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Sex, Size & Gender Roles

Evolutionary Studies of Sexual Size Dimorphism

Daphne J. Fairbairn, Wolf U. Blanckenhorn and Tamás Székely

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OXFORD
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Great Clarendon Street, Oxford OX2 6DP

Oxford University Press is a department of the University of Oxford.
It furthers the University's objective of excellence in research, scholarship,
and education by publishing worldwide in

Oxford New York

Auckland Cape Town Dar es Salaam Hong Kong Karachi
Kuala Lumpur Madrid Melbourne Mexico City Nairobi
New Delhi Shanghai Taipei Toronto

With offices in

Argentina Austria Brazil Chile Czech Republic France Greece
Guatemala Hungary Italy Japan Poland Portugal Singapore
South Korea Switzerland Thailand Turkey Ukraine Vietnam

Oxford is a registered trade mark of Oxford University Press
in the UK and in certain other countries

Published in the United States
by Oxford University Press Inc., New York

First published 2007

British Library Cataloging in Publication Data
Data available

Library of Congress Cataloging in Publication Data
Data available

Typeset by Newgen Imaging Systems (P) Ltd., Chennai, India
Printed in Great Britain
on acid-free paper by
Antony Rowe, Chippenham, Wiltshire

ISBN 978–0–19–920878–4

10 9 8 7 6 5 4 3 2 1

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Acknowledgments

The chapters in this volume are derived from an international workshop on the evolution of sexual dimorphism held at Ascona, Switzerland, in August of 2005. The three editors jointly conceived and organized this workshop in response to the burgeoning literature on sexual size dimorphism, and in the hope of providing a forum for the exchange of ideas across traditional disciplinary and taxonomic boundaries. The 42 participants in the workshop (Figure i.1) engaged in 5 days of intense discussion and exchange, and the breadth and excitement of these exchanges is evident in the resulting chapter essays. The editors are very grateful to all of the participants, and particularly to the chapter authors whose excellent contributions form the substance of the book. We are also grateful to the staff of the Centro Stefano Franscini and the Hotel Monte Verità for their excellent infrastructure and competent organization, and to Rosemarie Keller and Yves Choffat (Zoological Museum, Zurich) for administrative and technical assistance. We also thank the following organisations for providing financial and/or organizational support for the workshop: the Association for the Study of Animal Behaviour, Centro Stefano Franscini, Ethologische Gesellschaft e.V., Kontaktgruppe für Forschungsfragen (KGF Basel, Switzerland, including Novartis, Roche, Serono, and Syngenta), Swiss National Fund's SCOPES programme, Swiss Academy of Natural Sciences (SCNAT), Swiss Zoological Society, and Zoological Museum, University of Zurich.

Figure i.1 Participants in the international workshop on the evolution of sexual size dimorphism held in Ascona, Switzerland, August 21–26, 2006. The photo is taken on the lawn in front of the Hotel Monté Verita, overlooking Lake Maggiore. From left to right, front row: Alex Kupfer, Ellen Kalmbach, Derek Roff, Lynda Delph, Isabella Capellini, Tiit Teder, Henry John-Alder, Wolf Blanckenhorn, Evgeny Roitberg, Lee Ann Galindo, Daphne Fairbairn, Doug Emlen, Jacob Gonzales-Solis, and Antigoni Kaliontzopoulou. Middle row: Alois Honek, Martin Schäfer, Toomas Tammaru, Robert Cox, Virginia Salaver-Andres, Jordi Figuerola, Vojtěch Jarošík, Stéfanie Bedhomme, Jordi Moya-Laraño, Marguarita Ramos. Back row: Daniel Frynta, Martin-Alejandro Serrano-Meneses, David Carrier, Lukáš Kratochvíl, Subhash Rajpurohit, Toomas Esperk, Tamás Székely, Craig Stillwell, Matthias Foellmer, Terje Lislevand, Maria Martinez Benito, Turk Rhen, Patrik Lindenfors. Missing from the photo: Marguerite Butler, Michael Cherry, Krzysztof Koscinski, Sergiusz Pietraszewskj, and Abdul Jamil Urfi.

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CHAPTER 1

Introduction: the enigma of sexual size dimorphism

Daphne J. Fairbairn

1.1 The phenomenon to be explained: patterns and extremes of sexual size dimorphism

In the dry grass of a California meadow, the taut spiral of an orb web catches the early morning sun. A fat, yellow and black spider rests in the middle of the web, a crazy zig-zag of white silk marking the web below her (Figure 1.1). You stop and look more closely. This is a female *Argiope aurantia* and she is waiting for a morning meal. Her body is almost 20 mm long, and she seems gigantic, with a great round abdomen. Curiously, on the same web a much smaller, thinner, less brightly coloured spider seems to be moving cautiously toward the waiting female. This is a mature male *A. aurantia* and he is attempting to court the female and induce her to mate with him. He is only a fraction of her size (less than 6 mm long), and would easily make a meal. However, if he is successful in seducing her, he may fertilize all of the 300–400 eggs in her next egg sac, a worthy prize indeed (Foellmer and Fairbairn 2004). This is a dangerous enterprise for him because even if he escapes being eaten he will surely die in the end, spontaneous death during copulation being the fate of males of this species (Foellmer and Fairbairn 2003, 2004). Even to achieve his position close to the center of the web, he has had to battle with other males waiting for the female to become reproductively mature. In this contest, larger males had the advantage (Foellmer and Fairbairn 2005a) and yet all of the males are much smaller than their potential mate. Why is this? Surely larger males could out-compete other males and would also be less likely to be treated as prey by the waiting females. Why are the males so small?

Not far away, on the coast of central California at Piedras Blancas, another curious mating drama plays out each winter. In late fall, male northern elephant seals (*Mirounga angustirostris*) haul themselves on to the beach and set up breeding territories from which they attempt to exclude all other males. Males battle with each other, striking blows with their sharp teeth, and most bulls have deep scars over their necks and chests. Although fights are common, much of the competition among males takes the more benign form of bellowing, chasing, and rearing up to display size and strength. Females come ashore a little later than males to give birth and nurse their pups, and they only stay ashore for about a month before abruptly abandoning their pups and going back to sea. Mating occurs only during the last 3–5 days of nursing, and a single bull will attempt to monopolize all the females on his territory (Figure 1.2; and see www.elephantseal.org for a detailed description of this colony). Males are much larger than females, weighing an average of 2275 kg, while females average only 700 kg (Bininda-Edmonds and Gittleman 2000). The great size and aggressiveness of males can be a liability for the females, for both they and their pups are at risk of being crushed during mating attempts or male–male interactions (Le Boeuf and Mesnick 1991; Figure 1.2). In spite of this risk, large males sire more offspring than smaller males because of their ability to exclude other males from their mating territories (Alexander *et al.* 1979; Galimberti *et al.* 2002; Lindenfors *et al.* 2002).

Although this may explain why males grow so large, why are females (and their pups) not also larger? Why are the females so much smaller than their mates?

These curious cases are just two examples of differences in the average body sizes of adult males and females in natural populations, a phenomenon known as sexual size dimorphism (SSD). Moderate SSD, in which the sexes differ in size by 10% or less, occurs commonly in both animal and plant lineages whenever reproductive roles are segregated into separate sexes (e.g. Ralls 1976, 1977; Lloyd and Webb 1977; Parker 1992; Andersson 1994; Fairbairn 1997; Geber *et al*. 1999; and chapters in this volume). Dimorphism in our own species, *Homo sapiens*, falls in this range, males being on average about 7% taller than females (Gustafsson and Lindenfors 2004). More extreme examples such as those described above are less common but by no means rare. For example, in the avian order Galliformes (gamebirds) and the mammalian orders Carnivora, Primates, and Pinnipedia (seals, sea lions and walruses), males in some of the larger species typically weigh more than twice as much as females (Greenwood and Adams 1987; Fairbairn 1997; see also Chapters 2 and 3 in this volume). The most extreme male-biased dimorphism among birds and mammals occurs in the southern elephant seal, *Mirounga leonina*, where the 3510-kg males weigh seven times more than females (Greenwood and Adams 1987; Bininda-Edmonds and Gittleman 2000; Lindenfors *et al*. 2002). The record for male-biased SSD, however, belongs to a small shell-spawning cichlid fish in Lake

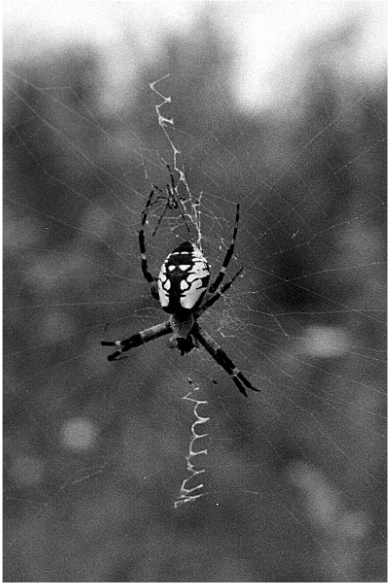

Figure 1.1 Male (above) and female (below) orb-web spiders, *Argiope aurantia*, on a mating web. Photo credit: Matthias Foellmer.

Figure 1.2 Breeding male (top), pup and female (bottom) northern elephant seals, *Mirounga angustirostris*, on the beach at the Piedras Blancas rookery in central California, USA. Photo credit: Daphne Fairbairn.

Tanganyika (Schütz and Taborsky 2000). Male *Lamprologus callipterus* weigh only 23–33 g but this is more than 12 times the average weight of females. Even though larger females lay more eggs, female size is constrained by the size of the gastropod shells available for spawning because they must enter the shells to spawn. Males, on the other hand, collect the shells and carry them in their mouths to their territories. They have to be large enough to transport the shells, as well as defend their territory, with its harem of females, against other males. The net effect of these selection pressures has been a decrease in female size relative to male size as this breeding system evolved (Schütz and Taborsky 2000).

Although such examples of extreme male-biased SSD are impressive, they pale in comparison to the extremes reached in many taxa where females are the larger sex. Moderate, female-biased SSD is by far the most common pattern in both animals and dioecious flowering plants (Greenwood and Adams 1987; Fairbairn 1997; Geber *et al*. 1999; see also other chapters in this volume). Even among birds and mammals, where male-biased SSD generally predominates, several major lineages are characterized by moderate female-biased SSD (e.g. bats (Chiroptera), rabbits and hares (Lagomorpha, Leporidae), baleen whales (Mysticeti), raptors (Falconiformes), and owls (Strigiformes)), and many other lineages include at least some species in which females are slightly larger than males (Ralls 1976; Fairbairn 1997; see also Chapters 2 and 3 in this volume). Female-biased SSD predominates in most other vertebrate and invertebrate lineages, and in these groups extreme SSD, where females are at least twice as large and sometimes several hundred times larger than males, has evolved repeatedly (Ghiselin 1974; Poulin 1996; Vollrath 1998). The most familiar example of this occurs in orb-weaving spiders (Araneidae), as illustrated by the example of *Argiope aurantia* at the beginning of this chapter, but dwarf males and giant females occur in several other spider families as well (Vollrath 1998; Hormiga *et al*. 2000; see also Chapter 7 in this volume). Even more extreme female-biased SSD, with females several hundred times larger than males, has evolved repeatedly in aquatic environments and examples can be found in several lineages of crustaceans, annelid worms, cephalopod mollusks, and deep-sea fishes (e.g. Gotelli and Spivey 1992; Raibault and Trilles 1993; Anderson 1994; Norman *et al*. 2002; Rouse *et al*. 2004; Zardus and Hadfield 2004; Berec *et al*. 2005; Pietsch 2005). In numerous cases, males have become structurally reduced sperm donors that live permanently in or on the female. Well-documented examples of this form of parasitic SSD include deep-sea marine tube worms in the genus *Osedax* (Rouse *et al*. 2004), the bottom-dwelling echiuran marine worm *Bonelia viridis* (Berec *et al*. 2005), and the barnacles *Trypetesa lampas* (Gotelli and Spivey 1992) and *Chelonibia testudinaria* (Zardus and Hadfield 2004). These examples from diverse taxa share a common mating system, where large, relatively sedentary females accumulate males throughout their reproductive lives, and the tiny, short-lived males compete for attachment sites on or within the female. Among vertebrates, several different lineages of deep-sea Anglerfishes (suborder Ceratioidei) have evolved a similar pattern of SSD in which dwarf males attach themselves to females hundreds of times their size (Pietsch 2005). In some of these species, males become structurally reduced, and remain permanently attached as parasitic sperm donors, and multiple males have been found on a single female. Although these examples suggest that dwarf males typically spend much of their lives attached to larger females, the most extreme female-biased SSD discovered to date occurs in the blanket octopus (*Tremoctopus violaceous*) where both sexes are free-living. In this species females are up to 2 m long and are 10 000–40 000 times heavier and at least 100 times longer than males (Norman *et al*. 2002). Like male *A. aurantia*, males of this species die after inseminating the female.

These examples serve to illustrate the astounding range of SSD. Even in this brief overview, general patterns begin to emerge, such as the relative dominance of male-biased SSD in endothermic vertebrates and of female-biased SSD in other groups. Another apparent trend is the association of extreme SSD with aquatic environments (spiders being a notable exception) and with skewed mating ratios wherein only the larger sex accumulates multiple mates. A third pattern, most obvious in cases of extreme SSD, is that divergence in body size between males and females is generally accompanied by divergence in life history and ecological variables. For example, SSD is frequently associated with differences between the sexes in age at maturity (Stamps and Krishnan 1997; Vollrath 1998; Blanckenhorn *et al*. 2007; see also Chapters 5, 15, and 20 in this volume) and survival or lifespan (e.g. Norman *et al*. 2002; Foellmer and Fairbairn 2003, 2004). Some degree of habitat or trophic segregation between the sexes is also common (Blanckenhorn 2005; Ruckstuhl and Neuhaus 2005). The striking variation in SSD and the covariation of ecological and life history variables provide powerful illustrations of the many ways that gender roles have evolved in organisms with separate sexes. Even within a single evolutionary lineage, the teleost fishes, the contrast between the shell-spawning, polygynous freshwater cichlid, *Lamprologus callipterus*, where males are 12 times heavier than females, and the deep-water, open-ocean Anglerfishes with attached, dwarf males hundreds of times smaller than females, could hardly be more extreme.

How and why such diversity has evolved is the subject of this volume. The chapters that follow are a compendium of studies of the evolution, adaptive significance, and genetic and developmental bases of SSD. In a series of separate overviews and case studies, evolutionary biologists attempt to answer the question: why do adult males and females so frequently differ markedly in body size and morphology? Throughout the volume the emphasis is on sexual dimorphism in overall size but the scope of enquiry encompasses gender differences in body shape, the size and structure of secondary sexual characteristics, patterns of growth (ontogeny), life history, and genetic architecture. From a variety of perspectives, the authors examine the role of natural and sexual selection in shaping these differences. Adaptive hypotheses allude to gender specific reproductive roles and associated differences in trophic ecologies, life-history strategies, and sexual selection. This adaptationist approach is balanced by more mechanistic studies of the genetic, developmental, and physiological bases of SSD. These describe how organisms have responded to gender-specific patterns of selection to produce present-day patterns of SSD and remind the reader that the evolution of sexual dimorphism occurs in the face of major biological constraints: divergent phenotypes must be produced from largely identical sets of genetic instructions.

1.2 The major integrative themes: adaptive significance and genetic constraint

The broad sweep of research on SSD presented in this volume can be viewed in the context of two central questions. One question concerns the adaptive significance of SSD. What selective forces drive divergent evolution of the two sexes and maintain SSD in contemporary populations? On a general level, there is broad consensus that SSD primarily reflects the adaptation of males and females to their disparate reproductive roles (e.g. Greenwood and Adams 1987; Andersson 1994; Short and Balaban 1994; Fairbairn 1997; Geber *et al*. 1999; Mealy 2000; Blanckenhorn 2005; see also other chapters in this volume). Because body size tends to be related to reproductive success through different pathways in males and females, most typically through fecundity in females and through mating success in males, the body size associated with maximum fitness (i.e. the optimal body size) often differs between the sexes. In such cases, selection favors SSD, and males and females are expected to evolve toward their separate optimal sizes (Figure 1.3a). Sexual dimorphism in traits not closely related to reproductive function, such as feeding or locomotory structures, is less readily explained. Such differences are generally associated with ecological differences between the sexes and this has given rise to the hypothesis that SSD could reflect adaptation of the two sexes to different ecological niches rather than to different reproductive roles (Slatkin 1984; Hedrick and Temeles 1989). It seems unlikely that ecological niche divergence between adult males and females (more recently termed sexual segregation) is ever truly independent of sexual divergence in reproductive roles (e.g. Shine 1991; Braña 1996; Geber *et al*. 1999; Blanckenhorn 2005; Ruckstuhl and

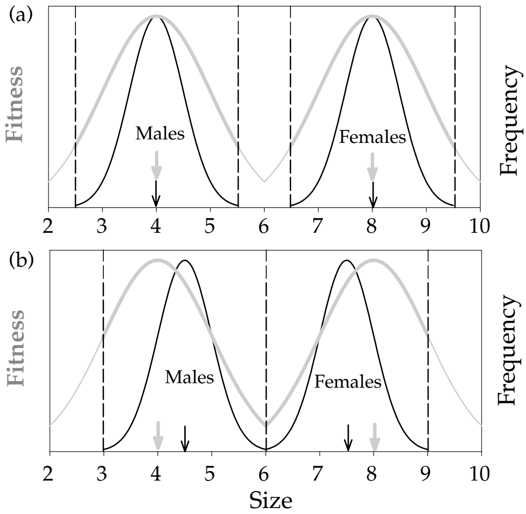

Figure 1.3 A schematic representation of selection on body size in which the optimal body size (i.e. the size that maximizes fitness) is higher for females than for males. The gray lines show lifetime fitness as a function of body size. The black lines are frequency distributions of body sizes for males and females in the population. (a) A population in which the mean sizes of the two sexes (black arrows) match the optimal sizes (gray arrows) and hence SSD is at evolutionary equilibrium. Within the range of sizes present in the population (bounded by the dashed lines) selection is stabilizing in both sexes. (b) A population in which the mean sizes of both sexes are displaced toward the common mean and away from their optimal values. Within the range of sizes present in the population, selection would appear as primarily directional and antagonistic (in opposite directions in males and females). This pattern is expected during an evolutionary transition to increased SSD and may persist for many generations if the genetic correlation between sexes is high (Lande 1980a; Fairbairn 1997; Reeve and Fairbairn 2001).

Neuhaus 2005; see also Chapter 5 in this volume). Nevertheless, whether ecological differences between the sexes are causes or consequences of SSD, or have evolved independently, is the subject of continuing research (e.g. Pérez-Barbería and Gordon 2000; González-Solís 2004; Forero *et al.* 2005), and selection favoring divergent ecological roles should be considered in any comprehensive explanation of SSD (e.g. see Chapters 3–5, and 9 in this volume).

The second major question addressed in various ways throughout this volume is to what extent the evolution of SSD is constrained by the shared genomes of males and females. Selection that favors different optima in males and females, known as sexually antagonistic selection, results in genomic conflict if the traits are determined by the same genes in both sexes (Rice 1984; Gibson *et al.* 2002; Bonduriansky and Rowe 2005a, see also Chapters 16–18 in this volume). Theory predicts that, if there is no independent genetic variance for the trait in either sex (i.e. if the genetic correlation between sexes is perfect; $r_{\mathrm{Amf}} = 1$), SSD cannot evolve. In such a situation, antagonistic selection will result in a compromise, intermediate average trait value (Lande 1980a, 1987; Fairbairn 1997; Reeve and Fairbairn 2001; see also Chapters 8 and 16–18 in this volume). However, genetic correlations are seldom perfect, and provided that some independent genetic variation exists, trait values are expected to eventually reach their independent selective optima within each sex (Lande 1980a, 1987; Reeve and Fairbairn 2001). The major effect of the shared genes (i.e. genetic correlations) is to greatly slow the rate of attainment of equilibrium SSD so that the mean sizes of the two sexes may remain displaced from their optima for many generations (Figure 1.3b; Lande 1980a; Reeve and Fairbairn 2001; see also Chapter 18 in this volume). A second effect of strong between-sex genetic correlations is to produce correlated evolution of body size in males and females, even when selection is antagonistic. This is expected in the early stages of the evolution of SSD, when selection for increased (or decreased) size in one sex causes a lesser, correlated response in the other sex. Size initially evolves in the same direction but at different rates in the two sexes, resulting in a temporary covariance between the sexes and between mean size and SSD (Lande 1980a; Fairbairn 1997; Reeve and Fairbairn 2001). Such a scenario has been proposed as an explanation for the common pattern of interspecific allometry for SSD known as Rensch's rule (Maynard-Smith 1977; Leutenegger 1978). However, because genetic correlations between the sexes should produce such allometry only very early in the evolutionary trajectory, most authors have rejected this explanation (Clutton-Brock 1985; Fairbairn and Preziosi 1994; Abouheif and Fairbairn 1997; Fairbairn 1997). The only system in which this hypothesis has been specifically tested is that of allometry for SSD among populations of the water strider, *Aquarius remigis*, and there it was definitively rejected (Fairbairn and Preziosi 1994; Preziosi and Fairbairn 2000; Fairbairn 2005). Nevertheless, the extent to which genetic constraints and genomic conflict influence patterns of SSD is largely unknown.

These two themes, adaptive significance and genetic constraint, weave their way through the 19 contributed chapters that follow. In the first section of the book, six chapters describe broad patterns of variation in SSD within and among major phylogenetic lineages. The studies in this section combine literature reviews with new comparative analyses to both discern patterns and deduce broad-scale underlying evolutionary mechanisms. The second section of the book presents a collection of eight case studies where researchers have measured patterns of selection and genetic architecture within single species or groups of closely related species. These studies emphasize the mechanisms of adaptation and constraint within populations (i.e. at the microevolutionary level) and provide excellent examples of morphological evolution in response to selection for diverse gender roles. The final section of the book consists of five chapters that more directly address the proximate, functional basis of SSD. These studies describe how developmental and genetic mechanisms are able to overcome the basic constraints of a shared genome to produce males and females uniquely adapted for their disparate gender roles. The studies presented in the three sections represent diverse approaches for studying SSD and utilize many different taxa, but all authors emphasize common themes and general patterns. Brief introductions to each of three sections serve to summarize and highlight these.

1.3 Caveats and limitations of this collection of studies

The comparative analyses, case studies, and conceptual reviews that comprise this volume represent a very broad array of approaches to the study of SSD and utilize many different organisms at both macroevolutionary and microevolutionary levels. Both alone and in concert, the chapters provide comprehensive introductions to research on SSD and establish goals and directions for future research. Nevertheless, readers should be cautioned that the volume is not encyclopedic. Limitations on both the number of chapters and the length of each chapter meant that we could sample only some of the burgeoning literature in this area (an ISI keyword search uncovered 1469 papers using the term sexual size dimorphism published between 1976 and September 2006). Because each author was permitted only a limited number of citations, more recent review articles are often cited in preference to lists of the older, original studies. Readers are encouraged to refer to these reviews for the original citations. To help readers access the literature in more detail, a list of suggested readings is provided at the end of each chapter.

We have not attempted to include studies of every major organismal lineage and the empirical studies clearly emphasize tetrapods, insects, and spiders. These lineages all offer abundant data on many different species, facilitating broad inferences about both pattern and process. Plants are represented by only a single chapter, Lynda Delph's case study of *Silene latifolia* (Chapter 11). Studies of sexual dimorphism in plants have tended to emphasize the evolution of dioecy itself or differences between sexes in physiology, life history, flower size, or flower number, rather than dimorphism for overall size, and, as a result, it remains difficult to discern general patterns of SSD (Dawson and Geber 1999; Geber *et al*. 1999). Nevertheless, the concepts and theories applied to the evolution of sexual dimorphisms in plants are the same as those applied to animal systems (Geber 1999), and there is nothing to suggest that generalizations cannot be made across the two kingdoms. Excellent introductions to the literature on sexual dimorphism in plants are provided by Lloyd and Webb (1977) and in the edited volume by Geber *et al*. (1999).

Fish are also conspicuously absent from our empirical chapters, an omission that is particularly regrettable given the extreme range of SSD even just within the teleosts. As illustrated by the examples in the introductory paragraphs, the magnitude and direction of SSD in fish appears to be strongly related to the breeding system (e.g. Clarke 1983; Parker 1992; Roff 1992; Erlandsson and Ribbink 1997; Schütz and Taborsky 2000; Pietsch 2005). The available data suggest that fecundity selection generally favors large size in female fish and that female-biased SSD is the more common pattern, particularly in open-ocean species. Male-biased SSD tends to be associated with contest competition among males to defend resources or females, or provision of parental care by males, and may be more common in shallow-water and reef fishes. These generalities are tentative, however, and await more rigorous, phylogenetically controlled comparative analyses.

Aquatic and parasitic invertebrates are also absent from our collection of empirical studies. As illustrated in the introductory examples, extreme female-biased SSD has evolved repeatedly in this group (e.g. Ghiselin 1974; Gotelli and Spivey 1992; Poulin 1996; Vollrath 1998; Norman *et al*. 2002; Rouse *et al*. 2004; Zardus and Hadfield 2004; Berec *et al*. 2005). The little evidence available suggests that male dwarfism tends to evolve in aquatic habitats when larvae are pelagic and mature females are rare and widely dispersed. Transition to a parasitic lifestyle may also promote increased SSD through either increase in female size or decrease in male size (Poulin 1996; Vollrath 1998). Unfortunately, for most lineages of aquatic and parasitic invertebrates we lack sufficient data to make valid generalizations about the frequency and causes of SSD. When such data become available, it will be interesting to discover whether patterns common in insects and tetrapods, such as the association between male-biased SSD and sexual selection favoring large males (but not necessarily the reverse) and the pattern of allometry for SSD called Rench's rule, also hold in these lineages. Evidence from parasitic crustaceans and spiders suggests that these patterns may not be general in taxa with extreme female-biased SSD (Poulin 1996; Vollrath 1998; Hormiga *et al*. 2000; see also Chapter 7 in this volume) but quantitative and comparative studies of other lineages are sorely needed.

1.4 General methodological issues in estimating SSD

Although the term sexual size dimorphism can refer to sexual dimorphism in the size of a particular body component, most studies in this volume refer to dimorphism for overall body size. Unless otherwise specified, this is the sense in which we use the term and its abbreviation, SSD. Three basic methodological issues arise when we attempt to estimate SSD, and I will consider these in turn.

1.4.1 Measuring body size

The first methodological issue is simply choosing how to measure body size. Standard measures of exist but differ among taxa. For example, snout–vent length is the standard for snakes, lizards, frogs, and salamanders (see Chapters 4 and 5 in this volume) while body mass is the most common measure for birds (see Chapter 3). Body mass is the most general measure in mammals (see also Chapter 2 in this volume), but skeletal measures such as skull length or shoulder height are also used (see Chapter 12). In insects, head width, lengths of leg segments, wings, or wing covers (tegmina), or total body length are all used (e.g. see Chapters 6 and 8–10), whereas in spiders, maximum carapace width and total body length are most often used (Hormiga *et al*. 2000; see also Chapter 7). While it is appropriate to use any measure of size that is repeatable within and between individuals, if the goal is to study SSD for overall body size, not all measures are equally desirable (Lovich and Gibbons 1992; see also Chapter 6). Although mass might seem the gold standard for estimating overall size, it can have poor repeatability within individuals because of the effects of food in the gut, hydration, nutritional status, and reproductive condition. Skeletal measures may have the advantage of higher repeatability but tend to underestimate the variance in body size. This is because, for any isometric change in body dimensions, a change in length or width by a factor of z will increase volume (and hence mass) by z^3. Thus, a sexual size ratio of 2 based on a length measure (e.g. males twice the length or height of females) would correspond to a weight ratio closer to 8. Using any single skeletal measure as an index of overall size is also problematic because it assumes a strong and isometric relationship between the trait measured and overall body size. Although multivariate morphometric analyses invariably find strong positive correlations among linear measures of body components, each trait shows some independent variation and thus the correlations are not perfect. Further, allometric growth of body components is the rule, not the exception, leading to variation in organismal shape as well as size (e.g. Gould 1966; Baker and Wilkinson 2001; Bonduriansky and Day 2003; Emlen and Allen 2004). The pattern of selection may also differ among body components so that the perceived adaptive significance of SSD may depend upon which measure is used as an index of size (e.g. see Chapters 3, 5, 7, and 9–11). The take-home message is that no single measure, including mass, is ideal for estimating overall body size and, by extension, for studies of the evolution and adaptive significance of SSD. Researchers (and readers of this volume) need to be aware of the limitations of the measures used, and comparisons among studies using different measures should be made with caution.

1.4.2 Estimating average size of males and females

The second methodological issue concerns selecting an appropriate parameter for estimating the average size of adult males and females. In organisms such as insects and spiders that have determinate growth (i.e. skeletal growth stops at the final molt), mean body size estimated from an unbiased sample of adult males and females in a given population or species should suffice. However, many organisms, including most vertebrates other than birds, continue to grow after reproductive maturity. In these species, sex-specific patterns of growth or survival after maturity can alter SSD with age. Depending upon the question of interest, it may still be appropriate to estimate SSD using the mean sizes of all adult males and females in the population. However, parameters of the growth curves such as size at maturity, asymptotic size, or maximum size may be more appropriate measures of adult size in each sex. I refer readers to Stamps and Andrews (1992), Stamps (1993), and Chapter 14 in this volume (Box 14.1) for more detailed discussions of this problem. Chapters 5, 15, and 19 in this volume also provide brief discussions and explain how this problem has been resolved for different study systems.

1.4.3 Selecting an appropriate index for SSD

Once a measure of average size and has been adopted, researchers face the final challenge of deciding how to quantify SSD. Numerous quantitative indices exist in the literature, but no single index has emerged as the standard. Lovich and Gibbons (1992) and Smith (1999) provide excellent critical reviews of these methods and I will only highlight a few key issues here. Most commonly, SSD is expressed as a raw size ratio between males and females (M/F or F/M) or a proportional difference in size, as I have done in the examples in this chapter. These are both ratio estimators and are readily interchangeable (e.g. $(M-F)/F = (M/F)-1$). Unfortunately, although superior to difference estimators, ratio estimators tend to be statistically problematic and suffer from lack of standardization among studies (Lovich and Gibbons 1992; Smith 1999). For example, raw ratios have a highly asymmetrical distribution because values over 1.0 are unbounded, while values below 1.0 can vary only between 1 and 0. This exaggerates our perception of the magnitude and variance in SSD for ratios greater than 1.0 relative to those less than 1.0. For example, if females are twice as large as males, the size ratio equals 2 if female size is the numerator, but 0.5 if male size is the numerator. If females are 10 times larger than males, these values are 10 and 0.1, respectively. Because of this asymmetry, ratios are never a good choice for comparisons among taxa or traits unless the same sex is always larger, the convention in that case being to put the mean for the larger sex in the numerator (Smith 1999).

Following the arguments of Lovich and Gibbons (1992) and Smith (1999), we can define four characteristics as desirable for estimators of SSD. The first is linearity: a doubling of the magnitude of the dimorphism should cause a doubling of the estimator. The second is symmetry: males twice the size of females and females twice the size of males should yield values equidistant from the neutral value. The third is directionality: the sign of the index should indicate which sex is larger. The fourth is intuitive appeal: the magnitude and direction of the dimorphism should be obvious on a standard numerical scale. Most ratio and percentage difference estimators do not satisfy these four criteria (e.g. see Table 2 in Smith 1999). Several, such as Storer's index ([male − female]/[(male + female)/2]), do a good job for values close to equality, but fail at extreme values. The only estimator that satisfies the criteria for a wide range of values of SSD is the modified ratio index proposed by Lovich and Gibbons (1992), the size dimorphism index, which we will abbreviate as simply SDI. This is estimated by taking the ratio of the larger to the smaller sex and subtracting 1, which sets the neutral value at 0 rather than 1. The resulting value is then made negative if males are the larger sex and positive if females are the larger sex. This index has the intuitive appeal that it can easily be translated into a raw ratio or a percentage difference. For example, an SDI of 0.3 means that females are 1.3 times or 30% larger than males. One only need remember that a negative SDI means males are larger, something that should always be explicitly stated when this index is used.

The authors of the chapters in this volume have used either log (M/F) or the SDI of Lovich and Gibbons for their statistical analyses. Log (M/F) has excellent statistical properties except at extreme values of SSD (Smith 1999), and satisfies the criteria of symmetry and directionality listed above. However, it represents SSD on a logarithmic scale, and hence does not satisfy the criteria of linearity and intuitive appeal. We therefore asked all of the authors to also incorporate the SDI of Lovich and Gibbons (1992), at least as a descriptive statistic. The presence of this single, common index allows interested readers to readily compare SSD among the many different types of organisms and traits—from calyx width in the flower, *Silene latifolia*, to body mass in Primates—that are the focus of the 19 contributed chapters.

1.5 Summary

SSD, defined as a difference between the average size of adult males and females, is very common in organisms with separate sexes. In this introductory chapter, I review overall patterns of SSD and provide brief summaries for several taxa (plants, fishes, and aquatic invertebrates) not included in the survey chapters that follow. I also highlight examples of extreme SSD such as *Lamprologus callipterus*, a shell-brooding cichlid fish, where males are more than 12 times heavier than females, and the blanket octopus (*Tremoctopus violaceous*), where females can be 40 000 times larger than males. I then briefly review the structure and content of this book, which consists of 20 contributed chapters reflecting current research on SSD. These chapters focus on two major themes: the adaptive significance of SSD in contemporary populations and the extent to which the evolution of SSD is constrained by genomic conflict. I review these themes and conclude that both theory and empirical evidence support the hypothesis that SSD primarily reflects the adaptation of each sex to its distinct reproductive role. However, the extent to which genetic constraints prevent males and females from reaching their equilibrium body sizes in natural populations remains to be determined. I note the limitations of this book, which can provide only an introduction to the burgeoning literature in this area, and close by considering several methodological difficulties associated with estimating adult body size and SSD in natural populations.

1.6 Acknowledgments

Many thanks to my fellow editors, Wolf Blanckenhorn and Tamas Székely, for their helpful comments on earlier drafts of this chapter. I am also grateful to Matthias Foellmer for his help with the description of *Argiope aurantia* and for kindly allowing me to use his photograph.

1.7 Suggested readings

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Fairbairn, D.J. (1997) Allometry for sexual size dimorphism: pattern and process in the coevolution of body size in males and females. *Annual Review of Ecology and Systematics* **28**, 659–687.

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SECTION I

Macro-patterns: explaining broad-scale patterns of variation in sexual size dimorphism

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Introduction

Tamás Székely

One of the fundamental ideas in biological research is the progression from pattern to function and mechanism. Thus on the road to understanding *how* selection may influence a trait, and *what* are the underlying physiological, developmental, and genetic mechanisms of adaptation, the first challenge for evolutionary biologists is often to quantify the overall distribution of traits within and between populations, species, genera, and families. Our volume on sexual size dimorphism (SSD) attests this progression by devoting Section I to overviews of distribution and functional hypotheses of SSD in some of the best-studied organisms in the wild.

Section I addresses three major questions. The first and most fundamental question is, what is the overall distribution of SSD in various animal taxa? During the last few decades impressive data-sets have been gathered on the distribution, ecology, and behavior of animals in nature. Luckily, some of these data have been summarized so that they are readily accessible in handbooks, review papers, and online databases. Capitalizing on these advances, one of the main thrusts of Chapters 2–7 is to map the distribution of SSD in invertebrates (spiders and insects) and vertebrates (amphibians, reptiles, birds, and mammals). These chapters provide the vital statistics of SSD by using some of the largest data-sets available to date.

Chapters in Section I provide three major insights into the distribution of SSD. First, invertebrates and poikilothermic vertebrates have largely female-biased SSD (see also Chapter 1 in this volume), although monomorphism and male-biased dimorphism also occur in these taxa. In contrast, mammals and birds have statistically significant male-biased dimorphism overall, as conjectured by Darwin (1874). However, a caveat, at least in those organisms that grow throughout their lives, is that different ages of males and females at maturation may create a false impression of biased SSD at adulthood, whereas in reality none may exist (see Chapter 5). Second, the frequency distribution of SSD is leptokurtic, at least in birds and mammals, since fewer species exhibit extreme SSD than predicted by normal distribution. This is unexpected and further investigation will be needed to determine whether the deviation from normality is a statistical artifact emerging from the shared phylogenetic history of closely related species, or a real biological phenomenon that may be driven by stabilizing selection acting across a group of taxa. Third, SSD in a given morphological trait may only be loosely correlated with SSD in other morphological traits, as shown in spiders and birds (see Chapters 3 and 7). This suggests that different selection (intensity and/or direction) may be acting upon on different body parts (e.g. see Chapter 9).

The second major question addressed in Section I is, how does selection act on the sizes of males and females? With the advent of inexpensive DNA sequencing, powerful computers and new statistical methods for testing adaptive hypotheses, cross-species analyses are proliferating. The comparative approach, as the latter is often called (see Boxes I.1 and 7.1), benefits from the immense "experiment" nature has carried out in producing diverse body sizes and shapes. Researchers studying the results of these natural experiments seek to identify the ecological and life-history traits that facilitated the evolution of SSD. Although the chapters in Section I use different traits representing SSD, and different proxy variables

Box I.1 The comparative approach

Comparative analysis of traits is one of the fundamental research methods in biology (Harvey and Pagel 1991). Evolutionary biologists use comparative methods to reveal patterns that hold across a broad range of taxa, to test hypotheses that are not open to experimental manipulation, and to reveal the timing and mode of evolution (Bennett and Owens 2002).

The comparative approach has two major uses in evolutionary biology (see examples in Pagel 1999 and Martins 2000). First, one may reconstruct the evolution of a trait using an evolutionary model such as maximum parsimony or maximum likelihood. Such reconstructions allow researchers to infer transitions in trait values (or states), and to test whether the direction and frequency of these transitions differ from an appropriate null model.

Second, comparative analyses may reveal relationships between traits; one trait is usually considered the response trait, whereas the others are the explanatory traits. A statistical problem with using species data in a simple cross-species analysis (such as least-squares regression or multiple regression) is that the units of the analysis (usually the species) are not independent from each other because closely related taxa are more similar to each other than to a distantly related taxon. Several methods have been proposed to deal with this statistical non-independence. These include the methods of phylogenetically independent contrasts (Felsenstein 1985; see example in Box 7.1 in this volume) or generalized least squares (Martins and Hansen 1997; Pagel 1997). For details of these methods see reviews by Harvey and Pagel (1991), Freckleton *et al.* (2002), and Blomberg *et al.* (2003). Appropriate software packages are available for most of these methods (e.g. CAIC, COMPARE, CONTINUOUS), and their manuals provide detailed examples. For further explanations of how to access and use such software see the websites of Joe Felsenstein (http://evolution.genetics.washington.edu/phylip/software.html), Emilia Martins (http://www.indiana.edu/~martinsl/index_files/programs.html), and the Evolutionary Biology Group at the University of Oxford (http://evolve.zoo.ox.ac.uk/software.html).

representing functional explanations, their main conclusion is consistent with Darwin's (1874) assertion: sexual selection is a major contributor to SSD, at least in mammals, birds, and reptiles (see Chapters 2–4). However, this broad-brush view of sexual selection favoring large size *via* male–male combats or by female choice is modulated by various other processes. First, comparative analyses provide mixed support for fecundity selection. For instance, fecundity selection appears to have a strong positive influence on female size in spiders (see Chapter 7), a negative influence in mammals (see Chapter 2), and weak (or non-detectable) effects in reptiles and birds (see Chapters 3 and 4). Second, in addition to fecundity selection, the cost of mate search favoring small size in males has a strong predictive power among spiders (the so-called gravity hypothesis of Foellmer and Moya-Laraño; see Chapter 7). Third, the agility of male displays in birds, which can be viewed as an energy-saving mechanism that favors small male size, came up as a significant predictor of SSD in comparative analyses of over 30 avian families (see Chapter 3). Note that the latter two hypotheses (gravity selection and male agility) are nevertheless associated with sexual selection. It will be interesting to see whether these two hypotheses, which are currently viewed as only subsidiary explanations of SSD, may have general predictive power in other organisms beyond spiders and birds.

The third major question addressed in this first section is, do organisms exhibit an allometry consistent with the Rensch's rule? As one might expect, the answer to this question is affirmative in some taxa, but negative in others. In mammals and birds there is an overall consistency with Rensch's rule (see Chapters 2 and 3), whereas among insects the evidence is mixed at best (see Chapter 10). Spiders appear to exhibit an allometry that is the reverse of Rensch's rule (see Chapter 7). It is unlikely that these diverse results are driven by different methodologies of testing the allometric relationship; rather, they appear to be genuine. Nevertheless, it is somehow striking that Rensch's rule appears to be prevalent in those taxa that show signs of intense sexual selection (Székely *et al.* 2004; Fairbairn 2005). Furthermore, as Blanckenhorn *et al.* point out in

Chapter 6, the strength of the allometric relationship may vary even within a given group of organisms depending on the level of analysis, such as genus, species, or population.

Chapters in Section I also highlighted gaps in current research agendas, and directions where research on SSD should head in future. First, we need more data and better phylogenies. Data on body sizes are needed for a vast number of organisms, especially plants, fish, insects, and other invertebrates, which so far have been understudied in this context. Since field research has typically focused in the northern hemisphere, more work is needed on species that live in the tropics and/or the southern hemisphere, where most species actually live.

Second, better data are needed on proxies for functional explanations. For instance, sexual selection is represented only by binary (or ordinal) scores in comparative analyses of reptiles, birds, and mammals. Similarly, quantitative descriptions of male displays are not available for the vast majority of species, so that current work often suffers from merely rough scores for male agility. Better resolution of comparable data across a broad range of organisms will likely boost the statistical power of comparative analyses in future.

Third, many functional explanations of SSD need further attention. For instance, Andersson (1994) listed dozens of functional explanations for the body sizes of males and/or females, and Blanckenhorn (2000) has argued convincingly for considering viability selection; most of these potential explanations have not been evaluated using comparative analyses. Mate search and pre- and post-copulatory sexual selection (i.e. sperm competition and cryptic female choice) may differentially affect the evolution of SSD, and these also need further analyses (Blanckenhorn 2005).

Finally, more advanced comparative analyses are needed in SSD research. Comparative analyses are often branded as correlational, especially by experimental biologists. True, some comparative analyses, such as the popular phylogenetically independent contrasts (see Box I.1), can only reveal correlations but no causation. Directional comparative methods, however, infer sequences of events along a particular phylogeny (Pagel 1997; Perez-Barbeira *et al*. 2002); this is probably as close to causality as one may get in the comparative context.

In conclusion, the chapters in Section I provide much needed syntheses of the distribution and functional hypotheses about SSD in several major animal taxa. Progress in the future will depend on data availability, better phylogenetic hypotheses, and willingness of researchers to use advanced phylogenetic methods. A challenging task remains the integration of analyses at different levels of selection (e.g. population, subspecies, species, family) to investigate where most variation accumulates. Are patterns, for instance Rensch's rule, consistent between different levels of selection? What is the relevance of intraspecific allometry for interspecific allometry? I concur with Cox *et al*. (Chapter 4) that integrating cross-species comparisons in a group of species that exhibit a broad range of SSD with detailed demographic analyses of its species will likely provide fundamental insights on how selection may shape SSD in nature.

CHAPTER 2

Sexual size dimorphism in mammals

Patrik Lindenfors, John L. Gittleman, and Kate E. Jones

2.1 Introduction

In this chapter we review the extent and direction of sexual size dimorphism in mammals using body-mass measurements for 1370 mammalian species, constituting almost 30% of those currently known (Wilson and Reeder 1993). Further, we investigate the role of sexual selection through male–male competition as a driver of male-biased sexual dimorphism in mammals. Since theoretical models predict that sexual selection on male size should also have a simultaneous effect on female size (Lande 1980a, 1987; Lande and Arnold 1983), we examine whether fecundity selection on females acts as a counteracting factor that selects for smaller female size (Lindenfors 2002). Finally, we investigate the suggestion that energetic demands placed on females from the need to rear large, successful males can constitute a selection pressure on female size that is correlated with sexual selection on male size (Fairbairn 1997; Lindenfors 2002) and thus explain why more dimorphic species also tend to be larger (Rensch's rule; Rensch 1950, 1959; Abouheif and Fairbairn 1997; Fairbairn 1997; Figure 2.1).

In most sexually reproducing animals, females are larger than males (Andersson 1994; Chapter 1 in this volume), a pattern often explained by fecundity selection on females (Darwin 1871). This is because more space is required for keeping eggs than keeping sperm and because egg production increases with body size (e.g. see Chapter 4 in this volume). Energetic demands on female mammals are comparatively higher than on females in other animal groups since mammals not only need energy for egg production but also for gestation and lactation. Female mammals should therefore be expected to develop a larger energy store and should consequentially be expected to exhibit even larger size differences with males than other animals without such demands.

However, even though there are numerous mammalian species where females are larger than males (Ralls 1976), earlier studies have reported that mammals are generally dimorphic, with a bias toward males (Alexander *et al.* 1979; Weckerly 1998), as is also commonly the case in birds (see Chapter 3 in this volume). In explaining this male size bias, sexual selection is often cited as a possible driver (Darwin 1871). This is especially likely in species where males provide little or no parental investment, as males in these species can increase their reproductive success directly by competing for matings (Trivers 1972, 1985). Sexual selection through male–male competition as an explanation for male-biased size dimorphism has found support in several comparative studies that have shown correlations between different estimates of polygyny and dimorphism. Such correlations have been reported for mammals in general (Alexander *et al.* 1979; Weckerly 1998), but also separately for primates (Clutton-Brock and Harvey 1977; Clutton-Brock *et al.* 1977; Clutton-Brock 1985; Mitani *et al.* 1996; Lindenfors and Tullberg 1998), ungulates (Geist 1974; Pérez-Barbería *et al.* 2002; Jarman 1974, 1983; Loison *et al.* 1999; but see Chapter 12 in this volume), and pinnipeds (Lindenfors *et al.* 2002). Although it is improbable that sexual selection on males is the sole causal agent behind mammal size dimorphism (see e.g. Isaac 2005), these empirical studies indicate that sexual selection can be the important determinant in a significant fraction—if not the majority—of cases where male-biased sexual size dimorphism has evolved in mammals.

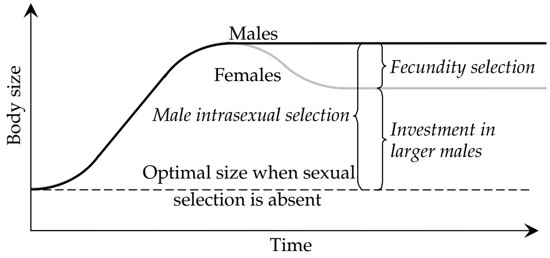

Figure 2.1 An idealized graph of a hypothetical path to male-biased sexual size dimorphism in mammals. Intrasexual competition in males results in larger male body size in species where physical competition is an important determinant of male reproductive success. Due to a genetic correlation between the sexes, female size also increases initially, but this increase is counteracted by fecundity selection, over time resulting in size dimorphism. Female size does not return to its initial level due to increased energetic demands of rearing larger male offspring. Sexual selection and fecundity selection should thus act as antagonistic selection pressures on body size in mammals, at least for females. Adapted from Lindenfors (2002).

If sexual selection acts on males, then what are the expected effects on females? Models indicate that sexual selection on male mass may directly affect female mass due to genetic correlations between the sexes in genes determining body mass (Maynard Smith 1978; Lande 1980a, 1987; Lande and Arnold 1983), but this is expected to only be a temporary phenomenon as female size gradually returns to its initial state due to some opposing natural selection (Lande 1980a; Fairbairn 1997; Reeve and Fairbairn 2001). However, indirect effects on females from selection on males might also be expected from correlated selection on females, because females may need to be larger simply due to the importance of producing larger male offspring (Fairbairn 1997; Lindenfors 2002). For example, sexually selected primate species have significantly longer periods of lactation (even after correcting for body mass; Lindenfors 2002). Resources transferred during lactation are typically more costly than the prenatal costs of gestation (Cameron 1998) and female body mass is positively correlated with milk yield in mammals (Oftedal 1984). For species under sexual selection, offspring production—especially when those offspring are males—should thus involve a longer lactation period, constituting a significant selection pressure to increase female body mass. Females in more polygynous species are therefore expected to be larger than females in their less polygynous sister taxa.

However, fecundity in mammals has been shown to decrease with increased body size (e.g. Boyce 1988; Harvey *et al*. 1989; Lee *et al*. 1991; Purvis and Harvey 1995). Both interspecific studies (e.g. Boyce 1988; Harvey *et al*. 1989; Lee *et al*. 1991; Purvis and Harvey 1995) and theoretical models (e.g. Charnov 1993) predict that there is a trade-off between somatic growth and reproduction. Growth to a large size takes time and energy, so life-history relationships with body mass are often thought of as physiologically constrained allometries, with resulting trade offs between body size and reproduction (Roff 1992; Stearns 1992; Charnov 1993). Increased female size due to sexual selection on males should therefore decrease female fecundity. Such effects already identified are smaller litter sizes in more dimorphic mammals (Carranza 1996) and longer interbirth intervals in more polygynous haplorhine primates (Lindenfors 2002).

When increases in male mass are correlated with smaller increases in female mass, a correlation between size and size dimorphism is produced (Figure 2.1), a pattern termed Rensch's rule (Abouheif and Fairbairn 1997; Fairbairn 1997): the tendency for size dimorphism to scale with body size (Rensch 1950, 1959). To test the scenario described above, we examine support for Rensch's rule in mammals by presenting the first analysis of allometry for sexual size dimorphism across all mammals as well as separately within each order (Abouheif and Fairbairn 1997). Note that our outlined model is not falsified if Rensch's rule is not supported (Lindenfors and Tullberg 2006); but that the presence of Rensch's rule nevertheless would provide a first indication that there exists parallel—but not equal—selection pressures on males and females. We also test whether more polygynous species are more dimorphic and have larger males and females than less polygynous species. To test for possible counteracting selection on females, we conduct life-history analyses to attempt to identify fecundity costs of larger female size due to sexual selection on males, but also costs of sexual selection per se, after the effects of body size have been removed. Finally, we examine whether there is a detectable increased investment in offspring in more sexually selected species, because of both their larger size and the effects of sexual selection on its own.

2.2 Materials and methods

We obtained data on adult body mass for males and females, mating systems, variables indicating female fecundity (age at first birth, gestation length, litter size, interbirth interval, birth rate, maximum longevity), and variables indicating investment in individual offspring (neonatal mass and weaning age) from the PanTHERIA v.1 database (K.E. Jones, J. Bielby, A. Purvis *et al.*, unpublished work). PanTHERIA has been compiled to summarize comparative variables among all mammal species and contains over 100 000 lines of data from over 3300 sources collected over a 2-year period by a collaboration of three academic institutions. Source papers were found systematically from relevant journals and secondary sources (e.g. *Journal of Mammalogy*, *Mammalia*, *Journal of Zoology*; Hayssen *et al*. 1993). Further sources for particular variables, clades, or individual species were found using the electronic search engine Web of Science (http://isi3.isiknowledge.com). Entries were checked for inconsistencies and complemented when additional data were required (Kitchener 1991; Creel and Macdonald 1995; Nowell and Jackson 1996; Mills and Hofer 1998; Smith and Jungers 1997; Smith and Leigh 1998; Creel and Creel 2002; Lindenfors 2002; Pérez-Barbería *et al*. 2002, Sunquist and Sunquist 2002; Macdonald and Sillero-Zubiri 2004). All variables were $\log_{10}$-transformed prior to analysis to meet the assumption that the data were normally distributed.

We used a composite dated supertree phylogeny of 4497 mammal species for our phylogenetic comparative analyses (Bininda-Emonds *et al.*, 2007). This phylogeny was compiled by combining previously published mammal supertrees (Purvis 1995; Bininda-Emonds *et al*. 1999; Jones *et al*. 2002; Grenyer and Purvis 2003; Cardillo *et al*. 2004; Price *et al*. 2005) with new interordinal and intraordinal supertrees constructed by Matrix Representation with Parsimony, using procedures outlined elsewhere (Bininda-Emonds *et al*. 2004; Cardillo *et al*. 2004). The supertree used here is the preliminary version also used by Cardillo *et al*. (2005). Branch lengths were $\log_{10}$-transformed to best meet the assumptions of the computer program CAIC (Purvis and Rambaut 1995).

For our analyses, we have used a $\log_{10}$-transformed ratio of male to female body mass as our measure of sexual size dimorphism but for comparisons with other studies in this volume we also show the size dimorphism index (SDI) of Lovich and Gibbons (1992) in Table 2.1. When describing the distribution of dimorphism in mammals, we placed an arbitrary cut-off point at 10% size difference between the sexes to term a species dimorphic (equivalent to $\log_{10}$(male mass/female mass) of ± 0.0414). To statistically test for the presence or absence of dimorphism, we used paired t tests where male mass was paired against female mass.

Mating system was used as an indication of the strength of sexual selection on males. Species were classified as having one of three mating systems which were ordered into degrees of increasing potential sexual selection through direct male–male competition (polyandrous/monogamous, polygynandrous, and polygynous) and treated as a discrete variable. The influence of sexual selection was analyzed utilizing the BRUNCH option in CAIC (Purvis and Rambaut 1995) which functions as normal independent contrasts (Felsenstein 1985) but allows the incorporation of a discrete independent variable, in this case mating system. When BRUNCH is used, only contrasts at nodes where the sister species differ in mating system are included in the final analysis. In this manner, "more" or "less" sexually selected taxa were compared, where polygynandrous species ended up as being either more or less polygynous depending on whether its sister taxa were monogamous or polygynous. Polytomies were handled using zero-length branches.

When checking for the presence or absence of Rensch's rule, we follow Abouheif and Fairbairn (1997), by first performing an independent contrasts analysis and then regressing male mass contrasts on to female mass contrasts, and finally testing for a deviation from a slope of 1.0. The alternative method of regressing size dimorphism on female size is to be avoided for statistical

Table 2.1 Summary of the patterns of dimorphism found in mammals. Dimorphism is given as the standard size ratio and, in parenthesis, as the SDI of Lovich and Gibbons (1992), calculated as (mass of the larger sex/mass of the smaller sex) – 1, with the sign arbitrarily given as negative when males are larger and positive when females are larger. Mammals and the majority of mammalian orders are, on average, male-biased dimorphic (average size ratio > 1.0, SDI < 0, $P < 0.05$), even if there exist a few orders with no significant dimorphism ($P > 0.05$) or female-biased dimorphism (Lagomorpha, average size ratio < 1.0, SDI > 0, $P < 0.05$). P values represent the significance of paired t tests where male body mass was paired with female body mass. Although analyses indicate that size dimorphism increases with size in mammals as a whole (Rensch's rule), upon closer inspection this only applies separately in Primates and Diprotodontia. The presence of Rensch's rule was tested using the procedure following Abouheif and Fairbairn (1997). Dashes indicate orders with too few data points for statistical analysis ($n < 3$ for tests of the presence of dimorphism; $n < 10$ for tests of the presence of Rensch's rule).

Order	Number of recognized species	Number of species with body mass data	Average dimorphism (SDI)	Sexual size dimorphism (*P* value)	Rensch's rule
		Mammalia			
All mammals	4629	1370	1.184 (–0.176)	≪ 0.001	Yes
		Subclass Prototheria			
Monotremata (monotremes)	3	2	1.273 (–0.273)	–	–
		Subclass Metatheria			
Didelphimorphia (American marsupials)	63	13	1.323 (–0.323)	0.002	No
Paucituberculata (shrew oppossums)	5	2	1.840 (–0.840)	–	–
Microbiotheria (Monito del monte)	1	1	1.044 (–0.044)	–	–
Dasyuromorphia (Dasyuroids)	63	24	1.465 (–0.464)	≪ 0.001	No
Peramelemorphia (bandicoots and bilbies)	21	9	1.496 (–1.496)	0.015	–
Notoryctemorphia (marsupial moles)	2	0	–	–	–
Diprotodontia (kangaroos, etc.)	117	63	1.306 (–0.298)	≪ 0.001	Yes
		Subclass Eutheria			
Insectivora (insectivores)	428	59	1.048 (–0.040)	0.081	No
Macroscelidea (elephant shrews)	15	5	0.964 (–0.020)	0.142	–
Scandentia (tree shrews)	19	1	–	–	–
Dermoptera (colugos)	2	0	–	–	–
Chiroptera (bats)	925	354	0.999 (0.017)	0.091	No
Primates (primates)	233	198	1.247 (–0.246)	≪ 0.001	Yes
Xenarthra (sloths, armadillos, and anteaters)	29	4	0.914 (–0.054)	0.216	–
Pholidota (pangolins)	7	3	1.767 (–0.825)	0.001	–
Lagomorpha (rabbits and pikas)	80	21	0.930 (0.087)	0.012	No
Rodentia (rodents)	2015	295	1.092 (–0.085)	≪ 0.001	No
Cetacea (whales, dolphins, and porpoises)	78	10	1.414 (–0.395)	0.082	No
Carnivora (carnivores)	271	180	1.476 (–0.472)	≪ 0.001	No
Tubulidentata (aardwark)	1	0	–	–	–
Proboscidea (elephants)	2	2	1.900 (–0.900)	–	–
Hyracoidea (hyraxes)	6	1	1.111 (–0.111)	–	–
Sirenia (dugongs and manatees)	5	0	–	–	–
Perissodactyla (horses, rhinos, and tapirs)	18	8	1.164 (–0.152)	0.156	–
Artiodactyla (antelopes, camels, pigs, etc.)	220	115	1.340 (–0.335)	≪ 0.001	No

reasons (e.g. Atchley *et al.* 1976; Ranta *et al.* 1994; Sokal and Rohlf 1995; but see Smith 1999), but also for conceptual reasons, because male and female body sizes are what selection acts on—not dimorphism *per se*. We use major-axis regressions through the origin as there is no reason *a priori* to put males or females on the x or y axis. For life-history analyses, ordinary regression analyses were carried out by placing female body mass on the x axis. For analyses of only continuous variables, the independent contrasts method (Felsenstein 1985), as implemented by the CRUNCH option in the computer program CAIC (Purvis and Rambaut 1995), was used.

2.3 Results

2.3.1 General patterns

We collected sex-specific body-mass data for 1370 species, constituting almost 30% of the 4629 extant and recently extinct mammalian species described (Wilson and Reeder 1993). The variances of male and female body masses were not significantly different (Cochran $P = 0.150$; Figure 2.2a), indicating that neither female nor male body mass is more variable. The distribution of body masses is significantly different from a normal distribution for both sexes (Kolmogorov–Smirnov $P < 0.01$). With the cut-off point at a 10% size difference in either direction, we found that mammals on average are male-biased size dimorphic (average male/female mass ratio = 1.184; paired t test $P \ll 0.001$; Table 2.1) with males larger than females in 45% of species (Figure 2.2b; Table 2.1). The majority of mammalian orders are also significantly male-biased dimorphic (average male/female mass ratio > 1.0; $P < 0.05$). Some orders exhibit no significant size dimorphism, and one (Lagomorpha) is significantly female-biased dimorphic on average (average male/female mass ratio < 1.0; $P < 0.05$; Table 2.1). The distribution of dimorphism in mammals is significantly different from a normal distribution (Kolmogorov–Smirnov $P < 0.01$), probably because the distribution is not phylogenetically corrected (see Lindenfors 2006).

A major-axis regression on male and female body mass contrasts revealed a significant allometric relationship between male and female body mass. This implies that size dimorphism increases with body mass in mammals in general, which supports Rensch's rule (Table 2.1; Figure 2.3), and that—contrary to our previous result—male body mass is more variable than female. However, further analyses of mammalian orders only finds support for Rensch's rule in Primates and Diprotodontia (Table 2.1).

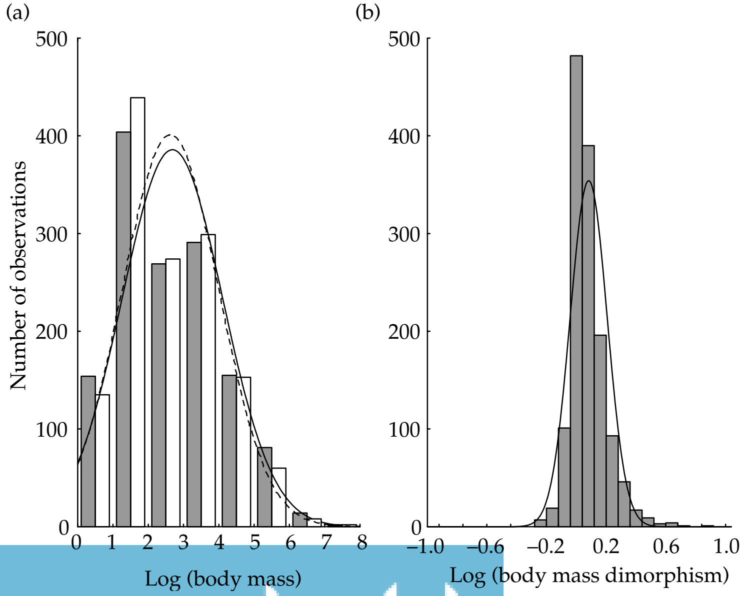

Figure 2.2 The distribution of (a) body mass and (b) sexual size dimorphism in mammals, where one species provides one observation. Sexual size dimorphism is measured as the log (male mass/female mass). The distributions of dimorphism and body mass for both sexes are significantly different from the normal distribution. In (a) the variances of body masses in males (shaded bars, continuous line) and females (open bars, striped line) are equal. Mammals are male-biased dimorphic, with an average male/female mass ratio of 1.184.

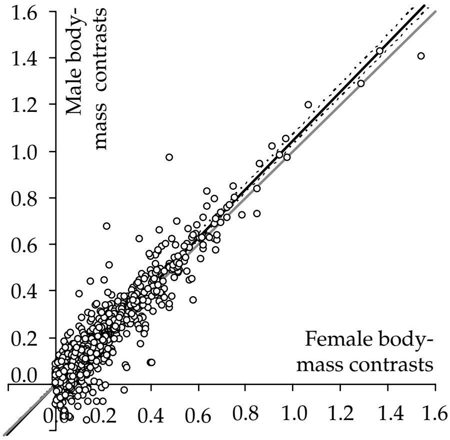

Figure 2.3 Major-axis regression through 0 (thick black line) on male and female body-mass contrasts in mammals. The 95% confidence intervals (thin dashed lines) exclude the slope of 1 (thick grey line), indicating that the relationship between male and female body mass is allometric, in extension indicating that body-mass dimorphism increases with increasing body mass in mammals, that Rensch's rule applies in mammals.

2.3.2 Sexual selection

We tested for the effects of sexual selection using mating system as a three-state unordered categorical variable, testing for differences in dimorphism between "more" and "less" sexually selected sister taxa utilizing the BRUNCH option in CAIC. These tests revealed that a higher degree of sexual selection was associated with a higher degree of male-biased dimorphism. Further, more polygynous taxa also had larger males and females than their less polygynous sister taxa. These patterns only hold separately in the mammalian orders of Primates and Artiodactyla (Table 2.2).

2.3.3 Fecundity selection

Since we were also interested in the female aspect of male-biased size dimorphism, we analyzed the relationship between female mass and several life-history characters using independent contrasts. Our results confirmed the pattern reported in earlier research (e.g. Boyce 1988; Harvey *et al.* 1989; Lee *et al.* 1991; Purvis and Harvey 1995), that all life-history traits are slower or energetically more costly in larger species of mammals (Table 2.3).

Table 2.2 Results from the BRUNCH algorithm in CAIC using mating system as a three-state unordered discrete character enabling comparisons of "more" and "less" sexually selected sister taxa (see text for an explanation of these categories). A significant difference between sister taxa differing in degree of polygyny is indicated by $P < 0.05$ (in bold; values close to significance are in italics). There is a significant effect of sexual selection on dimorphism as well as male and female body mass in mammals in general, but this pattern is no longer significant if Primates and Artiodactyla are excluded from the comparisons.

Variable	Number of comparisons	*t* value	*P*
Artiodactyla			
Dimorphism	15	2.015	*0.064*
Male mass	15	2.297	**0.038**
Female mass	15	2.124	*0.052*
Carnivora			
Dimorphism	10	1.594	0.146
Male mass	10	1.462	0.178
Female mass	10	1.059	0.317
Chiroptera			
Dimorphism	9	−0.057	0.956
Male mass	9	−0.629	0.547
Female mass	9	−0.696	0.506
Mammalia			
Dimorphism	69	3.360	**0.001**
Male mass	69	3.199	**0.002**
Female mass	69	2.764	**0.007**
Diprotodontia			
Dimorphism	4	−0.508	0.647
Male mass	4	−0.354	0.746
Female mass	4	−0.273	0.802
Primates			
Dimorphism	20	3.670	**0.002**
Male mass	20	3.090	**0.006**
Female mass	20	2.645	**0.016**
Rodentia			
Dimorphism	5	1.151	0.314
Male mass	5	1.036	0.358
Female mass	5	0.917	0.411
Mammalia except Artiodactyla and Primates			
Dimorphism	33	1.451	0.110
Male mass	33	1.272	0.256
Female mass	33	1.050	0.304

Repeating these analyses over several mammalian orders complicated the picture in that not all life-history traits in all orders were correlated with body mass (Table 2.4). This was particularly true for small-bodied orders such as Rodentia and Insectivora, but particularly the aerial Chiroptera. It is likely that flight adaptations play an important role in Chiropteran life-history evolution (Jones and MacLarnon 2001).

We further carried out analyses using the BRUNCH option in CAIC, with mating system indicating the strength of sexual selection and the life-history variables given in Table 2.4 as indicators of female fecundity. We used General Linear Models (GLMs) to enable the inclusion of female body mass as a covariate in subsequent tests (see below). These analyses revealed no effect of sexual selection on female fecundity in mammals (GLM, $P > 0.5$ for all variables). Separately analyzing three orders where sexual selection is a probable cause of dimorphism revealed no life-history correlates of mating system in Artiodactyla or Primates, while several correlates were found in Carnivora (GLM, age at female sexual maturity, $F = 10.612$, $P = 0.011$; litter size, $F = 40.899$, $P = 0.001$; birth rate, $F = 8.263$; $P = 0.026$; maximum longevity, $F = 5.318$, $P = 0.058$). These patterns in Carnivora remained significant after including female mass as a covariate, indicating an extra effect above that of size alone (GLM, age at female sexual maturity, $F = 6.238$, $P = 0.044$; litter size, $F = 420.350$, $P \ll 0.001$; birth rate, $F = 9.112$, $P = 0.032$; maximum longevity, $F = 15.538$, $P = 0.013$). Interestingly, in Primates the interbirth interval was indicated to be significantly longer in more polygynous species after the inclusion of mass (GLM, $F = 5.251$, $P = 0.045$).

2.3.4 Increased investment in offspring

Finally we examined whether there is an increased investment in offspring in species under more sexual selection. The BRUNCH option in CAIC showed that this effect could be found for weaning age, which was higher in mammals under greater sexual selection because of their larger mass (GLM, $F = 0.352$, $P = 0.034$). Separately analyzing the three orders in which sexual selection correlates with size dimorphism revealed larger neonates in Carnivora (GLM, $F = 4.275$, $P = 0.070$), whereas Primates have higher weaning ages in species under greater sexual selection (GLM, $F = 11.658$, $P = 0.006$). We then added mass as a covariate and tested for an effect of sexual selection above that caused by size increase alone. These analyses again showed that weaning age is significantly longer in species under more sexual selection, even after removing the effects of the increased mass (GLM, $F = 3.583$, $P = 0.039$). As above, no effect of sexual selection on female life histories was found in Artiodactyla, whereas Carnivora again had larger neonates (GLM, $F = 12.965$, $P = 0.010$), and Primates had higher weaning ages in species under greater sexual selection (GLM, $F = 5.251$, $P = 0.045$).

Table 2.3 Results of regressions through the origin on independent contrasts of the relationship between nine life-history variables and female body mass separately in mammals. *N* refers to the number of contrasts. All life-history characters are significantly correlated with female body mass.

Variable	*N*	*B*	*t*	R^2	*P*
		Mammalia			
Female maturity	490	0.170	10.216	0.176	0.000
Gestation length	606	0.076	10.673	0.158	0.000
First birth	291	0.190	10.974	0.293	0.000
Litter size	844	−0.035	−2.965	0.010	0.003
Interbirth interval	637	0.158	6.483	0.062	0.000
Birth rate	631	−0.190	−6.674	0.066	0.000
Maximum longevity	521	0.123	5.617	0.057	0.000
Neonate mass	562	0.665	22.238	0.468	0.000
Weaning age	581	0.129	7.732	0.093	0.000

2.4 Discussion

Generally, we found that mammals exhibit significant male-biased sexual size dimorphism, thus corroborating the results of earlier comparative studies (e.g. Greenwood and Wheeler 1985; Reiss 1989; Abouheif and Fairbairn 1997; Loison *et al.* 1999). Examining mammal orders separately, most taxa with sufficient numbers of species for statistical analyses also conform to this pattern; notable exceptions are Lagomorpha and Chiroptera, the former being significantly female-biased dimorphic and the latter showing a tendency ($P = 0.091$) in the same direction. The overwhelmingly largest mammal order—Rodentia, containing 45% of the extant mammal species—is,

Table 2.4 Results of regressions through the origin on independent contrasts of the relationship between nine life-history variables and female body mass separately in seven mammalian orders as well as in all mammals except Artiodactyla, Carnivora, and Primates. *N* refers to the number of contrasts. Neonate mass and age at weaning are correlated with body mass in all examined orders.

Variable	*N*	*B*	*t*	R^2	*P*	*N*	*B*	*t*	R^2	P
			Artiodactyla					*Carnivora*		
Female maturity	60	0.169	2.514	0.097	0.015	117	0.140	4.619	0.155	0.000
Gestation length	64	0.116	5.851	0.352	0.000	132	0.142	4.937	0.157	0.000
First birth	44	0.214	3.723	0.244	0.001	42	0.233	5.750	0.446	0.000
Litter size	66	−0.048	−2.049	0.061	0.044	149	0.036	1.092	0.008	0.277
Interbirth interval	58	0.008	0.163	0.000	0.871	119	0.109	3.565	0.097	0.001
Birth rate	57	−0.108	−2.252	0.083	0.028	119	−0.076	−1.680	0.023	0.096
Maximum longevity	64	0.113	3.016	0.083	0.004	131	0.157	5.251	0.175	0.000
Neonate mass	65	0.863	23.447	0.896	0.000	115	0.565	6.195	0.252	0.000
Weaning age	59	0.212	3.223	0.152	0.002	124	0.117	2.673	0.055	0.008
			Chiroptera					*Insectivora*		
Female maturity	40	0.201	2.274	0.117	0.028	13	0.207	0.991	0.076	0.341
Gestation length	81	−0.046	−1.069	0.014	0.288	25	0.130	2.867	0.255	0.008
First birth	33	0.086	0.975	0.029	0.337	4	0.158	0.661	0.127	0.556
Litter size	184	−0.010	−0.744	0.003	0.458	36	0.010	0.137	0.000	0.982
Interbirth interval	120	−0.018	−0.633	0.003	0.527	28	0.158	0.640	0.015	0.528
Birth rate	118	0.004	0.447	0.002	0.656	27	−0.030	−0.076	0.000	0.940
Maximum longevity	42	−0.102	−0.716	0.012	0.478	25	0.365	3.186	0.297	0.004
Neonate mass	97	0.923	13.662	0.660	0.000	21	0.845	9.454	0.817	0.000
Weaning age	73	0.213	1.985	0.052	0.051	19	0.103	1.745	0.145	0.098
			Diprotodontia					*Primates*		
Female maturity	34	0.109	2.193	0.127	0.035	74	0.070	1.150	0.018	0.254
Gestation length	26	−0.066	−1.346	0.068	0.190	94	0.017	1.036	0.011	0.303
First birth	21	0.104	2.126	0.184	0.046	78	0.071	1.382	0.024	0.171
Litter size	57	−0.127	−3.581	0.186	0.001	101	−0.051	−1.910	0.035	0.060
Interbirth interval	37	0.149	2.598	0.158	0.013	81	0.174	3.502	0.133	0.001
Birth rate	37	−0.276	−4.580	0.368	0.000	79	−0.373	−6.556	0.355	0.000
Maximum longevity	39	0.227	3.224	0.215	0.003	85	0.100	2.238	0.056	0.028
Neonate mass	21	0.581	7.556	0.741	0.000	78	0.607	12.544	0.671	0.000
Weaning age	38	0.275	9.168	0.694	0.000	86	0.340	4.324	0.180	0.000
			Rodentia				*Mammals except Artiodactyls, Carnivores, and Primates*			
Female maturity	81	0.171	3.461	0.130	0.001	239	0.174	8.069	0.215	0.000
Gestation length	113	0.117	6.786	0.291	0.000	329	0.002	0.157	0.000	0.875
First birth	38	0.258	5.016	0.405	0.000	130	0.180	7.694	0.314	0.000
Litter size	160	−0.040	−1.313	0.011	0.191	540	−0.078	−8.069	0.108	0.000
Interbirth interval	106	0.162	1.526	0.022	0.130	381	0.067	2.234	0.013	0.026
Birth rate	106	−0.146	−1.240	0.014	0.218	378	−0.142	−0.044	0.042	0.000
Maximum longevity	75	0.186	3.852	0.167	0.000	254	0.166	8.310	0.214	0.000
Neonate mass	103	0.788	26.422	0.872	0.000	308	0.804	32.671	0.777	0.000
Weaning age	105	0.115	3.907	0.128	0.000	315	0.168	9.945	0.240	0.000

however, significantly male-biased dimorphic. It is likely that the data we were able to examine are biased toward larger species, as these tend to be better studied than smaller species, which may affect the overall pattern we report.

A non-phylogenetic analysis indicated no significant difference between the variances of male or female body masses, thus giving no apparent indication of which sex changes size more often. Contrary to this result, our phylogenetic analysis of the relationship between size dimorphism and body mass (Rensch's rule) revealed a significant correlation between mass and mass dimorphism. This puts the focus on males for understanding size dimorphism in mammals, since male contrasts were significantly larger than female. Our result is also the first where Rensch's rule has been confirmed across such a high-taxon level (class Mammalia). Since Rensch's rule is based on empirical observations of patterns in the animal world (D.J. Fairbairn, personal communication), this broadens the generality of the rule. However, in contrast to an earlier study (Abouheif and Fairbairn 1997), we only found support for Rensch's rule on the level of order in Diprotodontia and Primates. Also, as has been shown elsewhere, the presence/absence of Rensch's rule can be due to factors not relating to the rule itself (Lindenfors and Tullberg 2006). More revealing is therefore to analyze the data for drivers of size dimorphism.

Since our results show that mammals exhibit male-biased sexual dimorphism and since this dimorphism has been shown in several mammal groups to relate to sexual selection on males (Geist 1974; Jarman 1974, 1983; Clutton-Brock and Harvey 1977; Clutton-Brock *et al*. 1977; Alexander *et al*. 1979; Clutton-Brock 1985; Mitani *et al*. 1996; Lindenfors and Tullberg 1998; Weckerly 1998; Loison *et al*. 1999; Lindenfors *et al*. 2002; Pérez-Barbería *et al*. 2002), we have here focused on male-biased dimorphism and its relation to sexual selection on males. Using mating system as a proxy for the strength of sexual selection indicates that mammals under greater sexual selection pressure are indeed more dimorphic. The same analysis applied to body mass reveals that species under more sexual selection have larger males, but also larger females, than do species under weaker sexual selection. Thus, we found sexual selection to be an important cause of sexual dimorphism, but also of large size itself.

This pattern only holds across all mammals and was not found within different orders (except for Primates and Artiodactyla). This lack of support may in some cases be due to a low statistical power, as sample sizes in some orders were small. The lack of a relationship between dimorphism and mating system is particularly interestingly in Carnivora as this order contains a large number of species and the most dimorphic mammal known (southern elephant seal, *Mirounga leonina*). Previous carnivore studies have found a significant relationship between canine dimorphism and mating system (Gittleman and Van Valkenburgh 1997). Also, a study on pinnipeds using harem size instead of mating system showed that sexual selection drives sexual dimorphism in pinnipeds (Lindenfors *et al*. 2002). It is therefore possible—or even probable—that sexual selection is also an important driver of size dimorphism in carnivores, but that our measurement of mating system is too crude to detect a relationship. This also acts as a cautionary note for the other orders where the influence of sexual selection could not be validated.

By confirming sexual selection on males as a correlate of male-biased dimorphism in mammals, however, we have only managed to explain half of the pattern. To make a dimorphic species, it is important also to explain what maintains smaller size in females (Lindenfors 2002). Our life-history analysis of female mammals confirmed that large size slows down and increases the expenditure of reproduction (Boyce 1988; Roff 1992; Stearns 1992; Charnov 1993). Thus, as fecundity is an important selection pressure on female size, it is not in the females' interest to grow larger (Lindenfors 2002).

Separate analyses of each mammalian order confirms the general pattern. Generally, the more variation in body mass that exists in an order, the more tight is the relationship between body mass and fecundity. For example, in Rodentia, Chiroptera, and Insectivora, many of the analyzed life-history variables are not at all correlated with body mass. This can be a statistical effect where the relationship becomes more detectable as more variation is included, but it can also indicate that, at small sizes, body mass is not a major determinant of life histories. In Chiroptera, for example—which is the order where our results indicate the fewest correlations between body mass and life histories—flight adaptations may play an important role (Myers 1978; Jones and MacLarnon 2001).

If sexual selection is the cause of size dimorphism through selection on males, and if female size is also greater in species under greater sexual selection, then females should be expected to pay some sort of life-history price for their larger size (Lindenfors 2002). Our results indicate that in general it is age at weaning that is later in species under more sexual selection. Interestingly enough, this result remains even if the effects of body mass are removed. Further, an earlier study has reported that, contrary to theoretical predictions, the ratio of weaning weight to adult weight scales with adult body mass (Purvis and Harvey 1995). These results indicate that mammals under more sexual selection wean at a later age and consequentially also at a larger size. Weaning age and body weight are especially important because resources transferred during lactation are typically more energetically costly than the prenatal costs of gestation (Cameron 1998), and female body mass is correlated with milk yield in mammals (Oftedal 1984). Thus, a longer suckling period constitutes a significant selection pressure on female size.

We did not find that the higher weaning age resulted in a longer interbirth interval, a result that we expected. It has been shown previously in primates (Lindenfors 2002) that higher weaning age corresponds with a longer interbirth interval, a result replicated in this study for primates but not for mammals overall. It is not unlikely, however, that our result outside primates stems from the low number of comparisons available when simultaneously utilizing mating system and interbirth interval. Future studies may shed more light on this question.

Overall, our results indicate that much of the male-biased dimorphism in mammals is caused by sexual selection on males. We also suggest that fecundity selection on females explains the female part of sexual size dimorphism. Nevertheless, females were found to be larger in more sexually selected species, most probably because a selection pressure correlated to sexual selection on males through the demands of lactation.

This review also highlights that there is ample variation in mammalian sexual size dimorphism left to explain. Although it is probable that much of the male-biased dimorphism we have not been able to explain here will also be tied to sexual selection on males, we still have no satisfying general answer for what causes female-biased dimorphism in mammals.

2.5 Summary

This chapter explores the pattern of sexual size dimorphism in mammals and the processes that underly its evolution. We find that, on average, male mammals are the larger sex (average male/female mass ratio 1.184), with males being at least 10% larger than females in over 45% of species. Most mammalian orders are also have male-biased sexual dimorphism, although some orders do not show any bias or are significantly female-biased (Lagomorpha). Sexual size dimorphism increases with body size across mammals (Rensch's rule), suggesting that there are parallel selection pressures on both male and female size. We found support for the hypothesis that male-biased dimorphism relates to sexual selection on males through male–male competition for females. We draw this conclusion from a positive correlation between the degree of sexual selection, as indicated by mating systems and the degree of male-biased size dimorphism. The degree of sexual selection was also positively correlated with male and female size across mammals. Further, a parallel selection pressure on female mass is identified in that age at weaning is significantly higher in more polygynous species, even when correcting for body mass. We also explore the processes maintaining smaller female size in sexually dimorphic species and confirm that reproductive rate is lower for larger females, indicating that fecundity selection selects for smaller females in mammals. Although the patterns we discuss hold across mammals as a whole, there is considerable variation across orders and many of these relationships are not significant. Further work is still needed to more closely investigate the pattern of sexual dimorphism and processes driving sexual dimorphism in different clades.

2.6 Acknowledgments

We thank Wolf Blanckenhorn, Tamás Székely, and Daphne Fairbairn for organizing the magnificent workshop and editing this volume. We also thank Isabella Capellini for comments on previous drafts of this chapter. This work was financed by the Swedish Research Council (P.L.), NSF (DEB-0129009; J.L.G. and K.E.J.), and the Earth Institute of Columbia University (K.E.J.).

2.7 Suggested readings

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CHAPTER 3

Sexual size dimorphism in birds

Tamás Székely, Terje Lislevand, and Jordi Figuerola

> "The males of many birds are larger than the females, and this no doubt is the result of the advantage gained by the larger and stronger males over their rivals during many generations."
>
> Darwin (1874)

3.1 Introduction

The difference in body size between males and females has been known by naturalists for hundreds of years. For instance, Charles Darwin (1874) wrote "The male [spider] is generally much smaller than the female, sometimes to an extraordinary degree", "...the female of almost all fishes is larger than the male", and "With mammals, when, as is often the case, the sexes differ in size, the males are almost always larger and stronger."

Birds exhibit a modest range of sexual size dimorphism (SSD) relative to spiders and fishes (see Chapters 1 and 7 in this volume). Nevertheless, they are excellent model organisms to test macroevolutionary patterns for several reasons. There are approximately 9700 bird species, and they inhabit all continents and occupy a variety of niches. Birds are exceptionally well studied in the wild, and data on body sizes, ecology, and behavior are readily accessible for many species. In addition, their taxonomy and phylogeny are reasonably well understood. Males and females can often be easily distinguished, whereas in many invertebrates detailed examination of genitalia is needed to tell sexes apart. Birds have determinate growth so most birds achieve adult size shortly after fledging whereas many invertebrates, fishes, and reptiles keep growing throughout their lives. Birds also exhibit exceptional variation in breeding systems, providing an excellent opportunity to test Darwin's assertion about sexual selection and its implication for SSD.

We have three objectives in this chapter. First, we will assess the distribution and pattern of SSD among birds and test whether Darwin's assertion about male-biased avian dimorphisms are consistent with data. Thus we explore the overall distribution of SSD in five readily measurable morphological traits. We show that SSD in one trait is often only loosely related to SSD in another trait, suggesting different selective forces are acting on different traits. Second, we test an allometric relationship between body size and SSD, termed Rensch's rule (Abouheif and Fairbairn 1997; Fairbairn 1997). Previous works in several avian taxa demonstrated the existence of such an allometry (Fairbairn 1997; Colwell 2000; Székely *et al.* 2004; Raihani *et al.* 2006). Our objective here is to establish whether this relationship occurs more often than expected by chance among avian families. Finally, we test four major functional explanations of SSD.

Body size and its components are the targets of several selective processes (Andersson 1994; Blanckenhorn 2000). Thus there are advantages of being large (e.g. contests over mates or resources, mate preference by the opposite sex, resilience to temporary food shortage), or small (e.g. early maturation with shorter generation time and more rapid reproduction, higher success in scrambles). SSD is expected to evolve if some of these selective processes are stronger in one sex than in the other, or the outcome of these processes do not cancel out between the sexes. Given that the reproductive physiology and breeding ecology of sexes are often different, we expect extensive SSD in many bird species.

Here we focus on four major functional hypotheses. First, the *mating-competition hypothesis* predicts increasing SSD, as measured by $\log_{10}$(male size) – $\log_{10}$(female size) (see also Chapters 2, 4, and 12 in this volume), with more intense male–male competition. This is because when males compete over females, sheer size is often advantageous. Second, the *display-agility hypothesis* predicts decreasing SSD with more manoeuvrable male displays (Payne 1984; Jehl and Murray 1986; Figuerola 1999). This hypothesis is likely to be relevant if females prefer males with acrobatic displays. Since manoeuvrability in the air increases with small size, selection for producing small males is expected by female choice (Andersson and Norberg 1981). Third, the *resource-division hypothesis* predicts increasing SSD with the potential for overall resource use. Thus to avoid exploiting the same resources when males and females forage together and use the same territory, one may expect enhanced SSD. Since resource division may emerge either via large males and small females or vice versa, we calculated the absolute difference between the sizes of males and females—that is, $|\log_{10}(\text{male size}) - \log_{10}(\text{female size})|$—and used the absolute difference as a response variable. Finally, the *fecundity hypothesis* predicts increasing female size (relative to male size) with fecundity. We tested the latter prediction by relating SSD to clutch size.

Previous reviews of avian SSD were insightful and thought-provoking (Table 3.1). Our work, however, is distinct from these earlier studies in several respects. First, we use five morphometric traits whereas most previous studies used only one (or two) *proxies* of body size. Second, our study is the first to test all four fundamental hypotheses of SSD. Whereas the mating-competition hypothesis has been tested extensively, the other three hypotheses were somehow neglected. Finally, we test these hypotheses using the hitherto broadest range of taxa that includes 3767 species (out of 9702 species; Monroe and Sibley 1993) and 125 avian families (out of 146 families).

3.2 Methods

Data were collected from handbooks that included *Birds of the Western Paleartic*, *Birds of Africa*, *Birds of North America Online*, and *Handbook of Birds of New Zealand and Australia* (T. Lislevand *et al.* 2007). Morphometric data of adult birds, preferably taken during breeding season, were compiled. If several data were available for a given species (e.g. from different subspecies), we preferred those with measurements available for more morphological variables, and the ones with larger numbers of individuals for each sex.

Explanatory variables were either taken from handbooks (see above), or from specific sources (T. Lislevand *et al.* 2007). Scores of mating competition were taken from Dunn *et al.* (2001), or from handbooks using the following scheme: (1) polyandry, when some females have several social mates; (2) monogamy (<5% of males polygynous); (3) mostly

Table 3.1 Summary of functional analyses of SSD in birds. Only broad-scale studies are listed that used several avian families. N/A indicates that a hypothesis was not tested, and Yes and No show whether a specific hypothesis was supported or not.

Morphometric trait	Functional hypothesis				No. of species (families)	Reference
	Mating competition	Display agility	Resource division	Fecundity		
Wing length	Yes	N/A	N/A	N/A	341 (12)	Payne (1984)
Body mass	Yes	N/A	N/A	N/A	73 (30)	Owens and Hartley (1998)
Body mass, tail length, wing length	Yes	N/A	N/A	No	1031 (91)	Dunn *et al.* (2001)
Body mass, wing length, tarsus length, bill length, tail length	Yes	Yes	No	No	3767 (125)	This work

monogamy, but occasional polygyny (5–15% of males polygynous); (4) mostly polygyny (>15% of males polygynous), and (5) lek or promiscuous. The latter category includes species in which the male attracts mates to courts or arenas, and he contributes no resource other than sperm to the raising of young (Dunn *et al.* 2001). This scoring reflects the notion that the intensity of male–male competition increases from one to five. Note that cooperative breeders (score 5 in Dunn *et al.* 2001, $n = 103$ species) were merged with monogamous species ($n = 955$ species) to reflect the assumption that sexual selection is weak in many (but not all) cooperative breeders. Excluding the cooperative breeders from the analyses of mating competition does not influence qualitatively our results (not shown). Data for extra-pair paternity are not yet available for vast majority of these species, and this prevented us from using extra-pair paternity in the analyses.

Descriptions of male display behaviors were taken from textbooks (T. Lislevand *et al.* 2007), and these descriptions were scored on a five-point scale: (1) ground displays only, including displays on trees and bushes; (2) ground displays with occasional jumps/leaps into the air; (3) both ground and non-acrobatic flight displays; (4) mainly aerial displays, non-acrobatic; and (5) mainly aerial displays, acrobatic (see further explanations in Raihani *et al.* 2006). A display was considered acrobatic if it included rapid changes in flight direction, twists, rolls, and turns. Three observers scored the descriptions blindly to the identity of species. The scores of the observers were highly consistent (Spearman rank correlations, $r_s = 0.829–0.848$, $n = 1113–1228$ species, $P < 0.001$). To increase the robustness of display scores, we only included species in the analyses that were scored by at least two observers, and the maximum difference between scores was ≤ 2. We use the median score of observers for each species.

To investigate the influence of resource sharing on the relative sizes of sexes, we collected information on territorial behavior and whether the birds feed on, or away from, their territories. Verbal descriptions of territorial behavior and feeding locations on (or away from) the territory were taken from the literature (T. Lislevand *et al.* 2007), and these descriptions were scored on a three-point scale: (0) males and females do not share resources and they feed away from their breeding territory; (1) males and females share resources on their territory only during the breeding season; and (2) males and females share resources on their territory all year round. As with male displays, three observers scored the descriptions blindly to the identity of species. The scores were consistent among observers ($r_s = 0.628–0.674$, $n = 1454–1629$ species, $P < 0.001$). To increase the robustness of these scores, we only included those species in the analyses that were scored by at least two observers, and the maximum difference between scores was ≤ 1. We use the median score for a given species. We took clutch size as a measure of fecundity, since data on clutch size are readily available for many species. Other measures, such as the number of clutches produced by females per year, are less universally available for the broad range of species we intended to cover.

In total, we had morphometric data for 3767 species, although due to missing data in one or several morphological measurements, the number of species we used in the analyses varied between 2348 species (tail length) and 2977 species (wing length), and for the explanatory data between 1218 species (display agility) and 2642 species (clutch size).

Comparative evolutionary biologists use a variety of phylogenetic methods to test functional hypotheses (Harvey and Pagel 1991; Martins 1996; Freckleton *et al.* 2002; Blomberg *et al.* 2003). A major constraint of these analyses is that they require a phylogeny. Whereas phylogenies are available for many avian families, they are rarely fully comprehensive, and even comprehensive phylogenies may have uncertain topology and/or branch lengths that may lead to potentially erroneous conclusions. To avoid losing species due to missing phylogenetic information, we decided to carry out the analyses separately for each family using species-level data, and then use the resulting test statistic (for instance, Pearson correlation coefficient, *r*) as a response variable to assess our working hypotheses. All morphometric data were converted to logarithm base 10 before the analyses.

The dispersion of SSD was compared across traits using Moses test (Daniel 1990) as implemented by the SPSS version 12.0 software package. To be conservative, we did not use 5% trimmed controls in Moses tests and report the two-tailed probabilities.

For testing the existence of Rensch's rule, we fitted a major-axis regression for each family separately. Only families with data from at least five species were used for fitting a major-axis regression between $\log_{10}$(male size) (dependent variable) and $\log_{10}$(female size). The distribution of principal axes (β) was tested using Wilcoxon one-sample test against the median of 1.0. Note that we are not concerned with the significance of β for a given family (this may be inflated due to phylogenetic non-independence; Fairbairn 1997). Rather, we took each family as a sampling unit, and test whether the distribution of β is different from 1.0 across avian families. Allometry consistent with the Rensch's rule would be indicated by slopes larger than 1.

Functional hypotheses were tested by calculating bivariate Spearman rank correlations (r_s) between morphometric traits (SSD in body mass, and in lengths of wing, tarsus, bill and tail), and explanatory variables (mating competition, display agility, resource division, fecundity). Then we tested the distribution of bivariate rank correlation coefficients (r_s) against a median of 0.0 using Wilcoxon one-sample test. We were unable to use partial rank correlations (Daniel 1990) for testing each explanatory variable while controling for the other three, because missing data resulted in too few families having enough data with five (or more) degrees of freedom. We use SPSS 12.0 or Minitab 13.31 for statistical analyses, unless otherwise stated. We mostly rely on non-parametric statistics, since SSD—somehow surprisingly—was not normally distributed (see below), and three out of four explanatory variables were scores; that is, measured on the ordinal scale.

3.3 Results

3.3.1 Distribution of SSD

Birds exhibit male-biased SSD in all five morphometric traits (Figure 3.1; Appendix, Table A3.1). This result is consistent between species-level and family-level analyses. In the latter analyses each family was represented by a single datum, the mean of their species.

The distributions of SSD are not normal at species level (Figure 3.1; Appendix, Table A3.1): the distributions are leptokurtic as there are more species around the mean than predicted by normal distribution. The deviation from normality becomes weaker at family level; nevertheless it remains significant for tail length, and marginally significant for body mass and bill length. These results suggest that strongly dimorphic species (either male-biased or female-biased) are rarer than predicted by a process of random evolution such as Brownian motion.

The dispersion of SSD in body mass is higher than in wing length, tarsus length, and bill length, both at species level (Figure 3.1a; Moses tests, $P < 0.001$) and at family level (Figure 3.1b; Moses tests, all four tests $P < 0.002$). Dispersion of SSD in body mass was not different from dispersion of SSD in tail length at species level, only at family level (Moses tests, $P = 1.000$ and $P < 0.001$, respectively).

Median SSDs are different between the traits: the largest SSD was exhibited in body mass and tail length (Figure 3.1; Appendix, Table A3.1), whereas the smallest SSD was exhibited in tarsus length (Friedman tests using only species (or families) with all five morphometric traits, species level: $\chi^2 = 273.592$, $P < 0.001$, $n = 1366$ species; family level: $\chi^2 = 23.781$, $P < 0.001$, $n = 95$ families).

SSD in one trait only correlates weakly with SSD in the other traits (Figure 3.2a; $r_s = 0.459$–0.685). This is indicated by a low Kendall's coefficient of concordance ($W = 0.050$, $\chi^2 = 273.592$, $P < 0.001$). The correlation is particularly poor between SSD in tail length and SSD in other traits, suggesting that different selective processes influence tail length and the four other traits. These results remain consistent at family level (Figure 3.2b), and Kendall's coefficient remains low ($W = 0.063$, $\chi^2 = 23.781$, $P < 0.001$).

3.3.2 Species and families exhibiting extreme SSDs

Some of the most male-biased SSDs are exhibited by bustards, grouse, widowbirds, waterfowl,

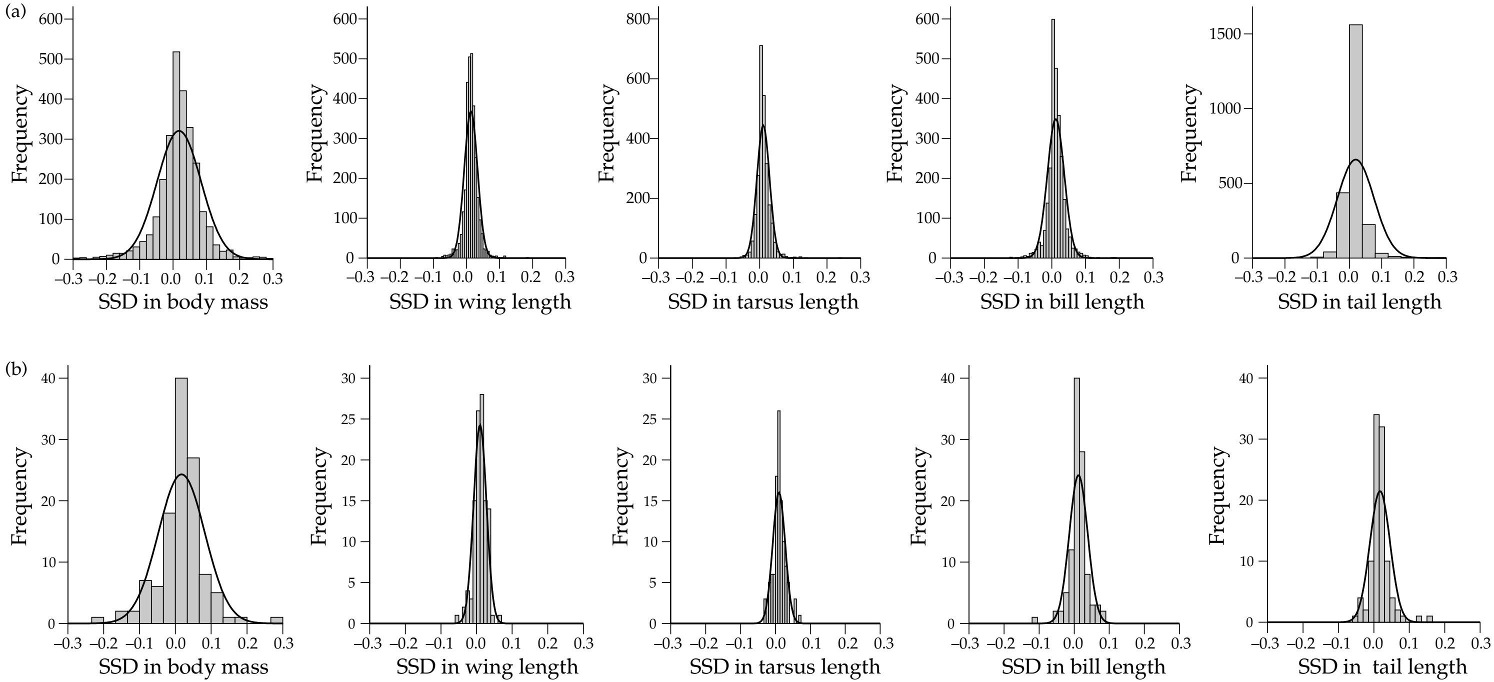

Figure 3.1 Distribution of SSD, calculated as $\log_{10}$(male trait)−$\log_{10}$(female trait) in five morphological traits at (a) species level and (b) family level, using the mean of each species. For sample sizes see Appendix, Table A3.1.

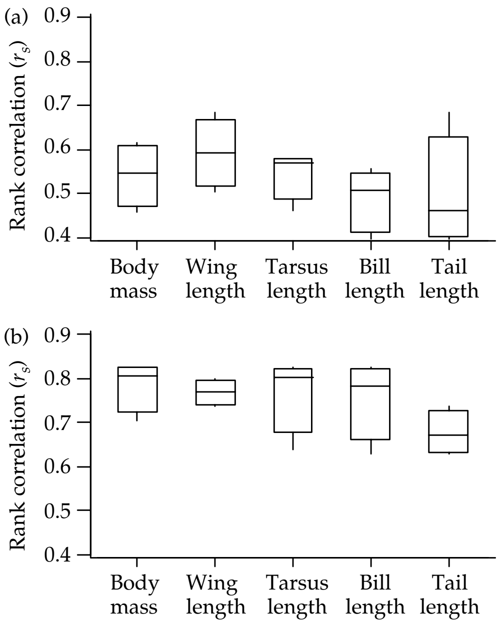

Figure 3.2 Correlations between SSDs of different traits (Spearman rank correlations, r_s). (a) Species level; (b) family level. The line is drawn across the median, and the bottom and the top of the boxes are lower (LQ) and upper quartiles (UQ), respectively. The whiskers extend from LQ and UQ to the lowest and highest observations, respectively, within the range defined by LQ − 1.5*(UQ − LQ) and LQ + 1.5*(UQ − LQ).

grackles, and brown songlark (Appendix, Table A3.2), whereas the most female-biased SSDs are exhibited by raptors (Appendix, Table A3.2). Interestingly, the most extreme bill dimorphisms are seen in hornbills (male-biased SSD), kiwis, and long-billed curlew (female-biased SSD). Families showing consistent male-biased SSD are Otididae and Phasianidae (Figure 3.3), whereas families showing consistent female-biased SSD are Accipitridae, Tytonidae, and Turnicidae (Appendix, Table A3.2). The largest ranges of SSD (as measured by the interquartile range) are exhibited by Otididae, Tytonidae, Centropidae, Bombycillidae, Gaviidae (body mass); Tytonidae, Otididae, Trochilidae, Ciconiidae, Falconidae (wing length); Tytonidae, Otididae, Phasianidae, Spheniscidae, Accipitridae (tarsus length); Eurylaimidae, Otididae, Trochilidae, Threskiornithidae, Pelecanidae (bill length); and Nectariniidae, Menuridae, Cerylidae, Spheniscidae, Tytonidae (tail length, Appendix, Table A3.2).

3.3.3 Rensch's rule

The distribution of major-axis slopes (see Methods) is significantly larger than 1.0 for all traits (Figure 3.4). This strongly suggests that most avian families exhibit the allometric relationship between male size and female size, and this relationship occurs in body mass, wing length, tarsus length, bill length, and tail length. The extent of allometry was not different between traits (Friedman test, $\chi^2 = 4.832$, $P = 0.305$, df = 4, $n = 50$ families).

Bird families exhibiting the strongest allometry consistent with Rensch's rule are Nectariniidae (mean β of five morphometric traits = 1.231), Otididae (mean $\beta = 1.183$), Passeridae (mean $\beta = 1.179$), Phasianidae (mean $\beta = 1.153$), and Cisticolidae (mean $\beta = 1.148$). Bird families exhibiting the strongest allometry in the opposite direction from the Rensch's rule are Threskiornidae (mean $\beta = 0.905$), Charadriidae (mean $\beta = 0.962$), Scolopacidae (mean $\beta = 0.977$), Regulidae (mean $\beta = 0.989$), and Columbidae (mean $\beta = 0.992$).

3.3.4 Functional explanations of SSD

We tested four major hypotheses of SSD by calculating Spearman rank correlations for each family separately (see Methods). Then we tested whether the distribution of rank correlation coefficients is different from 0. Medians of correlation coefficients between mating competition and all five morphometric traits were significantly larger than 0 (Table 3.2). SSDs in body mass and bill length were strongly associated with mating competition. These results suggest that increasing male-biased SSD is strongly associated with intense mating competition.

The median correlation coefficients were less than 0 between display agility and SSD in morphometric traits, although the deviation from 0 was only significant in body mass (Table 3.2). To test whether the relationships between display agility and SSDs are consistent with the prediction, we combined the probability of five tests into a single value (see Sokal and Rohlf 1981). The combined probability test revealed $P < 0.05$ for display agility and SSD ($\chi^2 = 18.984$, df = 10), consistent with the display-agility hypothesis. Thus support for the

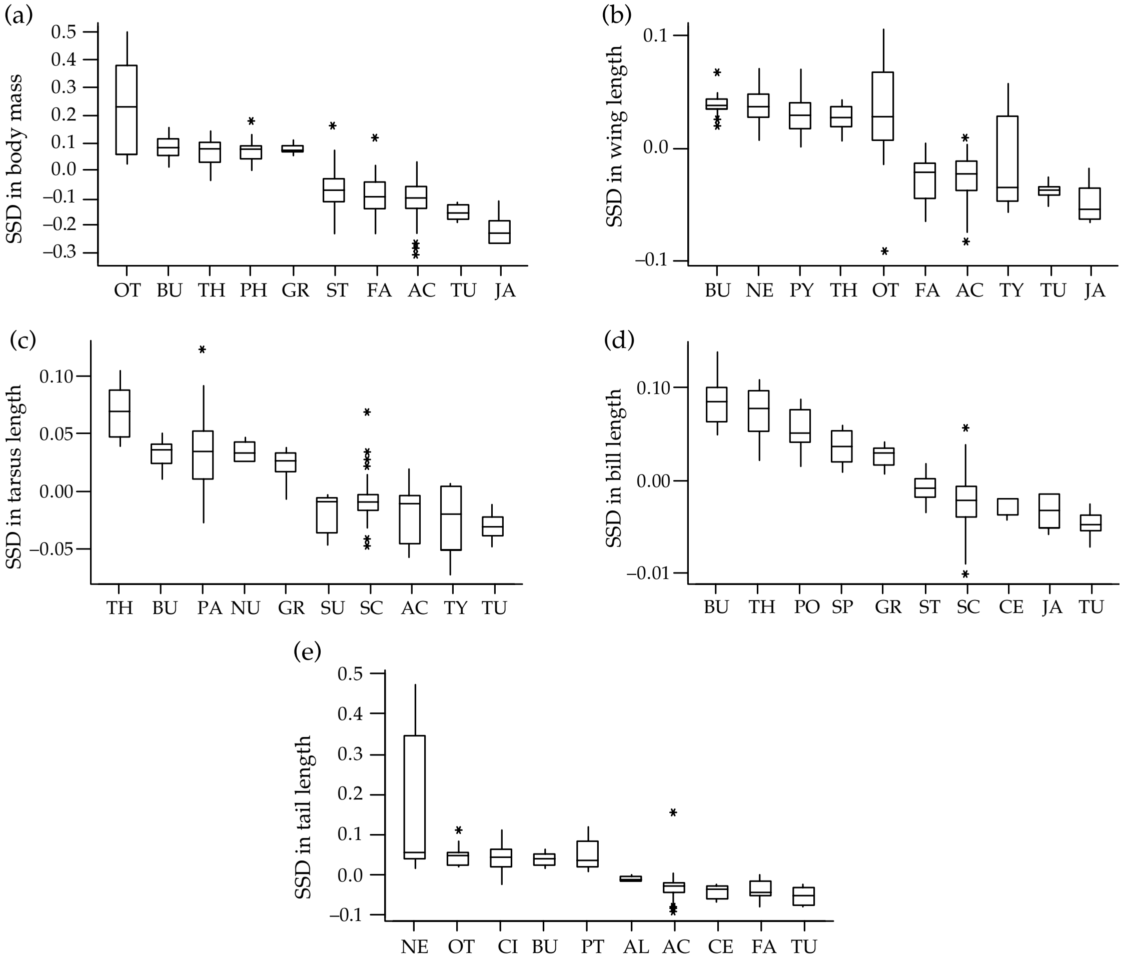

Figure 3.3 Families representing the most extreme male-biased and female-biased SSDs in body mass (a), wing length (b), tarsus length (c), bill length (d), and tail length (e). Only families with at least five data points are included. Shown are the families Accipitridae (AC), Alcedinidae (AL), Bucerotidae (BU), Centropidae (CE), Cisticolidae (CI), Falconidae (FA), Gruidae (GR), Jacanidae (JA), Nectariniidae (NE), Numididae (NU), Otididae (OT), Phasianidae (PA), Phalacrocoracidae (PH), Podicipedidae (PO), Pteroclidae (PT), Pycnonotidae (PY), Scolopacidae (SC); Spheniscidae (SP), Strigidae (ST), Sulidae (SU), Threskiornithidae (TH), Turnicidae (TU), Tytonidae (TY). Asterisks indicate outliers (see Figure 3.2 legend). For details of the boxplots see Figure 3.2. SSDs were calculated as $\log_{10}$(male trait)–$\log_{10}$(female trait).

Table 3.2 The distribution of Spearman rank correlations (r_s) between SSD traits and functional explanations. r_s was only calculated for families with data from at least five species. The median of rank correlations, the probability of Wilcoxon one-sample test (*P*) of difference from median = 0, and number of avian families (*n*) are given. *P* values of less than 0.05 are shown in italic.

Trait	**Mating competition**		**Display agility**		**Resource division**		**Fecundity**	
	Median	***P (n)***	**Median**	***P (n)***	**Median**	***P (n)***	**Median**	***P (n)***
Body mass	0.2481	*0.003* (18)	−0.1222	*0.016* (34)	0.0393	0.504 (36)	−0.0428	0.379 (61)
Wing length	0.1933	*0.013* (15)	−0.0618	0.237 (39)	0.0329	0.548 (44)	−0.0314	0.527 (63)
Tarsus length	0.1497	*0.038* (12)	−0.0511	0.442 (34)	0.0044	0.950 (39)	−0.0177	0.669 (55)
Bill length	0.2816	*0.001* (15)	−0.0658	0.200 (35)	0.0302	0.526 (38)	−0.0164	0.757 (57)
Tail length	0.2310	*0.008* (13)	−0.0566	0.225 (34)	0.0927	0.078 (39)	−0.0253	0.601 (55)

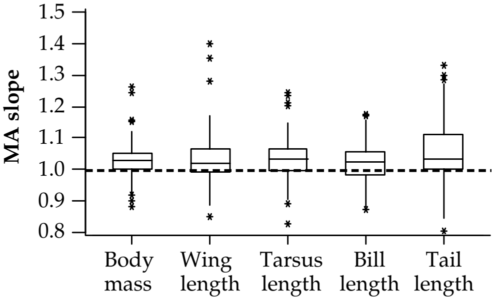

Figure 3.4 Rensch's rule in birds. The principal axis of major-axis (MA) regression $\log_{10}$(male size):$\log_{10}$(female size) was calculated separately for each family with data from at least five species. The median slope is significantly larger than 1.0 in all traits (Wilcoxon one-sample tests, body mass $W = 1596$, $P < 0.001$, $n = 64$ families; wing length $W = 1729$, $P < 0.002$, $n = 69$ families; tarsus length $W = 1411$, $P < 0.001$, $n = 59$ families; bill length $W = 1363$, $P < 0.003$, $n = 61$ families; tail length $W = 1546$, $P < 0.001$, $n = 61$ families). Asterisks indicate outliers (see Figure 3.2); two outliers in tail length are not shown, Nectariniidae (1.787) and Passeridae (1.697).

display-agility hypothesis is weaker than for the mating-competition hypothesis (combined probability test of mating competition and morphometric traits, $\chi^2 = 50.316$, df $= 10$, $P < 0.001$).

There is no clear pattern in Spearman rank correlations between SSD, resource use, and fecundity (Table 3.2). This is indicated by the non-significant combined probability values of resource use ($\chi^2 = 9.062$, df $= 10$, $P > 0.5$) and fecundity ($\chi^2 = 5.600$, df $= 10$, $P > 0.5$).

Avian families exhibiting the strongest relationship with SSD in the predicted direction are Trochilidae, Hirundinidae, Phasianidae, Passeridae, Anatidae (mating competition); Falconidae, Trochilidae, Musophagidae, Strigidae, Pardalotidae (display agility); Tytonidae, Falconidae, Pycnonotidae, Hirundinidae, Pardalotidae (resource division); and Jacanidae, Dendrocygnidae, Burhinidae, Maluridae, Petroicidae (fecundity). Families showing the strongest relationship with SSD in the opposite direction to the predicted directions are Tyrannidae, Muscicapidae, Sylviidae, Accipitridae, Meliphagidae (mating competition); Laniidae, Sturnidae, Cuculidae, Phasianidae (display agility); Centropidae, Threskiornithidae, Cuculidae, Otididae, Podicipedidae (resource division); and Tytonidae, Odontophoridae, Glareolidae, Ciconiidae (fecundity).

3.4 Discussion

Our work has confirmed Darwin's assertion that most birds exhibit male-biased SSD. This result was consistent between species and families, and among five morphometric traits. The frequency distribution of SSD, however, was significantly leptokurtic: more species were monomorphic than predicted by normal distribution. At family level the frequency distributions remained leptokurtic; nevertheless the deviation from normal was statistically weaker or non-significant. We consider three explanations for the non-normal distributions of SSD. First, the non-normality is a statistical artifact due to measurement error, or bias due to variable number of specimens measured for males and females. However, measurement error for a given sex should not produce bias toward more monomorphic species. Also, if only a few males and females are measured from a given species, this is likely to inflate SSD and thus produce strongly male-biased (or female-biased) SSDs, the opposite pattern to Figure 3.1. Second, non-normal distributions of SSD may be real biological features. For instance, genetic correlations between the sizes of males and females may pull the sexes toward the same mean (Merilä *et al*. 1999; see also Chapter 18 in this volume). Also, strong stabilizing selection may act on the sizes of males and females (Price and Grant 1985). The latter explanation appears to be relevant, since males and females spend much of their lives living in proximity to each other in many birds, so that using similar niches may require similar body sizes in males and females. Third, the extent of SSD is often related to sexual selection, and intense sexual selection in turn facilitates species diversification and may elevate the risk of extinction (Owens *et al*. 1999; Morrow and Pitcher 2003). Consequently, the deviations from normal distribution may be due to heterogeneous rates of extinction and/or speciation in regards to SSD.

SSD in body mass exhibited the widest range of values of all five morphometric traits. On the one hand, since the body masses of many birds change spectacularly between breeding and non-breeding seasons, and over a single day (Cuthill and Houston 1997), the different dates and/or times of measurements may inflate the extent of SSD in body mass. Female mass may also change from before to after egg laying. Given, however, that our data-set preferentially included measurements taken during the breeding season, these effects are likely to be minor. On the other hand, body mass is a three-dimensional trait whereas the lengths of wing, tarsus, bill, and tail are single-dimensional. Thus SSD as calculated from a three-dimensional trait may amplify the SSDs exhibited by single-dimensional traits (see Chapter 1 in this volume).

Interestingly, the correlations between the five measures of SSD were weak, particularly those between tail length and the other traits. The low correlations may have important implications. First, the ancestral patterns of integration between various morphometric traits may persist over considerable time, thus constraining possible evolutionary patterns (Arnold 1981). The apparent low correlations we report suggest that tail length responds to different selective forces than the other traits. A nested analysis of variance using taxonomic hierarchy (species, genera, family, and order) as a random factor suggests that different evolutionary processes are operating on SSD in tail length. Whereas for the other four morphological variables over 50% of variance is concentrated at family or order levels (50.8, 51.1, 51.3, and 66.3% variance in SSD of body mass, wing length, tarsus length, and bill length, respectively), in tail-length SSD the corresponding value was low (14.50%) and most variance occurred at species and genus levels (55.60 and 29.9%, respectively). Our results are thus consistent with those of Björklund (1990), who argued that different forces (or constraints) operate on different morphological characters (for examples from other taxa, see Chapters 9 and 11 in this volume).

Second, tail length is more variable than the other traits in Palearctic birds (Fitzpatrick 1997), an observation that is probably related to the implication of this trait in sexual selection. Møller and Cuervo (1998) identified 70 independent events in the evolution of ornamental tail feathers. The extreme elongation of tails has been related to sexual selection in several birds (Andersson 1982; Andersson and Andersson 1994; Winquist and Lemon 1994; Regosin and Pruett-Jones 2001; Møller *et al*. 2006). Third, low interspecific variation in wing length in comparison to tail length has been found in different bird taxa, and this low variation is considered to be the result of stabilizing selection on wing morphology (Alatalo 1988; Balmford *et al*. 1993; Thomas 1993; Fitzpatrick 1997; Groombridge *et al*. 2004). In comparison, tail length appears to be a compromise between aerodynamics and sexual selection. Thus further work is essential to evaluate how sexual selection and utilitarian processes such as aerodynamics, migratory behavior, and flight capacity influence each morphological trait.

Our analyses strongly suggest that Rensch's rule occurs in a broad range of avian taxa, and the rule appears to be exhibited by all five morphometric traits. These results expand on previous work that shows the existence of Rensch's rule among Passeriformes, Pelecaniformes, Procellariformes (Fairbairn 1997), Galliformes (Sæther and Andersen 1988; Fairbairn 1997), hummingbirds (Fairbairn 1997; Colwell 2000), bustards (Payne 1984; Rainahi *et al*. 2006), grouse (Payne 1984; T. Lislevand *et al*. 2007), and shorebirds (Székely *et al*. 2004). No evidence of allometry consistent with the Rensch's rule was found in Falconiformes, Strigiformes, Anseriformes, Charadriiformes (Fairbairn 1997), and seabirds (Serrano-Meneses and Székely 2006).

The discrepancy between some of the previous studies of Rensch's rule raises two important questions. First, what is the correct way of testing Rensch's rule? As Fairbairn (1997) argues, major-axis regression using phylogenetic control is desirable. Phylogenetic correction, however, can be carried out in a variety of ways (Freckleton *et al*. 2002), and the phylogenies themselves are prone to errors. Second, what is the correct taxonomic level of analysis: species, genera, or families? Rensch (1959, p. 159) suggested that "This rule, however, applies only to subspecies of a species, to related species of a genus, or to related genera of a family". Note that Rensch himself is inconsistent, illustrating his rule using three species of Scarabaeidae that represent three different genera (Rensch 1959, Figure 50, p. 160). In our view, the answer to both issues requires simulation studies to explore the sensitivity of the allometric relationship to phylogeny, comparative methods, and the taxonomic level of analyses.

We also identified a number of species and families with extreme SSDs and/or with large intra-familiar variation in SSD. These taxa will be excellent for comparative analyses across species, and for detailed observational and experimental studies within species. Note that our lists are not exhaustive, since our data-set only included about one-third of all bird species due to restricted data availability and time constraints in data compilation. For instance, display agility of males relates to SSD in a number of taxa (Figuerola 1999; Székely *et al*. 2004; Raihani *et al*. 2006; Serrano-Meneses and Székely 2006). None of these studies, however, used quantitative data on display behavior, because high-resolution comparable data are simply not available for the vast majority of species. Measures of agility (e.g. frequencies of rolls and turns, estimates of descending/ascending height; see Grønstøl 1996) from a range of species would be extremely useful for functional testing of the display-agility hypothesis using comparative methods. Behavior and ecology of many species are gradually better understood, partly due to efforts in the tropics and southern hemispheres where most species live. Also, with the advent of high-throughput sequence analyses that lead to better molecular phylogenies, we anticipate future comparative analyses to become more powerful.

Our results are consistent with the assertion of Darwin (1874) and previous comparative studies that intense mating competition between males predicts male-biased SSD (Table 3.1; Webster 1992; Winquist and Lemon 1994; Raihani *et al*. 2006; but see Björklund 1990; Oakes 1992). We also showed that the relationship between sexual selection and SSD is more complex than usually acknowledged, since display agility, a functional explanation that is often considered of minor importance, was related to reduced size in males relative to females. The latter effect, however, was weaker than the effect of mating competition on SSD. One potential explanation for the different predictive powers of mating competition and display agility may be data quality. Breeding system, a proxy we used for mating competition, is often better described in the literature than display agility, for which we used scores based upon verbal descriptions. Interestingly, mating competition is not only likely to select for large size in the sex competing more intensively for mates, but can also promote changes toward small size when small size is favored during displays. To what degree these results in birds elucidate the processes in other taxa is not yet known. We conjecture that male agility should influence SSD in many more taxa in which males display to and/or fight over females; for instance bats, primates, and pinnipeds.

We found no support for the fecundity and resource-division hypotheses. There may be good reasons why these hypotheses may only work in certain avian taxa (Selander 1972; Shine 1989; Temeles and Kress 2003). For instance, fecundity selection may only be important in capital breeders—those using resources from their own body to produce offspring—but not in income breeders. In sum, we agree with Andersson (1994) that discounting fecundity selection and resource division would be premature, since differences between species in foraging ecology, parental roles, and demands imposed by egg production may also affect SSD. To advance these hypotheses (and others we have not considered here; see Andersson 1994; Blanckenhorn 2000), one needs further comparative analyses, perhaps using higher-quality data from those groups that exhibit unusually large ranges in SSD.

We propose that future tests of functional hypotheses in avian SSD should use a two-pronged approach. First, we need to select a group of species for detailed quantitative description of selective forces in regards to major functional hypotheses. This may include observational or experimental tests of specific hypotheses. Second, these observational (or experimental) data should be compared among species using standard comparative methods to establish which (if any) hypotheses predict SSD across species and traits (see Chapters 2, 4, and 13 in this volume). Note that functional hypotheses may have integrated effects and there may be statistical interactions between these effects (Székely *et al*. 2004). Powerful statistical analyses of cross-species effects require precise data, a good number of species and sound phylogenetic hypotheses. Thus integrating the results of within-species and across-species approaches are likely to provide comprehensive functional explanations of SSD.

3.5 Summary

Birds are excellent model organisms for testing functional explanations of SSD, since many species are exceptionally well studied in nature. We review four major functional hypotheses of SSD, and test these using data on five morphometric traits from over 2500 bird species. We show that SSD is male-biased in most avian species and families. We also report that allometry consistent with Rensch's rule occurs in significantly more avian families than expected by chance. Finally, using cross-species analyses we show that SSDs are most consistent with sexual selection, specifically with the mating competition and the display agility hypotheses. Sexual selection, however, is unlikely to explain all variation in SSD, and further work is essential to test how ecological use of resources and fecundity selection may trigger, or amplify, changes in SSD. Further work is also essential to establish the interactive effects of these selective processes, and evaluate their significance in major avian lineages. We argue that these challenging projects are timely given rapid accumulation of data on natural history, improved estimates of phylogenetic relationships and recent advances in statistical analyses of cross-species data.

3.6 Acknowledgments

We appreciate the comments of Malte Andersson and Valerie Olson on a previous draft of this chapter. Monte Verita provided an excellent conference venue and facilities for our workshop on SSD. Alison Meredith, Alejandro Serrano-Meneses, René van Dijk, Hazel Watson, Akif Erdogan, Áron Székely, and Tamás Székely Jr contributed to data collection. Peter Dunn and his co-workers generously allowed us to use their mating-system scores. András Kosztolányi wrote the R code to calculate major-axis regression. The Ramón y Cajal program of the Spanish Ministry of Science of Technology funded J.F. visits to the University of Bath. T.S. was funded by a Leverhulme Research Fellowship (RF/2/RFG/2005/0279), by the BBSRC (BBS/B/05788), and the NERC (NE/C004167/1).

3.7 Suggested readings

Andersson, M. (1994) *Sexual Selection.* Princeton University Press, Princeton, NJ.

Fairbairn, D.J. (1997) Allometry for sexual size dimorphism: pattern and process in the coevolution of body size in males and females. *Annual Review of Ecology and Systematics* **28**, 659–687.

Székely, T., Freckleton, R.P., and Reynolds, J.D. (2004) Sexual selection explains Rensch's rule of size dimorphism in shorebirds. *Proceedings of the National Academy of Sciences USA* **101**, 12224–12227.

CHAPTER 4

The evolution of sexual size dimorphism in reptiles

Robert M. Cox, Marguerite A. Butler, and Henry B. John-Alder

4.1 Introduction

Reptiles figure prominently in both historical and current research on sexual size dimorphism (SSD), in part because of the considerable range of dimorphisms and life histories observed within this group. In this chapter, we describe the major patterns of SSD in reptiles and discuss the primary evolutionary hypotheses and ecological correlates proposed to explain these patterns. Our discussion of patterns in reptile SSD is based on a large dataset for which we compiled measures of adult SSD for 1314 populations representing 832 species (479 lizards, 277 snakes, and 76 turtles). To address the major evolutionary hypotheses for SSD, we focus our discussion on recent comparative studies that examine the relationships between SSD and various ecological and evolutionary correlates across multiple populations and species.

4.2 Phylogenetic distribution of reptile SSD

To date, the only comprehensive empirical review of SSD across reptiles is that of Fitch (1981). However, subsequent investigators have supplemented this monograph with new data and analyses for lizards (Stamps 1983; Carothers 1984; Braña 1996; Stamps *et al*. 1997; Butler *et al*. 2000; Cox *et al*. 2003), snakes (Shine 1994b), and turtles (Gibbons and Lovich 1990; Forsman and Shine 1995). Figure 4.1 summarizes our compilation of body-size measurements from these and other studies and provides the empirical basis for our descriptions of SSD in each reptile lineage. We follow convention in the reptile literature by focusing our analyses and discussion on sex differences in length (i.e. snout–vent, carapace, or plastron length), since body mass typically varies with reproductive status, fat storage, and digestive state. We use the index of Lovich and Gibbons (1992) to express SSD as (length of larger sex/length of smaller sex)–1, negative by convention when males are the larger sex and positive when females are larger than males.

4.2.1 Lizards

Males are larger than females in the majority of lizards, although female-biased SSD is common and occurs in nearly every family (Figure 4.1). Male-biased SSD reaches extremes in which males average 50% longer than females in some polychrotid anoles (*Anolis*), tropidurids (*Tropidurus*), marine iguanas (*Amblyrhynchus*), and varanid monitor lizards (*Varanus*). By contrast, females exceed males by as much as 20% in some polychrotids (*Polychrus*), skinks (*Mabuya*), and pygopodids (*Aprasia*). Male-biased SSD is the rule in several families (e.g. Iguanidae, Tropiduridae, Teiidae, Varanidae), whereas others exhibit considerable variation with no clear directional trend in SSD (e.g. Gekkonidae, Scincidae). At a finer taxonomic scale, many genera show consistent trends toward substantially larger males (e.g. *Ameiva*, *Leiocephalus*, *Microlophus*, *Tropidurus*) or females (e.g. *Phrynosoma*, *Diplodactylus*, *Aprasia*), whereas others show considerable phylogenetic lability in the direction of SSD (e.g. *Anolis*, *Lacerta*, *Mabuya*, *Sceloporus*).

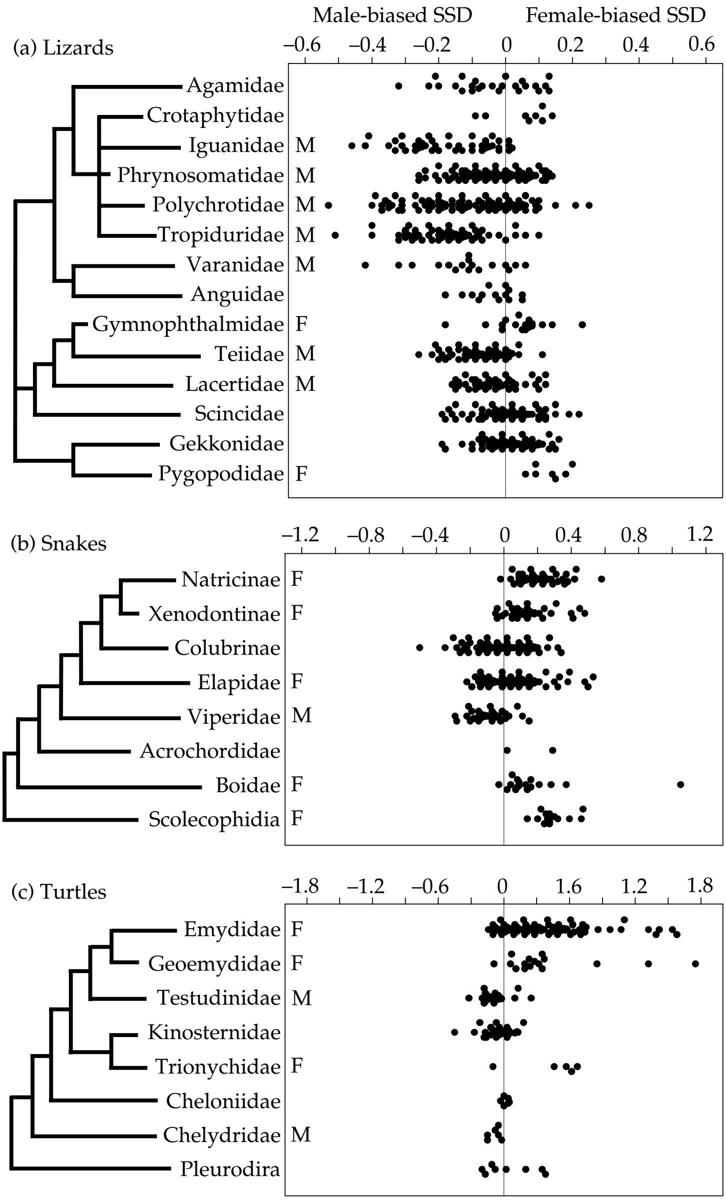

Figure 4.1 Distribution of SSD in major reptile lineages. SSD is calculated as (mean length of larger sex/mean length of smaller sex)−1, arbitrarily expressed as negative when males are larger and positive when females are larger. Lengths are snout–vent length (lizards and snakes) and carapace or plastron length (turtles). Each data point represents a single population or species. Letters indicate when mean SSD for a particular lineage is significantly ($P < 0.05$) male- (M) or female-biased (F). Phylogenetic relationships are provided for illustrative purposes. Axes are drawn to different scales in each panel on account of differences in the range of maximum SSD in each lineage. Snakes are actually a derived lizard clade (i.e. our depiction of lizards is paraphyletic with respect to snakes), but we have separated these lineages for graphical convenience.

4.2.2 Snakes

Although snakes actually comprise a derived lizard clade, they differ from lizards in that females are larger than males in the majority of species (Figure 4.1). Moreover, female-biased SSD is the rule in many lineages (e.g. Natricinae, Xenodontinae, Boidae, Scolecophidia) and only one family is characterized by ubiquitous male-biased SSD (i.e. Viperidae). Males are also larger than females in many elapids and colubrines, but these groups exhibit a broad range of SSD with no consistent directional trend. The overall range in SSD across snakes is comparable to that observed in lizards. Females exceed males in length by more than 50% in some natricine water snakes (*Nerodia*), xenodontines (*Farancia*), elapid sea kraits (*Laticauda*), boids (*Morelia*), and scolecophidian blind snakes

(*Ramphotyphlops*). Sex differences in body mass are quite impressive in large pythons (*Morelia*, *Python*) and boas (*Eunectes*), with females exceeding males by an order of magnitude in some cases. Males may average as much as 50% longer than females in some exceptional colubrines (*Drymoluber*) and frequently exceed females by 20–30% in some other colubrines (*Coluber*, *Lampropeltis*) and viperid rattlesnakes (*Crotalus*).

4.2.3 Turtles

As with lizards and snakes, turtles exhibit a broad range in SSD, although females are larger than males in the majority of species (Figure 4.1). Female-biased SSD is the rule in several families (e.g. Emydidae, Geoemydidae, Trionychidae), and male-biased SSD is characteristic of others (e.g. Testudinidae, Kinosternidae). The magnitude of SSD in many turtles is greater than that of most snakes and lizards, with females exceeding males by 50–60% in mean shell length for many aquatic emydids (*Chrysemys*, *Trachemys*), trionychid softshell turtles (*Apalone*), and pleurodire side-neck turtles (*Podocnemis*). Even more impressive are some geoemydids (*Kachuga*) and emydids (*Graptemys*) in which females average two or nearly three times the length of males. Extremes in male-biased SSD are more modest, although several testudinid tortoises (*Geochelone*, *Gopherus*) and kinosternid mud turtles (*Kinosternon*) typically exceed females by 20–30% in mean shell length.

4.2.4 Crocodilians

Although comparative data are few for crocodilians, male-biased SSD is the rule in this group, with males exceeding females by 20–40% in length for some large alligatorids (*Alligator*, *Caiman*) and crocodylids (*Crocodylus*). However, females may be slightly larger than males in smaller species such as *Alligator sinensis* and the dwarf crocodile, *Osteolaemus tetraspis*.

4.3 Rensch's rule in reptiles

Rensch's rule states that SSD characteristically increases with size when males are the larger sex and decreases with size when females are the larger sex, such that logarithmic plots of male against female size across species have a slope greater than one (Abouheif and Fairbairn 1997; see also Chapters 2, 3, and 6 in this volume). Although many studies have found support for Rensch's rule in reptiles (Fitch 1978; Berry and Shine 1980; Shine 1994a; Wikelski and Trillmich 1997; Shine *et al*. 1998; Kratochvil and Frynta 2002; Cox *et al*. 2003), others have not (Gibbons and Lovich 1990; Braña 1996; Butler *et al*. 2000). On the basis of our extensive literature data-set, we investigated allometry in SSD within each major reptile family or subfamily. Although we did not account for phylogenetic relationships in our analyses, previous studies involving subsets of these data have generally found that allometric patterns are similar in both conventional and phylogenetically based analyses (Abouheif and Fairbairn 1997; Butler *et al*. 2000; Kratochvil and Frynta 2002).

Figure 4.2 reports major-axis slopes from the regression of $\log_{10}$-transformed measures of male size on female size. Out of 24 reptile lineages, eight exhibit significant allometry consistent with Rensch's rule and several others show nearly significant trends toward this pattern. Only natricine snakes exhibit significant allometry opposite Rensch's rule, although several other snake and turtle lineages tend toward this pattern. The average major-axis slope is significantly greater than unity across lizard families ($t = 5.20$, $\mathrm{df} = 12$, $P < 0.01$) and across all reptile lineages ($t = 3.12$, $\mathrm{df} = 23$, $P < 0.01$), providing support for general tendency toward Rensch's rule.

The ultimate explanations for both this general tendency and its notable exceptions are not clear. Among snakes, Rensch's rule occurs only in those lineages in which male combat and male-biased SSD are common, whereas converse Rensch's rule tends to occur when female-biased SSD is prevalent. The picture is less clear in lizards and turtles. Rensch's rule is evident in several lizard families characterized by territoriality and male-biased SSD, but is conspicuously absent from others with similar characteristics (e.g. Phrynosomatidae, Polychrotidae). Of the two turtle lineages in which male combat and male-biased SSD are common, kinosternids follow Rensch's rule,

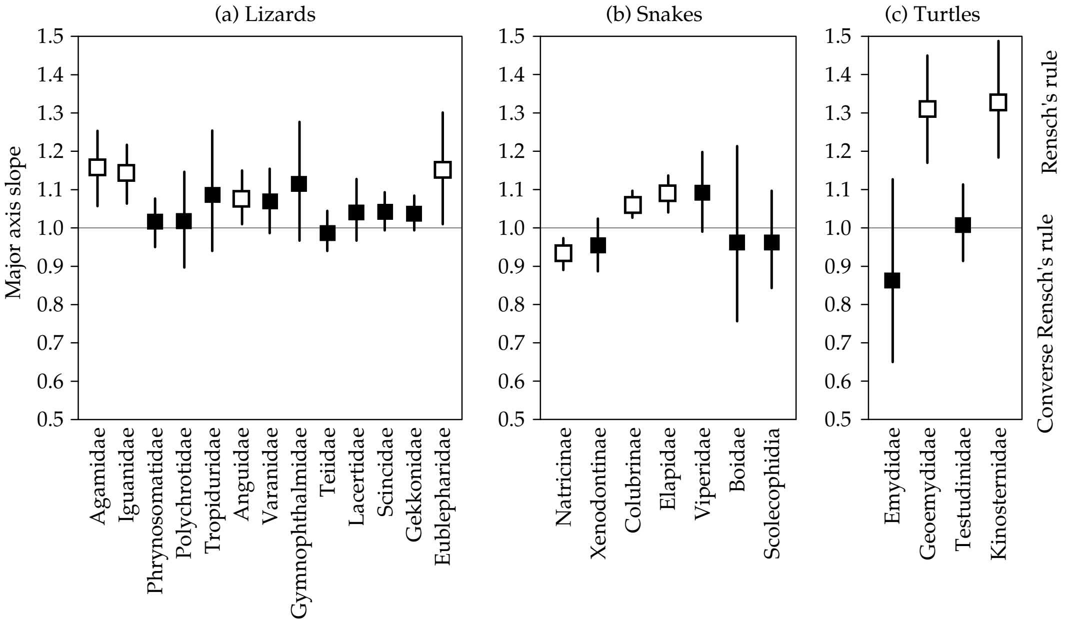

Figure 4.2 Tests for Rensch's rule in major reptile lineages. Symbols indicate slopes (±95% confidence intervals) from major-axis regressions of $\log_{10}$(male size) on $\log_{10}$(female size) within each lineage. Open symbols indicate significant deviations from isometric scaling of male and female body size, as determined by confidence intervals that do not include a slope of 1. These analyses do not account for phylogenetic relationships within lineages.

whereas testudinids do not. Although both emydids and geoemydids are characterized by extreme female-biased SSD, they differ dramatically with respect to Rensch's rule.

4.4 Geographic variation in reptile SSD

Shifts from male-biased SSD at low latitudes to monomorphism or female-biased SSD at higher latitudes have been found in the lizard genera *Sceloporus* (Fitch 1978) and *Leiocephalus* (Schoener *et al*. 1982), and across lizards in general (Cox *et al*. 2003). By contrast, higher latitudes are typically associated with male-biased SSD in *Anolis* lizards (Fitch 1976) and across snake species (Shine 1994b). In either case, these trends appear to be driven primarily by phylogenetic conservatism rather than any systematic tendency for the evolution of SSD in response to latitudinal range expansion within clades (Shine 1994b; Cox *et al*. 2003).

Considerable geographic variation in SSD also occurs *within* many reptile species. The Australian carpet python (*Morelia spilota*) exhibits the largest known geographic variation in SSD for any vertebrate species. Males from northeastern populations exceed females by a modest 10% in length and 30% in mass, whereas females from southwestern populations are more than twice as long and 10 times as massive as their "dwarf" male counterparts (Pearson *et al*. 2002). In some reptiles, phenotypic plasticity in growth and body size interact with population differences in food availability to drive intraspecific variation in SSD (Madsen and Shine 1993b; Wikelski and Trillmich 1997). Geographic variation in SSD of the slider turtle, *Trachemys scripta*, is related to variation in proximate environmental factors, influencing juvenile growth and the timing of maturation (Gibbons and Lovich 1990). Intraspecific variation in SSD also correlates with population differences in latitude, altitude, climate, and geophysical features (Fitch 1978, 1981; Iverson 1985; Lappin and Swinny 1999). Roitberg (in Chapter 14 in this volume) provides a more detailed discussion of patterns and causes of intraspecific variation in reptile SSD, illustrated by an extensive analysis of geographic variation in the widespread Eurasian sand lizard, *Lacerta agilis*.

4.5 Selective pressures influencing reptile SSD

Three major, non-exclusive selective pressures have received the majority of attention as ultimate explanations for SSD in reptiles: (1) sexual selection, which arises through variance in mating success and is usually invoked in the context of large male size conferring an advantage in male–male competition; (2) fecundity selection, which favors large female size when number of offspring increases with maternal size; and (3) natural selection for resource partitioning, which occurs when body size is related to resource use, such that SSD reduces intersexual competition. In turn, these distinct selective mechanisms may often vary predictably with certain suites of characteristics related to habitat or ecological niche. Table 4.1 summarizes recent comparative studies examining the first two hypotheses.

4.5.1 Sexual selection

In lizards, body size often determines success in agonistic encounters between males, and male reproductive success is known to increase with body size in some species (reviewed in Stamps 1983; Cox *et al*. 2003). Further, comparative studies have revealed associations between SSD and the occurrence of male combat or territoriality. Carothers (1984) showed that iguanids with male aggression exhibit strong male-biased SSD, whereas those lacking male aggression are monomorphic. Across lizard families, Stamps (1983) found that the mean SSD is strongly male-biased in

Table 4.1 Summary of recent studies using comparative data-sets (multiple species or populations) to test for correlations between SSD and various measures of sexual selection for large male size and fecundity selection for large female size. Support refers to significant correlations, although we emphasize that many caveats (e.g. strength of correlations, methods of analysis) apply to our simple categorizations of support (see text for further details). Studies that have been superceded by more comprehensive recent analyses are not presented here.

Taxon	Support	Measure	Study
Sexual selection			
Across lizards	Yes	Male aggression	Cox *et al.* (2003)
	Yes	Territoriality	Figure 4.3
	Yes	Female home range area	
	Yes	Ratio of male:female home-range area	
Eublepharid geckos	No	Male combat	Kratochvíl and Frynta (2002)
*Anolis sagrei**	No	Female density	Stamps (1999)
Anolis lizards	Yes	Female density	Stamps *et al.* (1997)
Across snakes	Yes	Male combat	Shine (1994b)
Fecundity selection			
Across lizards	Yes	Clutch size	Cox *et al.* (2003)
	No	Fecundity slope	Figure 4.3
	Yes	Reproductive frequency	
	Yes	Reproductive mode	
	No	Length of reproductive season	
Lacertid lizards	Yes	Fecundity slope	Braña (1996)
Emydid turtles*	No	Reproductive frequency	Forsman and Shine (1995)
Across snakes	No	Clutch size	Shine (1994b)
	No	Fecundity slope	
	No	Reproductive frequency	
	Yes	Reproductive mode	

*Phylogenetic relationships not explicitly taken into account.

territorial species, whereas non-territorial species show no overall directional trend in SSD.

Nonetheless, many territorial lizards do exhibit pronounced female-biased SSD, and many non-territorial species have strong male-biased SSD. Further, evolutionary changes in SSD are not associated with the evolution of male aggression in at least one lineage, the eublepharid geckos (Kratochvil and Frynta 2002; see also Chapter 15). In a comprehensive study across lizard families, Cox *et al*. (2003) showed that evolutionary shifts in male aggression and territoriality are generally correlated with changes in SSD, but concluded that these variables fail to explain most of the inter-specific variance in lizard SSD (Figure 4.3). In part, this may reflect the weak explanatory power of these categorical surrogates for sexual selection, since stronger correlations are observed between SSD and continuous measures such as the ratio of male to female home-range areas (Figure 4.3) and

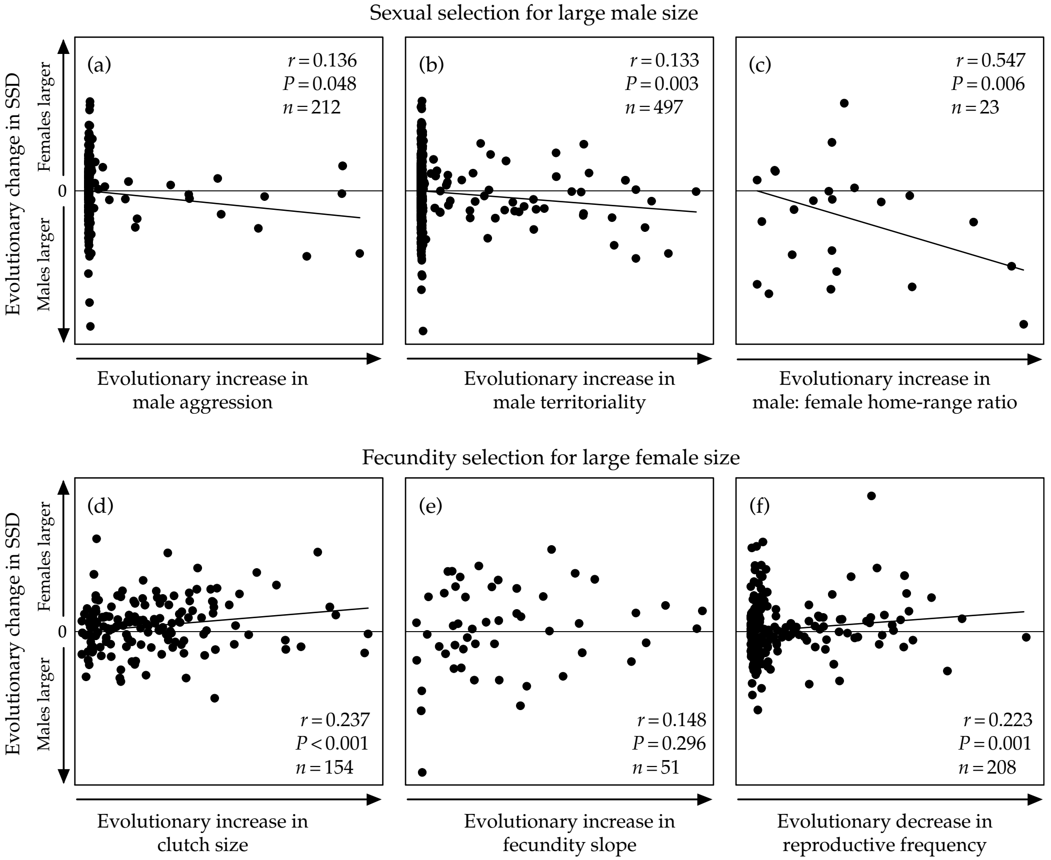

Figure 4.3 Comparative evidence for correlated evolutionary changes in SSD and several measures of sexual selection (top panels) and fecundity selection (bottom panels) in lizards. Values are 'positivized' independent contrast scores from phylogenetically based statistical analyses (see Cox *et al.* 2003 for details). The evolution of male aggression (a) and territoriality (b) are associated with shifts toward larger male size, but SSD also varies considerably in the absence of evolutionary change in either variable. The ratio of male to female home-range area (c) reflects the potential for a single male to defend multiple females within a territory (Stamps 1983). This measure of sexual selection yields a stronger correlation, but data are available for fewer species. The evolution of larger clutch size (d) and lower reproductive frequency (f) are associated with shifts toward larger female size, but SSD is not associated with fecundity slope (e), the slope of the regression of clutch size on maternal size within a population. Sample sizes indicate number of independent contrasts. Multiple regression including measures of sexual selection (territoriality) and fecundity selection (clutch size, reproductive mode, reproductive frequency) reveals that 84% of the intraspecific variation in lizard SSD is left unexplained even when simultaneously considering both hypotheses ($r^2 = 0.16$; $n = 84$; $P = 0.008$). Modified from Cox *et al.* (2003) with permission from *Evolution*.

female density (Stamps 1983; Stamps *et al*. 1997; Cox *et al*. 2003).

Recent intraspecific studies of lizards are revealing a complexity that challenges many of our conventional assumptions about sexual selection on male body size. For example, *Crotaphytus collaris* is a highly territorial, polygynous species in which Baird *et al*. (1997) found that large size confers success in male agonistic encounters for each of three populations with varying degrees of SSD. However, social organization varies with habitat structure, such that the opportunity for sexual selection is high in only a single population, and moreover one with a low index of SSD. Subsequent studies of this species using paternity analyses have revealed that male reproductive success is not correlated with body size, but rather with bite force, which provides a direct measure of performance in male contests (Lappin and Husak 2005). In other territorial species with male-biased SSD, paternity studies contradict the simplistic notion that sexual selection is uniformly directional with respect to male size: females of *Uta stansburiana* and *Anolis sagrei* mate with multiple males and then produce sons by large sires and daughters by small sires (Calsbeek and Sinervo 2004; R. Calsbeek, personal communication).

The majority of snake species exhibit female-biased SSD, with the occurrence of male-biased SSD restricted to derived lineages in which males engage in physical combat. Multiple evolutionary gains and losses of male combat are associated with evolutionary shifts in SSD (Shine 1994b), but considerable variation in the magnitude of SSD occurs even in the absence of variation in male combat. The python *Morelia spilota* is the only snake known to exhibit intraspecific variation in male combat. Interestingly, whereas males are slightly larger than females in the presence of male combat, females are more than twice as long and 10 times as massive as males in its absence (Pearson *et al*. 2002). Large body size generally confers an advantage in male combat (reviewed in Shine 1994b), and success in combat enhances mating success in some species (Madsen and Shine 1993c; Madsen *et al*. 1993; Fearn *et al*. 2005). Even when females are the larger sex and overt physical combat is absent, large male size may be advantageous for scramble competition (Madsen and Shine 1993a; Weatherhead *et al*. 1995), or forcible insemination of females (Shine and Mason 2005).

Turtles are similar to snakes in that the occurrence of male-biased SSD is primarily restricted to lineages with male combat, particularly tortoises, terrestrial emydids, and kinosternids (Berry and Shine 1980). Male combat usually occurs in the presence of receptive females, and large males dominate smaller males in some species (Kaufmann 1992; Niblick *et al*. 1994). The prevalence of male-biased SSD in crocodilians is also believed to result from sexual selection for large male size, which presumably confers an advantage in male aggression and territoriality (Fitch 1981). However, definitive comparative studies of sexual selection with respect to SSD are generally lacking for both turtles and crocodilians.

Historically, most attempts to explain reptile SSD in terms of sexual selection have focused on the advantages of large size in male–male competition. However, SSD may also be influenced by intrasexual competitive advantages of small male size (as in birds; see Chapter 3), sexual selection via female choice, and sexual selection on female size. For example, Zamudio (1998) concluded that patterns of female-biased SSD in horned lizards are consistent with the hypothesis that sexual selection favors small male size. Similarly, Berry and Shine (1980) hypothesized that small male size may favor efficient mate searching and agile precoital behaviors in aquatic turtles.

Although females mate preferentially with large males in some lizard species (Cooper and Vitt 1993; Censky 1997), the evidence for female choice related to male size is generally weak in reptiles (Olsson and Madsen 1995; Tokarz 1995), and available data are too sparse to support robust conclusions with respect to SSD. Interestingly, recent genetic data suggest that many lizards and snakes are polyandrous (Calsbeek and Sinervo 2004; Rivas and Burghardt 2005). Such promiscuity may seem paradoxical with respect to female preference, but may actually facilitate so-called cryptic female choice that resolves intersexual genetic conflict over body size and other traits (see Chapters 16 and 18). For example, females of several lizard species with male-biased SSD use sperm from large mates to produce male offspring and that of small mates to produce female offspring (Calsbeek and Sinervo 2004; R. Calsbeek, personal communication). This complexity underscores the general point that attempts to explain SSD via sexual selection may often be confounded by inferences drawn solely from behavioral observations in the absence of genetic paternity data. Finally, we note that sexual selection may also influence female size, as in the case of the snake *Thamnophis sirtalis*, in which males mate preferentially with large females (Shine *et al*. 2006).

4.5.2 Fecundity selection

In the majority of reptiles, the number of offspring in a clutch or litter increases with maternal body size, so selection for increased fecundity should favor large female body size. Consistent with this hypothesis, comparative studies have documented evolutionary increases in clutch or litter size associated with shifts toward female-biased SSD in lacertid lizards (Braña 1996) and across lizards in general (Cox *et al*. 2003; Figure 4.3), but not in horned lizards (Zamudio 1998) or Australian snakes (Shine 1994b). The slope of the relationship between clutch size and maternal size within a population presumably offers a more informative estimate of fecundity selection than mean clutch size, since this relationship describes the extent to which selection on female body size is likely to increase fecundity within a given species. Braña (1996) found a strong relationship between this so-called fecundity slope and SSD even after controlling for phylogenetic relationships among lacertids. However, broad-scale analyses across lizards and snakes revealed that correlations between SSD and fecundity slope are no longer significant when phylogeny is taken into account (Shine 1994b; Cox *et al*. 2003). Further, several lizard lineages that have independently evolved invariant clutch sizes of one or two eggs show no systematic tendency towards relatively male-biased SSD when compared to related species with variable clutch size (Shine 1988).

Fitch (1978, 1981) suggested that fecundity selection should be particularly intense in species that reproduce infrequently, as in viviparous species with lengthy gestation periods or species that inhabit temperate regions with short breeding seasons. In lizards, the evolution of viviparity and reduced reproductive frequency are generally correlated with shifts toward female-biased SSD (Cox *et al*. 2003; Figure 4.3). However, evolutionary shifts in these variables explain only a small portion of the associated variance in SSD, and many species that reproduce infrequently nonetheless exhibit strong male-biased SSD. Further, there is no relationship between SSD and continuous measures of reproductive frequency such as length of the reproductive season. The evolution of viviparity is also associated with shifts toward female-biased SSD in snakes, but continuous measures of reproductive frequency do not correlate with SSD (Shine 1994b). Finally, the magnitude of female-biased SSD actually increases with reproductive frequency in emydid turtles, challenging the assumption that the intensity of fecundity selection varies inversely with reproductive frequency (Forsman and Shine 1995). On the whole, comparative data for reptiles provide only weak and inconsistent support for Darwin's (1871) fecundity-advantage hypothesis as an explanation for SSD (Table 4.1).

4.5.3 Ecological hypotheses for SSD

In considering ecological causes for the evolution of SSD, most authors have focused on the role of SSD in reducing competition between the sexes. In particular, sex differences in food type are often associated with SSD, especially in gape-limited predators such as snakes (Shine 1989, 1991). Sea kraits (*Laticauda colubrina*) provide a good example: in populations where multiple prey types are available, large females feed primarily on large conger eels, while small male kraits prey upon small moray eels. However, female-biased SSD remains substantial (50%) even in populations where dietary partitioning does not occur and head-size dimorphism is greatly reduced (Shine *et al*. 2002). Many snake species provide similar evidence that dietary partitioning has influenced the evolution of sexual dimorphism in trophic morphology, but the evidence for a relationship with SSD is less clear (Shine 1991). Even when SSD and dietary differences are correlated, it is often difficult to determine the causal relationship between the two, since divergence in prey size would not be an unusual consequence of SSD resulting from other factors (Vitt and Cooper 1985). Furthermore, few studies have actually validated the assumption that SSD reduces intersexual competition. Interestingly, Stamps *et al.* (1997) found that intersexual competition coefficients in *Anolis aeneus* are actually predicted to be lower when males and females are the same size than when males are larger.

Even in the absence of intersexual competition, males and females may evolve to different body-size optima given a sufficiently complex adaptive landscape. Schoener (1969a) modeled optimal body size based on foraging energetics and showed that two size optima exist for ''sit-and-wait'' predators, whereas a single optimum is more likely for ''active'' foragers. The Lesser Antilles is a chain of small Caribbean islands that have either one or two species of *Anolis* lizards per island, and these lizards fit the assumptions of the sit-and-wait predator model. Across islands, various *Anolis* species follow a remarkably regular pattern of pronounced SSD, with male and female body sizes lying near the predicted body-size optima (Schoener 1967, 1969b, 1977). Although SSD is consistently male-biased, sexual selection alone is not sufficient to explain the similarity of SSD across islands (Schoener 1969b). In fact, if the strength of sexual selection were related to female density (Stamps *et al.* 1997), one would expect variability in SSD across islands. Pronounced SSD may allow solitary species to maximize population-level resource utilization and help explain the incredible densities observed (Rand 1967; Schoener 1967).

A very different situation exists in more complex *Anolis* faunas. With greater numbers of sympatric species, niche compression should result in reduced SSD (Schoener 1969a), which is indeed observed (Schoener 1969b). The most complex *Anolis* communities occur in the Greater Antilles. Each of the four major islands has been the site of an independent adaptive radiation producing the same suite of six ''ecomorph'' types characterized by different microhabitats and lifestyles. For example, species characterized as trunk-ground ecomorphs live close to the ground in relatively open habitat, use a sit-and-wait foraging strategy, and are generally territorial. In contrast, twig anoles live in the crowns of trees in dense matrices of thin twigs and tend to use an active foraging mode of searching for prey. This microhabitat specialization has resulted in the evolution of correlated differences in morphology, behavior, and—interestingly—SSD (Butler *et al.* 2000; Butler and King 2004). Trunk-ground and trunk-crown ecomorphs consistently evolve high SSD, whereas trunk, crown-giant, grass-bush, and twig anoles repeatedly evolve low SSD (Figure 4.4). The selective pressures driving the repeated evolution of convergent dimorphisms are not clear because precise information about mating system, niche breadth, and species and sex overlap in resource use are not available across all ecomorphs. However, the pattern is not an artifact of phylogenetic inertia, as SSD evolves repeatedly (Figure 4.4), and neither is it correlated with body-size evolution. Sexual dimorphism in shape is also partitioned by ecomorph type. When males and females are plotted in multivariate shape morphospace, the sexes form separate clusters in some ecomorphs (trunk-ground and trunk-crown), whereas the species/sex classes are interdigitated in the remaining ecomorphs (Butler *et al.* 2007). Thus, patterns of sexual dimorphism are not only highly convergent to microhabitat type, but also serve to increase ''species packing'' within these complex lizard assemblages.

Turtles provide another intriguing association between SSD and ecological specialization. Berry and Shine (1980) noted that most turtles could be placed into one of four major ecological categories: (1) aquatic swimmers, (2) semi-aquatic species, (3) aquatic bottom-walkers, and (4) terrestrial species. Females are larger than males in most aquatic swimmers, males equal or exceed female size in most semiaquatic species and aquatic bottom-walkers, and male-biased SSD reaches extremes in terrestrial tortoises and emydids. Berry and Shine (1980) suggested that male combat and forced insemination favor large male size in terrestrial, semi-aquatic, and aquatic bottom-walking species,

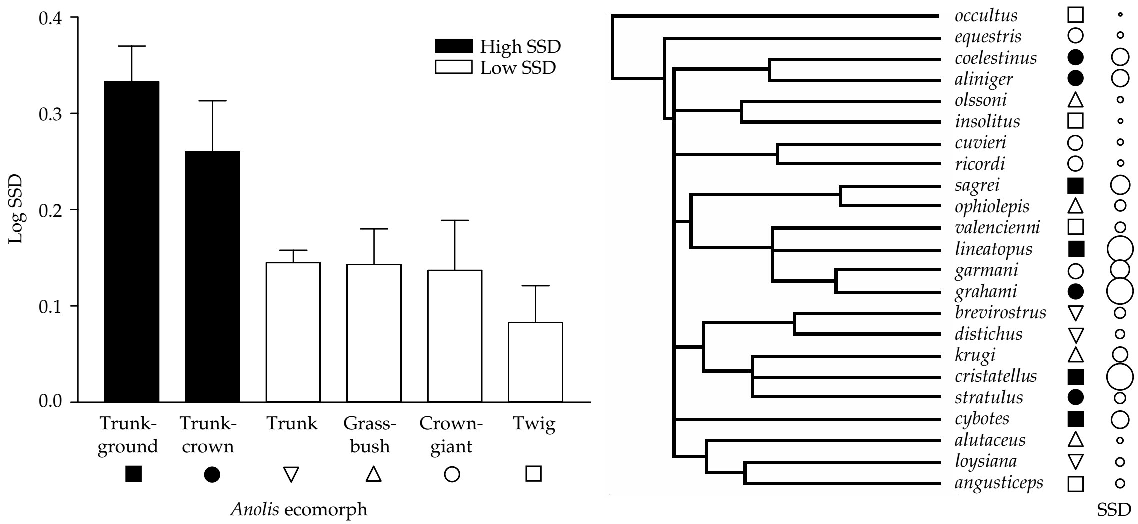

Figure 4.4 Association between ecomorph (habitat) type and SSD in 23 species of Greater Antillean *Anolis* lizards. The left-hand panel shows mean (±1 SE) log SSD for each ecomorph type. All species exhibit male-biased SSD, but the repeated convergent evolution of trunk-ground and trunk-crown ecomorphs (dark symbols and bars) is consistently associated with an increase in the magnitude of SSD (indicated by the size of the circles on the far right). Redrawn from Butler *et al.* (2000) with permission from *Evolution.*

whereas small male size confers an advantage in agile courtship behaviors and mate searching in aquatic species. However, Gibbons and Lovich (1990) suggested that size-dependent predation simply prevents most terrestrial males from maturing at the early ages and small sizes that are favored in aquatic species. Although there is some disagreement about the actual selective forces driving this correlation between SSD and habitat, the association remains striking.

4.6 Constraints on reptile body size

4.6.1 Female reproductive burden

In reptiles, the burden of a clutch or litter may impose substantial constraints on female morphology. An interesting example occurs in Asian flying dragons of the genus *Draco*, which glide from trees by extending their modified ribs and associated membranes to form crude airfoils. Despite the fact that males are territorial and large size enhances male reproductive success, many *Draco* species exhibit female-biased SSD, and *Draco melanopogon* females also exceed males in relative head size, wing size, and tail length. These atypical dimorphisms may represent sex-specific adaptations to permit gliding when females are encumbered by a clutch (Shine *et al.* 1998). However, studies of live animals suggest that small size actually enhances gliding, and that gravid females are reluctant to glide (McGuire and Dudley 2005; J. McGuire, personal communication). Thus, an additional possibility is that selection for enhanced gliding has favored small size in males, but opposing advantages of large size or reduced frequency of gliding have prevented the complementary evolution of small female size.

Many arboreal lizards have evolved reduced clutch size, presumably as an adaptation to facilitate arboreal locomotion (e.g. *Anolis*, gekkonids, and some skinks). Andrews and Rand (1974) observed that these taxa use adhesive toe pads for climbing and suggested that their adhesive properties may fail if mass is greatly increased. One consequence of reduced clutch size is that fecundity selection should favor increased reproductive frequency over the per-clutch fecundity advantage of large female size. However, Shine (1988) found no consistent trend toward male-biased SSD in species with invariant clutch size when compared to related species with variable clutch size. Arboreal species that rely on claws or grasping rather than adhesive toe pads tend to have relatively larger clutch and body sizes (e.g. *Polychrus*, *Iguana*, chameleons), indicating that mode of arboreal locomotion may influence both clutch and body size. However, implications with respect to SSD per se are less clear.

4.6.2 Energetic growth constraints

Most reptiles continue to grow after sexual maturation, such that energetic costs of reproduction may constrain energy allocation to growth. In some species, reproductive females expend nearly twice the total metabolizable energy as males, whereas in others males may have substantially greater respiratory expenditure than females during the mating season (Merker and Nagy 1984; Orrell *et al*. 2004). Given that males and females often differ in the timing and relative magnitude of reproductive investment, growth may often be differentially constrained in each sex, giving rise to SSD (see Chapter 19).

Adult male *Cophosaurus texanus* lizards average 10% larger than females because of a divergence in growth that occurs when females initiate reproduction. Estimates of the energetic costs of growth and egg production suggest that SSD would be essentially eliminated if females were to hypothetically allocate the energy content of a clutch into growth, rather than reproduction (Sugg *et al*. 1995). Similarly, male and female diamond-backed rattlesnakes (*Crotalus atrox*) grow at comparable rates until maturity, when females shift energy allocation to reproduction at the expense of growth, resulting in male-biased SSD (Duvall and Beaupre 1998). However, sex differences in growth are absent when captive snakes are raised on controlled diets, suggesting that proximate environmental factors predominate in the development of SSD (Taylor and DeNardo 2005). In several species of *Sceloporus* lizards, female-biased SSD may develop because male growth is constrained by metabolic costs (i.e. increased movement, activity, and home-range defense) associated with maturational increases in plasma testosterone (see Chapter 19).

Of course, even when the growth of one sex is constrained by energetic costs of reproduction, the continued post-maturational growth of the opposite sex implies that there is some additional selective advantage to large size. However, the important point is that the actual magnitude of SSD depends not only on the strength of selection on male or female size, but also the extent to which growth in each sex is constrained by energetic costs of reproduction. These constraints will depend upon the timing of maturation and the nature of reproductive investment in each sex, as well as the extent to which environmental factors (e.g. food availability) provide a context for energetic trade-offs. If such energetic growth constraints are prevalent in reptiles, this may help explain why so much of the interspecific variance in SSD is left unaccounted for by measures of sexual and fecundity selection (Cox *et al*. 2003).

4.7 Summary

Most studies interpret observed patterns of reptile SSD in light of sexual selection for large male size, fecundity selection for large female size, and natural selection to reduce resource competition. Although sexual selection for large male size has clearly influenced the evolution of reptile SSD, the broad explanatory power of this hypothesis is uncertain because we generally lack sufficient comparative data beyond simple categorizations of the presence or absence of male combat or territoriality. Future work would benefit from more precise descriptions of the intensity of sexual selection on male size and other traits, since recent paternity analyses have revealed complexity that goes beyond simple directional selection favoring large males, and that size may be less important than other traits in determining reproductive success.

Although fecundity increases with female body size in many reptiles, comparative data provide only weak and inconsistent support for the fecundity advantage of large female size as an explanation for SSD in this group. For most reptiles, we still lack quantitative data on lifetime fecundity as it relates to female growth and size, ecological determinants of optimal body size, and energetic costs of reproduction and their impact on growth of both males and females. Although broad comparative studies have been valuable for suggesting major patterns and hypotheses, the relative importance of these processes will likely remain uncertain until we are able to develop more detailed predictions incorporating linkages between behavioral strategies for acquiring energy, rates of energy expenditure for growth and reproduction, mating system, and fitness. We believe that the key to further understanding lies in the integration of comparative, demographic, and experimental techniques designed to simultaneously address both the ultimate evolutionary causes and proximate developmental mechanisms for SSD.

4.8 Acknowledgments

We thank D. Fairbairn, W. Blanckenhorn, and T. Szekely for organizing this volume and its preceding workshop, and for inviting us to contribute. Support from the Association for the Study of Animal Behavior enabled R.M.C. to participate in this workshop. Studies of lizard SSD by R.M.C. and H.B.J.-A. were supported in part by the National Science Foundation (IBN 0135167).

4.9 Suggested readings

Butler, M.A., Schoener, T.W., and Losos, J.B. (2000) The relationship between sexual size dimorphism and habitat use in Greater Antillean *Anolis* lizards. *Evolution* **54**, 259–272.

Cox, R.M., Skelly, S.L., and John-Alder, H.B. (2003) A comparative test of adaptive hypotheses for sexual size dimorphism in lizards. *Evolution* **57**, 1653–1669.

Gibbons, J.W. and Lovich, J.E. (1990) Sexual dimorphism in turtles with emphasis on the slider turtle (*Trachemys scripta*). *Herpetological Monographs* **4**, 1–29.

Shine, R. (1994) Sexual size dimorphism in snakes revisited. *Copeia* **1994**, 326–346.

Stamps, J.A., Losos, J.B., and Andrews, R.M. (1997) A comparative study of population density and sexual size dimorphism in lizards. *American Naturalist* **149**, 64–90.

CHAPTER 5

Sexual size dimorphism in amphibians: an overview

Alexander Kupfer

5.1 Introduction

Sexual size dimorphism (SSD) is a difference in body length or mass of sexually mature organisms and has been demonstrated in a great variety of animals including invertebrates and vertebrates (see other chapters in this volume). SSD may have important consequences for animal ecology and behavior, and is a key aspect in our understanding of the evolution of life-history traits and mating systems.

Amphibians are a diverse group of vertebrates renowned for variable life histories, which include both aquatic and terrestrial habitats (Frost *et al.* 2006). The three orders of amphibians—frogs (Anura), salamanders (Urodela), and caecilians (Gymnophiona)—are thought to have been already present in the Mesozoic era (San Mauro *et al.* 2005). The current diversity of frogs is 5421 species (www.amphibiaweb.org), which are distributed on all major land masses. The salamanders comprise of 559 species that are found mostly in temperate regions, but with members of several salamander families also being present in sub-tropical and tropical regions. The snake-like caecilians, around 171 species, are the least known group of modern amphibians. They are distributed exclusively in tropical biotas, excluding Madagascar and land masses east of the Wallace line (Himstedt 1996; Wilkinson and Nussbaum 2006).

SSD occurs in all amphibian lineages. There are a number of studies either describing the pattern (Shine 1979) or explaining and predicting the presence of SSD in amphibians (e.g. Woolbright 1983; Arak 1988; Monnet and Cherry 2002). These studies almost exclusively focus on anurans, whereas overviews on SSD in salamanders are incomplete (Shine 1979; for plethodontid salamanders see Bruce 2000) and non-existent for caecilians. So far no study has used comparative phylogenetic methods (Harvey and Pagel 1991) to investigate SSD in amphibians. This exercise would be timely, as the amphibian tree of life has just been published (Frost *et al.* 2006).

In this chapter I review sexual size and shape dimorphism in amphibians. I describe the diversity of intersexual differences, and discuss their proximal causes and adaptive significance. In comparison to other vertebrates (mammals, Chapter 2 in this volume; reptiles, Chapter 4; birds, Chapter 3) the pattern of SSD in amphibians is poorly understood, so the review also aims to outline the potential for future work.

5.2 Diversity and patterns of SSD in amphibians

5.2.1 Frogs

The fertilization of eggs in most frogs (Anura) is external, and males and females typically engage in an amplexus, in either aquatic or terrestrial breeding sites. There is a great diversity of reproductive modes in anurans with aquatic, terrestrial, or arboreal eggs, aquatic or terrestrial larvae, and different kinds of parental care by either males or females (Duellman and Trueb 1994; Lehtinen and Nussbaum 2003). Most frogs have a planktivorous aquatic larval stage (tadpoles), some have direct development without aquatic larvae, and a few species (e.g. the African bufonids *Nectophrynoides* spp. and *Nimbaphrynoides* spp.) are life-bearers (viviparous). Snout–vent length (or snout–urostyle length) is used as a standard to describe the body size in frogs.

The only comprehensive review on overall patterns of SSD is by Shine (1979). His study is based on 589 frog species, representing about 11% of contemporary frog species. This work revealed that females are larger than males in 530 species (90%, exemplified by African treefrogs in Figure 5.1). Males are the larger sex in only 18 species (3%) of several anuran lineages (e.g. Ranidae, Hylidae, Myobatrachidae). No SSD was found in 41 species (7%). Shine (1979) explained the dominant pattern of female-biased SSD by fecundity selection, and as probably being due to higher male mortality rates. Based on Shine's data, at least anuran SSD follows the pattern of many other lineages of poikilothermic vertebrates in which females are the larger sex (see Chapters 1 and 4 in this volume). Although Shine included both ancestral and modern anuran lineages, his analyses did not control for phylogeny.

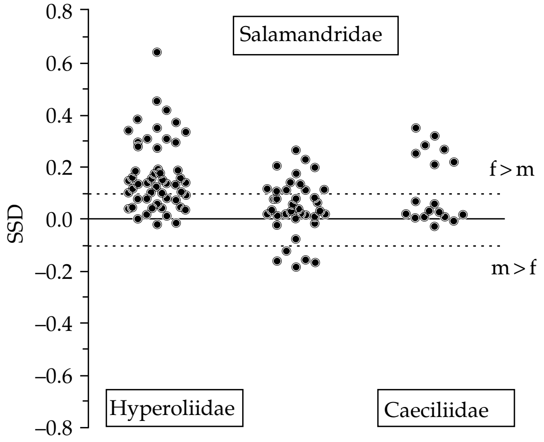

Figure 5.1 Distribution and range of SSD across selected families of three amphibian orders. SSD is calculated as size dimorphism index (SDI; (mean length of larger sex/mean length of smaller sex)−1; after Gibbons and Lovich 1990), arbitrarily expressed as negative when males are larger (m > f) and positive when females are larger (f > m). Body size is accessed via snout–vent length (frogs and salamanders) and total length (caecilians). Each data point represents a species (Anura: Hyperoliidae, 53 species; Urodela: Salamandridae, 38 species; Gymnophiona: Caeciliidae, 18 species). Note that an SDI of ≥ -0.1000 and ≤ 0.1000 corresponds to size differences of less than 10% in snout–vent and total length respectively, indicated by dashed lines.

Interestingly, in frogs that show male-biased SSD several morphological adaptations such as spines or tusks are present (Figure 5.2e and f). These species were also reported to show aggressive behavior and perform male combat. Shine (1979) concluded that such secondary characters are a good indicator for male combat and are subject to sexual selection.

Shine's analysis was criticized by Halliday and Verrell (1986) mainly on the basis that heterogeneity of data sources and types prevented precise estimates, and also for the simplistic interpretation that SSD is mainly a result of sexual selection. Halliday and Verrell (1986) proposed that sexual dimorphism in body size is the result of a variety of selective forces, and SSD cannot be attributed solely to sexual selection. They also noted that sexual differences in body size must take into account the effects of life history and age, because amphibians exhibit indeterminate growth and continue to grow throughout their life.

Studies of the adaptive causes of SSD in frogs mostly included species with female-biased SSD (Woolbright 1983; Arak 1988; Monnet and Cherry 2002); anurans with male-biased SSD have rarely been analysed. I briefly mention two examples consistent with Shine's (1979) sexual-selection hypothesis. "Fanged" frogs (genus *Limnonectes*, about 50 species), a monophyletic group of Ranidae distributed in southeast Asia that breed in streams, show pronounced sexually dimorphic characters (Emerson 1994). Male frogs are larger than females, and male secondary sexual traits include larger heads and fanged mandibles (Emerson 1994; Fabrezi and Emerson 2003). In addition, males are territorial and involved in male–male combat (Tsuji and Matsui 2002). In stream-breeding *Limnonectes kuhli* large males are favored by females (Tsuji 2004). One proposed reason for this rare SSD pattern in frogs is that limited oviposition sites along streams cause more intensive male–male combat, selecting for larger heads and fanged mandibles in males. Similar findings were also obtained in another frog, *Adelotus brevis* (Myobatrachidae) from Australia (Katsikaros and Shine 1997), where males have a larger body size and heads and in addition bear large paired projections (tusks) at the lower jaw

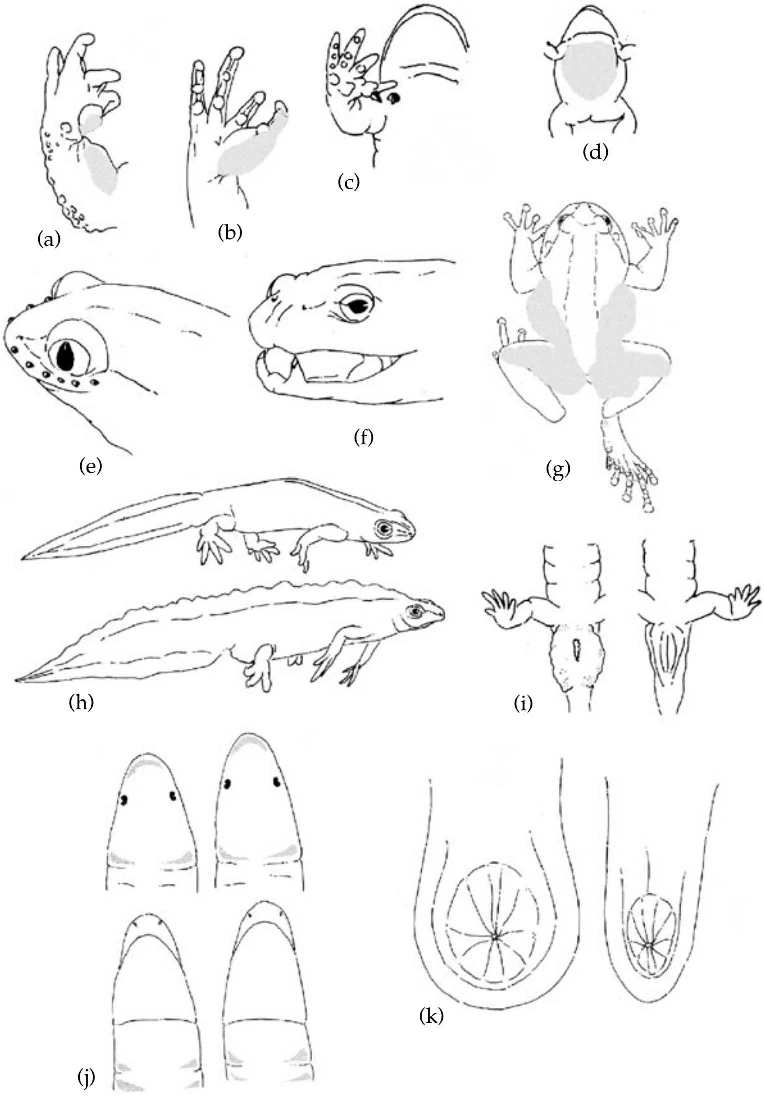

Figure 5.2 Sexually dimorphic traits in amphibians. (a) Keratinized nuptial pad on forearm of male *Bombina orientalis* (Anura: Bombinatoridae); (b) Keratinized nuptial pad on fourth finger of male *Rana maculata* (Anura: Ranidae); (c) Keratinized spines on fourth finger and breast of male *Leptodactylus pentadactylus* (Anura: Leptodactylidae); (d) ventral gland of male *Kaloula verrucosa* (Anura: Microhylidae); (e) labial spines of male *Vibrissaphora boringii* (Anura: Megophryidae); (f) enlarged mandibular odontids of *Adelotus brevis* (Anura: Myobatrachidae); (g) breeding male of *Trichobatrachus robustus* (Anura: Astylosternidae) showing hair-like dermal appendages on legs and lateral body; (h) sexual dimorphism in the smooth newt *Lissotriton vulgaris* (Urodela: Salamandridae; top, female; bottom, male) with the male (below) showing dorsal crest, enlarged tail fins, and foot webbing; (i) cloacal dimorphism in breeding *Ambystoma jeffersonianum* (Urodela: Ambystomatidae), with the male (left) showing swollen cloaca (right, female); (j) head dimorphism in *Geotrypetes seraphini* (Gymnophiona: Caeciliidae), males (right) have longer heads than females (left); (k) cloacal dimorphism in *Typhlonectes compressicauda* (Gymnophiona: Typhlonectidae), males (left) have a larger cloacal disk than females (right). Panels a–f and i after Duellman and Trueb (1994).

(see Figure 5.2f), which are used in territorial fights. In this species small males were practically excluded from the breeding sites, and large males obtained more mates. Furthermore, large males also mated with large females, which suggests that male size had a direct influence on reproductive success since large females are thought to be more fecund. A different adaptive cause for male-biased SSD has been reported for the giant African bullfrog *Pyxicephalus adspersus*, a very large and compact ranid where females reach just about 50% of the male snout–vent length (about 200 mm). Males are engaged in parental care of tadpoles, and male size relates directly to the successful defense of territories against predators (Cook *et al*. 2001).

Sexual dimorphism in frogs is evident in a variety of morphological traits (see Figure 5.2a–g), such as body size, shape, and coloration (Hoffman and Bloin 2000), and the sexes also differ in physiological traits. A striking feature that distinguishes frogs from salamanders and caecilians is the male vocal apparatus (Duellman and Trueb 1994). Males of most anurans vocalize. Acoustic communication is involved in defending and maintaining territories but also in attracting females (Wells 1977). In some anurans males call from single sites; inter-male spacing reduces interference, and therefore receptive females may locate individual callers easily. Since frogs have a polygynous mating system, variance in male reproductive success can be directly related to behavioral parameters; thus male advertisement calls can be sexually selected. In a typical population of frogs, whether they are explosive or prolonged breeders, not all males mate within a season (Wells 1977). Woolbright (1983) showed that in some frogs large male size co-varies with calling performance. Larger male body size also has advantages in the defense of calling sites in species where females are larger (Howard 1981). Parameters of the advertisement call (frequency and duration) are hugely variable, but they are also correlated with male body size (Lode and Le Jaques 2003). In midwife toads (*Alytes obstetricans*), for example, males carry terrestrial eggs and after the embryonic development is completed tadpoles are released into lentic or lotic water. Larger males obtained more matings than smaller conspecifics, and eggs carried by larger males had higher hatching success. Females chose males with a ''low'' call frequency, which is an indicator of male size because only larger males could produce these frequencies (Lode and Le Jaques 2003). However, in other anuran mating systems male body size seemed not to be the major factor in sexual selection (reviewed by Duellman and Trueb 1994).

Fecundity selection (i.e. the fecundity-advantage hypothesis) is a likely explanation for female-biased SSD in frogs. Fecundity is highly variable among frog species (Duellman and Trueb 1994); for example, female *Bufo* spp. may lay more than 1000 aquatic eggs, and a terrestrial clutch of less than 20 eggs is known in the genus *Eleutherodactylus*. It has been shown among species that larger females can accommodate more eggs (Salthe and Macham 1974), although this result has not been controlled for phylogeny. In addition, within a reproductive mode there is a positive correlation between ovum size and female body size. Regardless of the reproductive mode there is also a trade-off between clutch and ovum size, whereas ovum and hatchling size are positively correlated (Duellman and Trueb 1994). Within a species, larger females have larger clutch sizes (Wake 1978; Prado and Uetanabaro 2000).

Any hypothesis of ecological causes for the evolution of SSD could best be inferred in species in which the sexes differ in the morphology of the feeding apparatus (Shine 1989). It is not easy to test the niche-divergence hypothesis empirically since sexual selection and natural (ecological) selection have to be disentangled. Ecological causes of SSD have been tested in few anurans where males are the larger sex and have larger head size (Katsikaros and Shine 1997; Fabrezi and Emerson 2003). Although Katsikaros and Shine (1997) found marked differences in the diet of males and females in the tusked frog *Adelotus brevis*, these where largely attributed to the different foraging habitats during the breeding season. Male frogs spent most of their time in calling sites, and just preyed upon invertebrates that were locally abundant, which were different from the prey in the terrestrial habitats of females. Gut-content analysis may only reflect short-term foraging strategies, whereas stable isotopes in animal tissues reflect a combination of the source elements and tissue fractionation processes, and can thus reveal information on temporal and long-term feeding regimes (Dalerum and Angerbjörn 2005). In future, it would be most appropriate to test ecological causes for the evolution of SSD using naturally enriched isotopes.

5.2.2 Salamanders

The overall body architecture of most salamanders (Urodela) shows some striking similarities to lizards; however, due to largely reduced limbs (e.g. *Amphiuma* spp.) some species have a more snake-like appearance (Duellman and Trueb 1994). Fertilization in most salamanders is internal, and achieved via a spermatophore either in terrestrial or aquatic copulations. Most salamanders have a carnivorous aquatic larval stage, some have direct development without aquatic larvae, and a few species (i.e. *Salamandra* spp., *Lyciasalamandra* spp.) are viviparous.

Shine (1979) estimated that females are larger than males in approximately 61% of salamanders of 79 species reviewed. Male-biased SSD was only found in 19% of the species (15 taxa), mainly among species reported to have aggressive behavior and male combat (e.g. Salamandridae). About 20% of species expressed no dimorphism in body size. Recently Bruce (2000) summarized information about SSD in plethodontid salamanders, the most diverse family of salamanders. SSD patterns in plethodontids are variable, however; female-biased SSD is common in the Hemidactylinii, Bolitoglossini, and Plethodontini lineages, but only in desmognathine salamanders is SSD male-biased. Two genera of bolitoglossine salamanders (*Oedipina* and *Aneides*) show only weak or no SSD.

Sexual selection is characterized by individual variation in reproductive success, as influenced by competition over mates. It has been inferred as the cause of larger male size in salamanders that show combat behavior (Shine 1979), a rare feature in the behavioral repertoire of salamanders. Selection should favor male characters that directly increase reproductive success. Variation in mating and reproductive success could either arise from intrasexual competition (e.g. male–male combat) or intersexual processes (female choice). In a critique of Shine (1979), Halliday and Verrell (1986) argued that males are smaller than females in many salamanders where males engage in male–male combat.

Intersexual selection involves active female choice of males with enlarged and conspicuous secondary sexual ornaments. In terms of sexual selection, European newts are one of the best-studied amphibian systems, since during the aquatic breeding season males show several obvious secondary sexual characters such as bizarre dorsal crests (see Figure 5.2h) or enlarged tails, in addition to lekking behavior (reviewed by Halliday 1977; Andersson 1994; Griffiths 1996). It has been demonstrated that female newts actively choose large males exhibiting conspicuous dorsal crests (Hedlund 1990; Green 1991). The crest itself also increases the body surface area of the male, which in turn presumably affects the male's ability to transfer pheromones to the female during the display, and enhances the efficiency of cutaneous respiration and endurance, all of which are primary determinants of courtship success (Halliday 1977; Hedlund 1990). Female newts may interpret male body size enlarged by a fully developed crest as an indicator of age, viability, or experience (Hedlund 1990). Larger male *Triturus cristatus* with large crests were more likely to deposit spermatophores that were picked up by the female. It has also been shown that the number of testes lobes in *T. cristatus* and *Lissotriton vulgaris* is highly correlated with age (Dolmen 1982). Halliday (1977) argued that newt females should prefer older and larger males if longevity is a good indicator of male fitness. Other factors that may influence reproductive success in male newts are those improving courtship performance (Halliday 1977). Males of all species of European newts are highly mobile and perform an extensive courtship display in front of the female (Griffiths 1996). Body traits enhancing the performance of complex movement (e.g. longer legs or tails) can increase individual reproductive success and may be indirectly subjected to sexual selection.

Male–male competition has been rarely studied. Some evidence has been found in one terrestrial-breeding salamander species of the *Desmognathus ochrophaeus* complex, in which larger males were invariably more successful in matings when two males of different sizes were placed with a female (Houck 1988). However, higher reproductive success of males that actively dominate smaller males in species with male-biased SSD remains to be proven. Aggressive behavior (i.e. biting) has been reported for the newt *Ommatotriton ophryticus* (Raxworthy 1989). In addition to a larger body size other sexually dimorphic traits include crests, foot webbing, and coloration. This newt species might be a good system to test any sexual-selection hypothesis in combination with genetic mating success, since female salamanders store male sperm for some time and offspring are typically sired by multiple fathers (Garner and Schmidt 2003). Female choice is thus thought to be manifested in a greater tendency to pick up spermatophores from males that deposit many in courtship trails (Halliday 1977). Mate choice by males for larger and more fecund females has been demonstrated for two other aquatic-breeding newts (Halliday and Verrell 1986).

Natural selection should favor large females when female size is positively correlated with fecundity (Darwin 1871). The evaluation of fecundity selection includes information on egg and clutch size. Correlations between fecundity and body size have been found in salamanders. In his review on salamander reproductive modes, Salthe (1969) stated that an increase of overall body volume is correlated with an increase in size and clutch volume across salamander species. Intraspecifically there is also some evidence that larger females have higher fecundity at least in species with moderate clutch sizes, such as newts (Bell 1977). In salamanders with high reproductive investment and reduced clutch size, such as plethodontids, evidence indicates that clutch volume usually increases with female size but not in all species (Bruce 2000).

Tests for the niche-divergence hypothesis usually are invoked when males and females differ markedly in traits such as head dimensions (sensu Shine 1989). Although several salamanders show strong dimorphism in head shape correlated with SSD (Malmgren and Thollenson 1999; Bovero *et al.* 2003), any proximate hypothesis regarding the use of different food sources remains to be tested.

Body size in salamanders is usually assessed by snout–vent length, measured from the snout tip to the posterior end (sometimes the anterior end) of the cloaca (Bruce 2000). In some respect the overall body architecture of salamanders shows similarities to lizards, and newts and lizards were even put in the same genus originally by Linnaeus (1758). Thus some problems with the interpretation of SSD in lizards might also apply in salamanders. For example, character-scaling issues have been discussed in lizards (Kratochvil *et al.* 2003), and snout–vent length might not in all case describe body size adequately. However, in a study on two European newt species snout–vent length has been identified as a useful body-size trait (Malmgren and Thollenson 1999).

The SSD patterns in salamanders might only be detectable when other body traits, such as tail length or head size, are included in the analysis and adjusted for body size (i.e. snout–vent length; Malmgren and Thollensen 1999, Bovero *et al.* 2003). Detailed studies of SSD in several salamanders have revealed cryptic SSD patterns when several such variables have been analysed; for example, males of pond-breeding *Lissotriton vulgaris* have larger tails than females at the same body size (Malmgren and Thollenson 1999), and males of stream-breeding *Euproctus platycephalus* have larger heads than females (Bovero *et al.* 2003).

Although phylogenetically controlled comparative analyses (Harvey and Pagel 1991) have been used to study SSD in other vertebrates such as lizards, birds, and mammals (Székely *et al.* 2000; Cox *et al.* 2003; see also Chapters 2–4 in this volume), they have not yet been used in salamanders. A synthetic analysis of SSD in this group is much needed, which should best concentrate on salamander lineages showing a large degree of SSD variability. In some respects, salamandrids would be the ideal group for such a study, since they not only have multiple origins of male-biased SSD (Figure 5.1), but also show large variability in life histories (pond and stream breeding, or oviparity and viviparity).

5.2.3 Caecilians

Caecilians (Gymnophiona) are tropical snake-like, burrowing amphibians. Due to their secretive and subterranean habits their life history and ecology, including their mating systems, still remain largely unstudied (Himstedt 1996; Gower and Wilkinson 2005). However, it is known that caecilians have internal fertilization, and either oviparity with aquatic larvae or direct development, or viviparity, which is more common than in frogs and salamanders (Wake 1977; Himstedt 1996; A. Kupfer, unpublished work). Data on sexually dimorphic traits are available in the literature (Nussbaum 1985; Nussbaum and Pfrender 1998; Kupfer 2002), and hypotheses regarding proximate causes of SSD have been tested for several species (Delétre and Measey 2004; Kupfer *et al.* 2004a).

A general problem with caecilian morphology is that it largely lacks obvious secondary sexual characters. Frogs in comparison have a vocal apparatus and several secondary morphological characters such as breeding pads or glands. Sexes in some salamanders are distinguishable by coloration, and males of some aquatic breeding newts possess dorsal crests, which they display during courtship (Darwin 1871; Raxworthy 1989; Green

1991). Generally, total body length (snout–tip to tail–tip) is used to describe the body size of caecilians and reveal sexual dimorphism.

Data on SSD are available for 18 caecilian taxa (11 genera; see Figure 5.1). Interestingly many caeciliids, which are regarded as derived (Frost *et al*. 2006), are monomorphic for body size (Figure 5.1). A female-biased SSD has been found in ichthyophiids, caeciliids, and typhlonectids; however, there is no case reported yet of males being significantly larger in body size than females in any caecilian. In the oviparous caecilian *Ichthyophis* cf. *kohtaoensis* females are larger than males, and they also have a larger cloacal disk than males (Kupfer 2002). Since large females have large clutches, it is likely that fecundity selection has influenced the evolution of female body size (Kupfer *et al*. 2004b). Fecundity selection is also apparent in frogs and salamanders in which large females usually have large clutch sizes (reviewed by Duellman and Trueb 1994).

Caecilians show cryptic dimorphic traits that can only be identified when a large set of morphological characters is analysed and body size is used as a covariate or traits are adjusted to body size (e.g. Nussbaum 1985; Kupfer 2002). Strikingly, head-size dimorphism (i.e. larger and wider heads in males in comparison to females of the same body length) is found in six genera of caeciliids (*Boulengerula*, *Dermophis*, *Gegeneophis*, *Geotrypetes*, *Hypogeophis*, and *Schistometopum*; see Figure 5.2j). Other sexually dimorphic traits include differences in shape of the cloacal disk in many caecilian lineages (Taylor 1968; Kupfer 2002; Giri *et al*. 2004; Figure 5.2k), and differences in the number of body rings (annuli) and vertebrae (reported in one species, *Scolecomorphus ulugurensis*; Nussbaum 1985).

Only recently have proximate causes of SSD in caecilians been investigated either experimentally in the laboratory (Kupfer *et al*. 2004a) or by rigorous morphometric analysis (Kupfer 2002; Delétre and Measey 2004; Jones *et al*. 2006), including testing any dietary divergence hypotheses (*sensu* Shine 1989). In caecilians in which the sexes differ not in body size but in head size, it is not easy to distinguish between sexual and natural (ecological) selection (Shine 1989). Since head dimorphism is widespread in many genera of higher caecilians (see a recent phylogenetic tree of African caecilians by Wilkinson *et al*. 2003), this trait might be phylogenetically autocorrelated (see discussion in Abouheif and Fairbairn 1997). Although males have larger heads than females in *Schistometopum thomense*, Delétre and Measey (2004) failed to find any difference in diet between the sexes. However, they discussed several scenarios that might explain adaptive causes for larger male heads, such as aiding in terrestrial copulations by biting. Dietary differences were found in *Boulengerula boulengeri*, in which males have larger heads (Jones *et al*. 2006).

Caecilians show high degrees of parental investment and a diversity of reproductive modes (oviparity and viviparity) relative to other amphibians. To understand the evolution of mating systems and parental investment in caecilians, phylogenetically controlled comparative analyses should include not only SSD data of major caecilian lineages, but also reproductive traits.

5.3 Age, ontogeny, and SSD in amphibians

The body-size distribution within a population likely reflects different growth rates of females and males (Halliday and Verrell 1988; see Chapters 4 and 19 in this volume). In organisms with indeterminate growth such as amphibians, the actual body size is a result of a trade-off between growth and reproduction. Growth rates are often asymptotic after maturation and the sexes often mature at a different age (sexual bimaturity). Thus size data can be best interpreted when the age of animals is known. Estimating age by skeletochronology, counting lines of arrested bone growth on histological sections, is a widely accepted method for aging amphibians, and has successfully been used in many temperate and tropical species (Khonsue *et al*. 2000; Olgun *et al*. 2001; Ento and Matsui 2002; Monnet and Cherry 2002; Bovero *et al*. 2003). Despite finding lines of arrested growth in the vertebrae of caecilians (Measey and Wilkinson 1998; M. Orlik and A. Kupfer, unpublished work), skeletochronology has not been applied for any caecilian population in the wild.

Comparing the mean body size and age of 51 frog populations of 30 species, Monnet and Cherry

(2002) reported that most variation in SSD can be explained in terms of differences in age structure between the sexes; that is, females were larger because they were older than the males, which mature earlier at smaller size. Unfortunately, demographic studies on frogs mostly focus on species with female-biased SSD but have not been applied to species with male-biased SSD (e.g. *Limnonectes* spp., *Adelotus*). However, a skeletochronological study of an Asian ranid frog (*Rana nigrovittata*) revealed that males were larger after metamorphosis (Khonsue *et al*. 2000; see Figure 5.3a). Since these frogs show no dimorphism in head size and no aggressive behavior, the adaptive causes for this reversed SSD pattern remain to be studied.

Sexual bimaturity is common in salamanders (reviewed by Duellman and Trueb 1994, and Bruce 2000 for desmognathine salamanders). Males mature earlier than females in 29 (64%) of 45 salamander species listed in Duellman and Trueb (1994). In many cases when males mature earlier, they are also smaller than females (Table 5.1). The sexes may also mature at the same age and same body size; for instance, in the viviparous salamander *Lyciasalamandra luschani* both sexes mature at 3 years and in *Salamandra lanzai* at 8 years (Table 5.1). Surprisingly, in viviparous species with reduced fecundity and higher offspring quality that live at high altitude and have a short breeding season, the fecundity-advantage hypothesis predicts female-biased SSD (Shine 1989). Unfortunately, the relation between female body size and fecundity has not been analysed in any demographic studies on amphibians, and questions about age-related fecundity have remained unanswered.

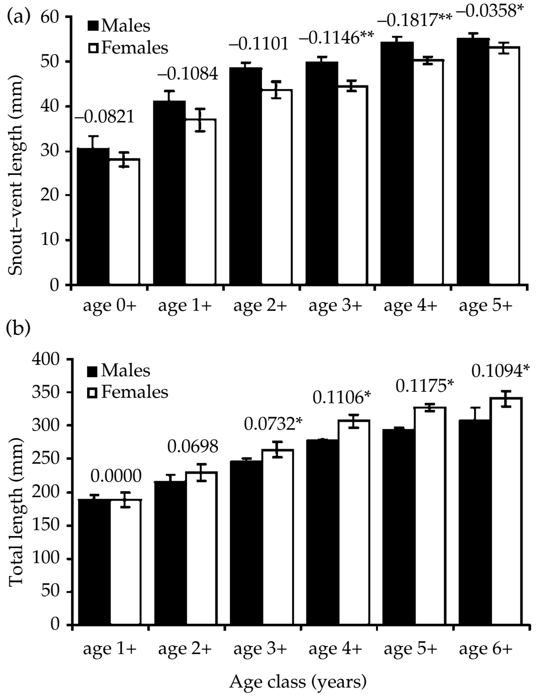

Figure 5.3 Age, ontogeny, and SSD in amphibians. (a) Development of snout–vent length (mean ± SD) and SSD of field-collected *Rana nigrovittata* (Anura: Ranidae) of different age classes estimated by skeletochronology (after Khonsue *et al.* 2000); (b) development of total length (mean ± SD) and SSD of captive *Ichthyophis* cf. *kohtaoensis* (Gymnophiona: Ichthyophiidae) of different age classes (after Kupfer *et al.* 2004a). SSD is indicated above each bar and calculated as SDI (as in Figure 5.1). Significant intrasexual differences: $^{*}P \leq 0.05$ and $^{**}P \leq 0.01$.

Dimorphic sexual size patterns during amphibian ontogeny have also been investigated by following growth patterns in controlled natural populations, or under laboratory conditions (Gramapurohit *et al*. 2004; Kupfer *et al*. 2004a). In a 3-year study of post-metamorphic growth patterns in Indian bullfrogs (*Hoplobatrachus tigerinus*), both sexes showed similar growth rates, although some males matured at smaller size than females. Sexual differences in body size in naturally occurring breeding populations of this species (males smaller than females) appear to be due to the presence of different age groups rather than differences in early growth rates (Gramapurohit *et al*. 2004). Sexually dimorphic growth patterns also exist in caecilians (Kupfer *et al*. 2004a). In a laboratory population of *I*. cf. *kohtaoensis* sexes showed no difference in body size in the first 3 years after metamorphosis; however, females were significantly larger in the fourth, fifth, and sixth years (Figure 5.3b). Furthermore, sex-specific growth rates were found in the first two growth seasons when males grew faster, while from the third growth season on females grew faster. All animals under laboratory conditions grew constantly after metamorphosis, demonstrating indeterminate growth for a caecilian as reported for frogs and salamanders.

Table 5.1 Size at maturity, age at maturity estimated by skeletochronology, and life history for males and females of selected salamander species. Body size (snout–vent length, SVL) is measured from the tip of the snout to the posterior end of the cloaca.

Taxon	Sex	Age at maturity (years)	SVL at maturity (mm)	Reproductive mode	Source
Hynobiidae					
Hynobius kimurae	Male	5–6	66	Aquatic eggs and larva in streams	Misawa and Matsui (1999)
	Female	7.5	72		
Hynobius nebulosus	Male	3	42	Aquatic eggs and larva in ponds	Ento and Matsui (2002)
	Female	4	47		
Salamandridae					
Mesotriton alpestris	Male	3	44	Aquatic eggs and larva in ponds	Miaud *et al.* (1993) in Olgun *et al.* (2001)
	Female	3–4	49.1		
Triturus cristatus	Male	2	65	Aquatic eggs and larva in ponds	Miaud *et al.* (1993) in Olgun *et al.* (2001)
	Female	2–3	66		
Ommatotriton ophyriticus	Male	4	53.3	Aquatic eggs and larva in ponds	Kutrup *et al.* (2005)
	Female	4	61.7		
Chioglossa lusitanica	Male	4–5	43–44	Aquatic eggs and larva in streams	Lima *et al.* (2001)
	Female	4–5	43–44		
Lyciasalamandra luschani	Male	3	45	Terrestrial, viviparous	Olgun *et al.* (2001)
	Female	3	44		
Salamandra lanzai	Male	8	70	Terrestrial, viviparous	Miaud *et al.* (2001) in Olgun *et al.* (2001)
	Female	8	68		
Salamandra salamandra	Male	2–3	80	Terrestrial, viviparous	Rebelo and Caetano (1995) in Olgun *et al.* (2001)
	Female	3–4	86		

5.4 Summary

Amphibians—frogs (Anura), salamanders (Urodela), and caecilians (Gymnophiona)—are diverse organisms that live in aquatic or terrestrial ecosystems. Female-biased SSD is the common pattern in frogs and salamanders as assessed for 589 species of frogs and 79 salamanders by Shine (1979). Male-biased SSD is rare among amphibians, and only present in few lineages (Anura: Megophryidae, Ranidae, Hylidae, Myobatrachidae; Urodela: Salamandridae, Desmognathinae), and some species show only weak or no SSD in body size. Preliminary SSD data for caecilians indicate that many are monomorphic in body size, whereas others exhibit female-biased dimorphism. Various sexually selected male morphological traits exist in many amphibian species that are monomorphic in body size. SSD may be partly explained by sex-specific growth trajectories during ontogeny and delayed maturity. Field studies on amphibians with male-biased SSD indicate associations with territoriality and male–male combat.

In comparison with other vertebrates (see Chapters 2–4), our understanding of SSD in amphibians is still incomplete. Phylogenetic comparative analyses are much needed to understand the complex evolutionary patterns of amphibian SSD and mating systems. Hypotheses based on fecundity and sexual selection or life-history theory (including ontogenetic development of SSD) have to be tested intra- and interspecifically. To assess the ecological-divergence hypothesis and differences in food utilization between sexes, comparative studies should analyse not only SSD using body length, but also other morphological traits together with information on reproductive behavior, feeding, and environment. A recent review on the conservation status on amphibians worldwide (Stuart *et al.* 2004) pointed out that in 23% of 5742 assessed amphibian species information on their life history, mating systems, and SSD is completely lacking.

5.5 Acknowledgments

D. Fairbairn, W. Blanckenhorn, and T. Székely are congratulated for organizing the magnificent SSD workshop. Many thanks for giving me the opportunity to contribute to this volume. W. Blanckenhorn, M. Foellmer, W. Himstedt, T. Székely, and E. Valk made valuable comments on drafts of the manuscript. An EU-Marie Curie fellowship (MEIF-CT-2003–501675) enabled me to participate in this workshop.

5.6 Suggested readings

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Duellman, W.E. and Trueb, L. (1994) *The Biology of Amphibians*. John Hopkins University Press, Baltimore, MD.

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CHAPTER 6

Rensch's rule in insects: patterns among and within species

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6.1 Introduction

Rensch's rule (so termed by Abouheif and Fairbairn 1997; Fairbairn 1997) describes a widespread pattern in the animal kingdom that male body size diverges faster than female body size over evolutionarily time among related species, such that male-biased sexual size dimorphism (henceforth dimorphism) increases and female-biased dimorphism decreases with body size (Rensch 1959). When first describing the phenomenon, Rensch (1950) did not offer an explanation, and its causes remain largely unclear to this day. Although it is unlikely that one single mechanism is responsible across the broad range of taxa in which it is observed (Fairbairn 1997, 2005), it has been suggested that Rensch's rule may be driven primarily by sexual selection for large male size in combination with a typically high genetic correlation in body size between the sexes (Fairbairn and Preziosi 1994; Fairbairn 1997). However, to date evidence for the general importance of sexual selection in producing Rensch's rule is equivocal at best (Fairbairn and Preziosi 1994; Fairbairn 1997, 2005; Kraushaar and Blanckenhorn 2002; Tamate and Maekawa 2005; Young 2005).

Almost 10 years ago, Abouheif and Fairbairn (1997) reviewed the evidence for Rensch's rule in animals and found support for it in a majority of taxa. However, arthropods, and especially insects, were greatly underrepresented in their survey and often displayed variation in dimorphism inconsistent with Rensch's rule (see also Chapter 7 in this volume). Since then a number of new data-sets on insects have become available, which prompted the update provided in this chapter.

The original formulation of Rensch's rule refers to a systematic pattern of variation in dimorphism among closely related species (Rensch 1950, 1959; Abouheif and Fairbairn 1997; Fairbairn 1997). Statistically, Rensch's rule is manifested in allometric slopes greater than 1 when male size is regressed on female size (described further below; Fairbairn 1997). Consequently, Rensch's rule can also be studied among populations within species. Primarily with the aim of investigating the putative mechanisms causing Rensch's rule, a number of studies have explored intraspecific variation in dimorphism in the past, but obtained mixed results (Fairbairn and Preziosi 1994; Fairbairn 1997, 2005; Kraushaar and Blanckenhorn 2002; Gustafsson and Lindenfors 2004; Tamate and Maekawa 2005; Young 2005; see also Chapters 8 and 14). Again, new intraspecific data have recently become available in connection with studies of Bergmann clines (Blanckenhorn *et al.* 2006), allowing a more comprehensive evaluation of the equivalent of Rensch's rule at this taxonomic level.

Patterns analogous to Rensch's rule can further be studied within populations of a given species, for example when animals are reared in the laboratory under different environmental conditions and several such treatments or genetic groupings (e.g. families) are compared. In such cases, body size of males and females can be affected differentially to produce allometries in dimorphism. Such phenotypic plasticity in dimorphism has recently been investigated in a comparative study of insects by Teder and Tammaru (2005), and in a more mechanistic framework by Fairbairn (2005; see also Chapter 14).

Contrary to patterns among species, where vertebrate data clearly dominate (Abouheif and Fairbairn, 1997), at this taxonomic level data are more likely to be available for smaller organisms that can be more easily reared in captivity, such as insects.

We here review the validity of Rensch's rule in insects and its extension to lower taxonomic levels: among species, among populations within species, and among families or environments within populations. We thus reduce Rensch's rule to its mere statistical manifestation: more variance in male than female body size. In so doing we ask whether allometries in dimorphism at these various taxonomic levels relate in any way, possibly in that patterns at a lower taxonomic level might uncover mechanisms generating Rensch's rule at this or higher taxonomic levels (see Fairbairn and Preziosi 1994; Kraushaar and Blanckenhorn 2002; Fairbairn 2005; Chapter 8). In this context we discuss potential proximate mechanisms producing variation in dimorphism whenever this is appropriate.

6.2 Patterns among species

Until recently, few studies of Rensch's rule in insects existed in the literature. Besides a data-set on beetles included in Rensch's (1950) original work, Abouheif and Fairbairn (1997) listed only Sivinski and Dodson's (1992) study on tephridid fruit flies, which included a parenthetical treatment of a large but unpublished data-set for stick insects (Phasmatodea; see Sivinski 1978), and work on one family of water striders (Heteroptera: Gerridae) by Fairbairn (1990, 1997) and Andersen (1994). Andersen (1997) in parallel published an extended study on additional water strider groups. Since then, data on ladybird beetles (Dixon 2000), stalk-eyed flies (Baker and Wilkinson 2001), caddisflies (Jannot and Kerans 2003), dragonflies (Johansson *et al.* 2005), and, most recently, a number of further insect groups (Blanckenhorn *et al.* 2007) have become available. As was customary, most of the earlier studies presented phylogenetically uncorrected data.

It has become standard to analyze dimorphism using allometric plots of ln(male size) on ln(female size) (or vice versa: Abouheif and Fairbairn 1997; Fairbairn 1997). Logarithmic transformations are necessary for reasons of scaling when studying such evolutionary allometries (Gould 1966; LaBarbera 1989). When (by convention) plotting female size on the x axis, Rensch‘s rule becomes statistically manifest in slopes $b > 1$ (i.e. hyper- or positive allometry; Fairbairn 1997). Because there is variance in both female and male size, and because the y and x variables are identical, major-axis (MA, or model II) regression should be used instead of least-squares regression (Sokal and Rohlf 1995), although this was not always done in the past (Table 6.1). In general, hypo- or negative allometry results when variance in y is less than in x, and hyper- or positive allometry results in the opposite case. Standard errors (SE) or 95% confidence intervals (CI; equal to 1.96*SE) based on error in x and y for MA slopes, or error in y only for least-squares slopes, can be calculated. Note that unless r^2 is very high, the MA slope is always greater than the least-squares slope, and the MA SE is always smaller (because in a right-angled triangle either of the two catheti, minimized in MA regression, are necessarily smaller than the hypotenuse minimized in least-squares regression).

Table 6.1 lists all allometric regression slope estimates available to date for insects, and Figure 6.1 plots the data for those groups yet unpublished (see Blanckenhorn *et al.* 2007). Phylogenetically uncorrected MA estimates based on the original data and/or corrected estimates based on independent contrasts assuming a particular phylogeny for the group are given in Table 6.1 (Felsenstein 1985; Purvis and Rambaut 1995). Because in the past least-squares estimates were often supplied, we list them for comparison. Least-squares and phylogenetically uncorrected estimates are clearly biased (Felsenstein 1985; Sokal and Rohlf 1995), so phylogenetically corrected MA estimates are preferred.

We have estimates for a total of seven insect orders, some of them featuring multiple estimates for various subtaxa. These estimates are based on different body-size traits, although this is of minor importance (but see section 6.4. below) as long as the same trait is used for both sexes and the traits are at the same scale (i.e. linear traits such as thorax or body length in contrast to volume traits

Table 6.1 Least-squares (LS) and MA allometric slopes (± 95% CI) of ln(male size) on ln(female size) for various insect orders and/or some subsets (asterisks indicate slopes significantly different from 1; $^{*}P < 0.05$; $^{(*)}P < 0.1$). The RR? column indicates whether the data support (+; MA slopes >1) or are opposite to (–; MA slopes <1) Rensch's rule, or are neutral (0; MA slopes = 1).

Taxonomic group	Phylogenetically uncorrected		Phylogenetically corrected		*N*	RR?	Reference	Trait
	LS slope (± 95% CI)	MA slope (± 95% CI)	LS slope (± 95% CI)	MA slope (± 95% CI)				
Coleoptera (beetles)	0.99 ± 0.024	0.99 ± 0.017	1.02 ± 0.039	1.02 ± 0.027	35	0	Blanckenhorn *et al.* (2006)	Body mass$^{0.33}$
Carabidae	0.97 ± 0.024*	0.97 ± 0.017*	–	–	9	–	Rensch (1950)	Body length
Coccinellidae (Ladybird beetles)	1.01 ± 0.039	1.02 ± 0.026	–	–	37	0	Dixon (2000)	Body mass$^{0.33}$
Diptera (flies)								
Diopsidae (stalk-eyed flies)	1.09 ± 0.113	1.14 ± 0.071*	1.13 ± 0.110*	1.18 ± 0.067*	30	+	Baker and Wilkinson (2001)	Thorax length
Drosophila spp. (fruit flies)	1.09 ± 0.168	1.18 ± 0.104*	0.98 ± 0.210	1.11 ± 0.139$^{(*)}$	23	+	Blanckenhorn *et al.* (2006)	Thorax length
				1.23 ± 0.245$^{(*)}$	20		Huey *et al.* (2006)	
				1.15 ± 0.059*	42		Pitnick *et al.* (1995)	
Scathophagidae (dung flies)	1.14 ± 0.096*	1.18 ± 0.058*	1.06 ± 0.142	1.14 ± 0.090*	32	+	W.U. Blanckenhorn, R. Meier, and M. Bernasconi, unpublished work	Hind tibia length
Sepsidae (black scavenger flies)	1.00 ± 0.093	1.03 ± 0.064	0.81 ± 0.168*	0.91 ± 0.132	29	0	W.U. Blanckenhorn and R. Meier, unpublished work	Head width
Tephritidae (fruit flies)	1.11*	1.12*	–	–	27	+	Sivinski and Dodson (1992)	Thorax length
Anastrepha spp.	1.20*	1.22*	–	–	9	+	Sivinski and Dodson (1992)	Thorax length
Hymenoptera	0.98 ± 0.037	0.99 ± 0.025	0.95 ± 0.060	0.96 ± 0.044$^{(*)}$	24	–	Blanckenhorn *et al.* (2006)	Body mass$^{0.33}$
Lepidoptera (butterflies)	1.03 ± 0.082	1.07 ± 0.055*	0.94 ± 0.106	1.00 ± 0.076	47	+	Blanckenhorn *et al.* (2006)	Body mass$^{0.33}$
Heteroptera (bugs)								
Gerrinae (water striders)	1.06 ± 0.065	1.08 ± 0.043*	1.14 ± 0.131*	1.22 ± 0.078*	33	+	Fairbairn (1990), (1997)	Body length
		1.22 ± 0.059*			65		Andersen (1997)	
Eotrechinae (water striders)	1.22 ± 0.059*	1.06 ± 0.133	–	–	23	+	Andersen (1997)	Body length
Halobatinae (water striders)	–	1.72 ± 0.125*	–	–	39	+	Andersen (1997)	Body length
Ptilomerinae (water striders)	–	1.35 ± 0.104*	–	–	18	+	Andersen (1997)	Body length
Rhagadotarsinae (water striders)	–	1.12 ± 0.098*	–	–	21	+	Andersen (1997)	Body length
Trepatobatinae (water striders)	–	1.15 ± 0.098*	–	–	39	+	Andersen (1997)	Body length
Odonata (dragonflies)	1.06 ± 0.043*	1.07 ± 0.028*	1.07 ± 0.170	1.12 ± 0.109*	21	+	Johansson *et al.* (2005)	Hind tibia length
Phasmatodea (stick insects)	0.84*	–	–	–	152	–	Sivinski (1978); Sivinski and Dodson (1992)	Body length
Trichoptera (caddisflies)								
Hydropsychidae	1.05 ± 0.100	–	1.04 ± 0.120	1.09 ± 0.720	29	0	Jannot and Kerans (2003)	Body length

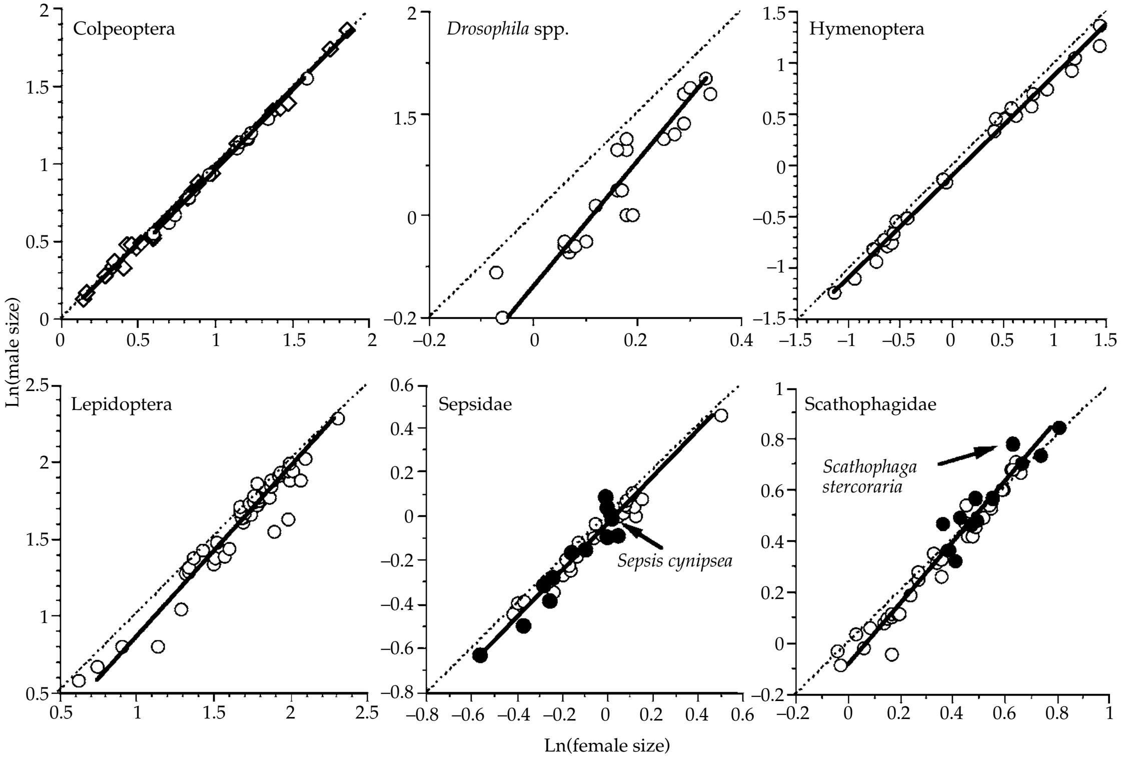

Figure 6.1 Allometric (least-squares) regression plots of mean male on mean female body size (natural-log-transformed; traits and slope estimates are given in Table 6.1) for six insect taxa (line of isometry hatched for comparison). Filled circles for the Sepsidae and Scathophagidae denote the genera *Sepsis* and *Scathophaga*, respectively.

such as body mass). At the order level, Coleoptera, Hymenoptera, and Phasmatodea show allometry that is inconsistent with Rensch's rule, with the latter two even revealing an opposite trend, whereas Diptera, Heteroptera, and (potentially) the Lepidoptera conform to Rensch's rule. Ironically, Rensch's (1950) original carabid beetle example does not follow Rensch's rule, although admittedly he had mentioned that this is not a particularly good example. This limited data-set suggests that Rensch's rule occurs in only about half of insect orders and may consequently not be the norm in insects. Note that the number of estimates within the different orders, as well as their quality (phylogenetic correction or not), varies considerably: for Diptera and Heteroptera several families have been investigated, whereas for most other orders species from all families were combined or only a single family (e.g. Trichoptera) were investigated. However, the various sub-estimates for Diptera and Heteroptera are rather consistent in supporting Rensch's rule. Nevertheless, as shall be shown further below for the Sepsidae (see Figure 6.2 below), within any group Rensch's rule might hold at one taxonomic level (e.g. the family) but not at another (e.g. the genus). Thus overall support for Rensch's rule in the insects remains rather mixed and probably does not deserve the attribute "rule", a pattern also true for spiders (see Chapter 7).

6.3 Patterns among populations within species

A long-standing hypothesis for the evolution of allometry consistent with Rensch's rule is that it is driven by sexual selection for large male size in combination with a generally very high genetic correlation in body size between the sexes (reviewed in Fairbairn 1997). Fairbairn and Preziosi (1994) investigated this hypothesis by comparing dimorphism together with the intensity of sexual selection on male size among isolated populations of the water strider *Aquarius remigis* (see also Chapter 9). Their reasoning was that if sexual selection on male body size is consistently stronger in one population compared to another living in a different environment (with viability and fecundity selection assumed to be equal), male size should increase, and hence dimorphism change, faster over evolutionary time in that population. Such divergent selection should eventually result in more variation in male than female size among populations, thus generating Rensch's rule (Fairbairn and Preziosi 1994). In so doing, they extended Rensch's rule to the within-species taxonomic level, following a major tenet of evolutionary biology in trying to explain a macroevolutionary pattern among species by studying the putative underlying selective mechanisms operating at the microevolutionary level.

The approach of Fairbairn and Preziosi (1994) was replicated in two species of dung fly by Kraushaar and Blanckenhorn (2002), and intraspecific variation in dimorphism was further studied in two vertebrates (humans and salmon) by Gustafsson and Lindenfors (2004) and Young (2005), yielding overall mixed results. Recently, Blanckenhorn *et al.* (2006) took advantage of sex-specific studies of latitudinal clines to investigate intraspecific patterns of Rensch's rule. Except for the studies by Fairbairn and Preziosi (1994) on Gerridae and Kraushaar and Blanckenhorn (2002) on Sepsidae and Scathophagidae, all estimates presented here stem from studies of sex-specific latitudinal clines (Blanckenhorn *et al.* 2006). Only few individual estimates differ significantly from a MA slope of 1 (shown in italics in Table 6.2) and the data reveal no overall pattern, as only 20 of 37 species have allometric slopes >1 that are consistent with Rensch's rule (mean slope ± 95% CI, 0.970 ± 0.078). That is, as for the interspecific pattern, there is no evidence for the prevalence of an intraspecific pattern analogous to Rensch's rule in insects. As is well known for insects, dimorphism is female-biased overall (only five of 37 species have larger males), as evidenced by a positive mean size dimorphism index (SDI) of 0.036 ± 0.035 ($\pm$ 95% CI).

Note that when investigating the relationship between male and female body size (as in Figure 6.1), it is actually sufficient to know body-size means and standard deviations. This is because the reduced MA slope of a regression of ln(male size) on ln(female size), which closely approximates the MA slope, can conveniently be calculated as the ratio of the standard deviations of ln(male size) and ln(female size) (Sokal and Rohlf 1995). This should facilitate further studies of Rensch's rule within species as undertaken here.

6.4 Patterns within populations of a given species

In studies examining Rensch's rule, dimorphism has been commonly assumed to have some narrow, species-specific range. In an extensive re-analysis of insect case studies, Teder and Tammaru (2005) demonstrated that this assumption is not necessarily correct. Instead, dimorphism can strongly vary as a function of developmental conditions. Typically, differences between female and male size increased as conditions improved and body size increased. The phenomenon was attributable to a disproportional increase in the size of the larger sex, which was the females in most species analyzed. As a result, female body size was usually more variable than male size at the intra-population level—a pattern of body-size plasticity opposite to that predicted by Rensch's rule. As a plausible explanation, Teder and Tammaru (2005) suggested that the two sexes may be differently constrained by growth conditions when attaining their optimal body sizes: the larger sex responds more strongly to a reduction in environmental quality, thus deviating more from its optimal size than the smaller sex.

Teder and Tammaru (2005) focused their analyses on body mass, the size trait most commonly available. However, some evidence exists that different size traits can show different sex-related patterns of variance. For example, van Alphen and Thunnissen (1983) showed in a parasitoid wasp that an equal increase in head width in the two

Table 6.2 Among-population MA allometric slopes (reduced MA in case of most butterfly data) of ln(male size) on ln(female size) and overall size dimorphism (SDI = (female size/male size − 1) when females are larger; SDI = −(male size/female size − 1) when males are larger; after Lovich and Gibbons 1992) for various insect species. All sizes are in millimeters except *Papilio canadensis* (mg); italic MA values are significantly different from 1; Asterisks indicate multiple estimates; see Blanckenhorn *et al.* (2006a) for references.

Order	Family	Species	Trait	*N*(populations)	Male size	Female size	SDI	MA slope
Coleoptera	Carabidae	*Carabus nemoralis*	Elytron length	26	14.15	14.98	0.059	1.039
Coleoptera	Chrysomelidae	*Phyllotreta striolata*	Elytron length	9	76.62	81.13	0.059	*1.176*
Coleoptera	Chrysomelidae	*Stator limbatus*	Elytron length	92	1.55	1.52	−0.020	*0.879*
Diptera	Drosophilidae	*Drosophila alduchi*	Wing length	5	1.94	2.08	0.072	0.674
Diptera	Drosophilidae	*Drosophila buzzanti*	Wing length	5	1.98	2.15	0.086	1.355
Diptera	Drosophilidae	*Drosophila melanogaster*	Thorax length	18	0.77	0.86	0.117	0.943
Diptera	Drosophilidae	*Drosophila serrata*	Wing length	20	1.19	1.30	0.092	1.047
Diptera	Drosophilidae	*Drosophila simulans*	Wing length	5	1.88	2.16	0.149	*0.609*
Diptera	Drosophilidae	*Drosophila subobscura*	Wing length	10	1.20	1.35	0.125	1.001
Diptera	Drosophilidae	*Zaprionus indianus*	Wing length	10	2.67	2.73	0.022	*1.267*
Diptera*	Scathophagidae	*Scathophaga stercoraria*	Hind tibia length	6	3.56	2.79	−0.276	1.074
				30	3.69	2.94	−0.255	0.931
				30	3.42	2.45	−0.396	1.197
Diptera*	Sepsidae	*Sepsis cynipsea*	Hind tibia length	25	1.36	1.42	0.044	1.002
				25	1.21	1.27	0.050	0.855
Hemiptera*	Gerridae	*Aquarius remigis*	Body length	8	12.83	14.33	0.117	*1.459*
				31				*1.250*
Lepidoptera	Lycaenidae	*Heodes virgaureae*	Wing length	16	15.60	14.80	−0.054	0.919
Lepidoptera	Lycaenidae	*Lycaena helle*	Wing length	12	13.20	13.30	0.008	1.215
Lepidoptera	Lycaenidae	*Palaeocrysophanus hippothoei*	Wing length	15	15.80	16.50	0.044	0.816
Lepidoptera	Lycaenidae	*Polyommatus icarus*	Wing length	10	15.60	14.84	−0.051	0.154
Lepidoptera	Lymantriidae	*Lymantrea dispar*	Wing length	36	24.25	30.27	0.248	*1.274*
Lepidoptera	Papilionidae	*Papilio canadensis*	Body mass$^{0.33}$	2	9.19	9.41	0.024	0.652
Lepidoptera	Satyridae	*Aphantopus hyperantus*	Wing length	15	20.10	21.90	0.090	0.921
Lepidoptera	Satyridae	*Coenonympha arcania*	Wing length	7	16.20	17.00	0.049	1.127
Lepidoptera	Satyridae	*Coenonympha hero*	Wing length	5	15.70	16.20	0.032	1.135
Lepidoptera	Satyridae	*Coenonympha pamphilus*	Wing length	20	14.40	15.80	0.097	0.907
Lepidoptera	Satyridae	*Coenonympha tullia*	Wing length	8	17.50	18.30	0.046	0.950
Lepidoptera	Satyridae	*Erebia ligea*	Wing length	14	22.30	22.50	0.009	1.050
Lepidoptera	Satyridae	*Hipparchia semel*	Wing length	6	24.60	26.70	0.085	0.880
Lepidoptera	Satyridae	*Lasiommata maera*	Wing length	10	24.30	25.20	0.037	0.541
Lepidoptera	Satyridae	*Lasiommata megera*	Wing length	5	21.10	22.70	0.076	1.189
Lepidoptera	Satyridae	*Lasiommata petropolis*	Wing length	8	20.30	20.90	0.030	1.234
Lepidoptera	Satyridae	*Lycaena phlaeas*	Wing length	10	14.00	14.60	0.043	0.790
Lepidoptera	Satyridae	*Maniola jurtina*	Wing length	12	20.90	23.20	0.110	0.767
Lepidoptera	Satyridae	*Pararge aegeria*	Wing length	7	21.20	21.80	0.028	1.012
Odonata	Coenagrionidae	*Enallagma cyathigerum*	Thorax length	7	4.05	4.08	0.007	0.792
Orthoptera	Acridinae	*Caledia captiva*	Pronotum length	8	3.84	4.96	0.292	1.284
Orthoptera	Gryllidae	*Allonemobius socius*	Femur length	21	6.51	7.06	0.084	*0.718*
Orthoptera	Gryllidae	*Pteronemobius fascipes*	Head width	10	1.72	1.86	0.081	1.023
Orthoptera	Gryllidae	*Telogryllus emma*	Head width	19	6.23	6.20	−0.005	*1.028*

sexes lead to a disproportional increase in female body mass, implying differences in body shape. Consequently, any index of dimorphism may strongly differ within species depending on the size trait used for its calculation. For example, a study on four parasitoid wasps revealed that dimorphism based on linear (hind tibia length) and volume (adult mass) measurements may differ even qualitatively: females were typically heavier, whereas males were the larger sex with regard to hind tibia length (Teder 2005). Similarly, Väisänen and Heliövaara (1990) measured a number of different linear size indices in a heteropteran bug, and showed that the corresponding SDI varied between 0 and 0.5 (see also Chapter 9).

To test whether the patterns of sex-related variance in linear structural traits coincide with patterns of variance in body mass found by Teder and Tammaru (2005), we here performed analogous analyses using linear size indices instead of body mass. We extracted relevant data for 58 insect species from the literature. A data-set for any particular species consisted of means of some linear measure of adult size, presented separately for males and females, and reported for at least two different population samples (e.g. in different environments). For each species, ln (male size) was plotted against ln (female size). A reduced MA regression slope $b > 1$ indicates greater variance in male size, whereas $b < 1$ indicates greater variance in female size.

The proportion of species in which linear traits of females responded more strongly to a reduction in environmental quality than those of males was nearly equal to the proportion of species with an opposite trend: $b < 1$ in 29 species (52%); $b > 1$ in 27 species (48%). In contrast, Teder and Tammaru (2005), analyzing an analogous data-set using body mass instead of structural traits, found female body mass to be more sensitive to environmental conditions in nearly 70% of species ($b < 1$ in 98 species; $b > 1$ in 44 species). The two distributions of linear structural and body-mass traits differed significantly (Fisher's exact probability test, $P = 0.03$). A similar tendency was found when comparing the allometric slopes based on body masses with those based on some linear size measure for a paired subset of 16 species for which both types of trait were available (Table 6.3). Within this set of species, the slope of the log–log regression of the structural trait of males on that of females was typically greater than the corresponding slope for male on female body mass (12 higher compared with four lower; binomial test, $P = 0.08$; Table 6.3). In other words, the tendency of female size to be more plastic was stronger when size was expressed in terms of body mass than when linear size traits were used. This is not merely a statistical artifact due to a common mean–variance correlation, which can be largely removed by proper (logarithmic) transformation of the data (Gould 1966; LaBarbera 1989).

Why then do the sex-related patterns of variance depend on the size measure used? A likely explanation is associated with the relative nature of dimorphism based on body mass and linear measures. It is well known in insects that sexual differences in body mass are to a considerable degree attributable to sexual differences in abdomen size. For example, Wickman and Karlsson (1989) demonstrated in seven butterfly species and a calliphorid fly that the proportion of abdomen mass relative to the total body mass is higher in females than in males. The relatively larger abdomens of females have been commonly interpreted as resulting from fecundity selection: a larger abdomen can hold more eggs (Karlsson and Wickman 1990; Preziosi *et al.* 1996; Chapter 9). In the extreme, there may be no optimum for female size as larger (abdomen) size may always be better (e.g. Tammaru *et al.* 2002). In line with this, Wickman and Karlsson (1989) showed that the proportion of abdomen mass relative to total body mass increases with total mass. Male fitness, however, is often determined by his ability to find mating partners, and selection on larger abdomen mass (sperm production) may therefore be counterbalanced by selection on better locomotory abilities (Ghiselin 1974; e.g. Blanckenhorn *et al.* 1995). In contrast, sex-related differences in selection pressure on the sizes of structural traits associated with head and thorax (including wings and legs) are expected to be generally less striking. It follows that, with environmental conditions improving (and body size increasing), females and males should diverge in body mass more than in linear traits.

Table 6.3 Paired comparison of reduced MA regression slopes of ln(male size) on ln(female size) and minimum and maximum size dimorphism across samples (SDI = (female size/male size − 1) when females are larger, and SDI = −(male size/female size−1) when males are larger) for body mass and linear traits.

Order	Family	Species	Linear trait	Slope (body mass)	Slope (linear trait)	Min; max SDI (body mass)	Min; max SDI (linear traits)	Reference
Coleoptera	Carabidae	*Notiophilus biguttatus*	Pronotum width	0.884	1.027	0.032; 0.119	0.032; 0.039	Ernsting *et al.* (1992)
Coleoptera	Carabidae	*Poecilus cupreus*	Elytra length	0.333	0.658	−0.010; 0.058	0.004; 0.007	Zangger *et al.* (1994)
Coleoptera	Scolytidae	*Ips sexdentatus*	Pronotum width	0.721	1.245	−0.149; −0.020	−0.061; −0.026	Colineau and Lieutier (1994)
Diptera	Muscidae	*Musca autumnalis*	Wing length	0.610	1.068	0.462; 0.679	0.080; 0.104	Gaaboub and Hayes (1984)
Diptera	Tachinidae	*Eucelatoria rubentis*	Tibia length	2.671	2.758	−0.214; −0.005	−0.120; −0.056	Reitz (1996)
Hymenoptera	Cephidae	*Cephus cinctus*	Forewing length	0.923	1.125	0.821; 1.087	0.039; 0.162	Cárcamo *et al.* (2005)
Hymenoptera	Encyrtidae	*Syrphophagus aphidivorus*	Wing length	0.550	0.001	0.000; 0.200	0.039; 0.117	Buitenhuis *et al.* (2004)
Hymenoptera	Megaspilidae	*Dendroceru*s *carpenteri*	Hind tibia length	0.963	0.970	−0.124; 0.612	−0.025; 0.156	Otto and Mackauer (1998)
Orthoptera	Acrididae	*Chorthippus brunneus*	Hind femur length	0.515	0.527	0.443; 0.910	0.161; 0.281	Willott and Hassall (1998)
Orthoptera	Acrididae	*Myrmeleotettix maculatus*	Hind femur length	0.784	0.915	0.360; 0.419	0.154; 0.157	Willott and Hassall (1998)
Orthoptera	Acrididae	*Omocestus viridulus*	Hind femur length	0.676	0.910	0.660; 0.721	0.246; 0.250	Willott and Hassall (1998)
Lepidoptera	Lycaenidae	*Hemiargus isola*	Forewing length	2.409	2.059	0.041; 0.139	−0.001; 0.022	Wagner and Martinez del Rio (1997)
Lepidoptera	Noctuidae	*Agrotis ipsilon*	Forewing length	1.048	1.172	0.122; 0.132	0.044; 0.052	Sappington and Showers (1992)
Lepidoptera	Noctuidae	*Spodoptera frugiperda*	Forewing width	0.823	0.389	−0.085; 0.038	−0.036; 0.035	Ferguson *et al.* (1994)
Lepidoptera	Tortricidae	*Bactra verutana*	Wing length	1.067	0.935	0.451; 1.250	0.121; 0.183	Frick and Wilson (1982)
Trichoptera	Limnephilidae	*Potamophylax cingulatus*	Wing length	0.763	1.123	0.204; 0.475	0.017; 0.060	Svensson (1975)

6.5 Relationships among the various taxonomic levels

After investigating the evidence for Rensch's rule at three taxonomic levels (among species, among populations within species, and within populations), we now ask whether the patterns correlate. As outlined in the Introduction, plots of male on female size (Figure 6.1), indicating sexual differences in body-size variance, and hence Rensch's rule, can formally be generated at all these levels by plotting species means, population means, or family or group means in various environments, respectively, as done here. Direct comparisons are possible if such estimates are available for a given group of species, and we here present two such examples for the sepsid and scathophagid flies (Figure 6.2). Data for the higher taxonomic levels (species, genera) stem from field-caught, pinned specimens at the Zoological Museum, Copenhagen, Denmark, whereas laboratory and field estimates at lower taxonomic levels were gathered at the Zoological Museum, Zurich, Switzerland. The species estimates refer to the genera *Sepsis* spp. and *Scathophaga* spp., and the population and family estimates refer to *Sepsis cynipsea* and *Scathophaga stercoraria* (data from Blanckenhorn 1997b, 1998a, unpublished work; Kraushaar and Blanckenhorn 2002). In most sepsids, as is the case for *S. cynipsea*, females are larger than males, and in many scathophagids, as is the case for *S. stercoraria*, males are larger than females (Figure 6.1).

Four observations can be gathered from this admittedly limited comparison of allometric body-size slopes at various taxonomic levels in these two species groups (Figure 6.2). First, in the scathophagids all estimates are congruent in that males show greater variance than females at all taxonomic levels, with slopes generally >1, consistent with Rensch's rule. In the sepsids, in contrast, the estimates are incongruent: only the interspecific estimates tend to conform to Rensch's rule (slope >1), males thus exhibiting more variance, whereas the intraspecific estimates show slopes ≤1, indicating greater variance among females (or equal variances for both sexes). In the sepsids, therefore, intraspecific patterns do not predict interspecific patterns, whereas in the scathophagids they do (see Kraushaar and Blanckenhorn 2002). Second, in both families intraspecific body-size variance tends to be greater in the larger sex (females in *S. cynipsea*, males in *S. stercoraria*; Figure 6.2; see section 6.4). This is consistent with a correlation between mean and variance that is frequently observed in metric data: often a data-set with a greater mean also displays greater variance, which is one of the prime reasons for statistical data transformation (Sokal and Rohlf 1995). It also suggests that intraspecific patterns largely reflect mechanisms generated by phenotypic plasticity, whereas interspecific patterns should rather reflect

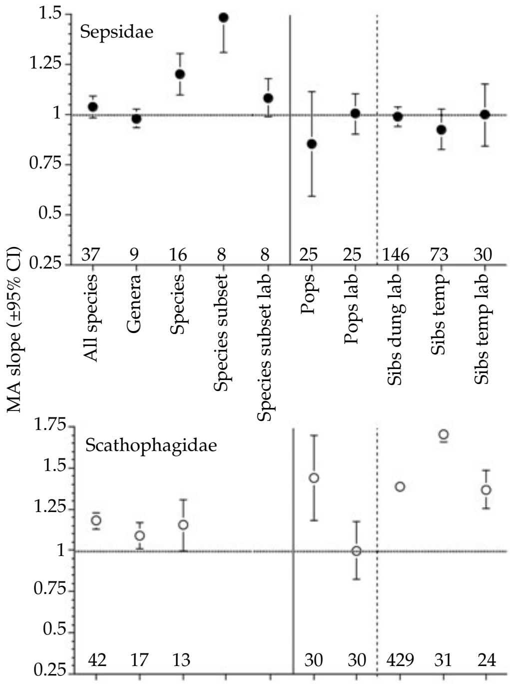

Figure 6.2 MA regression slopes (±95% CI) at various taxonomic levels (from left to right: among species, among populations, and among families of *Sepsis cynipsea* and *Scathophaga stercoraria*), for field-caught and laboratory-reared specimens of the Dipteran groups Sepsidae and Scathophagidae (sample sizes given underneath). The species subset for the Sepsidae refers to eight species of *Sepsis* for which field and laboratory data were available. Sibs dung lab: full-sib offspring (families) of one population, reared in the lab at various dung (= food) conditions; Sibs temp: full-sib offspring (families) of one population, reared in the field throughout the season at various temperatures; Sibs temp lab: full-sib offspring (families) of one population, reared in the lab at various temperatures.

mechanisms related to the speciation process, with possibly little correspondence between the two (see Fairbairn 2005). Thus interspecific patterns are unlikely to be generally predictable from intraspecific (among-population) studies, as originally envisioned by Fairbairn and Preziosi (1994) and Kraushaar and Blanckenhorn (2002). Third, at least in the sepsids (Figure 6.2) even the interspecific estimates are quite variable: allometric slopes among *Sepsis* species are clearly >1, following Rensch's rule, whereas among genera (averaging various species within a given genus) and overall the slopes are equal to 1. Thus interspecific patterns at various taxonomic levels (species, genus, family, etc.) are not necessarily consistent, and it would be interesting to systematically investigate this pattern in other groups. Such variation in interspecific dimorphism at various taxonomic levels, typically revealed by nested analysis of variance, is known from other taxa (e.g. Kappeler *et al.* 1996; Jannot and Kerans 2003). Fourth, again in the sepsids, allometric slopes generated from field-caught specimens were substantially steeper than those obtained when the same eight species were reared in the laboratory (Figure 6.2). This suggests that standardized and rather benign rearing procedures in the laboratory, which typically reduce the degree of phenotypic plasticity and hence produce adults of maximal body size, can affect even interspecific allometric slopes and ultimately the extent of Rensch's rule (see section 6.4). More data-sets of this kind are clearly needed to evaluate the generality of these findings.

6.6 Summary and conclusions

Abouheif and Fairbairn (1997) found Rensch's rule to be a common pattern among animal species, a result largely dominated by vertebrates, with data on invertebrates being rare in their sample. We here re-evaluated the evidence for insects with new data-sets and found Rensch's rule consistently in Diptera (flies) and Heteroptera (Gerridae; water striders), but not in other insect groups (except perhaps in Lepidoptera; Table 6.1), suggesting that the mechanisms causing the pattern are unevenly distributed among taxa. Extending our investigation to the level among populations within species also revealed no consistent evidence for Rensch's rule (Table 6.2), although when populations are ordered by latitude a pattern consistent with Rensch's rule was found more commonly than expected by chance (Blanckenhorn *et al.* 2006). In contrast, at the level within populations of a given species at different environmental conditions, reflecting phenotypic plasticity, the majority of insects show more variation in female (typically the larger sex) than male body size, opposite to Rensch's rule (Teder and Tammaru 2005), a result that weakened when linear structural traits were used as a size measures instead of body mass. A specific comparison of these three taxonomic levels revealed congruence in scathophagid flies, typically featuring male-biased dimorphism and allometry consistent with Rensch's rule at all levels, but no congruence in sepsid flies, in which female-biased dimorphism dominates (the common pattern in insects). Patterns of body size allometry at the three taxonomic levels consequently generally do not correspond well. Whether patterns at lower levels can reveal the (selective) mechanisms causing Rensch's rule at higher levels therefore remains questionable and should be scrutinized further. To extend or correct the patterns found here, we strongly encourage researchers to gather more data on female and male body size variation at multiple taxonomic levels for a given species group, taking both linear structural and body mass traits for direct comparison and analyzing the data using the standardized methods exemplified here.

6.7 Acknowledgments

W.U.B. and R.M. acknowledge Swiss matching funds for the European exchange program COBICE to visit the Zoological Museum Copenhagen in 2001. W.U.B. and R.M. also thank K.-D. Klass (Copenhagen) for measuring museum specimens. We further thank F. Johansson (Umeå), R. Baker and G. Wilkinson (Maryland), and R. Huey (Seattle) for sending us their data. T.T. thanks T. Tammaru for comments and the Estonian Science Foundation (grant no. 6619) for financial support.

6.8 Suggested readings

Abouheif, E. and Fairbairn, D.J. (1997) A comparative analysis of allometry for sexual size dimorphism: assessing Rensch's rule. *American Naturalist* **149**, 540–562.

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Teder, T. and Tammaru, T. (2005) Sexual size dimorphism within species increases with body size in insects. *Oikos* **108**, 321–334.

CHAPTER 7

Sexual size dimorphism in spiders: patterns and processes

Matthias W. Foellmer and Jordi Moya-Laraño

7.1 Introduction

Spiders (Araneae) are known for the most spectacular cases of sexual size dimorphism (SSD) among terrestrial animals. In several species of web-building spiders females are giants compared to their tiny male counterparts and may outweigh them by more than 100 times (Head 1995; Vollrath 1998). The evolution of such extreme SSD has puzzled researchers since Darwin (Darwin 1871; Gerhardt 1924; Elgar 1992; Vollrath and Parker 1992; Andersson 1994; Head 1995; Coddington *et al.* 1997). In fact, its evolutionary significance is far from resolved and remains controversial (e.g. Vollrath and Parker 1992; Coddington *et al.* 1997; Prenter *et al.* 1998, 1999; Moya-Laraño *et al.* 2002a, Blanckenhorn 2005; Foellmer and Fairbairn 2005a, 2005b). Apart from the most extravagant cases, spiders exhibit the whole range of SSD, from extreme female-biased to male-biased, with females being larger than males in the majority of species (Head 1995; Vollrath 1998). Interestingly, both male-biased SSD and extreme female-biased SSD occur in several distinct spider taxa, and extreme SSD has evolved several times independently, even within the orb-web spiders (Hormiga *et al.* 2000). Spiders are the only terrestrial animal taxon that exhibits such a broad range of SSD and in which extreme SSD is relatively common (Ghiselin 1974; Andersson 1994). Hence, spiders offer a unique and tangible system to study the ultimate and proximate factors that drive the evolution of SSD. In this chapter, we first clarify important issues regarding spider morphology as they relate to size dimorphism and then elucidate the patterns of SSD within the spiders. Finally, we present the hypotheses for the adaptive significance of SSD in spiders as well as the current evidence for and against these and emphasize areas for future research.

7.2 Spider morphology: dimorphism in size and shape

Spiders have two major body parts, the anterior prosoma and the posterior opisthosoma (Figure 7.1). The prosoma is a cephalothorax and encompasses the head region with eyes, fangs, and pedipalps, plus the thorax region to which the four pairs of walking legs are attached. The opisthosoma is the spider's abdomen containing most of the visceral organs, the gonads, and the silk glands (Foelix 1996). To understand spider size it is important to consider the pattern of growth in spiders. As arthropods, spiders undergo a series of molts during the ontogeny, shedding their cuticle in each of the molts (Foelix 1996). The prosoma and legs grow only during a molt when liquefied reserves from the abdomen are pumped into the anterior regions of the body to expand the new and still soft cuticle (Foelix 1996). The vast majority of spider species exhibit determinant growth and do not molt after maturity (Foelix 1996). Thus, prosoma and leg traits are frequently referred to as fixed traits. Prosoma traits, such as carapace width, are typically highly correlated with body mass at maturation (Foelix 1996) and are therefore very useful and easy to measure for estimating a spider's size. On the other hand, the abdomen's

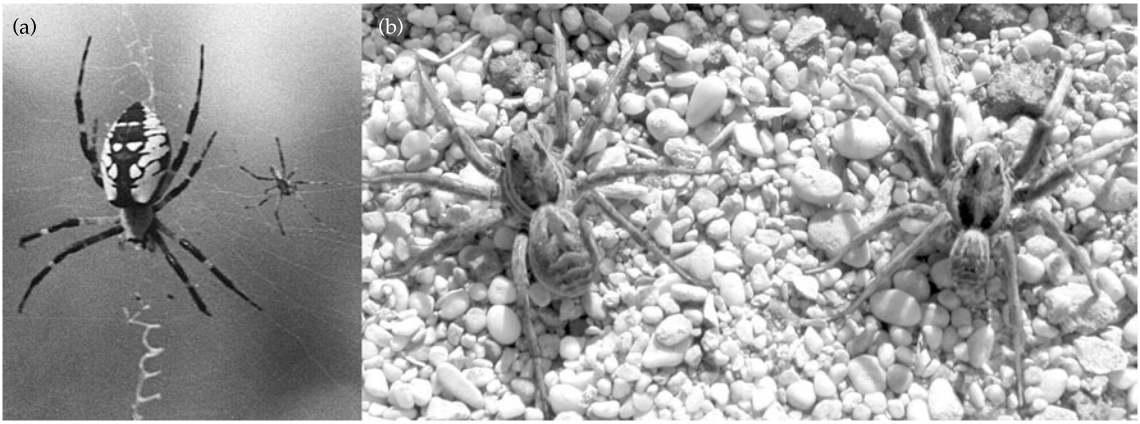

Figure 7.1 (a) A female (left) and a male of the orb-web spider *Argiope aurantia*, a species with extreme SSD. (b) A female (left) and a male of the wolf spider *Lycosa tarantula*, a species with little SSD. Note that panels a and b are not to the same scale. (a) M. Foellmer Photo credit: (b) E. de Mas.

cuticle is flexible. Its dimensions change with changing body mass as a function of foraging success and reproductive state (e.g. female egg load) and are thus condition-dependent (Prenter *et al.* 1995; Moya-Laraño 2002). Adult males in many species do not feed and hence their abdomen shrinks over time as reserves are used up (e.g. Foellmer and Fairbairn 2005b). The same also applies to body length, which depends partly on abdomen length. Hence, body-mass and abdomen traits are commonly employed in indices of body condition (e.g. Moya-Laraño 2002; Moya-Laraño *et al.* 2003; Foellmer and Fairbairn 2005a, 2005b).

In many spider species, if not all, the sexes typically differ not only in size, but also in shape; that is, in the relative size of body parts (e.g. Prenter *et al.* 1995). Males have relatively longer legs than females, and in males, but not females, legs exhibit a positive allometric relationship with carapace width (Eberhard *et al.* 1998; but see Uhl *et al.* 2004). Leg length as a size trait will thus often underestimate SSD and should only be used in combination with carapace width in multivariate selection studies to discern selection on body size and body-size components (Foellmer and Fairbairn 2004, 2005a, 2005b). Little is known about sex-specific investment in the prosoma compared with the abdomen at maturation, which warrants further study. We thus recommend using carapace width as a standard size trait for spiders along with other relevant traits to capture shape and condition.

7.3 The pattern of SSD in spiders

Although in most spider species females are the larger sex, there is great variation in SSD across species (e.g. Head 1995; Vollrath 1998). Extreme SSD occurs mostly in, but is not limited to, the Orbiculariae (orb-web spiders) and Thomisidae (crab spiders), where females may weigh 100 times as much as males or, when expressed on a linear scale, be about five times as long, and these are not even the upper limits (Head 1995; Vollrath 1998; Hormiga *et al.* 2000). The evolution and coevolution of male and female body size in spiders are still not fully understood. Of interest are two questions: (1) do spiders exhibit interspecific body-size allometry consistent or inconsistent with Rensch's rule (see Chapters 1 and 6 in this volume)?; (2) is the evolution of body size in the sexes uncoupled? Answers to these questions may well turn out to be different for different spider groups and are essential for testing hypotheses about selection processes that drive the evolution of SSD within the Araneae. Rensch's rule posits that within a clade males evolve to a large size at a faster rate than females, and that this is manifested in an allometric trend: SSD increases with mean size in taxa in which males are the larger sex, and decreases in those in which females are larger (Fairbairn 1997). Rensch's rule is prominent but not universal in the animal kingdom (Abouheif and Fairbairn 1997; Chapter 6 in this volume). The second question addresses the extent to which the sexes evolve in the same direction. In most animal taxa, male and female body sizes are highly correlated, suggesting tight coevolution (Fairbairn 1997).

Abouheif and Fairbairn (1997) and Fairbairn (1997) suggested that spiders do not exhibit body-size allometry consistent with Rensch's rule, and that the correlation between male and female size may be lower in spiders than in most other animal taxa, indicating relatively uncoupled evolution of their sizes. Other comparative studies also suggested that SSD in spiders increases with increasing female size and that it depends little on male size, supporting the notion that females have diverged more in size over evolutionary time (Head 1995; Prenter *et al.* 1998, 1999). A phylogenetic analysis of the Orbiculariae showed that extreme SSD has evolved several times independently and that this has involved different evolutionary pathways (Hormiga *et al.* 2000). Increases in female size contributed most to SSD evolution, and SSD has even been lost in some lineages. Taken together, these results suggest that, overall, changes in female size have been more important for generating current SSD in spiders than changes in male size.

Almost all studies and claims about the pattern of SSD in spiders have been based on body-length data taken from identification manuals and similar literature (Vollrath and Parker 1992; Head 1995; Abouheif and Fairbairn 1997; Coddington *et al.* 1997; Prenter *et al.* 1997, 1998; Hormiga *et al.* 2000; but see Prenter *et al.* 1999). As stated in section 7.2, this may entail problems because body length is confounded with condition. Thus, in comparative analyses of the evolutionary divergence of male and female size the use of body length might lead to wrong conclusions due to the introduction of considerable error in the detection of evolutionary trends. Prenter *et al.* (1999) used carapace width in their comparative analysis and could confirm some of the results obtained in other studies. However, the problem remains that for interspecific comparisons most of the literature considers only body-length data.

Here we present an updated evaluation of the distribution of SSD and its allometry in spiders and examine specifically whether and to what extent the interpretation of results differs depending on the body-size measure used (body length compared with carapace width). We further examine whether body-size allometry differs between two large spider clades for which we have data, the Orbiculariae and the RTA clade (Coddington 2005). The Orbiculariae comprise orb-web spiders and derived web-weavers and include most of the spider species with extreme SSD (Hormiga *et al.* 2000). Most taxa in the RTA clade do not build prey-catching webs, and with the exception of some crab spiders (LeGrand and Morse 2000) most species show little dimorphism (for methods see Box 7.1).

The SSD estimates based on body length (BL) and those based on carapace width (CW) not surprisingly are correlated significantly (Spearman's rank correlation coefficient, 0.648, $P < 0.001$), but there is considerable scatter (Figure 7.2). SSD based on body length is significantly larger than SSD based on carapace width (Figures 7.2 and 7.3): for SDI-BL mean = 0.29, median = 0.23, range = -0.07 to 3.52; for SDI-CW mean = 0.11, median = 0.08, range = -0.52 to 3.09 (Wilcoxon signed ranks test, $Z = -18.04$, $P < 0.001$). The discrepancy between the two size measurements likely reflects the fact that body length is confounded by condition, especially by female egg load. Additionally, it is possible that body length as a trait is more dimorphic than carapace width independent of condition. Nevertheless, females are larger in most species regardless of which size estimator is used.

Figure 7.3 summarizes SSD for our sample by taxonomic category. The most extreme cases of SSD are found within the Araneidae. Note that some prominent families such as the sheet-web weavers (Linyphiidae), which contain probably many species with larger males (Lang 2001), are not included in our sample, because they are not covered in the books we used as our data sources. For other family-level summaries of SSD in spiders based on body length see Prenter *et al.* (1997, 1998) and Vollrath (1998).

The use of body length or carapace width has relatively little effect on estimates of body-size allometry (Table 7.1). The major-axis regression slopes are essentially identical when all species are

Box 7.1 A comparative analysis of the pattern of SSD in spiders

Data were taken from identification manuals published in the series *The Insects and Arachnids of Canada* (Dondale and Redner 1978, 1982, 1990; Platnick and Dondale 1992; Dondale *et al.* 2003), which for each species provides data for both body length and carapace width. Thus we base our analysis on species from a large and diverse geographical area. We used the updated species classification following the World Spider Catalog (version 6.5; http://research.amnh.org/entomology/spiders/catalog/INTRO1.html). A total of 489 species from 15 families and 86 genera were included in the analyses. As an index of SSD we used the size dimorphism index (SDI; Lovich and Gibbons 1992). The SDI is calculated as the larger sex divided by the smaller sex minus 1, arbitrarily set to negative when males are larger. To evaluate body-size allometry we followed the standard approach and present the results both for $\log_{10}$-transformed species data, not corrected for phylogeny (so-called tips), and for phylogenetically independent contrasts (Fairbairn 1997). Independent-contrast analysis corrects for similarity between species that is due to common ancestry (reviewed in Garland *et al.* 2005). We used PDAP version 6.0 (Garland *et al.* 2005) to calculate independent contrasts based on the current knowledge of spider phylogeny (Coddington 2005, Murphy *et al.* 2006). Unresolved nodes were entered as polytomies, so taxonomy was assumed to reflect phylogeny. That is, if no other information was available, all genera descended from the common family node and all species from the common genus node. In the absence of estimates for branch lengths we set all branch lengths arbitrarily equal to 1, and diagnostic methods (Garland *et al.* 2005) did not reveal any problem with our branch lengths. Independent-contrast analysis has been shown to be robust in case of incomplete phylogenies (Garland *et al.* 2005).

We used model II (major-axis) regression to estimate the allometric slope of log(male size) on log(female size), since both variables can be expected to have similar measurement errors and the assignment to axis is arbitrary (Fairbairn 1997). The corresponding regression for independent contrasts was forced through the origin (Garland *et al.* 2005). A slope >1 indicates allometry consistent with Rensch's rule.

combined and within the RTA clade. A slight difference is noticeable for the Orbiculariae. The lower orbicularian body-length tips slope is likely the result of gravid females being included, but this disappears when independent contrasts are considered. This result can be seen as comforting: the measure provided in most identification manuals can be used without the danger of bias. The slopes for the uncorrected species tips data are all <1, and two of them significantly so (all spiders combined and the RTA clade based on carapace width) as judged by their 95% confidence intervals not encompassing 1 (Table 7.1, Figure 7.4). Orbiculariae show greater scatter, so their confidence interval overlaps 1 (Table 7.1, Figure 7.4). Independent-contrast analyses generally confirm the slopes based on uncorrected tips data in our data-set, although none is significantly different from a slope of 1. Interestingly, the Orbiculariae and the RTA clade do not differ with respect to the independent-contrast regression slopes. Thus, spiders do not show SSD allometry consistent with

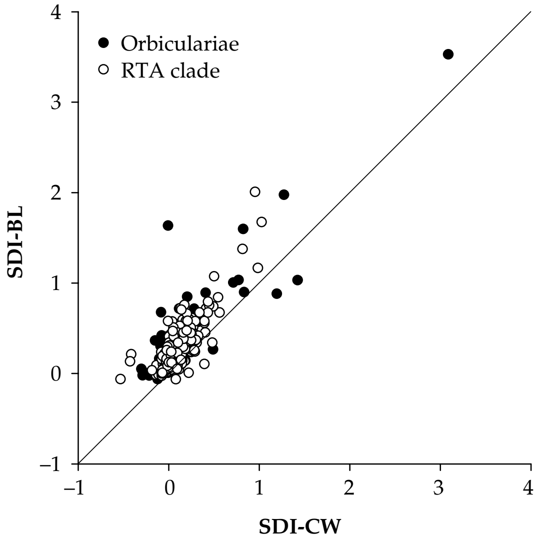

Figure 7.2 The relationship between SSD (calculated as the Lovich and Gibbons (1992) size dimorphism index; see text) based on body length as a size measurement (SDI-BL) and SSD based on carapace width (SDI-CW). Data points are shown for the two spider clades. The diagonal line depicts the line of equality between the two indices.

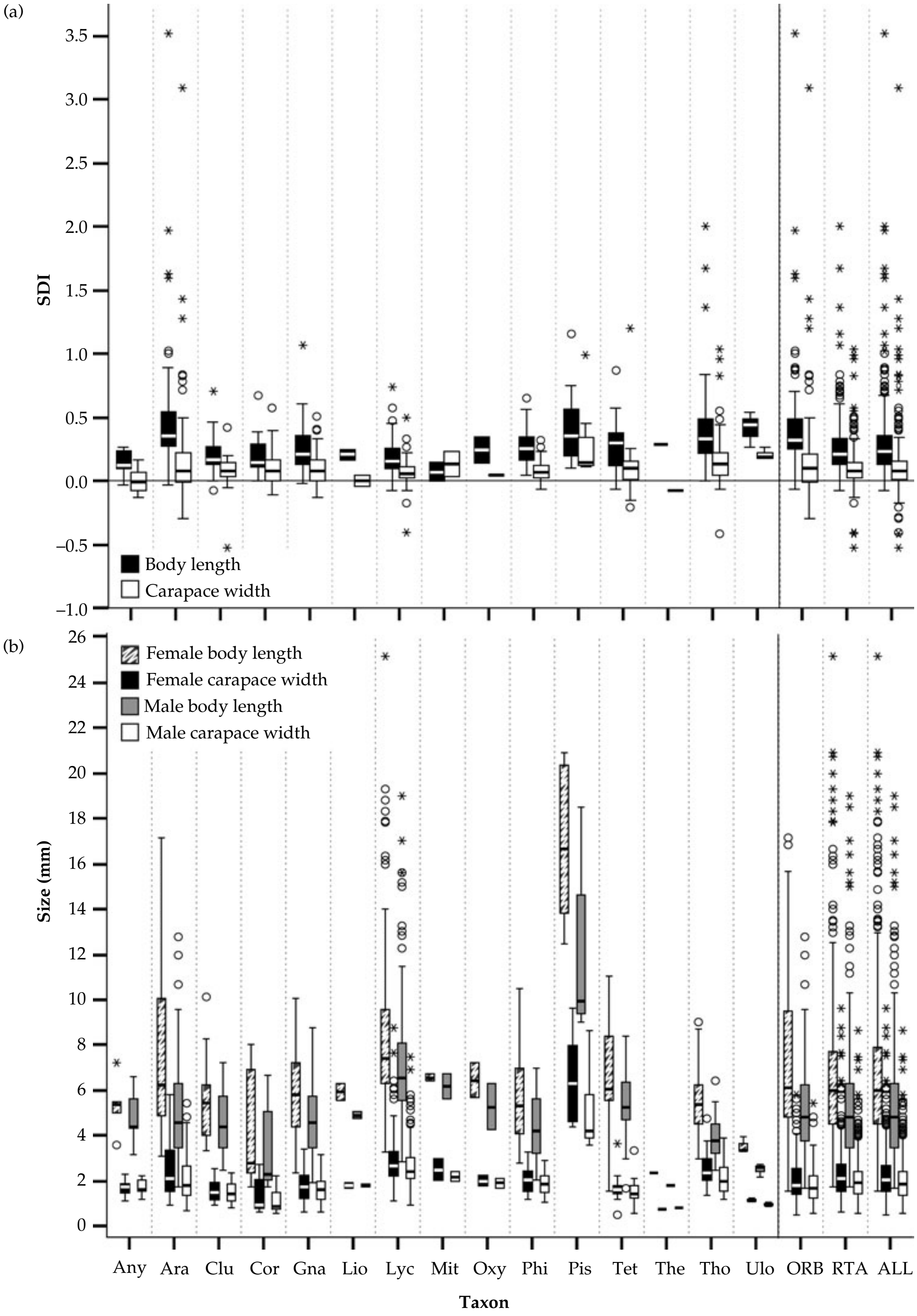

Figure 7.3 (a) Box plots for the distributions of SDI based on body length and carapace width. The horizontal reference line indicates no dimorphism (SDI = 0). (b) Box plots for the distributions of body length and carapace width for males and females. Taxonomic categories are the families included in our analysis as well as the RTA clade, the Orbiculariae, and all species combined. Horizontal lines within boxes are the medians; lower and upper box limits are the 25th and 75th percentiles respectively. Circles depict outliers that are 1.5–3 box lengths (i.e. interquartile ranges) from the end of the boxes; asterisks show extreme values (> 3 box lengths). Any, Anyphaenidae; Ara, Araneidae; Clu, Clubionidae; Cor, Corinnidae; Gna, Gnaphosidae; Lio, Liocranidae; Lyc, Lycosidae; Mit, Miturgidae; Oxy, Oxyopidae; Phi, Philodromidae; Pis, Pisauridae; Tet, Tetragnathidae; The, Theridiosomatidae; Tho, Thomisidae; Ulo, Uloboridae; ORB, Orbiculariae; RTA, RTA clade; ALL, all species combined.

Table 7.1 Major-axis regression slopes for log(male size) on log(female size) for all spiders combined and for the Orbiculariae and the RTA clade separately. Also given are the Pearson correlation coefficients, *r*. Size is either based on body length (BL) or carapace width (CW). Tips, regression based on log-transformed species data; ICs, regression based on phylogenetically independent contrasts.

			N	**MA slope**	**95% CI**	**MA intercept**	***r***
All species	BL	Tips	489	0.96	0.04	−0.07	0.92
		ICs	152	0.96	0.11		0.86
	CW	Tips	489	0.96	0.03	−0.03	0.94
		ICs	152	0.95	0.10		0.87
RTA clade	BL	Tips	396	0.98	0.04	−0.08	0.94
		ICs	97	0.98	0.14		0.86
	CW	Tips	396	0.96	0.03	−0.03	0.97
		ICs	97	0.96	0.11		0.90
Orbiculariae	BL	Tips	93	0.87	0.14	−0.04	0.85
		ICs	54	0.93	0.20		0.85
	CW	Tips	93	0.95	0.15	−0.04	0.85
		ICs	54	0.92	0.23		0.81

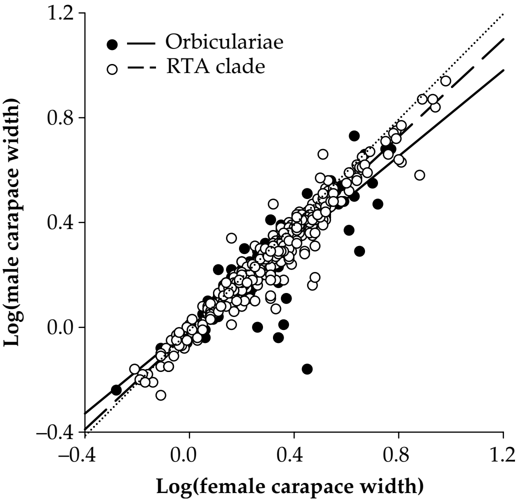

Figure 7.4 The relationship between log (male carapace width) and log(female carapace width) for the Orbiculariae and the RTA clade. The dotted line depicts a slope of 1. Also shown are the least-squares regression lines. For major-axis regression results see text and Table 7.1.

Rensch's rule; instead, females appear to have diverged more in size over evolutionary time, conforming to previous interpretations (Fairbairn 1997; Prenter *et al.* 1999).

Conspicuous are the relatively low Pearson correlation coefficients for the independent contrasts (Table 7.1). Figure 7.4 illustrates the scatter; that is, the relatively low correlation between male and female size. This suggests that male and female body size can indeed evolve in a relatively uncoupled fashion in some species, especially in orb-weavers, which is truly unusual for animals (Fairbairn 1997). Below we discuss possible reasons for this. Future studies should also focus on single subgroups such as families to investigate when and why the evolution of male and female body size is decoupled. On a proximate level, such uncorrelated changes in body size between the sexes are probably mediated by an asynchronous change in the number of instars, combined with adjustment of growth rates to ensure timely maturation in seasonal habitats (Higgins 2002; Blanckenhorn *et al.* 2007). Spiders are known for their high inter- and intraspecific variability in instar number (e.g. Hallas 1989). Possible constraints limiting the evolution of SSD still need to be identified. For instance, there is a great need for quantitative genetic studies of sex-specific growth strategies in spiders (Uhl *et al.* 2004). A recent study revealed that SSD can have an impact on the mating system of a species and that SSD may be constrained by genital mechanics (Ramos *et al.* 2005). In species with extreme female-biased SSD the female genitalia are larger relative to male genitalia than in species with moderate or no SSD. This should facilitate multiple mating by females, because mating with several males may be necessary to fill the female's spermathecae (Ramos *et al.* 2005). At the same time, the relationship between SSD and genital dimorphism possibly sets limits to the evolution of extreme SSD if the sexes cannot evolve apart in size beyond a necessary genital match (Ramos *et al.* 2005). This point is illustrated by the highly dimorphic cob-web spider genus *Tidarren,* in which the tiny males voluntarily remove one of their relatively large pedipalps prior to maturation, which greatly improves their locomotory performance and endurance (Ramos *et al.* 2004), demonstrating also how selection has favored male strategies that increase the probability of reaching females (see below).

7.4 Hypotheses for the adaptive significance of SSD in spiders

Until the maturation molt, males and females of a given spider species have very similar lifestyles (e.g. building prey-catching webs). Invariably, and even in actively hunting spiders (Persons 1999; Moya-Laraño *et al.* 2002a), males are the searching sex, which upon maturation change lifestyles considerably and stop building prey-catching webs or even feeding (Foelix 1996; Foellmer and Fairbairn 2005b). Hence, most of the adaptive hypotheses for the evolution of SSD in spiders focus on male agility or the ability to find a receptive female. Below we review sex-specific patterns of selection in spiders as they pertain to the evolution and maintenance of SSD.

7.4.1 Selection on female body size

There is good evidence that fecundity selection favoring large size in females is a major factor contributing to the evolution and maintenance of SSD in spiders. Female size correlates positively with clutch size in spiders, both at the inter- and intraspecific level (Marshall and Gittleman 1994; Head 1995; Prenter *et al.* 1999; Higgins 2002). Further, SSD correlates positively with female body size and clutch size (Head 1995; Prenter *et al.* 1998, 1999). However, the relationship between female size and reproductive success is more complex because female lifetime reproductive success depends not only on clutch size, but also on clutch number and fertility (Higgins 2000, 2002; Roff 2002). Adding an instar greatly increases clutch size (Higgins 2002) but also prolongs development time, which may translate into higher cumulative juvenile mortality, less time for reproduction in a seasonal environment (Higgins 2000; Roff 2002), and potentially mate limitation (Higgins 2000; Moya-Laraño *et al.* 2003). Hence, if being large and maturing early is strongly favored, then in turn selection should favor fast growth and efficient resource-acquisition abilities (Higgins 2000; Blanckenhorn *et al.* 2007), balanced by increased mortality as a result of voracious but risky foraging (Arnqvist and Henriksson 1997; Higgins and Rankin 2000). The relative importance of these factors and the trade-offs involved are still poorly understood in spiders.

It has also been hypothesized that large size is favored in females because they may outgrow their predators (Hormiga *et al.* 2000; Higgins 2002). For this hypothesis to hold, it remains to be demonstrated that the cost imposed by voraciousness on juvenile mortality is outweighed by substantially lower mortality of larger adult females.

Which factors contribute to the large interspecific variation in female body size is not well known. Why have females in some spider species grown into giants, while females in others have not (Hormiga *et al.* 2000)? It has been argued that differences in prey availability (i.e. habitat productivity), habitat structure, foraging mode, and phenology are important constraints on the fecundity benefits of large size and thus determine the reproductive schedule and output (Enders 1976; Craig 1987; Head 1995). An interesting example of probable physiological and ecological constraints on female size is provided by the aquatic spider *Argyroneta aquatica*. In this species, females are smaller than males. Females have to collect air more frequently than males and appear to be limited by the costs of building air bells, the size of which is correlated with female body size (Schütz and Taborsky 2003).

7.4.2 Selection on male body size

We discuss a number of non-exclusive hypotheses for the adaptive significance of small male size in spiders. All major hypotheses are based on one or more of the following premises: (1) when population densities are low, selection for large size by male–male interference competition is relaxed; (2) in general, but most importantly when population densities are low, receptive females are scattered, thus limiting resources, and selection must favor those male morphologies or strategies that are better for reaching females and confer an advantage either in scramble competition or in anti-predatory behavior; and (3) females may impose direct selection on male size via either sexual cannibalism or mate choice.

The sexual-cannibalism hypothesis

Sexual cannibalism is relatively common in spiders (Elgar 1992). The original sexual-cannibalism hypothesis tried to explain the evolution and maintenance of extreme female-biased SSD (Darwin 1871). According to this hypothesis, small males have an advantage because they may be more agile and thus faster at escaping female attacks, or may fall below a presumed threshold above which females can detect approaching males or consider them valuable prey (Darwin 1871; Elgar 1992). This hypothesis has been refuted in all direct and indirect tests conducted to date in highly dimorphic species (reviewed in Foellmer and Fairbairn 2004; but see Elgar and Fahey 1996), and in less dimorphic species larger males are actually better at escaping female attacks (e.g. Persons and Uetz 2005; reviewed in Foellmer and Fairbairn 2004).

Hypotheses based on low population densities and/or early maturation

The next three hypotheses trying to explain extreme SSD in spiders are based on related assumptions. The protandry hypothesis posits that maturing earlier than females is adaptive for males because males that mate first with a female will sire most or all of her offspring (Morbey and Ydenberg 2001). This should lead to female-biased SSD assuming a positive correlation between development time and adult size (Roff 2002). In most spider species males indeed mature earlier than females (Jackson 1986; Maklakov *et al.* 2004). The Ghiselin–Reiss hypothesis (Ghiselin 1974; Reiss 1989) posits that in species living at low densities the probability of males congregating around receptive females is so low that male–male interference competition is relaxed, thus conferring no advantage to larger males (Andersson 1994). Selection by scramble competition to reach females would then favor a morphology adapted for mate-searching and early maturation at a smaller size to increase the probability of survival to adulthood (Ghiselin 1974; Andersson 1994). The differential mortality model (Vollrath and Parker 1992) is also based on the assumptions of low densities and early maturation. However, in this model the lower densities only pertain to males of sedentary spiders. This hypothesis states that in species in which females stay relatively sedentary throughout their life (e.g. web-builders and crab spiders), males suffer from higher (size-independent) mortality than females during mate search, as compared to actively hunting species in which male and female mortality would be similar (Vollrath and Parker 1992). This would relax male–male interference competition in sedentary species and in turn viability selection would favor reduced growth and early maturation at male small size to increase the number of males reaching females.

Protandry could confer an advantage to males if females are not overly choosy (Maklakov *et al.* 2004) or if male interference competition were truly uncommon. Whereas in several spider species females appear to mate indiscriminately with respect to male body size (e.g. Kotiaho *et al.* 1996; Maklakov *et al.* 2004), in many other species, ranging from species with male-biased SSD to orb-weavers with extreme female-biased SSD, male–male interference competition is common and probably favors larger males because of their advantage in direct combat (reviewed in Foellmer and Fairbairn 2005a). Thus, the assumption of relaxation of male–male interference competition seems not to hold in many cases. In addition, females in many species mate multiply, and recent evidence suggests that sperm mixing is the most common pattern of sperm use by females (e.g. Schneider *et al.* 2000), although males may guard or plug females to prevent other males from mating (Cohn *et al.* 1988; Foellmer and

Fairbairn 2003; Fromhage and Schneider 2006). No study has yet attempted to demonstrate the adaptive significance of protandry in spiders, which requires showing that early-maturing males indeed have higher reproductive success (del Castillo and Núñez-Farfán 1999).

The Ghiselin–Reiss hypothesis predicts that small male size may also be favored in scramble competition if adult males have to feed regularly to maintain stamina, because lower metabolic requirements enable small males to spend more of their time and energy searching for females and mating (Reiss 1989; Blanckenhorn 2000). However, in most spider species adult males rely largely on energy reserves and rarely feed (Foellmer and Fairbairn 2005b). In such species large males may actually have an energetic advantage because of their lower mass-specific metabolic rate, or if energy-storing capacity scales hyper-allometrically with size (Calder 1984). Foellmer and Fairbairn (2005b) did not find a size-dependent energetic advantage in *Argiope aurantia*, a species in which adult males do not feed. Such an effect has yet to be demonstrated. The highly dimorphic crab spider *Misumena vatia* seems to fit the Ghiselin–Reiss hypothesis (LeGrand and Morse 2000). Population densities are low, males feed regularly, do not engage in fights over females, and can mate with several females (LeGrand and Morse 2000; Anderson and Morse 2001). Also, in species of the orb-weaver genus *Metepeira*, males are relatively smaller than females in populations of lower densities (Piel 1996).

There is major lack of support for the differential-mortality hypothesis, which predicts that sit-and-wait predators exhibit more pronounced female-biased SSD than active hunters and assumes a stage-dependent mortality difference between males and females (Prenter *et al.* 1997, 1998; Moya-Laraño *et al.* 2002a, Walker and Rypstra 2003). However, male mortality during mate search has been suggested to be high (approximately 80%) in some highly dimorphic web-building spiders (e.g. Andrade 2003). More studies are needed to elucidate whether high travel mortality is common in other spiders as well and whether it can balance sexual selection for large size due to interference competition.

The gravity hypothesis

The gravity hypothesis (Moya-Laraño *et al.* 2002a) posits that in species in which females live in high places where males must climb to reach them, males will be selected to be small, either because they have an advantage in scramble competition by reaching females faster or because they escape predators more efficiently while moving on vertical surfaces. Due to the constraint imposed by gravity, a simple biomechanical model based on physical first principles shows how, all other things being equal, the speed at which an animal can climb (v) is inversely proportional to its body length (L) or body mass (M). Relevant data are available for two highly dimorphic orb-weavers. In *Nephila clavipes*, in which females live in high to very high places, smaller males were more likely to reach females (Linn 2001). However, in *A. aurantia* large male size was actually favored in one of two populations (Foellmer and Fairbairn 2005b). This apparent paradox might be explained by the complex empirical relationship found between climbing speed and body size in spiders, which we now investigate here.

We conducted an experiment to investigate whether an animal shaped like a spider exhibits a negative relationship between climbing speed and body size, as predicted by the gravity hypothesis (J. Moya-Laraño, M. Foellmer, and C. Allard, unpublished work). Using a large body-mass range of spiders of different instars (0.2–881.4 mg) and phylogenetic affiliation we found surprisingly that the empirical relationship between body size and climbing speed is not purely negative but curvilinear (Figure 7.5), with an optimal body size for climbing at approximately 42.5 mg (approximately 7.6 mm; Edwards 1996), beyond which the negative relationship predicted by the gravity hypothesis arises. This may explain why Foellmer and Fairbairn (2005b) found positive directional selection on male body size during mate search in *A. aurantia*, as males weigh only approximately 20 mg.

Furthermore, we found a curvilinear pattern of SSD (log(male body length) against log(female body length)) in spiders that live in habitats high off the ground and a linear pattern in spiders that live at ground level for the data-set of Moya-Laraño *et al.* (2002a). The pattern of SSD is

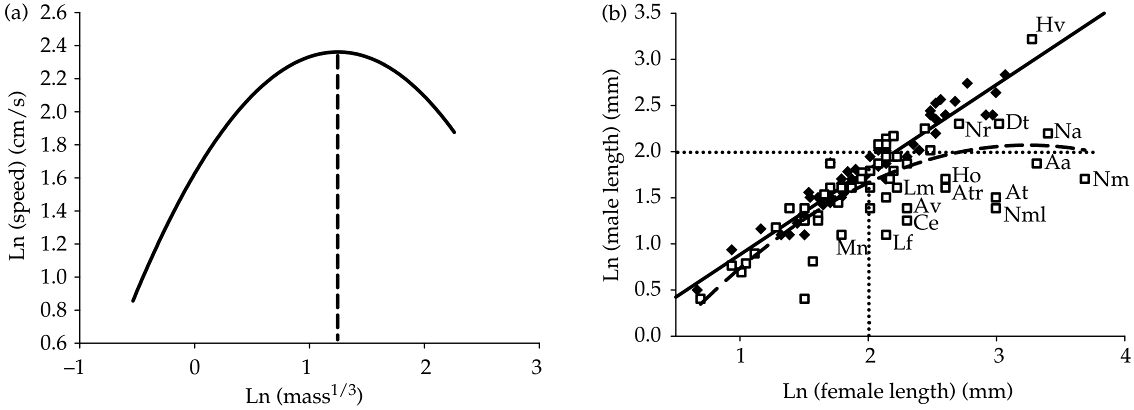

Figure 7.5 Empirical test of the gravity hypothesis and the influence of the (curvilinear) pattern on spider SSD. (a) Relationship between body size (ln(mass)) and ln(climbing speed) in spiders of variable instars. The fitted curve is: $\ln(\text{speed}) = 1.63 + 1.18{*}\ln(\text{mass}^{1/3}) - 0.05{*}\ln(\text{mass}^{1/3})^2$. Both the linear and quadratic mass terms are significant. The dashed vertical line shows the optimal body mass for climbing (approximately 42.5 mg). This relationship predicts a curvilinear pattern of SSD in spiders from habitats located high off the ground. (b) A plot of ln(male size)−in(female size) (as used throughout this book) for spiders living at or close to ground level (low habitats; ◆, solid line) and high above ground level (high habitats; ❐, dashed line). The horizontal and vertical dotted lines show the male and female body lengths respectively, which correspond to the optimal climbing speed (approximately 7.6 mm) extrapolated from (a). Note how in high-habitat spiders the curvilinear trend starts very close to the female threshold, as would be predicted by the pattern of climbing speed, and how beyond this threshold for all species but one (Hv) male sizes fluctuate around the threshold (horizontal dotted line). The linear (least-squares) model for low-habitat spiders is: $\ln(\text{male body length}) = 0.92{*}\ln(\text{female body length})$ ($P < 0.0001$). The curvilinear model for high-habitat spiders is: $-0.72 + 1.72{*}\ln(\text{mass}) - 0.27{*}\ln(\text{mass})^2$ (both the linear and quadratic mass terms were significant). Note that spiders from distant taxa are responsible for the curvilinear pattern: Araneidae (Aa, *Argiope aemula*; At, *A. trifasciata*; Atr, *Araneus trifolius*; Av, *A. versicolor*; Ce, *Cyrtophora exanthematica*; Nr, *Neoscona rufofemorata*), Nephilinae (Ho, *Herennia ornatissima*; Lf, *Leucauge fastigiata*; Na, *Nephila antipodiana*; Nm, *N. maculata*; Nml, *N. malabarensis*), Pisauridae (Dt, *Dolomedes tenebrosus*), Theridiidae (Lm, *Latrodectus mactans*), Thomisidae (Mn, *Misumenops nepenthicola*), and that there is one clear outlier (Hv, *Heteropoda venatoria*) which, like all Sparassidae, has a very flat body, lateral legs and abundant fine hair (*scopulae*), suggesting that this species may be highly adapted to climb.

linear in both spider groups up to the 7.6-mm threshold for female body size (the *x* axis), beyond which the correlation between male and female body size vanishes for high-habitat spiders, although it remains in ground-dwelling spiders (Figure 7.5). Thus, the concave relationship between male and female body size (Figure 7.5b) suggests that SSD in spiders living in high habitats is indeed mediated by male climbing ability. Our analyses therefore support the gravity hypotheses and also explain the lack of support for the hypothesis in some instances (Foellmer and Fairbairn 2005b). Furthermore, the gravity hypothesis provides an explanation for why male and female size are uncoupled in large orbicularians. However, climbing is not the only kind of movement necessary for spider males when females live in tall places. Males in this context have to also walk (or run) horizontally, bridge (walk upside-down from one branch to another using a silk strand), and drop (from a higher to a lower place using a silk strand), and all these different types of movement should affect an optimal male body size.

Copulatory and post-copulatory processes

There is evidence for additional factors that could affect the evolution of SSD in the context of mating. In the highly dimorphic orb-weaver *Nephila edulis*, small males have been shown to employ a more efficient mating tactic in the absence of (large) competitors that confers a fertilization advantage (Schneider *et al.* 2000). However, larger males often prevent smaller ones from mating in *N. edulis*, which might help explain the large variability in male size in this species (Schneider and Elgar 2005).

7.4.3 The adaptive significance of SSD: integrating male and female effects

It is important to remember that it is the difference in net selection on size between males and females that will ultimately determine SSD (the differential equilibrium hypothesis of SSD; Blanckenhorn 2000; Preziosi and Fairbairn 2000; Chapters 1, 9, and 10). Net selection is the sum of all effects during all relevant selection episodes (Arnold and Wade 1984b). Such data do not exist for any spider species so far and will be very difficult to obtain (Foellmer and Fairbairn 2005a). In most cases data are available for either females or males (e.g. Higgins 2002; Foellmer and Fairbairn 2005a). One exception is the burrowing wolf spider *Lycosa tarantula*. In spite of its moderate to low SSD (based on carapace width), selection acts quite differently on adult males and females. Whereas large carapace width confers higher male mating success (C. Fernández-Montraveta and J. Moya-Laraño, unpublished work), small carapace width confers lower mating success in females (Moya-Laraño *et al.* 2003) but favors females in fights over burrows and territories (Fernández-Montraveta and Ortega 1993; Moya-Laraño *et al.* 2002b). That is, body size seems to be under directional selection in males but under net stabilizing selection from opposing selective forces (sensu Preziosi and Fairbairn 2000) in females. Thus, even in a species with moderate SSD, selective pressures can act very differently on each sex.

7.5 Summary and conclusions

We have shown that estimation of the direction and magnitude of SSD in spiders strongly depends on the size measure chosen, but also that this has probably no large effect in phylogenetic comparative analyses. Whenever possible the use of carapace width is recommended, as this structural measure is common and less affected by condition than body mass or length. Our updated evaluation of body-size allometry supports previous work in demonstrating that spiders do not exhibit allometry consistent with Rensch's rule. Instead, females appear to have diverged more in size over evolutionary time, and male and female body size show relatively uncorrelated coevolution, which is unusual for animals. This finding requires further research. Quantitative genetic analyses of sex-specific growth strategies are urgently needed if we are to understand the role of genetic constraints in the evolution of extreme SSD. Although much progress has been made over the past 10 years, our knowledge is very patchy with regard to the various hypotheses proposed to affect sex-specific selection. So far, fecundity selection favoring large size in females and gravity selection favoring small size in males are probably the only hypotheses that have some general explanatory power. Nevertheless, many different processes are operating in different species and SSD requires a case-by-case explanation. Importantly, attempts should be made to gain a comprehensive view of selection operating on male and female size in any given species. We hope that this review will stimulate such work.

7.6 Acknowledgments

We would like to thank W. Blanckenhorn, D. Fairbairn, and T. Székely for the invitation to the workshop, J. Dykeman for helping with the data entry, and E. de Mas for the *Lycosa tarantula* picture.

7.7 Suggested readings

Blanckenhorn, W.U. (2005) Behavioral causes and consequences of sexual size dimorphism. *Ethology* **111**, 977–1016.

Foellmer M.W. and Fairbairn, D.J. (2005) Competing dwarf males: sexual selection in an orb-weaving spider. *Journal of Evolutionary Biology* **18**, 629–641.

Moya-Laraño, J., Halaj, J., and Wise, D.H. (2002) Climbing to reach females: Romeo should be small. *Evolution* **56**, 420–425.

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SECTION II

Micro-patterns: case studies of patterns and evolutionary processes within and among species

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Introduction

Wolf U. Blanckenhorn

The first section of this book comprises a number of chapters comparing patterns of variation in sexual size dimorphism (SSD) at the higher, macroevolutionary level. The second section takes a microevolutionary perspective in presenting a collection of case studies within species or groups of closely related species. This follows the logic implicit in much of the research in evolutionary ecology, in that macroevolutionary patterns should reflect microevolutionary processes. Consequently, many of the adaptive hypotheses and patterns found or tested via comparative analyses in Section I reappear in Section II, now being tested empirically as processes occurring within and among populations. We have assembled a total of eight fine case studies on a variety of taxa.

I start with some general methodological issues that should help readers appreciate the effort required when investigating sexual dimorphism intraspecifically. It is widely agreed that fecundity selection in females and sexual selection in males are the major evolutionary forces selecting for larger body size in many organisms. Large body size often increases mating success due to intrasexual (largely male–male) competition or female choice (Andersson 1994). Clutch size and sometimes also egg or offspring size, and consequently female reproductive success, also typically increase with body size, at least in ectotherms (Darwin's fecundity-advantage hypothesis; Honek 1993; Preziosi *et al*. 1996). Even larger females of warm-blooded species produce not necessarily more, but often better-quality offspring (Clutton-Brock 1988). Opposing such fecundity and sexual selection are potential disadvantages of large body size in terms of viability that are frequently invoked but for which evidence is comparatively rare in the literature (Blanckenhorn 2000). Within some limits set by genetic (Reeve and Fairbairn 1996), phylogenetic (Cheverud *et al*. 1985), developmental (Badyaev 2002), or physiological (Peters 1983) constraints, the three major selective forces are thought to equilibrate differentially in the sexes, resulting in the SSD observed in a particular species (Price 1984a; Arak 1988; Schluter *et al*. 1991; Blanckenhorn 2000; Chapter 1 in this volume).

Although this so-called differential equilibrium model for the evolution of SSD within species seems widely accepted (Andersson 1994), for any particular species it requires demonstration of the complete sex-specific costs and benefits of body size (see depictions in Figures 1.3 and 10.1). This is very difficult and hence rare, but can, should be, and is occasionally attempted (see Price 1984b; Koenig and Albano 1987; Grant 1985; Ward 1988; Harvey 1990; Björklund and Linden 1993; Badyaev *et al*. 2000; Fedorka and Mousseau 2002; Olsson *et al*. 2002; Boutellier and Perrin 2005; and Chapters 8–10 for excellent examples of such studies; see also Table 10.3). There are essentially two avenues to obtain the necessary estimates of size-dependent lifetime fitness, reflecting the well-known life-table approaches in ecology. One way is to conduct longitudinal studies of individuals over their whole life, in which case one can estimate the entire lifetime reproductive success of a set of males or females in relation to their body size. This is clearly the preferred and most complete approach, and it has been successfully applied particularly in larger vertebrates that can be marked and followed in the wild with relative ease (Clutton-Brock 1988). Naturally, such an approach is difficult to execute in small animals, particularly those with complex life cycles such as frogs or holometabolous insects, because they cannot be followed easily in nature and because the size measure used in juveniles will necessarily differ from that used in adults. The alternative is a cross-sectional, piecemeal approach in which the effects of body size on the standard fitness components (survival, fecundity, mating success) are investigated for a sample of individuals only at a particular life stage. Several such estimates at various stages, often called selection episodes, for various fitness components can ultimately be integrated, in the ideal case yielding a measure equivalent to lifetime reproductive success for a given species. This is the approach often taken in studies of selection in the wild for smaller and abundant species by applying the standard methodology of estimating selection differentials or gradients (Arnold and Wade 1984a, 1984b; Endler 1986; Brodie *et al*. 1995). Both the longitudinal and cross-sectional approaches can be, and in practice often are, studied phenomenologically; that is, without necessary regard to the behavioral means producing the effect of body size on reproductive success (e.g. whether large males have an advantage in sexual selection due to male–male competition or female choice), although additionally studying the underlying, behavioral mechanisms is certainly more complete (Blanckenhorn 2005).

Cross-sectional estimation of several separate selection episodes and fitness components makes a number of assumptions if it is to correctly reflect overall selection over the entire lifetime of an organism in a variable environment (see Chapters 9 and 10). First, it assumes that any sample correctly reflects the age structure of the population, thus including older and younger individuals. Second, it assumes that there are no systematic effects of age on the fitness component estimated; otherwise, for example, early fecundity may systematically overestimate lifetime fecundity if, say, fecundity diminishes with age. Third, selection depends strongly on the environmental conditions at the time. Therefore multiple (e.g. seasonal) samples at various times or environmental conditions at more than one place, or in several populations, are necessary to encompass the possibility of spatiotemporal variation in selection (Istock 1981). Assessment in more than one environment is particularly advised for any experimental estimation of selection in the field or laboratory (as emphasized by all the Chapters 8–11). Fourth, selection at any life stage is contingent upon the probability of an individual reaching this life stage (e.g. adult success is contingent upon surviving the juvenile phase), so the magnitude of selection has to be adjusted for this probability (Blanckenhorn *et al*. 1999b; Chapter 10). If these assumptions are not fulfilled, biased estimates of selection can result. Of course, any natural (e.g. time of season) or experimentally manipulated extraneous variable (e.g. food availability) that can affect selection intensity can be entered into the statistical model to arrive at an average estimate of selection over several environments (Arnold and Wade 1984b).

With these methodological caveats in mind it should be easier for the reader to understand and at the same time appreciate the case studies comprising section II of this book. The first three chapters (Chapter 8–10) by Fox *et al*., Fairbairn, and Blanckenhorn, represent some of the most comprehensive single-species studies ever undertaken to determine the adaptive significance of SSD and test the differential equilibrium hypothesis. All three happen to be studies of insects, which generally require a cross-sectional approach, as argued above, but note that Preziosi and Fairbairn 2000 (see also Chapter 9) managed to obtain estimates of adult lifetime reproductive success even for a small animal such as the water strider *Aquarius remigis*. Blanckenhorn (Chapter 10) briefly reviews other available studies in the literature, including some on vertebrates (op. cit.). Chapter 11 by Delph is also a single-species study, in fact the only plant chapter in this volume, nevertheless showing that SSD is an issue in dioecious plants as well. This chapter also addresses differential selection on males and females, but, together with Chapters 8 and 9, additionally emphasizes the role of the underlying genetic architecture in potentially constraining the expression of sexual dimorphism in particular traits in case of strong genetic correlations among them (Lande 1980; Reeve and Fairbairn 1996). Chapters 9 and 11 further emphasize that dimorphism may strongly vary among traits because often selection acts on components of body size rather than overall body size, in which case both direct and correlated responses to selection affect the evolution of body size and shape. Together with Chapter 10, Chapter 11 also illustrates the value of artificial selection in this context. Taken together, the single-species case studies in Chapters 8–11 demonstrate that the conceptual framework of SSD in any particular species being the (adaptive) outcome of complex sex-specific selection, as depicted in Figures 1.3 and 10.1, is by and large at least qualitatively correct, despite the fact that a quantitative match between current selection pressures and current SSD is not often shown (Blanckenhorn 2000). The latter is perhaps not so surprising given the many possible methodological pitfalls when measuring selection (discussed above) and potential constraints on attaining SSD equilibrium (Chapter 1). Chapters 8–11 all emphasize the necessity of incorporating the investigation of constraints into any study of the adaptive significance of SSD.

Chapters 12–15 carry the question up one level of biological organization in comparing populations or closely related species rather than emphasizing measures of selection within populations. Chapter 13 by Kalmbach and Benito investigates the relationship between SSD and juvenile mortality in birds, emphasizing that selection may not directly target body size per se, but instead correlated life-history traits such as development time or growth rate. Chapter 12 by Capellini attempts to link the extent of dimorphism in body size and fighting structures in a number of closely related African antelopes to the intensity of sexual selection experienced by them and the productivity of their habitat. In so doing, this chapter reiterates some of the adaptive hypotheses investigated in the broader-scale comparative studies of section I. The latter is also true for Chapter 14 by Roitberg, who investigates latitudinal and altitudinal variation in body size and, once again, Rensch's rule, among populations of the widespread Old World lizard *Lacerta agilis*; and for Chapter 15 by Kratochvíl and Frynta, who again use comparative methods (in this case trait mapping) to reconstruct the historical evolution of SSD and associated morphological and behavioral traits among closely related gecko species.

Thus, it is evident that the chapters in Section II utilize a variety of approaches including studies of geographic variation, quantitative measures of selection in wild populations, experimental manipulations of body size or environmental factors in natural or laboratory populations, and descriptions of underlying quantitative genetic architecture. This beautifully exemplifies the multi-faceted approaches possible and even necessary in research on SSD.

CHAPTER 8

Variation in selection, phenotypic plasticity, and the ecology of sexual size dimorphism in two seed-feeding beetles

Charles W. Fox, R. Craig Stillwell, and Jordi Moya-Laraño

8.1 Introduction

Most animals show some degree of sexual size dimorphism. However, the degree and direction of dimorphism vary substantially among taxa and even among populations within species. Major progress has been made in the study of sexual size dimorphism in the last decade. Yet detailed studies on the proximate and ultimate causes of sexual size dimorphism in a single animal taxon are few (e.g. Chapters 9–20 in this volume). In this chapter we examine sexual size dimorphism in two well-studied species of seed beetle that differ in the direction of dimorphism (female-biased and male-biased) and that show substantial variation in dimorphism among populations within species. Seed beetles are an excellent system for studies of evolutionary biology because of their ease of laboratory rearing, allowing for large-scale studies that are impractical with many other organisms. We review studies on the sources of selection on body size, how this selection varies between species and among populations, and the consequences of this variation for the evolution of sexual size dimorphism.

8.2 Selection on male body size in *Stator limbatus* and *Callosobruchus maculatus*

In most insects, including seed beetles in the genus *Callosobruchus*, females are larger than males, presumably because of substantial fecundity selection on females. For insect species where males are larger than females the male-biased size dimorphism is typically associated with male–male interference competition that imposes selection for large male size. However, males are larger than females in the genus *Stator* despite an absence of direct male–male conflict. Laboratory experiments (Savalli and Fox 1998b) show that, when presented simultaneously with both large and small males, females are more likely to mate with the large male, but the effect is small and appears to be due to scramble competition among males rather than active female choice. However, this slight advantage of large males in scramble competition is likely offset by scramble competition favoring small males when flying (see the discussion on temperature, below).

So why are males larger than females in *Stator limbatus*? We have identified two sources of selection favoring large males: fecundity selection mediated via nuptial gifts, and effects of male body size on female receptivity to future matings.

8.2.1 Fecundity selection

Like many insects, male seed beetles transfer nuptial gifts to females in the form of a large volume of seminal fluid (Takakura 1999). In *Callosobruchus maculatus*, virgin males contribute 6–10% of their body mass to females during mating (Fox 1993a; Savalli and Fox 1998a), although the proportion of their mass transferred declines substantially in subsequent matings (Fox *et al.* 1995; Savalli and Fox 1999b). Male *S. limbatus* produce similar-sized ejaculates, averaging approximately 7% of their mass (Moya-Laraño and Fox 2006). For all seed-beetle species in which nuptial gifts have been studied, substances in male ejaculates are incorporated into female eggs and somatic tissues (e.g. Boucher and Huignard 1987). Females treat these male-derived nutrients as a food source: females with limited access to food, or access to only low-quality food, increase their mating rate (Takakura 2004). Male ejaculates can also be a source of water for females (Arnqvist *et al.* 2005). These male nuptial gifts appear to have positive effects on female reproduction. For example, studies manipulating female mating frequency generally demonstrate that multiply mating females have higher fecundity (Fox 1993b; Savalli and Fox 1999a; Wilson *et al.* 1999; but see Arnqvist *et al.* 2005), increased adult lifespan (Fox 1993b; but see Savalli and Fox 1999a), and their egg size declines more slowly with age (Wasserman and Asami 1985; Fox 1993a), all consistent with females using materials in male nuptial gifts for egg production and somatic maintenance. Also, females that mate with non-virgin males (which produce smaller ejaculates than virgin males) have lower fecundity and are more likely to remate than are females that mate with virgin males (Savalli and Fox 1999a), an effect not likely due to sperm limitation.

Male nuptial gift size is positively correlated to male body size in *S. limbatus*, driving substantial fecundity selection on male body size (Savalli and Fox 1998b; Moya-Laraño and Fox 2006). Females mated to large males lay more eggs than do females mated to small males, and the effect of male body size on female fecundity is nearly as great as the effect of female body size on her own fecundity (partial R^2 is approximately 75% for both effects; Savalli and Fox 1998b). When pairs are confined together until death the total mass lost through a male's lifetime explains 32% of the variance in female fecundity, whereas female mass loss explains 36% of female fecundity, suggesting that males are contributing much of the biomass used by females to make eggs. However, the relative effects of male and female size on female fecundity varies among oviposition hosts (Czesak and Fox 2003; Fox and Czesak 2006) and among studies. This fecundity selection on male size is clearly mediated by the size of the male nuptial gift. Using path analysis, Moya-Laraño and Fox (2006) showed that first male size has no direct effect on female fecundity. Instead, the entire effect is via the body size → ejaculate size → female fecundity pathway. Thus, in contrast to many species (but see Vahed 1998) fecundity selection acts quite substantially on male *S. limbatus* via nuptial gifts and this fecundity selection on males is similar in intensity to fecundity selection acting on females.

Although male nuptial gift size is also large and positively correlated to male body size in *C. maculatus* (Savalli and Fox 1998a), fecundity selection on male body size appears to be much weaker in *C. maculatus* than in *S. limbatus*. For example, the partial R^2 for the male size effect is only about one-third as large as that for the effect of female size on her own fecundity (Savalli and Fox 1999b). Using a different population of *C. maculatus*, Eady and Brown (2000) found a negative relationship between male size and female fecundity, whereas two further studies failed to find any relationship between male body size or nuptial gift size and female fecundity (Edvardsson and Tregenza 2005; Fox *et al.* 2007). Although nuptial gift size likely affects female reproduction and adult survival in *C. maculatus*, variation in gift size does not appear to mediate strong fecundity selection on male body size. This potentially explains the large difference in sexual dimorphism between *S. limbatus* and *C. maculatus* but raises the intriguing question of why *S. limbatus* males experience substantial fecundity selection and male *C. maculatus* do not when both species produce similarly sized ejaculates that are positively correlated with body size.

8.2.2 Female receptivity to remating

A second source of selection on male body size in *S. limbatus* is through effects of male size on female post-mating behavior. Although females show no active preference for large over small males during their first mating, females that mate with larger males are less likely to accept a second mate and have a longer refractory period before remating (Savalli and Fox 1998b; Moya-Laraño and

Fox 2006). Although sperm competition has not been studied in *S. limbatus*, second-male sperm precedence is very high in other seed beetles (Eady 1994, 1995; Eady *et al.* 2004). Thus, smaller males are likely to get fewer fertilizations than are larger males. However, a recent analysis demonstrated that nuptial-gift size has little effect on female receptivity: females were more likely to remate if the first male was small or the second male large, regardless of the size of the nuptial gift (Moya-Laraño and Fox 2006). Moreover, females mating with larger second males laid more eggs independently of the ejaculate size transferred by these males, suggesting some kind of post-mating sexual selection acting on male body size (Moya-Laraño and Fox 2006).

In contrast to *S. limbatus*, receptivity of female *C. maculatus* is not influenced by male body size (Savalli and Fox 1999b). Females are more likely to remate after mating with a non-virgin male (suggesting that male nuptial gifts do indeed affect female behavior; Savalli and Fox 1999a), if their initial copulation is short (and thus the amount of ejaculate transferred is small; Edvardsson and Canal 2006), and when food is restricted (Savalli and Fox 1999b). However, we have no evidence that this foraging for ejaculates translates into significant selection on male nuptial gift size or male body size.

8.3 Within-species variation in sexual size dimorphism

The difference in sexual size dimorphism between *Stator* and *Callosobruchus* appears to be due, at least in part, to differences in (1) fecundity selection and (2) sexual selection on male body size. However, sexual dimorphism and body size also vary substantially among populations within species (Kraushaar and Blanckenhorn 2002; Blanckenhorn *et al.* 2006; see Chapter 6). Numerous hypotheses have been proposed to account for variation in dimorphism. The most common of these is that sexual selection varies among populations (e.g. Blanckenhorn *et al.* 1995; reviewed in Fairbairn 2005). Alternatively, abiotic and other biotic factors may have different effects on males compared with females, either because the fitness consequences of body size differ between males and females or because the sexes differ in the degree of plasticity they exhibit in response to climatic or ecological variables (Fairbairn 2005; Blanckenhorn *et al.* 2006; Stillwell and Fox, in press; see Chapter 6). For example, in *S. limbatus*, body size and sexual size dimorphism vary with latitude—beetles are smaller but more dimorphic at lower latitudes (Figure 8.1). This cline in dimorphism reflects genetic variation in body size among populations (Amarillo-Suárez and Fox 2006) and occurs because females exhibit a steeper latitudinal cline in body size than do males (R.C. Stillwell, G.E. Morse, and C.W. Fox, unpublished work), suggesting that males and females are responding differently to selection imposed by abiotic and biotic factors that covary with latitude.

We explored the potential causes of systematic geographic variation in *S. limbatus* body size and sexual size dimorphism by testing whether climatic variables (based on weather-station data) and seed size can explain the observed latitudinal clines (R.C. Stillwell, G.E. Morse, and C.W. Fox, unpublished work). In contrast to many other studies examining latitudinal clines in body size, the latitudinal cline in *S. limbatus* body size is not correlated with a gradient in mean annual temperature but instead with host-plant seed size

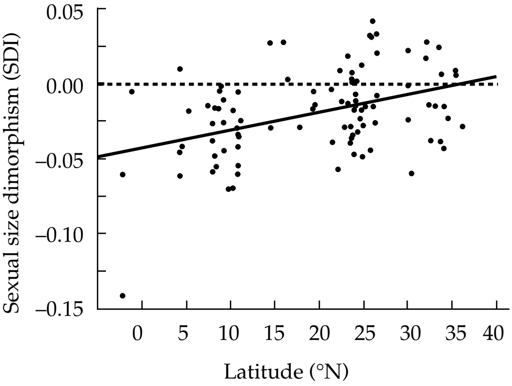


Figure 8.1 The latitudinal cline in sexual size dimorphism (pronotum width), estimated as (mean size of the larger sex/mean size of the smaller sex) − 1, made positive when females are the larger sex and negative when males are the larger sex (the SDI statistic of Lovich and Gibbons 1992), in the seed beetle *S. limbatus*. The dashed line indicates the point where populations are monomorphic (no dimorphism). Latitudes to the left of zero are located south of the equator (°S) while latitudes to the right of zero are located north of the equator (°N). Beetles are larger, but also less sexually dimorphic (the regression line approaches the dashed line), at higher latitudes. Data are based on field collections from 95 localities throughout the New World (R. C. Stillwell, G. E. Morse, and C. W. Fox, unpublished data).

(beetles are larger when adapted to large-seeded hosts), moisture/humidity (beetles are smaller in more moist/humid locations), and seasonality (beetles are larger in locations where seasonality is most pronounced). Only humidity covaries (positively) with geographic variation in sexual size dimorphism, but the cline in dimorphism persists even after removing the humidity effect, suggesting that other environmental variables are responsible for producing this dimorphism cline.

8.3.1 Variation in selection on male and female size

Our latitudinal cline study suggests a variety of ecological variables that may have effects on the fitness consequences of male compared with female body size, including host-plant characteristics (e.g. seed size and possibly seed quality), seasonality (including seasonal variation in temperature), and humidity. Below we explore how these variables affect selection on body size in *S. limbatus* and *C. maculatus* and, most importantly, examine whether these variables have different effects on the fitness consequences of male and female size.

Host plant affects selection on male and female body size

Both *C. maculatus* and *S. limbatus* are generalist feeders. *S. limbatus* uses more than 70 legume species as hosts. The natural diet of *C. maculatus* is less broad; their natural hosts are all in the genus *Vigna*, but beetles have colonized a wide variety of agricultural crops to which they rapidly adapt. These various hosts of *S. limbatus* and *C. maculatus* vary substantially in seed size and quality. Beetles develop from egg to adult completely inside a single seed so the resources available for development depend greatly on seed size and the density of larvae inside the seed. Beetle populations have evolved considerably in growth, life history, and behavior in response to their local hosts. For example, we commonly study a *C. maculatus* population from Burkina Faso (BF) adapted to the large-seeded cowpea (*Vigna unguiculata*) and one from South India (SI) adapted to the small-seeded mung bean (*Vigna radiata*). Although females are larger than males in both populations, the SI population is more sexually dimorphic than the BF population (Stillwell and Fox in press). In a recent experimental evolution study, replicate SI populations were allowed to adapt to cowpea (the host of the BF beetles). These new cowpea-adapted beetles evolved to be smaller and less sexually dimorphic than the ancestral populations maintained on their native host (mung), consistent with the difference between the SI and BF populations (Messina 2004). Apparently the switch in rearing host changed the relative magnitude of selection on male and female body size, driving the evolution of sexual dimorphism. Exactly how selection changed is unknown but female size evolved faster than male size, suggesting greater sensitivity of female body size-mediated effects on fitness to larval competition and resource availability (Messina 2004).

Body size and sexual dimorphism also vary among host plants for *S. limbatus*. Two of the most common seeds used in the Sonoran desert of the southwestern USA are cat-claw acacia (*Acacia greggii*) and blue paloverde (*Parkinsonia florida*). Using path analysis, Fox and Czesak (2006) showed that this difference in selection on egg size indirectly affects the relative magnitude of selection on male versus female body size (Figure 8.2). When females lay their eggs on seeds of *A. greggii*, larval survival is very high and not affected by egg size. Because fecundity selection is of similar magnitude on male and female body sizes, total selection on male and female body sizes are nearly identical when eggs are laid on seeds of *A. greggii*. In contrast, when offspring are reared on seeds of *P. florida*, egg size affects offspring survival (larvae from small eggs die while trying to penetrate the seed; Fox and Mousseau 1996; Fox *et al.* 2001) and, consequently, directly affects parental fitness. Because egg size is affected by female size, there is selection on female body size through both the fecundity (body size → fecundity → fitness) and egg size (body size → egg size → fitness) paths. However, egg size is not correlated with male body size such that selection on egg size does not translate into indirect selection on male size. Thus, because of the difference in seed suitability for larval development, (1) total selection on male body size is much lower when eggs are laid on

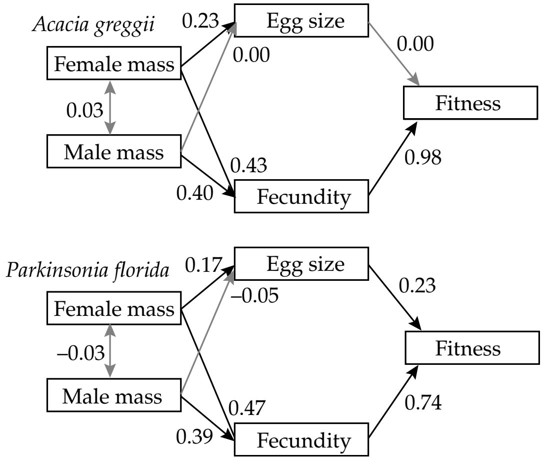


Figure 8.2 Path analysis showing how oviposition host affects the magnitude of selection on body size in the seed beetle *S. limbatus*. Black paths are statistically significant and gray paths are non-significant. Fitness is defined as the number of larvae produced that successfully survive until completely inside their host seed. All standard errors are less than 0.035. From Fox and Czesak (2006).

seeds of *P. florida* and (2) the host upon which females lay their eggs causes a large change in the relative magnitude of selection on male compared with female size by an amount similar in magnitude to the median total amount of directional selection observed in nature in studies of morphological traits (Kingsolver *et al.* 2001). This shift in relative selection on males and females is a consequence of where females lay their eggs, independent of any changes in male or female investment into reproduction, variation in sexual selection, or any other direct effects on adult beetles. It is caused by variation among hosts in offspring survival and not caused by differential mortality of males and females, large or small beetles, or any direct effect of male size on fitness. We suspect that variation among hosts in such indirect selection on body size is a major source of variation in selection on *S. limbatus* in nature.

Temperature affects selection on male body size

Although male seed beetles appear to experience very little direct contest competition for females, they are under intense (scramble) competition to find mates. Laboratory experiments with *S. limbatus* have demonstrated that selection favors small males because these males can reach potential mates more quickly than can large males. The advantage of being small is especially great at low temperature (20 compared with 30°C; J. Moya-Laraño, M. El Tigani El-Sayyid, and C.W. Fox, unpublished work). This strong selection against large males at low temperature is probably due to their decreased ability to initiate flight: at low temperature large males take off much more slowly than do small males, whereas there is no difference at high temperature. Because temperature and diel variation in temperature vary among *S. limbatus* populations, we interpret these scramble competition results as evidence that variation in temperature can alter the fitness consequences of male body size. Although females also fly to search for host seed pods, plants are sedentary, such that the selection for rapid take-off is likely to be less. The mechanism for the temperature effect on male flight is not yet known. However, if beetles generate metabolic heat to warm up flight muscles, smaller beetles may more quickly reach the minimum muscle temperature required to take off, a relationship observed for other insects (Harrison and Roberts 2000).

8.3.2 Sex differences in phenotypic plasticity in body size

Body size can be highly plastic in response to rearing conditions. Two of the most important environmental factors affecting plasticity in body size of ectothermic animals are diet and temperature (Nylin and Gotthard 1998; Angilletta and Dunham 2003). Variation among populations in sexual size dimorphism can be produced when environmental conditions vary among populations and males and females exhibit different responses to these environmental variables (differential-plasticity hypothesis; Fairbairn 2005).

Effect of temperature on sexual size dimorphism

In most ecotherms, body size increases with decreasing rearing temperature (Angilletta and Dunham 2003). Females and males generally exhibit plastic responses that are in the same direction but the sexes can differ in their sensitivity to rearing temperature, generating temperature-induced variation in dimorphism. In *C. maculatus*, males reared at 20°C were on average 63% larger than males reared at 35°C, whereas females were only 38% larger (Stillwell and Fox, in press). This creates substantial variation in sexual dimorphism across rearing temperatures (Figure 8.3). This plasticity is caused primarily by sex differences in growth rate: growth rate increased with rearing temperature but females grew approximately 25% faster than males when reared at 30°C and only approximately 9% faster when reared at 20°C (Stillwell and Fox, in press), a pattern observed for other arthropods (Blanckenhorn *et al.* 2007).

The effect of temperature on growth rate and body size typically differs between male and female insects (Chapter 20) but the causes of this difference are unknown. In beetles, temperature may have non-random effects on larval mortality of large and small phenotypes. The proportion of males to females emerging successfully declines with decreasing temperature and becomes significantly female-biased at 20°C. If smaller males are experiencing greater mortality at low temperature, then temperature-mediated non-random mortality could generate the observed temperature effect on dimorphism (Stillwell and Fox, in press). Size dimorphism likewise changes with temperature in dung flies, concurrent with a change in sex ratio of emerging flies, suggesting that temperature may likewise shift the relative magnitude of larval mortality of large and small flies (Blanckenhorn 1997a).

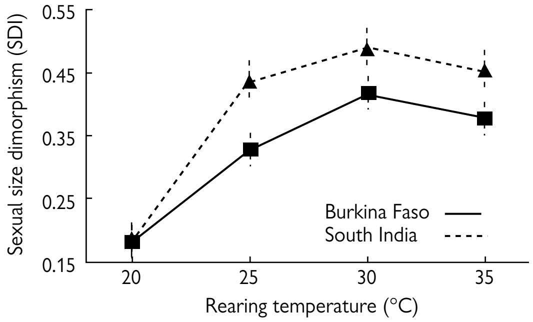


Figure 8.3 The effect of temperature on sexual size dimorphism of two populations of *C. maculatus*, estimated as (mean female size/mean male size) − 1. Dimorphism was calculated separately for each family, then averaged across families. The figure pools data from three different rearing hosts; rearing host did not affect dimorphism in this study (R.C. Stillwell and C.W. Fox, unpublished work).

Alternatively, temperature-induced variation in dimorphism could reflect greater canalization of female body size against environmental perturbation, which may be adaptive because of the large effect female body size on fecundity (Fairbairn 2005). Recent work on butterflies supports this hypothesis (Fischer and Fiedler 2000, 2001). Because male size has little effect on male fitness in *C. maculatus* (Savalli and Fox 1999b) male size might be less canalized and thus more susceptible to environmental conditions, as observed in our study. Interestingly, sexual size dimorphism does not appear to vary with temperature in *S. limbatus* (Stillwell and Fox 2005), the species for which body size has large effects on fitness of both males and females, consistent with the prediction of the adaptive canalization hypothesis.

Implications of phenotypic plasticity in body size for Rensch's rule

A common phenomenon observed in almost all animals is that male body size varies more than female size among species, or among populations within species, a pattern known as Rensch's rule (Fairbairn 1997; see Chapter 6). This pattern is generally assumed to be due to differences in selection on males and females but, when applied to variation within species, could also be generated by sex differences in plasticity of body size (Fairbairn 2005). To illustrate this point, Figure 8.4 depicts a plot of male size against female size for two populations of *C. maculatus* reared at a variety of temperatures (Stillwell and Fox, in press). Suppose that each rearing temperature represents a different field population and that these populations do not differ genetically in size but do vary in the temperatures that larvae experience during development. If our field populations varied in temperature only between 30 and 35°C we would conclude that female body size varies more among populations than does male body size, as the slope of the regression of male size against female size would be <1, opposite to Rensch's rule. In contrast, if our range of temperatures experienced in nature was <25°C we would conclude that male body size varies

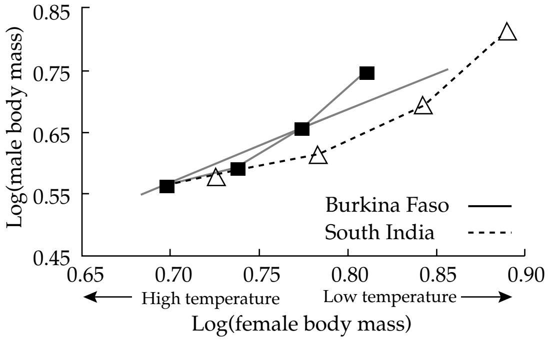


Figure 8.4 Reduced major-axis regression of log(male body size) on log(female body size) for two populations of *C. maculatus* reared at four different temperatures. Lines connect the four temperature treatments for each population. Small beetles are those reared at high temperature and large beetles are those reared at low temperature. The gray line denotes the linear reduced major-axis regression slope of 1.0 through all points. Note that the slope of the relationship changes non-linearly from <1 to >1 depending on which pair of temperatures we compare (R.C. Stillwell and C.W. Fox, unpublished work).

more among populations than does female body size, as the slope of the regression would be >1, following Rensch's rule. However, both conclusions would be wrong: our populations do not differ genetically in body size, only in the temperatures experienced by larvae during development. Hence, sex differences in plasticity can severely impact evaluations of Rensch's rule (Fairbairn 2005).

8.4 Evolutionary genetics of sexual size dimorphism

Adaptive hypotheses for the evolution of sexual size dimorphism assume that organisms can evolve quickly in response to changing patterns of selection. Indeed, when genetic and phenotypic variances are the same for the sexes, the rate of evolution of dimorphism will be a function of the difference in selection on male and female body size (Reeve and Fairbairn 2001; Badyaev 2002). However, some researchers have argued that patterns of dimorphism may be better explained by genetic constraints, such as phylogentic inertia, allometry, and genetic correlations between the two sexes (Cheverud *et al.* 1985; Cowley *et al.* 1986; Fairbairn 1997).

The degree to which body size of males and females can evolve independently can be quantified as a cross-sex genetic correlation, r_G. When r_G is non-zero selection on one sex will necessarily affect evolution of the opposite sex (Lande 1980a) and if r_G is high then sexual size dimorphism will evolve very slowly. When r_G is 1.0 then sexual dimorphism can evolve only if the genetic and/or phenotypic variance for body size differs between males and females (see below; Reeve and Fairbairn 2001; Badyaev 2002). Experimental studies have consistently demonstrated that between-sex genetic correlations (r_G) for body size are quite high (generally >0.80) but that they vary substantially among taxa (Roff 1997) and even within studies depending on the trait used to estimate body size (Cowley *et al.* 1986; del Castillo 2005; Chapter 9). For *C. maculatus* we estimated r_G for body mass using data from a variety of full-sib and half-sib experiments conducted by Fox and colleagues over the last 16 years. All estimates were >0.80 and only one estimate differed significantly from 1.0 (Fox 1994). Likewise, for *S. limbatus*, estimates of r_G were all >0.95 and not significantly less than 1.0, with one exception (Fox 1998). Also, r_G does not vary with temperature or host species (R.C. Stillwell and C.W. Fox, unpublished work); the between-sex r_G is approximately 1.0 at all temperatures and on all hosts upon which beetles were reared, suggesting that environmental effects on r_G are unlikely to be a major influence on the rate and trajectory of dimorphism evolution.

But how much do high genetic correlations constrain the evolution of sexual size dimorphism? High genetic correlations do not constrain males and females from ultimately attaining their 'optimal' body size unless $r_G = 1.0$ (Lande 1980a; Reeve and Fairbairn 2001), but r_G does affect the rate and trajectory of body size and dimorphism evolution (Fry 1996). Yet we know that dimorphism can evolve very quickly in *C. maculatus*, despite very high values of r_G: Messina (2004) demonstrated substantial evolution of dimorphism after just 40 generations of natural selection following a host shift. Why? First, r_G is only one of the important genetic parameters for the evolution of dimorphism. Despite high genetic correlations between the sexes, sexual size dimorphism can evolve when the heritability (h^2) or phenotypic variance (V_P) for body size differ between the sexes (Reeve and Fairbairn 1996, 2001; Badyaev 2002). It is common to find that genes have sex-specific effects in *Drosophila*, and several studies (including seed beetles) have shown that genetic architecture changes with rearing conditions (Kawecki 1995; Guntrip *et al.* 1997), but the heritability of body size in *C. maculatus* and *S. limbatus* rarely differs between males and females (Fox 1994, 1998; Fox *et al.* 2004; R.C. Stillwell and C.W. Fox, unpublished work). Studies on other seed beetles likewise suggest that h^2 for body size and genetic covariances between body size and other traits (such as development time) are similar for both sexes (Tucić *et al.* 1998; Šešlija and Tucić 2003). Thus, neither sex differences in h^2 or V_P for body mass, nor changes in h^2 or V_P in males relative to females associated with a change in diet, are likely explanations for the rapid evolution of dimorphism in Messina's study (2004).

A more likely explanation for why the high genetic correlation between males and females is not a major constraint on the evolution of sexual size dimorphism is that genetic correlations are not good predictors of correlated responses to selection when few loci contribute to differences between the sexes. Most quantitative genetic modeling is based on the Gaussian infinitesimal model, in which r_G is a very good predictor of correlated responses to selection regardless of the direction of selection and the trait on which selection acts. However, real-world traits are affected by a finite number of genes that often have asymmetric effects on the two sexes. When the number of loci affecting two traits is finite and the pleiotropic effects of alleles at those loci are asymmetrical (i.e. some loci have large effects on only one sex) then r_G poorly predicts correlated responses to selection (Czesak *et al.* 2006); even when r_G is 1.0 dimorphism can evolve rapidly, or fail to evolve, depending on the genetic architecture underlying the genetic correlation.

8.5 Future directions and summary

Studies with seed beetles have shown that variation in sexual size dimorphism observed within and among species of seed beetles is due to both differences in the sources of selection on males and females and differential phenotypic plasticity of the sexes. However, our studies also raise a variety of exciting unanswered questions, as follows.

- Male ejaculate size clearly affects male fitness in *S. limbatus*, via both fecundity and sexual selection, imposing selection on male size. In contrast, neither of these sources of selection appears to be significant in *C. maculatus*. This difference in selection can contribute to explaining the difference in size dimorphism between species but leaves us wondering why male *C. maculatus* produce such large ejaculates.
- Female *S. limbatus* lay more eggs when mating with large males. Does this reflect direct nutritional benefits obtained from male ejaculates or increased allocation of resources by females following mating with large males?
- Variation in body size among populations probably reflects genetically based differentiation in most species. However, plasticity in body size is the norm rather than the exception, and the degree of plasticity frequently differs between the sexes, at least for some environmental variables. Why does plasticity in body size frequently differ between the sexes, and how much does this sex difference in plasticity influence patterns of dimorphism observed in nature (see Fairbairn 2005)?
- A substantial literature is developing on how genetic and phenotypic covariance matrices (i.e. V_G, h^2, and r_G) vary among species and among populations within species. However, few studies have examined how genetic covariance matrices, and sex differences in genetic covariance matrices, vary with environmental conditions. Yet environmental effects on these genetic parameters can have substantial influence on the evolutionary dynamics of sexual dimorphism and may provide an explanation for evolutionary dynamics observed in nature.

8.6 Acknowledgments

We thank various colleagues, including A. Amarillo-Suárez, M.E. Czesak, F. Messina, T. Mousseau, and U. Savalli, for collaborating on the various projects discussed here. The research reviewed here was funded by grants from the US National Science Foundation (DEB-98-07315, DEB-99-96371, DEB-01-10754, and DEB-02-71929), Kentucky EPSCoR, and the USDA Kentucky Agricultural Experiment Station (to C.W.F.), and from Fundación para la Promoción de la Investigación y la Tecnología (to A. Amarillo-Suárez and C.W.F.).

8.7 Suggested reading

Blanckenhorn, W.U., Stillwell, R.C., Young, K.A., Fox, C.W., and Ashton, K.G. (2006) When Rensch meets Bergmann: does sexual size dimorphism change systematically with latitude? *Evolution* **60**, 2004–2011.

Blanckenhorn, W.U., Dixon, A.F.G., Fairbairn, D.J., Gibert, P., van der Linde, K., Meier, R. *et al.* (2007) Proximate causes of Rensch's rule: does sexual size dimorphism in arthropods result from sex differences in development time? *American Naturalist* **169**, 245–257.

Fairbairn, D.J. (2005) Allometry for sexual size dimorphism: testing two hypotheses for Rensch's rule in the water strider *Aquarius remigis*. *American Naturalist* **166**, S69–S84.

Teder, T. and Tammaru, T. (2005) Sexual size dimorphism within species increases with body size in insects. *Oikos* **108**, 321–334.

CHAPTER 9

Sexual dimorphism in the water strider, *Aquarius remigis*: a case study of adaptation in response to sexually antagonistic selection

Daphne J. Fairbairn

9.1 Introduction

Much of the research on sexual size dimorphism (SSD) centres on two primary goals. The first is to identify the adaptive significance of differences in body size between males and females (e.g. see Chapters 7, 8, 10, and 12 in this volume) and the second is to determine to what extent the evolution of SSD is constrained by conflict within and among genes influencing male and female fitness (e.g. see Chapters 16–18). Realization of these two goals is a rather daunting task because the necessary empirical investigations ultimately require estimation of the effect of body size on the lifetime fitness of males and females in natural populations. Theory predicts that if SSD has reached its evolutionary equilibrium, lifetime fitness functions should be convex in both sexes, indicating net stabilizing selection, and the mean size of each sex should be close to its optimum (Lande 1980a; Reeve and Fairbairn 2001; see Chapters 1 and 10). In contrast, the signal of evolutionary lag introduced by genetic conflict would be directional selection on males and females in opposing directions (Lande 1980a; see Chapter 1, 16, and 18). Because of the difficulty of measuring lifetime fitness, most studies focus on the adaptive significance of dimorphic traits only in certain contexts or selective episodes. For example, one may test the hypothesis that sexual selection favors large size of a male ornament by measuring mating success as a function of trait size. Such studies are an essential step in discovering the functional or adaptive significance of a trait, but they do not tell us whether the current mean value of the trait is optimal. Why, for example, is the size of the male ornament not greater than it is? To truly understand the adaptive significance of any trait, we need to measure direct and indirect selection on that trait throughout the lifespan of the organism. For SSD, this also means measuring selection on the traits of interest in both sexes because indirect selection can arise from correlations between sexes as well as among traits within sexes.

In this chapter, I describe our attempts to do this for the water strider, *Aquarius remigis* (Hemiptera, Gerridae). We have combined measures of selection in natural populations, common garden rearing experiments, and studies of behavior and functional morphology to discern the adaptive significance and quantitative genetic architecture of SSD. Although there is still much to be done, we have come a long way toward achieving the two major goals outlined above. Our studies reveal that SSD reflects the adaptive divergence of males and females in response to selection associated with their disparate reproductive roles, primarily fecundity selection in females and sexual selection in males. We also find that the mean overall sizes of the two sexes are close to their selective optima, suggesting that SSD is at equilibrium with the current selective regimes. Our quantitative genetic experiments reveal a web of genetic correlations that would be expected to constrain the evolution of SSD. However, significant concordance between the pattern of genetic correlations and the pattern of SSD suggests that the genetic architecture has evolved in response to sexually antagonistic selection in a manner that facilitates adaptive responses to changing selective regimes.

In the following sections I first describe the characteristics of *A. remigis* that have made it a uniquely suitable organism for these studies and then briefly review the data that have led to these comprehensive conclusions.

9.2 Why study SSD in *A. remigis*?

A. remigis is a large (mean length 12–16 mm) semi-aquatic bug that lives on the surface of streams, small rivers, and impoundments across much of temperate North America. Juveniles (nymphs) and adults share a similar ecology, foraging for insects and other arthropods trapped in the surface film. The relatively large size and visibility of the adults as they skate along the water surface make them particularly well-suited for both behavioral observations and mark-and-recapture studies (e.g., Fairbairn 1985, 1986; Kaitala and Dingle 1992, 1993; Krupa and Sih 1993; Blanckenhorn 1994; Blanckenhorn and Perner 1994, 1996; Ferguson and Fairbairn 2000; Preziosi and Fairbairn 2000). In cooler habitats, where we have done most of our work, *A. remigis* has an annual life cycle that greatly facilitates estimation of natural selection. The adults eclose in the late summer and fall but remain non-reproductive until the following spring. As soon as the ice melts in spring, both sexes begin mating and continue to mate an average of once per day throughout the reproductive season, which lasts until early summer, by which time all the overwintered adults have died (Fairbairn 1985; Blanckenhorn and Fairbairn 1995; Ferguson and Fairbairn 2000; Preziosi and Fairbairn 2000). Reproduction is thus synchronous and the generations are non-overlapping. Mating pairs typically remain *in copula* for several hours and are easily observed and captured for assays of sexual selection (Figure 9.1 Fairbairn 1988; Sih *et al.* 1990; Weigensberg and Fairbairn 1994; Campbell and Fairbairn 2001; Vermette and Fairbairn 2002). A further advantage of these populations is that most adults lack wings and so dispersal among streams is rare. Local populations are thus essentially closed: adults found on a given stream have developed on that stream and are the offspring of parents from that population (Calabrese 1979; Fairbairn 1986; Preziosi and Fairbairn 1992). This permits adaptation to local selective regimes and, indeed, adaptive divergence of body size has been documented for populations separated by as little as 6 km (Blanckenhorn 1991a).

As is typical of many insects, female *A. remigis* are slightly larger than males (see Chapter 6) but this moderate overall SSD masks considerable variation in SSD among body components (Figures 9.2 and 9.3; Table 9.1; Fairbairn 1992, 2005). The components associated with feeding and locomotion (head, thorax, and legs) tend to show little SSD, whereas those with clear reproductive functions (abdomen and genitalia) are strongly dimorphic. Forefemur width may appear to be an

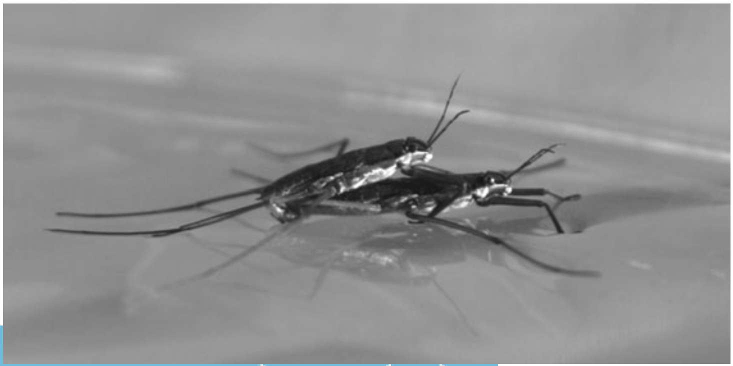


Figure 9.1 A copulating pair of *A. remigis* on the water surface. The male is riding on the female's back, grasping her with his forelegs and with his external genital segments extended downward and under the female. Photo credit: G. Roff and D. Fairbairn.

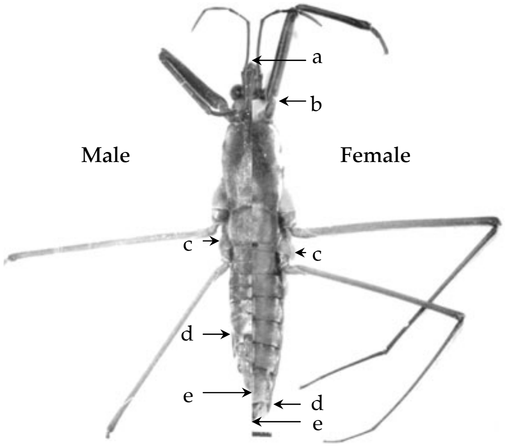


Figure 9.2 Composite ventral view of an adult male (left) and female (right) *A. remigis* illustrating the pattern of SSD. Arrows indicate the approximate locations of the sutures used as landmarks for measuring body components. All measures are taken where the relevant sutures cross the midline. a–e, total length; a–d, soma; b–c, thorax; c–d, abdomen; d–e, genitalia. The scale bar indicates 0.9 mm.

exception to this generality, but the forelegs are used to grasp females during mating (Figure 9.1) and hence serve a function in reproduction (Weigensberg and Fairbairn 1996). Thus, without even measuring selection, one might deduce that the disruptive selection driving the evolution of SSD in this species is associated primarily with divergence in reproductive roles rather than in ecological roles. As we shall see, this deduction is confirmed by our assays of the ontogeny of SSD and of selection in natural populations.

9.3 The adaptive significance of SSD in *A. remigis*

9.3.1 Pre-adult stages: the ontogeny of SSD

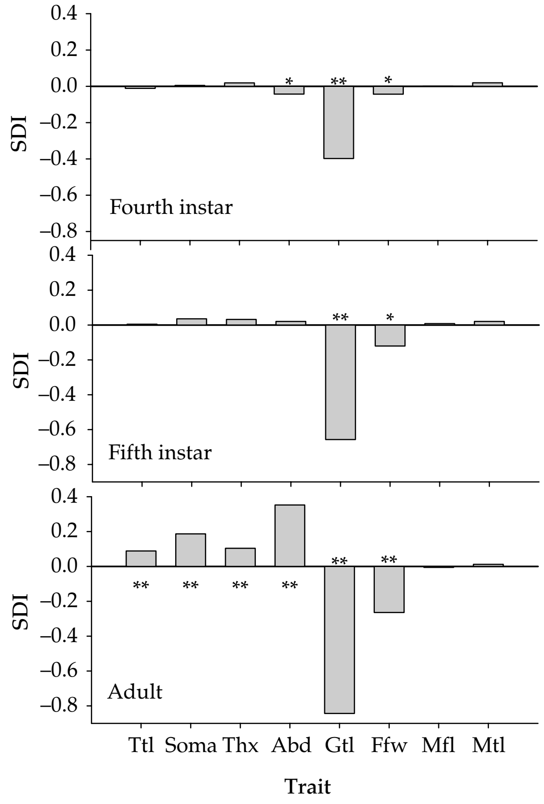


Figure 9.3 The ontogeny of SSD for various body and leg components of laboratory-reared nymphal and adult *A. remigis*. All measures were made in dorsal aspect (rather than ventral as in Figure 9.1) on the sixth day following molting. Asterisks indicate significant differences between males and females: $*P < 0.05$; $**P < 0.006$, the critical P after correction for multiple comparisons. Sample sizes (m, f): 20, 23 fourth-instar nymphs; 21, 33 fifth-instar nymphs; and 30, 27 adults. Mtl, length of the tibia of the mid-leg; all other abbreviations are as in Table 9.1. Data are from V. Simoneau and D.J. Fairbairn, unpublished work.

If SSD is adaptive in the nymphal stages we would expect it to appear early in ontogeny and to be associated with somatic rather than reproductive structures. To test this hypothesis, we compared the sizes of laboratory-reared males and females preserved as fourth-instar nymphs (when the sexes can first be distinguished), fifth-instar nymphs, or adults (Figure 9.3; V. Simoneau and D.J. Fairbairn, unpublished work). Contrary to the above predictions, the only trait that was significantly dimorphic during the nymphal stages was genital length. This result suggests strongly that the adaptive significance of SSD lies in the adult phase of the life cycle.

9.3.2 SSD as a correlated response to selection on development time

Many organisms show sexual bimaturism—that is, males and females become reproductively mature at different ages—and in insects this is manifest by differences in development time (Thornhill and Alcock 1983; Blanckenhorn *et al.* 2007; see Chapter

Table 9.1 Sexual size ratio, SDI*, and heritabilities for morphological traits from a representative population of *A. remigis* from southern Quebec, Canada. Trait abbreviations are shown in parentheses. Data are from 726 male and 723 female offspring from 180 full-sib families (D.J. Fairbairn and J.P. Reeve, unpublished work).

Trait[‡]	Size ratio (f/m)	SDI	Heritability (SE)	
			Males	Females
Total (Ttl)	1.08	0.08	0.43 (0.11)	0.52 (0.11)
Soma	1.27	0.27	0.47 (0.08)	0.58 (0.08)
Thorax (Thx)	1.07	0.07	0.42 (0.08)	0.53 (0.08)
Abdomen (Abd)	1.70	0.70	0.25 (0.07)	0.55 (0.08)
Forefemur width (Ffw)	0.81	−0.24	0.18 (0.07)	0.41 (0.08)
Midfemur (Mfl)	1.01	0.01	0.67 (0.08)	0.71 (0.08)
Genitalia (Gtl)	0.30	−2.33	0.48 (0.09)	0.50 (0.08)
Segment 8 (S8)	0.49	−1.06	0.48 (0.09)	0.41 (0.08)
Pygophore (Pg)[†]			0.26 (0.09)	
Dorsal plate of the vesica (Dp)[†]			0.58 (0.08)	
Apical extension of the Dp (Ae)[†]			0.71 (0.08)	
Ae width (Aew)[†]			0.53 (0.08)	

*SDI = (size of the larger sex/size of the smaller sex)−1, set as positive when females are the larger sex and negative when males are the larger sex (Lovich and Gibbons 1992).

[‡] All measures are lengths along the ventral midline unless otherwise indicated.

[†] Genital components found only in males.

20). If size at maturity is correlated with development time, as would be the case under the simple assumption of equal growth rates, sexual bimaturism will be associated with SSD. This is important because it implies that SSD could arise as an indirect effect of selection acting on development time rather than on body size per se.

To determine whether this could be true for *A. remigis*, we have measured adult body size and development time (the number of days from egg to adult eclosion) under a variety of laboratory conditions. For example, A. Rigler and I (unpublished work) reared *A. remigis* under densities differing by an order of magnitude but with abundant food. Both survivorship and development time were significantly reduced at high density ($P < 0.001$), but body size (total length) was not affected ($P > 0.17$). Neither development time nor the effect of density on development time differed between the sexes ($P > 0.30$ for the effect of sex on development time and $P > 0.75$ for the interaction between density and sex). Overall, we have conducted 10 separate rearing experiments and in every case body size differed significantly between males and females but development time did not. The difference in development time between the sexes was always very slight and in five of the 10 cases, males actually took slightly longer to develop than females (Fairbairn 1990; A. Rigler and D.J. Fairbairn, unpublished work). Clearly, SSD in *A. remigis* is not associated with sexual bimaturism and cannot be attributed to selection on development time.

9.3.3 Selection on pre-reproductive adults

Pre-reproductive males and females do not differ with respect to date of eclosion, activity, stride rate, foraging success, behavior in dyadic encounters, position in the stream, reaction to current, probability of surviving from eclosion to the spring reproductive season, or date of emergence from overwinter diapause (Fairbairn and Brassard 1988; Blanckenhorn and Perner 1996; Ferguson and Fairbairn 2000). In contrast, during the reproductive season, males are more mobile and spend much less time foraging and feeding than females, mainly because they are searching for mates or *in copula* (Kaitala and Dingle 1993; Blanckenhorn *et al.* 1995; Blanckenhorn and Perner 1996). These comparisons suggest that ecological divergence between the sexes is negligible prior to the onset of reproductive activity. Disruptive selection favoring different optima in the two sexes therefore seems unlikely during this life stage.

To test this hypothesis, we estimated pre-reproductive selection on body size in two populations at Mont St. Hilaire, Quebec, Canada (Ferguson and Fairbairn 2000, 2001a; Preziosi and Fairbairn 2000). In these small, closed populations, it was possible to capture and individually mark every adult on eclosion and then recapture those that survived to the spring. Body size was measured from photographs taken of each animal on first capture (Figure 9.2) and selection was estimated using either selection-gradient analysis or stepwise multiple regression, with survival to the reproductive season (''pre-reproductive survival'') as the fitness measure. Over the four winters spanned by our studies, pre-reproductive survival ranged from 17 to 30% (see also Matthey 1974 and Blanckenhorn 1994 for similar estimates from other northern populations), and was the largest contributor to variance in net adult fitness (Ferguson and Fairbairn 2001a). However, in spite of very large samples (2476 females and 2140 males) we found no evidence of selection on female size in any year, while selection on males was significant in only two of the four years, being positive one year and negative the next. Blanckenhorn (1994) found a similar pattern of weak and inconsistent selection over three consecutive winters in his population in New York State.

We have little information about the causes of overwinter mortality, but increased probability of survival has been shown to be positively associated with both lipid reserves and date of eclosion, neither of which differ between males and females (Blanckenhorn 1991b, 1994; Ferguson and Fairbairn 2000). Thus, we have no evidence to suggest either consistent selection on body size or disruptive selection on males and females during the pre-reproductive phase. Selection on pre-reproductive adults cannot explain SSD.

9.3.4 Selection on reproductive adults

To assess selection on body size during the reproductive phase of the life cycle, it is convenient to partition reproductive fitness into three components: reproductive longevity, fecundity (number of eggs produced by females), and mating success (number of matings obtained by males). I will describe these sequentially.

Reproductive longevity

Our intensive mark-and-recapture protocol at Mont St. Hilaire enabled us to estimate reproductive longevity as the number of days each adult was known to be alive after the winter diapause (Preziosi and Fairbairn 1996, 1997, 2000; Ferguson and Fairbairn 2000, 2001a). Neither mean reproductive longevity nor the opportunity for selection generated by the variance in reproductive longevity differed between males and females (Ferguson and Fairbairn 2000, 2001a). Preziosi and Fairbairn (1997, 2000) found that total length was negatively related to reproductive longevity for females in both years of their study and for males in one year. Selection-gradient analysis indicated that this selection specifically targeted abdomen length in females but was not associated with any specific body component in males. In contrast, Ferguson and Fairbairn (2000) found no association between body size and reproductive lifespan in either sex in the subsequent two generations. This discrepancy between studies may merely reflect lack of power in the second study because sampling frequency was reduced from twice to once per week. However, the relationship between body size and reproductive longevity is quite labile and sensitive to food availability (Blanckenhorn *et al.* 1995), so the difference between years at Mont St. Hilaire may reflect interannual variation in ecological conditions. Our results indicate at least intermittent selection favoring smaller abdomen size in females, and a weaker trend for selection favoring smaller overall size in males.

Fecundity

Fecundity tends to be positively correlated with female total length in both laboratory and field populations of *A. remigis* (Fairbairn 1988; Blanckenhorn 1991c, 1994; Preziosi *et al.* 1996; Preziosi and Fairbairn 1997, 2000) and multivariate analyses have revealed that this correlation is caused by the positive regression of fecundity on abdomen length (Preziosi *et al.* 1996; Preziosi and

Fairbairn 1997, 2000). This is true whether fecundity is assayed as daily fecundity, cumulative fecundity, or "instantaneous" fecundity (the total number of mature eggs carried by females preserved on capture from natural populations). This pattern of positive fecundity selection on abdomen size in females is nicely congruent with the pattern of SSD, abdomen length being the only trait that is much larger in females than in males (Table 9.1; Figures 9.2 and 9.3).

Mating success

The mating system of *A. remigis* has been characterized as convenience polyandry (Weigensberg and Fairbairn 1994; Arnqvist 1997). Males repeatedly attempt to mount single females without any form of courtship, while females typically struggle vigorously to repel these attempts (Weigensberg and Fairbairn 1994; Watson *et al.* 1998; Sih *et al.* 2002; Fairbairn *et al.* 2003). Once a male achieves intromission, there is a minimum latency of 15–20 min before insemination (Rubenstein 1989; Campbell and Fairbairn 2001). However, beyond this initial latency period, prolonging copulation has a negative impact on male fitness (Vermette and Fairbairn 2002). Males maximize their total paternity success by transferring sperm quickly, dismounting and seeking other potential mates rather than prolonging copulations to guard against female remating (Vermette and Fairbairn 2002). In such a mating system, one would expect sexual selection to favor two types of male characteristics: (1) traits that enable males to make many mating attempts and (2) traits that increase the probability of success of each attempt. Evidence suggests that both forms of sexual selection have influenced the evolution of male body size.

Numerous studies have documented a large male mating advantage in *A. remigis* (Fairbairn 1988; Sih and Kruppa 1992, 1995; Krupa and Sih 1993; Fairbairn and Preziosi 1994; Preziosi and Fairbairn 1996, 2000; Weigensberg and Fairbairn 1996; Sih *et al.* 2002), and multivariate analyses of selection have consistently shown that the target of this selection is the length of the external genitalia rather than total length (Preziosi and Fairbairn 1996, 2000; Sih *et al.* 2002; Bertin and Fairbairn 2005). Evidence suggests that this selection occurs because longer genitalia aid males in overcoming female reluctance to mate. If a male is successful in grabbing and mounting a female, he attempts to achieve intromission by extending his genital segments and swinging them down and behind the female. The phallus then emerges to reveal a unique, shoehorn-shaped, sclerotized plate (the apical extension of the dorsal plate of the vesica) which the male inserts between the female's gonocoxae to initiate intromission (Fairbairn *et al.* 2003; Bertin and Fairbairn 2005; Figures 9.1 and 9.4). When the phallus is deflated, the dorsal plate including its apical extension occupies 75% of the length of the pygophore (the second genital segment) and its length is genetically correlated with total genital length (Table 9.2; Figure 9.4; Fairbairn *et al.* 2003). Hence, one might surmise that the apparent selection on external genital length is an indirect effect of selection for the long dorsal plate. However, multivariate analyses indicate that the main target of selection is the first genital segment (segment 8), with somewhat weaker selection on the pygophore and no direct selection on the dorsal plate (Bertin and Fairbairn 2005). These results support the alternative hypothesis that longer genitalia give males a mechanical advantage in manipulating and positioning the phallus for intromission (Preziosi and Fairbairn 1996; Sih *et al.* 2002; Fairbairn *et al.* 2003). In this sense, the male genitalia serve as a tool or armament for overcoming female resistance.

The pattern of sexual selection on other components of male size is much weaker and less consistent but there is an overall trend for males with smaller somas (thorax and abdomen) to be favored (Fairbairn and Preziosi 1996; Preziosi and Fairbairn 1996, 2000; Ferguson and Fairbairn 2000; Sih *et al.* 2002; Bertin and Fairbairn 2005). Evidence from laboratory experiments suggests that males with small somas have an advantage because they are able to spend more time looking for mates rather than foraging and to make more mating attempts when food is limiting (Blanckenhorn *et al.* 1995). Sih *et al.* (2002) have also suggested that females may prefer smaller males because of the energy demands of mate-carrying. Whatever the mechanism, the general pattern is for sexual selection acting through differential mating success to favor males with relatively small somas but large genitalia, a pattern strongly congruent with the pattern of SSD (Figures 9.2 and 9.3).

9.3.5 Net adult fitness

To determine whether SSD is at evolutionary equilibrium in our populations, we approximated lifetime fitness by estimating fitness over the entire adult lifespan, which we term net adult fitness. Although this estimate omits possible selection acting through size-specific nymphal survival, our evidence indicates that if such selection occurs, it does not act differentially on males and females (see Section 9.3). Preziosi and Fairbairn (2000) and Ferguson and Fairbairn (2000) calculated longitudinal estimates of net adult fitness for 2028 males and 1191 females marked and measured on eclosion and followed through their adult lifespan, in four consecutive generations at Mont St. Hilaire. Net fitness was estimated as total number of matings obtained for males and total number of eggs laid for females, in both cases including zeros for adults who did not survive to the mating season. In the first two generations, net selection on total length was clearly stabilizing for both males and females and the mean sizes were very close to their optima (Preziosi and Fairbairn 2000). However, net selection was very weakly directional or not detectable in the two subsequent generations (Ferguson and Fairbairn 2000). This difference may simply reflect the lack of power in the second study due to the reduced sampling intensity (once rather than twice per week). However, a pattern of weak directional selection is also consistent with the expectation of a decline in the intensity of selection as the size of each sex approaches its optimum (Lande 1980a). In females, net stabilizing selection on total length in the first two generations was caused by a balance between positive

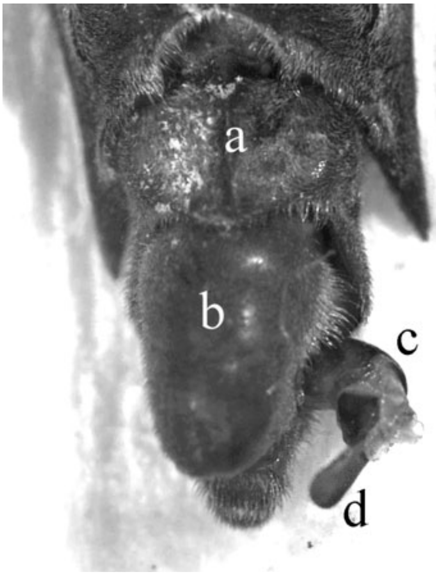


Figure 9.4 Male genital segments in ventral aspect, with the partially inflated phallus emerging laterally. a, Segment 8; b, pygophore; c, partially inflated phallus; d, apical extension of the dorsal plate of the vesica.

Table 9.2 Genetic correlations between sexes (on the diagonal; bold) and within sexes (off-diagonal; males above, females below) for body-size components in *A. remigis*. Within-sex correlations were estimated according to Becker (1985), corrected for unequal family sizes as in Roff (1997). Between-sex correlations were estimated using mixed-model analysis of variance and restricted maximum likelihood (Fry 1992; Roff 1997). Correlations whose confidence limits overlap zero are italicized. Data source and abbreviations are as in Table 9.1.

	Soma	Thx	Abd	Ffw	Mfl	Gtl	S8	Pg	Dp	Ae	Aew
Soma	**0.80**	0.87	0.56	0.47	0.39	0.36	0.32	0.46	0.31	*0.10*	0.33
Thx	0.84	**0.86**	0.49	0.56	0.49	0.34	0.42	0.55	0.34	*−0.12*	*0.15*
Abd	0.87	0.69	**0.85**	0.47	*0.12*	*0.18*	*0.18*	*0.27*	*−0.05*	*0.10*	0.27
Ffw	0.46	0.39	0.29	**0.94**	*0.15*	0.52	0.56	0.59	*0.22*	*0.10*	*0.05*
Mfl	0.51	0.60	0.28	0.30	**1.00**	0.37	0.24	0.44	0.26	*0.02*	0.24
Gtl	*0.21*	*0.18*	*0.17*	*0.21*	0.28	**0.62**	0.88	0.43	0.48	0.34	*−0.08*
S8	0.38	0.25	0.39	0.25	0.25	0.77	**0.60**	0.44	0.32	0.30	*−0.04*
Pg									*0.19*	*0.21*	*0.11*
Dp										*0.75*	0.20
Ae											*0.14*

fecundity selection and negative longevity selection during the reproductive season (Preziosi and Fairbairn 2000). The underlying patterns were less obvious for males, but it is likely that both a trade-off between mating frequency and reproductive longevity and the antagonistic selection on genitalic versus somatic body components contributed to the net stabilizing selection. For both sexes, the absence of strong directional selection in any generation, the evidence of stabilizing selection in two generations, and the close approximation of the mean sizes to their optima all support the hypothesis that SSD is at or close to evolutionary equilibrium in these populations.

9.4 The quantitative genetics of SSD in *A. remigis*

Although analytical models have demonstrated that SSD can reach equilibrium with no change in the genetic correlation between sexes, a more realistic expectation is that the genetic architecture will evolve in response to consistent selection (Lande 1980a; Reeve and Fairbairn 1996, 2001; Bonduriansky and Rowe 2005a; Fairbairn and Roff 2006; and see Chapters 16–18). Specifically, we expect selection favoring divergent evolution of male and female traits to cause a decline in the genetic correlation between sexes through the evolution of sex linkage and sex-specific patterns of gene expression. The same prediction can be made for divergently selected traits within sexes. The converse is also true: SSD will evolve more readily for traits that are not highly correlated either between sexes or with other traits. Both of these arguments predict a negative association between SSD and the genetic correlations of the dimorphic traits within and between sexes (Bonduriansky and Rowe 2005a; Fairbairn and Roff 2006; see Chapter 17).

To test this hypothesis, we have estimated genetic correlations using half-sib, full-sib, and parent–offspring rearing designs (Preziosi and Roff 1998; D.J. Fairbairn and J.P. Reeve, unpublished work) as well as directly from field samples (Ferguson and Fairbairn 2001b). These studies indicate significant heritabilities for all of our standard traits (Table 9.1), highly similar phenotypic and genetic correlation matrices, and genetic correlations generally as high or higher than their phenotypic counterparts (Table 9.2; Figure 9.5; Preziosi and Roff 1998; Ferguson and Fairbairn 2001b). The genetic correlation between males and females for total length is high (0.86, SE = 0.17; Preziosi and Roff 1998), suggesting considerable constraint on the evolution of SSD. However, as predicted, the between-sex genetic correlations for body components decline significantly as SSD increases (Figure 9.5b). The lowest between-sex correlations are for the two genital measures and these are also tend to have low or non-significant correlations with somatic components within each sex, a trend that is particularly

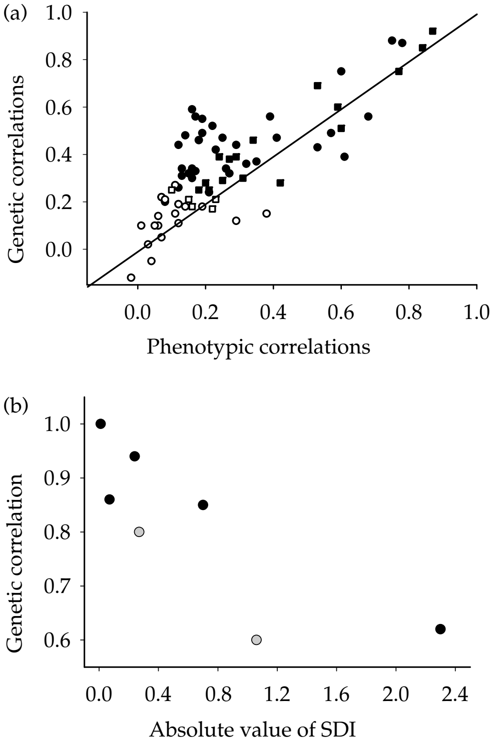


Figure 9.5 Genetic correlations within and between sexes for body components of *A. remigis*. Details as in Table 9.2. (a) A scatter plot illustrating the strong correlation between genetic and phenotypic correlations ($r_{19} = 0.95$ for females and $r_{53} = 0.74$ for males; Mantel tests, $P < 0.001$). White symbols denote non-significant genetic correlations. Circles are males, squares are females. (b) Between-sex genetic correlations plotted against the absolute value of SDI. Black symbols are linearly independent measures, from left to right: Mfl, Thx, Ffw, Abd, Gtl. Gray symbols are, from left to right, composite (soma) or component (S8) measures. Spearman $r = -0.89$, $P_{1\text{-tailed}} = 0.01$ for all seven traits. With soma and S8 excluded: Spearman $r = -0.90$, $P_{1\text{-tailed}} = 0.05$.

pronounced for genital–abdomen correlations (Table 9.2; Figure 9.5; Preziosi and Roff 1998; Ferguson and Fairbairn 2001b). These patterns are congruent with both the pattern of SSD and the pattern of antagonistic selection on genital and somatic body components. Our genetic analyses thus support the hypothesis that the genetic architecture has evolved in response to long-term divergent selection on males and females. Conversely, the relative genetic isolation of male genital length, particularly from abdomen length, should facilitate rapid adaptive evolution of SSD in response to changing local selective regimes. This may explain our observation that SSD is at or close to its optimum with respect to local selection regimes in spite of strong between-sex genetic correlations for total length.

9.5 Summary

This chapter describes a series of studies designed to determine the adaptive significance of SSD in the water strider, *A. remigis,* and to address the fundamental question of whether SSD is at evolutionary equilibrium in local populations of this species. Female *A. remigis* are about 8% longer than males overall but this moderate SSD masks much more extreme dimorphisms for body components: the abdomen is 70% longer in females, while the genitalia are on average three times longer in males. We discover that, with the exception of the genitalia, SSD is negligible until the adult stage and there is no evidence of sexual bimaturation, ecological niche divergence, or sex-specific selection prior to the onset of reproductive maturity. In contrast, during the reproductive season, sexual selection on males strongly favors longer genitalia while somewhat weaker sexual and longevity selection favors small somatic size. At the same time, fecundity selection favors longer abdomens in females, and this is balanced by a negative relationship between female size and reproductive longevity. These patterns of balancing and antagonistic selection result in net stabilizing selection on total length in both sexes. Further, both sexes appear to be close to their optimal sizes, indicating that SSD is close to evolutionary equilibrium in our field populations. A general negative relationship between SSD and the genetic correlations within and between sexes indicates that the genetic architecture has evolved in response to these sex-specific patterns of selection, as predicted by quantitative genetic theory. This pattern of genetic architecture can also be expected to facilitate rapid response of SSD to changing patterns of selection, and may explain why SSD can be close to equilibrium in local populations in spite of strong between-sex genetic correlations for overall size.

9.6 Acknowledgments

The progress described in this chapter would not have been possible without the considerable efforts of undergraduate students Jonathan Brassard, Veronique Campbell, Adrienne Rigler, Valerie Simoneau, and Ilana Wiegensberg; graduate students Ian Ferguson, Richard Preziosi, Jeff Reeve, and Richard Vermette; and postdoctoral scholars Wolf Blanckenhorn and Angeline Bertin. I am grateful to all of them for their scholarly contributions and for the joy and enthusiasm that they brought to our research endeavors. I am also grateful to the Natural Science and Engineering Research Council of Canada, Le Fonds québécois de la recherche sur la nature et les technologies, Concordia University in Montréal, Canada, and the University of California at Riverside for generously supporting this research program.

9.7 Suggested readings

Bertin, A. and Fairbairn, D.J. (2005) One tool, many uses: precopulatory sexual selection on genital morphology in *Aquarius remigis*. *Journal of Evolutionary Biology* **18**, 949–961.

Preziosi, R.F. and Fairbairn, D.J. (2000) Lifetime selection on adult body size and components of body size in a waterstrider: opposing selection and maintenance of sexual size dimorphism. *Evolution* **54**, 558–556.

Reeve, J.P. and Fairbairn, D.J. (2001) Predicting the evolution of sexual size dimorphism. *Journal of Evolutionary Biology* **14**, 244–254.

Sih, A., Lauer, M.L., and Krupa, J.J. (2002) Path analysis and the relative importance of male-female conflict, female choice and male-male competition in water striders. *Animal Behaviour* **63**, 1079–1089.

CHAPTER 10

Case studies of the differential-equilibrium hypothesis of sexual size dimorphism in two dung fly species

Wolf U. Blanckenhorn

10.1 Introduction

This book makes evident that research on sexual size dimorphism (SSD) can be and is conducted successfully at the macroevolutionary (Section I), microevolutionary (Section II), and mechanistic (Section III) levels. In this chapter I integrate various studies of selection on body size in two species of dung fly, the yellow dung fly *Scathophaga stercoraria* (Diptera: Scathophagidae) and the black scavenger fly *Sepsis cynipsea* (Diptera: Sepsidae), that we have conducted over numerous years. This aims at investigating the differential-equilibrium model (Price 1984; Arak 1988; Schluter *et al.* 1991; Blanckenhorn 2000; Figure 10.1; see also Chapters 1 and 9 in this volume, and the Introduction to Section II) by asking whether current sex-specific selection on body size predicts, or is consistent with, the current SSD of the species (or population). The two species are ecologically similar but display opposing SSD, females being larger in *S. cynipsea* (the common pattern in insects) and males being larger in *Sc. stercoraria*. Thus the comparison is particularly interesting and general because the model should work in both situations. The majority of our data stem from one particular study population near Zurich, Switzerland, although we have also investigated variation in selection on body size among populations in Switzerland (Kraushaar and Blanckenhorn 2002). Most of the studies discussed are phenomenological, but we have also conducted numerous supplementary studies investigating underlying behavioral mechanisms of sexual selection in particular (not further treated here). I shall compare our data with similar data from other species available in the literature, and discuss potential reasons for the frequent lack of quantitative evidence supporting the equilibrium model of SSD. I start by describing the nature of our available data before presenting and integrating the results for the two species.

10.2 Estimation of selection in the field in dung flies

Phenomenological coefficients of selection—that is, univariate selection differentials or multivariate selection gradients (Brodie *et al.* 1995)—are measured in a standardized way using established (regression) methods and expressed in standard deviation units (Arnold and Wade 1984a, 1984b). To test the equilibrium model, I here consider selection on body size during four selection episodes reflecting the main individual fitness components (Figure 10.1): (1) sexual selection (males only), (2) fecundity selection (females only), (3) juvenile (= egg, larval, and pupal) viability selection, and (4) adult viability selection (both sexes). Individual flies cannot be followed throughout their lives, necessitating a piecemeal or cross-sectional (as opposed to longitudinal) approach. For discussion of these approaches and their assumptions and caveats please refer to the Introduction to Section II.

Our sexual-selection estimates generally refer to instantaneous, dichotomous pairing success. That

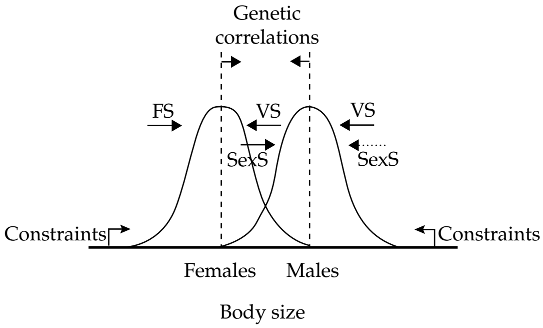


Figure 10.1 The differential-equilibrium model of the evolution of SSD within species. Body-size distributions for the (arbitrary) case where males are larger than females are depicted. Fecundity selection (FS) tends to select for increased body size in females, and sexual selection (SexS) for increased body size in males (but occasionally in the opposite direction). Adult and juvenile viability selection (VS) select against large body size in both sexes. If these major selective pressures equilibrate differentially in the sexes, SSD results in a given species. Some general (physiological, developmental, or phylogenetic) constraints as well as genetic correlations between the sexes that potentially limit the expression of the optimal SSD are indicated (adapted from Blanckenhorn 2000).

is, we compare the body size of the males that have acquired a mate in a given sample at a given time and place with those that have not. Note that other types of estimate are possible and presented regularly, for example the number of mates acquired by males over a certain period of their life (or their lifetime). Furthermore, male pairing success ultimately translates into male fecundity (i.e. his total number of offspring sired) as the product of his number or probability of obtaining mates times his mates' fecundities. Such male fecundity selection estimates are sometimes reported (e.g. Badyaev and Martin 2000). We have estimated something similar in our species (Blanckenhorn *et al.* 1999a; Jann *et al.* 2000) by considering the body size of the mating partner, which is strongly correlated with her fecundity.

We generally estimate female fecundity selection as clutch size, or equivalently eggs laid per day, as a function of body size. We generally let the females oviposit in the laboratory, even when they were collected in the field. Typically these represent single estimates at abundant food, but we have occasionally obtained repeated measures for single females over time (age), as well as fecundity estimates at limited food (Jann and Ward 1999).

We generally estimate juvenile viability selection as adult emergence as a function of body size, thus reflecting egg-to-adult viability, under various field or laboratory conditions (Blanckenhorn 1998a; Blanckenhorn *et al.* 1999a). Although such mortality data are by nature dichotomous (dead or alive), in practice we typically consider the proportion of offspring emerged from a clutch of eggs (i.e. a family). However, there is a general problem with measuring juvenile viability selection, particularly in animals with complex life cycles: the character under selection (here body size) cannot always be reliably estimated from the egg or the juvenile, and the adult size of those individuals that die during development cannot be measured. One way to circumvent this problem, and the method we generally use, is to estimate adult body size from relatives (parents, full-, or half-sibs) that survived, at any environmental conditions of interest. The mean phenotype of a family at ideal conditions is arguably the best possible body-size estimate of a genotype because the environmental-variance component is minimized (Blanckenhorn *et al.* 1999a).

Adult viability selection is generally best estimated as (adult) longevity as a function of body size. However, in small and abundant animals such as insects that cannot be marked individually or easily tracked in nature, age may be used as a substitute. In insects age can be estimated, for instance, from wing wear (Burkhard *et al.* 2002). One can alternatively estimate the remaining lifespan in the laboratory after capture of individuals. We have used both methods.

10.3 Body-size selection in the yellow dung fly *Sc. stercoraria*

10.3.1 Study species

The yellow dung fly, *Scathophaga stercoraria* (sometimes *Scatophaga*), is 7–13 mm long and occurs in north-temperate regions of the Old and New Worlds. Larvae of this species are coprophagous, meaning that they feed on the dung of large mammals, which they thereby decompose, together with many other species of primarily earthworms, beetles, and flies (Hammer 1941).

Adult yellow dung flies, in contrast, are sit-and-wait predators of small insects and lick nectar from flowers in addition to fresh dung (Hammer 1941). Adult flies require feeding on prey (primarily protein and lipids) beyond the nutrients they acquire during the pre-adult stage in order to produce eggs and sperm (Foster 1967). The distribution of *Sc. stercoraria* up to places like Iceland and high elevations reveals a preference for colder temperatures (Sigurjónsdóttir and Snorrason 1995; Blanckenhorn 1997b). Toward the south its distribution appears to be limited by hot temperatures, which this species is susceptible to and evidently avoids. This often splits the year into a spring and an autumn season, as flies are not present at the dung in the hottest summer months in the warmer regions of their distribution (Hammer 1941; Parker 1970; Gibbons 1987; Ward and Simmons 1990; Jann *et al.* 2000; Blanckenhorn *et al.* 2001). In north-central Europe, *Sc. stercoraria* is one of the most abundant and widespread insect species associated with cow dung, probably relating to human agricultural practices, as this species is considered a cow-dung specialist.

Many males wait on and around fresh dung pats and immediately seize incoming females. Females show few behaviors indicating pre-copulatory choice of particular males. Copulation takes place in the surrounding grass or on the dung pat. During the ensuing oviposition the male guards the female against other competitors. Females lay clutches of 30–70 eggs into the dung, on which the developing larvae feed. Individuals have to complete larval development in order to overwinter as pupae, at which point adult body size is fixed but pupal development (i.e. metamorphosis) still requires time to be completed. Body size and development time in this species are greatly affected by the amount of dung individuals have available as larvae (Amano 1983; Blanckenhorn 1998a; Teuschl *et al.* 2007), but they are also heritable (Blanckenhorn 2002). Males are larger than females on average (Borgia 1981, 1982; Jann *et al.* 2000; Kraushaar and Blanckenhorn 2002).

10.3.2 Selection estimates

Table 10.1 lists the average selection coefficients we have obtained for the yellow dung fly. Large body size typically and consistently confers a strong mating advantage to males, as was also qualitatively evident from earlier studies (Borgia

Table 10.1 Available sex-specific field estimates of linear sexual (pairing success), fecundity, and viability selection differentials or gradients on body size (hind tibia length) for the yellow dung fly *Sc. stercoraria*, with reference to the type of environmental variation encompassed. Each individual sample is based on hundreds to thousands of individual flies, although the confidence interval refers to variation among estimates.

	Females (mean ± 95% CI)	Males (mean ± 95% CI)	Environmental factor varied or manipulated	Reference (no. of estimates)
Pairing success	–	+0.505 ± 0.011	Seasonal, temperature, food	Jann *et al.* (2000) (2)
	–	+0.289	Population	Kraushaar and Blanckenhorn (2002) (1)
	–	+0.275 ± 0.232	Seasonal, population	Blanckenhorn *et al.* (2003) (2)
Fecundity	+0.187	−0.001	Seasonal, temperature, food	Jann *et al.* (2000) (1)
	+0.223	+0.019	Population	Kraushaar and Blanckenhorn (2002) (1)
Juvenile viability				
Seasonal	+0.225 ± 0.177	−0.234 ± 0.349	Seasonal, temperature, dung	W.U. Blanckenhorn, unpublished data (3)
	−0.014 ± 0.042	−0.048 ± 0.047	Dung (laboratory)	Teuschl *et al.* (2007) (4)
	−0.128 ± 0.219	−0.202 ± 0.236	Temperature, dung (laboratory)	Teuschl *et al.* (2007) (4)
Winter	−0.073 ± 0.100	−0.150 ± 0.336	Seasonal, temperature, dung	W.U. Blanckenhorn, unpublished data (3)
	−0.311 ± 0.317	−0.237 ± 0.128	Seasonal, temperature, dung	Teuschl *et al.* (2007) (2)
Adult viability	+0.122 ± 0.014	+0.005 ± 0.065	Seasonal (general)	Burkhard *et al.* (2002) (2)
	−0.208 ± 1.405	+0.062 ± 0.537	Seasonal (fungal parasite)	W.U. Blanckenhorn, unpublished data (2)

1982; Sigurjónsdóttir and Snorrason 1995; Otronen 1996). Sexual selection for large male size is extraordinarily strong compared to other species, particularly in relation to the large sample size of our studies (Kingsolver *et al.* 2001). The comprehensive 2-year study by Jann *et al.* (2000) based on approximately 6000 individual males additionally revealed an overall positive and significant quadratic selection differential, indicating accelerating selection with body size (Figure 10.2). However, this non-linearity was not apparent in our study of 30 Swiss populations (Kraushaar and Blanckenhorn 2002).

A strong fecundity advantage to females also generally occurs (Borgia 1981; Jann *et al.* 2000; Kraushaar and Blanckenhorn 2002; Table 10.1). The data of Jann *et al.* (2000; based on approximately 800 field-caught females) also revealed significant positive (i.e. accelerating) quadratic selection with body size (Figure 10.2), which also occurred in the study by Kraushaar and Blanckenhorn (2002).

Male fecundity selection as estimated in our studies (see Section 10.2) was nil (Table 10.1), reflecting the general lack of assortative pairing by size (potentially mediated by male choice of larger, more fecund females). However, this estimate of male fecundity selection is limited because we have no cumulative measures of pairing success for males.

As each of the individual estimates listed in Table 10.1 is based on large sample sizes encompassing a wide range of environments, we are confident that our sexual (males) and fecundity (females) selection estimates correctly reflect the average conditions over several years and populations. Note that (directional) fecundity selection favoring large female size is generally weaker than sexual selection favoring large male size (Table 10.1).

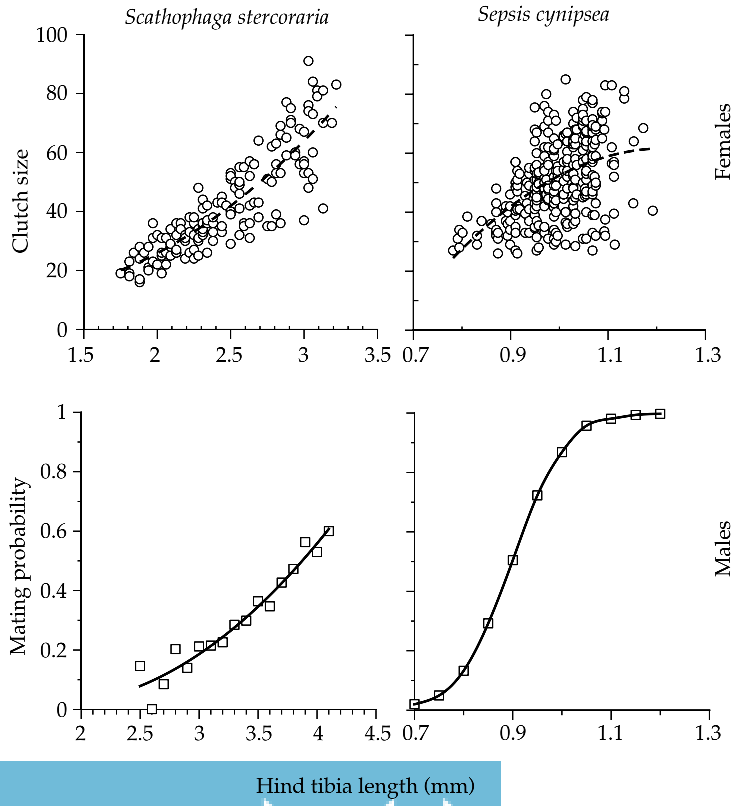


Figure 10.2 Clutch size of female (top) and mating probability of male (bottom) *Sc. stercoraria* (left) and *S. cynipsea* (right) as a function of body size (field data from Jann *et al.* 2000 and Blanckenhorn *et al.* 1999a, based on approximately 800 females and 6000 males and 300 females and 1500 males, respectively).

Adult viability selection over two seasons was estimated by Burkhard *et al.* (2002) based on age as reflected by wing wear. Larger females tended to be older, presumably indicating greater longevity conferring an advantage, whereas patterns for males were inconsistent and weak overall (Table 10.1). These field estimates should reflect abiotic (e.g. hot temperature, food limitation) as well as biotic (e.g. predation and parasitism) mortality sources. However, Burkhard *et al.* (2002) concluded that in *Sc. stercoraria* wing wear is a problematic estimator of age because it is also strongly affected by aggressive interactions among individuals, so these estimates have to be treated with caution. An as-yet unpublished data-set investigated size-specific parasitism of *Sc. stercoraria* by the fungal parasite *Entomophtora scathophagae* in the spring and autumn seasons of 2002 based on a relatively small sample of approximately 170 females and 370 males. This fierce parasite, which kills adult individuals within a few days, is typically rare in our populations but there are outbreaks in some years. Selection on body size by this parasite was inconsistent and not significant. Overall we conclude that viability selection against large body size, presumed to counterbalance strong body-size advantages in terms of mating and fecundity, is not strongly apparent in yellow dung flies (Figure 10.1; Table 10.1).

We have estimated juvenile viability selection in four separate experiments. All these were experimental investigations of mortality effects of abiotic conditions (larval food (dung), season, temperature), yielding several sub-samples, two in the field and two in the laboratory (Table 10.1). Therefore, effects of juvenile predators, parasites, or parasitoids, which undoubtedly occur in and around the dung (Hammer 1941), are excluded. Moreover, Teuschl *et al.* (2007) worked with yellow dung flies artificially selected for large and small body size in the laboratory for 11–24 generations to extend the body-size range available to increase the chance of detecting potentially cryptic disadvantages of large size. The data show that viability selection in both sexes is predominantly negative, thus favoring smaller individuals under a variety of conditions (Table 10.1). Rather than food limitation per se, higher seasonal or winter mortality of larger genotypes is primarily mediated by their longer development time (because it takes time to get large; Roff 1980), which is positively genetically correlated with body size (Blanckenhorn 1998a; Teuschl *et al.* 2007). That is, dung flies face severe time constraints as individuals have to reach the pupal stage before the dung pat dries or is depleted and before the first winter frost.

As selection coefficients of consecutive life stages and selection episodes are additive, because fitness components are cumulative and hence multiplicative (Arnold and Wade 1984a, 1984b), we can, albeit only very crudely because of copious averaging, quantitatively test the differential-equilibrium model using the estimates in Table 10.1. We can thus add the overall, averaged sex-specific juvenile viability selection coefficient, weighting seasonal viability by two-thirds because in Switzerland there are about three generations per year, only one of which overwinters, and the adult viability coefficient, adjusted for the estimated overall sex-specific probability of a juvenile to survive to adulthood (Blanckenhorn *et al.* 1999b) based on Blanckenhorn's field data (Blanckenhorn 1998a). This yields $(2/3) * (+0.028) + (1/3) * (-0.192) + 0.788 * (-0.043) = -0.080 \pm 0.307$ ($\pm$95% CI) for females and $(2/3) * (-0.161) + (1/3) * (-0.194) + 0.780 * 0.034 = -0.146 \pm 0.108$ for males. The corresponding confidence intervals can be derived from the variance among individual estimates within episodes (Table 10.1) because variances are additive. According to the differential-equilibrium model (Figure 10.1), these values should balance the positive mean fecundity selection coefficient for females, which is $0.788 * 0.205 = +0.162 \pm 0.031$, and the mean sexual plus fecundity selection coefficient for males, which is $0.730 * (0.356 + 0.009) = +0.267 \pm 0.125$ (both again adjusted for survival probability). It is evident that the latter net selection for large body size in both sexes has about twice in magnitude of the opposing viability selection. I therefore conclude that our cross-sectional data do not support the differential-equilibrium model of SSD in the yellow dung fly, as seems often the case (Blanckenhorn 2000). Nevertheless, because net sexual selection on males is stronger than fecundity selection on females, current selection can explain why males are larger (see Arak 1988). Even though our juvenile viability selection estimates exclude effects of various egg, larval, and pupal predators and parasitoids in and around the dung (Hammer 1941) and are therefore incomplete, it is conceivable that none of these, nor the whole set together, exert significant size-selective selection pressure.

10.4 Body-size selection in the black scavenger fly *S. cynipsea*

10.4.1 Study species

Black scavenger or dung flies of the genus *Sepsis* are common in Eurasia and Africa (Pont and Meier 2002). Many similar-looking species coexist in dung of various animals, some of them being dung specialists and others generalists (Hammer 1941; Pont and Meier 2002). *S. cynipsea* is approximately 4 mm long, the most common and abundant European sepsid and specialized on cow dung. Similar to yellow dung flies, female *S. cynipsea* oviposit into the dung, on which the developing larvae feed (Hammer 1941). However, unlike the yellow dung fly, *S. cynipsea* is most abundant during the hot summer.

Again, large numbers of *S. cynipsea* males typically wait on and around fresh cow pats for females coming to lay eggs (Parker 1972a), so operational sex ratios are highly male-biased. Males scramble to secure arriving females by clasping her wing base with their armoured forelegs, and harassment is common. Females respond with characteristic shaking behavior, indicating reluctance to mate or some sort of male assessment (Blanckenhorn *et al.* 2000). Once females stop shaking, males guard them during oviposition and subsequently attempt to copulate away from the dung (pre-copulatory guarding; Parker 1972a, 1972b; Ward *et al.* 1992). Only about 40% of the pairs formed in the field eventually copulate (Parker 1972b; Ward 1983). Males are smaller than females and thus cannot force copulation, even though large males enjoy a mating advantage in this species too (Ward 1983; Blanckenhorn *et al.* 1998, 1999a, 2000). Direct aggressive or territorial interactions among males are rare (Ward *et al.* 1992; Blanckenhorn *et al.* 2000). From laboratory rearing we know that adults acquire the protein needed for the production of eggs and sperm by feeding on dung, and that individuals require sugar, which in the field they acquire from nectar. *S. cynipsea* overwinter as adults (Blanckenhorn 1998b).

10.4.2 Selection estimates

Table 10.2 summarizes our previously published selection estimates for *S. cynipsea* (Blanckenhorn *et al.* 1998, 1999a, 2004; Kraushaar and Blanckenhorn 2002). Note that due to the much smaller size of *S. cynipsea* adults, adult viability selection estimates are very difficult to obtain, so our data-set for this species is much more limited.

Table 10.2 Available sex-specific field estimates of linear sexual (pairing success), fecundity, and viability selection differentials or gradients on body size (hind tibia length) for the black scavenger fly *S. cynipsea*, with reference to the type of environmental variation encompassed. Each individual sample is based on hundreds of individual flies, although the confidence interval refers to variation among estimates.

	Females (mean ± 95% CI)	**Males (mean ± 95% CI)**	**Environmental factor varied or manipulated**	**Reference (no. of estimates)**
Pairing success	–	+0.190 ± 0.129	Seasonal, population, general	Blanckenhorn *et al.* (1999a) (4)
	–	+0.090	Population	Kraushaar and Blanckenhorn (2002) (1)
	–	+0.045 ± 0.065	Seasonal, population	Blanckenhorn *et al.* (2004) (2)
Fecundity	+0.123 ± 0.014	+0.030 ± 0.042	Seasonal, temperature, food	Blanckenhorn *et al.* (1999a) (3)
	+0.078	+0.003	Population variation	Kraushaar and Blanckenhorn (2002) (1)
Juvenile viability: seasonal	−0.032 ± 0.038	+0.027 ± 0.094	Dung (laboratory)	W.U. Blanckenhorn, unpublished data (2)
Adult viability*	−0.038 ± 0.020	−0.005 ± 0.030	Population (general)	Blanckenhorn *et al.* (1999a) (3)

*Residual longevity in the laboratory.

Sexual selection favoring larger males also occurs in *S. cynipsea* (Parker 1972a, 1972b; Ward 1983; Ward *et al.* 1992), although in this species it is overall weaker, more variable (Blanckenhorn *et al.* 1999a, 2004), and generally mediated by direct or indirect female choice rather than male–male competition as in *Sc. stercoraria* (Blanckenhorn *et al.* 1999a, 2000; Table 10.2). Fecundity selection favoring larger females also occurs, again being weaker than in *Sc. stercoraria*. Moreover, and unlike *Sc. stercoraria*, both Blanckenhorn *et al.* (1999a) and Kraushaar and Blanckenhorn (2002) found a negative quadratic component indicating that fecundity selection asymptotes (i.e. diminishes) at larger sizes (Figure 10.2). Again, assortative pairing by size, here classified as male fecundity selection (Table 10.2), is weak. Our few estimates of adult viability selection (here estimated as residual longevity in the laboratory after field capture; Blanckenhorn *et al.* 1999a) and juvenile viability selection on body size are weakly negative (Table 10.2), indicating only slight disadvantages of larger flies.

As for *Sc. stercoraria*, I conclude that this limited cross-sectional data-set for *S. cynipsea* does not support the differential-equilibrium model (Figure 10.1). Mean sexual selection favoring larger males—that is, $0.800 * (0.108 + 0.016) = +0.100 \pm 0.078$ ($\pm 95\%$ CI)—is roughly of similar strength as fecundity selection favoring larger females—that is, $0.802 * 0.101 = +0.081 \pm 0.039$—even though females are larger on average in this species. Again, these values are adjusted by estimated sex-specific survival probability (in the laboratory; Blanckenhorn *et al.* 1998; Table 10.2). In females there is some countervailing viability selection when adding the juvenile and mortality-adjusted adult viability coefficients from Table 10.2, which almost counterbalances the fecundity selection advantage: $(-0.032) + 0.802 * (-0.038) = -0.062 \pm 0.045$. However, this is not the case for males: $(+0.027) + 0.800 * (-0.005) = +0.023 \pm 0.100$. Therefore, we cannot explain why males do not increase in size to become larger than females.

10.5 Possible constraints on SSD in dung flies

Besides the factors relating to sampling issues (see Section 10.2 and the Introduction to Section II), there are a number of other biological explanations for why we often fail to find congruence between current patterns of selection and SSD (see Chapters 1, 9, 16 and 18). I briefly discuss these here in relation to our dung fly results. Most of these explanations actually concede that the differential-equilibrium model may not be fulfilled, that there is indeed often persistent directional rather than net balancing selection (see Figure 10.1) in many species (as evident from Table 10.3). Thus, what requires explanation is the apparent lack of evolutionary response (here in body size or SSD) to this directional selection.

The evolution of SSD can be genetically constrained if there is little genetic variation for body size, but this is rare (Mousseau and Roff 1987).

Table 10.3 Available sex-specific field estimates of linear sexual, fecundity, or viability selection differentials or gradients on any morphological trait for a number of animal species (from Kingsolver *et al.* 2001). Additional, non-sex-specific adult viability selection coefficients averaged $+0.072 \pm 0.078$ ($n = 9$), and there was only one estimate for juvenile viability. There were nine invertebrate and six vertebrate species for which both fecundity and sexual selection estimates were available (paired data).

	Females (mean ± 95% CI; *n*)	Males (mean ± 95% CI; *n*)	Category
Fecundity or sexual selection	+0.127 ± 0.063 (13)	+0.255 ± 0.120 (22)	Differentials (unpaired data)
	+0.079 ± 0.114 (8)	+0.333 ± 0.221 (16)	Gradients (unpaired data)
	+0.149 ± 0.084 (9)	+0.256 ± 0.139 (9)	Invertebrates* (paired data, both types)
	+0.063 ± 0.155 (6)	+0.239 ± 0.150 (6)	Vertebrates† (paired data, both types)
Adult viability selection	−0.039 ± 0.113 (9)	+0.042 ± 0.073 (9)	All estimates and species

**Allenomobius socius, Aquarius remigis, Callosobruchus maculates, Clibanarius dugeti, Gammarus pulex, Plathhemis lydia, Scathophaga stercoraria, Sepsis cynipsea, Stator limbatus.*

†*Crocidura russula, Carpodacus mexicanus, Geospiza conirostris, Geospiza fortis, Niveoscineus microlepidates, Parus major.*

Further, a high genetic correlation between the sexes in body size can prevent or at least slow down the evolution of SSD despite consistent differences in selection between the sexes (Lande 1980a; see also Chapter 18). However, genetic variation for body size is high and genetic correlations between the sexes are less than one for our two species (Blanckenhorn 1998a, 2002; Reusch and Blanckenhorn 1998), which, after all, have become dimorphic. So this is unlikely.

Akin to genetic constraints are putative developmental constraints, which are biases or limitations on phenotypic variability caused by the developmental system (Badyaev 2002). For example, to express SSD, the larger sex is often assumed to require longer developmental periods in order to get larger (Roff 1980; Fairbairn 1990; Blanckenhorn *et al.* 2007; but see Chapter 20), and this has to occur in essentially the same genetic background. However, this problem can be and is largely overcome by differential gene expression or regulation in the sexes (Badyaev 2002; Chapter 16).

Phylogenetic constraints reflect the phenomenon that despite strong (directional) selection, species will require considerable time to evolve dimorphism markedly different from that of their ancestors and closely related species (Fairbairn 1990). For the two dung fly species studied here there is little evidence for such phylogenetic constraints: their SSD is either right on (*S. cynipsea*) or even beyond (i.e. more extremely male-biased; *Sc. stercoraria*) the SSD predicted for their body size from comparisons of closely related species (see Figure 6.1).

The differential-equilibrium model (Figure 10.1) actually refers to a given population, and not to a species as a whole, because selection may vary not only temporally (e.g. Gibbs and Grant 1987) but also spatially between populations (e.g. Badyaev *et al.* 2000). If so, gene exchange with other populations may prevent the evolution of a locally adapted SSD in a given population. This might occur in our dung fly species, as they are both abundant and widespread in Europe. However, we considered both multiple populations (Kraushaar and Blanckenhorn 2002) and several seasons (Blanckenhorn *et al.* 1999a; Jann *et al.* 2000) to acquire overall estimates for the species in Switzerland, which we know from population genetic studies to be not strongly genetically differentiated (Kraushaar *et al.* 2002).

Finally, cryptic evolution describes the phenomenon that an evolutionary response in a trait (here body size) is not observed despite consistent directional selection favoring large size because concomitant deteriorating environmental (e.g. food) conditions produce smaller phenotypes, or because selection primarily targets the environmental rather than the additive genetic component of the trait in question (Kruuk *et al.* 2001). It remains to be seen how frequent this problem is. By chance one would expect that environments are as likely to improve as they are to deteriorate, so one should as often expect the evolutionary response to be in accord with the environmental change as not.

10.6 Evidence from other species

Following up an earlier study by Endler (1986), Kingsolver *et al.* (2001) reviewed the literature on selection estimates for all organisms. Their data-set is publicly available, so I extracted sexual, fecundity and viability selection coefficients (i.e. gradients and/or differentials) for all animal species. I supplemented these data with data from a few studies published since 1999 (the time limit of the Kingsolver *et al.* data-set). For a particular species, multiple estimates for any morphological trait were averaged to arrive at one estimate per species. There was only one estimate available for juvenile viability selection, and only half of the available adult viability selection coefficients were sex-specific. Only for a subset of nine invertebrates and six vertebrates were data on both fecundity and sexual selection (and occasionally also viability selection) available (paired data in Table 10.3).

Table 10.3 shows two clear patterns. First, sexual and fecundity selection coefficients are typically positive, and sexual (or fecundity) selection favoring large male size is generally stronger than fecundity selection favoring large female size. Second, adult viability selection is weak on average, not showing the expected counteracting selection disfavoring large size (Schluter *et al.* 1991; Blanckenhorn 2000). If consistent and representative, and everything else (particularly viability selection) being equal for the sexes, this should result in an evolutionary trend towards male-biased SSD, potentially explaining Rensch's rule (Fairbairn and Preziosi 1994; Fairbairn 1997). Rensch's rule will also result if (sexual) selection on male size is more variable than (fecundity) selection on females. That is, if in some populations or species large male size is consistently favored but in others smaller size is consistently favored, and if this is not the case for females, then male body size will diverge more than female body size. Inspection of the confidence intervals in Tables 10.1–10.3 suggests such a trend.

10.7 Summary

Price (1984a) and Arak (1988) were the first to formally suggest and test the differential-equilibrium model of SSD (Figure 10.1). Such integrative tests are rare because lifetime reproductive success can hardly ever be measured, data require long times to be generated, sub-studies are often published separately, and some selection episodes are likely missing for any particular species so that fitness estimates with respect to body size often remain incomplete. In agreement with the general situation in most single species (Table 10.3; Blanckenhorn 2000), our studies of two common dung fly species with contrasting SSD reveal overwhelming evidence for sexual and fecundity selection favoring large body size but only sparse evidence for opposing selection, and consequently do not support the differential-equilibrium model. For the smaller *S. cynipsea*, data and evidence for viability disadvantages of body size are largely lacking, particularly in males, probably the prime reason for the lack of support in this species. However, in the yellow dung fly *Sc. stercoraria* considerable effort was spent in detecting selection against large individuals, including multiple viability selection estimates covering a wide and representative range of environmental conditions and artificial extension by artificial selection of the body-size range available (Teuschl *et al.* 2007). The latter permits assessment of the fate of flies larger than occur in nature, which otherwise may regularly die early during development (e.g. due to genetic malfunctions), because if survival declines very steeply only at the very fringes of a strongly platykurtic (i.e. flat) fitness function, any viability disadvantages of large body size will be difficult to detect in practice (Teuschl *et al.* 2007). Phylogenetic, genetic, or developmental constraints are unlikely to be responsible for lack of support of the differential-equilibrium model in dung flies, but physiological constraints (e.g. Peters 1983) have not yet been properly addressed.

10.8 Acknowledgments

I thank the many colleagues and students who contributed to the work reviewed here, only some of whom appear as coauthors of my work. I also thank the funding agencies, above all the Swiss National Fund, the University and Zoological Museum Zürich, for providing me with the means to conduct this research over the years.

10.9 Suggested readings

Blanckenhorn, W.U. (2005) Behavioral causes and consequences of sexual size dimorphism. *Ethology* **111**, 977–1016.

Fairbairn, D.J. (1997) Allometry for sexual size dimorphism: pattern and process in the coevolution of body size in males and females. *Annual Review of Ecology and Systematics* **28**, 659–687.

Schluter, D., Price, T.D., and Rowe, L. (1991) Conflicting selection pressures and life history trade-offs. *Proceedings of the Royal Society of London Series B* **246**, 11–17.

CHAPTER 11

The genetic integration of sexually dimorphic traits in the dioecious plant, *Silene latifolia*

Lynda F. Delph

11.1 Introduction

Dioecy is a breeding system of plants wherein there are distinct male and female individuals. Once dioecy evolves within a plant lineage this opens the door for sexual dimorphism, or differences between the sexes, to evolve. Following individuals throughout their life is relatively easy with plants, allowing researchers to investigate sexual dimorphism in life history, plant physiology, biotic interactions, as well as a multitude of morphological traits (see reviews in Geber *et al*. 1999).

One important question about sexual dimorphism is which traits are directly under selection to differ between the sexes and which differ because of indirect selection on correlated traits (e.g. see Chapter 9 in this volume). This question arises because sexually dimorphic traits often range beyond those obviously under sexually differentiated selection, to dimensions of the phenotype that do not have obviously different fitness consequences for the two sexes. Moreover, one or both sexes can exhibit phenotypes that seem maladaptive (Chapter 18), raising the question of how such dimorphism can be maintained in natural populations.

Aspects of these questions can be addressed by examining trait–trait correlations within each sex as well as between-sex correlations. If selection on one trait differs between the sexes and has cascading effects throughout the phenotype, then this should show up as suites of traits in natural populations that show strong within- and between-sex genetic correlations, and a pattern of trait covariation that suggests trade-offs among traits. My laboratory colleagues and I have been investigating this cascade question for over a decade, via observations of natural populations and quantitative-genetic experiments with the dioecious plant *Silene latifolia*. Our research was primarily motivated by the finding that males of this species exhibited a higher cost of reproduction than females and this could not be explained by straightforward measurements of investment in growth and reproduction (Delph and Meagher 1995; Delph 1999). Here I compile some of our work into a case study of why the two sexes of *S. latifolia* look the way they do morphologically and also why they exhibit different life histories. Taken together, the various studies support the hypothesis that direct selection on flower production differs between the sexes, and that constraints on the independent evolution of other traits exist as a consequence of strong genetic correlations with flower production.

11.2 Sexual dimorphism in the study species, *S. latifolia*

Sexual dimorphism has been studied extensively in the dioecious plant *S. latifolia* (Table 11.1), perhaps in part because it is a short-lived, herbaceous perennial that commonly flowers in its first year, making it highly amenable to both phenotypic and genotypic analyses. It is Eurasian in origin, but has naturalized in North America (McNeill 1977). It has white, scented flowers that open at dusk

Table 11.1 Sexual dimorphism exists in many traits in *S. latifolia*. The magnitude of the dimorphism for each trait is calculated here using the sexual dimorphism index (SDI) of Lovich and Gibbons (1992): (larger mean/smaller mean)−1, with values shown as positive when the mean for females is larger than the mean for males (F > M) and negative when the mean for males is larger than the mean for females (M > F). For those traits whose magnitude of dimorphism could not be quantified as above, the direction of the magnitude of dimorphism is indicated as F > M or M > F. Traits followed by an asterisk compare males with pollinated females.

Trait	Magnitude of dimorphism	References
Morphological/mass		
Plant height	0.15 to 0.44	Lyons *et al.* (1994)
Leaf size	0.11 to 0.24	Delph *et al.* (2002), Steven *et al.* (2007)
Calyx width	0.34 to 0.80	Meagher (1992), Delph *et al.* (2002), Delph *et al.* (2004a), Delph *et al.* (2004b), Steven *et al.* (2007), Carroll and Delph (1996)
Calyx length	0.06 to 0.23	Delph *et al.* (2002), Steven *et al.* (2007)
Petal–limb length	0.06 to 0.18	Carroll and Delph (1996), Delph *et al.* (2002), Delph *et al.* (2004b)
Petal–limb diameter	0.07	Carroll and Delph (1996)
Flower mass	1.10 to 2.28	Gross and Soule (1981), Carroll and Delph (1996), Laporte and Delph (1996), Gehring and Linhart (1993), Lyons *et al.* (1994), Delph *et al.* (2004a), Delph *et al.* (2004b), Steven *et al.* (2007)
Pedicel mass	3.8	Carroll and Delph (1996)
Flower number*	−13.23 to −16.32	Carroll and Delph (1996), Delph and Meagher (1995), Laporte and Delph (1996), Gehring *et al.* (2004)
Allocation		
Investment in leaf biomass	0.13 to 0.20	Gross and Soule (1981), Delph and Meagher (1995), Steven *et al.* (2007)
Investment in reproduction	0.42 to 0.79	Gross and Soule (1981), Gehring and Linhart (1993), Delph and Meagher (1995)
Investment in vegetative biomass	0.07	Delph and Meagher (1995)
Total biomass	0.10 to 0.74	Lovett Doust *et al.* (1987), Gehring and Linhart (1993), Lyons *et al.* (1994), Delph and Meagher (1995)
Nectar sugar/flower	1.82 to 2.86	Gehring *et al.* (2004)
Nectar volume/flower	3.09 to 4.00	Gehring *et al.* (2004)
Total nectar sugar/plant*	−6.70	Gehring *et al.* (2004)
Ecophysiological/life-history		
Leaf life-span	F > M	J. Gehring and L. Delph, unpublished work, Delph *et al.* (2005)
Specific leaf area	−0.02 to −0.08	Delph *et al.* (2002, 2005)
Stomatal conductance	−0.36 to −0.47	Gehring and Monson (1994), Delph *et al.* (2005)
Photosynthetic rate*	−0.03 to −0.17	Gehring and Monson (1994), Laporte and Delph (1996), Delph *et al.* (2005)
Transpiration rate	−0.24 to −0.29	Delph *et al.* (2005)
Dark respiration rate	−0.14 to −0.80	Laporte and Delph (1996), Delph *et al.* (2005)
Water-use efficiency	0.36	Gehring and Monson (1994)
Percentage oxygen sensitivity	F > M	Laporte and Delph (1996)
Tolerance to competition	F > M	Lovett Doust *et al.* (1987), Lyons *et al.* (1994)
Seedling emergence time	−0.06	Purrington and Schmitt (1998)
Age at first flowering	0.02	Purrington and Schmitt (1998)
Longevity	F > M	Correns (1928), Gehring and Linhart (1993)

(Jürgens *et al*. 2002) and is primarily pollinated by night-flying moths that feed on nectar, including moths in the genus *Hadena*, which oviposit within the ovary (Shykoff and Bucheli 1995; Wolfe 2002; Young 2002). *S. latifolia* has heteromorphic sex chromosomes, wherein three genes located in the non-recombining portion of the Y chromosome turn plants into males by both preventing ovule production and allowing anther development (Lengerova *et al*. 2003).

Females are larger than males in overall biomass and plant height, but as can be seen in Table 11.1 a host of morphological/mass, allocation, and eco-physiological/life-history traits have been shown to be sexually dimorphic. For example, flowers from females are larger than those from males in terms of the dimension, mass, and nutrient content of homologous parts, and they also contain more nectar (Table 11.1; see also Carroll and Delph 1996). In contrast, males make up to 16 times more flowers over the same time period as pollinated females (Laporte and Delph 1996; Meagher and Delph 2001). This highly dimorphic production of flowers alters the architecture of males relative to females because every time a new flower is produced a new branch has to be made (Figure 11.1). Their greater flower production also leads to males investing more in nectar on a per-plant basis than females (Gehring *et al*. 2004).

In terms of allocation of carbon, females invest more than males in leaf biomass (in part by making bigger leaves), stem biomass, and reproductive biomass, a phenomenon that runs counter to the idea that females must trade-off something in order to invest more in reproduction relative to males. In fact, females invest more in all components of growth even though males have higher rates of gas exchange (Table 11.1). Lastly, not only do females grow larger than males, they are also more tolerant of competition and live longer.

Figure 11.1 Flowering branches of an individual female (top) and male (bottom) *S. latifolia*, exhibiting sexual dimorphism 1 month after the onset of flowering. As seen here, males typically produce more flowers, each of which is smaller than those on females, and as a consequence males branch more than females. Scale: width of figure = 50 cm.

11.3 Multi-population common-garden experiment

To more fully investigate sexual dimorphism and as a start to looking into the question of trait integration, we grew seeds from nine populations from around the world in a common-garden experiment (Delph *et al*. 2002). This allowed us to do several things. First, it allowed us to fully characterize sexual dimorphism in the species. For example, did all populations exhibit sexual dimorphism in the same traits and did the degree of sexual dimorphism in any given trait vary among the populations? Lande (1980a) has argued theoretically that the mean of a trait should evolve more readily than the degree of sexual dimorphism. Hence our prediction was that population trait means would differ from each other more than would the degree of dimorphism. Second, which trait was the most dimorphic? We were interested in this question because we thought that this would give us insight into the trait most likely to be directly under disruptive selection. Third, was the degree of sexual dimorphism in other traits influenced by their correlation with the most sexually dimorphic trait? Our rationale here was that if traits were genetically correlated and selection on one trait was driving indirect selection on other traits (Figure 11.2), then a correlation should show up. We grew plants in a greenhouse and measured a total of eight traits, including flower-size traits, leaf traits, and allocation traits (Table 11.2).

We found that trait means differed quite remarkably among the populations for all eight traits, but the degree of sexual dimorphism was much less variable, as was predicted (Table 11.2). Only calyx width and calyx length exhibited a significant sex-by-population interaction, indicating that the degree of dimorphism varied among populations. The most sexually dimorphic trait was flower number. Moreover, there was a significant positive relationship between the degree of sexual dimorphism for each trait and the phenotypic correlation of each trait with flower number. This result supports the hypothesis that correlations among traits might be constraining the independent evolution of some traits. Lastly, a continuum was revealed, with plants from Portugal at one end and those from Croatia at the other. Plants from Portugal produced few, large flowers, thick leaves, and invested relatively heavily in leaf biomass. In contrast, plants from Croatia produced many relatively small flowers, thin leaves, and invested relatively heavily in stem biomass.

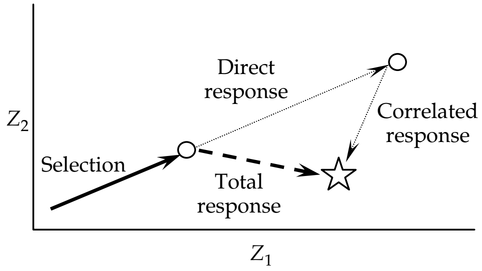


Figure 11.2 Schematic view of correlated response to selection on two traits. The vector of selection on two traits is shown as a solid arrow pushing the bivariate mean of two traits (circles). In the absence of genetic correlations, the direct response to selection represents all evolutionary change. When two traits are genetically correlated, the correlated response to selection can cause evolution to deviate significantly from the direction of selection (star). In the illustrated example, a negative genetic correlation with Z_1, which experiences stronger selection, causes Z_2 to evolve in the direction opposite to selection on Z_2.

Table 11.2 Traits measured in the among-population study and whether they differed significantly (a) among populations, (b) between the sexes (percentage sexual dimorphism calculated as the difference between the female and male trait means, divided by the male mean, multiplied by 100), and (c) whether the degree of dimorphism varied among populations.

Traits	(a) Are there among-population differences in trait?	(b) Is there sexual dimorphism in the trait?	(c) Does the degree of dimorphism vary among populations?
Flower number	Yes	Yes (71%)	No
Calyx width	Yes	Yes (51%)	Yes
Calyx length	Yes	Yes (12%)	Yes
Petal–limb length	Yes	Yes (6%)	No
Leaf length	Yes	Yes (28%)	No
Leaf thickness	Yes	No (6%)	No
Leaf mass	Yes	Yes (9%)	No
Stem mass	Yes	Yes (32%)	No

11.4 Quantitative-genetic crossing experiment

The correlations in the multi-population study were phenotypic rather than genetic. Consequently, the results, which suggested that selection on one trait could influence the evolution of other traits, while informative, were nevertheless inconclusive because several processes can cause apparent links among traits even when they are not actually genetically correlated (Armbruster and Schwaegerle 1996). We therefore undertook a quantitative-genetic crossing experiment to quantify the heritability of traits and the between-sex and among-trait genetic correlations (Steven *et al*. 2007). This genetic variance–covariance matrix, referred to as the **G** matrix, quantitatively characterizes how net selection on a focal trait can be affected both directly by selection and by selection on other traits correlated with the focal trait (Lande 1980b).

We started with seeds from over 100 different maternal plants from a single population, grew up seeds from these families, and did a cross-classified breeding design in which each father was crossed to each of three non-sib, unrelated mothers to produce 150 full-sib families nested within both paternal half-sib and maternal relationships. We then grew up multiple offspring from each of these families and measured seven traits, which included flower-size traits, flower number, leaf traits, and allocation traits.

The results from this experiment were in concordance with the multi-population study. All traits were found to have significant heritability and flower number was again found to be the most sexually dimorphic trait. Furthermore, flower number was significantly genetically correlated with all of the other measured traits. Specifically, flower number and all measures of flower size were negatively genetically correlated, substantiating the size/number trade-off. Furthermore, flower number was strongly correlated with leaf thickness: plants with few flowers had thicker leaves compared to those with more flowers (J. Steven and L. Delph, unpublished work). In general, the various traits were genetically integrated, with only one genetic correlation not being significantly different from 0 in males, and with two-thirds of the correlations being significant in females. Lastly, the between-sex genetic correlations were all significantly greater than 0 and less than 1, ranging from 0.59 to 0.86. The two highest between-sex correlations were for calyx width and leaf length, 0.81 and 0.86, respectively. These correlations suggest that variation in these traits is affected by some of the same alleles in both sexes, but also that some of it is affected by alleles with sex-limited effects. Overall, the results indicate that selection to change flower or leaf size in one sex will indirectly result in a change in the same trait in the other sex, and that suites of traits will change in response to selection on any one of the traits.

11.5 Artificial-selection experiment

A powerful way to test for genetic integration among traits is to artificially select on one trait and look for correlated responses in others (Conner 2003). This process allows one to calculate realized heritabilities and genetic correlations. We therefore designed an experiment to reduce the sexual dimorphism in flower size and number via artificial selection (Delph *et al*. 2004a). Of the two traits, flower size and flower number, flower size seemed to be fairly canalized, whereas flower number appeared quite plastic, varying with such things as pot size and nutrient addition (L. Delph, personal observation; see also Steven *et al*. 2007). Hence, we chose to artificially select on a measure of flower size, calyx width, rather than flower number, essentially betting on there being a genetically based size/number trade-off that would allow us to simultaneously alter both traits. We performed two separate experiments for replication, with similar results.

Our artificial selection took the form of sex-specific selection in which we selected for flowers on males to be more female-like—that is, larger—and for flowers on females to be more male-like—that is, smaller. We also had control lines in which we randomly selected individuals for the next generation. We grew a total of five generations for each experiment, starting with the base generation and ending after four generations of selection.

We measured calyx width in every generation, and in the last generation we measured gametophyte production and a host of morphological, allocation, and physiological traits, looking for correlated responses. We considered a correlated response to be significant if there was a significant difference among selection lines within a sex, but we also considered it informative if an existing difference between the sexes was eliminated or if one were created.

11.5.1 Changes in flower size and number

We found a strong response to direct selection on flower size (Delph *et al*. 2004a). Females selected for small flowers actually produced flowers with smaller calyces than did males selected for large flowers (Figure 11.3). We were able, therefore, to affect a reversal of the normal pattern of sexual dimorphism across selection lines via selection. In addition to reversing the pattern of dimorphism, we also expanded the phenotypic range of calyx size for each sex across selection lines because of a strong realized between-sex genetic correlation (Figure 11.3). In other words, males selected for large calyces produced daughters with exceptionally large calyces relative to other females, and vice versa for the sons of females selected for small calyces. Although between-sex genetic correlations are theoretically not supposed to be larger than 1.0, averaged over both experiments our mean value (1.08) was higher than this, because the sex not under selection sometimes responded more than the sex under selection. Clearly, variation in this trait is controlled by some of the same alleles in the two sexes.

In addition to seeing a strong response to selection on flower size, we also saw the predicted correlated response in flower number, with the average strength of the correlation between size and number being −0.52 (Delph *et al*. 2004a). Even so, we were not able to completely eliminate the sexual dimorphism in this trait—males still always made more (and lighter) flowers than females. Nevertheless, the expansion of phenotypic variation within each sex for both flower size and number afforded us an opportunity to measure how other traits covaried with this variation.

11.5.2 Correlated responses in gametophyte production

Our measurements of how gametophyte (pollen and ovule) production per flower covaried with flower size gave us insight into why sexual dimorphism evolved in the direction it did, namely the unusual case of flowers on males being smaller than those on females (for a temperate species; see Delph *et al*. 1996). Whereas ovule

Figure 11.3 Calyces of flowers from the artificial selection on calyx width, exhibiting the range of phenotypes among the selection lines and within each sex. Calyces of flowers from females are in the top row, and those from males are in the bottom row. The flowers on the left and right end of each row represent extreme individuals from the small- and large-selection lines, respectively. The two central flowers represent individuals with a calyx width close to the mean for the small (second from left) and large (third from left) selection lines.

number increased significantly with calyx width, pollen production did not (Delph *et al*. 2004a). The same number of pollen grains was produced in large flowers as in small flowers. Hence, because of the size/number trade-off, a male that made larger flowers would make less pollen than a male that made small flowers. In contrast, a female that made larger flowers would make more ovules per flower than a female that made small flowers and could therefore pay fewer fixed costs (Charnov 1979) for the same number of ovules.

How does this help us envision why sexual dimorphism evolved in the direction it did? Consider calyx width to be a homologous trait and assume an ancestral state of monomorphism in size. If there were selection for greater flower production in males, perhaps via mating success, then this would have led to selection for smaller flowers because of the negative genetic correlation between size and number. Elaborate floral displays have been shown to enhance mating success more for males than females in some species (e.g. Bell 1985), and pollinators have been shown to prefer plants with large floral displays in *S. latifolia* (Shykoff and Bucheli 1995). Conversely, given the correlation between calyx width and ovule number it seems plausible that there might be selection to keep flower size large (and therefore not increase flower number) or perhaps even increase flower size (and actually decrease flower number). Hence, selection for more flowers in males but large flowers in females may be the form of disruptive selection that took place to create males with smaller flowers than females.

11.5.3 Correlated responses in traits affecting life-history trade-offs

In addition to looking for a flower size/number trade-off and a flower size/gametophyte trade-off, we were also interested in determining whether flower number traded off with traits that affect life history, such as allocation and physiological traits (Delph *et al*. 2005). For example, would a plant that made many, small flowers allocate less biomass to leaves and have an upregulated physiology? We already knew that males had higher rates of photosynthesis and respiration than females, suggesting this might be true (Gehring and Monson 1994; Laporte and Delph 1996). Would the leaves of a plant with many, small flowers senesce earlier than those on plants with few, large flowers? Or are these traits independent of one another? To answer these questions we measured a host of ecophysiological traits. Overall we predicted that genetic correlations between floral display and ecophysiological traits might lead to a higher cost of reproduction for plants with elaborate floral displays and, in particular, males.

We found a host of correlated responses (Delph *et al*. 2005). In both sexes, the individuals that made the fewest, largest flowers also invested more in leaf biomass and had thicker leaves than small-flowered individuals (Figure 11.4a–c). Large-flowered individuals also had lower rates of gas exchange compared to those that made a lot of small flowers. One month after flowering began, plants in the small-flowered selection line had the highest photosynthetic and transpiration rates and the most negative respiration rates (Figure 11.4d–f). In other words, individuals producing a relatively large number of flowers were acquiring more carbon, but were losing more water as a result, and they were also "breathing" carbon out at a higher rate. The consequence of this upregulated physiology was that leaves on many-flowered plants senesced at a younger age, and were thereby not able to fix carbon for as long as leaves on few-flowered plants (Delph *et al*. 2005).

Overall, these results mirrored the observations from the multi-population study in that suites of traits went together. For example, the small-flowered selection lines were similar to Croatian plants in making a lot of small flowers and having thin leaves, and the lines in which plants made a few large flowers were similar to Portuguese plants, with thick, long-lasting leaves. They also matched the conclusions of the quantitative-genetic experiment of there being genetic correlations between flower size/number and other traits such as leaf mass, stem mass, and leaf thickness.

11.6 Summary

In this chapter, I have described three studies investigating patterns of genetic integration

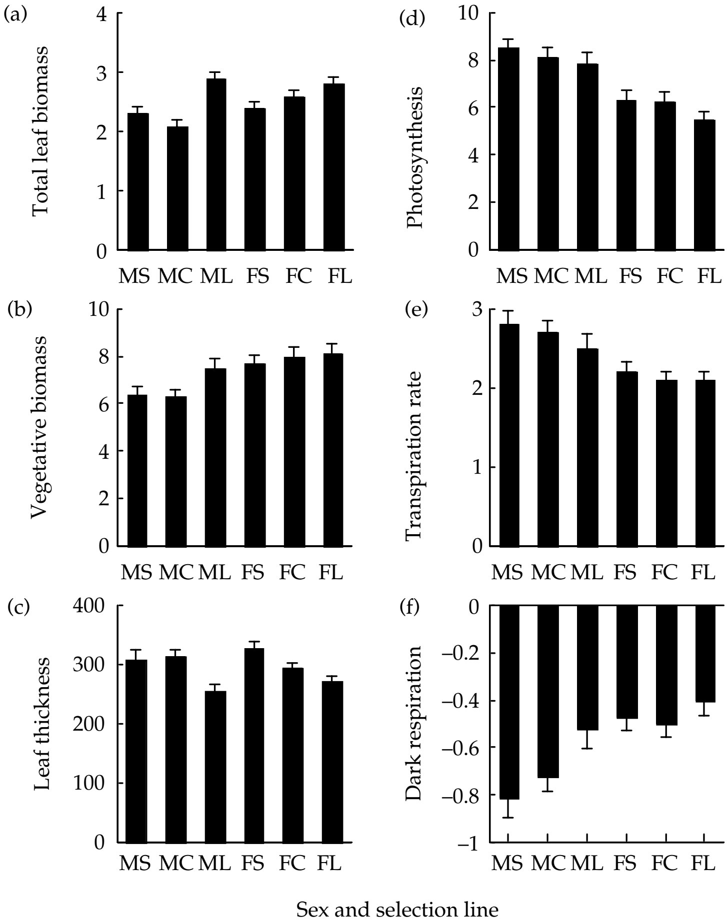


Figure 11.4 Means (± SE) of traits for the different selection lines in the last generation of one of the artificial-selection experiments (Selection Program 1, Delph *et al.* 2005): MS, males from the small-calyx selection line; MC, males from the control line; ML, males from the large-calyx selection line; FS, females from the small-calyx selection line; FC, females from the control line; FL, females from the large-calyx selection line. Units of measure are as follows: total leaf biomass (g), vegetative biomass (g), leaf thickness (specific leaf area, cm^2/g), photosynthesis ($\mu mol/m^2$ per s), transpiration ($mmol/m^2$ per s), and dark respiration ($\mu mol/m^2$ per s).

among sexually dimorphic traits in the dioecious, flowering plant *S. latifolia*. The first study compared trait values among populations from across the geographic range of the species. The second described the quantitative-genetic architecture of these traits, based on a half-sib pedigree breeding design. In the third study, we selected on flower size and observed the direct and indirect responses of our correlated traits. All three studies strongly support the hypothesis of genetic integration among sexually dimorphic traits in *S. latifolia*, such that selection for sexual dimorphism in any one trait will lead to a host of changes in other traits and thereby affect the phenotype and extent of sexual dimorphism of many traits. The most sexually dimorphic trait, and therefore plausibly the trait under direct selection to differ among the sexes, is flower number. Flower production was likely selected to be high in males as a way of making more pollen and low in females as a way of making large flowers containing more ovules. This scenario is based on the presence of a flower size/number trade-off combined with the fact that larger flowers produce more ovules but do not produce more pollen. Flower number was found to be genetically correlated with all measured traits, and the pattern of covariation of flower number and traits expected to impact life-history trade-offs was in accord with the hypothesis that the production of large numbers of flowers leads to a cost of reproduction that cannot be easily understood by simply measuring biomass allocation. Taken together, the results from this work highlight the utility of taking a multi-trait, quantitative-genetic approach to understanding why the sexes differ from each other.

11.7 Acknowledgments

I thank the editors for the invitation to contribute a chapter on sexual dimorphism in plants. I am grateful to all those who worked with me on the research summarized herein, including M. Arntz, E. Brodie III, S. Carroll, F. Frey, J. Gehring, F. Knapczyk, M. Laporte, M. Levri, T. Meagher, and J. Steven. I thank I. Capellini and C. Lively for comments on an earlier version of this chapter.

The National Science Foundation supported this research.

11.8 Suggested readings

Ashman, T.-L. (2005) The limits on sexual dimorphism in vegetative traits in a gynodioecious plant. *American Naturalist* **166**, S5–S16.

Bond, W.J. and Maze, K.E. (1999) Survival costs and reproductive benefits of floral display in a sexually dimorphic dioecious shrub, *Leucadendron xanthoconus*. *Evolutionary Ecology* **13**, 1–18.

Kohorn, L.U. (1994) Shoot morphology and reproduction in jojoba: advantages of sexual dimorphism. *Ecology* **75**, 2384–2394.

CHAPTER 12

Dimorphism in the hartebeest

Isabella Capellini

12.1 Introduction

Sexual size dimorphism (SSD) is highly variable across mammals and birds (see Chapters 2 and 3 in this volume). Sexual-selection theory predicts that, in polygynous species, different lifetime reproductive strategies of the sexes lead to more intense intrasexual competition among males for access to mates (Darwin 1871; Andersson 1994). This will promote the evolution of increased male size relative to females, as well as more complex fighting structures or extravagant and exaggerated traits, if males bearing such traits gain an advantage over competitors and achieve higher reproductive success (Darwin 1871; Andersson 1994). It follows that species with greater potential for polygyny should exhibit larger dimorphism in size and in structures linked to male intrasexual competition.

However, some mammals and birds under relatively intense sexual selection exhibit low dimorphism (see Chapters 2 and 3). Whereas sexual selection for smaller and more agile males can explain the low SSD in birds (Székely *et al*. 2004; Raihani *et al*. 2006; Chapter 3), natural selection opposing sexual selection has been invoked in explaining the low SSD of strepsirhine primates (Kappeler 1990). I will explore the interaction between sexual selection and natural selection in the evolution of SSD in the hartebeest (*Alcelaphus* spp.), a group of African antelopes with little dimorphism, and investigate whether forces linked to natural selection may constrain the evolution of a greater dimorphism in this lineage. Because body size is likely to be under different selective forces, I will also investigate whether, and to what extent, sexual and natural selection interact in the evolution of dimorphism in hartebeest weaponry, and finally whether fighting structures are expensive traits to grow.

Comparative analyses have shown that mating system and the potential for polygyny explain much variation in SSD across mammals (see Chapter 2). Similarly, dimorphism in canine size is greater in primates and carnivores under more intense sexual selection (Gittleman and Van Valkenburgh 1997; Thoren *et al.* 2006). Horn length in male African bovids, and antler length in male cervids, correlate with group size (a surrogate measure for the potential for polygyny), suggesting that investment in weaponry is under sexual selection (Clutton-Brock and Albon 1980; Popp 1985) and implying that dimorphism in fighting structures should be greater in polygynous than in monogamous species. Behavioral studies in ungulates also support the sexual-selection hypothesis by showing that big males achieve higher fighting and/or mating success than small ones (e.g. Clutton-Brock *et al.* 1982; Apollonio *et al.* 1989; Gosling and Petrie 1990). Similarly, Soay sheep rams (*Ovis aries*) that are more successful in monopolizing females and reproducing, are heavier, in better physical condition, and have more massive horns for their size (Preston *et al.* 2003).

Some species under moderate intensity of sexual selection exhibit lower than expected SSD, and in these taxa natural selection may counterbalance the selection for size divergence between the sexes (e.g. the strepsirhine primates; Kappeler 1990). In ungulates, habitat primary productivity may be an important limiting factor in the evolution of a larger SSD. Long-term data on cohort variation in size in temperate ungulates show that not only are individuals born in years of limited food supply smaller as adults than those born when resources are abundant, but also that their SSD is lower; indeed, male growth appears more affected by food scarcity than female growth (Post *et al.* 1999; Toigo *et al.* 1999; Le Blanc *et al.* 2001). In addition, investment in horns (at a given body size) decreases when environmental conditions are unfavorable, and males allocate more resources to body growth rather than weaponry (Festa-Bianchet *et al.* 2004). Although these studies highlight the importance of habitat productivity for the development and phenotypic expression of body size and horn dimensions, they also suggest that the evolution of SSD and investment in weaponry can be opposed by natural selection in poor environments.

The hartebeest lineage represents an ideal model in which to test the interaction of sexual and natural selection in the evolution of dimorphism in body size and fighting structures. Although hartebeest have evolved recently (less than 1 million years ago; Vrba 1997; Flagstad *et al.* 2001), the eight allopatric subspecies (grouped into the two species *Alcelaphus lichtensteini* and *Alcelaphus buselaphus*) have spread across all the African savannahs and diverged in body size, coloration, and horn size and shape (Kingdon 1997). Compared to other antelopes, hartebeest have low levels of dimorphism, as both sexes bear horns and have similar body masses (Jarman 1983). Previous work on four subspecies showed that the degree of dimorphism varies across hartebeest taxa; whereas males are about 8% heavier than females in Swayne's (*A. b. swaynei*; Mattravers Messana 1993) and Lichtenstein's hartebeest (*A. lichtensteini*; Booth 1985), they are 23% heavier in red hartebeest (*A. b. caama*; Smithers 1971).

Male hartebeest fight fiercely to defend (or gain) a territory, and thus access to reproduction, and severe injuries are not unusual (Gosling 1975; Booth 1985). When fighting, the opponents drop on their knees and deliver a hammer-like blow; further clashes may follow before horns are interlocked and males begin wrestling (Gosling 1975). During the wrestling phase, they push forward with great energy and may also attempt to force the opponent's head on one side, so that his shoulders and throat would be exposed and could be stabbed with a hooking movement of the horn tips (Gosling 1975). The pedicel, a bony structure that bears the horns (Figure 12.1), is a typical and unique trait of the alcelaphines, and is particularly developed in the hartebeest (Vrba 1997). The pedicel is believed to be an adaptation to fighting that improves protection of the head by displacing the impact point of clash farther away from the braincase (Gosling 1975), and therefore should be under sexual selection (Grubb 2000). Similarly, males with more massive skulls should be better protected against the opponent's blow, but also able to deliver more powerful blows themselves (Geist 1966; Grubb 2000).

Here I test whether (1) dimorphism in body size in hartebeest is under sexual selection and (2) natural selection balances the evolution of a larger body-size dimorphism. Furthermore, I will

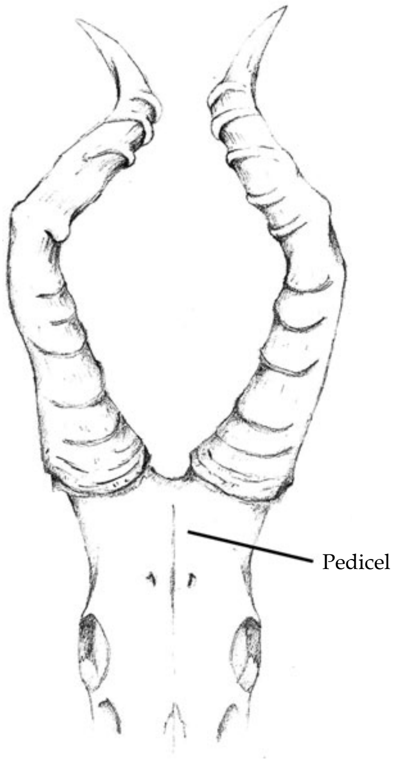


Figure 12.1 Horn morphology and pedicel in a female red hartebeest specimen from the Seeis Conservancy (Namibia). Horn shape varies greatly across subspecies (Kingdon 1997), but not between sexes within each subspecies.

compare the findings on body-size dimorphism with previous results on dimorphism in fighting structures. According to the sexual-selection hypothesis, dimorphism in body size and fighting structures should be greater in hartebeest subspecies under more intense sexual selection. If natural selection opposes the evolution of dimorphism via environmental productivity, dimorphism in body size and weaponry should be higher in more productive and less seasonal habitats, since seasonality limits the temporal availability of resources (Bourliere 1983) for growing bigger and building up weaponry.

12.2 Methods

I measured horn dimensions, pedicel height, skull weight, and basal skull length on 382 (126 females and 256 males) museum specimens belonging to eight hartebeest subspecies (details in Capellini and Gosling 2006). Only adult skulls of known sex, taxon, and locality of collection were considered. Age was determined on the basis of tooth wear after Gosling (1975). Horn dimensions were measured with a plastic non-elastic rope, commonly used for trophy records, whereas a folding ruler was used for pedicel and skull length, and a spring balance was used for skull weight (details in Capellini and Gosling 2006).

Basal skull length (from the anterior edge of the foramen magnum to the tips of the premaxillae) significantly correlated with mean shoulder height using data from the literature (females: $F_{1,7} = 21.36$, $R^2 = 0.78$, $P = 0.004$; males: $F_{1,7} = 21.61$, $R^2 = 0.78$, $P = 0.004$; Capellini and Gosling 2007), and thus was used to quantify variation in body size across taxa and between the sexes. It could be argued that body mass is more important in intrasexual competition and should be used in place of any linear measurement of size. However, Gosling and Petrie (1990) showed that the most successful topi males (*Damaliscus lunatus*) in a lekking population were taller than the least successful ones. Furthermore, in a detailed study on fallow deer (*Dama dama*), linear measurements of size, but not body mass, predicted mating success (McElligott *et al.* 2001).

Investment in horns was assessed through horn length (along the anterior midline), as in previous comparative studies, and basal horn circumference. Biomechanical analyses showed that larger horn bases better absorb and disperse the forces released during clashes, and that species in which males fight more fiercely have larger horn bases (Schaffer and Reed 1972; Kitchener 1985, 1988). Broken horns were not measured and only prime age skulls were included in the analyses on horn length, since old individuals, particularly males, have shorter horns than younger ones, due to horn grounding and fighting (Gosling 1975). Pedicel height was assessed as the length from the middle point, on the line connecting the superior edges of the orbits, up to the top of the pedicel (Capellini and Gosling 2006). In addition, I measured skull weight as a general estimate of investment in fighting structures (horns, pedicel, skull robustness). Only complete specimens were weighed (Capellini and Gosling 2006).

Two-way analysis of variance (ANOVA) was used to investigate variation in fighting structures and skull length across subspecies, the sexes, and their interaction. Dimorphism within each subspecies was assessed with independent-samples *t* tests (two-tailed). Trait dimensions were divided by basal skull length to correct for size, and ratios log-transformed to achieve normality, prior to statistical analysis. The critical level of statistical significance was 0.05 in all tests.

Dimorphism was quantified as the log ratio of male to female trait size (log(M/F); Smith 1999), and regressed against independent factors linked to sexual and natural selection (see below). Phylogenetic independent contrasts were employed to correct for similarity between taxa due to common ancestry (Harvey and Pagel 1991; Garland *et al.* 1992). Contrasts were calculated with CAIC (Purvis and Rambaut 1995), and the phylogeny and branch lengths were taken from Flagstad *et al.* (2001).

The intensity of sexual selection was measured by group size and duration of the peak breeding season, surrogate indicators of the potential for polygyny. Data on group size were extracted from numerous studies (references in Capellini and Gosling 2006); weighted means were calculated for each subspecies and represented an estimate of the potential for polygyny in space. The duration of the peak breeding season, when most copulations occur (Gosling 1975; Mattravers Messana 1993), was assumed to reflect the potential for polygyny in time, with shorter seasons leading to increased intensity of male competition (Gosling 1986). No data were available on the length of the reproductive season in the extinct bubal (*A. b. buselaphus*) of North Africa and Tora hartebeest (*A. b. tora*) of Ethiopia.

Mean annual rainfall represented a proxy for habitat productivity (defined here as grass quality and quantity; for details Capellini and Gosling 2007), as it strongly influences grass productivity across African regions, and within one region between years (Bourliere and Hadley 1970; Bourliere 1983). Because savannah productivity varies also temporally in response to climatic seasonality (Bourliere 1983), the index of relative seasonality described in Walsh (1981; eqn 12.1) was chosen to express the distribution of precipitation over the year. This index ranges between 0 and 1.83, with higher values indicating greater seasonality. Climatic data were extracted from the tables of the Meteorological Office of Great Britain (1972) and Griffiths (1972), and values assigned to each specimen from the closest climatic station to the locality of collection (details in Capellini and Gosling 2007). Means of the environmental predictors were then computed for each subspecies range.

$$\mathrm{SI} = \frac{\sum_{n=1}^{n=12} \left| \bar{X}_n - \left(\frac{\bar{R}}{12} \right) \right|}{\bar{R}} \qquad (12.1)$$

In eqn 12.1, SI is the index of seasonality, $\bar{X}_n$ is the mean rainfall of month n, and $\bar{R}$ is the mean annual rainfall.

12.3 Results

12.3.1 Investment in fighting structures and in body size across subspecies and sexes

Fighting structures varied between hartebeest subspecies (two-way ANOVAs; horn circumference, $F_{6,215} = 20.28$, $P < 0.001$; horn length, $F_{5,95} = 81.87$, $P < 0.001$; pedicel height, $F_{6,200} = 11.76$, $P < 0.001$; skull weight, $F_{6,189} = 16.64$, $P < 0.001$), the sexes (horn circumference, $F_{1,215} = 590.28$, $P < 0.001$; horn length, $F_{1,95} = 119.98$, $P < 0.001$; pedicel height, $F_{1,200} = 65.47$, $P < 0.001$; skull weight, $F_{1,189} = 311.95$, $P < 0.001$), and the subspecies × sex interaction was significant for horn circumference ($F_{5,215} = 7.86$, $P < 0.001$) and horn length ($F_{5,95} = 3.06$, $P = 0.013$) but not for pedicel height ($F_{5,200} = 1.64$, $P = 0.150$) and skull weight ($F_{5,189} = 0.59$, $P = 0.734$). Further analyses showed that males invest more in fighting structures than females, even after accounting for differences in body size (Figure 12.2a–d; Table 12.1; details in Capellini and Gosling 2006). Furthermore, the degree of investment differed across subspecies (Capellini and Gosling 2006). For example, female investment in horn circumference was similar across taxa, but it varied in males (Figure 12.2b).

Thus hartebeest subspecies could be broadly classified as heavily armed (Lelwel (*A. b. lelwel*), Lichtenstein's, western (*A. b. major*), and red hartebeest) or lightly armed (Coke's (*A. b. cokei*), Swayne's, Tora, and bubal hartebeest). When computed as log(M/F), dimorphism in all fighting structures was relatively large, ranging, for example, between 0.086 (Coke's) and 0.170 (Lichtenstein's) in horn circumference (Table 12.1; Figure 12.3). The largest dimorphism was found in skull weight, from 0.213 (Coke's) to 0.295 (Swayne's; Table 12.1; Figure 12.3; Capellini and Gosling 2006).

Body size varied among subspecies ($F_{6,215} = 47.48$, $P < 0.001$) and the sexes ($F_{1,215} = 30.10$, $P < 0.001$; interaction, $F_{5,215} = 0.46$, $P = 0.806$). The sexes differed significantly in skull length in five out of eight hartebeest subspecies (Table 12.1). There was no significant difference between the sexes in Swayne's hartebeest ($t = 1.35$, df $= 7$, $P = 0.219$), but sample sizes were particularly small in this subspecies ($N = 4$ females, $N = 5$ males). However, dimorphism in skull length was low in all taxa, ranging between 0.011 and 0.021 (Table 12.1; Figure 12.3). Therefore, albeit dimorphic in body size, the difference between the sexes was small in all subspecies. Not only do male hartebeest invest more in fighting structures than females (Capellini and Gosling 2006), they also appear to invest relatively more in weaponry than in body size (Figure 12.3), and the degree of such an investment varies across subspecies (Figure 12.3),

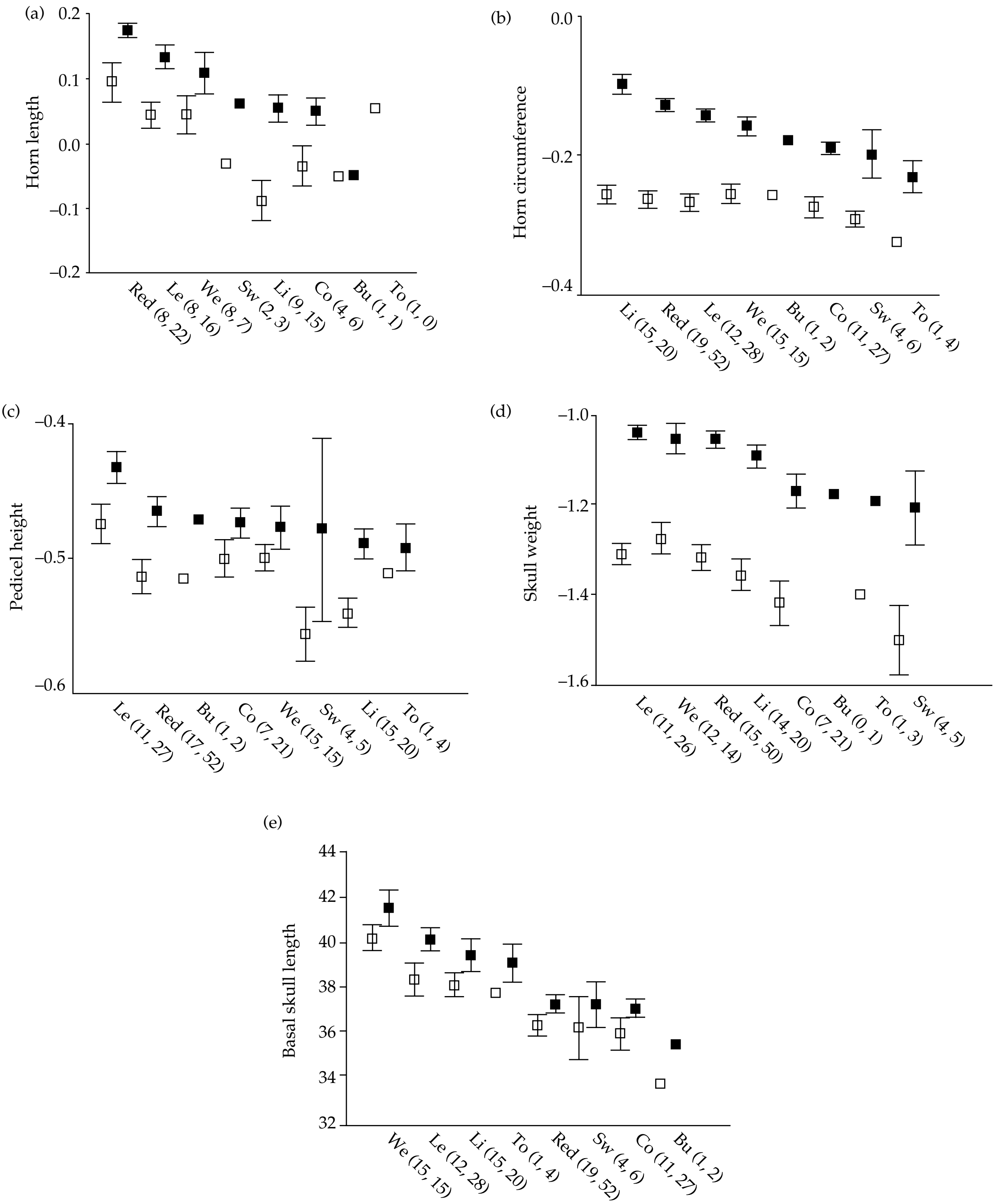


Figure 12.2 Mean ± 2 SE in (a) horn length, (b) horn circumference, (c) pedicel height, (d) skull weight, and (e) basal skull length in male and female hartebeest. Trait measurements were divided by skull length and log-transformed. Basal skull length (in cm) was not transformed. Males, black squares; females, white squares. Subspecies order follows male trait size from the biggest to the smallest. Subspecies names are as follows: Bu = bubal, Co = Coke's. Le = Lelwel, Li = Lichtenstein's, Red = red, Sw = Swayne's, To = Tora, We = Western. Sample sizes, for females and males respectively, are in brackets after the subspecies name on the X-axis.

Table 12.1 Dimorphism in horn circumference, horn length (only prime-age individuals, see text), pedicel height, skull weight and skull length in each hartebeest subspecies. Dimorphism is given as log(M/F) and as SDI ((size of the larger sex/size of the smaller sex)−1), set as negative when males are the larger sex (Lovich and Gibbons 1992). Independent-samples *t* tests were carried out on $\log_{10}$(trait size/body size) except in Tora and bubal hartebeest due to small sample size.

Subspecies	**Dimorphism, SSD, SDI (df, *P*)**				
	Horn circumference	**Horn length**	**Pedicel height**	**Skull weight**	**Skull length**
Bubal	0.111, −0.290	0.023, −0.053	0.066, −0.163	–	0.021, −0.050
Red hartebeest	0.144, −0.393 (69, <0.001)	0.075, −0.189 (28, <0.001)	0.065, −0.162 (67, <0.001)	0.275, −0.885 (63, <0.001)	0.011, −0.026 (69, 0.012)
Coke's hartebeest	0.086, −0.220 (36, <0.001)	0.099, −0.255 (8, 0.001)	0.036, −0.086 (26, <0.001)	0.213, −0.632 (26, <0.001)	0.013, −0.031 (36, 0.004)
Lelwel hartebeest	0.139, −0.377 (38, <0.001)	0.121, −0.320 (21, <0.001)	0.060, −0.149 (36, <0.001)	0.283, −0.921 (35, <0.001)	0.020, −0.046 (38, 0.008)
Lichtenstein's hartebeest	0.170, −0.480 (33, <0.001)	0.157, −0.434 (22, <0.001)	0.070, −0.175 (33, <0.001)	0.268, −0.852 (32, <0.001)	0.015, −0.034 (33, 0.010)
Western hartebeest	0.116, 0.307 (28, <0.001)	0.076, 0.192 (13, 0.011)	0.043, 0.105 (28, 0.025)	0.229, 0.695 (24, <0.001)	0.013, 0.031 (28, 0.016)
Swayne's hartebeest	0.105, −0.273 (7, 0.006)	0.097, −0.249 (3, 0.036)	0.064, −0.159 (6, 0.049)	0.295, −0.971 (7, 0.002)	0.014, −0.033 (7, 0.219)
Tora hartebeest	0.099, −0.257	–	0.034, −0.081	0.228, −0.069	0.015, −0.034

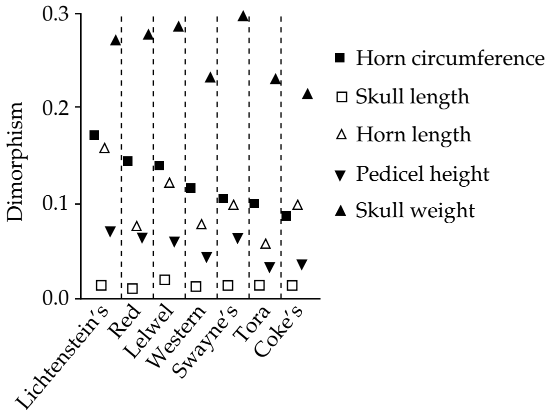


Figure 12.3 Dimorphism as log(M/F) in horn length, basal skull length, pedicel height, skull weight, and horn circumference. Species are arranged from the largest to the smallest value in horn circumference.

probably in response to different intensity of selective pressures.

12.3.2 Dimorphism and sexual selection

Group size did not influence dimorphism in fighting structures (Table 12.2), but the length of the breeding season negatively affected pedicel height and skull weight, showing a similar, non-significant tendency for horn circumference (Table 12.2; Capellini and Gosling 2006). Neither predictor correlated with dimorphism in horn length (Capellini and Gosling 2006) and skull length (Table 12.2). Hence variation in the overall investment in fighting structures across subspecies, as quantified by skull weight, appeared to be determined by differences in the intensity of sexual selection, and specifically by the temporal availability of receptive females (Capellini and Gosling 2006).

Capellini and Gosling (2006) argued that, although group size is a good proxy for the potential for polygyny in cervids (Clutton-Brock and Albon 1980) and bovids (Popp 1985), it might not be so for analyses at lower taxonomic levels such as between subspecies. Perhaps sexual selection on males might be better quantified by direct measurements of the intensity and frequency of fights that, for example, correlate with canine size dimorphism across primates (Plavcan *et al.* 1995).

Results on the pedicel support the hypothesis that this structure is an adaptation to fighting and is under sexual selection (Capellini and Gosling

Table 12.2 Correlations (*r*) and statistical probabilities (*P*) derived from phylogenetic comparative analysis using bivariate least-squares regressions through the origin of independent contrasts in dimorphism in response variables against contrasts in group size, length of the breeding season, annual rainfall, and seasonality. Dimorphism was quantified as $\log_{10}$(male trait/female trait). Significant results are highlighted in italics. Seven subspecies were involved in all analyses, except in length of breeding season ($n = 6$ subspecies).

Response variable	Correlation (*r*), statistical probability (*P*)			
	Group size	Length of breeding season (months)	Mean annual rainfall (mm/yr)	Index of seasonality
Horn circumference	0.17, 0.68	−0.73, 0.10	0.53, 0.17	−0.04, 0.93
Horn length	−0.14, 0.73	−0.46, 0.36	*0.83, 0.01*	0.00, 0.99
Pedicel height	0.01, 0.98	*−0.96, 0.02*	0.15, 0.73	−0.42, 0.30
Skull weight	0.32, 0.49	*−0.91, 0.01*	0.04, 0.94	−0.09, 0.85
Skull length	−0.17, 0.69	−0.53, 0.28	0.09, 0.83	−0.62, 0.11

2006). Unexpectedly, neither horn length nor horn circumference correlated with the intensity of sexual selection. However, horn circumference exhibited a tendency to increase when the peak of the breeding season is short. If the pedicel increases protection of the head, this might lead to less intense selection for larger horn bases in this group of antelopes (Capellini and Gosling 2006), hence the weaker correlation between horn circumference dimorphism and breeding-season length.

12.3.3 Dimorphism and natural selection

Climatic factors linked to habitat productivity and environmental seasonality did not influence size dimorphism in hartebeest (Table 12.2). Dimorphism in fighting structures was not correlated with mean annual rainfall, with the sole exception of horn length (Table 12.2; Capellini and Gosling 2006), a trait that was previously found unrelated to sexual selection. In agreement with studies on environmental effects on horn development in temperate bovids (Toigo *et al.* 1999; Le Blanc *et al.* 2001; Festa-Bianchet *et al.* 2004), these results suggest that horns are expensive traits to grow. Therefore, both sexual selection and natural selection have to be considered when studying horn evolution and, more in general, the evolution of weaponry.

Finally, seasonality was not associated with dimorphism in any trait (Table 12.2). This climatic factor may lead to contrasting selective pressures linked to both natural and sexual selection (Capellini and Gosling 2006). On the one hand, in more seasonal environments high-quality trophic resources are limited to a brief period (Bourliere 1983), hence investment in weaponry and size should be constrained. On the other hand, the length of the breeding season tends to be shorter in more seasonal habitats (Gosling 1986; Capellini and Gosling 2006), leading to more intense male competition for access to reproduction, and thus promoting investment in larger male body size and more massive fighting structures.

12.4 Conclusions

Investment in fighting structures appeared to be under both positive sexual selection, through the temporal availability of receptive females, and natural selection in the opposite direction, limiting the investment in weaponry (horn length) through habitat productivity (as quantified by mean annual rainfall). These conclusions are in agreement with observational studies in Coke's and Lichtenstein's hartebeest showing that males compete fiercely for access to reproduction, and fights can lead to the death of one opponent (Gosling 1975; Booth 1985). It follows that if sexual selection has promoted the evolution of fighting structures in the hartebeest, it should also act on body size and favor larger male size. However, body-size dimorphism (skull length) was low, varied little across hartebeest subspecies in comparison to dimorphism in fighting structures, and was unrelated to any surrogate measure of the intensity of sexual selection. Therefore, other selective forces might oppose sexual selection and limit investment in male size in these antelopes. Hartebeest size appears to have evolved in response to habitat productivity, so that subspecies living in more productive savannahs are larger than those in poorer environments (Capellini and Gosling 2007), and the evolution of longer horns seems to be constrained by savannah productivity (Capellini and Gosling 2006). Likewise grass productivity might represent an important limiting factor for the evolution of a higher body-size dimorphism in this group of antelopes. Contrary to this prediction, neither habitat productivity nor seasonality explain dimorphism in body size, suggesting that lower savannah productivity in space and time does not limit the investment in male size, and thus the evolution of greater dimorphism.

Natural selection may oppose sexual selection for larger male size through other mechanisms. For example, in many strepsirhine primates that exhibit low dimorphism in body mass despite a polygynous mating system, selection for agility in relation to anti-predator strategies may oppose the evolution of larger male size (Kappeler 1990). Agile males are preferred by females in pronghorn antelope (*Antilocapra americana*), an ungulate with intense male–male competition but little sexual dimorphism (Byers *et al.* 1994). Byers (1998) suggested that smaller males are more agile and better able to escape predators, and argued that a similar scenario might occur in some African antelopes. The alcelaphines are among the fastest bovids in Africa, and are mostly preyed upon by lions (*Panthera leo*) and hyaenas (*Crocuta crocuta*; Dowsett 1966; Gosling 1975; Gosling and Petrie 1990; Scheel and Packer 1995), although occasionally also by cheetahs (*Acinonyx jubatus*; Dowsett 1966; Gosling 1975). Because predation pressure appears to be higher in young subadult males excluded from female groups than in other social classes (Gosling 1975), agility and speed to escape predators may favor the survivorship of smaller agile males in hartebeest and, more generally, in antelopes. Agility may also have influenced the evolution of dimorphism in relation to sexual selection and male competition, rather than natural selection. In birds, species with more acrobatic displays have lower SSD (Székely *et al.* 2004; Raihani *et al.* 2006; Chapter 3). Similarly, agility may also be an important component in male competition in antelopes. In case of the hartebeest, male fights are fierce and agility during fighting is probably a minor component. However, satellite males may gain an advantage by being smaller and more agile, for example when they attempt to disperse female groups guarded by territorial males and possibly sneak copulations.

Alternatively, selective pressures such as intrasexual competition and/or fecundity advantage may favor larger female size, resulting in lower body size dimorphism. As in males, large females might be favored in agonistic interactions. Competition among female ungulates occurs in several species (e.g. Clutton-Brock *et al.* 1982; Festa-Bianchet 1991; Fairbanks 1994) and arises through limited access to high-quality food (Clutton-Brock *et al.* 1982, Dennehy 2001) and, at least in topi, also to high-quality mates (Bro-Jorgensen 2002). Female hartebeest interfere overtly during copulations of territorial males in Lichtenstein's (Dowsett 1966), Coke's (L.M. Gosling, personal communication), and red (I. Capellini, personal observation) hartebeest. Large females may also achieve higher reproductive success (Andersson 1994). For example, large females are more likely give birth to heavier offspring, which in turn have better chances of survival and future reproductive success (Clutton-Brock *et al.* 1982; Albon *et al.* 1983; Steinheim *et al.* 2002). At present no data are available for hartebeest to assess the importance and role of these factors in the evolution of dimorphism in body size and fighting structures. Future field studies are needed to address these issues and to achieve a better understanding of the evolution of size dimorphism in mammals in relation to female intrasexual selection, female reproductive strategies, and agility.

12.5 Summary

Sexual selection favors the evolution of dimorphism in body size and fighting structures when large males with massive weaponry achieve high reproductive success. However, some mammalian species under moderate sexual selection exhibit unexpectedly low dimorphism, suggesting that sexual selection may be opposed by natural selection. I used hartebeest, a group of African savannah antelopes, to test the interaction between natural and sexual selection in the evolution of dimorphism in body size and fighting structures (horns, pedicel, skull robustness). In all hartebeest subspecies the sexes differed significantly in the dimensions of weaponry, and the degree of dimorphism was high and variable among them. Conversely, although the sexes differed significantly in body size in at least five subspecies, size dimorphism was small. Hence, not only do males invest more in weaponry than females, but they also invest more in fighting structures than in size.

The potential for polygyny, a surrogate for the intensity of sexual selection, explained dimorphism in fighting structures across hartebeest subspecies, although it did not predict dimorphism in body size, suggesting that sexual selection toward large dimorphism has probably been opposed by natural selection. Habitat productivity, which drives the evolution of hartebeest body size, explained dimorphism in horn length across hartebeest subspecies, supporting the hypothesis that horns are expensive traits to grow. However, savannah productivity was not a limiting factor for larger size dimorphism in hartebeest. Anti-predator advantages of smaller and more agile males might oppose sexual selection and limit the evolution of a larger male size. Alternatively, intrasexual competition for food and/or mates among female hartebeest or a fecundity advantage might select for an increase in female size, resulting in the low dimorphism of these antelopes.

12.6 Acknowledgments

I am grateful to all the museums that allowed access to their hartebeest collections and to all the collection managers for their help and assistance: Natural History Museum, London, UK; Royal Belgian Institute and Museum of Natural Sciences, Brussels; Royal Museum for Central Africa, Tervuren, Belgium; Museum für Naturkunde, Berlin; Senckenberg Museum of Natural History, Frankfurt, Germany; Muséum National d'Histoire Naturelle, Paris, France; Museo di Storia Naturale La Specola, Florence; Museo di Storia Naturale, Milano; Museo di Storia Naturale G.Doria, Genova, Italy. Special thanks to Morris Gosling for useful discussions and allowing me access to his hartebeest collection; to the Seeis Conservancy (Namibia) and Aldo Oriani for access to their private collections; Seth Eiseb, the Seeis Conservancy, and Birgit and Harald Förster for their assistance in Namibia; and Ted Garland and Mark Pagel for help with the phylogenetic analysis. I am grateful to Lynda Delph, David Carrier, Tamas Székely, and Wolf Blanckenhorn for their valuable comments on earlier versions of the manuscript. This research was supported by the ABC Grant Improving Human Resource Potential Program of Brussels, the Coldparsyst Program of Paris, the University of Milan, and the University of Newcastle upon Tyne.

12.7 Suggested readings

Perez-Barberia, F.J., Gordon, I.J., and Pagel, M. (2002) The origins of sexual dimorphism in body size in ungulates. *Evolution* **56**, 1276–1285.

Roberts, C.S. (1996) The evolution of hornedness in female ruminants. *Behaviour* **133**, 399–442.

CHAPTER 13

Sexual size dimorphism and offspring vulnerability in birds

Ellen Kalmbach and Maria M. Benito

13.1 Introduction

Evolutionary theories trying to explain the existence and patterns of sexual size dimorphism (SSD) across taxa often focus on selection on body size at the adult stage, mainly driven by sexual selection acting on males or fecundity selection on females. However, the size dimorphism observed in adults can be determined not only by selection during adulthood (Blanckenhorn 2000), but also by selection on growth or size at earlier stages. It is therefore necessary to include ontogeny as an important period for determining final size dimorphism (e.g., Badyaev 2002; see also Chapters 7, 9, 19, and 20 in this volume).

Besides genetic constraints on how to achieve dimorphic growth while conserving the genes for the complete developmental programme in both sexes, physiological constraints during development can also limit final size. In sexually dimorphic species, size-related viability and health costs can become detectable as sex-biased effects. Increased mortality of the larger sex is the most extreme result, but other sub-lethal fitness effects can also be size- and sex-specific. A main focus in this respect is body mass, or size, of offspring, as this is often related to survival or probability of recruitment and regarded as a prime measure of offspring quality (Hochachka and Smith 1991; Potti *et al.* 2002). More recently, aspects of immunocompetence have been investigated as another measure of sex differences in physiological health and quality (Fargallo *et al.* 2002; Tschirren *et al.* 2003; Laaksonen *et al.* 2004; Bize *et al.* 2005; Chin *et al.* 2005; Müller *et al.* 2005a, 2005b). Although mortality, body mass, and immunocompetence are very diverse aspects of development, sex-biased reductions in offspring quality or survival can all be seen as manifestations of some disadvantage of one sex during the growth period. Collectively, these and any other negative effects on offspring quality and fitness are referred to as offspring vulnerability.

Differential offspring survival in a size-dimorphic species was probably first observed in humans: male fetuses and infants have a higher risk of dying than females (e.g. Süßmilch 1765). Male bias in offspring mortality has also been documented in other mammals (Clutton-Brock *et al.* 1985) and birds (Roskaft and Slagsvold 1985; Teather and Weatherhead 1989; Griffiths 1992; Müller *et al.* 2005a, 2005b). Most of these species have in common that males are the larger sex. To achieve their larger size, males are likely to have higher energy demands during growth, which in turn might make them more vulnerable to a shortage of resources, leading to increased mortality.

Alternative, size-independent explanations have been proposed to explain the observed male-biased offspring vulnerability in many mammals and birds. The one that has received most attention is the male-phenotype hypothesis. Size-independent aspects of physiology, in particular the high levels of testosterone needed for male sexual differentiation, might negatively impact on other aspects of development, such as immunocompetence (Olsen and Kovacs 1996; Fargallo *et al.* 2002). In order to tease apart the importance of male phenotype compared with the size effect on offspring mortality, it is necessary to include species where females are the larger sex.

In this chapter we will use recent studies of birds to explore patterns of sex-specific offspring vulnerability in relation to SSD in both directions; that is, female-biased as well as male-biased SSD. We will combine results on sex-specific offspring performance, and analyze mortality and plasticity of fledging mass in relation to SSD. If indeed size is the main reason for increased mortality of male offspring, then female offspring of species with female-biased SSD should experience similar disadvantages as males in species with male-biased SSD.

13.2 Measuring sex-biased offspring vulnerability in birds

Studies of sex-specific patterns of growth and mortality in birds have benefited hugely from the development of molecular sexing methods in the mid-1990s (Griffiths 1992; Ellegren 1996; Griffiths *et al.* 1998). Bird nestlings can usually not be sexed visually except in extremely size-dimorphic species, but even then only during the second half of the growth period (Cronmiller and Thompson 1980). A few earlier studies used laparotomy, a surgical incision of the abdomen, to inspect the gonads, but this could only be carried out in older chicks, not in hatchlings (Roskaft and Slagsvold 1985). Reports of sex-specific mortality between hatching and fledging could therefore not be based on individual fates. They were mostly inferred by comparing fledging sex ratios in nests with and without mortality (assuming equal hatching sex ratios in both nest categories), or by comparing fledging sex ratios with a sample of dissected clutches (Howe 1977) . As avian hatching sex ratios are frequently skewed in relation to such variables as parental condition or social status, the progressing season or territory quality (e.g. Komdeur *et al.* 1997; Heg *et al.* 2000; Kalmbach *et al.* 2001), comparing hatching and fledging sex ratios between different sub-samples of nests can lead to wrong conclusions about sex-biased mortality.

The most widely reported measure of nestling mortality is the survival probability from hatching to fledging. Using the difference between hatching sex ratio and fledging sex ratio as a measure for sex-specific mortality, a relationship between larger size and increased mortality was found across species with different degrees of SSD (Clutton-Brock *et al.* 1985). Sex differences in nestling mortality correlated with adult size dimorphism: the larger the males were in relation to females, the higher their survival disadvantage as nestlings. However, as only one species with female-biased size dimorphism was included in that review (which showed no sex bias in offspring mortality: Eurasian sparrowhawk, *Accipiter nisus*; Newton 1979), the size–mortality relationship therefore was shown only for species with larger males. Additionally, as the study dates before the advent of molecular sexing, its data suffer from the above-described methodological problems of obtaining true hatching and fledging sex ratios within the same nests. We will remedy this problem by employing strict selection criteria for the studies we include in our comparative analysis of nestling mortality (see Section 13.3.1).

Sex-biased mortality represents the extreme case of sex differences in offspring vulnerability. As mentioned above, growth rate and size at fledging are also regarded as a measure of offspring performance. Because of its likely negative impact on future life stages, reduced size at fledging is seen as a manifestation of non-optimal conditions during ontogeny (Hochachka and Smith 1991; Haywood and Perrins 1992; Potti *et al.* 2002). Assuming that under ideal conditions individuals will grow to the maximum possible size (given their species, genes, and sex), the degree of size reduction under suboptimal conditions gives an indication of how much the growing organism was struggling.

Considering that the larger sex is likely to have a higher energy demand during growth than the smaller one, we would predict that during periods of scarce resources the larger sex would be affected disproportionately. To test this prediction, we will compare fledging mass of males and females under varying circumstances (Section 13.3.2). We use mass rather than some structural measure of size, such as wing or tarsus length, for two reasons. Body mass is probably the easiest of those measures to record in the field, and is the one most frequently reported in publications. Second, our choice of mass reflects the fact that for birds adult SSD is most commonly reported as the dimorphism in mass.

13.3 Comparative analysis of SSD and nestling vulnerability

The modulation of vulnerability differences between the two sexes by environmental conditions is referred to as sex-biased environmental sensitivity. It is generally assumed that poor conditions increase the disadvantage of the weaker sex. In order to investigate environmental sensitivity, comparisons of offspring performance under varying environmental conditions need to be made (Sheldon *et al.* 1998). Most simply, this can be a dichotomy between a ″good″ and a ″poor″ environment. Increasingly, these contrasting situations are created by experimental manipulation of the environment during ontogeny. Such experimental approaches include brood size increase and decrease, manipulation of parental condition and workload, provision of supplementary food, or changes of the parasite load (Richner 1992; Sheldon *et al.* 1998; Nager *et al.* 2000; Bize *et al.* 2005; Råberg *et al.* 2005). However, comparisons might also be made between naturally occurring good and poor conditions, for example between first and last hatchlings in asynchronous broods or between seasons of abundant and low food availability (Wiebe and Bortolotti 1992; Brommer *et al.* 2003; Goymann *et al.* 2005). As restricting data to either experimental or observational studies would greatly reduce the number of available species, we included both types of study in the following comparative analyses.

To correct for the species' phylogenetic relatedness, we employed a comparative approach following the method of phylogenetically independent contrasts (Harvey and Pagel 1991; Garland *et al.* 1992). Contrasts were calculated using the program CAIC (Purvis and Rambaut 1995), and the phylogeny was taken from Sibley and Ahlquist (1990). All statistical results were obtained using this comparative method, and are reported in Table 13.1. However, for illustrative purposes we show species data, including species-level trend lines, in our graphs. These are more accessible because of their biologically interpretable values. Regression lines are only shown for those relationships for which a significant effect was found in the analysis based on phylogenetically independent contrasts.

Table 13.1 Regression results of sex-specific vulnerability against SSD, using phylogenetically independent contrasts. (a) Nestling mortality from hatching to fledging against SSD. The dependent variable was hatching sex ratio, fledging sex ratio, or sex-specific chick mortality (calculated as fledging sex ratio minus hatching sex ratio). (b) Intraspecific fledging mass change under good and poor conditions against SSD. The dependent measure was the mass-change difference (Δflm female–Δflm male; see text), mass-change difference for experimental studies only, male change only, or female change only. SSD is the independent variable in all models. Models are based on phylogenetically independent contrasts. For the analysis presented here we used the molecular phylogeny by Sibley and Ahlquist (1990). The results were qualitatively the same when using a morphological phylogeny. All regressions are forced through the origin. The analyses were run with the program CAIC (Purvis and Rambaut 1995). R^2 is the proportion of variance in the independent variable explained by the predictor variable; r is the Pearson correlation coefficient.

Dependent variable	No. of species	No. of contrasts	R^2	r	P
(a) Nestling mortality					
Hatching sex ratio	45	13	0.02	−0.14	0.622
Fledging sex ratio	45	13	0.09	−0.29	0.303
Sex-specific mortality	45	13	0.29	−0.54	0.047
(b) Fledging mass change					
Female–male difference	21	19	0.32	0.57	0.008
Female–male difference (experimental studies only)	14	13	0.40	0.63	0.015
Male change	21	19	0.25	−0.50	0.025
Female change	21	19	0.00	0.00	0.980

13.3.1 Sex-biased mortality and sex ratios

As highlighted above, for the following sex ratio and mortality analyses, we only used data from studies that report sex ratio at hatching *and* fledging from the same study nests. Sex-ratio data for the cross-species analysis were taken from observational studies or from experimental studies, in cases where the sex ratios between experimental and control treatments did not differ.

Across species, we found a negative correlation between sex-biased mortality and size dimorphism that was consistent for species with male-biased and female-biased SSD (Table 13.1). The larger of the two sexes appears to suffer greater mortality; that is, more females die as nestlings in species with larger females, and more males die in species with larger males. The survival disadvantage increases with increasing size dimorphism. In other words, the larger sex always suffers higher mortality, indicating that to achieve a larger final body size both males and females pay a survival cost. On the species level, overall nestling mortality seemed slightly male-biased (Figure 13.1). This impression is supported by a negative average mortality value in the comparative analysis, suggesting that offspring survival was negatively affected by male-specific traits other than size.

Neither hatching nor fledging sex ratio showed a correlation with SSD (Table 13.1). At the population level, parents neither overproduced the smaller sex (as predicted by Fisher's (1930b) equal-investment sex-ratio theory) nor the larger sex to compensate for its higher mortality up to fledging. Despite the trend of increased mortality of the larger sex, and the unbiased hatching sex ratios, overall fledging ratios were not significantly biased

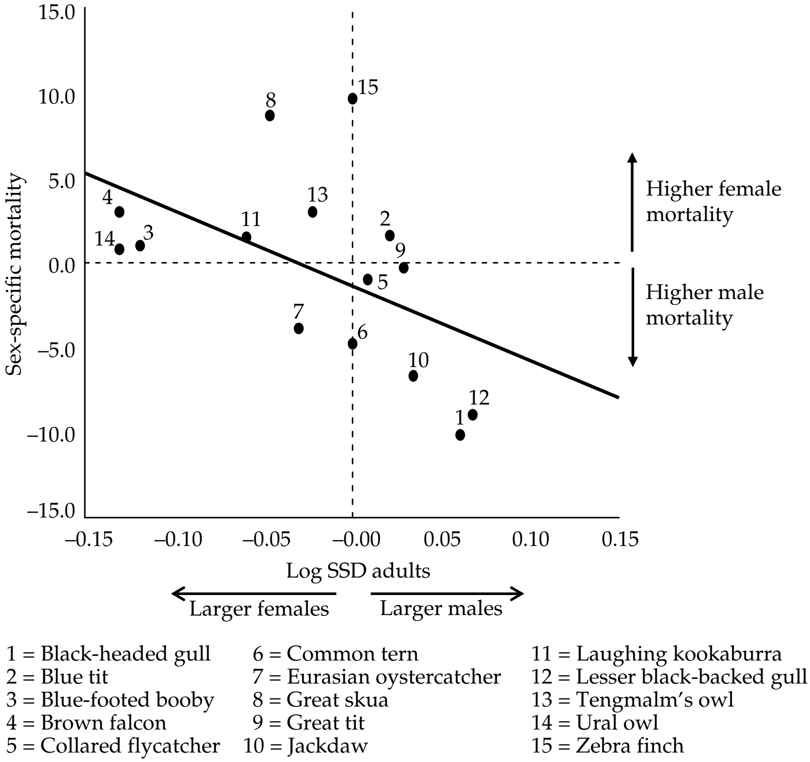


Figure 13.1 Relationship between SSD, calculated as log(male adult weight/female adult weight) and sex-specific chick mortality, calculated as fledging sex ratio minus hatching sex ratio. Species references: 1, Müller *et al.* (2005b); 2, Råberg *et al.* (2005); 3, Torres and Drummond (1999); 4, Mcdonald *et al.* (2005); 5, Sheldon *et al.* (1998); 6, Gonzalez-Solis *et al.* (2005); 7, Heg *et al.* (2000); 8, Kalmbach *et al.* (2005); 9, Oddie (2000); 10, Arnold and Griffiths (2003); 11, Legge *et al.* (2001); 12, Griffiths (1992); 13, Hornfeldt *et al.* (2000); 14, Brommer *et al.* (2003); 15, Bradbury and Blakey (1998).

towards the smaller sex (Table 13.1). This is likely due to the high variation of sex ratios among species and the relatively small number of species we could include based on our methodological criteria.

13.3.2 Fledging mass

In the following cross-species analysis, we used data from studies which reported sex-specific fledging mass under two different conditions that could be classified as either good or poor. In most studies those conditions were created through experimental manipulations, although we also included data from observational studies reporting sex-specific fledging mass (see Table 13.2 for classification of good and poor conditions). For each sex we set the average fledging mass under good conditions as the reference value, and expressed the difference between that and fledging mass under poor conditions as a percentage of the reference mass. We will call this difference Δ*flm* (delta fledging mass). As we are mainly interested in the difference between males and females with respect to their reaction to environmental conditions, we compared Δ*flm* of males and females within each species. We subtracted Δ*flm* of males from Δ*flm* of females to obtain one value per species. When positive, this value indicates that males lose relatively more mass compared to females, whereas when this value is negative males lose relatively less mass. For example, the value of −10.6 for great skua (*Stercorarius skua*) means that males lost 10.6% less of their reference body mass than females during poor rearing conditions (Kalmbach *et al.* 2005).

Across species, and across both directions of size dimorphism, birds of the larger sex suffered a greater mass reduction under poor conditions (Table 13.1; Figure 13.2). For monomorphic species the fledging mass differences are clustered around 0. This suggests that in the absence of size dimorphism neither sex has a consistently higher vulnerability. The overall pattern could indicate that having to grow to a larger size under suboptimal conditions is similarly difficult for males and females. However, when plotting Δ*flm* for males and females separately, we see that the pattern is mainly generated by a correlation between male fledging mass reduction and SSD (Figure 13.3). The more male-biased the SSD, the larger the impact of poor rearing conditions on male fledging mass, while female mass differences between good and poor conditions are independent of whether they are the larger or the smaller sex. This pattern remains when non-experimental studies are excluded from the data-set (Table 13.1).

Our results prompt an interesting consideration. The relative demands of having to grow large (for a given species) might not be as high as is generally assumed. Only in conjunction with the rest of the male phenotype does aiming for being large—that is, following a developmental program which leads to large size for a given species—appear to make the growing organism more vulnerable. Testosterone and its allies are much-cited candidates for mediating male vulnerability. Remarkably, in the species with the largest females and highest female mass loss (African black coucal), the breeding system is polyandrous. Although female behavior is 'masculinized', daughters' testosterone levels are lower than those of sons and even lower than those of nestlings of other species (Goymann *et al.* 2005).

13.4 SSD and environmental sensitivity of immunocompetence

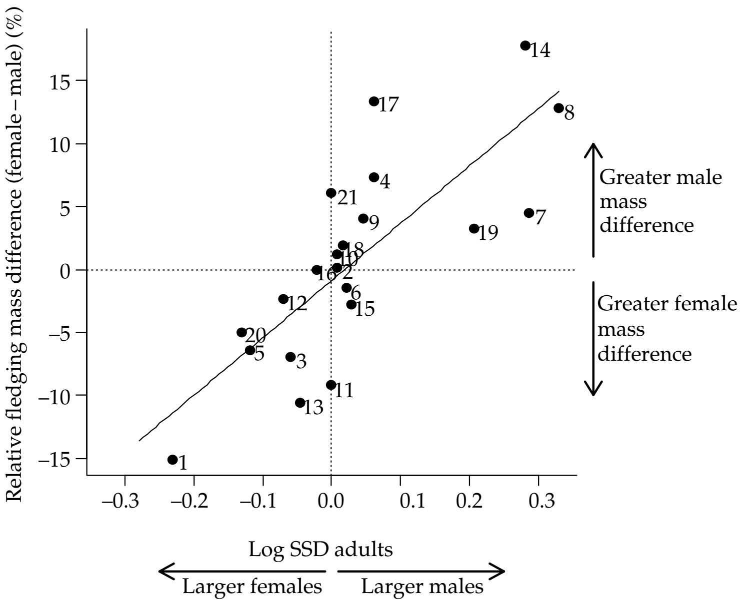
The immune system provides a potential link for life-history trade-offs (Sheldon and Verhulst 1996). It is relatively expensive to develop and maintain, but crucial for a successful life. Reduced immune capacity of nestlings is likely to indicate suboptimal conditions during development when resources have to be invested in other parts of the growing organism. Recently, a few studies investigated sex-linked differences of immunocompetence in varying environmental conditions.

In two of four studies there was no differential decrease in immunocompetence under poor conditions (great tit and alpine swift, adult SSD 1.07 and 1.02, respectively; Oddie 2000; Bize *et al.* 2005). In food-restricted nests of Eurasian kestrels (adult SSD 0.78), the (smaller) males showed a slightly

Table 13.2 Circumstances representing good and poor conditions in the studies which were included in the cross-species analysis of fledging mass. Log SSD is log(male adult mass/female adult mass); where available taken from the same study population, otherwise from reference literature. Type of study: obs, observational; exp, experimental.

Species	Log SSD	Type of study	Good/poor environment	Reference
Capercaillie, *Tetrao urogallus*	0.33	obs	Good against poor growth year due to temperature difference	Lindén (1981)
Helmeted guineafowl, *Numida meleagris*	−0.02	exp	Summer against winter rearing conditions	Baeza *et al.* (2001)
Lesser snow goose, *Anser caerulescens cearulescens*	0.06	obs	Seasonal environmental decline; earliest against penultimate category	Cooch *et al.* (1996)
African black coucal, *Centropus grillii*	−0.23	obs	Hatching order; "middle" against "late" chicks; earliest chicks were older at fledging	Goyman *et al.* (2005)
Alpine swift, *Apus melba*	0.01	exp	De-parasitized against parasitized broods	Bize *et al.* (2005)
Ural owl, *Strix uralensis*	−0.13	obs	Good and poor food years (vole cycles)	Brommer *et al.* (2003)
Great skua, *Stercorarius skua*	−0.05	exp	Control eggs against small replacement eggs	Kalmbach *et al.* (2005)
Lesser black-backed gull, *Larus fuscus*	0.06	exp	Control against poorer condition parents	Nager *et al.* (2000)
Black-headed gull, *Larus ridibundus*	0.06	exp	First against last hatched chick in all female and all male broods	Müller *et al.* (2005b)
Common tern, *Sterna hirundo*	0	obs	First against third hatched chicks	Becker & Wink (2003)
Eurasian kestrel, *Falco tinnunculus*	−0.07	exp	(a) Unisex broods in poor food years; (b) control against enlarged brood	(a) Laaksonen *et al.* (2004); (b) Dijkstra *et al.* (1990)
American kestrel, *Falco sparverius*	−0.06	obs	Good against poor food years	Wiebe & Bortolotti (1992)
Blue-footed booby, *Sula nebouxii*	−0.12	exp	Feather-clipping of mothers; chicks of control against chicks of clipped mothers	Velando (2002)
Carrion crow, *Corvus corone*	0.05	exp	Food-supplemented against un-supplemented nests in a food-limited population	Richner (1992)
Collared flycatcher, *Ficedula albicollis*	0.01	exp	Reduced against enlarged broods	Sheldon *et al.* (1998)
Great tit, *Parus major*	0.03	exp	Experimental nests of "large" and "small" nestlings; "large" against "small" nestlings	Oddie (2000)
Blue tit, *Parus caeruleus*	0.02	exp	Reduced against enlarged broods	Råberg *et al.* (2005)
Zebra finch, *Taeniopygia guttata*	0	exp	Abundant against restricted food	Kilner (1998)
Red-winged blackbird, *Agelaius phoeniceus*	0.21	exp	Control against enlarged broods	Cronmiller and Thompson (1980)
Boat-tailed grackle, *Quiscalus major*	0.29	obs	First against third hatched chicks	Bancroft (1984)
Great-tailed grackle, *Quiscalus mexicanus*	0.28	exp	Experimentally synchronized last hatchlings; having female nest mate against having male nest mate	Teather and Weatherhead (1989)

stronger decrease of cell-mediated immunity (CMI) than the (larger) females compared with control nests (Fargallo *et al.* 2002). CMI of male nestlings (larger sex) in large broods of European starlings (adult SSD 1.05) also decreased more strongly than CMI of female nestlings compared to values in smaller broods (Chin *et al.* 2005). So far these studies have reported either no sex bias or a



1= African black coucal
2 = Alpine swift
3 = American kestrel
4 = Black–headed gull
5 = Blue–footed booby
6 = Blue tit
7 = Boat tailed grackle
8 = Capercaillie
9 = Carrion crow
10 = Collared flycatcher
11 = Common tern
12 = Eurasian kestrel
13 = Great skua
14 = Great tailed grackle
15 = Great tit
16 = Helmeted guineafowl
17 = Lesser black–backed gull
18 = Lesser snow goose
19 = Red–winged blackbird
20 = Ural owl
21 = Zebra finch

Figure 13.2 Relative change of fledgling mass between good conditions and poor conditions against SSD, calculated as log(male adult weight/female adult weight). Each species value is calculated as female difference (Δ*flm* of females) minus male difference (Δ*flm* of males). Negative values indicate that males lost relatively less mass than females; that females are more vulnerable. Positive values indicate that males lost relatively more mass than females; that males are more vulnerable. The relationship between sex-specific change of fledging mass and SSD is significant using phylogenetic contrasts ($P = 0.008$; see Table 13.1). See Table 13.2 for references.

male bias, but no study has yet found decreased CMI for female nestlings. A second study of Eurasian kestrels, which investigated haematocrit as a measure of physiological condition, found a lower value for (larger) females under increased competition (Laaksonen *et al*. 2004).

The small number of studies and remaining controversy over the interpretation of CMI tests as well as hematocrit values make it clear that at this point no generalization about SSD and immunocompetence of fledglings can be made.

13.5 Intra-brood competition and size-related vulnerability

The dichotomy of good and poor conditions for reasons of comparison is of course a simplification of the much more complex, naturally occurring situation. In reality, rearing conditions vary across a multitude of gradually changing and interacting factors, not just in two extremes (although the latter happens, to some extent, in experimental studies). So far we have assumed physiological disadvantages of large size, which could be regarded as intrinsic vulnerability of the larger sex. However, nestlings interact with each other and size is often implicated in the outcome of intra-brood competition. Following the terminology of intrinsic vulnerability, we will call growth and viability disadvantages that result from social interactions extrinsic vulnerability.

In contrast to intrinsic disadvantages, larger individuals generally have a competitive advantage at the behavioral, extrinsic level (Anderson

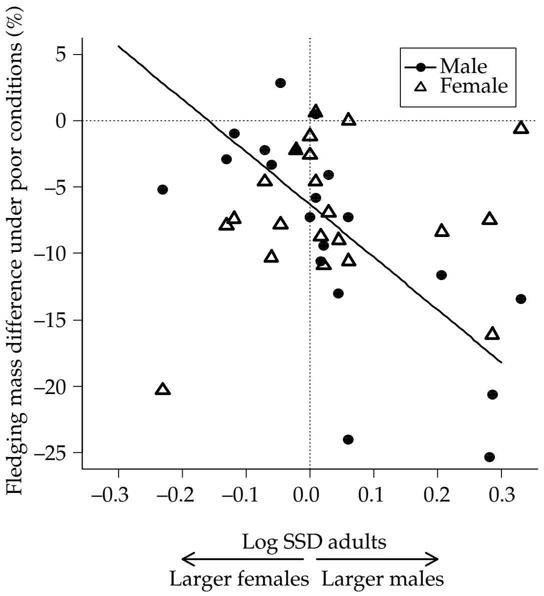


Figure 13.3 Relative difference of fledging mass between good and poor conditions against SSD, calculated as log(male adult weight/female adult weight) for male and female nestlings separately. The regression, based on phylogenetic contrasts, is significant for male nestlings, but not for female nestlings ($P = 0.025$ for males and $P = 0.978$ for females; see Table 13.1).

et al. 1993). Oddie (2000) showed experimentally that increased mortality of the smaller female great tit nestlings was mainly due to their competitive disadvantage. Similarly, Råberg *et al*. (2005) found that female blue tit nestlings (again the smaller sex) suffered more (reduced fledging size). They suggested that brood size, as an indication of the strength of intra-brood competition, could explain part of the variation around the overall pattern. Besides brood size, sex composition, and size and age differences among nest mates determine within-brood dynamics and add another layer of complexity. Depending on the social circumstances, for example in large broods, the competitive disadvantage of the smaller sex can outweigh its physiological advantages.

13.6 Sex-biased vulnerability and the evolution of SSD

Our cross-species comparison highlights two aspects of size-related offspring vulnerability that affect the extent of SSD exhibited in adult birds. First, across species there is a pattern that the larger sex has a viability disadvantage during ontogeny. This will cause a certain amount of viability selection during ontogeny against growing large. How strong this selection is will depend on many other aspects of each species' particular life history. For example it will be modulated by the ability of parents to adaptively skew primary sex ratios in response to environmental conditions, by the strength of sibling competition, by the type of breeding system and reproductive skew between the sexes, or by differential food allocation to offspring (Anderson *et al*. 1993; McDonald *et al*. 2005; Råberg *et al*. 2005).

Second, we found that across species the larger sex shows a stronger modulation of its relative fledging mass according to environmental circumstances. This can lead to a smaller degree of size dimorphism than would be predicted as optimal for adults. In the short term, sex-biased size reduction during ontogeny will create shifting patterns of SSD between cohorts or even within a season, tracking changes in environmental conditions (Cooch *et al*. 1996). If environmental degradation is a continuing process, size dimorphism in a population could decrease over time even though fecundity and sexual selection favor an increase.

Our results show a size-dependent modulation of male fledging mass in response to environmental conditions, but a size-independent mass reduction in female nestlings. This pattern suggests greater plasticity of male growth. On average, quantitative genetic studies indicate a slightly higher heritability of size in female birds (e.g. Jensen *et al*. 2003), which could reflect greater size plasticity in male fledglings. It remains a challenge to uncover the mechanisms permitting sex-biased evolution of growth patterns despite the shared gene pool between the sexes (Merilä *et al*. 1998; see also Chapters 16, 17, and 19).

13.7 Future studies

An important aspect of sex-specific environmental sensitivity is the timing of the occurrence of poor conditions relative to critical stages of offspring development. When cell numbers of specific organs are limited during a small time window of development, metabolism and growth during all subsequent stages can be affected. Such a mechanism is thought to be involved in increased health risks of persons who showed poor growth during gestation (Bateson *et al.* 2004). It is likely that the metabolic machinery to build differently sized individuals of the same species differs from early development onwards. Sex differences in energy allocation to specific organs might already cause higher vulnerability of the eventually larger sex before size dimorphism and differential energy requirements become apparent (Kalmbach *et al.* 2005). Similarly, poor conditions during a developmental phase when the sexes are still equal in size can cause sex- or size-specific effects later (Gorman and Nager 2003). Physiological studies are required to determine sex differences in physiology and energy allocation at very early stages. To tease apart intrinsic and extrinsic size-related vulnerability, growth experiments with hand rearing, having chicks raised as singletons by parents (Kalmbach *et al.* 2005), or creating same-sex and same-size broods (Oddie 2000; Müller *et al.* 2005b), will be useful.

The measures we used for the present analysis are rather broad, including the necessary dichotomous classification into good and poor conditions for the analysis of fledging mass. This was mainly determined by the availability of comparable variables for a larger number of species. Although mortality is no doubt an aspect of fitness, and fledging mass also appears to be fitness-related (Haywood and Perrins 1992; Potti *et al.* 2002), other aspects of an organism's state might be crucial for its subsequent performance. Studies of immunocompetence address this issue.

The between-sex effect of expected size (predicted by the average size of males and females of the species) on mortality and fledging mass indicates that size-related viability selection also occurs within each sex. To address this, it would be necessary to have prior individual-level knowledge of expected size, beyond the classification by sex, and to investigate how individuals of different predicted sizes of a given sex react to varying conditions. This approach was taken by Weatherhead and Dufour (2005), who analysed 30 years' of data for red-winged blackbirds. They found no survival differences between (predicted) large and (predicted) small males. As a predictor of size they used the mid-parent value, but the chicks were reared by their natural parents. A phenotypic correlation between large size and good parental abilities might thus mask size-related offspring vulnerability. The sizes of parents are themselves modulated by plasticity and are not a direct measure of genetic size. Using multi-generation animal models of wild populations or captive selection lines could reduce this problem (e.g. Kruuk *et al.* 2001; Teuschl *et al.* 2007).

13.8 Summary

We found cross-species correlations between sex-biased vulnerability (mortality and reduced fledging mass under poor conditions) and the extent of SSD in both directions (males or females larger). This indicates that being programmed to grow large carries viability costs. However, our comparison between fledging mass reached in good and poor environments suggests that having to grow large is mainly disadvantageous when coupled with the male phenotype. Female fledging mass differences between good and poor conditions were independent of SSD. On a behavioral level, larger size generally influences competitive ability positively. Despite physiological disadvantages of the larger sex, in unmanipulated broods the smaller sex might de facto be more vulnerable; that is, exhibit higher mortality or stunted growth (Anderson *et al.* 1993; Oddie 2000; Råberg *et al.* 2005).

Differences in environmental sensitivity between the two sexes during ontogeny, in the form of either increased mortality or reduced size, may select against dimorphism during development, affecting existing patterns of SSD in a given species. As such, environmental conditions are likely to play a major role in modulating SSD within or between generations. Given that there is a correlation of vulnerability with size predicted by sex, a similar size-related vulnerability would be expected within sexes. However, to determine the predicted size of an individual is much more difficult. We suggest that more experimental studies should be carried out with the aim of distinguishing between the physiological basis for vulnerability of being large and behavioral factors that can counteract such disadvantages.

13.9 Suggested readings

Kalmbach, E., Furness, R.W., and Griffiths, R. (2005) Sex-biased environmental sensitivity: natural and experimental evidence from a bird species with larger females. *Behavioral Ecology* **16**, 442–449.

Le Galliard, J.F., Ferriere, R., and Clobert, J. (2005) Juvenile growth and survival under dietary restriction: are males and females equal? *Oikos* **111**, 368–376.

Råberg, L., Stjernman, M., and Nillsson, J.-Å. (2005) Sex and environmental sensitivity in blue tit nestlings. *Oecologia* **145**, 496–503.

Sheldon, B.C., Merilä, J., Lindgren, G., and Ellergren, H. (1998) Gender and environmental sensitivity in nestling collared flycatchers. *Ecology* **79**, 1939–1948.

CHAPTER 14

Variation in sexual size dimorphism within a widespread lizard species

Evgeny S. Roitberg

14.1 Introduction

Lizards exhibit pronounced variation in the extent and direction of sexual size dimorphism (SSD; Fitch 1981; Cox *et al.* 2003; see Chapters 4 and 15 in this volume), and in recent decades they have been among the model groups for studying this phenomenon (Blanckenhorn 2005, p. 981). Most papers on SSD in lizards present either broad comparisons across species (e.g. Braña 1996; Chapters 4 and 15) or detailed analyses of individual populations (e.g. Watkins 1996; Rutherford 2004). Studies of patterns of intraspecific variation in SSD are less numerous and generally involve only few study populations (regional samples), or the study populations come from a small geographic area (Jenssen *et al.* 1995; Censky 1996; Wikelski and Trillmich 1997; Lappin and Swinney 1999; Flemming and Mouton 2001; Hasegawa 2003; Molina Borja 2003; Roitberg and Smirina 2006a). Only few studies (Parker and Pianka 1975; Fitch 1981; Zamudio 1998) provide more extensive data on geographic variation in SSD. Even for animals in general, extensive studies of geographic variation in SSD within species are quite rare (Rising 1987; Storz *et al.* 2001; Pearson *et al.* 2002; Fairbairn 2005; Tamate and Maekawa 2006). However, intraspecific variation is particularly promising for testing adaptive hypotheses (and other hypotheses related to current environmental conditions) because at this level the effect of phylogenetic conservatism is very small (Shine and Fitzgerald 1995; McCoy *et al.* 2003).

This chapter considers geographic variation in SSD for a widespread Eurasian lizard species, *Lacerta agilis*. First I document the variation in SSD across a large part of the species' range, examine its major trends, and check for correlations of this variation with morphology (body size), environment (climate), and phylogeny. Then, using samples of aged individuals, I evaluate the relative contribution of sex differences in growth trajectories and adult mortality in shaping adult SSD. Finally, I put my findings into the context of recent discussions on ultimate and proximate determinants of variation in SSD.

14.2 Study species

Lacerta agilis is a small to medium-sized lacertid lizard that occupies much of the temperate Palaearctic from the Pyrenees in Western Europe to the Baikal Lake in Siberia (Figure 14.1). This species is often abundant, easy to catch, and highly polymorphic, and has become a model species for comprehensive microevolutionary studies (Yablokov *et al.* 1980). Recent studies have provided an intraspecific phylogeny (Kalyabina *et al.* 2001; Kalyabina-Hauf and Ananjeva 2004) and detailed life-history data for several populations (Strijbosch and Creemers 1988; Olsson 1992, 1993; Olsson and Shine 1996; Gullberg *et al.* 1997). Together, these characteristics make *L. agilis* a particularly suitable subject for studying intraspecific variation in SSD.

14.3 Methods

14.3.1 Study samples and estimating adult body size

I collected original and published data on snout–vent length (SVL) from 52 local or regional samples

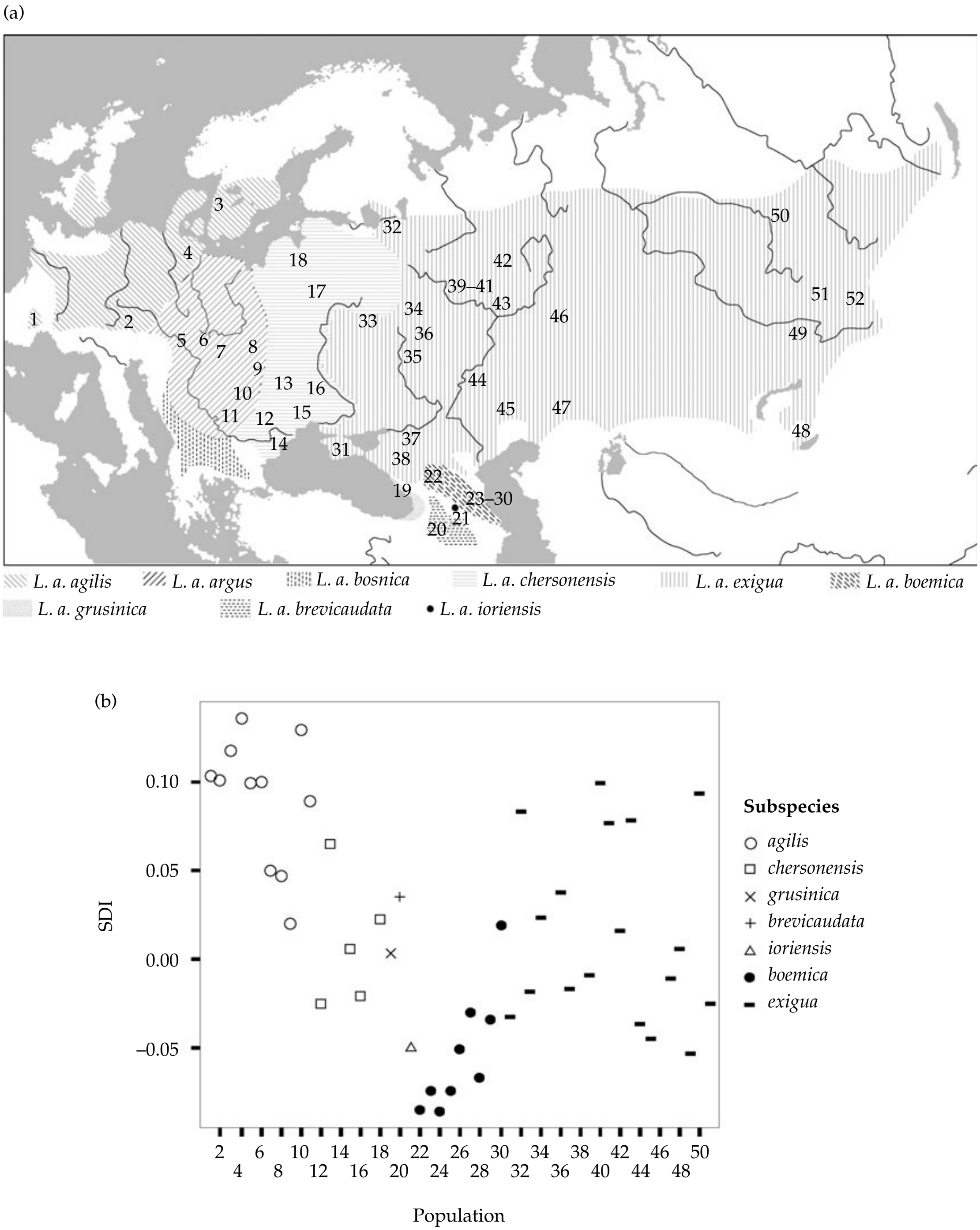


Figure 14.1 Geographic distribution of different subspecies of *L. agilis* (after Kalyabina *et al.* 2001, with modifications), study samples (a), and their variation for SSD (b). Following Rahmel (1988) I consider *L. a. argus* as a synonym of *L. a. agilis* in all analyses. SSD is estimated using the index of Lovich and Gibbons (1992): SDI = (size of larger sex/size of smaller sex) − 1, set as negative if males are the larger sex and positive if females are the larger sex (see text for further explanation).

across the species range (Figure 14.1a; see Appendix, Table A14.1). Each sample included at least 10 individuals of each sex (median sample size was 33 for males and 34 for females). A few samples were excluded from analyses for means because they exhibited unusually high variances and obviously included immature animals. Even for the rest of the data, criteria for including an individual in the sample may not have been identical among researchers. Moreover, in animals with substantial postmaturation growth, the size distribution of adults in a particular sample can be affected by proximate factors such as local and temporal variation in the proportion of newly matured animals, size at maturity, growth rates, and adult mortality (Stamps and Andrews 1992; Stamps 1993; Watkins 1996). The choice of an appropriate statistic for estimating adult body size is therefore an important methodological problem. Average and extreme values are the most widely used statistics, and they are often the only parameters available in publications. Average size is statistically powerful and provides reasonable estimates even for small sample sizes. However, the mean is particularly sensitive to the confounding factors mentioned above (Stamps and Andrews 1992; Stamps 1993). The maximum value and the higher percentiles are less powerful than the mean, but they are more resistant to any variation outside the upper area of the character distribution. These statistics have been proposed as estimators of the typical asymptotic size (the size of full-grown animals) in the population (Box 14.1).

To validate the use of means in my study, I repeated some analyses using maximum values and (whenever individual SVL data were available) the 80th percentiles of the size distributions. Estimates of SSD (see Section 14.3.2) based on these three statistics for characteristic body size showed very concordant variation (Table 14.1), validating the use of means in this study.

14.3.2 Estimating SSD

I quantified SSD with the sexual dimorphism index, SDI, equal to (size of the larger sex/size of the smaller sex) − 1, arbitrarily expressed as positive if females are larger and negative if males are larger (Lovich and Gibbons 1992). I chose this index because it generates values that are intuitive, directional, properly scaled, and symmetrical around 0 (Lovich and Gibbons 1992).

Table 14.1 Spearman rank correlations (r_s) between SSD calculated from different estimators of adult body length. The sexual dimorphism index, SDI = (size of larger sex/size of smaller sex) − 1, is arbitrarily expressed as positive if females are larger and negative if males are larger (Lovich and Gibbons 1992).

	SDI for 80th percentiles	SDI for maximum values
SDI for means	0.968 ($P < 0.01$, $N = 20$)	0.747 ($P < 0.01$, $N = 39$)
SDI for 80th percentiles		0.846 ($P < 0.01$, $N = 19$)

Box 14.1 Estimators of asymptotic size

In lizards and most other ectotherms, linear growth after maturity is usually asymptotic; that is, it slows progressively with size and virtually ceases at advanced size and age. The mean (typical) growth curve and its asymptote (A) can be developed from individual growth increments or body sizes of aged individuals (e.g. Brown *et al.* 1999). For comparative studies focusing on differences among populations or between sexes, asymptotic size (A) is a preferable statistic because it is affected by a much shorter list of proximate factors than average size (Stamps and Andrews 1992; Stamps 1993; Brown *et al.* 1999). As growth curves are often not available, some other simple statistics have been proposed as estimates of asymptotic size. Use of the maximum value (the largest-individual method, Stamps and Andrews 1992) clearly overestimates A and it is highly dependent on sample size (Brown *et al.* 1999). Instead, the 80th or other higher percentiles have been recommended for theoretical reasons (Brown *et al.* 1999) and have been shown to conform to the growth-based estimates in several sets of lizard data (Brown *et al.* 1999; Kratochvil and Frynta 2002; Roitberg and Smirina 2006b).

Whenever possible, three SDI values, based on means (SDI_X), maximum values (SDI_{MAX}), and the 80th percentiles (SDI_{P80}) were computed for each study sample.

14.3.3 Estimating allometry of SSD

Following Fairbairn (1997) the slope of major-axis regression (model II) of log(male SVL) on log (female SVL) was used to quantify the allometry of SSD. The slopes (β) and their 95% confidence intervals were computed with a program designed by P. Legendre (available at www.fas.umontreal.ca/biol/legendre). They were tested against the null hypothesis of $\beta = 1$ (isometry). The pattern with $\beta > 1$ is most common and referred to as Rensch's rule (Fairbairn 1997; Chapters 3 and 6).

14.3.4 Estimating sex differences in body growth and survival

As male and female lizards rarely differ in terms of hatchling size, the primary proximate mechanisms to shape adult SSD are sex differences in (1) postnatal growth trajectories (e.g. Chapter 19) and (2) survival schedules. The corresponding patterns that can be revealed in cross-sectional samples from populations are sex differences in (1) age-specific SVLs and (2) age compositions. Data available for two populations of *L. a. agilis* (Strijbosch and Creemers 1988; Olsson and Shine 1996) and five populations of *L. a. boemica* (Roitberg and Smirina 2006b) have been extracted from published figures and summarized in Figures 14.2 and 14.3.

Although the age at sexual maturation is likely to differ among these populations (and between males and females within some populations), in all cases, all or the vast majority of yearlings are juveniles or subadults, and virtually all 2-years-olds are adults or at least subadults. In my analyses, I have therefore considered all animals of 2 or more years of age to be adults.

14.4 Results

14.4.1 Geographic patterns

The main geographic pattern in SSD is a contrast between the Western European *L. a. agilis* and the

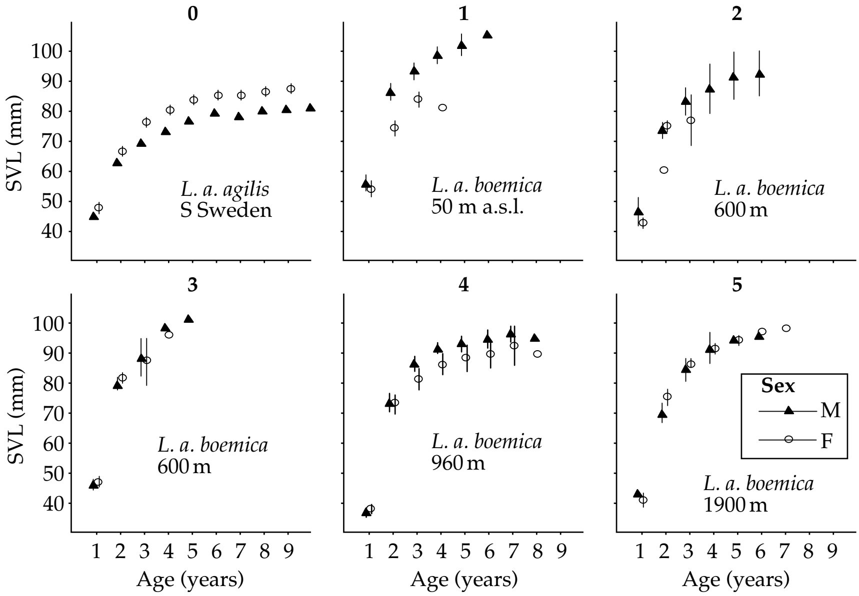


Figure 14.2 Age-specific SVLs (mean ± 2 SE) in different *L. agilis* populations. Data from: Olsson and Shine (1996) for South Sweden; Roitberg and Smirina (2006) for *L. a. boemica* (shown with elevations above sea level, a.s.l.).

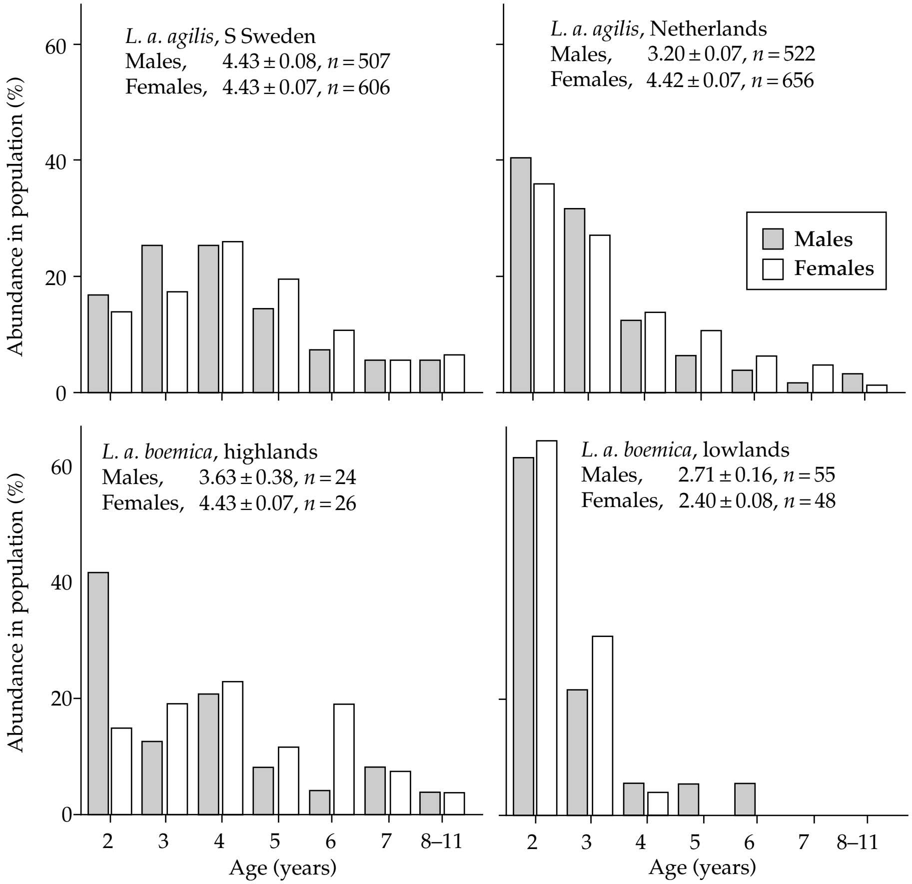


Figure 14.3 Age compositions of individuals of 2 or more years old in different *L. agilis* populations. Means ± SE are also given. Data from: Olsson and Shine (1996) for South Sweden; Strijbosch and Creemers (1988) for Netherlands; Roitberg and Smirina (2006b), for *L. a. boemica*.

North Caucasian *L. a. boemica*. Whereas SSD was consistently female-biased in *L. a. agilis*, *L. a. boemica* exhibited either no sex differences or a clearly male-biased SSD (Figure 14.1b). The other subspecies tend to occupy intermediate positions along the SSD axis (Figure 14.1b).

SSD also varied within subspecies (Figure 14.1b). In *L. a. exigua* and *L. a. boemica*, this variation is apparently related to climate. In *L. a. exigua* the SDI exhibited a positive correlation with the latitude (Figure 14.4a) and in *L. a. boemica* with the altitude (Figure 14.4b). That is, in both subspecies, the male-biased SSD is associated with low latitudes and altitudes.

14.4.2 Allometry

Despite marked geographic variation in SSD, patterns of geographic variation in body length were highly concordant between the sexes both within and across subspecies (Table 14.2). For the whole data-set, the major-axis regression slope of log (male SVL) on log(female SVL) was significantly greater than 1 (Figure 14.5; Table 14.2), which is consistent with Rensch's rule. However, this pattern is shaped solely by the contrast between the small-sized and female-larger *L. a. agilis* and the large-sized and male-larger *L. a. boemica* (Figure 14.5). If these two forms are excluded from

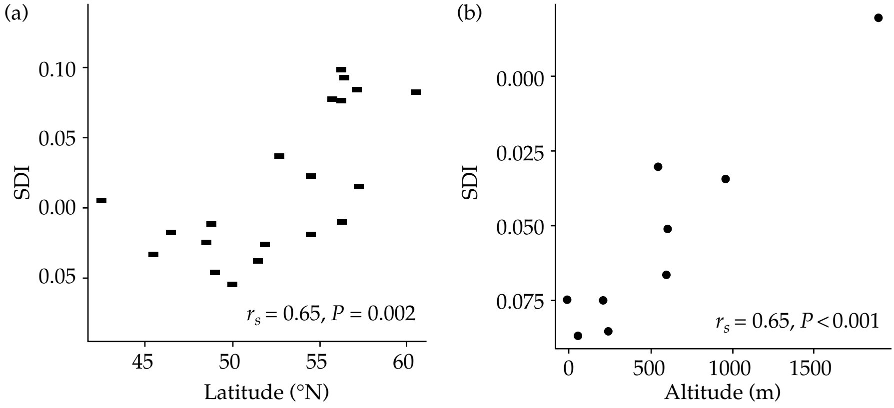


Figure 14.4 Spearman rank correlation (r_s) between the SSD index (SDI) and latitude or altitude within subspecies. (a) *L. a. exigua*; (b) *L. a. boemica*.

Table 14.2 Major-axis regression slopes of male size on female size (log-transformed mean SVL) among populations within and across subspecies of *L. agilis*.

Data-set	Slope estimate (95% CI)	Pearson correlation coefficient (*r*) between male and female SVL
All samples, $n = 47$	1.48 (1.17–1.91)	$0.78^{\dagger}$
All, without *L. a. agilis* and *L. a. boemica*, $n = 27$	0.83 (0.56–1.21)	$0.73^{\dagger}$
L. a. agilis, $n = 11$	0.94 (0.69–1.27)	$0.90^{\dagger}$
L. a. chersonensis, $n = 5$	0.57 (0.34–0.85)	0.95*
L. a. boemica, $n = 9$	0.73 (0.21–1.74)	0.72*
L. a. exigua, $n = 19$	0.85 (0.44–1.54)	$0.66^{\dagger}$

$^*P < 0.05$; $^{\dagger}P < 0.01$.

analysis, the remaining variation across subspecies and the variation within subspecies actually exhibit a weak tendency toward the converse of Rensch's rule (Table 14.2).

14.4.3 Relative impact of sex differences in growth and survival

Figure 14.2 summarizes data on age-specific body length in males and females in a Swedish population (*L. a. agilis*) and five populations from the southeastern North Caucasus (*L. a. boemica*). In the Swedish population, mean SVL of females was consistently higher than that of the same-age males (see also Olsson and Shine 1996). In contrast, populations of *L. a. boemica* exhibited either no consistent differences in average growth curves of males and females or age-specific SVLs were clearly larger in males. The latter pattern occurred in the lowland population whose SSD was strongly male-biased. Thus, sex differences in averaged growth trajectories correspond well to the patterns of adult SSD: the larger sex (females in *L. a. agilis* and males in the lowland *L. a. boemica*) grow faster than the smaller sex.

Figure 14.3 shows age compositions of adult males and females for the two contrasting subspecies. For *L. a. boemica*, I pooled three samples from the lowland and submontane sites and two samples from the mountain sites because there were only small differences within these groups. Both Northern European populations showed a high longevity (mean adult age was 3.3–4.4 years), with females being slightly older than males (Mann–Whitney U test: $Z = -3.45$, $P < 0.001$ for Sweden; $Z = -2.76$, $P = 0.006$ for The Netherlands). Noteworthy, the mountain *L. a. boemica* were comparable to the Swedish and Dutch *L. a. agilis* for their mean adult age and the pattern

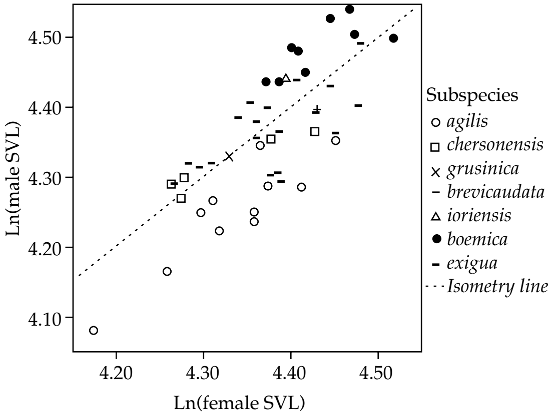


Figure 14.5 Plot of log-transformed male size on log-transformed female size for 52 study samples of *L. agilis*.

of female-biased survival (Figure 14.3), although in *L. a. boemica* this bias was not statistically significant ($Z = -1.69$, $P = 0.09$). In contrast, the lowland *L. a. boemica* showed a much younger mean adult age than both the mountain *L. a. boemica* and the North European *L. a. agilis*, and exhibited no signs of female-biased survival (Figure 14.3). The variation in age structure thus tends to conform to the variation in SSD, but the sex differences in age composition are minor as compared to the differences in growth curves.

14.5 Discussion

14.5.1 Comparing variation in SSD within and between subspecies

SSD in *L. agilis* exhibits a pronounced geographic variation. For mean adult SVL, SSD ranges from 7–9% in favor of males to 10–13% in favor of females. A comparable magnitude of divergence in SSD has been documented among related lizard species (Lappin and Swinney 1999; Chapter 19) but not within a single species. In snakes, a unique case of a much more dramatic geographic variation in SSD was found in the python, *Morelia spilota* (Pearson *et al.* 2002). In other vertebrates, SSD varying from male-biased to female-biased in different geographic populations within a species has been reported for only few species (e.g. Storz *et al.* 2001; Tamate and Maekawa 2006).

My study revealed two robust patterns of geographic variation in SSD: a clear contrast between *L. a. agilis* and *L. a. boemica* (pattern 1) and ecogeographical clines within subspecies (latitudinal in *L. a. exigua* and altitudinal in *L. a. boemica*) with more male-biased SSD in warmer climates (pattern 2). Pattern 1 is consistent with the temperature-mediated clines (i.e. summer is cooler in Western Europe than in the North Caucasus), but it is likely that the two patterns have at least partly different causation. Pattern 1 is greater in magnitude and is shaped primarily by divergence in male size (Rensch's rule), whereas female size variation contributes equally or more than male size variation to pattern 2. Further, phylogeographic studies reveal pronounced genetic divergence between *L. a. agilis* and *L. a. boemica*, but no substantial substructure within either subspecies (Kalyabina *et al.* 2001; Kalyabina-Hauf and Ananjeva 2004). Thus, pattern 1 is associated with substantial genetic divergence whereas pattern 2 is not.

14.5.2 Possible determinants of the SSD divergence between *L. a. agilis* and *L. a. boemica*

The patterns described above suggest that the divergence in SSD between subspecies (pattern 1) includes an adaptive component related to geographic differences in patterns of sexual selection. A basal position of *L. a. boemica* in the species phylogeny (Kalyabina *et al.* 2001; Kalyabina-Hauf and Ananjeva 2004) suggests that the small male size and female-biased SSD of *L. a. agilis* is a derived state. An adaptive shift to a smaller male size and female-biased SSD can be predicted by the so-called small-male-advantage hypothesis (Zamudio 1998; Cox *et al.* 2003). Let us assume that the formation of the nominate subspecies in Western Europe was accompanied by a shift to a social system with lower male aggression and higher rate of promiscuity. Such a shift in social behavior and SSD in regions with cooler climate and lower population density as compared to conspecifics from densely populated regions with warmer climates has been reported for another widespread lizard (an iguanid, *Uta stansburiana*; Tinkle 1969; Parker and Pianka 1975; Fitch 1981) and a snake (a python, *Morelia spilota*; Pearson *et al.* 2002). The SSD variation among populations of horned lizards (*Phrynosoma*) has occurred primarily by changes in male size arguing for the small-male-advantage hypothesis (Zamudio 1998).

The available evidence suggests that in Western Europe, *L. agilis* generally occurs at much lower population densities than in the North Caucasus. In many Western European territories this species is classified as endangered (Blanke 2004 and references therein), whereas in the forest-steppe and steppe zone of Eurasia, including North Caucasus, *L. agilis* is often very abundant, its density reaching up to 1000 individuals per hectare (Baranov and Yablokov 1976). There is also anecdotal supportive evidence from animals kept in terraria that *L. a. boemica* is more aggressive than *L. a. agilis* (Hemmerling and Obst 1967). Also, the prevalence of bite scars, which is often used as a proxy of the intensity of male–male agonistic encounters in snakes and lizards (e.g. Shine and Fitzgerald 1995; Hasegawa 2003), is significantly higher in *L. a. boemica* (23.1%, $N = 78$) than in *L. a. agilis* (0.0%, $N = 46$; E.S. Roitberg, unpublished work).

Although male–male sexual aggression appears to be lower in *L. a. agilis* than in *L. a. boemica*, larger male *L. a. agilis* are more successful in agonistic interactions than smaller males (Olsson 1992). Nevertheless, the rate of agonistic encounters and their contribution to male mating success in *L. a. agilis* may well be lower than in *L. a. boemica*. Competition for access to mates is only one component of sexual selection; others include mate searching and the postcopulatory phase (Blanckenhorn 2005). In mate searching, which seems to increase at low population density, small males should have advantage due to their higher mobility and earlier maturation (Blanckenhorn 2005 and references therein). Interestingly, a trade-off between fighting capacities and mobility among individual males has been recently demonstrated for another lacertid lizard, *Lacerta monticola* (López and Martín 2002).

Another possible explanation for pattern 1 involves geographic differences in growth constraints (Chapter 19) or viability selection for small body size (Blanckenhorn 2000). Cool and humid summer climates in most of the species' range in Western Europe should reduce activity and energy acquisition opportunities relative to those in more continental Eurasia. This might constrain body growth in a similar way as resource limitation (Congdon 1989). Under such conditions, environmental constraints for growth and viability selection for small body size are expected to be strong in both sexes, but in females these forces can be partly counterbalanced by fecundity selection (Kratochvíl and Frynta 2002). Indeed, the correlation between female size and clutch size (egg number) is quite high in *L. a. agilis* (Olsson 1993; Amat *et al*. 2000). Moreover, the available data, limited to a few females from single localities, suggest that *L. a. agilis* is characterized by higher relative clutch mass and smaller egg and hatchling size than the more eastern forms, including *L. a. boemica* (Rykena 1988; Warnecke 2000). The above points argue for a high potential for fecundity selection in the Western European populations.

A third hypothesis for pattern 1 is that the SSD difference between the two genetically diverged subspecies is at least partly caused by evolutionary lag in the response of *L. a. agilis* to anthropogenic changes in habitat availability. Before the Middle Ages, low population densities might have been even more characteristic for *L. a. agilis* than in later times, because the natural deficiency of steppe and forest-steppe landscapes in Western Europe had not yet been mitigated by human deforestation activity (see Bischoff 1984). Anthropogenic changes in habitat availability and hence lizard density may favor increased male size, but the SSD has not yet reached evolutionary equilibrium. The virtual lack of overlap between the SDI values for the two taxa (Figure 14.1b), in spite of obviously overlapping density levels, offers some support for this hypothesis.

14.5.3 Possible determinants of eco-geographic clines within subspecies

Geographic differences in patterns of sexual selection might also contribute to pattern 2 because the northern *L. a. exigua* (Peters 1959; Bulakhova 2005) and the high-elevation *L. a. boemica* (Roitberg and Smirina 2006a) populations generally exhibit relatively low densities. However, the variation in SSD within subspecies appears not to be genetically based (i.e. does not reflect genetic divergence among populations) and is strongly influenced by variation in female as well as male size (see Section 14.4.2). This clinal variation can be most parsimoniously addressed in terms of differential trade-offs between growth and reproduction (proximate causation, the nonadaptive hypotheses of Cox *et al*. 2003). Based on the model of Adolph and Porter (1996) and growth data for five populations of *L. a. boemica* (Roitberg and Smirina 2006b), I propose the following explanation. In warm climates of lowland and southern localities, juveniles grow sufficiently to reach their maturation size by late May or early June of their second year, and to reproduce as yearlings. For females, this means a substantial allocation of energy to egg production, possibly at the expense of body growth. In cooler climates, the yearling females do not reach the maturation size until mid-summer (when it is too late for reproduction) and continue to invest energy in body growth. They start reproduction 1 year later but at a larger mean size than lowland females. As established for many lizard species, size at maturity strongly correlates with final size (Stamps *et al*. 1998). Thus, early maturation might be responsible for smaller mean body length of adult females in the lowland populations. Another possible reason for smaller female size in warmer climates may be higher annual reproductive expenditures because many females there make two clutches per season. Thus, the clinal variation in SSD within subspecies might be partly an epiphenomenon of selection on life-history variables, with no adaptive significance in terms of SSD per se (Roitberg and Smirina 2006b). Similar proximate factors might also contribute to pattern 1. However, in this case some additional forces related to male size must have contributed to the observed divergence.

14.5.4 Sex differences in growth, survival, and maturation time

My analyses of published data on age-specific SVLs and age composition in several populations of *L. a. agilis* and *L. a. boemica* (Figures 14.4 and 14.5) suggest sex differences in growth trajectories to be the major proximate determinant of adult SSD. The larger sex also tends to have higher survival and that may contribute to SSD as well, but this bias in age composition is generally small compared to sex differences in growth curves. In other lizard studies, differential growth was also more important in shaping SSD than differential survival (Watkins 1996; Rutherford 2004).

An additional related mechanism is sexual bimaturation (i.e. later maturation of the larger sex; Stamps and Krishnan 1997). Female *L. a. agilis* do appear to mature a year later than the males in some populations (Rahmel and Meyer 1988; Strijbosch and Creemers 1988) but no bimaturation was found for another *L. a. agilis* population with a strongly female-biased SSD (Nöllert 1989). Thus, the possible contribution of sexual bimaturation to adult SSD in this species remains to be determined.

14.6 Final remarks

Although numerous factors unrelated to geographic variation could affect SSD in particular study samples, these effects are unlikely to create a strong and regular pattern shaped by a large number of independently collected data units. With no doubt, both patterns revealed in the geographic variation of SSD of *L. agilis*—pronounced differences between *L. a. agilis* and *L. a. boemica*, and eco-geographic clines within subspecies—are biologically relevant. Another firm conclusion is that female-biased SSD of *L. a. agilis* and male-biased SSD of the lowland *L. a. boemica* result primarily from differential growth, the larger sex exhibiting higher growth rate. However, within a correlational study it was impossible to reliably differentiate between the different hypotheses that predict similar geographic patterns of variation in SSD.

14.7 Future research

Along with general body size (SVL), absolute and relative size of particular body segments related to female fecundity (abdomen length) or male fighting capacity (head dimensions) should be examined for variation in sexual dimorphism among populations (see Braña 1996; Chapters 4 and 15). Such data coupled with comparative data on different aspects of reproductive output (particularly the slope of the regression of fecundity on female size; see Braña 1996; Cox *et al*. 2003) could help to assess applicability of the sexual-selection and fecundity-advantage hypotheses for the revealed SSD patterns. Intensive mark–recapture or skeletochronological studies on northern (female-larger) and southern (male-larger) populations of *L. a. exigua* would estimate whether this divergence arose through the same proximate mechanisms as a parallel but stronger divergence between *L. a. agilis* and *L. a. boemica*.

Common-garden experiments involving populations that exhibit contrasting SSD patterns could determine whether observed growth differences between the sexes (and those between males of *L. a. agilis* and *L. a. boemica*) are genetically fixed or constrained by environment at the proximate level (see John-Alder and Cox, this volume for relevant experiments with *Sceloporus* species). Behavioral studies of *L. a. agilis* and *L. a. boemica* in the field and laboratory (cf. Tinkle 1969; Shine and Fitzgerald 1995; McCoy et al. 2003; Hasegawa 2003; chapter 15) could additionally address the sexual selection hypothesis. The use of paternity analysis to assay sexual and fecundity selection on body size would be a powerful tool. Such investigations have been made for a Swedish population of *L. a. agilis* (e.g. Gullberg *et al*. 1997), and it would be of great interest to similarly investigate a conspecific population that exhibits an opposite, male biased SSD.

14.8 Summary

The sand lizard, *Lacerta agilis* occupies a large part of temperate Eurasia from the Pyrenees to the Baikal Lake. This chapter presents an analysis of geographic variation in SSD within this species based on original and published data on SVL of adult males and females in 52 local or regional samples. The major pattern, distinctive differences between the consistently female-larger *L. a. agilis* (West Europe) and the predominantly male-larger *L. a. boemica* (the south-eastern North Caucasus), is primarily determined by divergence in male size (Rensch's rule). The other subspecies (*L. a. chersonensis*, *L. a. exigua*, and the three Transcaucasian forms) tend to occupy intermediate positions along the SSD axis. Within subspecies, the variation in SSD is characterized by latitudinal (*L. a. exigua*) and altitudinal (*L. a. boemica*) clines towards a male-biased SSD in warmer climates, with female size varying as much or more than male size.

Data on age-specific SVLs and age compositions for *L. a. agilis* and *L. a. boemica* show that sex differences in body growth are the major proximate determinant of adult SSD, the sex-biased adult survival being of minor importance. Selective and proximate-level factors are discussed as possible determinants of the geographic patterns in SSD. These include sexual, fecundity and viability selection; growth limitations by environmental constraints for energy intake; and a trade-off between growth and egg production in females. The available correlational data are not sufficient to permit adequate evaluation of these hypotheses, but future directions for research are proposed.

14.9 Acknowledgments

I am grateful to E.M. Smirina for our excellent cooperation in skeletochronological investigations from which the present study has been developed. I thank V.F. Orlova and E.A. Dunayev for their help and hospitality during my work with collections at the Zoological Museum of Moscow University. K. Yu. Lotiev, E.M. Smirina, and V.A. Yakovlev provided their unpublished SVL data. Fruitful discussions with H. Strijbosch and A.M. Rudyk contributed to my understanding the sand lizard's ecology. Valuable comments and suggestions of R. Cox, D.J. Fairbairn, and L. Kratochvíl resulted in substantial text improvements. M. Stöck helped to develop Figure 14.1. I greatly appreciate the efforts of W.U. Blanckenhorn, D.J. Fairbairn, and T. Székely who arranged that beautiful workshop in Monte Verita, and I thank them for inviting me to contribute to this volume. The Ethologische Gesellschaft supported my participation in the workshop.

14.10 Suggested readings

Cox, R.M., Skelly, S.L., and John-Alder, H.B. (2003) A comparative test of adaptive hypotheses for sexual size dimorphism in lizards. *Evolution* **57**, 1653–1669.

Pearson, D., Shine, R., and Williams, A. (2002) Geographic variation in sexual size dimorphism within a single snake species (*Morelia spilota*, Pythonidae). *Oecologia* **131**, 418–426.

Roitberg, E.S. and Smirina, E.M. (2006) Age, body size and growth of *Lacerta agilis boemica* and *L. strigata* (Reptilia, Lacertidae): a comparative study of two closely related lizard species based on skeletochronology. *Herpetological Journal* **16**, 133–148.

Roitberg, E.S. and Smirina, E.M. (2006) Adult body length and sexual size dimorphism in *Lacerta agilis boemica* (Reptilia, Lacertidae): between-year and interlocality variation. In *Mainland and Insular Lizards. A Mediterranean Perspective* (Corti, C., Lo Cascio, P., and Biaggini, M., eds). Florence University Press, Florence, Italy, 175–187.

Storz, J.F., Balasingh, J., Bhat, H.R., Nathan, P.T., Doss, D.P.S., Prakash, A.A., and Kunz, T.H. (2001) Clinal variation in body size and sexual dimorphism in an Indian fruit bat, *Cynopterus sphinx* (Chiroptera: Pteropodidae). *Biological Journal of the Linnean Society* **72**, 17–31.

Zamudio, K.R. (1998) The evolution of female-biased sexual size dimorphism: a population-level comparative study in horned lizards (*Phrynosoma*). *Evolution* **52**, 1821–1833.

CHAPTER 15

Phylogenetic analysis of sexual dimorphism in eye-lid geckos (Eublepharidae): the effects of male combat, courtship behavior, egg size, and body size

Lukáš Kratochvíl and Daniel Frynta

15.1 Introduction: phylogenetic reconstruction of sexual dimorphism

The origin of different forms of sexual dimorphism and their distribution across living organisms are unequivocally evolutionary questions. As evolution is an historical phenomenon, and as organismal characters generally represent the influence of genealogy, macroevolutionary patterns of sexual dimorphism are mostly an outcome of unique past processes. Therefore, the causes of sexual dimorphism in particular groups should be explored within an explicit phylogenetic framework using methods of phylogenetic systematics (cladistics) and comparative biology to reconstruct the history of organisms and their characters (Hennig 1966; Harvey and Pagel 1991).

We view sexual dimorphism as a potentially adaptive character with its own evolutionary history; that is, a character that is inherited from ancestors and amenable to transformations during the evolutionary history of organisms. This viewpoint corresponds to the evolutionary definition of adaptation, which emphasizes past evolutionary history. According to this definition, an adaptation is a derived character that emerges in response to a specific selective process (Harvey and Pagel 1991). To identify a character as an adaptation, we first have to trace historical relationships among taxa, and conduct historical analysis of character origin, stasis, and modification. After assuming the evolutionary polarity of character states (identification of derived states), we can detect points of character changes; that is, points of emergence for potential adaptations. Subsequently, we may infer the selective process responsible for a particular evolutionary change in a given time to solve the questions of interest: What was the reason for a change at a given point? What preceded this change?

To assess whether sexual dimorphism is indeed an adaptation, one has to apply a comparative approach to uncover whether it is an evolutionary novelty, and to reconstruct probable causes of its emergence. Since Darwin (1871), a number of specific selective processes have been suggested to drive the evolution of sexual dimorphism (e.g. see Chapter 1 in this volume). Which process is the correct one? We suggest fitting different evolutionary models (as many as possible) by testing their ability to explain the observed phylogenetic pattern in sexual dimorphism. Such historical analysis involving multiple traits is a more conservative procedure than a correlational study, as it is in many cases able to infer chronological succession and thus causal connections.

Since clades may exhibit considerable phylogenetic conservatism in their sexual dimorphism (e.g. Chapter 4), we consider lineages in which closely related taxa differ in the direction of sexual dimorphism, or in the presence of sexually dimorphic traits that are most interesting and informative (see also Chapter 19). Therefore, we choose a small monophyletic group that exhibits substantial variation in sexual dimorphism, including the disappearence of dimorphism in several traits and reversals in sexual size dimorphism (SSD). Here we summarize our ongoing research on eye-lid geckos (Squamata: Eublepharidae; aproximately 27 species) in this context. We integrate data on three sexually dimorphic morphological traits (body size, head size, and presence of precloacal scent glands in males), three behavioral traits (male aggressive behavior, complexity of courtship display, and female choice), and one life-history trait (egg size relative to body size). We also comment on methods of morphometric measurement of sexual dimorphism. Subsequently, we use the distribution of character changes to evaluate which hypothesis might best explain the phylogenetic pattern of sexual dimorphism in eublepharids. We consider this chapter as a progress report, and we hope that this review will stimulate further phylogenetically oriented research on dimorphism based on historical analyses involving multiple traits.

15.2 Eublepharid geckos and their phylogeny

The family Eublepharidae is a small monophyletic assemblage of primitive geckos, sister to all other gecko groups (Kluge 1987). Species of this old lineage are scattered over the world. Genera *Aeluroscalabotes*, *Eublepharis*, and *Goniurosaurus* live in Asia, *Hemitheconyx* and *Holodactylus* in Africa, and the genus *Coleonyx* in North and Central America. The phylogenetic relationships among the eublepharid species and genera are relatively well corroborated (phylogeny based on morphology, Grismer 1988; molecular phylogeny, Ota *et al.* 1999; total evidence, Kratochvíl and Frynta 2002; Starostová *et al.* 2005). Throughout this study we use the phylogenetic hypothesis proposed by Kratochvíl and Frynta (2002), which is based on the combination of morphological and molecular data.

Our conclusions are based on our work with *Coleonyx brevis*, *Coleonyx elegans*, *Coleonyx mitratus*, *Coleonyx variegatus*, *Eublepharis angramainyu*, *Eublepharis macularius*, *Hemitheconyx caudicinctus*, *Holodactylus africanus*, *Goniurosaurus luii*, *Goniurosaurus kuroiwae*, and published data on a few other species. Representatives of all major evolutionary lineages of Eublepharidae are included in our analyses. However, not all extant species of eye-lid geckos were available to us, because some of them are extremely rare, endangered (Kratochvíl 2006; Stuart *et al.* 2006), or live in politically unstable regions.

15.3 Sexually dimorphic morphological traits in eye-lid geckos

15.3.1 SSD

In animals with indeterminate growth, age structure of samples may strongly bias estimates of body size and thus SSD. Therefore, to estimate body size, we need to know individual growth trajectories of animals (Stamps 1993; Stamps and Krishnan 1997; Chapters 14 and 19). To evaluate the growth rates of eublepharids, we examined growth curves of both sexes in a common-garden experiment; that is, under standardized laboratory conditions (details in Kratochvíl and Frynta 2002, 2003). This allowed us to control for environmental variation in growth and sexual dimorphism, which is well documented in reptiles (Madsen and Shine 1993b; Autumn and DeNardo 1995; Chapter 19).

Growth in four eye-lid gecko species was asymptotic—meaning that growth decelerates markedly after sexual maturity (see Box 14.1)—hence we used the logistic-by-length model (Schoener and Schoener 1978) to estimate the asymptotic snout–vent length (SVL). Although we would prefer to use asymptotic SVL estimated from common-garden growth experiments as a measure of body size for all species, growth curves were not available for other species. However, we found that maximum SVL provided a reasonable estimate of asymptotic values computed by the logistic model. Therefore, we use maximum SVL as an estimate of body size. Wherever possible, we used published data on SVL of those species for which we had insufficient data (references in Kratochvíl and Frynta 2002). We use body length instead of body mass to estimate SSD because body mass is often more influenced by environmental conditions than structural measures, such as SVL.

Eublepharids differ in the magnitude and direction of SSD, with ratios in maximum male-to-female SVL among species ranging from 0.93 to 1.18 (the range of ratios for mass are naturally much higher); both female-larger and male-larger species occur within this family. The male-larger species are *C. elegans*, *C. mitratus*, *C. reticulatus*, *E. angramainyu*, *E. macularius*, and *H. caudicinctus*. Females are the larger sex in *C. brevis*, *C. variegatus*, *Ho. africanus*, *G. luii*, and *G. kuroiwae* (for descriptive statistics see Kratochvíl and Frynta 2002).

Body size varies considerably within Eublepharidae: the largest species (*E. angramainyu*, maximum SVL 170 mm) is 2.5 times longer and over 25 times heavier than the smallest one (*C. brevis*, maximum SVL 67 mm).

15.3.2 Head-size dimorphism

Males and females of some eublepharids differ conspicuously in body shape, with males having bulkier heads. We tested intersexual differences in relative head size, comparing head size allometries on SVL. Head size was estimated as the geometric mean of head length and head width. Morphometric data were log-transformed before analysis. To exclude individuals in transitional allometry between juveniles and adults, only those reaching at least 70% of maximum SVL were included in the analysis of head-size dimorphism (HSD). Males have relatively larger heads than conspecific females in all but two examined species (*Ho. africanus* and *G. kuroiwae*; see details in Kratochvíl and Frynta 2002).

Demonstration of the sexual differences in relative sizes of body parts has some caveats. The traditional method used in assessing HSD in lizards is a comparison of head size relative to SVL between males and females, the same test we used in eublepharids. However, this method can be misleading in many lizard groups (Kratochvíl *et al.* 2003) as SVL naturally encompasses abdomen length, which is often sexually dimorphic (larger in females; Olsson *et al.* 2002). As a result, head size relative to SVL necessarily comes out 'larger' in males. Size-adjusted heads traditionally reported to be larger in males than females in many lizards could then be merely an artefact of inappropriate scaling to a sexually dimorphic composite trait (SVL). For example, the proximate mechanism for male-biased HSD found in the common lizard (*Lacerta vivipara*) is, ironically, the larger number of trunk vertebrae in females and the positive growth of female abdomens after maturation (Kratochvíl *et al.* 2003 and unpublished work).

Why then is male-biased HSD not such a computational artefact in eublepharids? We have three lines of evidence. First, at maturation, males depart from juvenile allometry in head size (Figure 15.1), contrary to females. Second, the proximate mechanism of head widening at maturation in males of *E. macularius* is mediated by increased levels of testosterone (Crews 1998; Crews *et al.* 1998). Finally, as mentioned above, two species of eye-lid geckos do not demonstrate male-biased HSD, an improbable situation if HSD only reflected sexual dimorphism in abdomen size.

15.3.3 Presence of precloacal scent glands

> The male alone of the gecko *Cyrtodactylus rubidus* of the Andaman Islands possesses pre-anal pores; and these pores . . . probably serve to emit an odour.
>
> Darwin (1871)

Not only males of Darwin's *Cyrtodactylus*, but also males of most species of eye-lid geckos produce waxy secretions from a row of macroscopic glands, so called precloacal or pre-anal pores. The glands are functional throughout the year in aseasonal species, but repose during the non-breeding season in species that live in seasonal environment. Pores are present in males of most eublepharid species (females possess only rudimentary, nonfunctional pores). Among the species examined in our analyses, pores are completely lacking only in *Ho. africanus* and members of the *Goniurosaurus kuroiwae* group (Kratochvíl and Frynta 2002). Interestingly, precloacal pores are functional in both sexes of *Aeluroscalabotes felinus*, a poorly known oriental species.

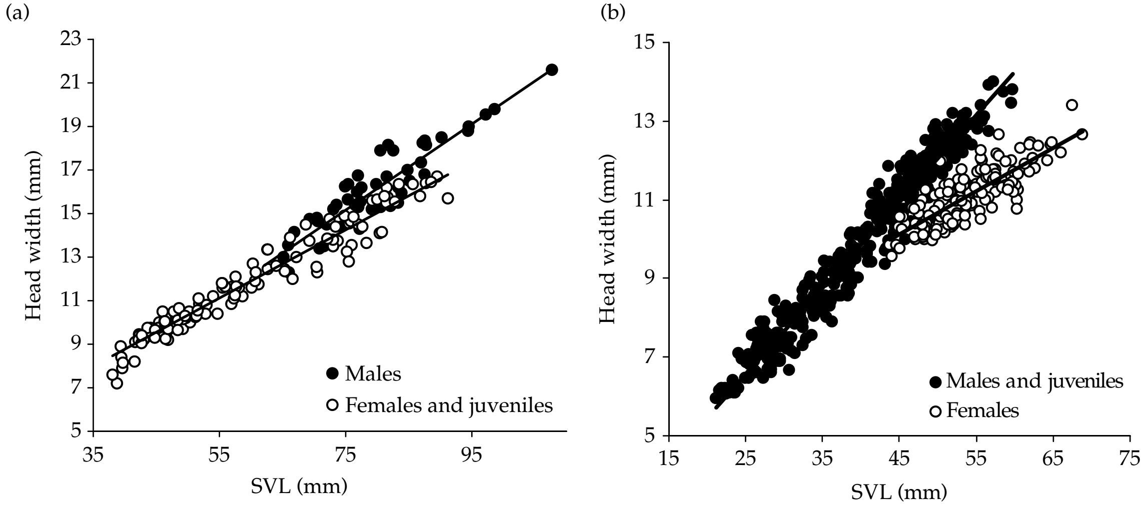


Figure 15.1 Scatterplot of head width against SVL showing the ontogenetic trajectory in body shape in (a) the eublepharid gecko *C. elegans* and (b) the lacertid lizard *Lacerta vivipara*. In both cases, males possess wider heads than females relative to SVL. However, this pattern is achieved by the departure from juvenile allometry in male geckos (which enlarge heads at sexual maturation) but female lizards (which enlarge abdomen length at sexual maturation).

15.4 Overview of potential determinants of sexual dimorphism

We tested four potential determinants of SSD: presence of male aggressive behavior, complexity of courtship display, body size, and egg size relative to body size. In this section we explain why these four attributes are hypothesized to drive the evolution of sexual dimorphism.

15.4.1 Male combat

Probably the most popular explanation for the origin and maintenance of sexual dimorphism in reptiles is Darwin's (1871) sexual-selection theory (e.g. Chapters 4, 14, and 19). This theory predicts a relationship between the presence or absence of sexually selected traits and forms of competition among males (Wiens 2001). Males should be the larger sex, and they should exhibit exaggerated body parts related to rivalry success or territory advertisement in lineages exhibiting male–male aggression or territoriality, respectively. In lizards, success in combat usually correlates with body size (Olsson 1992; Zucker and Murray 1996). Hence, the occurrence of male combat suggests sexual selection for larger male size, and a phylogenetic correlation between male-biased SSD and male aggressive behavior is predicted. However, sexual selection for large males will not occur unless success in combat also translates into greater reproductive success (Cox *et al.* 2003).

Functional analyses in lizards also show that large heads generate greater bite force and a stronger grip (Herrel *et al.* 1999). Large heads in male lizards are hypothesized to serve as weaponry during combat (Lappin and Husak 2005). This hypothesis predicts an evolutionary association between male-biased HSD and male–male combats.

Pore secretions are thought to be important for territory marking (Duvall 1979; Alberts 1991; Cooper *et al.* 1996), or a source of pheromones allowing sex recognition (Cooper *et al.* 1994). Only the former explanation predicts an association between territorial (or aggressive) behavior and the presence of precloacal pores.

15.4.2 Complexity of courtship display and female choice

Complexity of courtship display and the presence of courtship (or mating) behavior have also been suggested to influence sexually dimorphic traits (Chapter 3). Contrary to the explanation based on the presence of male combat, large heads in male lizards could function as an adaptation to hold a female during copulation (Gvoždík and Van Damme 2003). An association between male-biased HSD, the use of jaws during courtship, and copulatory behavior is then predicted.

Female choice is expected to be associated with complex courtship behavior and other exaggerated secondary sexual traits in males (Darwin 1871). Male-biased SSD (or HSD) could then reflect female choice for males possessing large heads or overall body size. Such preference, however, has been documented only rarely in lizards (but see Censky 1997).

15.4.3 Body size

Females in various animal clades tend to be larger than males in small species, whereas males are larger than females in large species. This phenomenon is commonly known as Rensch's rule (Fairbairn 1997; Abouheif and Fairbairn 1997; Colwell 2000; Chapters 2–4, 6, and 14). Although the functional and adaptive causes and consequences of this empirical allometry are unclear (Fairbairn 1997), comparative studies of sexual dimorphism should generally encompass body size as a potential determinant of SSD.

15.4.4 Relative egg size

We included one life-history trait, egg size relative to body size, in our analysis. All eublepharid geckos invariably lay two large eggs per clutch (Kratochvíl and Frynta 2006a, 2006b). The selective advantage of large female size due to higher fecundity (the fecundity-advantage hypothesis; Chapters 2–4) is therefore unlikely in eublepharids. As clutch mass in lizards typically corresponds to volume accessible for eggs within a female abdomen (Shine 1992), we may expect that eublepharids with larger eggs faced selection for larger abdomens and consequently larger female body size. If this is true, female-biased SSD should be evolutionarily associated with larger relative egg size.

15.5 Character states in potential determinants of sexual dimorphism

15.5.1 Presence of male aggressive behavior

Eublepharid geckos include both aggressive and non-aggressive species. Males of most eublepharids are strongly agonistic towards conspecific males during laboratory contests (Dial 1978; Kratochvíl and Frynta 2002). In contrast, combats between males of *Ho. africanus* and *G. kuroiwae* have never been observed (author's own observation; Tanaka and Nishihira 1987, 1989). Female–female contests do not occur in eublepharids.

15.5.2 Complexity of courtship display and female choice

Based on our observations of courtship and copulatory behavior, we divided the species into two groups. One group included species with elaborate courtship display (*E. macularius*, *E. angramainyu*, *H. caudicinctus*, *G. luii*, *G. lichtenfelderi*, *C. brevis*, and *C. variegatus*). These species have long precopulatory phase lasting up to 20 min with a typical high posture (an animal extends its legs and characterically bends its head down) and stereotypic tail vibrations (quick movements with the tip of the tail on the substrate surface) in males. The other group included *C. elegans* and *C. mitratus*, which exhibit limited courtship: their precopulatory phase is short, and the males display neither tail vibrations nor high posture.

In *C. elegans* and *E. macularius*, two male-larger species with contrasting courtship behavior, we found no female choice. Females refused all males when gravid or unreceptive, but mated willingly with all available males when receptive (up to 12 times per day) regardless of male size (K. Zelená, L. Kratochvíl, and D. Frynta, unpublished work).

15.5.3 Relative egg size

We gathered data on sizes of freshly laid eggs in 12 species of eublepharid geckos (Kratochvíl and Frynta 2006a, 2006b). The mass of eggs ranged from 0.3 g in *C. brevis* to 13.5 g in *E. angramainyu* (Figure 15.2), but relative clutch mass exhibited a narrow range: 0.14–0.22.

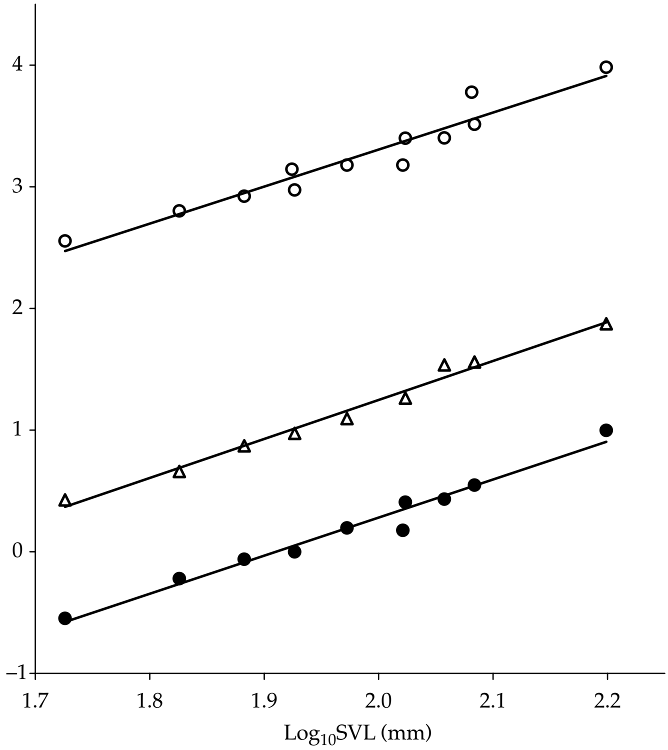


Figure 15.2 Interspecific allometry of egg mass (g, black circles), egg volume (mm^3, white circles), and postpartum female mass (g, triangles) with mean female SVL for eublepharid geckos. All variables are $\log_{10}$-transformed. Least-squares regression lines are depicted. Each symbol represents a species. Note that egg size increases proportionally to female size. From Kratochvíl and Frynta (2006a), reproduced with permission of Blackwell Publishing, Oxford.

15.6 Phylogenetic analyses of sexual dimorphism and its potential determinants

Evolution is a historical process and we need to use historical analyses to uncover homology, polarize character changes and determine evolutionary novelties in sexual dimorphism in search of their adaptive significance. Historical analysis of macroevolutionary patterns based on maximum parsimony shows that, in eye-lid geckos, the number of changes in character states is low and largely restricted to tips of the phylogenetic tree (Figures 15.3 and 15.4). Most probably, the character state of their common ancestor was a medium-sized gecko (Grismer 1988; Starostová *et al.* 2005) in which males were larger than females, and which possessed precloacal pores and exaggerated head size. This reconstruction does not allow us to further search for the selective mechanism responsible for the evolutionary origin of male-biased SSD, HSD, and precloacal pores since these three characteristics were likely present in the common ancestor of eublepharids, and are not evolutionary novelties within this family. For reconstruction of their origin, we would need to descend deeper into the phylogeny of squamate reptiles, which is beyond the scope of this chapter. Such analysis would be complicated by unknown phylogeny within other gecko clades (Han *et al.* 2004), the equivocal position of geckos within the Squamata (Estes *et al.* 1988; Vidal and Hedges 2005), and unexplored character states of sister groups of eublepharids.

Derived states of sexual dimorphism within eublepharids are (1) two independent disappearances of HSD and precloacal pores, and (2) three independent inversions from male-biased to female-biased SSD (Figure 15.3). The macroevolutionary pattern of sexual dimorphism in eyelid geckos is congruent with that in most other animal groups: loss of sexual dimorphism is more frequent than its new origin (Wiens 2001; Ord and Stuart-Fox 2006).

Which character can explain best the changes in sexual dimorphism? The two independent losses of male combat in the ancestors of *Ho. africanus* and

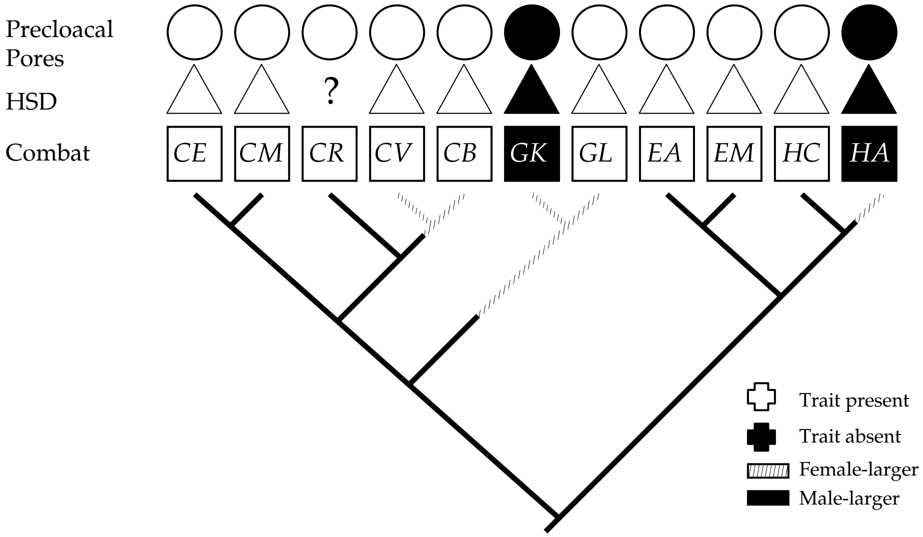


Figure 15.3 Historical analysis of male combat and morphological sexually dimorphic characters in eublepharid geckos (presence of precloacal pores, SSD, and HSD). CE, *Coleonyx elegans*; CM, *C. mitratus*; CR, *C. reticulatus*; CV, *C. variegatus*; CB, *C. brevis*; GK, *Goniurosaurus kuroiwae*; GL, *G. luii*; EA, *Eublepharis angramainyu*; EM, *E. macularius*; HC, *H. caudicinctus*; HA, *Ho. africanus*. Redrawn from Kratochvíl and Frynta (2002) with permission of Blackwell Publishing, Oxford.

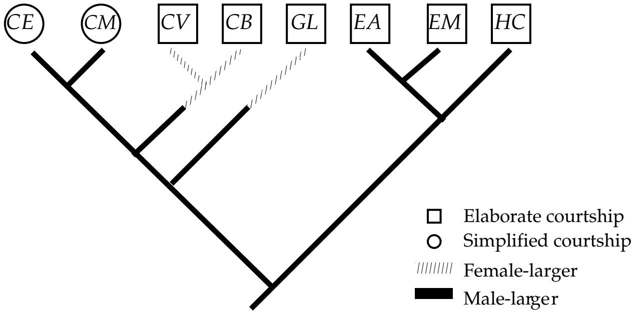


Figure 15.4 Phylogeny of the courship display and SSD in eublepharid geckos. Only species with a known state of courtship display are included. Abbreviations as in Figure 15.3. Redrawn from Kratochvíl and Frynta (2002) with permission of Blackwell Publishing, Oxford.

G. kuroiwae are correlated with the disappearances of HSD and precloacal pores (Figure 15.3). This can be taken as support for the interpretation that larger heads and precloacal pores of males are exaggerated for their function in intrasexual male competition (large heads as weapons, pores as organs related to territory advertisement). Under this scenario, the disappearances of male combat in the ancestors of both non-aggressive species were subsequently followed by the losses of exaggerated organs no longer needed. Aggression, expansion of head width, and the development of precloacal pores in males are under control of the hormone testosterone in *E. macularius* (Crews 1998). It is highly probable that these traits are also regulated by testosterone in other eublepharid species exhibiting the same characters—remember that aggressiveness, HSD, and pores are ancestral in eublepharids, and thus probably homologous in all species possessing them. At the proximate level, the evolutionary association of changes in HSD, pores, and aggressiveness may thus reflect common proximate mechanisms controlling expression of these three sex-specific traits (Chapters 16 and 19). They could change simultaneously, at the same evolutionary time, as a result of their phenotypic integration (sensu Pigliucci 2003), and it is therefore difficult to say which trait was the original target of selection for elimination. The phenotypic integration of these traits may reflect their functional links in coercive competition among males, or developmental connections between them since all three traits begin to be expressed in males at the age of sexual maturation, but this condition probably evolved in the common ancestor of eublepharids and we lack sufficient information on its evolution to differentiate these two explanations.

In contrast to HSD and preanal pores, evolutionary changes in male aggressiveness cannot readily explain evolutionary patterns of SSD in eublepharids. The shift to female-biased SSD in the ancestor of *C. brevis* and *C. variegatus* was not associated with the loss of combat, and the inversion in *Goniurosaurus* preceded, not followed, the loss of combat (Figure 15.3).

The lack of female preference for large males in two distantly related male-larger species (*C. elegans* and *E. macularius*) suggests that female choice for large males is not associated with male-biased SSD in eublepharids. Our analysis indicates that changes in complexity of courtship display are not correlated with female-biased SSD (Figure 15.4), nor with the loss of male-biased HSD. To the best of our knowledge, males of all eye-lid geckos use their jaws to hold the female during copulation. This ancestral behavior occurs in both male-larger (*E. macularius*, *E. angramainyu*, and *H. caudicinctus*) and female-larger species (*G. luii*, *C. brevis*, and *C. variegatus*). Further, two species (*C. elegans* and *C. mitratus*) retained male-biased SSD despite the loss of elaborate courtship display in their common ancestor (Figure 15.4). Tail vibration, a component of elaborate courtship behavior, increases female receptivity in *E. macularius* (Crews *et al.* 1998), and thus could be a result of female choice for this trait. In *C. elegans*, we observed high incidence of forced copulations with unreceptive females, which were almost never observed in *E. macularius* (K. Zelená, L. Kratochvíl, and D. Frynta, unpublished work). Elimination of courtship display in the ancestor of *C. mitratus* and *C. elegans* may reflect higher incidence of forced copulations, but is uniformative for the evolution of SSD.

We found only a single correlate of SSD in eyelid geckos. Following Fairbairn (1997), we estimated the slope of the regression of log$_{10}$(male SVL) on log$_{10}$(female SVL) among eublepharid species after controlling for their phylogeny using independent contrasts (Felsenstein 1985). The slope was significantly larger than 1 (Figure 15.5; computational details in Kratochvíl and Frynta 2002). Eublepharids thus demonstrate the full scope of Rensch's rule; that is, small species tend to be female-larger, larger species male-larger. The SSD pattern hence relates to body-size variation. Rensch's rule means that male size is evolutionarily more plastic than female size. When selection for small or large size occurs, males thus decrease

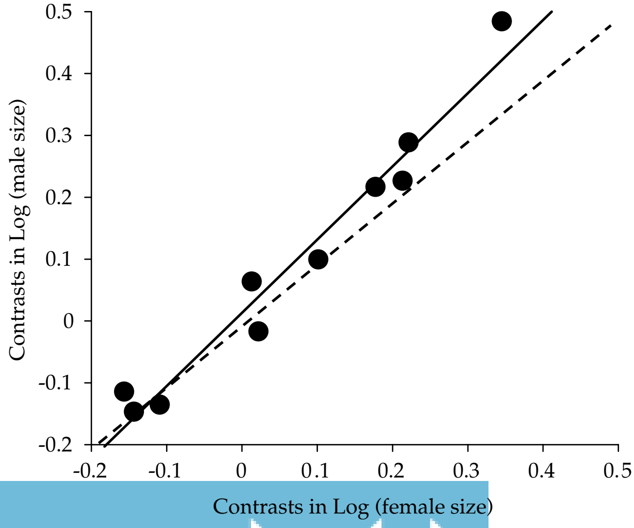


Figure 15.5 Phylogenetic independent contrasts in female size (SVL) and male size for eublepharid geckos. The solid line is the reduced major axis forced through the origin (slope ± SE, 1.22 ± 0.08), which is statistically different from 1; $P = 0.02$), showing consistency with Rensch's rule. The dashed line indicates isometry. Redrawn from Kratochvíl and Frynta (2002), with permission of Blackwell Publishing, Oxford.

or increase (respectively) their body size more than conspecific females. We can only speculate on what may constrain female size more than male size. Noteworthy candidates are differences in optimal resource allocation into growth against reproduction and maintainance in males and females between small and large species (Kozłowski 1989), or constraints on litter (egg) size operating in small species (Kratochvíl and Frynta 2002, 2006b).

The variation in relative egg size and clutch mass we found cannot explain the inversions in SSD or the pattern described by Rensch's rule. All species share similar relative clutch masses, and there is no trend for small species to have large relative clutch mass. Conversely, egg size and clutch mass in eublepharids increase nearly proportionally with female body size (Figure 15.2; Kratochvíl and Frynta 2006a, 2006b; Kratochvíl and Kubička 2007).

15.7 Summary

We here advocate an explicit phylogenetic framework for understanding the evolution of sexual dimorphism. Phylogenetic analysis of changes in dimorphism and their putative determinants in a group of related organisms exhibiting variation in these characters is a powerful tool for testing hypotheses on the origin, maintenance, and adaptive significance of sexual dimorphism. We summarized our research on eye-lid geckos (family Eublepharidae), and their sexual dimorphism integrating data on morphological (body size, SSD, HSD, presence of precloacal scent glands in males) and behavioral traits (presence of male aggressive behavior, complexity of courtship display, particularly female choice), and one life-history trait (relative egg size). We conducted phylogenetic analyses to test which factors can best explain the distribution of sexual dimorphism within this group. Male combat has disappeared twice within the Eublepharidae. In keeping with predictions of sexual-selection theory, both events were associated with losses of male-biased HSD and male scent glands. However, these associations may merely reflect phenotypic integration of the three traits involved via pleiotropic effects of testosterone, rather than functional linkage. Our analyses indicate that neither changes in the presence of male–male aggression nor in the complexity of courtship display or relative egg size were correlated with reversals from male-biased to female-biased SSD. Eublepharids demonstrate the full scope of Rensch's rule, since in small species females tend to be larger whereas in large species males are larger. To explain SSD patterns in eye-lid geckos, therefore, we need to explain Rensch's rule, which has been empirically demonstrated in many animal clades but is not yet fully theoretically elucidated.

15.8 Acknowledgments

Thanks to our collaborators (especially K. Zelená, E. Landová, M. Fokt, and I. Rehák) for stimulating discussions and parts of the data. Comments of E. Roitberg, R. Cox, Z. Starostová, J. Červenka, L. Kubička, M. Pokorná, W.U. Blanckenhorn, and T. Székely greatly improved the earlier versions of the text. The research was supported by the GAAV ČR (no. A6111410). Institutional support was given by the MŠMT (project no. 0021620828). We greatly appreciate the efforts of D.J. Fairbairn, W.U. Blanckenhorn, and T. Székely in preparation of the excellent workshop in Monte Verita and the editing of this volume.

15.9 Further readings

Braña, F. (1996) Sexual dimorphism in lacertid lizards: male head increase vs. female abdomen increase? *Oikos* **75**, 511–523.

Dial, B.E. and Grismer, L.L. (1992) A phylogenetic analysis of physiological-ecological character evolution in the lizard genus *Coleonyx* and its implications for historical biogeographic reconstruction. *Systematic Biology* **41**, 178–195.

Emerson, S.B. (2000) Vertebrate secondary sexual characteristics–physiological mechanisms and evolutionary patterns. *American Naturalist* **156**, 84–91.

Fairbairn, D.J. (1997) Allometry for sexual size dimorphism: pattern and process in the coevolution of body size in males and females. *Annual Review of Ecology and Systematics* **28**, 659–687.

SECTION III

Proximate developmental and genetic mechanisms

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Introduction

Daphne J. Fairbairn

The chapters in Sections I and II have described patterns of sexual size dimorphism (SSD) with a decidedly adaptationist perspective. Whether the patterns of variation occur across species within major clades, among populations within species, or within populations, the authors have sought ultimate, evolutionary explanations for SSD in terms of sex-specific patterns of selection. The chapters in Section III approach the evolution of SSD from a more mechanistic perspective, emphasizing its genetic and developmental basis rather than its adaptive significance. The authors assume that natural selection has favored the evolution of SSD but do not explicitly address this hypothesis. Instead, they ask how genetic and developmental systems function to generate sex-specific growth trajectories and adult body morphologies. From an evolutionary perspective, they ask about the proximate, biological mechanisms that facilitate or constrain responses to sex-specific patterns of selection. The five chapters present a mix of descriptive, theoretical, and experimental approaches that nicely illustrate the diverse methods for addressing these questions.

The section begins with Rhen's comprehensive review of basic genetic, physiological, and ecological determinants of sexual dimorphism (Chapter 16). This chapter takes the reader back to the macro-evolutionary perspective of the first section of the book but with the emphasis on proximate biological mechanisms. Rhen begins with the evolution of meiosis, syngamy, and gametes specialized for male and female roles (anisogamy). He then introduces genomic responses to sexually antagonistic selection, including specialized sex chromosomes, sex-limited gene expression, and transgenerational epigenetic effects such as genomic imprinting. Plasticity of SSD in response to social and environmental factors, as well as modulation by hormonal effects, are also described. Rhen argues convincingly that these characteristics have evolved repeatedly in different eukaryote lineages (i.e. plants and animals), providing striking examples of convergent evolution in response to similar selective regimes.

The following two chapters extend the concepts introduced in Chapter 16, with emphasis on genetic and epigenetic mechanisms in organisms with chromosomal sex determination. In Chapter 17, Bonduriansky argues that sexually antagonistic selection will favor imprinting (i.e. silencing) of genes inherited from the opposite-sex parent, and that this pattern of sexually dimorphic genomic imprinting could be sufficient to produce sexual dimorphism. He also considers the role of condition-dependence in the evolution of sexual dimorphism for sexually selected traits, predicting a positive covariation between the magnitude of SSD and condition-dependence. Although the chapter has a very strong conceptual and theoretical perspective, the predictions of these novel hypotheses are supported by Bonduriansky's own recent empirical studies, which are cited and described briefly.

The chapter by Bedhomme and Chippindale (Chapter 18) continues this theme with emphasis on the sexual conflict that occurs when alleles at a given locus exhibit sexually antagonistic fitness effects (intralocus sexual conflict). Bedhomme and Chippindale join the authors of the previous two chapters in proposing that this type of sexual conflict can be mitigated by sex-limited gene expression, sex linkage, and parent-of-origin genomic imprinting. They also propose that unresolved sexual conflict results in an average loss of fitness in populations, which they term the gender load. They describe several ingenious experiments demonstrating significant gender load in experimental laboratory populations and then discuss the difficulties faced by researchers seeking evidence of gender load in other organisms. This chapter highlights the complexities of "tuning individual gene expression to each sex separately," and suggests that genetic constraints may be more pervasive than envisaged in the traditional equilibrium model of SSD.

The final two chapters focus on developmental and physiological processes that generate sex-specific growth trajectories. In Chapter 19, John-Alder and Cox describe their studies of hormone-mediated growth trajectories in three lizard species with contrasting patterns of SSD. Rhen's description of how hormones regulate sex-specific growth patterns in vertebrates (Chapter 16) is a good introduction to this work, and John-Alder and Cox build on this by providing a clear and concise description of the basic physiology and methodologies necessary to understand their experiments. By experimentally manipulating testosterone levels in male lizards, they demonstrate that testosterone promotes growth in a species where males are larger than females, but inhibits growth in two species where females are the larger sex. They also uncover complex relationships between male activity and territorial behavior, also stimulated by testosterone, and phenotypic plasticity for growth. The story that they tell is a fascinating example of how environmental conditions, physiological mechanisms, and sexual selection interact to produce population- and species-specific patterns of SSD.

In the final chapter, Jarošik and Honek explore the hypothesis that sexual dimorphism in insects is meditated by differences between the sexes in rate of development and hence time to maturity (development time). In most insects, males are smaller than females (Chapter 6), and Jarošik and Honek ask whether males therefore develop faster and mature earlier than females, a phenomenon known as protandry. By using the concept of "developmental rate isomorphy" they are able to combine data from the literature on male and female development rates for 122 species from 11 insect orders. A meta-analysis of these data demonstrates that, on average, males do develop faster than females, especially in species that lack a true pupal stage. This major synthesis establishes that protandry is prevalent across all insect orders. However, SSD can arise through sex-specific modulation of growth rate rather than development time and so there may be little relationship between protandry and SSD (e.g. Blanckenhorn *et al*. 2007). A key challenge for future research will be to determine to what extent development rate and growth rate in insects evolve as correlated responses to selection favoring SSD, and, conversely, to what extent SSD may reflect selection acting primarily on growth and development rates rather than on adult size.

Taken together, the five chapters in this section provide fascinating insights into how genetic and developmental systems may evolve in response to selection favoring different phenotypes in males and females. Some aspects, such as chromosomal sex determination, appear to be quite labile, having evolved numerous times in different lineages. Other aspects, such as the hormonal cascade determining sexual differentiation in vertebrates, are highly conserved. We are only beginning to explore epigenetic influences on sexual differentiation, but there is increasing support for the hypothesis that genomic imprinting plays a key role. Empirical and theoretical evidence also suggests that sexually dimorphic traits tend to show high levels of condition-dependence and phenotypic plasticity, and we should therefore expect phenotypic plasticity in SSD. Finally, we are reminded that differences in adult body size between males and females require the evolution sex-specific patterns of growth and development. This means that SSD cannot be regarded as a characteristic restricted to the adult phase of the life cycle; it can be influenced by, and can have an influence on, processes occurring during juvenile development.

CHAPTER 16

Sex differences: genetic, physiological, and ecological mechanisms

Turk Rhen

16.1 Introduction

To fully understand the evolution of sexual size dimorphism (SSD), we need to examine the basic developmental, genetic, and physiological mechanisms that produce sex differences, as well as environmental factors that impinge on these mechanisms. To appreciate how these mechanisms came to be, we must recap the evolution of eukaryotes. Briefly, the evolution of meiosis and syngamy (i.e. the fusion of two cells) in eukaryotes was a prerequisite for the evolution of dimorphic gametes (i.e. anisogamy) and the subsequent evolution of all other sex differences. Although this is an obvious point, it is not a trivial one, for a phylogenetic perspective reveals that analogous mechanisms of sexual differentiation evolved independently in different lineages. In fact, if a recent hypothesis for the origin of major eukaryotic groups were correct, the two genders arose separately in plants and animals, but are essentially nonexistent in other eukaryotes. Moreover, gender differences can sometimes evolve rapidly. These observations are intriguing because there is an inherent genetic constraint to the evolution of phenotypic differences between the sexes; that is, the same genes control homologous traits in the initially monomorphic sexes (see Chapters 1, 17, and 18 in this volume).

In this chapter I briefly describe what is known about the evolution of the eukaryotic life cycle, including mitotic (asexual) and meiotic (sexual) cell division and syngamy. It is generally thought that divergent selection on the cells that fuse during syngamy led to the evolution of anisogamy. Additional sex differences evolved through elaboration of traits, like overall body size, that increased an individual's sexual fitness. In the bulk of the chapter, I illustrate four basic mechanisms that play a role in sexual differentiation, including genetic differences between the sexes, sex-limited or differential expression of autosomal genes, transgenerational epigenetic effects, and environmental influences on development. While these mechanisms are conceptually distinct, it is important to note that they act upon a common developmental process (i.e. somatic growth) and can therefore interact to influence SSD.

16.2 The evolution of eukaryotes and sex

Although early stages in the evolution of life are difficult to reconstruct, advances are being made. As recently as a decade ago, prokaryotes and eukaryotes were considered the two main lineages of life on earth. An important revision based on molecular systematics, genomics, and biochemical characteristics indicates that eubacteria and archaebacteria are as distinct from one another as they are from eukaryotes, leading to a three-domain classification that is now widely accepted (Figure 16.1). Whereas the first cells certainly lacked a membrane-bound nucleus and replicated by binary fission, the origin of the first nucleated cells remains a mystery (Martin 2005). Nevertheless, two distinct

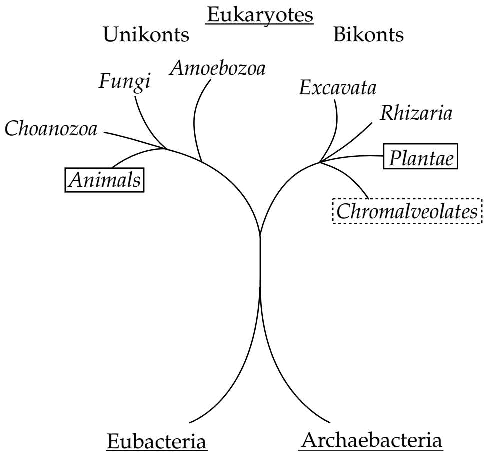

Figure 16.1 Relationships among the three domains of life: eubacteria, archaebacteria, and eukaryotes. Note the split between unikonts and bikonts and the independent origin of sex differences in animals and plants. Anisogamy also occurs in a few chomalveolates (i.e. *Plasmodium* sp.)

scenarios can be set apart. On one hand is the notion that the nuclear membrane arose *de novo* or through invagination of the plasma membrane (Martin 2005). On the other hand, there is the concept that the nucleus resulted from an endosymbiotic event analogous to the origin of mitochondria and chloroplasts (Martin 2005).

In either case, a fundamental difference in microtubule assembly characterizes two groups that split early in the history of eukaryotes (Figure 16.1; Richards and Cavalier-Smith 2005). Animals, Choanozoa (protists), Fungi, and Amoebozoa are unikonts, which have a single microtubule-organizing center. In contrast, Plantae (plants and red and green algae), Chromalveolates (protists), Excavata (protists), and Rhizaria (protists) are bikonts that have two microtubule-organizing centers. Despite this difference, mitosis is basically the same in both groups: sister chromatids are attached and pulled to opposite poles by microtubules. Several derived characters support a deep split between unikonts and bikonts, including protein phylogenies and complex gene fusions unique to each lineage.

Meiosis is also highly conserved in eukaryotes. It has even been proposed that meiosis was present in the last common ancestor of all eukaryotes and that there are no primitively "asexual" eukaryotes (Ramesh *et al.* 2005). This proposition counters the prevailing notion that some extant eukaryotes are members of a lineage that split before the evolution of sex. In any case, three relatively simple mechanistic changes transform mitotic into meiotic cell division. First, homologs align and cross over during prophase I of meiosis. Pre-existing mechanisms for DNA repair were co-opted during the evolution of synapsis: these mechanisms are found in prokaryotes. Secondly, kinetochores on sister chromatids are in a unipolar orientation during meiosis I. Thirdly, additional proteins near the centromere hold sister chromatids together during meiosis I. As a result, sister chromatids are pulled to the same pole whereas homologs are pulled to opposite poles during meiosis I. Reduction division during meiosis II is virtually identical to mitosis: sister chromatids are pulled to opposite poles because chromatid cohesion is lost and bipolar kinetochore orientation is regained at the end of meiosis I. In summary, synapsis, sister chromatid cohesion, and unipolar kinetochore geometry explain the origin of meiosis.

The other key innovation during eukaryotic evolution was syngamy, which completes the sexual cycle. Numerous hypotheses deal with the adaptive significance of sex (e.g. West *et al.* 1999), but for the current discussion, the most important consequence of sex is that it opens the door for selection to produce gender differences. Yet, most eukaryotes (i.e. Fungi and Protists) display no sign of sexual dimorphism other than complementary mating types. Mating types may be bipolar, tetrapolar, or include hundreds of alleles that might be more fittingly called self-incompatibility loci (Charlesworth 1994). The cells that fuse during syngamy are the same size (isogamous) in these groups. In contrast, anisogamy and more derived sex differences are found almost exclusively in animals and plants (including red and green algae). These observations suggest that isogamy was the ancestral state and that sexual dimorphisms evolved independently on either side of the unikont/bikont split (Figure 16.1).

The secret to understanding the evolution of sex differences lies in the evolution of dimorphic gametes. Parker and colleagues (1972) outlined a classic model in which individuals have finite resources available for producing gametes. Thus, there is an inherent trade-off between gamete size and number. Opposing patterns of selection are evident when, on one hand, individual fitness increases with the number of offspring produced, which is a function of gamete numbers. On the other hand, individual fitness increases with gamete size when zygote survival is a function of zygote size, which is a function of the size of the gametes that fuse. Isogamy with small gamete size evolves when the advantage of producing more gametes exceeds the advantage of provisioning zygotes (i.e. the slope of the fitness function for zygote size is shallow). Isogamy with large gametes evolves when these conditions are reversed (i.e. the slope of the fitness function for zygote size is steep). Disruptive selection, anisogamy, and disassortative mating (fusion of small and large gametes) arise when the fitness function is non-linear (i.e. the slope of the fitness function for zygote size is shallow at small sizes, but increases disproportionately at larger sizes; see Figure 16.2). Other factors, including sperm competition and sperm limitation, can influence the evolution of gamete size.

In multicellular organisms like plants and animals, each zygote gets half its genome from its father and half from its mother. In effect, sperm and egg are parallel and, on average, equivalent means to reproductive success. However, success through male function (i.e. sperm) must be measured relative to the male function of other individuals. Conversely, success through female function (i.e. eggs) must be measured relative to the female function of other individuals. This is Darwin's revolutionary concept of sexual selection, which can favor dramatic differences in phenotype between males and females. Paradoxically, sex hinders adaptive divergence between males and females because they share the same genome. Antagonistic selection on genes that are expressed in the same way in males and females imposes a significant fitness cost (Rice 1992; Chapters 1, 17, and 18). The evolution of dimorphism for any trait, including body size, is in essence the evolution of mechanisms that relieve this genetic constraint.

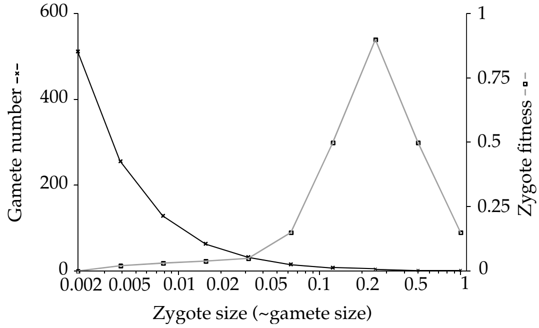

Figure 16.2 Hypothetical relationship among gamete and zygote size (on a log scale), gamete numbers, and zygote fitness that would produce disruptive selection on gamete size.

16.3 Cellular and developmental mechanisms underlying SSD

Before reviewing specific mechanisms of sexual differentiation, I outline the basic developmental mechanisms that produce sex differences in size. At an organismal level, SSD simply results from differences in the duration and/or rate of growth (Chapter 19). Male polar bears, for instance, reach a larger asymptotic body size because they grow faster and for a longer period of time than females (Derocher *et al.* 2005). Examining SSD in more detail reveals that growth in animals depends on both behavioral and physiological characteristics. Sex differences in adult size in spotted hyenas are likely due to differences in food acquisition. Whereas their linear dimensions are almost identical, females are approximately 10% heavier than males. Females are dominant to males in all situations, but are even more aggressive when feeding, thus relegating males to eat after females have had their fill (Frank 1996). Pacific white shrimp, another species with female-biased SSD, display a dramatic sex difference in the assimilation of food (Moss and Moss 2006). Males outcompete females when given limited rations despite their smaller size, suggesting that females are more physiologically efficient at converting food into body mass. These examples also illustrate the basic concept of external (i.e. nutritional) compared with internal (i.e. genetic and physiological) influences on body size. Ultimately, the rate and/or duration of cell growth, proliferation, or death produce differences in the size of specific organs as well as variation in overall body size (Hafen and Stocker 2003).

An interesting case is the evolution of clines in wing size in *Drosophila subobscura* after its introduction from Europe to the Americas (Calboli *et al.* 2003). In North America, the cline in wing size results from an increase in cell size with latitude. In contrast, the wing-size cline in South America is based on increasing cell numbers with increasing latitude, just as in Europe. Despite the distinct cellular basis of these clines, females have larger wings than males because they have more *and* larger cells in all populations studied. Although these findings highlight the importance of cell growth and proliferation in generating sex differences in organ size, more studies of their contribution to SSD are warranted.

Sex differences in cell proliferation and death are also important, particularly for development of sex-specific structures. Flower buds are initially bipotential in monoecious and dioecious plants (i.e. they have primordial male *and* female tissue). Male flowers develop in one of two basic ways: cell proliferation in the female organ may be arrested or the female organ may develop to a certain point and then degenerate via cell death. The converse occurs during development of female flowers. Interestingly, the cellular mechanisms responsible for the evolution of unisexual flowers vary among species (Dellaporta and Calderon-Urrea 1993). The significance of cell proliferation and death is not limited to plants. Two distinct sets of genital ducts develop in vertebrate embryos: Wolffian ducts are the anlagen for the male reproductive tract whereas Müllerian ducts give rise to the female reproductive tract. In male embryos, the testes synthesize testosterone, which acts as a cell-survival factor in the Wolffian ducts, and anti-Müllerian hormone (AMH), which triggers cell death in the Müllerian ducts. Female embryos do not produce testosterone or AMH. Accordingly, the Wolffian ducts regress via cell death and the Müllerian ducts grow and differentiate. These examples show that males and females initially develop along identical trajectories and that sex differences in cell growth, proliferation, and death produce sex differences in organ size and presumably body size.

Although AMH does not regulate body size, it is under sexually antagonistic selection and as such is useful for illustrating the links between gene expression, cell and organ growth, and organismal fitness (Jamin *et al.* 2003). Ectopic expression of AMH in female embryos is disastrous: such females lack a uterus and cannot reproduce. Conversely, disruption of AMH signaling in male embryos causes infertility. Such strong selection would presumably favor loss of the *AMH* gene in females and its retention in males (i.e. Y linkage). Yet, AMH is not dispensable in females because it plays a role in follicle development in adulthood (La Marca and Volpe 2006). The gene for AMH is thus located on autosomes in humans and mice. We must also consider the pleiotropic effects of genes that influence growth and body size. Next, I describe mechanisms that relieve the fitness load imposed by sexually antagonistic selection.

16.4 Sex linkage

Sex linkage is conceptually one of the simplest mechanisms for producing sex-specific gene expression (Rice 1996b; Chapter 18). Translocation of autosomal genes favored in XY males, but disfavored in XX females, to the Y chromosome would be beneficial for both sexes. The opposite scenario applies to genes that benefit females and harm males, which would ideally be W linked in species with ZZ males and ZW females. But how does sex-linked inheritance evolve from an ancestral state with no sex chromosomes? Furthermore, what happens to Z- and X-linked genes that are found in both sexes? Briefly, a new sex-determining locus initially evolves on an autosome. Such a gene might have a dominant allele F for femaleness and a recessive allele f for maleness. The only possible genotypes with this mode of inheritance are Ff females and ff males (i.e. Ff individuals mate with ff individuals to produce offspring, which will be one-half female (Ff) and one-half male (ff)).

By chance, loci under sexually antagonistic selection may be located on the same chromosome as the novel sex-determining gene. Selection then favors modifiers that suppress recombination between the sex-determining gene and the locus with opposing effects on female and male fitness.

This generates tighter linkage between alleles that benefit females and the female determining allele F, resulting in a nascent sex chromosome. Alleles on the new W chromosome that are not under strong selection (i.e. for their role in female reproduction) accumulate mutations and become non-functional. Deterioration of the W chromosome occurs gradually and the W and Z begin to differentiate over evolutionary time. This leaves Z-linked alleles with the entire functional burden and a basic difference in allelic interactions between the sexes. Whereas ZZ males remain diploid for these loci, ZW females become hemizygous. Specific mechanisms have evolved to ameliorate sex differences in gene dosage, a phenomenon called dosage compensation. During the process of chromosome degeneration, selection also favors linkage between alleles that benefit males and the male allele f. The X and Y chromosomes evolve in a perfectly analogous fashion to Z and W chromosomes.

Based on the independent origin of sex chromosomes in diverse animals and plants, it would appear that sex linkage evolves with little trouble (Bull 1983; Tanurdzic and Banks 2004). Although sex-linked inheritance is clearly important in the evolution of sexual dimorphism, its contribution to sex differences in quantitative traits like body size is unknown. Theory predicts a correlation between the relative contribution of sex-linked genes to trait development and the degree of sexual dimorphism for that trait (Fairbairn and Roff 2006). If we examine the proportion of genes that are sex-linked on a genome-wide scale, there is remarkable variation among groups. In fruit flies, roughly 16% (2309/14 449) of genes are X-linked. In contrast, just 0.06% (9/14 449) of fruit fly genes are on the Y chromosome. Whereas 5.6% of genes (1344/24 000) are X-linked in humans, 0.19% of genes (45/24 000) are Y-linked. Fewer genes are sex-linked in chickens, with 1.4% (328/23 000) on the Z and 0.2% (47/23 000) on the W chromosome. The degree of sex-chromosome differentiation even varies within groups (Ezaz *et al.* 2006). Whereas most birds share a derived pair of Z and W chromosomes, ratites have monomorphic or slightly dimorphic sex chromosomes. The degree of morphological divergence between sex chromosomes is also graded in snakes, with primitive boids having monomorphic sex chromosomes and colubrids, elapids, and vipers having progressively more dimorphic chromosomes.

16.5 Sex-limited expression of autosomal loci

Even in species with relatively large sex chromosomes, most genes reside on autosomes (i.e. approximately 84% of genes in fruit flies). This raises the question of what happens when selection favors different autosomal alleles in males and females. Consider a gene like *AMH* that is detrimental for females but beneficial for males. A null allele would be favored in females whereas a constitutive allele would be favored in males. Sexually antagonistic selection will maintain polymorphism at this locus, but neither sex is able to reach its phenotypic optimum. A third allele that is expressed in males but not in females, like *AMH* during embryogenesis, provides a simple solution to this dilemma. Sex-limited mutations of this sort are rapidly fixed by sexually antagonistic selection and can also increase in frequency with other patterns of selection (Rhen 2000).

Two distinct mechanisms produce sex-limited or differential expression of autosomal genes. The first involves epistasis between sex-linked and autosomal loci (Montagutelli *et al.* 1996; Perry *et al.* 2003; Chase *et al.* 2005). Such interactions are best characterized in the sex-determining cascade of *Drosophila melanogaster*. Sexual differentiation results from differences in dosage of X-linked and autosomal genes (Cline 1993). Four X-linked genes act as numerators in a chromosome-counting mechanism, and autosomal genes act as denominators. Whereas two copies of the numerator genes are expressed in XX females, just one copy is expressed in XY males. The numerator and denominator proteins can interact to form complexes that activate a gene called sex-lethal (*Sxl*). A high ratio of numerator to denominator proteins (i.e. XX:AA; 1:1) results in transcription of *Sxl* in females. In contrast, this ratio is too low (i.e. X:AA; 1:2) for activation of *Sxl* in males. Once *Sxl* expression is initiated in females, the protein acts in a positive-feedback loop to maintain its own expression. *Sxl*, which happens to be X-linked, is the master regulator of other genes involved in sexual differentiation. Many of these genes reside on the autosomes: i.e. transformer, double-sex, and fruitless. Interestingly, *Sxl* also interacts with another autosomal gene, cubitus interruptus, to enhance growth and female-biased SSD (Horabin 2005).

Sex steroids in vertebrates exemplify the second mechanism for producing sex-limited or differential expression of autosomal loci (Hughes 2001; Chapter 19), but analogous hormonal mechanisms have evolved in plants (Yamasaki *et al.* 2005). Sex steroids act independently of sex chromosomes and are the main mode of sexual differentiation in vertebrates. At first glance, sex-determining mechanisms in amniotes appear to be unrelated. The sex-determining gene *SRY* is variable in its regulatory and coding sequence among closely related mammals and has even been lost in some rodents (Whitfield *et al.* 1993). Although birds and mammals have chromosomal sex determination, sex chromosomes evolved separately in these groups. Snakes have sex chromosomes analogous but not homologous to birds. Some lizards have temperature-dependent sex determination and others have genotypic sex determination (Viets *et al.* 1994). Embryonic temperature determines sex in many turtles and all crocodilians examined to date (Ewert *et al.* 1994; Lang and Andrews 1994). Despite this diversity, there is genetic, cellular, morphological, and functional evidence for conservation of a core mechanism of sexual differentiation.

Genes downstream of *SRY* in mammals have been implicated in avian sex determination and temperature-dependent sex determination in reptiles. For example, *SOX9*, *DMRT1*, and *AMH* show higher expression in incipient testis compared with ovary in all species studied to date, including human, mouse, rat, chicken, and alligator. These genes are expressed in pre-Sertoli and Sertoli cells and are necessary for testis differentiation in mice and humans. Moreover, AMH causes Müllerian-duct regression in mammals, birds, and alligators (Austin 1994; Eusebe *et al.* 1996; Jamin *et al.* 2003). Gonadal differentiation is highly conserved: the gonadal anlagen is initially bipotential and consists of a medullary region that gives rise to the testis and a cortical region that gives rise to the ovary. The key cell types in the testis (Sertoli and Leydig cells) and the ovary (Granulosa and Theca cells) are also conserved, as are the steroids they produce. Leydig cells produce androgens whereas Granulosa and Theca cells synthesize estrogens and progestins.

Phylogenetic analyses indicate that three steroid receptors are present in jawless fish and that a genome-wide duplication in the last common ancestor of jawed vertebrates created the six receptors present in fish and tetrapods (Thornton 2001). Two estrogen receptors, α and β, evolved from the ancestral estrogen receptor. Glucocorticoid and mineralocorticoid receptors evolved from the ancestral corticoid receptor. Finally, androgen and progesterone receptors evolved from the 3-ketogonadal steroid receptor. The classic mode of action of steroid hormones is to enter cells, interact with their cognate receptor, and stimulate or inhibit transcription of target genes via *cis*-regulatory sequences. Androgens and estrogens regulate expression of various growth factors in this manner (Leung *et al.* 2004; Vanderschueren *et al.* 2004; Chapter 19). The population genetics model referenced above is based on natural polymorphism for hormone responsiveness (Rhen 2000); that is, an allele expressed in both sexes, an allele expressed in neither sex, and a third allele expressed in one sex only (under the control of hormone-response elements). In summary, many sex differences in phenotype are due to differential regulation of autosomal genes by sex-linked loci and/or sex-specific hormones.

16.6 Epigenetics and SSD

Although the genetic and hormonal mechanisms discussed so far are intrinsic to the developing organism, it is important to consider extrinsic factors that influence sex differences. These can be divided into two types of variable. Whereas the first includes transgenerational epigenetic effects, the second encompasses all other biotic and abiotic factors (see the next section). Parents, for example, may influence offspring phenotype through genomic imprinting, a phenomenon in which alleles inherited from the mother and the father are differentially expressed in offspring (Wilkins and Haig 2003; Chapters 17 and 18). Imprinting results from an epigenetic modification (i.e. DNA methylation) of maternal or paternal alleles that are otherwise identical. Hence, the difference in expression of parental alleles is not due to a difference in their nucleotide sequence per se, but rather a transient mark that is erased in embryonic germ cells and reapplied during sperm and egg development in each generation. At the extreme, alleles from one parent are completely silenced. For example, the paternally inherited allele for insulin-like growth factor 2 is expressed in the placenta and promotes embryo growth in mammals while the maternal allele is silent. Imprinting occurs in both plants and animals and its evolution is fairly well understood (Wilkins and Haig 2003; Gutiérrez-Marcos *et al.* 2006). However, its potential role in the evolution of sex differences is currently theoretical. Models suggest that imprinting of X-linked loci can enhance, eliminate, or even reverse sex differences in gene expression in offspring, depending on whether the locus is dosage-compensated or not (Seymour and Pomiankowski 2006; Chapter 17).

Parents also influence offspring through investment of critical resources. The basic idea is that increased allocation of resources should increase offspring fitness. Furthermore, this benefit must outweigh the cost of investment measured in terms of parental survival and fecundity. Given variation in the kinds of resources parents invest, as well as the costs and benefits of different resources, it is not surprising that parental investment varies widely. Parents may produce thousands or even millions of small offspring with miniscule investment in each or just a handful of large costly offspring. Another decision is whether to invest the same resources in daughters and sons or to invest differently in the two sexes (Trivers and Willard 1973). For example, there is a significant relationship between maternal condition and offspring sex ratio in ungulates and this relationship is stronger in species with more male-biased SSD (Sheldon and West 2004). Based on inheritance of sex chromosomes in mammals, offspring sex ratio is expected to be binomially distributed around one-half male and one-half female. Yet, females in better condition tend to produce a male-biased sex ratio. This would be adaptive if maternal condition influences offspring size and male offspring benefit more than females from larger body size. Evidence in red deer indicates that the size of male calves is indeed more strongly influenced by maternal condition than is the size of female calves (Loison *et al.* 2004). Despite significant deviations from a 1:1 ratio, the mechanism by which female ungulates modify offspring sex ratio is unknown. Sex ratios also vary in birds, but it is unclear whether skewed ratios are related to patterns of parental investment (Hasselquist and Kempenaers 2002).

Unlike most eukaryotes with chromosomal sex determination, haplodiploid hymenoptera are not constrained by their sex-determining mechanism. In fact, females can choose offspring sex by laying fertilized eggs (females) or unfertilized eggs (males). Female hymenoptera often modify progeny sex ratio, as predicted by sex-allocation theory. For instance, female organ-pipe wasps provision brood cells with all the resources required for offspring development, they deposit a single egg in each cell, and then seal these cells (Molumby 1997). Body size at emergence depends on the amount of food allocated to each cell, resulting in a strong maternal effect on offspring size. Although the effect of maternal provisioning on body size is similar in both sexes, females preferentially put female offspring in cells with more food. Consequently, females are larger than males at emergence. In accord with predictions, female fitness is correlated with body size, while male fitness is not. Female organ-pipe wasps appear to be maximizing their fitness by investing more resources in daughters.

In summary, the effect of maternal allocation of resources on male and female offspring is fairly well understood. In contrast, the role of other maternally derived factors in the evolution of sexual dimorphism has not been considered or is just beginning to be studied. Maternal RNA deposited in eggs influences offspring development in fruit flies and the African clawed frog (Deshpande *et al.* 2005; King *et al.* 2005). Maternally derived steroids can shape offspring phenotype in oviparous and viviparous vertebrates (Groothuis and Von Engelhardt 2005; Owen *et al.* 2005). While fathers can also have a big impact on offspring (Ketterson and Nolan 1994; Tallamy 2001), paternal effects on sons and daughters have not been studied as thoroughly as maternal effects.

16.7 Phenotypic plasticity and SSD

An organism's niche extends beyond its parents to include other conspecifics, the biotic environment, and the physical environment, all of which can influence sexual differentiation. The effects of extrinsic factors on sexual phenotype are usually mediated by the same mechanisms outlined above. Sexual plasticity may be adaptive, just like other phenotypic responses to environmental heterogeneity. For example, alternative reproductive tactics within a sex may be regulated by environmental cues (Rhen and Crews 2002). Furthermore, males and females often differ in their level of phenotypic plasticity, with one sex being more or less susceptible to environmental perturbations than the other sex. Finally, sex differences can even be caused by ecological, social, or cultural factors (Rhen and Lang 2004; Sakata and Crews 2004; McCarthy and Konkle 2005). Recall how sex differences in aggression and access to food may cause SSD in spotted hyenas. Sex-specific competition has also evolved in a dioecious grass: seedlings of both sexes grow more slowly when surrounded by females than they do in the presence of males (Epply 2006).

Another well-known phenomenon is environmental sex determination: factors like photoperiod and temperature trigger the development of male- or female-biased sex ratios. Long days induce male development whereas short days stimulate female development in the crustacean *Gammarus duebeni*. Day length has no inherent effect on the fitness of males and females but serves as a cue to the length of the growing season. Individuals that develop early are exposed to longer days and have more time to grow than individuals that develop later in the season (McCabe and Dunn 1997). Given that males benefit more than females from large size, individuals maximize their fitness by becoming male in environments that enhance growth. Conversely, individuals minimize fitness losses by becoming female in environments that restrict growth. A similar scenario applies to the evolution of temperature-dependent sex determination in the Atlantic silverside. Females develop at cool temperatures early in the season while males develop at warm temperatures late in the season. Females thus have a longer period for growth and are more fecund than if they were to develop later in the season. Body size has little effect on male fitness in this fish. In contrast to simply serving as a cue, incubation temperature has long-lasting effects on the physiology of snapping turtles (Rhen and Lang 2004). Turtles incubated at temperatures that normally produce males grow faster after hatching than do turtles incubated at female-producing temperatures. This effect on growth persists even when turtles from different incubation temperatures are placed in the same environment after hatching. Moreover, the temperature effect on growth in the laboratory is consistent with sex differences in growth and SSD in wild snapping turtles. In essence, different environmental conditions have different fitness effects on males and females and each sex develops under conditions that increase its marginal fitness. The mechanism that transduces the environmental cue into a physiological signal that determines sex has yet to be identified in any organism.

Recent studies have begun focusing on the condition dependence of sexual characteristics (Chapter 17). If sexually selected traits are energetically expensive to produce, one might expect that nutrient availability during development would influence the size of these traits. For example, food restriction during suckling reduces growth and adult body size in male and female rats (Houdijk *et al.* 2003). However, growth hormone and insulin-like growth factor levels only differ between control and food-restricted males. In accord with the differential effect of food restriction on hormones in males and females, males are more susceptible to the growth-inhibitory effects of streptozotocin-induced diabetes (Cortright *et al.* 1996). Yet, to fully understand sex differences, we must consider the flip side of the coin. That is to say, why are female size and hormone levels less sensitive to food restriction and diabetes than homologous traits in males? One answer is that male rodents are able to reproduce regardless of body size whereas female reproduction appears to require a minimum size (Hamilton and Bronson 1986). Hence, the hormonal mechanisms underlying growth in females may have been selected to be relatively insensitive to normal variation in nutrient intake. In summary, organisms must be able to perceive environmental cues, integrate or process those cues, and then react in an adaptive manner. It is also important to remember that the degree to which sex differences are sensitive to environmental input varies among species and even among traits within species.

16.8 Summary

The evolution of the eukaryotic life cycle represents a major transition in the history of life on earth. Advances in our understanding of the origin and evolution of mitosis, meiosis, and syngamy, along with clarification of relationships among eukaryotic lineages, are providing a new context for studying gender differences. For instance, females and males appear to have evolved independently in plants and animals. The evolution of gender itself epitomizes a paradox. Females and males share the same genome, which places a significant constraint on the evolution of sex differences. In this chapter, I reviewed four mechanisms that relieve this constraint and contribute to sexual differentiation. There has been convergent evolution of (1) genetic differences between the sexes, (2) sex-limited or differential expression of autosomal loci, (3) transgenerational epigenetic effects, and (4) phenotypic plasticity for sexual traits (i.e. environmental influences on sexual development). Future research should seek to integrate evolutionary and mechanistic approaches in the study of SSD. It is through such studies that we will understand exactly how sex-specific selection interacts with genetic (and physiological) variation to produce sexual dimorphism.

16.9 Suggested readings

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Yang, X., Schadt, E.E., Wang, S., Wang, H., Arnold, A.P., Ingram-Drake, L. *et al.* (2006) Tissue-specific expression and regulation of sexually dimorphic genes in mice. *Genome Research* **16**, 995–1004.

CHAPTER 17

The genetic architecture of sexual dimorphism: the potential roles of genomic imprinting and condition-dependence

Russell Bonduriansky

17.1 Introduction: the puzzle of sexual dimorphism

Differences between the sexes in morphology, physiology, behavior, and life history are ubiquitous, but we still have much to learn about how genomes produce strikingly different phenotypes in different sexes. In this chapter, I explore some emerging research that promises to enrich our understanding of the evolution and genetic architecture of sexually dimorphic traits. Building on the ideas and findings outlined in Section 17.1, I consider the potential roles of two genetic mechanisms, genomic imprinting and condition-dependence. I outline recent advances in theory and empirical knowledge that link these phenomena to sexual dimorphism, and suggest some questions for future investigation.

17.1.1 Sex-specific selection

The fundamental dimorphism in gamete size (anisogamy) is thought to engender the contrasting reproductive strategies of females and males that, in turn, select for sexual dimorphism. Competition among the numerous, tiny male gametes for access to a limited number of large, resource-rich female gametes selects for the 'primary' sex differentiation of the reproductive system, and ultimately leads to elaborate and often spectacular forms of male–male competition for access to females, mediated by 'secondary' sexual traits such as weapons, signals, clasping devices, or specialized sensory adaptations. Sex-specific reproductive strategies also typically comprise life-history traits such as growth rates, reproductive schedules, and aging rates. Thus, numerous male traits are subject to sexual selection, whereas the homologous traits of females are not. We still know very little about sex-specific selection (but see Preziosi and Fairbairn 2000; Chenoweth and Blows 2005). Nonetheless, it is clear that sex-specific selection favors the independent evolution of the sexes towards sex-specific (sexually dimorphic) phenotypic optima. As illustrated by previous chapters in this volume, sexual size dimorphism, where one sex expresses a trait such as an appendage, or the entire body, at a greater size than the other sex, characterizes many sexually homologous traits, including some spectacularly exaggerated secondary sexual traits.

17.1.2 Intersexual genetic correlations and intralocus sexual conflict

The puzzle of sexual dimorphism, first clearly formulated by Fisher (1930a, 1931), reflects the fact that sex-specific selection acts on genes that are expressed in both sexes and transmitted from mother to son and from father to daughter (Mendelian genes). Trait expression in females and males is therefore typically subject to an intersexual genetic correlation which can impede the evolution of sexual dimorphism (Lande 1980a, 1987; and see Chapters 1, 16, and 18 in this volume). Sexual selection on male traits can cause correlated evolution in homologous female traits, displacing the female phenotype from the optimum for viability and fecundity. Likewise, viability and fecundity selection on female traits can constrain the evolutionary response of homologous male traits. Consequently, genes subject to sex-specific selection may have sexually antagonistic fitness effects, increasing fitness when expressed in one sex, but reducing fitness when expressed in the other sex (Rice 1984; Rice and Chippindale 2001; Chapter 18). Genes with sexually antagonistic fitness effects have been documented in the fly *Drosophila melanogaster* (Chippindale *et al*. 2001; Rand *et al*. 2001; Chapter 18) and the cricket *Allonemobius socius* (Fedorka and Mousseau 2004). Such genes contribute to intralocus sexual conflict, a deviation from the optimal genotype at a locus as a result of a different pattern of selection on the same locus in the opposite sex, manifested in sub-optimal expression of traits affected by loci under sex-specific selection. Although the most intense intralocus sexual conflict is associated with sexually antagonistic selection (i.e. selection acting in opposite directions in females and males), some degree of intralocus sexual conflict is likely under any pattern of sex-specific selection (see Section 17.2).

An autosomal-Mendelian genetic architecture may be regarded as the genetic null model and primitive condition for most sexually homologous traits. This genetic architecture generates a high intersexual genetic correlation (see Lande 1987; Chapter 1). If, in one sex, such a trait is displaced from its viability optimum by sexual selection, then the genes affecting the expression of this trait will have sexually antagonistic fitness effects and generate intralocus sexual conflict. Lande (1980a, 1987) argued that sex-specific selection would ultimately lead to a reduction of the intersexual genetic correlation, allowing sexual dimorphism to evolve more rapidly. Although this prediction remains controversial (see Reeve and Fairbairn 2001; Fairbairn and Roff 2006), it is supported by recent evidence, from a fly, a bug, a moss, and a gynodioecious strawberry, showing that the more dimorphic traits within species tend to exhibit lower intersexual genetic correlations than traits with little or no dimorphism (Ashman 2003; Bonduriansky and Rowe 2005a; McDaniel 2005; Chapter 9). The most parsimonious explanation for this pattern is that traits that are (or have been) subject to intense intralocus sexual conflict evolve modifications to autosomal-Mendelian genetic architecture, and these genomic adaptations reduce the intersexual genetic correlation and facilitate the evolution of sexual dimorphism. But what are these genomic adaptations?

17.1.3 Genomic adaptations to intralocus sexual conflict

Genomic modifications that may reduce intralocus sexual conflict and facilitate the evolution of sexual dimorphism can be separated into two non-exclusive categories: those based on sex-linked segregation of loci located on the sex chromosomes, and those based on sex-limited epistasis. The former may reduce intersexual genetic correlations because sex chromosomes exhibit sex-dependent dosage. Fisher (1930a, 1930b, 1931) recognized that the Y chromosome is absent from female genomes, so any male-benefit genes on that chromosome will be expressed in males only. Consequently, Y-linked genes do not contribute to intersexual genetic correlations or intralocus sexual conflict (see Roldan and Gomendio 1999). However, Rice and Chippindale (2002) argued that the small, degenerate Y chromosome is unlikely to accommodate a sufficient number of genes to substantially mitigate intralocus sexual conflict. The much larger X chromosome is present in double dose in females, relative to males (although dosage compensation or X inactivation may reduce or eliminate this dosage difference). Rice (1984) showed that sex-linked segregation may facilitate the evolution of sexually antagonistic genes on the X chromosome. Nonetheless, because the X chromosome is expressed in both sexes, X-linked genes are not immune from intralocus sexual conflict (Rice 1984). It remains unclear whether sexually antagonistic genes are disproportionately located on the sex chromosomes (see Reinhold 1998; Roldan and Gomendio 1999; Lindholm and Breden 2002; Parisi *et al*. 2003; Fitzpatrick 2004). However, because the sex chromosomes (in species that have them) are necessarily the basis of all other differences between the sexes, sex-linked segregation is likely to play an important role in genomic adaptation to intralocus sexual conflict.

Sex-linked genes may serve as 'switches' for mechanisms of sex-limited epistasis (gene interaction patterns that occur in one sex only) that mitigate intralocus sexual conflict. One mechanism of sex-limited epistasis that may be of considerable importance is the duplication and sex limitation of autosomal loci (Rice and Chippindale 2002; Proulx and Phillips 2006; Chapter 16). If an autosomal locus carrying a male-benefit gene is duplicated, and one of the resulting loci subsequently evolves male-limited expression (under the control of a sex-linked genetic switch), the intersexual genetic correlation will be reduced, and this locus will evolve towards the male optimum, unopposed by antagonistic selection on females. Sexually antagonistic selection may similarly favor sex-limited expression of some alleles at autosomal loci (Rhen 2000; Chapter 16; and see Montgomery *et al*. 1996; Chase *et al*. 2005, for empirical examples). A long-recognized form of sex-limited epistasis is the role of sex-hormones in sexual differentiation (Jost *et al*. 1973; Chapter 16). Hormonal control of sexual dimorphism is well known in mammals (Renfree 1992; Renfree *et al*. 2001) and insects (Stern and Emlen 1999; Emlen *et al*. 2006). However, sex-limited epistasis can also take the form of 'direct' (i.e. not hormone-mediated) genetic control of sexual differentiation. Direct genetic control can involve both sex-linked and autosomal genes, and has been observed in mammals (O *et al*. 1988; Glickman *et al*. 2005; Chase *et al*. 2005) and insects (Kopp *et al*. 2000). Sexual dimorphism may often reflect a combination of hormonal and direct genetic mechanisms (see Emlen *et al*. 2006). We still know very little about variation among traits and taxa in the genetic architecture of sexual dimorphism, and it is likely that novel mechanisms await discovery.

In the following sections, I examine two other forms of sex-limited epistasis that may contribute to the reduction of genomic conflict and the evolution of sexual dimorphism: genomic imprinting and condition-dependence of sexually selected traits. These genomic adaptations are expected to be particularly relevant for secondary sexual traits (which can include overall body size), rather than primary sexual traits, for two reasons. First, secondary sexual traits are thought to undergo rapid (co)evolutionary cycles (Gavrilets and Hayashi 2006), and hence may be of relatively recent origin and characterized by abundant genetic variation. As I explain below, sufficient genetic variation is a key precondition for the evolution of genomic imprinting via intralocus sexual conflict. Second, such traits are expected to evolve strongly condition-dependent expression (Rowe and Houle 1996).

17.2 Genomic imprinting

17.2.1 Intralocus sexual conflict and the evolution of offspring–parent resemblance

For traits under sex-specific selection, individuals benefit by minimizing resemblance to their opposite-sex parent because the opposite-sex parent is likely to transmit low-fitness genes for such traits (Day and Bonduriansky 2004). Intralocus sexual conflict may thus be unavoidable when traits inherited from both parents are under sex-specific selection. Since both sex-specific selection and intersexual inheritance characterize many autosomal and X-linked loci, intralocus sexual conflict is likely to beset much of the genome, and impose substantial fitness costs (Chapter 18).

To illustrate this, consider a hypothetical sexually selected male trait, elongated antennae used by male flies as a signal in courtship (see Bonduriansky and Rowe 2003 for an empirical example). To become a father, a male must normally succeed in sexual competition, and his performance will depend, in part, on the length of his antennae, so fathers will have longer antennae than the average for all males. In contrast, sexual selection does not act on antenna length in females, so mothers will not have longer antennae than females that fail to breed. Assuming that the phenotypic variation reflects additive genetic variation, fathers will be more likely to transmit genes for long antennae than mothers will. Consequently, on average, a male offspring will be more likely to inherit a high male-fitness allele from its father than from its mother. This will be true even for a locus with male-limited expression, because females will shelter and pass on alleles that would have been eliminated by sexual selection had they been expressed in a male. Thus, for male secondary sexual traits, selection should favor mechanisms that diminish a male's resemblance to its mother, or, more formally, reduce the expression of maternally inherited alleles and weaken maternal heritability. For traits under sexually antagonistic selection, selection will also favor reduced expression of paternally inherited alleles in female offspring. But how could such inheritance patterns evolve?

Unequal expression of maternally and paternally inherited alleles, resulting in differential resemblance to the mother and father, can result from genomic imprinting. The DNA at an imprinted locus receives an epigenetic label (an imprint) in either eggs or sperm: in mammals, the imprint consists of cytosine methylation, but other taxa employ different molecular mechanisms (see Lloyd 2000). Imprints are retained in the zygote, and replicated through somatic cell divisions. They affect the rate of transcription, resulting in differential expression of alleles inherited from the mother and father and, often, the complete silencing of genes from one parent in some tissues. However, the imprint is removed in the germ line, and reapplied during gametogenesis in one sex. In a quantitative genetic analysis, genomic imprinting is manifested as unequal heritability through the mother and father (Spencer 2002). For example, silencing of maternally inherited alleles results in reduced maternal heritability for traits affected by the imprinted locus. Genomic imprinting has been identified in diverse organisms, including mammals (de Koning *et al*. 2000; Moore 2001; Suzuki *et al*. 2005), *Drosophila* (Lloyd *et al*. 1999; Lloyd 2000) and other insects (Herrick and Seger 1999), and plants (Alleman and Doctor 2000). Indeed, it appears that cytosine methylation is frequently applied to novel chromosomal regions as a means of silencing the promoters of selfish transposable elements (Bestor 2003), so it is not unreasonable to expect novel imprinted regions to evolve in response to intralocus sexual conflict.

A simple genetic model can illustrate selection on genomic imprinting under intralocus sexual conflict (Figure 17.1). Imagine a trait under sexual selection in males. The trait phenotype is determined by an autosomal locus with two alleles: *p* increases trait size and *q* decreases trait size. These alleles have additive phenotypic effects, so that heterozygous phenotypes are intermediate between those of the two homozygotes. Sexual selection favors large trait size in males so that, on average, *pp* males are most successful and *qq* males least successful. For simplicity, assume that females' probability of breeding is not strongly affected by this locus (corresponding to male-limited expression, or weak stabilizing selection in females). However, directional selection on the male trait is maintained through infusion of *q* alleles by mutation and gene flow. Now imagine a modifier locus where an 'imprinter' allele arises, silencing maternally inherited alleles at the trait locus (maternal silencer). The imprinter allele will alter the phenotypes of heterozygotes (denoted hereafter with the paternally inherited allele

	Maternal genotype		
Paternal genotype	*qq*	*pq*	*pp*
2×*pp*	4*pq*	2*pp* 2*pq*	4*pp*
1×*pq*	2*pq* 2*qq*	*pp pq qp qq*	2*pp* 2*qp*
0.5×*qq*	4*qq*	2*qp* 2*qq*	4*qp*

$=15pp+15pq+6qp+6qq$

Figure 17.1 A genetic model illustrating selection on genomic imprinting (with maternal silencing) of a trait under sexual selection in males (see text). The relative fitness of each paternal genotype is given by the factors to the left (with fitness of *pq* and *qp* fathers averaged, for simplicity), whereas maternal fitness is assumed to be unaffected by this locus. Offspring genotypes are shown for each possible cross (for heterozygotes, the paternally inherited allele is shown first). The tally at the bottom shows that, because males are more likely to pass on *p* alleles to their offspring, *pq* heterozygotes (whose fitness is increased by imprinting) are more common than *qp* heterozygotes (whose fitness is reduced by imprinting).

indicated first): *pq* males will express the same phenotype as *pp* homozygotes, whereas *qp* males will express the same phenotype as *qq* homozygotes. Net positive selection on the imprinter allele occurs because sexual selection weeds out males carrying *q* alleles, insuring that *pq* genotypes are more common than *qp* genotypes in offspring (Figure 17.1). The imprinter allele should therefore increase in frequency, and simulations for this two-locus system show that this is indeed what happens, provided that genetic variation is maintained (Day and Bonduriansky 2004).

Similar logic applies under sexually antagonistic selection. If selection is stronger on males than on females (but genetic variation persists), then breeding males will be more likely to carry and transmit *p* alleles, whereas breeding females will tend to transmit *q* alleles. In this case, a maternal silencer will decrease the fitness of female offspring, but this cost will be more than offset by the benefit to male offspring. Thus, as shown in Figure 17.2, an imprinter allele that silences the maternally inherited trait allele will increase in frequency if selection acts more strongly on males (Day and Bonduriansky 2004).

In the above examples, as in well-studied imprinted genes like *igf2* and *igf2r* of humans (Moore 2001), alleles from parents of a particular sex are silenced in all offspring. However, under sexually antagonistic selection, this type of imprinting would be costly to one sex. Indeed, if sexually antagonistic selection is equally strong on both sexes (balanced), a situation envisioned by Lande (1980a) as an intermediate stage in the evolution of sexual dimorphism where intralocus sexual conflict is most intense, then the net cost of maternal silencing to females will completely negate the net benefit to males. In such cases, selection would favor a more complex form of imprinting where male offspring silence maternally inherited alleles and female offspring silence paternally inherited alleles (Day and Bonduriansky 2004). Such sexually dimorphic imprinting would benefit both sexes. Moreover, unlike conventional imprinting, sexually dimorphic imprinting would reduce the intersexual genetic correlation (Bonduriansky and Rowe 2005a).

Note that the strength of selection for genomic imprinting reflects the magnitude of additive genetic variation for the imprinted trait. This suggests that genomic imprinting may be especially likely to evolve in traits with recently acquired secondary sexual functions, where genetic variation is abundant. Imprinting may also evolve when gene flow between populations with differing optima for sexually selected traits prevents these populations from attaining their local optima, or when genetic variation is maintained by balanced sexually antagonistic selection.

The intralocus sexual-conflict model (Day and Bonduriansky 2004) provides a more general alternative to previous theories of the evolution of genomic imprinting under sexual conflict. The most widely accepted of these, the parental-conflict theory (Moore and Haig 1991; Moore 2001), proposes that genomic imprinting evolves because paternally inherited alleles in embryos are more selfish towards their mother than are maternally

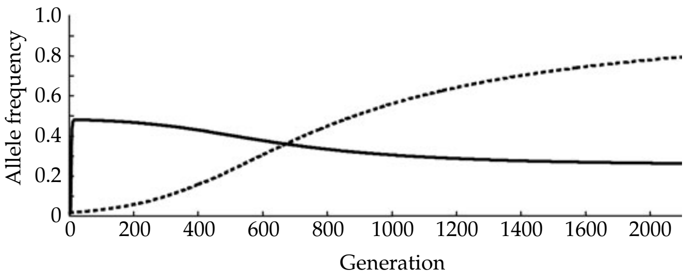


Figure 17.2 A simulation illustrating the evolution of genomic imprinting (with maternal silencing) for a secondary sexual trait subject to sexually antagonistic selection (see text). A male-benefit allele (*p* allele, solid line) that increases trait size occurs at a frequency of 0.01 at generation 0. An imprinter allele (dashed line) that silences maternally inherited alleles at the trait locus also has an initial frequency of 0.01. In each generation, 1% of *p* alleles are replaced by *q* alleles (which reduce trait size) as a result of mutation and gene flow, resulting in stronger selection on males than on females.

inherited alleles, and applies to traits involved in the extraction of maternal resources by offspring in species with polyandry and maternal provisioning after fertilization. The X-linked genomic imprinting theory (Iwasa and Pomiankowski 1999) shows that genomic imprinting can result in differential levels of expression of X-linked genes in males and females, so that imprinting of X-linked genes with sexually dimorphic expression optima is favored by selection. This theory is applicable to X-linked (or Z-linked) genes. In contrast, the intralocus sexual conflict model is potentially applicable to any trait under sex-specific selection in any species. Distinguishing between these theories, which predict imprinting in different sets of genes, is a problem of both theoretical and medical importance, given that genomic imprinting is directly implicated in the development of cancer and other disorders (Horsthemke 1997; Jirtle 1999).

17.2.2 Sexual dimorphism via genomic imprinting

Curiously, in addition to reducing the intersexual genetic correlation and mitigating intralocus sexual conflict, the sexually dimorphic form of genomic imprinting produces phenotypic sexual dimorphism in the imprinted trait when that trait is subject to sexually antagonistic selection (Day and Bonduriansky 2004). This phenotypic effect simply reflects unequal probabilities of inheriting sexually antagonistic alleles from the mother and father. In the sexually antagonistic selection example outlined above, fathers disproportionately transmit *p* alleles to their offspring, whereas mothers disproportionately transmit *q* alleles. Because, under sexually dimorphic imprinting, individuals only express alleles inherited from the same-sex parent, males are more likely than females to express *p* alleles, which produce a greater mean trait size (Figure 17.3). Thus, in theory, sexual dimorphism can result from a combination of sexually antagonistic selection and sexually dimorphic genomic imprinting.

17.2.3 Empirical evidence

The intralocus sexual-conflict model (Day and Bonduriansky 2004) predicts a role for genomic imprinting in the genetic architecture of sexually

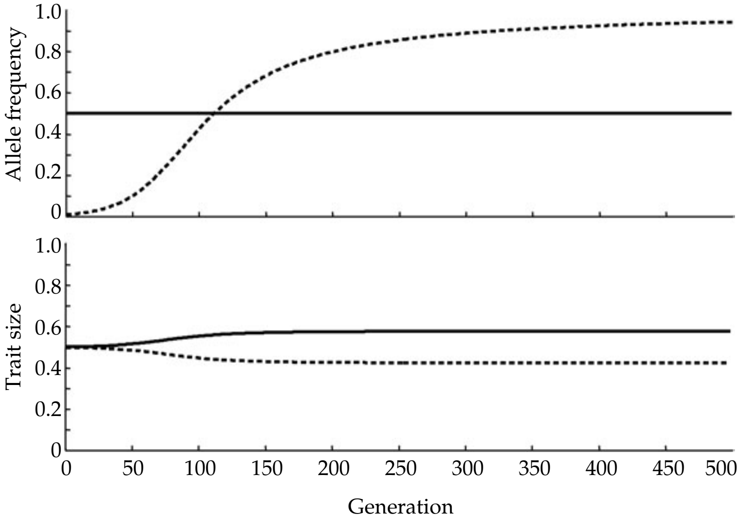


Figure 17.3 A simulation illustrating the evolution of a sexually dimorphic imprinter allele that causes silencing of maternally inherited alleles in males and paternally inherited alleles in females (top panel), and resulting evolution of phenotypic sexual dimorphism in the imprinted trait (bottom panel). The imprinter allele (top panel, dashed line) occurs at a frequency of 0.01 at generation 0. The imprinter allele modifies the expression of a secondary sexual trait under balanced sexually antagonistic selection. The male-benefit *p* allele (top panel, solid line) is present at a frequency of 0.5 in generation 0, and there is no mutation or gene flow. The bottom plot shows the evolution of the secondary sexual trait phenotype, assuming that a *p* allele contributes a phenotypic value of 1, and a *q* allele contributes a phenotypic value of 0. As the imprinter allele increases in frequency, the mean trait sizes of males (bottom panel, solid line) and females (bottom panel, dashed line) diverge.

dimorphic traits. Bonduriansky and Rowe (2005a) tested this prediction by comparing maternal and paternal heritabilities of sexually dimorphic body-shape components in the piophilid fly *Prochyliza xanthostoma*. As predicted, sexual traits tended to exhibit stronger heritabilities through the father than through the mother, whereas non-sexual traits tended to exhibit more similar heritabilities through both parents. Notably, the most strongly dimorphic sexual trait was heritable only through the same-sex parent, a pattern consistent with sexually dimorphic imprinting. Similar patterns have been reported previously (see Bonduriansky and Rowe 2005a). However, directional differences between maternal and paternal heritabilities do not provide unequivocal evidence of genomic imprinting. Further studies, using quantitative genetic and molecular techniques, are needed to test for genomic imprinting of autosomal loci affecting sexually selected traits. It may also be possible to use artificial sexually antagonistic selection as a direct test of the theory.

17.3 Condition-dependence

17.3.1 Coevolution of condition-dependence and sexual dimorphism

In many species, striking variation among males in the degree of 'exaggeration' of their secondary sexual traits appears to reflect variation in individual condition (see Cotton *et al*. 2004b). This suggests a conceptual link between condition-dependence and sexual dimorphism: if sexual dimorphism reflects mean trait exaggeration in males, relative to females, then sexual dimorphism is a function of condition-dependence. Yet, the association between condition-dependence and sexual dimorphism has received little attention. In this section, I argue that condition-dependence may play a key role in the evolution and genetic architecture of sexual dimorphism.

According to theory, condition-dependence evolves because it allows individuals to optimize the trade-off between viability and secondary sexual trait expression (see Nur and Hasson 1984; Rowe and Houle 1996). Condition reflects the quantity of metabolic resources available to an individual and the efficiency with which it can convert those resources into fitness. Thus, condition depends on both the quality of genes affecting resource acquisition and utilization, and the availability of resources in the ambient environment. Genetic variation in condition is difficult to quantify, and remains poorly understood (Hunt *et al*. 2004). In contrast, numerous experimental manipulations have confirmed the importance of environmental effects on condition, showing that individuals exposed to more abundant dietary resources are more vigorous and typically exhibit more exaggerated secondary sexual traits (Emlen 1997; Cotton *et al*. 2004a; Bonduriansky and Rowe 2005b; Bonduriansky 2007). The magnitude of such environmental treatment effects reflects the strength of condition-dependence.

Life-history theory predicts that condition-dependence and sexual dimorphism will coevolve (Bonduriansky and Rowe 2005b; Bonduriansky 2007). Because sexual selection displaces male traits from their viability-selected optima, the degree of trait exaggeration in males, relative to the viability-selected optimum approximated by the female phenotype, should reflect both the degree of sexual dimorphism and the viability costs of trait expression for males. These viability costs, in turn, favor the evolution of condition-dependence. In other words, all else being equal, the (mean) degree of trait exaggeration in males should also reflect the strength of condition-dependence that is favored by selection.

The coevolution of condition-dependence and sexual dimorphism may result in a common genetic and developmental basis (i.e. a positive genetic correlation) for these traits. Empirically, it also predicts phenotypic covariation among traits between condition-dependence and sexual dimorphism. If an organism possesses a suite of traits targeted to varying degrees by sexual selection, then the more dimorphic traits, which are targeted most directly by sexual selection, should also exhibit stronger condition-dependence. As predicted, the magnitude of condition-dependence of body-shape components is positively correlated with the degree of sexual dimorphism in the piophilid fly *P. xanthostoma* (Bonduriansky and Rowe 2005b) and the neriid fly *Telostylinus angusticollis* (Bonduriansky 2007).

These studies support the prediction that condition-dependence coevolves with sexual dimorphism, although tests using other taxa and other types of secondary sexual traits (e.g. genitalic traits, which tend to exhibit low phenotypic variances) are needed to assess the generality of this pattern. The prediction can also be tested interspecifically: species with greater dimorphism in the size of a trait (or overall body size) should exhibit stronger condition-dependence.

17.3.2 Intralocus sexual conflict and genic capture

Rowe and Houle (1996) hypothesized that directional sexual selection on a trait drives the evolution of condition-dependence via "genic capture", a form of epistasis linking the expression of the targeted trait with variation at numerous loci affecting the efficiency of resource acquisition and allocation. Their model is based on the implicit assumption that genic capture can evolve in a sex-limited manner (i.e. in males only, without a correlated evolutionary response in females). This assumption reflects the idea that sexual selection favors the evolution of condition-dependent expression in male secondary sexual traits, but not in the homologous traits of females (Figure 17.4).

If genic capture represents a form of sex-limited epistasis, as assumed by Rowe and Houle (1996), then the evolution of condition-dependence in secondary sexual male traits may reduce intersexual genetic correlations and facilitate the (co)evolution of sexual dimorphism in those traits (see Section 17.1.3). The capture of variation at numerous loci affecting resource acquisition and allocation efficiency by male secondary sexual traits can result in dramatic phenotypic differences between females and high-condition males. However, because the modifying effects of these genes (loci L_a–L_e in Figure 17.4) are assumed to be male-limited, they are expected to contribute little to intralocus sexual conflict. Nonetheless, even under genic capture, it is likely that some non-condition-dependent genes (such as L_f in Figure 17.4) will still affect trait expression in both sexes, exacerbating intralocus sexual conflict. Interestingly, covariation among traits between the strength of condition-dependence and the degree of sexual dimorphism (see Section 17.3.1) suggests that traits can evolve varying degrees of genic capture, corresponding to the intensity of intralocus sexual conflict.

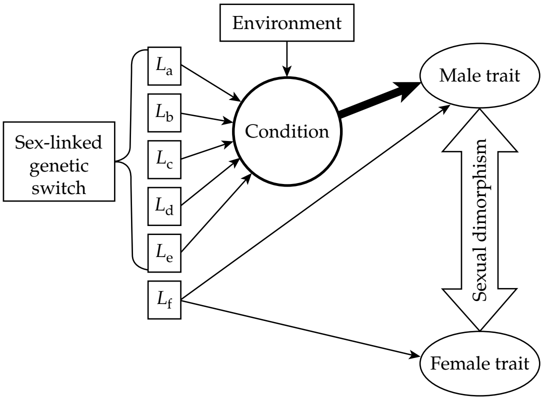


Figure 17.4 The genic-capture model postulates a form of sex-limited epistasis that has the potential to mitigate intralocus sexual conflict and facilitate the evolution of sexual dimorphism. Ancestrally, trait expression is affected by the same locus in both sexes (locus L_f) , and is independent of condition. Once the trait assumes a function in male sexual competition, the genic-capture model predicts that male trait expression will come to reflect variation at numerous loci affecting the efficiency of resource acquisition and allocation (loci L_a–L_e) and, thus, the genetic component of condition. Male trait expression will also reflect the availability of resources in the ambient environment. In contrast, it is assumed that female trait expression will remain independent of condition, and unaffected by genic capture. The sex-limited nature of genic capture requires some form of sex-linked genetic switch to activate this epistatic architecture in males.

However, if the evolution of condition-dependence in male traits results in correlated responses in females, then condition-dependence might exacerbate intralocus sexual conflict by imposing two distinct costs on females: over-allocation of resources to the homologues of male secondary sexual traits, and over-expression of those traits relative to the female optimum. Whether the evolution of condition-dependence is likely to mitigate or exacerbate intralocus sexual conflict thus depends on the intersexual genetic correlation for condition-dependence. The magnitude of this genetic correlation may reflect the degree of sex-limitation of the genetic switch that "activates" genic capture (see Figure 17.4). The assumption of sex limitation presupposes a genetic correlation of zero. However, an analysis of reaction norms for sexually dimorphic body shape components in the fly *P. xanthostoma* suggested otherwise: although male traits were more strongly condition-dependent than homologous female traits, a positive correlation between the sexes for condition-dependence strength was observed (Bonduriansky and Rowe 2005b).

17.3.3 The genetic architecture of condition-dependent sexual dimorphism

The theory and empirical observations outlined above suggest that condition-dependence and sexual dimorphism may have a common genetic and developmental basis and, thus, may be regarded as distinct pleiotropic consequences of the same genes. These findings point to a need to integrate genetic and evolutionary models of condition-dependence and sexual dimorphism. Although considerable thought has been given to the genetic architecture of sexual dimorphism (see Section 17.1.3), current models fail to account for the condition-dependent expression of sexually dimorphic secondary sexual traits. Conversely, theory on the genetic architecture of condition-dependence (Rowe and Houle 1996; Tomkins *et al*. 2004) fails to address its sex-specific nature, and the assumption that genic capture can evolve in a sex-limited manner has received little theoretical or empirical examination. This gap calls for models that can account for the wholly or partially sex-limited effects of resource acquisition and allocation genes and environmental factors on the expression of secondary sexual traits, as well as variation among traits in the strength of condition-dependence (see Bonduriansky and Rowe 2005b; Bonduriansky 2007).

17.4 Summary

In Section 17.2, I outline new theory showing that genomic imprinting may play a role in the genetic architecture of sexually dimorphic traits, and that it can contribute to the expression of a sexually dimorphic phenotype (Day and Bonduriansky 2004). Because sex-specific selection results in an elevated risk of inheriting low-fitness alleles from the opposite-sex parent in one or both sexes, an imprinter gene that causes the silencing of those alleles will be favored by selection. In traits under sexual selection in males, the silencing of maternally inherited alleles is predicted. However, under sexually antagonistic selection, greater fitness advantage results from a hypothetical form of imprinting whereby males silence maternally inherited alleles and females silence paternally inherited alleles. Interestingly, this form of imprinting, in conjunction with sexually antagonistic selection, is sufficient to produce a sexually dimorphic trait phenotype. The theory is tentatively supported by empirical evidence (Bonduriansky and Rowe 2005a).

In Section 17.3, I consider the potential role of condition-dependence in the evolution and genetic architecture of sexual dimorphism. Condition-dependent expression of secondary sexual traits allows individual males to optimize the trade-off between viability and reproductive rate. Life-history theory predicts that sexual dimorphism and condition-dependence will coevolve because the degree of exaggeration of male traits by sexual selection (i.e. the magnitude of sexual dimorphism) reflects the viability costs of trait expression and, therefore, the benefits of condition-dependence. This prediction is supported by positive covariation of sexual dimorphism and condition-dependence among morphological traits (Bonduriansky and Rowe 2005b; Bonduriansky 2007). Besides the hypothesized fitness benefits to males, however, I argue that condition-dependence may also contribute to the reduction of intersexual genetic correlations, thus benefiting both sexes by mitigating intralocus sexual conflict and facilitating the evolution of sexual dimorphism.

17.5 Suggested readings

Bonduriansky, R. (2007) The evolution of condition dependent sexual dimorphism. *American Naturalist* **169**, 9–19.

Bonduriansky, R. and Rowe, L. (2005) Intralocus sexual conflict and the genetic architecture of sexually dimorphic traits in *Prochyliza xanthostoma* (Diptera: Piophilidae). *Evolution* **59**, 1965–1975.

Bonduriansky, R. and Rowe, L. (2005) Sexual selection, genetic architecture, and the condition dependence of body shape in the sexually dimorphic fly, *Prochyliza xanthostoma* (Diptera: Piophilidae). *Evolution* **59**, 138–151.

Day, T. and Bonduriansky, R. (2004) Intralocus sexual conflict can drive the evolution of genomic imprinting. *Genetics* **167**, 1537–1546.

CHAPTER 18

Irreconcilable differences: when sexual dimorphism fails to resolve sexual conflict

Stéphanie Bedhomme and Adam K. Chippindale

18.1 Introduction

Sexual dimorphism occurs predominantly because selection shapes the two sexes in different ways, moving each closer to its fitness optimum. However, the ability of the genome to respond to this divergent selection may be limited by the architecture of intersexual genetic correlation (see also Chapters 1, 16, and 17 in this volume). Since most traits will be genetically correlated between the sexes when they first arise, divergent selection can drive fitness down in one sex as a direct consequence of selection on the other, defining a pattern of sexually antagonistic (SA) gene expression. The cost of the SA genes involved in this intralocus sexual conflict should motivate the evolution of sex-specific gene regulation and other mechanisms to allow the sexes to evolve towards separate fitness optima. Intralocus sexual conflict is therefore a precursor state to the evolution of sexual dimorphism and may persist if gender limitation is incomplete. Although this idea is not new, it has only recently been the focus of much empirical attention. Accumulating evidence suggests that intralocus sexual conflict may be common and consequential, creating a load in populations, but at the same time difficult to detect and quantify. Here we briefly discuss the relationship between sexual conflict and sexual dimorphism, the genetic basis of intralocus sexual conflict, summarize the empirical evidence to date, and discuss prospects for future work.

18.2 Definition and causes of sexual conflict

18.2.1 The origin of sexual conflict

Anisogamy—a difference in the size or morphology of male and female gametes—is both cause and consequence of many evolved sex differences. Males and females often invest differentially in offspring production and care, secondary sexual characters, and behaviors, pursuing different reproductive strategies that reflect divergent selection pressures. Typically, though by no means exclusively, it is females who invest more directly in reproduction and more heavily in individual offspring, creating selection on males to gain access to this limiting resource (Bateman 1948; Trivers 1972). The codependence of the sexes for fertility despite different reproductive optima creates two distinct forms of genomic conflict over reproduction: inter- and intralocus sexual conflict.

Interlocus conflict and its evolutionary consequences have attracted a lot of attention in the past 10 years (reviewed extensively by Arnqvist and Rowe 2005), but intralocus conflict (our current focus) has been much less studied. This discrepancy probably exists because intralocus sexual conflict, which arises when the same gene's expression has opposite effects on the fitness of the two sexes, is inherently difficult to disentangle from other evolutionary forces, and interlocus conflict is usually more colorful and conspicuous. However, intralocus conflict is intimately related to the evolution of sexual dimorphism, one of the features of life evolutionary biologists have tried to explain right from the beginning (Darwin 1874). Recent evidence, summarized herein, suggests that intralocus sexual conflict is widespread and may strongly contribute to the maintenance of genetic variation in fitness and its components. Whereas the two forms of conflict predict different evolutionary processes and forms of genetic variation, both promote sexual dimorphism and have the net effect of reducing population fitness. We call the reduction of fitness resulting from sexual conflict the *gender load* and suggest that it is a ubiquitous feature in the evolution of separate sexes.

18.2.2 Interlocus sexual conflict

Although not a perfectly clean dichotomy, the two forms of sexual conflict—inter- and intralocus—can be distinguished if we look at the traits involved and the underlying genetic mechanisms. Interlocus conflict involves loci expressed in one sex that negatively influence fitness of the opposite sex through direct interaction. For example, male bedbugs (Cimicidae) of some species fertilize their mates directly through the cuticle, an act with considerable direct negative consequences for their mates (Carayon 1966). The fitness costs of injury and infection have favored the evolution of counteracting mechanisms in females, involving immune function and various morphological adaptations to limit damage (Reinhardt *et al*. 2003). Female counteradaptations are generally going to involve different structures and behaviors controlled by different loci, and this has the potential to drive an evolutionary arms race (Dawkins 1976; Parker 1979; Rice and Holland 1997; Holland and Rice 1998; Gavrilets *et al*. 2001). As with the Red Queen process between parasites and hosts (Van Valen 1973), this process may promote rapid evolution of the loci involved in the conflict, as confirmed by the screening of *Drosophila melanogaster* (Jagadeeshan and Singh 2005) and *Homo sapiens* (Nielsen *et al*. 2005) genomes which revealed that the loci bearing the molecular signature of rapid evolution are very frequently involved in the immune system or in reproduction. At the population level, rapid coevolution between loci may promote divergence between isolated populations, and thus speciation (e.g. Rice 1996a; Gavrilets and Waxman 2002; Martin and Hosken 2003). Because this kind of sexual conflict is predicted whenever the correlation established between the two sexes' fitness through the reproductive interactions is less than 1—a correlation of 1 only being achieved with lifelong monogamy (Rice 2000)—it is expected to be common and manifested in many characters.

18.2.3 Intralocus sexual conflict

Intralocus sexual conflict, less readily apparent, occurs when male and female optima are different for a particular character. This means that the same allele will exhibit a SA pattern of fitness effects, being selected positively in one sex and negatively in the other. SA alleles therefore contribute to a pattern of negative genetic covariation between the sexes for fitness. Unlike interlocus conflict, in intralocus conflict the same traits, and the loci underlying them, are caught in a tug-of-war between selective forces acting in opposite directions in the two sexes (see Figure 18.1). These reversed selection gradients in the two sexes should impede the rate of directional change, a very different outcome from the self-reinforcing, cyclical patterns predicted by interlocus conflict evolution.

A common intralocus sexual-conflict scenario involves the opposition of natural and sexual selection pressures, usually with natural selection on females opposing sexual selection in males. This appears to be the nature of conflict over bill color in the zebra finch *Taeniopygia guttata*. In this species male and female bill-color distributions overlap but display significant sexual dimorphism: males are concentrated in the red end and females in the orange end of this color spectrum. Bill color has been shown to have significant heritability (0.56 ± 0.49) in both sexes and a high genetic correlation between the sexes (0.91 ± 0.12; Price and Burley 1993). In an aviary experiment, Price and Burley (1994) measured the selection gradients on bill color in males and females and established that selection pressures were in opposition for that trait (Figure 18.2). Moreover, they were able to look at the selection pressures at the different steps

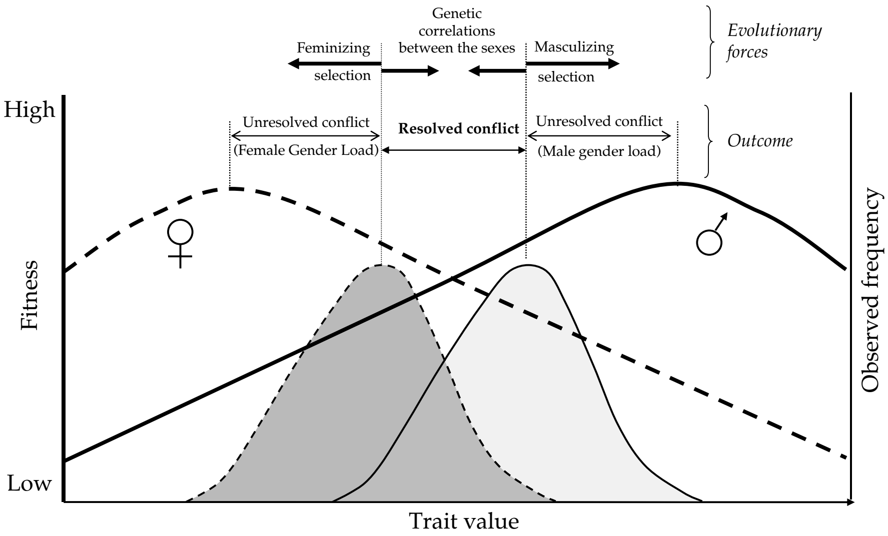


Figure 18.1 An example in which males (solid lines) and females (dashed lines) have different optima for the same trait, creating divergent selection pressures driven by distinct male and female fitness functions (thick lines). Because they share the same genome, genetic correlations between the two sexes constrain the independent evolution of the trait in each sex. The resulting distribution of phenotypes (shaded normal curves) in the population does not match the fitness optimum in each sex. Part of the conflict is resolved, since males and females don't have the same phenotypes. This is possible because the genetic correlations between males and females are different from 1. The resolved part of the conflict is expressed through sexual dimorphism. Another part of the conflict remains unresolved and is represented here as the difference between the position of the fitness optimum for a sex and the position of the maximum of its phenotype distribution. This unresolved conflict results in the existence of a gender load, since each gender is maintained far away from its optimum.

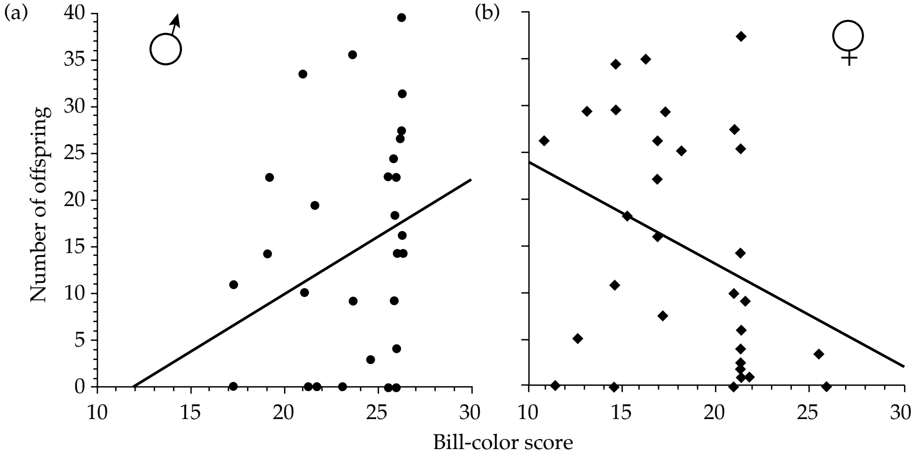


Figure 18.2 Number of offspring reaching independence (2 weeks after fledging) produced by male (a) and female (b) zebra finches (*Taenopygia guttata*) as a function of bill-color score. The lines represent the best least-squares regression. The selection differential for males is 0.24 ($P = 0.036$) and for females is −0.35 ($P = 0.015$), clearly showing diverging selection pressures on bill color in males and females. Redrawn from Price and Burley 1994 (with permission).

between the release of individuals in the aviary and fledging of their offspring. For males, the selection gradient was attributed to the influence of bill color on traits known to be indicators of success in sexual selection (time to first nesting and reproductive rate), confirming the female preference for red bills. For females, the estimated selection gradient was mainly due to the correlation between bill color and survival. These data suggest that sexual selection on males creates a cost to females paid in the currency of natural selection.

18.3 Sexual dimorphism and sexual conflict

18.3.1 Sexual dimorphism, a resolution of the conflict?

The existence of sexually dimorphic characters in a species is, in and of itself, both evidence of the pattern of selection that underlies intralocus sexual conflict and its resolution. Positive genetic correlation between the sexes, expected for most characters at equilibrium (Lande 1980), presents a constraint on the evolution of dimorphism because selection pressures applied to either sex will result in concordant evolution of the trait in both sexes. The sexual dimorphism we observe is thus the result of the action of opposite selection pressures on a trait for which the genetic architecture has allowed some independent evolution in each sex (Figure 18.1; Chapter 1).

We may ask whether the sexual dimorphism observed at a particular time is a complete resolution of conflict, whether the species has reached a limit to the dimorphism allowed by the genetic architecture of the trait involved, or whether the current level of dimorphism is a transient state on the way to one of the previous outcomes. The outcome predicted by quantitative genetic models (e.g. Lande 1980; Reeve and Fairbairn 2001) is that the initial genetic correlation between the sexes slows the response to selection for each sex but does not prevent them from reaching their respective optima. However, the genetic correlation between the sexes may change when the sexual dimorphism is evolving and the potential for independent evolution in each sex may be altered by this evolution. Lability of the genetic architecture of intersexual correlation will therefore be important in determining the degree of sexual conflict in a population at any given time. Hence, the present discussion bears analogy to the broader debate surrounding the evolutionary stability of genetic correlation matrices between traits (Chippindale *et al.* 2003; Prasad and Shakarad 2004).

18.3.2 Genetic mechanisms of conflict resolution and maintenance

Now we have touched upon the general case, here we discuss the specific mechanisms involved in resolving intralocus sexual conflict. These mechanisms fall under the categories of (1) sex-limited gene expression, (2) sex chromosomes, and (3) parent-of-origin silencing (imprinting).

The extensive occurrence of sex-limited gene expression has been confirmed by several approaches: developmental geneticists have described the cascade of gene activation and repression leading to sexually differentiated individuals in the animal models *Drosophila melanogaster* and *Caenorhabditis elegans* in great detail (Cline and Meyer 1996; Chapter 16) and sex-specific quantitative trait loci (QTL) are widely documented (e.g. Nuzhdin *et al.* 1997; Morgan and Mackay 2006). Moreover scans of the genome-wide transcription profiles with microarrays (Parisi *et al.* 2003) revealed that in *D. melanogaster* more than 20% of the 14 142 loci analysed had sex-biased transcription (i.e. their transcription level was at least twice as high in one sex as in the other). Sex-dependent expression would seem to be a panacea for the resolution of intralocus sexual conflict, as genomes apparently cater the expression of thousands of genes to each sex independently. However, the same information could also raise the suspicion that sexual conflict is rife, if gene regulation is variable, imprecise, or slow to evolve. The resolution of this problem is more an issue for empirical science than for theory.

Another mechanism by which sex-specific expression may be achieved is through localization of SA loci to a sex-determining chromosome, such as the Y chromosome in organisms with an XX, XY system of sex determination (Chapter 16). Genes with male-benefit SA effects should be drawn to the sex-determining region, thus (1) limiting their expression to the sex they benefit (see Figure 18.3) and (2) linking them to other male-benefit genes. This idea has been extensively theorized to drive the origin of the Y (or W in species with female heterogamety), its recombinational shutdown to prevent genetic exchange with its homolog, and its ultimate degeneration (Rice 1987, 1994, 1996b).

The third known mechanism of resolution of the sexual conflict is genomic imprinting, an epigenetic phenomenon whereby the expression of an allele depends on the parent it has been inherited from (see Chapters 16 and 17). It has first been studied in the context of parent–offspring conflict in the growth of placental mammals (Trivers 1972; Haig and Graham 1991; Moore and Haig 1991; Hurst 1999). This represents an interesting instance of intralocus sexual conflict over offspring provisioning. Alleles involved in increasing offspring nutrition and growth become SA (male-benefit) in expression because in promiscuous species fathers benefit from highly nourished offspring more than mothers do. Day and Bonduriansky (2004) have suggested that imprinting may commonly evolve due to intralocus sexual conflict. If, for example, high fitness males transmit male-adapted SA alleles, this could select for paternal imprinting of these alleles when transmitted to daughters. The importance of this mechanism would be enhanced by 'foreknowledge' of which sex will inherit the SA variation, a situation that exists for the sex chromosomes. For example, the paternal X is always passed down to daughters, making it potentially profitable to imprint SA variation on this chromosome.

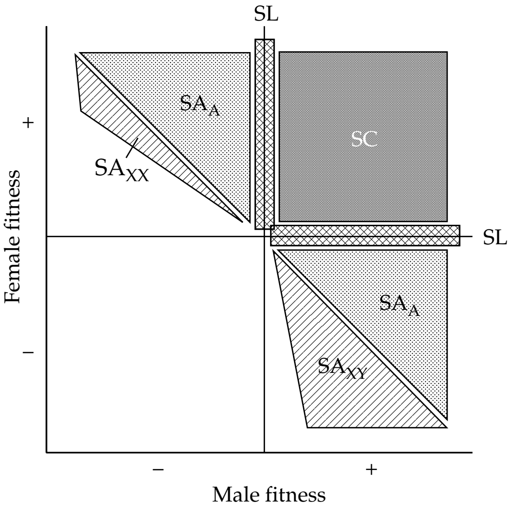


Figure 18.3 A key describing the distribution of allelic effects in terms of their predicted accumulation. Straightforward mutation–selection balance theory predicts the accumulation of alleles with benefits to both sexes (male+, female+) and the elimination of unconditionally bad variation (−, −) via selection. This form of selected variation is labeled SC, or sexually concordant, in the figure. Sexually antagonistic (SA) variation (+, −; −, +) can also accumulate in quadrants 1 and 3. When this variation is autosomal, the benefits to the favored sex must outweigh the detriment to the disfavored sex for the allele to be selected (SA_A sectors). According to theory, and supported by some recent evidence, X linkage can extend the SA sector so that alleles with substantial harming effects can accumulate to appreciable frequencies. This effect is particularly strong for male-benefit, female-detriment (+, −) alleles in XY systems (hence the larger area of SA_{XY} in quadrant 3) but should be greater for (−, +) alleles in ZW systems (e.g. birds and Lepidoptera). A common remedy for SA genes may be to render them sex-limited (SL) or sex-biased in expression, or to otherwise modify the harming effects on the sex whose fitness they reduce. This would move the gene's effect from the SA portions of the figure to the SL zones.

18.4 Investigating the impact of sexual conflict experimentally

18.4.1 The evidence for intralocus conflict and the gender load

Despite the variety of potential mechanisms for resolving intralocus sexual conflict, there is considerable experimental evidence emerging that SA alleles are common in populations. The most direct demonstration comes from *D. melanogaster* via the expression of whole-genome clones in males and females. These genomic haplotypes were sampled from an outbred laboratory population and expressed in a random genetic background (Chippindale *et al*. 2001). A positive correlation between males and females was found for juvenile survival whereas a strong negative correlation was found for adult fitness. This means that during adult life, when selection pressures are different for males and females, haplotypes producing high-fitness females resulted in low-fitness males and vice versa. This experimental result supports the idea that sexual conflict is not completely resolved in *D. melanogaster*, and that its effects are strong enough to overturn any underlying positive genetic correlation generated by mutation–selection balance.

Other putative examples have recently emerged in a variety of organisms, including plants (Delph *et al*. 2004a), insects (Fedorka and Mousseau 2004), reptiles (Forsman 1995; Calsbeek and Sinervo 2004), and possibly humans (Camperio-Ciani *et al*. 2004). Here we briefly describe two examples. First, in the lizard *Uta stansburiana*, body size is heritable and associated with fitness in opposite way in each sex: small females and large males survive better. It creates a cost to mating with large territory-holders and adds indirect benefits to females for mating with smaller 'sneaker' males, in terms of daughter's fitness, generating an interesting sexual selection problem. To mitigate these costs, polyandrous females appear to cryptically choose sperm from larger sires to produce sons and sperm from smaller sires to produce daughters (Calsbeek and Sinervo 2004).

In humans, some recent evidence suggests that intralocus sexual conflict may help resolve the Darwinian paradox of homosexuality. Based on a survey of gay and straight men in Italy, Camperio-Ciani *et al*. (2004) concluded that the female relatives of homosexual men have higher fertility than those of heterosexual men. Gay men also had a higher proportion of male homosexual relatives. Their data pointed to a genetic factor, presumably reducing the average fitness of sons by promoting homosexuality, but with a compensating benefit to daughters.

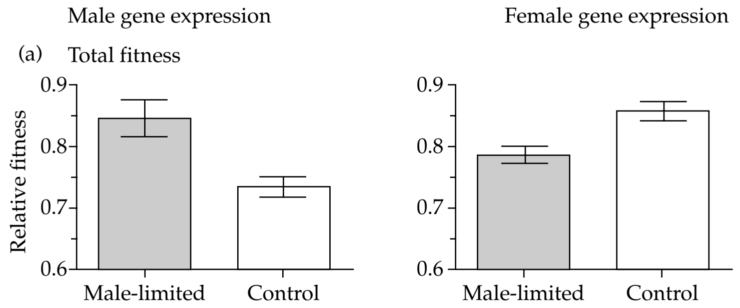
If we sum up, there is accumulating evidence that, despite the evolution of mechanisms to resolve sexual conflict and promote sexual dimorphism, SA alleles are segregating in populations and may have substantial effects. Because of this unresolved conflict, each sex may be some distance from its optimum, supporting a gender load.

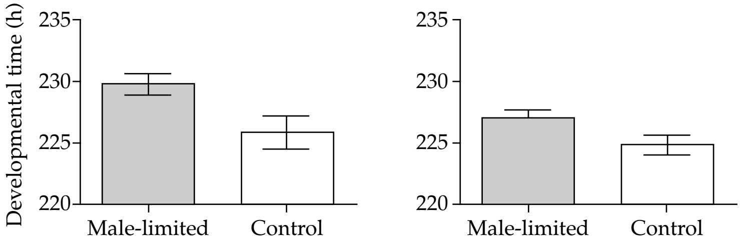
18.4.2 Experimental removal of intralocus conflict

To quantify the load resulting from intralocus sexual conflict, we used an ingenious experimental technique developed by William Rice (Rice 1996a). Using special genetic constructs in *D. melanogaster*, genomic haplotypes (the X and all major autosomes) can be transmitted together from father to son as if they were a single male-limited (ML; Y-like) chromosome. Whereas Rice used this technique primarily to investigate male–female interactions and interlocus conflict, we have been concerned with intralocus conflict. Because all chromosomes are patrilinealy transmitted, ML genomes are completely freed from female selection pressures, and therefore from intralocus sexual conflict. This selection regime should lead to populations of males that have evolved closer to the male optimum phenotype and are enriched for male-benefit SA alleles.

Four large and outbred ML populations were established, along with four matched control (C) populations with normal transmission of genetic material (see Prasad *et al*. 2007 for details). After 25 generations of experimental evolution, ML and control genomes were expressed in both sexes and their fitness, developmental time, and body weight were measured. Male fitness was measured as the proportion of offspring sired after 10 ML (or C) males have competed with 10 standard competitor males. Female fitness was measured as their offspring production after 10 ML (or C) females competed for yeast with five standard competitor females. Males expressing ML genotypes (heterozygous with a random, unselected haplotype) had 15% higher fitness than control males, whereas females expressing the ML genotypes had 10% lower fitness than the control (see Figure 18.4 and Prasad *et al*. 2007 for detailed statistics). The rapid gain in male fitness and decline of female fitness is most parsimoniously explained by a negative genetic correlation for fitness in the original base population. In this model, selection has 'masculinized' the genome, with deleterious effects for daughters produced by these males.

Our next logical step toward understanding the evolved differences was to describe the phenotype associated with ML evolution and thus identify traits involved in intralocus sexual conflict. Sexually dimorphic traits are obvious candidates because we know that they have historically been exposed to different patterns of selection in each sex. We first measured two dimorphic life-history traits: developmental time and body weight in


(a) Total fitness


(b) Developmental time

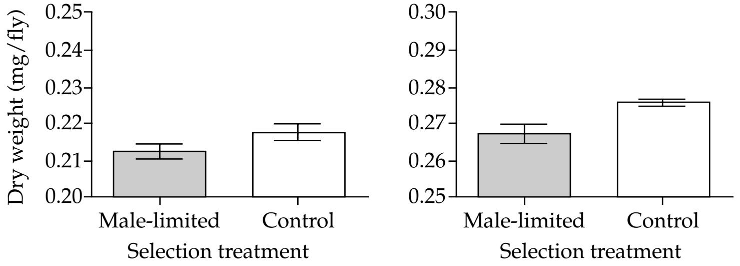

(c) Body size

Figure 18.4 (a) Total fitness, (b) developmental time, and (c) dry body weight of *D. melanogaster* males (left) and females (right) expressing genomes with a history of male-limited expression (shaded bars) or normal, bisexual, gene expression (white bars). Fitness was measured as relative lifetime survival and reproductive success under competitive conditions. Error bars represent standard errors.

males and females expressing ML or control genomes. For these two traits, the differences between ML and C populations are consistent with masculinization of the phenotype: when expressing ML chromosomes, both sexes grow more slowly, taking longer to eclose and doing so at a smaller size, as is typical of males in this species (see Figure 18.4 and Prasad *et al*. 2007 for detailed statistics). These data suggest that selection for female function has made males larger, on average, than their optimal size. Freed from such a constraint, males evolved towards a different pattern of growth. Current investigations, focused on chemical communication and the behavioral phenotypes of these ML populations, suggest the involvement of numerous traits in intralocus sexual conflict. They are thus revealing the reality of divergent selection pressures on males and females and the magnitude of SA effects.

18.5 Genetic factors predisposing sexual conflict

The experimental data we summarize here have led us to view the genome of sexually reproducing species as a patchwork of resolved and unresolved conflict. The resolved conflict is materialized by loci determining sexual dimorphism, by the various mechanisms described earlier. The unresolved conflict takes the form of the SA alleles maintained at intermediate frequencies (the conflict we can detect) and SA alleles that are fixed (the conflict we cannot generally detect). Previous results and our present results suggest that an important part of the sexual conflict is unresolved in sexually reproducing population, therefore generating a gender load. Here we ask whether any features of the genome may predispose conflict.

If we consider an autosomal SA locus, the allele with the highest net fitness should fix; that is, the allele that maximizes $|w_{\text{male}} + w_{\text{female}}|$, where w denotes relative fitness (Rice 1984). For this reason, autosomal SA loci should be only transiently polymorphic and finally fix the allele having the highest fitness when summed across the sexes. This predicts a series of allelic substitutions over evolutionary time, with a majority of the loci fixed at any time. The sexual conflict at these fixed loci is undetectable, because of the absence of polymorphism, but still present since the allele fixed is decreasing the fitness of one of the sexes compared to the ancestral situation. This type of sexual conflict is represented by the two SA_A triangles in Figure 18.3.

However, sex chromosomes are an obvious starting point in the search for a genetic mechanism maintaining SA variation, since the origin of a sex-determining locus and later heteromorphism of sex chromosomes is believed to be related to sexual conflict genes (e.g. see Rice 1984; Chapter 16). Rice (1984) suggested that, in species with a XY system, the X chromosome may be favored for the accumulation of SA alleles. Indeed, as a result of the creation of the Y chromosome, frequency-dependent selection on the former homolog becomes an important issue: the X chromosome is expressed twice as frequently by females, having two copies, than by males and is thus submitted more often to female selection pressures. On the other hand, due to hemizygosity, a recessive allele on the X chromosome is expressed in males at many times the rate it is in females, particularly when it is rare (e.g. expressed 10 times more frequently in males if its allele frequency is 0.1). Because of these asymmetries in expression, in theory (Rice 1984) SA alleles can be maintained at intermediate frequencies even if the cost to the sex they are detrimental to is higher than the benefit for the other sex, as represented in Figure 18.3 by the SA_XX and SA_XY triangles. Empirical evidence for X linkage comes from *D. melanogaster*, where Gibson *et al*. (2002) estimated that 97% of the SA variation can be attributed to the X chromosome: considerably more than predicted by the size of the chromosome (20% of the genome). It is interesting to note that the X chromosome has also been linked to genetic factors enhancing female fecundity and promoting homosexuality, presumably reducing male fitness, by a recent study of gay and straight men in Italy (Camperio-Ciani *et al*. 2004).

Moreover, the X chromosome, by its particular features, seems to both maintain SA variation and create a strong selection pressure for the evolution of imprinting. Indeed, the ideal conditions, as theoretically shown by Day and Bonduriansky (2004), for the evolution of imprinting are a high concentration of SA loci and a ‘foreknowledge’ of the sex of the offspring inheriting the genetic material, which is exactly the case for the males’ X chromosome.

The role of the X chromosome as a magnet for SA variation is particularly interesting from the perspective of sexual selection. As noted above for lizards, sexual selection on ‘masculine males’ may have deleterious consequences for daughters. But when SA genes are X-linked, they are *only* handed down to daughters in the next generation and their effects will oppose indirect benefits accrued from ‘good genes’ by mate choice on males. Our research with laboratory *Drosophila* (Chippindale *et al*. 2001; Gibson *et al*. 2002; Pischedda and Chippindale 2006) suggests that these effects may be considerable and contribute to the maintenance of variation in the face of sexual selection (i.e. help resolve the lek paradox). The same problem of transmission of fitness from father to son does not exist in ZW systems, where females are the heterogametic sex, suggesting that sexual selection may be more efficient in those taxa (Albert and Otto 2005). This prediction fits with the often discussed speculation that ZW species’ males are more spectacular and more sexually dimorphic (e.g. Reeve and Pfennig 2003).

18.6 Sexual conflict and environmental variation

Until now, we have considered the questions associated with sexual conflict and the evolution of sexual dimorphism in the context of a constant environment. However, environmental variation can interact with sexual conflict and make the evolution of sexual dimorphism more complex. Because of different phenotypes and patterns of gene expression, a change in the environment can cause new differential or even opposite selection pressures on females and males. For example, survival in many environmental circumstances will be size-related. Desiccation stress associated with drought or desertification will probably be easier for the larger sex to handle, because of a smaller surface/volume ratio leading to lower rates of transpirational water loss. Selection may therefore favor enhancements of traits already related to survival of the stress in the large sex, but such a response is not possible for the smaller sex because the stress leaves no survivors. New characters may therefore be recruited to the selection response, such as behavioral avoidance, migration, or alternate reproductive timing, which may be in conflict with the evolutionary response of the larger sex.

Although the preceding example may seem fanciful, the general principle may be widespread: selection from external sources, acting upon a dimorphic species, may create differential or opposing selection gradients on the sexes. One source of evidence for this is adaptive sex-specific phenotypic plasticity shown when a sexually dimorphic species is confronted with environmental variation. For example, when intraspecific larval competition was experimentally increased in the mosquito *Aedes aegypti*, each sex paid the cost of this environmental modification by changing life-history traits less closely related to its fitness, namely developmental time in females and body size and weight in males (Bedhomme *et al*. 2003). This kind of adaptive sex-specific adjustment of life history helps resolve conflict between the sexes that may be induced by the changing environment.

18.7 Prospectus

Despite our view that intralocus conflict is ubiquitous, its detection and quantification will be complicated in most organisms for at least three reasons. First, much of the conflict may be inaccessible to experimental investigation when alleles are fixed and allelic substitutions rare. Intralocus conflict will only be detectable with quantitative genetic approaches, including selection, when loci are polymorphic. Second, the footprint of SA variation is negative covariance between the sexes for fitness. Mixed in with the general expectation of positive intersexual covariances from mutation–selection balance, noncorrelation or weak correlation may be the most frequent outcomes when conflict is existing, presenting an interpretive problem. Third, measurements of genetic variation in fitness (let alone experimental manipulations) are not practical in most organisms. Even with superficially tractable systems, novel environment effects predispose positive genetic correlations for fitness components, which will obscure the signal from sexual conflict genes. The challenge ahead is therefore to find systems that are amenable to the study of intralocus sexual conflict using conventional methods, and to find new tools for its measurement. Comparative genomics may prove to be a very fruitful mode of investigation, because gene regulation is critical to the remediation of intralocus sexual conflict. The decades ahead will show that the complexities of tuning individual gene expression to each sex separately are overwhelming, explaining why sexual dimorphism usually produces intergradation between the sexes and why so much diversity exists in sexual form, function, and preference.

18.8 Summary and conclusions

We have presented evidence that intralocus sexual conflict is a widespread and potentially important contributor to several basic evolutionary phenomena. For example, the tug-of-war created by SA gene expression is likely to contribute to the maintenance of genetic diversity in the face of selection. Even in large laboratory populations adapted to standardized conditions, abundant genetic variation for fitness is commonly found in sexual species. Apparently, even with every opportunity to adapt, the average fitness of individuals often remains low relative to the fittest. We submit that this load upon fitness is partially the result of feminizing/masculinizing selection having detrimental effects on males/females that are manifested as low fertility, physical or behavioral phenotypes that are intermediate between the male and female optima. Intralocus sexual conflict is therefore an important vantage point for the study of gender diversity because it blurs the distinction between the sexes.

Intralocus sexual-conflict alleles are certain to exist in populations at levels higher than can be detected through quantitative genetic investigations of extant variation, because a significant proportion of them is evolutionarily fixed and thus undetectable. Hence, unless an argument can be made from design principles, we will usually only observe intralocus sexual conflict as a transient phenomenon under resolution by the genome. However, complex or changing environments may foster the evolution of new sex-specific reproductive strategies, and thereby impel sexual-conflict evolution. At the genome level, frequency-dependent selection seems to convert the X chromosome into a hotspot for the maintenance SA variation, making it a logical starting point for analysis of intralocus sexual conflict.

18.9 Suggested readings

Arnqvist, G. and Rowe, L. (2005) *Sexual Conflict*. Princeton University Press, Princeton, NJ.

Rice, W.R. and Chippindale, A.K. (2001) Intersexual ontogenetic conflict. *Journal of Evolutionary Biology* **14**, 685–693.

CHAPTER 19

Development of sexual size dimorphism in lizards: testosterone as a bipotential growth regulator

Henry B. John-Alder and Robert M. Cox

19.1 Introduction

Sexual size dimorphism (SSD) is widespread in lizards (see Chapter 4 in this volume). However, we cannot unambiguously answer the simple question of *why* adult males are characteristically larger than females in most species of lizards, when the opposite is true in many others. We do not know the relative importance of past evolutionary (i.e. genetic) as opposed to current ecological (i.e. environmental) processes in the development of SSD, in part because in most species we do not know *how* adult SSD develops.

SSD in populations of lizards can reflect sex differences in age distributions or age-specific body sizes (Stamps 1993; Watkins 1996; Chapter 14), and it can be expressed before or only after reproductive maturity. Factors that can contribute to SSD include (1) neonatal body size, (2) growth rate and/or duration, (3) survival, (4) migration and/or recruitment, and (5) behavioral segregation of size classes (see Watkins 1996). Because of these multiple contributing factors, the developmental origin of SSD must be resolved for every population of interest. This resolution is a necessary prerequisite for studies on ultimate causation of SSD, which typically invoke adaptive evolutionary hypotheses (Chapter 4).

Many authors consider SSD to be a reflection of sex differences in selective optima for body size (see Hedrick and Temeles 1989; Chapters 1 and 18), a view that is supported by empirical evidence mainly in species with short generation intervals (e.g. see Chapters 9–11). In lizards and most other vertebrates, however, we know much less about (1) developmental origins of SSD (Badyaev 2002) and (2) how male and female body sizes respond to selection. Even when SSD is known to reflect age-specific differences in body size, we rarely know the roles of such markedly different processes as sex differences in size-dependent survival and sex-specific growth patterns. On the other hand, we know that SSD is subject to proximate environmental influences on growth and body size (e.g. Haenel and John-Alder 2002; Krause *et al*. 2003; Aday *et al*. 2006; Cox *et al*. 2006; Chapters 4, 14, and 16) and that SSD can result indirectly from selection on growth parameters and other life-history traits (e.g. Mignon-Grasteau *et al*. 1999) instead of body size per se.

This chapter presents case studies of the development of SSD in three species of lizards in the genus *Sceloporus* (Iguania: Phrynosomatidae), representing both male-larger and female-larger patterns of adult SSD. We first describe studies that identify age-specific sex differences in growth rate as the developmental cause of SSD in all three species. We then show through common-garden experiments that the development of SSD depends upon environmental context, which in our experiments has been mediated primarily by environmental sensitivity of growth in males, not females. We then focus on the regulation of male growth, postulating that testosterone serves as a bipotential mediator of sex differences in growth rate. We provide the first direct experimental evidence for opposite effects of testosterone on male growth in closely related species with opposite patterns of SSD. We close with a discussion of possible mechanisms through which testosterone can both stimulate and inhibit male growth, whether through direct effects on the endocrine growth axis (i.e. somatotrophic axis) or indirect effects involving energy acquisition and trade-offs in energy allocation.

19.2 *Sceloporus* lizards as a model system for studies on the development of SSD

To date, we have focused on three species of *Sceloporus*, a large genus of North and Central American lizards in which SSD varies from males being 25% larger than females to females being 15% larger than males (Fitch 1978; Cox *et al.* 2003). Using the index of Lovich and Gibbons (1992) and snout–vent length as our measure of body size, this corresponds to a range in SSD of −0.25 to 0.15, where negative values indicate male-larger SSD by convention. The phylogenetic histories of Phrynosomatidae in general and the genus *Sceloporus* in particular are well characterized (Figure 19.1), even if subject to continual taxonomic revision (e.g. Leaché and Reeder 2002; Schulte *et al.* 2006). Male-larger SSD is the ancestral condition in this family; female-larger SSD has evolved independently in *Phrynosoma* (horned lizards) and in several lineages within the genus *Sceloporus* (Figure 19.1). For our studies, we have focused on species in which adult males and females differ by about 10% in body length, a difference large enough to provide clear and consistent contrasts. (Absolute characterization of a species' index of SSD can be problematic because of geographical (see Chapters 4 and 14) and developmental variation in SSD and because the magnitude of SSD that can be statistically resolved is inversely related to the sample sizes of known-aged individuals. Thus, an absolute threshold to distinguish dimorphism from monomorphism cannot readily be identified.)

We have studied the development of SSD in *Sceloporus undulatus* and *S. virgatus*, in which adult females are about 10% larger than males, and in *S. jarrovii*, in which males are about 10% larger than females (Fitch 1978; Haenel and John-Alder 2002; Cox 2005). We have studied a population of *S. undulatus* at the Rutgers University Pinelands Research Station on the coastal plain in central New Jersey, USA (approximately 40°N, 74°35′W) and sympatric populations of *S. jarrovii* and *S. virgatus* in Cave Creek Canyon near the American Museum of Natural History's Southwestern Research Station in the Chiricahua Mountains of southeastern Arizona, USA (approximately 31°53.5′N, 109°13′W). Detailed information on these populations and experimental design is published in Haenel and John-Alder (2002), Cox *et al.* (2005a), and Cox and John-Alder (2005c).

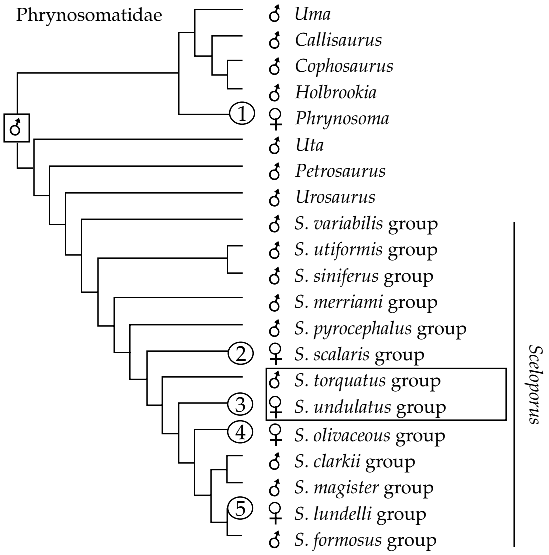


Figure 19.1 Phylogenetic relationships among phrynosomatid lizards (based on Reeder and Wiens 1996; Wiens and Reeder 1997). Symbols indicate the typical direction of SSD in each clade (♂, male-larger; ♀, female-larger). Male-larger SSD is the ancestral and dominant pattern, but female-larger SSD has evolved in at least five independent lineages (numbered circles). The box indicates the two *Sceloporus* clades discussed in this chapter (*S. jarrovii* = *torquatus* group; *S. virgatus* and *S. undulatus* = *undulatus* group).

19.3 SSD develops because of sexually dimorphic growth rate

To begin studies on SSD in a new species, we characterize growth and survivorship of known individuals in the field, using snout–vent length as the preferred measure of body size to avoid size fluctuations not reflecting progressive body growth (e.g. fat storage, reproductive condition, food intake; Dunham 1978; Andrews 1982; Haenel and John-Alder 2002). We use nonlinear growth equations to model asymptotic size and characteristic growth rate (Haenel and John-Alder 2002; Cox 2005), but we focus our quantitative analyses on linear growth rates of males and females of known age recaptured over discrete time intervals, which enables us to identify the precise seasonal and ontogenetic periods during which sex differences in growth rate give rise to SSD. We can then examine correlated sexual divergence in other factors that could influence growth and SSD, such as testosterone and associated reproductive behaviours (below).

In the species we have studied, the development of SSD is driven primarily by sexual differences in yearling growth rate (Figure 19.2). In no case is the development of SSD due to differential survival of either sex (Haenel and John-Alder 2002; Cox 2005). In *S. undulatus*, males and females hatch at similar body sizes and grow at similar rates prior to and after emergence from hibernation until about 10 months of age (Haenel and John-Alder 2002). Subsequently, females grow significantly faster than males, and in just 2 months SSD develops from an insignificant female bias to its full magnitude by 12 months of age (prior to first reproduction).

S. Sceloporus virgatus is similar to *S. undulatus*: males and females hatch at similar sizes, and SSD develops to its fullest extent during the first full

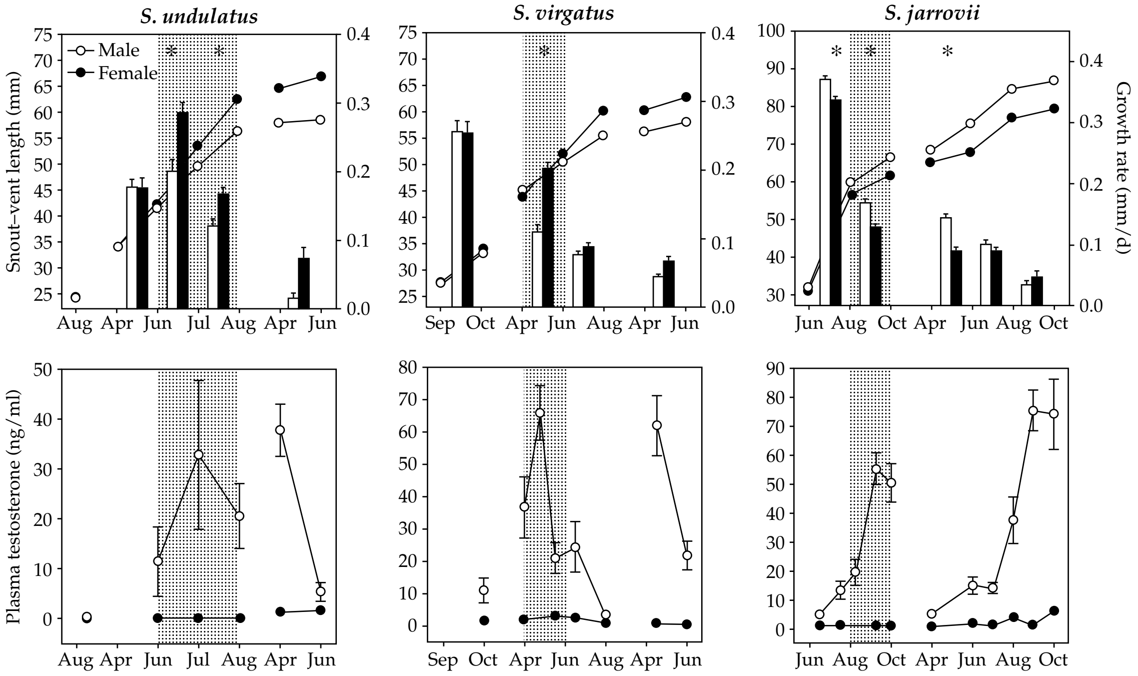


Figure 19.2 Ontogenetic development of sexual differences in growth rate and snout–vent length (top panels) and plasma testosterone levels (bottom panels) for three *Sceloporus* species. Data are means (±1 SE) for free-living males (white symbols) and females (black symbols) of known age. Asterisks indicate significant sexual differences in growth rate (bars), which give rise to sexual dimorphism in snout–vent length (circles). Breaks in connecting lines indicate periods of winter dormancy. Shaded areas indicate the timing of subsequent testosterone manipulations (see Figure 19.3). In the two female-larger species (*S. undulatus* and *S. virgatus*), sexual differences in growth rate correspond to seasonal peaks in male plasma testosterone levels. By contrast, yearling males of *S. jarrovii* grow more quickly than females regardless of seasonal changes in plasma testosterone. Figures for *S. undulatus* are redrawn from data in Haenel and John-Alder (2002; with permission from *Oikos*) and Cox *et al.* (2005a; with permission from the University of Chicago Press). Figures for *S. virgatus* and *S. jarrovii* are redrawn from data in Cox and John-Alder (2005c; with permission from The Company of Biologists) and Cox (2005).

activity season because females grow faster than males (Cox 2005). Unlike *S. undulatus*, however, *S. virgatus* breeds in its first year, and sex differences in growth rate are most pronounced during this first reproductive season. Females continue to grow faster than males during the summer months, and SSD develops to its fullest extent by 12 months of age. In both *S. undulatus* and *S. virgatus*, females grow more quickly than males during certain periods beyond the yearling stage, particularly during the breeding season, but the relative sexual difference in adult body size (i.e. SSD) remains essentially constant at about 10%.

In *S. jarrovii*, body sizes of males and females are very similar at birth, but males grow significantly faster than females from the beginning of postnatal life and through the ensuing summer months. SSD develops progressively, and the index of SSD calculated from male and female snout–vent lengths reaches its maximum value for this species at 12 months of age. This chronology applies equally well to both low- and high-altitude populations, even though females do not reproduce until their second year in the high-altitude population (Cox 2006).

19.3.1 Environmental sensitivity of sexual growth divergence

Comparisons of same-aged cohorts of yearling lizards demonstrate that sexual differences in growth rate and the development of SSD can be strongly influenced by environmental conditions. In both *S. undulatus* and *S. jarrovii* raised under favorable laboratory common-garden conditions, yearling males and females grow at the same rate, and SSD therefore fails to develop by the time lizards reach the size of first reproduction (Haenel and John-Alder 2002; Cox *et al*. 2006). Captive male *S. undulatus* grow as fast as females and about 60% faster than field-active males, whereas females grow equally fast in the field and the laboratory. In other words, SSD develops under natural conditions in *S. undulatus* because growth rate in juvenile males (but not females) is lower than its potential physiological maximum. Males appear to be particularly sensitive to environmental conditions (i.e. field versus laboratory), and plasticity in male growth is as great as the sex difference in growth rate that leads to the development of SSD in the field.

In *S. jarrovii*, environmental plasticity is again much more prominent in males than in females, but in this species males grow not more quickly but about 20% more slowly in captivity. Just as in *S. undulatus*, environmental plasticity in male growth is nearly as great as the sexual difference in growth rate that leads to the development of SSD under natural circumstances. Although the direction of the environmental effect on growth differs between the two species, males are the more variable sex in both cases. Thus, with regard to the natural development of SSD, the question of interest is the following: what factor or factors influence juvenile male growth leading to sexual differences in growth rate and the development of SSD in the wild?

19.3.2 Sexual divergence in growth and plasma testosterone

In *S. undulatus*, SSD develops because males grow more slowly than females in conjunction with maturational increases in male home range, territorial/aggressive behavior, and male-specific coloration (Skelly and John-Alder 2002), traits known to be at least partially dependent on testosterone (Marler and Moore 1989, 1991; Smith and John-Alder 1999; Quinn and Hews 2003; Klukowski *et al*. 2004; Cox *et al*. 2005b). In *S. virgatus*, SSD develops because males grow more slowly than females in conjunction with first reproduction. Together, these natural-history data indicate that sexual growth divergence in both species occurs during periods when males and females diverge in plasma testosterone levels. To directly address this issue, we characterized the ontogeny of sexual divergence in plasma testosterone by collecting blood samples from free-living males and females. In both species, plasma testosterone becomes markedly higher in males than in females in association with divergence in growth rate (Figure 19.2; Cox *et al*. 2005a; Cox and John-Alder 2005c), implicating plasma testosterone as a potential inhibitor of male growth. It follows that testosterone could serve as a mediator of the development of SSD.

In *S. jarrovii*, growth rate is higher in males than in females throughout the first year of life. Plasma testosterone is also significantly higher in males than in females at every measurement point, dramatically peaking during the reproductive season. However, in contrast to the relationship in *S. undulatus* and *S. virgatus*, both growth rate and plasma testosterone are higher in yearling males than females of *S. jarrovii*. For testosterone to serve as a developmental mediator of SSD in all three species, it must have opposite effects on growth in species characterized by male- and female-larger SSD.

19.4 Testosterone has opposite effects on growth in male- and female-larger species

We conducted experiments on field-active lizards to test the hypotheses that testosterone inhibits growth in yearling males of *S. undulatus* and *S. virgatus* while stimulating growth in yearling males of *S. jarrovii*. As illustrated in Figure 19.2, our experiments coincided with critical periods in the development of SSD marked by natural peaks in male testosterone and maximal sexual divergence in growth rate. The basic design was similar in all experiments (see Cox *et al*. 2005a; Cox and John-Alder 2005c): treatments involved (1) sham surgery, (2) surgical castration to remove the primary endogenous source of testosterone, and (3) castration accompanied by replacement of testosterone via an intraperitoneal Silastic® tubule containing 300 μg of testosterone (see Cox and John-Alder 2005c). These tubules maintained plasma testosterone in the mid-range of a reference group of free-living, same-aged males (Cox *et al*. 2005a; Cox and John-Alder 2005c). *S. virgatus* and *S. jarrovii* males were released after surgery at their sites of capture, whereas experiments on *S. undulatus* were conducted in an enclosed tract of natural habitat at the Rutgers Pinelands Research Station. Experiments on *S. undulatus* were replicated on separate cohorts of lizards in consecutive summers, and we allowed animals from the second replication to overwinter in the enclosure so that we could examine long-term growth effects during the subsequent activity season.

Our experiments yielded consistent and unambiguous results (Figures 19.3 and 19.4). In both of

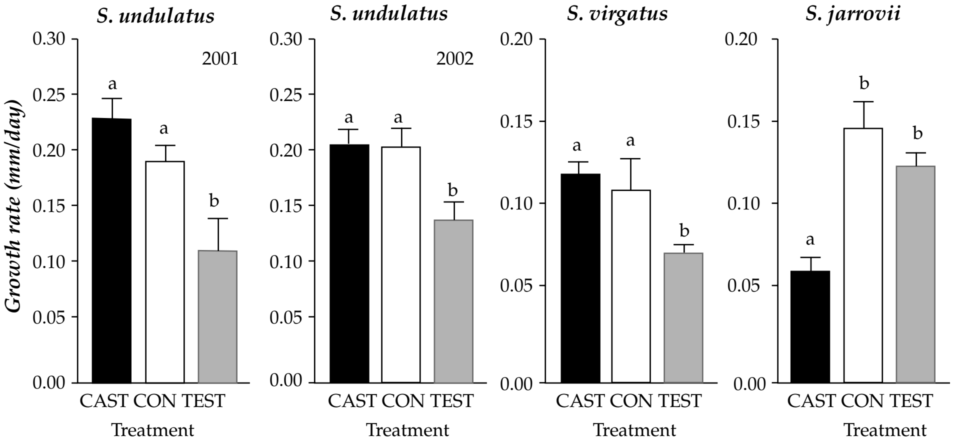


Figure 19.3 Mean (±1 SE) growth rate over the 6–8-week period following surgical castration and treatment with exogenous testosterone for yearling males of three *Sceloporus* species in their natural field environments. This experiment was replicated in two separate years for *S. undulatus*. Experiments were carefully designed to coincide with natural sexual divergence in growth rate and seasonal peaks in yearling male plasma testosterone levels (see Figure 19.2). Lower-case letters denote statistical separation among treatment groups. In the two species with female-biased SSD (*S. undulatus* and *S. virgatus*), testosterone strongly inhibits male growth and castration has no effect or a slight stimulatory effect (see Figure 19.4) on growth. By contrast, castration strongly inhibits growth in male-larger *S. jarrovii*, whereas exogenous testosterone restores growth of castrated males to the rate of intact controls. CAST, castration; CON, control (sham surgery); TEST, castration and testosterone replacement. Data are redrawn from Cox *et al.* (2005a; with permission from the University of Chicago Press) and Cox and John-Alder (2005c; with permission from The Company of Biologists).

the female-larger species (*S. undulatus* and *S. virgatus*), surgical castration caused growth rate to increase, and testosterone replacement caused growth rate to decrease. In the male-larger species (*S. jarrovii*), treatment effects were just the opposite: castration caused growth rate to decrease, and testosterone replacement restored growth rate to that of controls.

In *S. undulatus*, exogenous testosterone caused growth rate to decrease relative to castrates and intact controls (Figure 19.3), and control males grew less quickly than females (Cox *et al*. 2005a). The stimulatory effect of castration on growth did not attain statistical significance during the immediate 2-month periods following manipulation, but was readily apparent from animals recaptured the following summer (Figure 19.4a; Cox *et al*. 2005b).

In *S. virgatus*, testosterone replacement in castrates significantly reduced growth rate relative to castrates receiving blank implants, regardless of body size (Figure 19.3). However, growth rate was strongly size-dependent in intact controls (Figure 19.4b), yielding a significant size-by-treatment interaction. Growth rate was comparably high between small controls (≤44 mm SVL) and castrates (Figure 19.3), and comparably low between large controls (≥45 mm SVL) and testosterone-replaced castrates (Figure 19.4b, inset). In this larger size class alone, growth rate was significantly increased by surgical castration and was reduced to the rate of controls by testosterone replacement. The explanation for this treatment-by-size interaction may stem from an analysis of plasma testosterone in intact males.

Plasma testosterone is higher in large than in small yearling *S. virgatus* males and is positively correlated with body size in our experimental control group (Figure 19.4c). Thus, while surgical castration had a marked overall effect on plasma testosterone (Cox and John-Alder 2005c), its effect was slight in small lizards, as plasma testosterone was already naturally low in this size class. On the other hand, surgical castration markedly reduced plasma testosterone in larger lizards. In this light, one would predict that if testosterone were to influence growth in experimental groups relative to controls, then the growth-stimulatory effect of surgical castration would be greater in large than in small yearling males, whereas the growth-inhibitory effect of testosterone replacement would be greater in small than in larger yearlings. Testosterone replacement in castrates inhibited growth uniformly regardless of body size because castrates had uniformly low plasma testosterone. Thus, the complicated treatment-by-size interaction is actually consistent with the hypothesis and the experimental result that testosterone inhibits growth rate in *S. virgatus*.

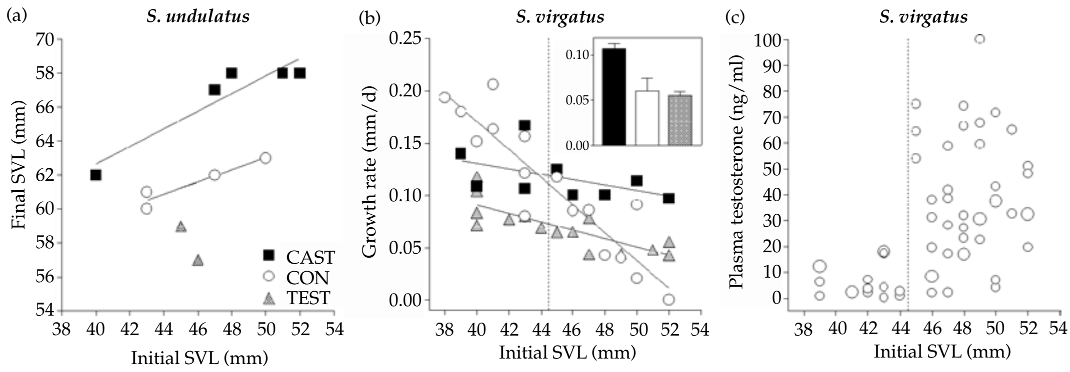


Figure 19.4 Stimulatory effect of castration on male growth in two *Sceloporus* species with female-biased SSD. (a) For any given initial size, castrated *S. undulatus* males averaged 3–5 mm larger than intact control males at 420 days post-treatment. Redrawn from Cox *et al.* (2005a) with permission from the University of Chicago Press. (b) Treatment effects on growth rate are strongly size-dependent in *S. virgatus*, because growth of control males decreases with size. (c) Yearling *S. virgatus* males under 44 mm have low plasma testosterone levels, and males over 44 mm have elevated plasma testosterone levels. When growth comparisons are restricted to males over 44 mm, castration has a stimulatory effect on male growth (b, insert). Treatments are as for Figure 19.3. Modified from Cox and John-Alder (2005c) with permission from The Company of Biologists.

In striking contrast to the experimental effects in the two female-larger species, growth rate was reduced by surgical castration and restored by testosterone replacement in *S. jarrovii*. The size dependence of growth rate was very similar in all groups of *S. jarrovii*, so the effects of experimental treatments relative to controls are clearly evident at all body sizes. In all species, treatment effects on growth in mass were nearly identical to those for growth in length, indicating that growth responses were not indirect effects, secondary to changes in nutritional status.

It has proven to be critically important to conduct experimental studies on field-active lizards, because responses to castration and testosterone are strongly dependent on environmental conditions. In two experiments on captive yearling *S. jarrovii* males of the same age as those we studied in the field, we were unable to detect growth inhibition by castration or stimulation by testosterone replacement under conditions favorable for growth in the laboratory (Cox *et al*. 2006), even though treatment effects on plasma testosterone were comparable between the laboratory and the field. Furthermore, hormonal responses to experimental manipulations in the laboratory were not without physiological effect: for example, castration reduced and testosterone replacement increased the intensity of gular pigmentation. This environmental sensitivity of testosterone-mediated male growth regulation is consistent with our observation that natural sex differences in growth are also eliminated under laboratory common-garden conditions (above).

19.5 Synthesis and interpretation

Here we present the first unequivocal evidence of growth promotion by testosterone in any squamate reptile (see Hews *et al*. 1994; Crews *et al*. 1995; Abell 1998a; Klukowski *et al*. 1998; Lerner and Mason 2001; Uller and Olsson 2003; Cox *et al*. 2005a; Cox and John-Alder 2005c). In part, our novel results may reflect inherent physiological differences in the growth-regulatory effects of testosterone among different reptile species (e.g. *S. undulatus* and *S. virgatus* compared with *S. jarrovii*). However, several important modifications in experimental design cannot be discounted as contributing factors. These include (1) precision-loading of Silastic® implants with small quantities of testosterone (see Cox and John-Alder 2005c), (2) the use of relevant natural history to inform the scheduling of experiments, (3) the return of experimentally manipulated lizards into their natural habitat, and (4) the use of both castration and testosterone implants to directly address the consequences of both removal and replacement of testosterone. Indeed, our experiments on captive *S. jarrovii* demonstrate how the outcome of laboratory experiments can be discrepant (Cox *et al*. 2006), and our evidence for growth promotion in this species is critically dependent upon the comparison of castrated males receiving placebo with those receiving testosterone implants.

Of greater significance in the context of the present volume, we report here the first direct evidence that testosterone can act as a bipotential regulator of male growth in closely related species with opposite patterns of SSD. This finding raises the possibility that testosterone may generally be either growth-stimulatory or growth-inhibitory in *Sceloporus* and other organisms, depending on the pattern by which differential growth leads to the development of SSD. In other classes of vertebrates, testosterone is generally considered to be a growth-promoting anabolic steroid (Ford and Klindt 1989; Borski *et al*. 1996; Gatford *et al*. 1998; Holloway and Leatherland 1998). However, most previous work on mammals, birds, and fishes has involved male-larger species, although isolated reports suggest that testosterone may hold bipotentiality even in those classes of vertebrates. Swanson (1967) reported that castration promotes growth in female-larger golden hamsters, implying that testosterone itself may inhibit growth in this species, and more recently, Sockman and Schwabl (2000) and Sockman *et al*. (2005) reported that pre-hatching injection of testosterone reduces post-natal growth in female-larger American kestrels.

Although our results clearly show opposite effects of testosterone on organismal growth, our explanations of underlying mechanism(s) are at this point largely conjectural. An obvious possibility is that testosterone stimulates both growth and growth-promoting functions of the somatotrophic

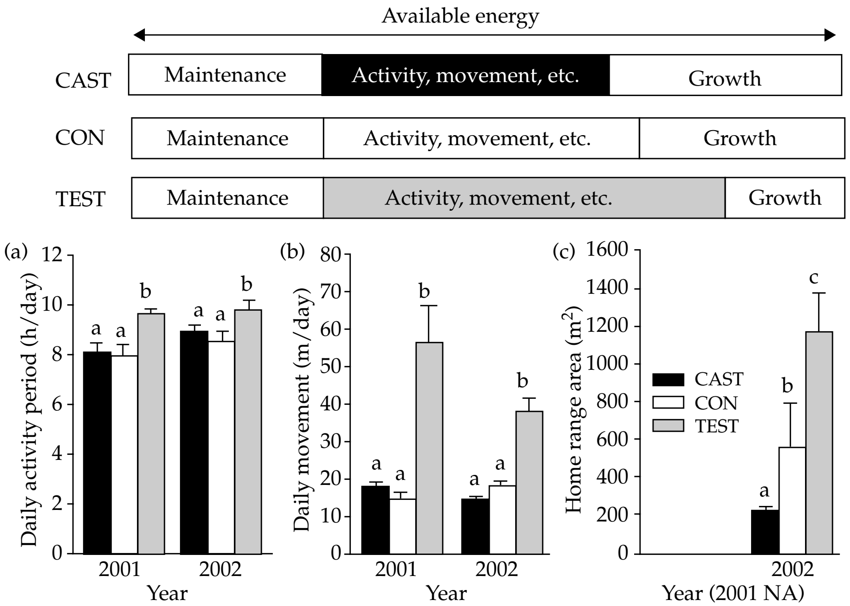


Figure 19.5 Testosterone increases (a) daily activity period, (b) daily movement, and (c) home-range area of *S. undulatus* males. Lower-case letters denote statistical separation of treatment groups. This experiment was replicated in two separate years, although home-range areas were only calculated for the second year. Energetic costs of increased activity, movement, and home-range area may explain why testosterone inhibits growth this species. Treatments are as for Figure 19.3. Data redrawn from Cox *et al.* (2005a) with permission from the University of Chicago Press.

axis in male-larger species while inhibiting these functions in female-larger species. (The somatotrophic axis is the central endocrine axis that regulates somatic growth in vertebrates. Hypothalamic factors regulate the secretion of growth hormone from the anterior pituitary, and growth hormone stimulates the production of insulin-like growth factor-1 (IGF-1) from the liver. IGF-1 in turn stimulates cell division and growth in many tissues. The transport and activity of IGF-1 are mediated by IGF binding proteins.) It is well established in mammals and fishes that growth and the growth-promoting functions of the somatotrophic axis are enhanced by testosterone and other androgenic steroids, whereas estrogenic hormones often have opposite effects (Jansson *et al.* 1985; Eden *et al.* 1987; Millard *et al.* 1987; Devesa *et al.* 1991; Painson *et al.* 1992; Borski *et al.* 1996; Pincus *et al.* 1996; Riley *et al.* 2002a, 2002b; Sparks *et al.* 2003; Larsen *et al.* 2004; Arsenault *et al.* 2004). Thus, as summarized by Gatford *et al.* (1998), "the somatotrophic axis may be a major pathway through which steroids act to produce sex differences in growth." One can easily imagine that testosterone could inhibit growth-promoting functions of the somatotrophic axis (either directly or via aromatization to estrogens) in female-larger species, an hypothesis that we are currently investigating. To date, however, no laboratory has investigated the effects of androgens and estrogens on the somatotrophic axis in a female-larger species in any class of vertebrates. A great advantage of *Sceloporus* is the prevalence of both male- and female-larger SSD in closely related species, thus providing a model system for studies on growth-regulatory processes that lead to SSD.

An alternative possibility is that testosterone may actually stimulate growth-promoting functions of the somatotrophic axis in both male-larger and female-larger species. Despite the fact that yearling males grow more slowly than females in *S. undulatus* and *S. virgatus*, large size confers an advantage when males of these species compete for access to mates (Vinegar 1975; Smith 1985; Haenel *et al.* 2003a), and male mating success is itself correlated with body size (Abell 1998b; see Haenel *et al.* 2003b;

G.J. Haenel and H.B. John-Alder, unpublished work). It therefore seems unlikely that selection for small male size would have led to the evolution of a mechanism by which testosterone inhibits growth while promoting other correlates of reproductive success. Instead, androgenic stimulation of the somatotrophic axis may be conserved regardless of sexual differences in organismal growth. In addition to its direct effects on growth, testosterone also stimulates energetically costly reproductive activities, and in species such as *S. virgatus* and *S. undulatus*, energy may be allocated to these activities at the expense of growth (see Riley *et al*. 2003). Indeed, we have previously shown that exogenous testosterone increases daily activity period, movement, and home-range area in males of *S. undulatus* (Figure 19.5; Cox *et al*. 2005a), and our estimates indicate that the increased energy requirements of these behaviors can account for at least 80% of the reduction in growth rate induced by testosterone. Thus, even while testosterone promotes growth through the somatotrophic axis, it may indirectly inhibit organismal growth in some species due to energetic trade-offs with reproductive investment. This energy allocation trade-off may be further exacerbated by additional costs of testosterone-induced ectoparasitism (Cox *et al*. 2005a; Cox and John-Alder 2007). Interspecific differences in the growth effect of testosterone may be related to life-history variation in the relative energetic demands of competing functions stimulated by testosterone and the balance between total organismal energetic demands and the environmental availability of energy due to differences in habitat and/or breeding phenology. In any case, if testosterone is generally stimulatory with regard to the somatotrophic axis while having opposite effects on organismal growth, then clearly the life histories of species such as *S. jarrovii* must somehow differ from *S. undulatus* and *S. virgatus* so that testosterone-induced energetic costs do not detract from growth.

19.6 Summary: implications for SSD

How are our findings relevant to SSD? As noted at the outset of this chapter, mechanism(s) that give rise to SSD in general and to sexual growth divergence in particular are poorly understood in lizards and other vertebrates. We have begun to develop *Sceloporus* lizards as a model system for comparative studies on the development of SSD in closely related species characterized by opposite patterns of adult SSD. In all species examined to date, mark–recapture studies have demonstrated conclusively that SSD arises due to sexual differences in growth rate before and during first reproduction. Our experimental results indicate that testosterone can be either growth-stimulatory or growth-inhibitory and identify this androgenic sex steroid as a potentially general mediator of sexual differences in growth rate that lead to the development of SSD. However, by focusing on males alone at the exclusion of females, we cannot be certain that testosterone's bipotential effects on growth are directly related to species differences in SSD. Nonetheless, our results raise interesting questions as to how testosterone may mediate sexual differences in growth and body size, thereby minimizing the potential for intersexual genetic conflict (see Badyaev 2002). Further research on *Sceloporus* and other genera with inherent advantages for comparative studies on SSD will strengthen our understanding of the proximate targets of selection that lead to sexual differences in growth and adult body size.

19.7 Acknowledgments

We thank J. Dighton of the Rutgers Pinelands Research Station and W. Sherbrooke, D. Wilson, and the staff of the American Museum of Natural History's Southwestern Research Station (SWRS) for logistical support and the use of laboratory facilities. We thank G. Haenel, S. Skelly, and V. Zilberman, who inspired and co-authored works cited in this chapter, and we thank the legions of graduate and undergraduate students who contributed, including M. Barrett, L. Branagan, K. Facente, M. Gleba, J. Malisch, J. Mangan, L. Smith, L. Swanson, R. Trikha, R. Tsao, L. Walker, and staff of the Cook College Farm for assistance with animal care. This project was funded by the American Museum of Natural History (Theodore Roosevelt Memorial Fund and SWRS Student Support Fund), the Graduate School-New Brunswick at Rutgers University, the

Society for Integrative and Comparative Biology (Grant-in-Aid of Research), and the National Science Foundation (IBN 9507529 and 0135167). This research was conducted in accordance with the Arizona Game and Fish Department, the United States Forest Service, the New Jersey Department of Environmental Protection, Division of Fish and Wildlife, and the Rutgers University Animal Care and Facilities Committee (protocol 01-019).

19.8 Suggested readings

Badyaev, A.V. (2002) Growing apart: an ontogenetic perspective on the evolution of sexual size dimorphism. *Trends in Ecology and Evolution* **17**, 369–378.

Cox, R.M. and John-Alder, H.B. (2005) Testosterone has opposite effects on male growth in lizards (*Sceloporus* spp.) characterized by opposite patterns of sexual size dimorphism. *Journal of Experimental Biology* **208**, 4679–4687.

Duvall, D. and Beaupre, S.J. (1998) Sexual strategy and size dimorphism in rattlesnakes: integrating proximate and ultimate causation. *American Zoologist* **38**, 152–165.

Haenel, G.J. and John-Alder, H.B. (2002) Experimental and demographic analyses of growth rate and sexual size dimorphism in a lizard, *Sceloporus undulatus*. *Oikos* **96**, 70–81.

Watkins, G.G. (1996) Proximate causes of sexual size dimorphism in the iguanian lizard *Microlophus occipitalis*. *Ecology* **77**, 1473–1482.

CHAPTER 20

Sexual differences in insect development time in relation to sexual size dimorphism

Vojtěch Jarošík and Alois Honek

20.1 Introduction

In this chapter we address sexual differences in insect development time. Although sexual size dimorphism in insects is well documented and has been elaborated theoretically (see Chapter 6 in this volume), sexual differences in development time are understood imperfectly. Differences in development time between the sexes are one of the major proximate mechanisms to produce sexual size dimorphisms (growth rate differences being the other), as both traits are typically assumed to be highly correlated (it takes time to get large: Roff 1980; Fairbairn 1990; Blanckenhorn *et al*. 2007). In insects, sexual differences in development time are often small and their experimental determination difficult. An abundance of experimental data exists on the length of male and female pre-imaginal (i.e. pre-adult) development, largely on insects of economic importance (Honek 1997). However, error in estimating the duration of development prevents precise calculation of thermal constants, which are necessary for establishing the rate of development of the sexes over a range of ecologically relevant temperatures, and hence rigorous testing of real differences between males and females. By using the developmental-rate isomorphy concept of Jarošík *et al*. (2002, 2004) we here show that insect development is, on average, faster in males than females, and that this pattern is more pronounced in insects without a true pupal stage.

20.2 Development time and body size in insects

For any given insect species variation in adult body size is large (Honek 1993), and part of this variation is related to development time (Honek 1999). Given a particular growth rate, final size of an insect should be proportional to the duration of growth. We can thus expect a positive relationship between development time and body size, and a trade-off between these characteristics (Roff 1980). This means that an individual may either shorten its development at a cost of being small, or may grow large at a cost of long development.

In insects, female lifetime reproductive success (i.e. fecundity) is more closely correlated with body size (Honek 1993) than the major components of male reproductive success, in particular his mating ability. Thus, in terms of fitness females gain more than males from being large (Charnov *et al*. 1981). With few exceptions, insect males are therefore smaller (Chapter 6) and hence should develop faster than females. Protandry, i.e. the faster development of males, can also increase male mating success, thus further enhancing his fitness (Godfray 1994).

20.3 Temperature and insect development time

As ectotherms insects rely on external sources of heat. Consequently, we cannot say that ectotherms require a certain length of time for development. They require a certain combination of time and temperature called physiological time. The concept of physiological time enables us to ask two central questions concerning the rate of development of males and females: (a) How to measure the rate of development of ectotherms? (b) How to analyse differences in the rate of development between males and females to reach a general conclusion?

20.3.1 How to measure the rate of development of ectotherms?

The rate of development of ectotherms is slow in the cold. As temperature increases, development rate increases up to an optimum temperature, and decreases again at high supraoptimum temperatures. In the wide range of ecologically relevant temperatures below the optimum the relationship between the rate of development and temperature is practically linear (Figure 20.1).

The linear approximation of the relationship between the rate of development and temperature enables us to calculate two constants: the sum of effective temperatures (*SET*)—that is, the amount of heat needed to complete a developmental stage—and the lower developmental threshold (*LDT*), the temperature below which development ceases. Thus the relationship between the rate of development, *RD*, and temperature, *T*, can be expressed as a linear equation in which a is the intercept with the y axis and b is the slope: $RD = a + bT$. The lower developmental threshold, at which the rate of development ceases (i.e. $RD = 0$), can then be calculated as $LDT = -b/a$. Furthermore, when development is completed (i.e. $RD = 1$), the sum of effective temperatures can be calculated as $SET = -1/b$. Then the number of day-degrees above the lower developmental threshold gives the sum of effective temperatures that is necessary for completion of a developmental stage (or total development). This linear relationship between the rate of development and temperature was first described by Ludwig (1928) and its suitability evaluated by Ikemoto and Takai (2000). Several non-linear models were also proposed (e.g. Logan *et al*. 1976; Lactin *et al*. 1995; Briére *et al*. 1999) and tested (Kontodimas *et al*. 2004). Here we use simple linear models which are convenient for meta-analysis (Jarošík *et al*. 2002).

Until recently it seemed that each developmental stage for each species had its own, specific lower developmental threshold (Honek and Kocourek 1990; Hodek and Honek 1996; Honek 1996; Kiritani 1997). This notion would change if, as shown in our example (Figure 20.2), the proportion of development time spent in individual developmental stages did not change with temperature; then the lower developmental threshold would remain the same for all developmental stages within a population of a given species.

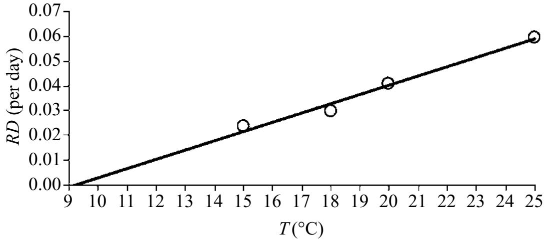


Figure 20.1 An example of a linear relationship between the rate of development (*RD*) and temperature (*T*) for the coccinellid beetle *Propylea japonica* (Thunberg). Data from Kawauchi (1983).

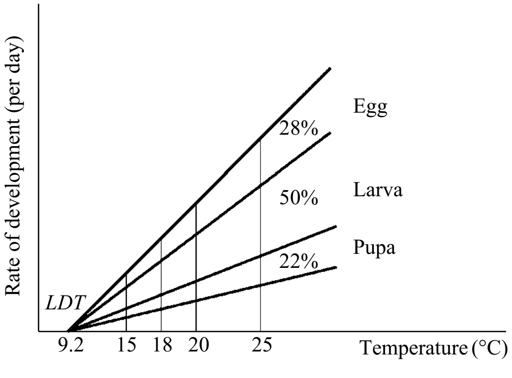


Figure 20.2 The concept of developmental isomorphy. Effect of temperature on the additively plotted rate of development, within the linear range of the relationship, for the coccinellid beetle *P. japonica*. The population is isomorphic and spent 28% of its total development in the egg, 50% as a larva, and 22% as a pupa at temperatures of 15, 18, 20, and 25°C. Therefore, all developmental stages have a common lower developmental threshold (*LDT* = 9.2). Because rate isomorphy implies no change with temperature in the proportion of time spent in a particular developmental stage, for assessment of the number of day degrees above the LDT necessary to complete a particular development stage, the sum of effective temperatures can be determined at any temperature within the linear range. Jarošík *et al*. (2003); data from Kawauchi (1983).

We call this notion *developmental-rate isomorphy* (Jarošík *et al*. 2002, 2004; Box 20.1).

The existence of developmental isomorphy thus facilitates measuring the rate of development of ectotherms to determine sexual differences more precisely. This is so because, as shown by Jarošík *et al*. (2002), the proportion of time spent in individual developmental stages typically does not change with temperature for males or females of a particular species (Figure 20.3a). Consequently, males and females must have the same lower developmental threshold, and the rate of development of males and females can be compared based on regression slopes of their rates of development on temperature (Figure 20.3b). Having an efficient tool for measuring the rate of development of males and females, we can now turn to the second question.

20.3.2 How to analyse differences in the rate of development between males and females to reach a general conclusion?

Reaching a general conclusion from particular experiments on any given species is an ambitious task because each experiment on the relationship between the rate of development and temperature is limited to those particular circumstances. We here use meta-analysis, a statistical synthesis of separate, independent experiments (Hedges and Olkin 1985; Hedges 1994; Shadish and Haddock 1994; Gurevitch and Hedges 2001) to analyse the differences in the rate of development between males and females as effect sizes that are independent of sample size and the scale of measurement (Box 20.2). We use the convention that negative effect size means shorter developmental time of males; that is, faster male than female development.

20.4 The data-set

Overall, we gathered data on the duration of non-dormant (i.e. direct) development of males and females, at two or more constant temperatures, for 132 populations of 122 insect species from 11 orders. All data fell within the range of the linear relationship between the *RD* and temperature. Because a previous study (Jarošík *et al*. 2002) has

Box 20.1 Concept of developmental-rate isomorphy in ectotherms

Rate isomorphy (Figure 20.2) means that the proportion of the development time spent in individual developmental stages does not change with temperature. Then the lower developmental threshold (*LDT*) remains the same for all developmental stages, and (1) the *LDT* can be established from data on any one developmental stage and (2) the sum of effective temperatures (*SET*) can be calculated from the duration of development at only one temperature.

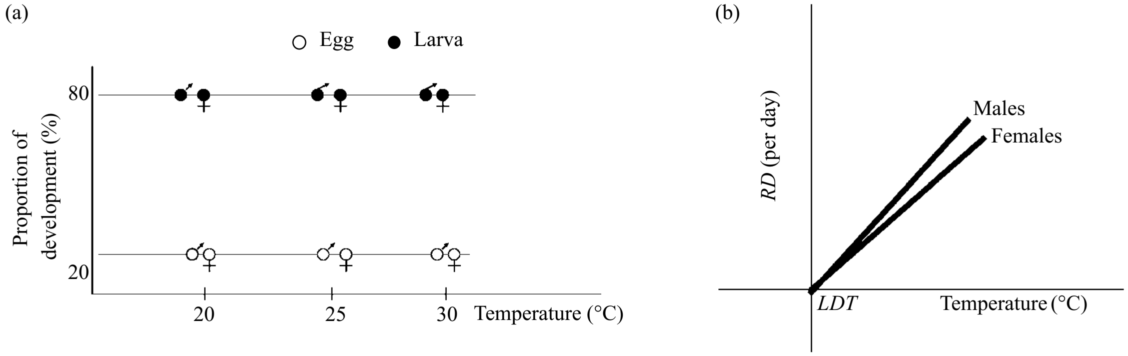


Figure 20.3 How to measure the rate of development of ectotherms. (a) The proportion of time spent in particular developmental stages of an ectotherm, exemplified by the cockroach *Periplaneta fuliginosa* (Serville), does not change with temperature for males and females. (b) Consequently, males and females must have the same lower developmental threshold (*LDT*), and the rate of development (*RD*) of males and females can be compared based on regression slopes of their rates of development on temperature. Data from Benson *et al*. (1994).

Box 20.2 Meta-analysis: statistical issues

Meta-analysis begins by representing the outcome of each experiment by a quantitative index of the effect size. This effect size is chosen to reflect differences between groups in a way that is independent of sample size and the scale of measurement used in the experiment. Meta-analytical techniques most commonly serve to test whether the effect size is significantly different from 0 and to examine potentially causative differences in the effect size among studies. The data necessary from each study to calculate the effect size and its variance are the means of the experimental groups, the standard deviations about these means, and the sample size of each group.

We estimated the mean development rates (*RD*) of males and females and the standard deviations from the regression slopes of *RD* on temperature (Figure 20.3b). The sample size of each group was equal to the number of temperatures used in each experiment. The data were corrected for small-sample bias following Hedges and Olkin (1985). To indicate significant variation in the rate of development between males and females, we used heterogeneity summary tables and contrasts among mean effect sizes, expressing the homogeneity of effect sizes between and within analysed groups by *Q-sums* (Hedges 1994; Gurevitch and Hedges 2001); these approaches are principally similar to classical ANOVAs and orthogonal contrasts among means (e.g. Sokal and Rohlf 1995).

shown that developmental-rate isomorphy is not affected by factors such as genetic differences between populations and differences in geographical origin, food, humidity, photoperiod, or number of instars, the data on the duration of development were averaged across these factors for each population.

Some controversy exists about whether all studies on a topic should be included in the analysis, or whether low-quality studies (e.g. data for only a part of pre-imaginal development) should be excluded. Following Gurevitch and Hedges (2001) we included all studies unless the results of the low-quality studies differed from those of higher-quality studies. We had reliable data for the insect orders Blattodea and Thysanoptera, for which all the data on developmental time were available for the whole (egg-to-adult) pre-imaginal development. We also had reliable data for the insect orders Diptera and Hymenoptera, for which all the effect sizes covering just a subset of the developmental stages (i.e. egg, larva, or pupa) showed the same trend as for the whole (egg-to-adult) pre-imaginal development. However, this was not so for Coleoptera, Homoptera, and Lepidoptera. For the Coleoptera and Homoptera the effect sizes covering the total pre-imaginal development differed from those covering only some of the developmental stages. However, these differences were not significant, and therefore all data were used in the analyses. For the Lepidoptera the data for pupal development differed significantly from those for the other developmental stages and the total pre-imaginal development and were therefore excluded.

There was no possibility to evaluate the quality of the data *a priori* for the insect orders Aphaniptera (=Siphonaptera), Heteroptera, Neuroptera, and Orthoptera, because all available data were for one developmental stage only, so we used all of the data. However, the Aphaniptera, for which only data on the pupal stage were available, appeared to be a very strong outlier, showing a reverse trend compared with all the other data (Table 20.1). Therefore, in the *a priori* planned comparison between holometabolous and heterometabolous insects (i.e. insects having and lacking the true pupal stage, respectively), and in our comparison of groups within the Holometabola, the Aphaniptera data were excluded.

20.5 Results

The mean effect across all studies indicated that males develop significantly ($P < 0.05$) faster than females. Following a conventional interpretation of the magnitude of effect sizes (Cohen 1969), the

Table 20.1 Sample size (number of species, *N*), rate of development of males and females (per day), effect sizes (d_+; see Box 20.2) with their 95% confidence intervals (CI) of the differences between the rate of development of males and females within insect orders, and the corresponding test statistics (*Z*, *P*) for the null hypotheses of no differences. Negative effect sizes mean faster development of males and positive effect sizes the converse. 95% Confidence intervals ($d^L - d^U$) that do not include 0 and *Z* statistics with $P < 0.05$ indicate statistically significant differences between males and females.

Order	Sample size	Rate of development (per day)		Effect size	95% CI		Statistic	Probability
	N	Males	Females	d_+	d^L	d^U	*Z*	*P*
Aphaniptera	2	0.00534	0.00651	7.16	3.65	10.67	4.00	<0.001
Blattodea	1	0.000201	0.000195	−2.53	−4.68	−0.38	−2.31	0.028
Coleoptera	15	0.0043	0.00410	−0.80	−1.27	−0.34	−3.38	0.001
Diptera	15	0.00529	0.00517	−0.41	−0.80	−0.03	−2.12	0.042
Heteroptera	7	0.00376	0.00372	−0.33	−0.94	0.27	−1.08	0.223
Homoptera	13	0.00334	0.00338	−0.10	−0.57	0.37	−0.40	0.368
Hymenoptera	43	0.00474	0.00450	−0.80	−1.05	−0.56	−6.50	<0.001
Lepidoptera	30	0.00336	0.00329	−0.52	−0.84	−0.21	−3.23	0.002
Neuroptera	1	0.00295	0.00292	−0.25	−1.86	1.36	−0.31	0.381
Orthoptera	2	0.00141	0.00122	−3.90	−5.96	−1.84	−3.71	<0.001
Thysanoptera	3	0.00433	0.00419	−0.63	−1.27	0.01	−1.93	0.062

overall effect size, $d_+ = -0.598$ (variance, $s^2_{d+} = 0.0053$), is considered to be "medium". Most insect orders, namely the Blattodea, Coleoptera, Diptera, Hymenoptera, Lepidoptera, and Orthoptera, exhibit significantly faster development of males than females (Table 20.1). A similar difference was only marginally significant ($P < 0.1$) for the Thysanoptera. No such difference between males than females was apparent in the Heteroptera, Homoptera, and Neuroptera. Only in the Aphaniptera did female pupae develop significantly faster than male pupae.

A heterogeneity summary table (Table 20.2) indicates significant variation in the rate of development between males and females, both within and between insect orders. Most variation (85%) appeared within insect orders, suggesting that the systematic differences in the rate of development between males and females are not strongly affected by phylogenetic relatedness; thus the results should remain similar if the analysis were repeated using phylogenetically independent contrasts. The strong within-order variability evident in Table 20.2 also suggests that the overall average effect across all studies is of limited value.

An *a priori* planned comparison between Holometabola (insects having the true pupal stage) and Heterometabola (insects without the true pupal stage) demonstrated that males of the Heterometabola develop significantly faster ($Q = 6.56$; df = 1; $P = 0.01$) relative to females (effect size of the difference between males and females $d_+ = -7.50$) than males of the *Holometabola* ($d_+ = -2.80$). In search for further patterns, we first repeated the meta-analysis just for the *Holometabola*, with parasitoid/non-parasitoid insects as a grouping factor: no significant differences were found ($Q = 0.29$; df = 1; $P = 0.59$), as almost all variability remained within groups ($Q = 132.1$; df = 71; $P < 0.0001$), clearly suggesting that the traits related to a parasitoid life history do not crucially affect the differential rate of development of males and females. When repeating the meta-analysis just for the Heterometabola, subdivided into the three distinct subgroups of postembryonic development type Pauro-, Para-, and Remetabola (Box 20.3), the results again indicated no significant variation between these groups ($Q = 3.80$; df = 2; $P = 0.15$). Significant variability appeared only within the group with parametabolic development (i.e. the Coccoidea; $Q = 23.08$; $\mathrm{df} = 6$; $P = 0.001$).

Table 20.2 Heterogeneity summary table, expressing the homogeneity of effect sizes (Box 20.2) between the rate of development of males and females within and between insect orders. The test statistic (*Q-sums*) with corresponding degrees of freedom (df) and probability (*P*) indicates statistically significant results.

Source of heterogeneity in effect sizes	**Q-sums**	**df**	***P***
Between orders	41.727	10	<0.001
Within orders			
Aphaniptera	1.478	1	0.224
Blattodea	–	0	–
Coleoptera	35.036	14	0.001
Diptera	17.751	14	0.218
Heteroptera	3.829	6	0.700
Homoptera	29.267	12	0.004
Hymenoptera	76.547	42	0.001
Lepidoptera	61.613	22	<0.001
Neuroptera	–	0	–
Orthoptera	2.951	1	0.086
Thysanoptera	1.171	2	0.557
Total within orders	229.644	114	<0.001
Total	271.371	124	<0.001

Box 20.3 Postembryonic development types of heterometabolous insects

Paurometabola are insects with a classic postembryonic development of Heterometabola: insects lacking a true pupal stage and having several larval instars that are gradually more similar to adults (orders Orthoptera, Blattodea, Heteroptera, and most Homoptera in our analysis). Parametabola include males of Coccoidea (coccids; mealybugs, and scales) and Remetabola thrips (Thysanoptera); these two latter groups, similar to Paurometabola, do not have a true pupal stage, but include quiescent stages, ecologically similar to the true pupal stage of Holometabola (Heming 2003).

20.6 Discussion

Our work shows that in insects, males on average develop faster than females, indicating protandry, but this difference varies strongly among taxa. This result seems little affected by phylogenetic relatedness, except by the existence of a pupa in holometabolous insects, which seems to limit the rate (i.e. speed) of male development relative to females, as in holometabolous insects the difference in the length of pre-imaginal development of males and females is significantly smaller than in heterometabolous insects. In heterometabolous insects the gonads develop gradually during all larval stages, thus providing longer time for development. In contrast, holometabolous insects undergo a complete histolysis of larval tissues during pupation, with a new development of adult tissues starting from imaginal discs. Assuming similar patterns of sexual dimorphism in holo- and heterometabolous insects, it is therefore possible that particularly in holometabolous insects the pre-imaginal development of male gonads is more costly than that of female gonads (Blanckenhorn *et al.* 2007), potentially explaining the limitation in male development rate in holometabolous relative to heterometabolous insects found here.

A second potential explanation for our finding relates to possible systematic differences in mortality risk of males relative to females in heterometabolous and holometabolous insects, as in the latter group larvae and adults often live in completely different environments (Blanckenhorn *et al.* 2007). Thus it could be adaptive for a male to remain longer in the larval stage if this increases its survivorship to reproductive age, whereas for a female it may be adaptive to emerge earlier because adult female insects typically need to feed to mature their eggs before reproduction. Again assuming similar patterns of sexual dimorphism in holo- and heterometabolous insects, we would in this case expect a smaller difference in the development times of males and females in heterometabolous insects, in which larvae and adults live in the same environment, than in holometabolous insects. As we obtained the opposite result, however, we can reject this hypothesis.

20.7 Summary and conclusions

Using the concept of developmental rate isomorphy, meaning that the proportion of time spent in individual developmental stages does not change with temperature for males and females of any particular species, we compared the rate of development of males and females based on regression slopes of their rates of development on temperature. To reach general conclusions, we compared these rates for 122 insect species from 11 orders using meta-analysis, a statistical synthesis of separate, independent experiments. On average, males develop significantly faster than females. However, this overall effect is accompanied by large variation within insect orders, suggesting that the systematic differences in the rate of development between males and females are not strongly affected by phylogenetic relatedness. The faster male relative to female development is more pronounced in heterometabolous insects without a true pupal stage than in holometabolous insects with a true pupal stage, perhaps related to pre-imaginal development of male gonads being more costly than that of female gonads in the latter group. In contrast, the pattern was not affected by other life-history traits such as a parasitoid life history or the existence of quiescent stages in insects lacking the true pupal stage.

20.8 Acknowledgments

The work was supported by grant no. QC50081 from the Ministry of Agriculture of the Czech Republic (to A.H. and V.J.) and grant nos MSM 0021620828 and LC06073 from the Ministry of Education of the Czech Republic (to V.J.).

20.9 Suggested readings

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Supplementary Tables

Table A3.1 Distribution of SSD in five morphometric traits (given as $\log_{10}$(male trait)–$\log_{10}$(female trait), median, lower quartile (LQ)–upper quartile (UQ)) using (a) species-level and (b) family-level data. For comparability, we also provide means ± SD for the index of Lovich and Gibbons (1992), SDI. We tested whether SSD in each trait was different from 0 using Wilcoxon one-sample tests, and the probability of these tests are given (****P* < 0.001). The distributions of SSD were also tested against normal using Kolmogorov–Smirnov tests, and the probabilities of these tests are also provided (*P*).

	Body mass	**Wing length**	**Tarsus length**	**Bill length**	**Tail length**
(a) Species level					
Median	0.0192***	0.0133***	0.0087***	0.0109***	0.0139***
LQ–UQ	(−0.0111 to 0.0520)	(0.0038 to 0.0233)	(0.0000 to 0.0185)	(0.0000 to 0.0237)	(0.0018 to 0.0264)
Mean ± SD	0.0183 ± 0.0660	0.0134 ± 0.0203	0.0106 ± 0.0187	0.0119 ± 0.0247	0.0188 ± 0.0477
SDI (mean ± SD)	−0.0463 ± 0.1865	−0.0321 ± 0.0499	−0.0253 ± 0.0466	−0.0286 ± 0.0612	−0.0526 ± 0.2103
Kolmogorov–Smirnov (*P*)	<0.001	<0.001	<0.001	<0.001	<0.001
Number of species	2649	2979	2506	2625	2349
(b) Family level					
Median	0.0208***	0.0108***	0.0094***	0.0128***	0.0141***
LQ–UQ	(−0.0056 to 0.0523)	(0.0005 to 0.0202)	(0.0015 to 0.0196)	(0.0010 to 0.0245)	(0.0044 to 0.0269)
Mean ± SD	0.0177 ± 0.0659	0.0098 ± 0.0181	0.0097 ± 0.0181	0.0122 ± 0.0262	0.0171 ± 0.0285
SDI (mean ± SD)	−0.0466 ± 0.1888	−0.0234 ± 0.0437	−0.0234 ± 0.0441	−0.0296 ± 0.0655	−0.0447 ± 0.0821
Kolmogorov–Smirnov (*P*)	0.050	0.597	0.295	0.084	0.015
Number of families	119	110	108	106	102

Table A3.2 Avian species showing extreme SSDs. The value of SSD, given as $\log_{10}$(male trait)−$\log_{10}$(female trait), is in parantheses for a given species in a particular trait, followed by the SDI of Lovich and Gibbons (1992).

	Avian species (SSD; SDI)				
	Body mass	**Wing length**	**Tarsus length**	**Bill length**	**Tail length**
Male-biased SSD	*Otis tarda* (0.497; −2.138)	*Euplectes progne* (0.182; −0.520)	*Nectarinia habessinica* (0.237; −0.725)	*Tetrao urogallus* (0.187; −0.539)	*Euplectes progne* (0.819; −5.597)
	Cairina moschata (0.380; −1.400)	*Quiscalus mexicanus* (0.117; −0.309)	*Alaemon hamertoni* (0.137; −0.371)	*Tockus albocristatus* (0.137; −0.371)	*Euplectes ardens* (0.713; −4.158)
	Cincloramphus cruralis (0.363; −1.309)	*Euplectes axillaris* (0.116; −0.306)	*Tetrao urogallus* (0.122; −0.325)	*Quiscalus mexicanus* (0.112; −0.294)	*Euplectes psammocromius* (0.642; −3.387)
	Tetrao urogallus (0.330; −1.136)	*Euplectes hartlaubi* (0.115; −0.302)	*Francolinus ochropectus* (0.122; −0.324)	*Ceratogymna elata* (0.109; −0.285)	*Euplectes jacksoni* (0.610; −3.077)
	Psarocolius decumanus (0.296; −0.978)	*Euplectes psammocromius* (0.114; −0.301)	*Cincloramphus cruralis* (0.118; −0.312)	*Ceratogymna atrata* (0.108; −0.283)	*Clangula hyemalis* (0.485; −2.054)
Female-biased SSD	*Accipiter ovampensis* (−0.269; 0.857)	*Centropus grillii* (−0.073; 0.182)	*Galerida modesta* (−0.051; 0.125)	*Emberiza leucocephalos* (−0.092; 0.235)	*Falco peregrinus* (−0.080; 0.201)
	Micronisus gabar (−0.281; 0.911)	*Accipiter nisus* (−0.074; 0.186)	*Polemaetus bellicosus* (−0.055; 0.135)	*Rhodopis vesper* (−0.094; 0.241)	*Turnix hottentotta* (−0.080; 0.202)
	Accipiter nisus (−0.286; 0.933)	*Accipiter striatus* (−0.074; 0.187)	*Hirundo albigularis* (−0.056; 0.138)	*Numenius americanus* (−0.103; 0.266)	*Accipiter badius* (−0.081; 0.204)
	Accipiter novaehollandiae (−0.306; 1.022)	*Accipiter novaehollandiae* (−0.084; 0.213)	*Micronisus gabar* (−0.057; 0.141)	*Apteryx haastii* (−0.117; 0.310)	*Accipiter nisus* (−0.082; 0.208)
	Arcanator orostruthus (−0.336; 1.169)	*Eupodotis indica* (−0.091; 0.234)	*Tyto tenebricosa* (−0.071; 0.178)	*Apteryx australis* (−0.121; 0.323)	*Accipiter striatus* (−0.090; 0.230)

Table A14.1 Summary statistics for adult SVL of male and female *L. agilis* in 52 local and regional samples. See Figure 14.1a for geographic locations, and Figure 14.1b for the SDI for means. Means of samples 17, 35, 38, and 46 were excluded from analyses (see Section 14.3.1) because they exhibit unusually high standard deviations (SDs) and obviously include immature animals. No published data included 80th percentiles (P80): these were computed from histograms or scatter plots. If only total sample size was available (study samples 8 and 17), *N*/2 was assumed for male and female sample sizes.

	Study sample	Males						Females						Data source
		n	Min	Max	Mean	SD	P80	n	Min	Max	Mean	SD	P80	
1	Pyrenees	41			77.70	4.03		70			85.74	6.69		Amat *et al.* (2000)
2	Switzerland	30	63	78	68.18	3.35	70.6	28	68	83	75.05	4.02	78.4	Helfenberger and Bendel (1994)
3	South Sweden	44			70.00	5.97	77.5	45			78.20	4.70	85.0	Olsson (1988)
4	NE Germany	28	64	79	72.60	4.03		28	65	98	82.46	7.14		Nöllert (1988)
5	Lower Austria	41	48	74	59.21	8.30		41	49	85	65.09	9.26		Rahmel and Meyer (1987)
6	Moravia	17	48	82	64.30	7.42		17	61	80	70.70	5.77		Gvozdik and Boukal (1998)
7	East Slovakia	57	58	97	77.20	10.14		54	61	100	78.70	12.20		Majlath *et al.* (1997)
8	W Ukraine, Carpathians	55	61	85	71.24	1.93		55	62	91	74.57	1.19		Shcherbak and Shcherban' (1980)
9	Romania, E Carpathians	68	50	86	69.20	8.61		73	65	98	78.10	8.62		Fuhn and Vancea (1964)
10	Romania, S Carpathians	11	66	78	72.80	9.38		18	70	92	79.30	6.24		Fuhn and Vancea (1964)
11	Romania, Oltenia	28	50	81	70.00	4.20		22	50	93	73.50	6.18		Fuhn and Vancea (1964)
12	Romania,Valakhia	23	64	82	72.90	5.06		25	64	84	71.10	5.13		Fuhn and Vancea (1964)
13	Romania, Moldova	47	68	91	78.70	5.17		31	70	94	83.80	5.89		Fuhn and Vancea (1964)
14	SE Romania	20	44	91				18	54	90				Fuhn and Vancea (1964)
15	SW Ukraine	39	61	84	71.49			59	62	85	71.88			Kotenko and Tarashchuk (1982)
16	Ukraine, Uman'	18	59	86	73.62	6.46	79.0	24	56	84	72.10	7.59	78.0	E.M. Smirina, unpublished data
17	Belorussia	280		87	60.76	54.22		280		90	63.50	43.84		Pikulik *et al.* (1988)
18	Latvia, Daugavpils	20	68	90	77.90	5.61	83.6	26	72	90	79.65	4.8	83.8	E.S. Roitberg, unpublished data
19	Abkhasia	28	57	92	75.80	1.32		21	59	105	76.00	1.10		Darevsky *et al.* (1976)
20	Armenia	110	76	93	81.20	12.48		151	82	96	84.00	15.11		Darevsky *et al.* (1976)
21	East Georgia, Tianeti	37	74	91	85.00	4.87		22	74	89	81.00	4.69		Muskhelishvili (1970)
22	N Caucasus, Novokurskiy	34	73	106	92.50	7.39	100.0	34	74	98	85.24	6.63	92.0	E.S. Roitberg, unpublished data
23	N Caucasus, Groznyy	14	77	114	93.71	10.84	101.0	14	73	104	87.21	9.28	96.0	K.Yu. Lotiev, unpublished data
24	N Caucasus, Kostek	25	71	106	88.68	10.92	99.8	28	71	95	81.61	6.35	87.2	E.S. Roitberg, unpublished data
25	N Caucasus, Makhachkala	106	71	109	88.34	9.69	98.0	108	71	97	82.20	6.57	88.0	E.S. Roitberg, unpublished data
26	N Caucasus, Buinaksk	61	72	99	84.51	6.97	91.0	65	71	92	80.42	5.42	86.0	E.S. Roitberg, unpublished data
27	N Caucasus, Termenlik	14	79	100	90.36	7.02	97.0	16	75	99	87.69	6.55	93.4	E.S. Roitberg, unpublished data

28	N Caucasus, Sergokala	58	72	97	84.48	6.06	90.0	60	71	90	79.20	5.09	84.0	E.S. Roitberg, unpublished data
29	N Caucasus, Khuchni	25	73	103	85.68	7.92	93.4	29	71	98	82.83	7.53	90.0	E.S. Roitberg, unpublished data
30	N Caucasus, Kuli	11	73	100	89.91	8.07	97.0	11	78	100	91.64	6.96	97.0	E.S. Roitberg, unpublished data
31	Crimea	87	60	108	84.70	11.00	93.0	70	64	114	82.00	10.10	90.0	Shcherbak (1966)
32	Leningrad region	34	61	87	74.17			24	68	90	80.35			Peters (1959)
33	Kaluga region	18	63	84	74.80	6.23		32	61	99	73.40	8.37		Strel'tsov and Voronin (1973)
34	Ryazan region	333	60	112	78.64	12.69	88.4	380	60	112	80.43	13.96	94.0	Zharkova (1973)
35	Lipetsk region	136			72.02	36.15		197			72.80	39.30		Klimov *et al.* (1999)
36	Tambov region	18			80.90	7.64		42			83.90	8.42		Korneva and Yatsenko (1989)
37	W Cis-Caucasia	302	63	111	79.73	10.56	90.0	296	63	108	78.37	10.12	87.0	Lukina (1966)
38	Stavropol region	470	75	110	91.59	26.45		470	75	110	85.07	34.69		Tertyshnikov (2002)
39	Middle Volga, locality 1	30			75.20	4.05		63			74.48	6.03		Darevsky *et al.* (1976)
40	Middle Volga, locality 2	32			73.31	7.41		87			80.55	7.83		Darevsky *et al.* (1976)
41	Middle Volga, locality 3	36			73.92	8.58		80			79.59	9.30		Darevsky *et al.* (1976)
42	Vyatka region	21	74	91	83.52	4.55	87.6	30	74	98	85.30	5.21	89.8	E.S. Roitberg, unpublished data
43	Tatarstan	115	65	105	81.70	8.20	89.5	30	70	105	88.10	9.06	92.0	Garanin (1983)
44	Saratov region	56	62	98	75.20	15.19		68	57	94	72.50	15.59		Zavialov *et al.* (2000)
45	Volga-Ural	26			80.30	19.38		26			76.80	18.87		Darevsky *et al.* (1976)
46	S Ural, Bashkiria	33	33	91	69.00	88.12		40	54	98	76.90	67.36		Khabibullin (2001)
47	NW Kazakhstan, Emba	27	78	103	89.33	7.03	97.4	50	75	100	88.32	6.01	94.6	E.S. Roitberg, unpublished data
48	Kirgizia	17	71	87	77.93	4.58		15	68	88	78.37	6.51		Yakovleva (1964)
49	East Kazakhstan	13	67	97	82.00	7.93		20	65	86	77.80	6.26		Berdibayeva (1989)
50	S Siberia, Tomsk				78.50						85.80			Bulakhova (2005)
51	S Siberia, Altai	34	68	95	81.38	7.34	89.0	52	67	97	79.37	7.98	86.4	V.A. Yakovlev, unpublished data
52	Mongolia	10	56	85	73.00	9.17		10	50	80	71.30	9.17		Munkhbayar *et al.* (1998)

E, East; N, North; NE, Northeast; NW, Northwest; S, South; SE, Southeast; SW, Southwest; W, West.

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Glossary

adaptation 1. A trait that has evolved in response to natural selection and is currently maintained by natural selection. 2. A trait that functions to increase the lifetime reproductive success or *fitness* of a given biological entity. 3. The process of evolution in response to natural selection.

allometry Strictly defined as a departure from geometric similarity or a disproportionate change in the size of a body component with changes in some measure of overall size. More broadly defined as the disproportionate change in a given variable, not necessarily morphological, with body size. Allometry is detected statistically using the basic model $Y = aX^b$, which can be linearized as $\log Y = \log a + b \log X$. The allometric exponent can then be estimated as the slope of a regression of $\log Y$ on $\log X$. If the ratio of trait Y to trait X does not change with X, then $Y/X = a$ and $b = 1$. This is defined as *isometry* or geometric similarity. Allometry can be studied at several levels: (1) differential growth of body components is called ontogenetic allometry; (2) allometric covariation of traits among individuals of a given life stage and population is called static allometry; (3) allometric covariation of traits among species or higher taxa is called evolutionary allometry. Allometry for sexual size dimorphism occurs when the ratio of male to female body size changes systematically with either mean size or the size of either sex.

anisogamy Unequal size of eggs and sperm.

anlagen A group of relatively undifferentiated cells that subsequently differentiate to form a particular structure (i.e. tissue or organ). For example the optic anlagen is the group of cells in many vertebrate embryos that will ultimately become the eye.

autosome A chromosome present in equal dose in the genomes of both sexes and not involved in determining sex.

bikont A eukaryotic cell with two microtubule-organizing centers. Plantae (plants and red and green algae), Chromalveolates (protists), Excavata (protists), and Rhizaria (protists) are thought to have evolved from an ancestral bikont, and these groups are collectively called bikonts.

bipotential Having the property, or potential, to induce or effect two different outcomes, depending on experimental circumstances. For example, testosterone can be described as a bipotential growth regulator in that it stimulates organismal growth in a male-larger species and inhibits growth in female-larger species, all else apparently equivalent.

carapace The sclerotized dorsal plate of the *prosoma* or *cephalothorax* in spiders.

calyx The outermost part of a flower consisting of the sepals. In the bud stage, the calyx protects the developing inner parts of the flower.

cell-mediated immunity (CMI) Cell-mediated immunity represents the non-specific part of the immune reaction. A common way of testing general *immunocompetence* in birds is by injecting phytohemagglutinin (PHA) into the foot or wing web and measuring the subsequent swelling.

cephalothorax The anterior section of arachnids and many crustaceans, consisting of the fused head and thorax. Also called the *prosoma*.

co-dominance Full expression of two distinct alleles at a given *locus* in heterozygous individuals.

common-garden experiment An experiment in which the offspring of individuals from different origins (i.e. different populations, environments, families) are reared in a common environment to control for environmental influences on phenotypic traits. The term derives from agriculture and horticulture, where plants were literally reared in a common garden. However, the term applies more broadly to any controlled environmental condition such as a laboratory environment or growth chamber.

condition The quantity of metabolic resources available to an individual, and the efficiency with which it can utilize those resources to increase its fitness; condition is assumed to depend on both genetic quality and the abundance of resources in the ambient environment.

condition dependence A form of *phenotypic plasticity* whereby the expression of a trait reflects individual condition.

correlated evolution Most generally, the correlated evolution of two or more traits such that the evolutionary trajectory of one trait can be predicted from that of the other(s). The term is often used more specifically to refer to correlated evolution caused by a genetic correlation between traits, where direct selection acting on one trait causes an indirect, correlated response in the other trait.

cryptorchidism Testes not descended from the abdominal cavity into the scrotum.

day-degree The basic unit of *physiological time*; the thermal equivalent of 24 h at 1°C above the *lower developmental threshold*.

developmental constraint A developmental mechanism that limits or channels evolutionary change; a bias in or limitation of the pattern of phenotypic and genetic variation on which selection can act imposed by the structure or dynamics of the developmental system.

developmental-rate isomorphy The proportion of development time spent in individual developmental stages does not change with temperature. For example, an insect might spend 20% of its development time (time from egg to emergence as an adult) in the pupal stage, and this is true regardless of the temperature of rearing as long as all stages are reared at the same temperature.

dioecy A breeding system of plants wherein there are distinct male and female individuals.

dosage compensation Dosage compensation is a genetic regulatory mechanism that equalizes the phenotypic expression of characteristics determined by genes on the sex chromosomes so that they are equally expressed in the homogametic (XX, ZZ) and heterogametic sexes (XY, ZW).

epigenetic Relating to heritable factors other than the DNA sequence that regulate gene expression. Examples include DNA methylation, X-inactivation, and chromatin remodeling.

epistasis A non-additive interaction between alleles at different loci, reflected in phenotypic effects, most often referring to cases where alleles at one *locus* mask the effects of alleles at another locus. In quantitative genetics, epistatic variance is partitioned as V_I.

fecundity Reproductive output (number of eggs or offspring), usually of an individual.

fitness Most generally, success in contributing descendents to future generations. Fitness is often operationally defined as lifetime reproductive success (R), and this is appropriate if comparisons are made among individuals within a single generation and generations are non-overlapping. However, if generations overlap, reproductive rate (e.g. generation time, age at maturity, interbirth interval) can also contribute significantly to fitness, and the rate of increase, r, is a better measure. Life-history variables such as fecundity, mating success and survival are often used to estimate components of lifetime fitness. Assessing the adaptive significance of traits often requires estimation of these separate components of fitness.

fitness component Fitness estimated as survival and/or reproductive success through one component of the life history of an organism or other biological entity. Examples include survival to first reproduction, annual or lifetime fecundity, and mating or fertilization success.

gender In standard English, gender is a grammatical classification of objects into male and female classes, and it is often used colloquially as a synonym for sex, as in the male or female sex. However, in the sociological and psychological literature, gender is often defined as a person's psychological status concerning their sex, including innate and acquired behaviors, thoughts, and roles. One's gender identity need not correspond to one's biological sex. To make things even more confusing, in the biological literature, *sex* is often used as a synonym for genetic recombination or sexual reproduction, and colloquially, sex often refers to the act of coitus. Thus, neither sex nor gender has a single, unambiguous meaning. In this volume, we use gender as a synonym for male or female sexes in organisms where male and female sexual function occurs in separate organisms (gonochoric animals and dioeceous plants).

gender load The reduction of *fitness* resulting from sexual conflict.

gender role The life-history, ecological, and behavioral characteristics associated with male and female sexual function in a given species.

genetic architecture The set of genes and the relationships among them that underlie the expression of a given phenotypic trait.

genetic constraint Genetic factors that limit or bias evolutionary change; a bias in or limitation on the trajectory of evolution in response to natural selection imposed by the structure or dynamics of the genetic system. Examples of potential genetic constraints include lack of appropriate genetic variation and genetic correlations among traits arising from linkage or *pleiotropy*.

genetic correlation Correlated variation in the breeding values of two or more traits caused by the additive effects of overlapping sets of genes (*pleiotropy*) or genetic linkage.

genic capture A form of *epistasis* whereby the expression of a trait reflects genetic variation at loci that affect resource acquisition and allocation efficiency.

genomic imprinting An epigenetic mechanism whereby the degree to which a gene is expressed depends on the parent of origin.

gestation Period between conception and birth in viviparous animals.

heritability The proportion of the total variation in a trait that can be attributed to genetic variation within a given population (i.e. the ratio of genetic variance to total phenotypic variance). If the numerator is total genetic variance, this is referred to as broad-sense heritability, H^2. More commonly, in evolutionary biology, heritability is used in the narrow sense, referring to the ratio of additive genetic variance to total phenotypic variance. Narrow-sense heritability, h^2, quantifies the contribution of genetic variation to the resemblance between offspring and their parents and can be used to predict the response of traits to selection. For example, for a single trait considered in isolation, the predicted response to selection would be h^2s, where s (the *selection differential*) is a quantitative measure of the strength of selection.

homologous Refers to two or more characters (e.g. morphological structures, biochemical pathways, DNA sequences) found in different biological lineages (most commonly, different species) that are derived by evolution from the same ancestral character found in a common ancestor.

immunocompetence A term to describe the general immunological capacity of an organism without stating exactly which parts of the immune system are responsible for a good or poor immune reaction.

instar A developmental stage of arthropods, such as insects and spiders, between each molt (ecdysis) until sexual maturity is reached.

interference competition Competition over access to limited resources by direct interaction with other individuals, for example by fighting. Interference competition is a sexual-selection mechanism when members of one sex (most often males) compete over access to individuals of the opposite sex (most often females). Often large size or weapons are favored by this mechanism.

interlocus sexual conflict Interlocus sexual conflict occurs when loci expressed in one sex negatively influence fitness of the opposite sex through direct interaction.

intersexual genetic correlation Genetic correlation between traits expressed in males and traits expressed in females. Most commonly reported for sexually homologous traits but can also be estimated across traits (i.e. for non-homologous traits). Intersexual genetic correlations indicate that overlapping sets of genes influence trait expression in the two sexes and that the additive effects of these genes are similar.

intersexual inheritance The expression of genes inherited from the opposite-sex parent.

intralocus sexual conflict A deviation from the optimal genotype at a *locus* as a result of a different pattern of selection on the same locus in the opposite sex; intralocus sexual conflict is manifested in sub-optimal trait expression and reduced fitness.

isometry Geometric similarity or constant ratio; broadly defined as the proportionate change in a given variable with body size. Isometry for sexual size dimorphism occurs when the ratio of male to female body size remains constant or is independent of changes in mean size. See definition of *allometry* above.

kinetochore The protein structure in eukaryotes that assembles on the centromere and links the chromosome to microtubule polymers during mitosis and meiosis; part of chromosomes aligned during meiosis and mitosis.

lactation Process of milk production by mammary glands.

lek paradox Costly female choice of mates in the absence of direct fitness benefits for females. Derives from lek mating systems where females are presumed to choose among displaying males on the basis of male traits, but receive no direct fitness benefits from these males (e.g. nuptial gifts, protection from predators, paternal care of offspring, etc.). This is perceived as a paradox because females pay the costs of choice (i.e. time, predation risk) but apparently receive no compensating benefits. The lek paradox gave rise to the good-genes or indirect-benefits hypothesis of sexual selection through female choice.

locus A position on a chromosome occupied by a particular gene or set of allelic genes, relative to other genes (plural: loci).

lower developmental threshold (LDT) The temperature below which development ceases (base temperature Tb).

major-axis regression A form of model II regression in which the regression line is estimated by minimizing the sum of squared perpendicular distances from each observation to the fitted line. Both variables (X and Y) are assumed to be random (i.e. neither is fixed by the experimenter) and jointly distributed with a bivariate normal distribution. The major-axis regression estimates the slope of the major axis or principal axis of this bivariate distribution. Major-axis regression is most appropriate when the X and Y variables are measured on the same scale and have similar error variances, as is the case for most measures of male and female body size.

methylation Bonding of methyl groups to DNA nucleotides; methylation affects gene transcription.

ontogeny The period of development from conception to sexual maturity.

opisthosoma The posterior body part of a spider, also called the abdomen.

opportunity for selection The variance in relative fitness; sets the upper limit for the intensity of selection on any given trait.

Orbiculariae Orb-web spiders; a clade of spiders consisting of 14 families within the order Araneae, suborder Araneomorpha, characterized by construction of an orb web. Includes approximately one-third of all described spider species.

pedipalps A pair of appendages in spiders and other arachnids found just behind the jaws. In male spiders they are secondary copulatory organs and tend to be large and knob-like, resembling boxing gloves. They have to be loaded with sperm prior to copulation.

phenotypic integration The genetic, developmental, and physiological bases of the correlation and coordination of traits comprising complex organismal phenotypes; the processes by which different parts of an organism are integrated or coordinated during development to yield a functional whole.

phenotypic plasticity Variation in the phenotypic expression of a given genotype; usually refers to variation among individuals in response to variation in environmental conditions.

phylogenetic comparative methods A group of research methods that uses comparisons among related taxa to test evolutionary hypotheses. Phylogenetic hypotheses of relatedness are incorporated to identify independent evolutionary events and separate the effects of homology (similarity through common descent) from evolutionary innovation.

phylogenetic constraint A bias in or limitation on the trajectory of evolution in response to natural selection imposed by the phylogenetic history of a lineage. The genetic and developmental systems and the array of traits characteristic of any given lineage are the product of descent with modification and hence reflect the past history of the lineage. However, these phylogenetically determined characteristics also constrain the evolutionary trajectory of the lineage in response to current and future patterns of selection.

phylogeny Genealogy of a group of organisms, their evolutionary history; the set of ancestor–descendent relationships defining a given clade.

physiological time A concept of developmental time used for poikilothermic organisms whose rate of development depends on temperature. The temperature below which development cannot proceed is defined as the *lower developmental threshold*. Physiological time is measured in *day-degrees*, and developmental times are thus given as the number of day-degrees required to complete development.

pleiotropy The effect of a gene on more than one phenotypic trait.

polyandrous Most generally, refers to a mating system in which individual females may reproduce with more than one male. Usually refers to a mating system where at least some females mate with several males within a single breeding season or bout, but males tend to mate with only a single female.

polygynous Most generally, refers to a mating system in which individual males may reproduce with more than one female. Usually refers to a mating system where at least some males mate with several females within a single breeding season or bout, but females tend to mate with only a single male.

primary sexual trait A sex difference related directly to reproduction, such as gonads, components of the reproductive tract, and copulatory organs; sex differences that have evolved in response to natural selection (excluding sexual selection) for reproductive function. It excludes traits that have evolved in response to sexual selection but serve no other reproductive function.

prophase The first stage of mitotic and meiotic cell division.

prosoma The anterior body part of a spider, also called a *cephalothorax*.

protandry A form of sexual bimaturation where males mature earlier than females; for example, in many insects and spiders, the final molt to the adult stage occurs earlier in males than in females.

Rensch's rule A widespread pattern of variation in sexual size dimorphism in animals first noted by Rensch (1950). The rule is that sexual size dimorphism increases with body size in taxa where males are the larger sex but decreases with size in taxa where females are the larger sex. This pattern evolves when male body size diverges faster than female body size over evolutionarily time, and can be detected as a slope >1 in allometric regressions of log(male size) on log(female size). The rule applies primarily to species diverging from a common ancestor, but it has also been documented at various other taxonomic levels (e.g. among families, genera, subspecies, and populations), although many exceptions occur.

RTA clade A large spider clade named after the retrolateral tibial apophysis on the male copulatory organ, the *pedipalp*. Consists largely of non-web-building, active hunters with moderate or no sexual size dimorphism (exceptions to this are some highly dimorphic crab spiders).

scramble competition Competition over access to limited resources in which success is determined by the speed with which resources can be found and acquired. Scramble competition is a sexual-selection mechanism when members of one sex (most often males) compete over access to individuals of the opposite sex (most often females) through mate-searching abilities. Mate-search adapted morphologies and sensory organs are favored by sexual selection due to scramble competition.

secondary sexual trait A sex difference that has evolved in response to sexual selection. Note that, when sexual selection acts on components of the reproductive system, as in cryptic female choice, the distinction between primary and secondary sexual traits becomes blurred.

selection coefficient 1. In population genetics: the genotype-specific coefficients of Mendelian population-genetic models. 2. In quantitative genetics: the regression coefficients from regressions of relative fitness on standardized trait values.

selection differential A measure of the strength of selection on a single trait calculated as the difference between the phenotypic mean of the parents of the next generation (i.e. the selected individuals) and the overall population phenotypic mean.

selection episode Selection during a single event or life-history stage. Lifetime selection can be partitioned into selection acting during different components (episodes) of the life history.

selection gradient A standardized measure of the strength of selection defined as the covariance of relative fitness and the standardized trait value. It can be estimated as the slope of a univariate regression. For purely directional selection on single traits (univariate selection), the selection gradient is equivalent to the selection intensity. Selection gradients can also be calculated for non-linear selection (quadratic selection) and for multiple traits (multivariate selection) using multiple regression. In these cases, the term gradient can refer to either the entire matrix of regression coefficients or to the individual coefficients themselves.

selection intensity The standardized *selection differential*, calculated by dividing the selection differential by the phenotypic standard deviation.

Sertoli cells Cells of seminiferous tubules of the testes that provide nourishment to the sperm cells during spermatogenesis.

sex Commonly used as a synonym for biological *gender* (male or female) and also for sexual intercourse (coitus). In the biological literature, often used as a synonym for genetic recombination or sexual reproduction.

sex chromosome A chromosome containing at least one sex-determining *locus*, usually present in homologous pairing in the nucleus of the homogametic sex but alone or paired with a dissimilar homologue in the nucleus of the heterogametic sex (see *autosome*).

sex-linked gene A gene located on a *sex chromosome*.

sexual cannibalism Cannibalism that occurs when the female attacks and kills the male shortly before, during, or immediately after mating. Relatively common in spiders. Reverse cases, where males attack and kill females, are very rare.

sexually antagonistic selection Selection acting in opposite directions on a sexually homologous trait and its underlying loci in females and males.

sexually homologous traits Corresponding traits expressed in both sexes, such as the forelegs of females and males; sexually homologous traits are assumed to be affected by similar sets of genetic factors in both sexes (see *intersexual genetic correlation*).

Silastic® Dow Corning-registered trade name of an inert silicone rubber (polydimethylsiloxane). Small sections of Silastic tubing are commonly used to construct implants in experiments with testosterone and other steroid hormones. Silastic is commonly used in prosthetic medicine.

somatotrophic axis The endocrine growth axis in vertebrates, also called the somatotropic axis. Organ components include the hypothalamus, the pituitary, and the liver. Hypothalamic secretions of growth hormone-releasing hormone (stimulatory) and somatostatin (inhibitory) regulate secretion of growth hormone from the anterior pituitary. In the context of growth regulation, growth hormone stimulates secretion of insulin-like growth factor-1 (IGF-1). Hepatic IGF-1 becomes the primary source of circulating IGF-1 in blood plasma, and plasma IGF-1 is a mitogenic factor that stimulates growth in many target tissues. Activity of the somatotrophic axis is subject to nutritional and endocrine regulation, and the availability and activity of IGF-1 is a function of the presence of IGF-binding proteins in blood plasma.

spermatheca A sperm-storage organ found in female insects, spiders, and some other invertebrates; female spiders have two spermathecae, to each of which sperm has to be transferred separately.

sum of effective temperatures (SET) The amount of heat needed to complete a developmental stage.

syngamy Fusion of two gametes to form a single cell or fusion nucleus; fertilization.

taxon A generic term for organisms belonging to any single taxonomic entity, such as a species, genus, or family (plural: taxa).

unikont A eukaryotic cell with a single microtubule-organizing centre. Animals, Choanozoa (protists), Fungi, and Amoebozoa are thought to have evolved from a common unikont ancestor and these groups are known as unikonts.

univoltine Having one generation per year.

viability The capability to live and develop normally.

vulnerability An increased susceptibility to hazards that manifests itself in higher mortality or other aspects of decreased physical performance, such as growth or *immunocompetence*.

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Note: emboldened page numbers indicate terms appearing in the glossary.