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ORIGINAL ARTICLE

The evolution of simultaneous progressive provisioning revisited: extending the model to overlapping generations

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Abstract

"Simultaneous progressive provisioners" feed their offspring gradually as they develop—and typically feed more than one offspring simultaneously (SIM) at a time. In contrast, "sequential mass provisioners" supply offspring one after another (SEQ). Utilizing individual-based simulations, Field (Nature 404:869–871, 2005) compared the lifetime reproductive success of these strategies in different scenarios. Accordingly, SEQ should evolve in the majority of cases—SIM only has an evolutionary benefit if offspring depend on their mothers' protection until adulthood even past the provisioning period. However, this is only one potential explanation for the evolution of SIM. Here, we present an alternative mechanism for solitary individuals with overlapping generations. We propose an analytical model (comprising Field's former approach) utilizing growth rate instead of lifetime reproductive success as a measure of fitness. Our model shows that multiplicative geometric effects on fitness would typically compensate for the demographic disadvantages of SIM (due to prolonged dependency) and consequently support the evolution of SIM over SEQ for a wide range of life history parameters. The optimal level of SIM (i.e., the optimal number of eggs laid simultaneously) is determined by offspring development time, survival rates, and foraging efficiency of the mother. Only extreme values of these demographic parameters would favor a transition to SEQ behavior. Our model provides a coherent explanation of selective favoring of SIM over SEQ that may also contribute to understanding why SIM is the dominant strategy among social insect species.

Significance statement

Workers in social insects typically feed several offspring simultaneously while solitary species with parental care—apart from a few exceptions—provision brood cells one after another. The provisioning pattern might play a prominent role in the evolutionary pathway to higher social organization. Based on a novel theoretical approach, we show that geometric growth benefits increase selection pressure towards simultaneous progressive provisioning in species with generation overlap. Such geometric benefits may specifically emerge in seasonal eusocial species. This result alters former assessment of causal mechanisms and extends findings focusing on solitary insects. It adds a new and reasonable explanation for the dominance of simultaneous provisioning among social species.

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Introduction

The reproductive strategy of any organism is a core determinant of its fitness (Roff 2001)—and we observe huge variation in reproductive strategies across species. Whether parents support their offspring or not is one of the large discrepancies we can see among species. Parental care may not be widespread

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among insects in general—but it is typical in groups like solitary bees where larvae depend on a parental supply with critical food resources and it is even the rule in social insects (where brood care is often taken over by older siblings). In this case, "sequential mass" (SEQ) and "simultaneous progressive provisioning" (SIM) are two alternative strategies to provide food for offspring. The two strategies differ in the temporal patterns of egg laying and emergence of new adults: Sequential mass provisioners like pollen-feeding solitary bees typically seal each egg into an own brood cell stocked with all the food the offspring requires for reaching maturity (e.g., Bosch et al. 2001). Provisioning of a brood cell typically requires just a single or few days (much shorter than the total time needed to complete development from egg to eclosion) and has to be completed before the next egg may be laid. Progressive provisioners, in contrast, feed their offspring gradually as they develop and often provision more than one offspring at the same time. Consequently, the food provisioning period of each offspring is spread over a longer period than with SEQ. The progressively provisioning potter wasp *Synagris cornuta*, for example, typically feeds its offspring for 1 month, but occasionally this phase is extended to more than 3 months (Malyshev 1968). A principal difference between the two strategies is (i) that with SEQ offspring, dependency on food provisioning is limited to a brief period and (ii) that with SEQ, larvae will complete development sequentially whereas under SIM, several offspring may emerge at the same time.

Field (2005) already provided a comprehensive characterization of species groups as mass or progressive provisioners based on extensive reviews about bees (Michener 2000), sphecid wasps (Bohart and Menke 1976), and vespid wasps (Cowan 1991; Hunt 1999). Most solitary wasps and bees, as well as eusocial species of sweat bees (Halictidae), carpenter bees (Xylocopidae), and stingless bees (Meliponidae) are mass provisioners. Progressive provisioners on the other hand include a small fraction of solitary wasps in several genera, but most or all eusocial species among allodapine bees (Allodapinae), bumblebees (Bombinae), honeybees (Apinae), ants, and all eusocial vespid wasps (hover wasps: Stenogastrinae; paper wasps: Polistinae; yellowjackets: Vespinae). These species are often characterized by large ratios of the number of provisioning individuals to the number of feeding larvae, specifically at the beginning of the nest cycle (Spradbery 1973; Duchateau and Velthuis 1988; Mead et al. 1994; Reeve 1991) indicating that several offspring are provisioned simultaneously. In highly eusocial *Apis* species, the ratio might be above (e.g., *Apis mellifera*, *Apis cerana* (Dyer and Seeley 1991)) or below 1 (*Apis florea* (Seeley et al. 1982)).

SIM has been seen as key factor in the context of the evolution of sociality in insects. Wilson (2008) considered it—besides "fidelity to the nest, a preexisting disposition toward dominance behavior, and the choice of tasks according to opportunity"—as a preadaption for the final step in the evolution of eusociality. Indeed, the dominance of social species compared to a few solitary species is a striking pattern among the simultaneous provisioners. However, there are also eusocial species like halictid bees that are not simultaneous progressive provisioners (Michener 2000) and the temporal sequence in which SIM and eusociality evolved is not known in general (but see Hunt (1999)). Herre and Wcislo (2011) challenged the relevance of progressive provisioning for the evolution of eusociality by pointing to groups of species with eusociality but without progressive provisioning.

The only theoretical study about expected fitness consequences of different modes of provisioning was presented by Field in 2005. Field focused, however, on solitary species. As a consequence, insight into the general reasons responsible for the evolution of these diverging provisioning patterns is limited. Using individual-based simulations, Field (2005) analyzed the influence of provisioning patterns on the lifetime reproductive success of mothers. Under the assumption that immature offspring become independent as soon as they are fully provisioned, the model predicts "that the average mother always produces fewer offspring under simultaneous progressive provisioning than under mass provisioning." Without any further assumptions, sequential mass provisioning is thus always the superior strategy. This particularly holds for species with high mortality risk of adults, because of the substantial risk that the mother dies before the dependent offspring are fully supplied with food resources; Field's analysis clearly emphasizes the inherent "demographic disadvantage" of progressive provisioning. Progressive provisioning of several eggs at the same time prolongs the provisioning period for each egg compared to the case of sequential provisioning. It thus increases the risk that a mother dies before the egg is fully provisioned, resulting in the death of any affected brood together with her. Overall, the clear benefit of SEQ is that offspring are exposed to the shortest possible period with a risk of their mother's dying. However, we also have to concede that SIM allows producing offspring at a faster temporal rate as long as the parental provisioning rate remains above the larval consumption rate.

Field (2005) proposed that further mechanisms may support evolution of SIM in spite of the disadvantage explained above. He suggests, for example, that SIM may result in increased offspring survival and in fewer resources wasted into offspring that fail (Cowan 1991; Field and Brace 2004). In particular, Field argues that offspring may depend on mothers not just for food provisioning but also for protection, e.g., against predators and parasites, or nest cleaning beyond the phase of provisioning and included such added dependency in a modified version of the model (model 2 in Field (2005)). In this second model, offspring become independent only at adulthood and are exposed to a certain mortality risk if their

mother dies earlier. This assumption of "strong dependency" neutralizes the demographic benefit of sequential mass provisioning or may even reverse it: If dependence on such maternal support is very high (i.e., mortality risk is very large in case of mother's death), SIM may allow producing more offspring in a given time span. Consequently, Field's (2005) model demonstrates that SIM may become the superior strategy whenever the mortality risk for unattended (but fully provisioned) offspring is sufficiently high.

Field (2005) thus identifies continued offspring dependency on the mother's presence beyond the provisioning phase as a sufficient precondition for the evolution of SIM. Referring to vespid wasps as an example for an eusocial life cycle, he concludes that simultaneous progressive provisioning should evolve most easily in species with exposed nests, in danger of predation and parasitism, as well as extreme weather conditions (e.g., Wilson (1971), Chadab (1979), Jeanne (1979), Queller (1994), Eickwort et al. (1996), Kukuk et al. (1998), and Schatz and Wcislo (1999)). However, the model also predicts that SIM should only evolve if this dependency is rather strong: According to Field's simulations, the mortality risk of fully provisioned offspring in case of mother's death must be larger than 0.7 for the specific combination of life history traits given by Field (2005, Fig. 8, see also our Fig. 2) to provide at least a slight advantage of SIM over SEQ. Generalization of this result requires further calculations (see Fig. 3 here). Moreover, while the offspring's dependency on their mothers' (=foundresses') survival might in fact be a condition that favors simultaneous provisioning during the nest founding phase, its relevance necessarily drops when the first workers emerge and substitute the mother (and each other) in foraging and brood care. Thus, the suggestion that strong dependency caused the evolution of SIM in eusocial vespid wasps is not fully convincing. Similarly, the high numbers of simultaneous provisioners among social species with well-hidden or well-protected nests, e.g., like those of bumblebees, can hardly be explained with this argumentation. This poses the question whether other mechanisms may be more relevant when explaining the evolution of SIM and specifically the dominance of social species among the simultaneous provisioners.

In his simulations, Field (2005) uses lifetime reproductive success as measure of fitness to compare the different strategies. This is a common approach in behavioral ecology. However, this is an inadequate measure of fitness when offspring are allowed to reproduce after maturation—as it is the case for species with multiple, overlapping generations per season or when workers stay in the nest and actively enhance the fitness of their mother—as temporal variance and generation time significantly contribute to the long-term fitness of a strategy. In this case, the specific rate of increase (r) or the net reproductive rate (λ) is the most commonly used measure of fitness in life history studies (Benton and Grant 2000). To justify the use of lifetime reproductive success as a measure of fitness, it must be assumed that individual number is constant over time, which is hardly the case in annual species or species underlying strong seasonal fluctuations.

In the following, we will develop an analytical, demographic model for the life cycle of food provisioning insects. Our approach encompasses both individual-based models presented by Field (2005). Comparing lifetime reproductive success (R) and net reproductive rates (λ) of both SIM and SEQ, we will show that accounting for overlapping generations with offspring reproduction significantly increases the relative fitness of SIM and strongly alters the impact of life history traits under consideration. Whereas Richards and Richards (1951) in their comprehensive study on South American social wasps stated "It is difficult, therefore, to suggest any clear advantage of the third method [=SIM]," our results demonstrate that SIM is the better strategy under a broad spectrum of different conditions; particularly, strong dependency is not needed to explain the evolutionary success of SIM. Note that our approach considers a group of insects which can be interpreted both as a population of solitary organisms (as in Field 2005) and—with restrictions (see "Discussion" section)—as the individuals constituting the worker caste in social species during the ergonomic colony phase (Wilson 1971).

Model

We consider the entire life cycle of an individual from egg to death. Egg and larval development require a certain minimum time D_L. Fully developed offspring eclose after an additional pupal phase of time span D_P. To successfully complete the larval phase, individuals need a specific amount of food f. We assume that mothers collect food at constant rate (normalized to $\rho = 1$) and would thus need f time steps to fully provision a brood cell with a single egg. Throughout, mothers survive with rate s. Mothers lay b eggs simultaneously (=clutch size) and in discrete intervals as explained below. The number of eggs b represents the parental strategy to be analyzed: SEQ is characterized by $b = 1$ and SIM by $b > 1$.

In analogy with the model of Field (2005), we assume that (1) b is constant over time and (2) that new eggs are only laid once all older eggs are completely provisioned. Consequently, the time needed to provision b eggs defines the time interval between discrete egg laying events: $\Delta t = b \cdot f$. Like Field, we also assume that (3) collected resources are distributed equally between eggs and (4) that there is no lower starvation threshold, i.e., larvae will not die when provisioning rate decreases below a critical value. Note, however, that larval development time can become longer than the minimum duration D_L if a batch of eggs is not fully provisioned within this time span

(i.e., if $b \cdot f > D_L$). Thus, total development time D (including larval and pupal phases) is

$$D = max(D_L, b \cdot f) + D_P \tag{1}$$

Note that provisioning only happens during the larval phase.

Discrete generations without offspring reproduction

Field (2005) used an individual-based simulation approach to calculate mean lifetime reproductive success of a mother with a specific provisioning strategy b. Lifetime reproductive success (R) is calculated (Roff 2001) as

$$R = \sum_{i \in \mathbb{N}} m(i)l(i) \tag{2}$$

with fecundity $m(i)$ (i.e., the number of eggs laid at laying bout i) and survival $l(i)$ (i.e., the mother's probability to survive until bout i) for any oviposition event i. To calculate fecundity $m(i)$ and survival $l(i)$ from the model parameters, the life cycles can be considered to be partitioned by any fixed life history event, e.g., the onset of egg laying, in each generation of parents as well as in each generation of offspring. To include the total effect of mother's survival rate s (via individual mortality *and* offspring dependency) in the survival term $l(i)$ (compare Eqs. (4a) and (4b) to Eq. (3) below), we consider the egg to egg cycle (see Fig. 1). For the sake of simplicity, we assume that i, D_L, D_P, and D are natural numbers with time measured in days.

Providing explicit terms for fecundity and survival will lead to a compact analytical form of the model. Fecundity $m(i)$ and survival $l(i)$ can easily be derived from the verbal description above. Fecundity $m(i)$, i.e., the number of eggs laid, is constant for each bout

$$m(i) = b \tag{3}$$

Thus, Eq. (2) simplifies to $R = b\sum_{i \in \mathbb{N}} l(i)$. We enumerate bouts with index $i \in \mathbb{N}$ with $i = 1$ indicating the first egg laying event of an individual, which itself has finished development and has eclosed just before.

Figure 1 illustrates the main considerations for deriving survival $l(i)$. Before maturity, an individual has to survive its own developmental period of duration D (see Eq. (1)). If we assume—as in model 1 in Field (2005)—that offspring become independent of their mother as soon as they are fully provisioned, their probability of surviving to adulthood ($l(1)$) is equal to the probability of a mother to stay alive for a complete provisioning period: $l(1) = s^{f \cdot b}$. Note that this probability is independent of the length of time (D) needed to

become adult. Once matured, individuals will start egg laying with bouts separated by a time interval of $\Delta t = b \cdot f$ and accompanied by a bout to bout survival of $s^{f \cdot b}$. Thus, the probability of a mother surviving to the ith egg laying bout (each providing $b \cdot f$ offspring) is

$$l(i) = s^{i \cdot f \cdot b} \tag{4a}$$

and $R = b\sum_{i \in \mathbb{N}} s^{i \cdot f \cdot b}$. Field proposed a second model assuming that offspring depend on their parents not only during provisioning but until they become fully mature. With this prolonged dependency of offspring on their mother, the probability of offspring to survive to adulthood may decrease severely. We assume that fully provisioned offspring will die with probability μ if their mother dies before the offspring become mature. For a more intuitive presentation of the results, we use offspring mortality μ to express the level of dependency instead of Field's survival probability $h = 1 - \mu$. Only a fraction $q = s^{D - bf}$ of mothers will survive the final period of development after provisioning (lasting for $D - bf$ time steps and eventually including part of the larval period). Overall survival has now two components: (i) Offspring with mothers that survive until offspring are mature (fraction q) and (ii) those that survive although their mother died in the developmental phase but after provisioning is completed (fraction $(1 - q)(1 - \mu)$). Thus, Eq. (4a) can be generalized to

$$l(i) = (q + (1-q)(1-\mu))s^{i \cdot f \cdot b} \tag{4b}$$

The extreme cases of $\mu = 0$ (weak dependency) and $\mu = 1$ (strong dependency) are sketched in Fig. 1. Using Eqs. (3) and (4b), the terms in Eq. (2) form a convergent geometric series (Abramowitz and Stegun 1965). Conveniently, we do not need numerical calculations, but can determine $R = b\sum_{i \in \mathbb{N}}(q + (1 - q)(1 - \mu))s^{i \cdot f \cdot b}$ analytically as

$$R = b(q + (1-q)(1-\mu))\frac{s^{f \cdot b}}{1-s^{f \cdot b}} \tag{5}$$

In this generalized model, weak dependency sensu Field's model 2 corresponds to $\mu = 0$ and strong dependency to $\mu = 1$.

Overlapping generations with offspring reproduction

Next, we extend Field's approach to include generation overlap in the model. If we assume exponential growth, i.e., that offspring start to forage and reproduce right after eclosion, Field's measure of fitness (lifetime reproductive success of a mother) is not suitable for comparing the evolutionary value of different strategies. Instead, we have to calculate the exponential growth rates λ for different provisioning strategies.

Fig. 1 Schematic representation of the life cycle of an individual starting with the onset of egg development and ending with its death (for the case $D_L > b \cdot f$). *Filled dots* on the time axis denote life history events which correspond to a specific value of the time counter i; see text after Eq. (2). *Open dots* represent events that are implicitly considered in the calculations. Time intervals between events are given above the time axis. The *two boxes* show the day to day survival probability for the two extreme cases of weak ($\mu = 0$) and strong dependency ($\mu = 1$)
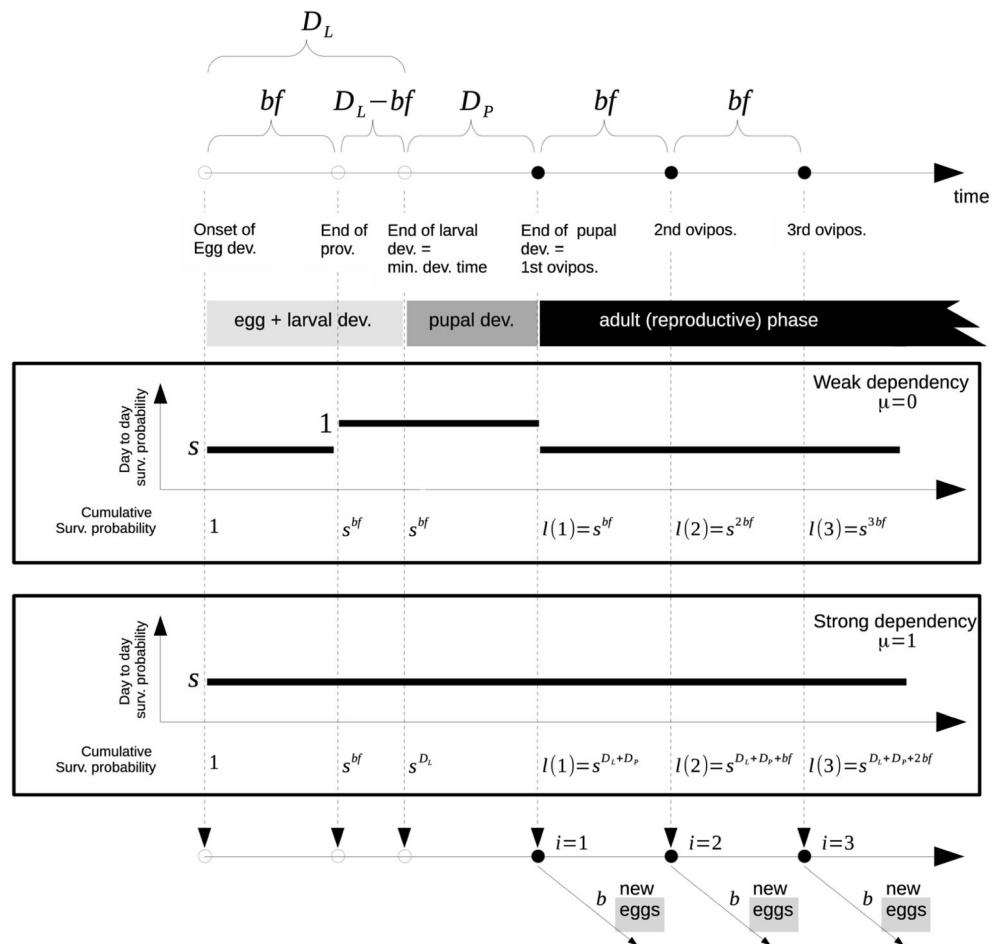
This can easily be done via the corresponding Leslie matrix or Euler-Lotka equation (Roff 2001)

$$1 = \sum_{i \in \mathbb{N}} \lambda^{t(i)} m(i) l(i) \qquad (6)$$

which implicitly defines the growth rate λ. In the context of offspring reproduction, the timing of egg laying (events) becomes crucial. To solve Eq. (6) for λ, we have to account for each moment in time $t(i)$ at which eggs are possibly laid. The first event ($i = 1$) occurs after time D when the mother's development is complete. It is followed by further reproductive bouts separated by a period equal to the time span $\Delta t = f \cdot b$ required to fully provision b eggs. Thus, the strategy-dependent temporal sequence of reproductive events follows:

$$t(i) = D + 1 + (i-1) \cdot f \cdot b \qquad (7)$$

Note that we assume that a female becomes reproductive when D days of her own development have fully passed, i.e.,

on day $D + 1$. Using Eqs. (3), (4b), and (7), the Euler-Lotka equation (Eq. (6)) can be written as

$$(q + (1-q)(1-\mu))b\lambda^{D+1} + \lambda^{bf} = s^{-bf} \qquad (8)$$

This equation must be solved for λ: For specific choices of the model parameters, this may be done analytically; otherwise, it has to be done numerically. Either way, the optimum value of b can be found by solving Eq. (8) for a range of clutch size values (see Table 1) followed by a numerical search for the maximum of growth rate λ. For this purpose, we utilized the function optim provided by the statistical software R (R Core Team 2014).

Numerical calculations for Figs. 2 and 3 are based on similar parameter ranges as chosen (and justified) by Field (see Table 1). Survival rates of mothers vary from 0.91/day to 0.99/day corresponding to mean life spans of approx. 10 to 100 days. These values cover empirical estimates for nonsocial digger wasps (Freeman 1980; Toft 1987) as well as for polistine (Queller 1996) and stenogastrine wasps (Field et al.

Table 1   Model parameters and corresponding range of analyzed values

Number of simultaneously laid eggs	b	1 … 30
Minimum duration of larval phase	D_L	5, 10, 15, 20, 25
Duration of pupal phase	D_P	0 … 30
Number of foraging days	f	1, 2, 3
Survival rate of mothers	s	0.91, 0.93, 0.95, 0.97, 0.99
Fraction of offspring dying due to the loss a mother before maturation	μ	0 (weak dependency), 0.4, 0.6, 0.8, 1 (strong dependency)

2000; Strohm and Marliani 2002). The level of offspring dependency covers the entire range of possible values from 0 to 1. Minimum larval development time and pupal development time vary between 0 and 30 days and comprise typical values compiled by Yanega (1997) for halictids and by Strassmann and Orgren (1983) for paper wasps.

No data were recorded for this theoretical study.

Results

The comparison of our model taking into account demographic aspects, namely overlapping generations and offspring reproduction (Eq. (8)), with Field's (2005) approach of discrete generations (Eq. (5)) clearly demonstrates the pronounced multiplicative effect of offspring reproduction on the evolutionary value of different strategies. Offspring reproduction leads to geometric growth similar to compound interest affecting the savings on a bank account.

Discrete generations (Field's model)

Equation (5) synthesizes Field's two models, and the mathematical determination of maximum net growth rates (R) confirms his simulation results (for formal proofs, see Propositions 1 and 2 in the Appendix): For the case of weak dependency ($\mu = 0$), lifetime reproductive success (R) is maximized for $b_{weak} = 1$. That is, whenever offspring dependency on mothers ends as soon as they are fully provisioned, SEQ ($b = 1$) always yields higher reproductive success (R) than SIM ($b > 1$). The opposite holds for the case of strong dependency ($\mu = 1$): If offspring are fully dependent on their mothers until they become fully mature, maximum lifetime reproductive success is achieved by SIM and optimal clutch size $b_{strong} = D_L/f > 1$ is determined by minimum larval development time and the number of days (f) required for provisioning a single larva. Thus, SIM always maximizes R for strong dependency and never for weak dependency. Further, the optimal number of eggs is completely independent of the
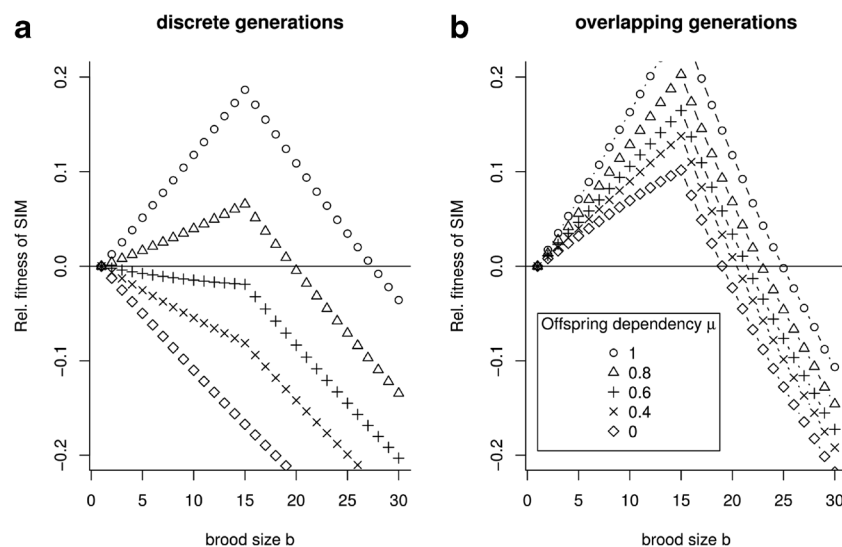

Fig. 2 Relative fitness gain by SIM compared to SEQ in dependence of clutch size b and offspring dependency μ. Results are shown for **a** the case that offspring do not reproduce during the lifetime of their mothers (discrete generations) and fitness is measured as lifetime reproductive success R (relative fitness gain = $(R(b) − R(1))/R(1)$) and **b** for the case that offspring reproduce as soon as they become mature (overlapping generations) and fitness is measured as the net reproductive rate λ (relative fitness gain = $(\lambda(b) − \lambda(1))/\lambda(1)$). Results of numerical solution of Eq. (5) in **a** and Eq. (8) in **b** for larval development time $D_L = 15$, pupal development time $D_P = 15$, mother's survival rate $s = 0.975$, food requirement $f = 1$, and offspring dependency $\mu = 0$, 0.4, 0.6, 0.8, and 1.0
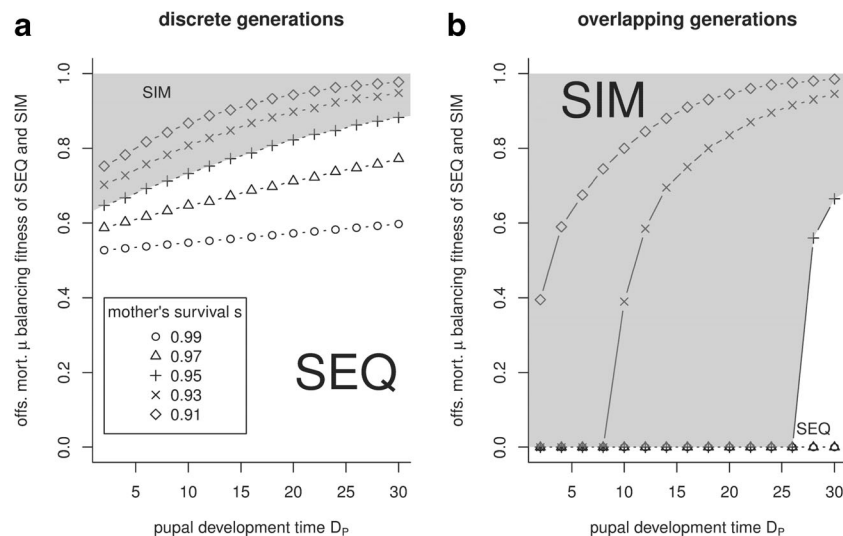
Fig. 3 Dependence of the critical offspring dependency μ_{crit} balancing fitness of sequential mass provisioning (SEQ) and simultaneous progressive provisioning (SIM) on pupal development time D_P. Results are shown for **a** the case that offspring do not reproduce during the lifetime of their mothers (discrete generations) and fitness is measured as lifetime reproductive success R ($R(\mu_{crit}, b_{opt}) = R(\mu_{crit}, 1)$) and for **b** the case that offspring reproduce as soon as they become mature (overlapping

generations) and fitness is measured as the net reproductive rate λ ($\lambda(\mu_{crit}, b_{opt}) = \lambda(\mu_{crit}, 1)$). Results of numerical solution of Eq. (5) in **a** and Eq. (8) in **b** for larval development time $D_L = 15$, different survival rates of mothers $s = 0.91, 0.93, 0.95, 0.97$, and 0.99 and food requirement $f = 1$. *Gray areas* indicate parameter combinations which lead to the evolution of SIM for mother's survival rate s = 0.95

degree of dependency on mothers. The latter only defines whether maximum fitness is reached for $b = 1$ or $b = D_L/f$.

Figure 2a shows the relative fitness gain of SIM compared to SEQ for a range of clutch sizes b (compare with Fig. 8 in Field (2005)). As long as offspring dependency (μ) is sufficiently high, SIM ($b_{strong} = D_L/f$) is favored. Below a critical value of offspring dependency μ_{crit} SEQ ($b_{weak} = 1$) yields a higher reproductive success than SIM. Note that obviously both strategies will perform better as μ becomes smaller; however, as brood remain longer in the state "fully provisioned but not adult" under SEQ than under SIM, the proportional benefit of a reduction in μ is larger for SEQ than SIM, thus shifting the benefits in favor of SEQ. No intermediate optimal values of clutch size, i.e., $1 < b < D_L/f$ can be observed (see also proof in Appendix). It is obvious that μ_{crit} decreases with increasing values of mothers' survival s. The analytical approach allows to calculate the exact limit value of μ_{crit} for $s \rightarrow 1$ which is one half for any combination of parameters (see Appendix, Corollary 5). This demonstrates that there is a hard lower limit for offspring dependency necessary for the evolution of SIM.

Overlapping generations

Taking account for the fact that offspring may start reproduction as soon as they become mature (overlapping generations) and thus considering net reproductive rate as a measure of fitness greatly increases the evolutionary benefits of SIM.

While in the model with discrete (non-overlapping) generations a substantial level of dependency ($\mu > 0.5$) is needed for SIM to become the "better" strategy (Fig. 2a), SEQ is now out-competed by SIM throughout the entire range of $0 \leqslant \mu \leqslant 1$ (Fig. 2b). That is, for any offspring dependency, the net rate of increase λ is maximized by SIM with $b > 1$ and the benefit of SIM increases with increasing offspring dependency μ.

For the specific set of model parameters used in Fig. 2 (particularly for the high survival rate of mothers $s = 0.975$ from Fig. 8 in Field (2005)), SIM is always the strategy that maximizes the net reproductive rate λ. However, this does not necessarily hold for all parameter combinations. As the relative benefit of SIM vs. SEQ depends on offspring dependency μ, we may determine a critical degree of μ_{crit} characterizing the fitness equivalence of SIM and SEQ. Thus, to assess the general impact of all model parameters on both model versions (maximizing lifetime reproductive success R or maximizing net reproductive rate λ), we calculate μ_{crit} for a broad range of model parameters. In the case of maximizing lifetime reproductive success R, this can be done analytically (see Corollary 4 in the Appendix), and for the model including offspring reproduction (maximizing λ), we did so by numerical solution. Figure 3 illustrates the influence of the length of pupal development time D_P and the survival rate of mothers s on the critical dependency μ_{crit}.

For both models, μ_{crit} increases with increasing pupal development time D_P and increasing mortality rates of mothers (Fig. 3). However, the range of parameter values that favor the

evolution of SIM is considerably increased with overlapping generation (Fig. 3b). With vanishing time for pupal development ($D_P = 0$) and if mothers die at a rate of 5% per day (mean lifetime = 20 days), SIM is the favorable strategy only for $\mu_{crit} > 0.65$ without offspring reproduction, while no dependency $\mu_{crit} = 0$ is needed if offspring reproduction is accounted for. For a more realistic choice of developmental time $D_P = 20$, severe offspring dependency $\mu_{crit} > 0.85$ is needed in the model with discrete generations while the model with overlapping generations still predicts SIM even with weak dependency ($\mu_{crit} = 0$), i.e., SIM can evolve even if all offspring survive the death of their mother. Low offspring dependency $\mu_{crit} < 0.6$ prevents any threshold effect of mother's survival rate in the discrete generation model and will always promote SEQ. In contrast, SIM is maintained in the model with overlapping generations until pupal development exceeds a critical value (e.g., 26 days for a mother's survival rate of 0.95 1/day). Both sensitivity to parameter variation (line spacing in Fig. 3) and the degree of parameter interactions (line curvature in Fig. 3) are more pronounced in the model with overlapping generations.

For the sake of completeness, we also tested the influence of larval development D_L and larval food requirement f for the selection benefit of SEQ over SIM for both model variants, that with and that without generation overlap. As these parameters do not qualitatively change the results in both model approaches, we do not show detailed results but just present their general tendency of influence (Table 2). Shorter larval development time will always decrease the critical value of offspring dependency and favor SIM. Increasing food demands on the other hand has the opposite effect. Both effects are rather weak for discrete generations but are more pronounced if generations overlap. For mechanistic explanation, see "Discussion" section.

Discussion

Our analytical model versions that utilize either lifetime reproductive success or growth rate as measures of fitness allow extending Field's (2005) simulations that were realized for just a restricted set of values from the entire parameter space. Field's model (with discrete generations) predicts that SIM may only evolve if offspring are highly dependent on their mothers even after they are fully provisioned. Here we show that overlapping generations with offspring reproduction significantly increases the relative benefit of SIM in comparison to SEQ: The multiplicative geometric effect in fitness typically compensates for the demographic disadvantage of SIM (due to prolonged dependency) and consequently supports the evolution of SIM over SEQ for a wide range of life history parameters. The optimal number of eggs laid simultaneously is determined by offspring development time, survival rates,

Table 2 Impact of different model parameters on whether SIM is favored over SEQ. Substantial quantitative differences of the strength of tendencies between the model with discrete generations and the model with generation overlap are not shown here but in Figs. 2 and 3

Increasing ...			... favors
mother's survival rate	s		SIM
minimum larval development time	D_L		SEQ
pupal development time	D_P		SEQ
food required per offspring	f		SEQ
offspring dependency	μ		SIM

and foraging efficiency of the mother. Only extreme values of these demographic parameters would favor a transition to SEQ behavior where $b_{opt} = 1$.

Mechanisms

SIM entails a fundamental fitness disadvantage because it prolongs the provisioning period for each egg and thus increases the risk that a mother dies before an egg is fully provisioned; in this case, all affected brood will perish with her. Expressed differently, the expected mean loss of resources provided to offspring that ultimately do not complete development (due to the death of a mother) increases with increasing clutch size b. This disadvantage can be balanced, however, by a demographic benefit if offspring start to reproduce themselves (species with generation overlap, see also below) or support the mother in raising the next generation (social species, see also below) when they become adults. This benefit comes about because, under SIM, offspring emerge on average earlier. Note that larval development is not extended by SIM, compared to SEQ, as several offspring can develop in parallel. The earlier an offspring emerges within a limited season, however, the more (earlier) it can contribute to the overall reproductive rate. This multiplicative geometric effect more than compensates the fitness loss due to prolonged provisioning under most conditions. The beneficial effect of offspring reproduction with a SIM strategy would be reduced whenever clutch size becomes so large as to prolong the larval developmental and thus total developmental time. This does not happen, however, as long as clutch size does not exceed the threshold value of D_L/f, i.e., the maximum number of eggs that can just be provisioned during a single larval development period without prolonging development. Consequently, the transition between $b_{opt} = 1$ (SEQ) and $b_{opt} = D_L/f$ (SIM) is typically dichotomous with respect to all model parameters (for formal proof, see Appendix) in the model version without generation overlap. With generation overlap, a very restricted range of parameter values exists where intermediate values $1 \leq b_{opt} \leq D_L/f$ can be optimal (not shown in detail).

In Fig. 3a, b, the entire risk that a mother dies during development increases from lines at the bottom to those at the top (declining survival rates of mothers). Thereby, the risk of

failed investment increases and a higher proportion of larvae dies before reaching the pupal stage. This always favors SEQ and explains the extension of the SEQ area from left to right and with increasing maternal mortality rate. Consequently, if the mother's mortality rate is rather high and offspring dependency rather low, geometric effects are not compensating the waste of provisions and the optimal strategy remains SEQ.

Less obviously, we also observe that SEQ is favored if the length of the pupal phase (D_P) is prolonged even though the fate of the brood in this period is—as such—not different between SEQ and SIM. In fact, due to simultaneous provisioning, more larvae will complete development within a single period of minimum larval development time, whereas under SEQ, only the first larva will complete development within that period. Whether SEQ or SIM is the better strategy depends on the balance between this advantage of SIM over SEQ and the added risk carried in the prolonged provisioning phase. Consequently, a prolongation of the pupal phase reduces the proportional effect of earlier completion of several larvae under SIM and thus shifts the balance in favor of SEQ.

Scope of the model

Our approach focuses on the growth rate λ as a proxy for fitness. This is justified only in situations when this is a suitable measure of fitness. This is true for continuous reproduction when strong environmental fluctuations favor r-selection (Engen and Sæther, 2017, and references there). It also might play a role for multivoltine solitary species in seasonal environments as long as geometric growth dominates the population dynamics early in the season. Under such conditions, details of life history may not matter for the argumentation in favor of SIM to apply. Geometric effects may occur in seasonal species with generation overlap when winter sets back population size to a much smaller level in each spring. It may also apply to annual social insects where colonies start with just a single foundress, but even in seasonal but perennial colonies where colonies lose a large proportion of their worker force during winter. Indeed, even in tropical systems, such effects may emerge if colonies would frequently lose a large proportion of workers to predators or other disturbances, maintaining worker number at levels below the environment's carrying capacity (more details below). Further, as growth limitations (due to competition) may set in later in the season, we at least speculate that transitions from a SIM to a SEQ strategy may occur over the course of the season, but it is hard to imagine that an inverse transition could ever be adaptive.

Note that our goal here is not to represent a specific life cycle, but to illustrate the geometric growth-effect in reproduction that favors SIM. Thus, even though tailored to a solitary life cycle, we can—with some restrictions—also apply the model to the ergonomic phase in the development of eusocial insect colonies (sensu Wilson 1971) when colony growth in terms of worker number substantially contributes to lifetime reproductive success of the colony, respectively the queen. The relationship between the number of workers at the end of ergonomic growth and sexual productivity (cumulative number of sexuals) can be inferred from the general model of colony dynamics proposed by Macevicz and Oster (1976) and included in the textbook by Oster and Wilson (1978). As soon as investment into workers is terminated in a typical bang-bang strategy (but see, e.g., Greene 1984), all resources collected by the workers are exclusively devoted to sexuals and the final number of sexuals as a simple measure of fitness can be calculated by integration over the exponentially declining number of workers. Thus, worker number at the beginning of the phase of sexual production affects the cumulative outcome in sexual number just linearly: doubling the number of workers at the beginning of sexual production would double the total number of sexuals produced (for detailed analysis including sexual mortality and formal proof, see Appendix).

The ergonomic phase of colony growth is comparable to reproduction with overlapping generations in solitary organisms if we acknowledge that the individuals under consideration are now the brood-caring workers of the colony. However, we have to be more careful in applying the model in a social context as we will now explain in detail.

(a) Egg laying and foraging: While in solitary species foraging and oviposition are performed by the same individual, egg laying is usually monopolized by the queen(s) in social colonies; yet queens often do not participate in brood care anymore. This separation of roles in the colony does not affect the applicability of the model, however. It does not matter whether the mother herself cares for the brood, or supporting workers. Whenever the term "mother" in the model section refers to an individual that provides food or shelter for the brood, it thus can be replaced by the more general concept of individual(s), not necessarily related, performing these tasks.

(b) In social insects, we have to consider optimal clutch size as the predicted per-worker number of larvae that are provisioned simultaneously. For SEQ, this ratio can even fall below 1 if several workers provision the same brood cell (see, e.g., Batra (1964)). If egg laying is monopolized by a queen, the optimal total number of eggs to be laid simultaneously by her would consequently be defined by the product of optimal clutch size per worker and worker number. If this value surpasses the, e.g., physiologically limited maximum egg laying rate of a queen, one might observe oviposition also before and after the optimal moments predicted by the model without limitation in egg laying rate, or even continuous egg production (as typically in *Polistes*) instead of the pulsed temporal pattern expected according to the model (and observed, e.g., after nest founding in bumble bees, see

Beekman et al. 1998, or in swarm-founding Polistinae, Jeanne 1991).

(c) In Field's (2005) original model, offspring dependency μ has a dominant effect on whether SEQ or SIM is the favored strategy. In particular, SIM is selected for only if offspring dependency is high. Note, however, that offspring dependency is not the probability of the loss of a caring individual but the broods' mortality risk resulting from such loss. This mechanism is not fundamentally different between solitary and social species. With more elaborate nest protection, the level of offspring dependency might typically be lower in social compared to solitary insects. In general, this would favor SEQ instead of SIM in the approach without generation overlap, but this effect is out-weighted by geometric increase in the extended version of the model.

(d) In the social context, mother's survival s reflects the probability of the presence of a caring individual, both during and after provisioning. In social insects, a single brood cell or egg is not necessarily attended by a specific individual: Workers lost can be substituted by others and parameter s should be quite high. Nevertheless, massive simultaneous loss of workers or bad environmental conditions, which reduce food availability and prolong development (Cartar and Dill 1991), may have the consequence that brood is eventually under-supplied and starves or dies (with risk μ, see paragraph (c) above). In Field's model, a minimum offspring dependency of 0.5 is required to favor SIM, even with the smallest risk of the mother dying. This restriction for solitary species is almost absent when considering overlapping generations.

(e) A typical annual colony cycle consists of a phase of ergonomic growth followed by sexual production. Similar to the solitary case with overlapping generations, our main argument for the benefits of geometric growth thus only applies during the period of worker production, as sexuals typically do not contribute to brood care. With the onset of sexual production, the model would consequently predict SEQ, except if the mechanism of strong dependency would become dominant. However, as pointed out before, dependency should in fact be weak in social insects, specifically when maximum colony size is reached at the end of the season. It would thus be interesting to screen empirical data for possible changes in provisioning behavior once production of sexuals is initiated.

In this first formal analysis of the provisioning patterns in social insects, we have ignored several other mechanisms that characterize the social life cycle and might affect the optimal provisioning strategy. Examples are queen-worker conflict, food storage in the nest, or strongly varying resource availability during the season which we will not consider in detail. Another obvious important factor is diminishing worker efficiency when worker number becomes larger. Like other analytical analyses of different characteristics of the social nest cycle, we started with simple assumptions and replaced this level of complexity by a linear approximation (Macevicz and Oster 1976, Oster and Wilson 1978). However, as soon as per worker efficiency decreases with increasing worker number, our argument based on the geometric growth effect is attenuated. Effects of resource shortage nearby the nest or inefficiency due to crowding inside the nest might be negligible right after colony foundation but have to be considered when colonies reach a saturation level in terms of worker number. In general, it is hard to say to what extent this is relevant in annual eusocial bees and wasps. At least for some wasps under specific environmental conditions, colony dynamics and transient mixed investment into workers and sexuals (instead of a dichotomous strategy switch) indicate density-dependent effects later in the season. In such cases, initial selection pressure in favor of SIM due to geometric growth will be reduced and it would be interesting to analyze the overall balance of selective forces with an extended model representing the entire nest cycle. However, this goes beyond the scope of this approach.

Finally, we have to consider that, in contrast to SEQ, the SIM strategy opens the opportunity for numerous additional behavioral choices not included in our model. This concerns the temporal pattern of oviposition and of allocation of food portions, which need not necessarily be identical for all brood cells and every moment in time, but can respond to the current distribution of age and supply state of offspring. In particular, satisfying offspring's needs "just in time," i.e., providing food not faster than consumed, but at the same time sufficiently fast not to delay development, can provide a temporal advantage in predictable environments. Yet, this strategy may be fatal when environmental conditions vary unpredictably and, for example, a substantial fraction of nearly fully provisioned brood would starve due to a sudden unexpected resource shortage. In that case, a bet-hedging strategy with less balanced distribution of care between offspring might be a better choice.

Further, if mothers are able to lay new eggs while others are still being provisioned, as indeed is the case in most social insects, a SIM-like state will not be arising through increased clutch size in discrete batches but rather by a continuous conveyor belt of brood. This could mitigate the risk (faced by discrete SIM breeders) of the mother dying before the larvae have completed their provisioning, because some offspring will have already been produced or at least fully provisioned and fewer resources will be wasted. Consequently, the conditions favoring SIM might even be greater than suggested by the model. A comprehensive analysis of such speculations would, however, require to relax the general rule "new eggs

only after former ones are fully provisioned" and add a huge number of degrees of freedom to the analysis. Here we restricted our approach to a simple case and postpone the analysis of intermediate strategies to the future.

A question of general interest is whether SIM evolved before or after sociality. In general, the advantage of increased geometric growth due to earlier offspring production would favor SIM whenever generations overlap—in perennial solitary as well as in social life histories. However, our analysis clearly demonstrates interactions between the level of selection towards SIM and the duration of developmental stages as well as the mortality rate of caring individuals and brood (Fig. 3b). We consequently expect differences in selection pressure whenever groups of species differ systematically in these characteristics. A lower risk for the loss of caring adult individuals as suggested for social insects (see above) might thus be accompanied by an increase in selection pressure in favor of SIM compared to perennial solitary organisms where such risks are assumed to be larger. In that context, Field (2005) discussed the relevance of well-hidden vs. well-exposed nests of solitary species as a suitable initial point of the analysis. He specifically emphasized that an initial evolution of progressive provisioning in well-hidden nests would provide favorable preconditions for the subsequent evolution of helping and sociality as a response to long periods of offspring dependency. Hunt and Amdam (2005) promoted the idea of a multivoltine life cycle as ancestral to eusociality. For example, bivoltinism is prevalent in solitary eumenines (Seger 1983)—thus, the eumenine-like solitary ancestor of the eusocial vespid *Polistes* presumably was bivoltine, too. In addition, brood provisioning can be observed in this subfamily in a few solitary species and all the species that show primitive social behavior (West-Eberhard 2005), but is typically rather sequential than simultaneous. However, *Odynerus tropicalis* (=*Antepipona tropicalis*) has been reported to provision more than one larva simultaneously, a pattern also observed in the parasitoidal wasp *Sphex albisectus* (Ferton 1902; Roubaud 1916; Malyshev 1968). It is unlikely that both the progressive and simultaneous characteristics of provisioning behavior evolved at the same time, but that in general progressive provisioning is ancestral to simultaneous provisioning. To this effect, our study specifically quantifies the strong selection pressure towards SIM in insect species that have already evolved sociality.

An interesting exception to the dominance of SIM among social insects are the eusocial halictid bee species that provision brood cells sequentially. Annual halictids show—in many regions—a peculiar temporal pattern within their nest cycle (Pesenko et al. 2000), however: Periods of foraging are interrupted by breaks, during which nests are closed and no activity outside the nests can be observed. This pattern has been shown to provide an evolutionary benefit under specific environmental conditions (Mitesser et al. 2006). Activity breaks can indeed limit foraging time to only half of the season (Weissel et al. 2006). This in turn reduces the benefit of SIM due to multiplicative effects. Further, like Field (2005), we considered provisioning as a component of parental care that is, in principle, freely distributable in time and between offspring. However, this may not always be the case. There are other tasks that cannot be performed in a progressive manner like provisioning. For example, the initiation of the nest (Field et al. 2007), construction of multi-purpose corridors in below ground nests, or preparation of the brood cell must possibly be completed before eggs can be deposited. If the total share of such inseparable components of parental investment is large, the benefit of SIM is reduced; this may apply to ground nesting halictids, which—other than for example bumble bees—do not use existing cavities but need to dig new ones. In addition, and unlike the species studied by Field and Brace (2004), progressive provisioning might in other species also increase the risk of parasitism (Longair 2004) if, e.g., brood attending behavior attracts parasites to potential victims and thus reduces the benefit of geometric growth. Nevertheless, it remains challenging to provide a full explanation why SIM has not evolved in halictids or in most non-social species.

Conclusion

In conclusion, by accounting for the geometric benefit of faster offspring reproduction that is associated with SIM in life cycles with generation overlap and specifically in social insects, we have identified an additional and important explanation for the evolution of simultaneously progressive provisioning. Together with Field's (2005) analysis of the role of offspring dependency on mother's survival, our findings provide a conclusive explanatory concept for the evolution of SIM in both solitary and social insects.

Appendix

Proposition 1: Lifetime reproductive success (LRS) is always decreasing with clutch size b if $b > D_L/f$.

Proof: If $b > D_L/f$, factor q is independent of b: $q = s^{D_P}$. LRS is $R = w \frac{bs^{f \cdot b}}{1 - s^{f \cdot b}}$ with $w = (q + (1-q)(1-\mu))$. Calculating the derivative with respect to b yields

$$R'(b) = -w \frac{s^{fb}(s^{bf} - bf \ln(s) - 1)}{(s^{bf} - 1)^2}$$

$$= -w \frac{s^{fb}(s^{bf} - \ln(s^{bf}) - 1)}{(s^{bf} - 1)^2} = w \frac{y(1 - y + \ln(y))}{(y-1)^2} \quad (9)$$

with $y = s^{bf}$ and $0 < y < 1$. Function $g(y) = 1 - y + \ln(y)$ decides on the sign of $R'(b)$. At the interval borders, $g(y \to 0) = -\infty$ and $g(1) = 0$. $g'(y) = 1/y - 1$ is always > 0 for $0 < y < 1$. Thus, $g(y)$ is always < 0 for $0 < y < 1$ and $R'(b)$ is always negative.

Proposition 2: If $b \leq D_L/f$, lifetime reproductive success is always decreasing with clutch size b for $\mu = 0$ and always increasing for $\mu = 1$.

Proof: If $b \leq D_L/f$, factor q depends on b: $q = s^{D_P + D_L - bf}$. LRS is $R = w'\mu \frac{b}{1 - s^{f \cdot b}} + (1-\mu) \frac{bs^{fb}}{1 - s^{f \cdot b}}$ with $w' = s^{D_L + D_P}$. If $\mu = 0$, the arguments from A1 can be applied to show that $R'(b)$ is always negative, too. If $\mu = 1$,

$$R'(b) = w' \frac{1 - y + y\ln(y)}{(1-y)^2} \quad (10)$$

Function $\tilde{g}(y) = -y + y\ln(y) + 1$ decides on the sign of $R'(b)$. $\tilde{g}(y \to 0) = 1$ and $\tilde{g}(1) = 0$. $\tilde{g}'(y) = \ln(y)$ is always negative, and thus, $\tilde{g}(y)$ is always positive for $0 < y < 1$. Thus, $R'(b)$ is always positive.

Proposition 3: There is no local relative maximum of lifetime reproductive success for $b \leq D_L/f$, and lifetime reproductive success is maximized for $b = 1$ or $b = D_L/f$.

Proof: In general, the derivative of LRS $R(b)$ is

$$R'(b) = w'\mu A - (1 - \mu)B$$

with $A = \frac{1 - y + y\ln(y)}{(1-y)^2}$ and $B = -\frac{y(1 - y + \ln(y))}{(y-1)^2}$

LRS $R(b)$ is increasing as long as $R'(b) > 0$. We further analyze this condition:

$$R'(b) > 0 \Leftrightarrow w'\mu A - (1-\mu)B > 0 \Leftrightarrow \frac{w'\mu}{1-\mu} > \frac{B}{A} \quad (11)$$
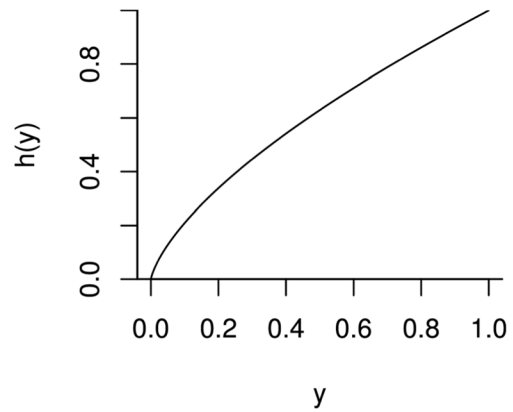

Fig. 4 Function $h(y) = B/A$ in dependence of y.

$h(y) = B/A$ is always increasing for increasing y within the interval $0 < y < 1$ (Fig. 4).

Thus, there must be a value y_0 such that if $y < y_0$, then $\frac{B}{A} < \frac{w'\mu}{1-\mu}$. It is not necessary to calculate y_0 —we further just make use of its existence. As $y = s^{bf}$, the derivative of LRS R' is always greater than 0 (and $R(b)$ is increasing) if $b > b_0$ with $b_0 = \ln \frac{y_0}{f\ln(s)}$. If b is smaller than this threshold, $R(b)$ is decreasing. In general, $R(b)$ is either always decreasing from $b = 1$ to $b = D_L/f$ or it is decreasing from $b = 1$ to $b = b_0$ and increasing from $b = b_0$ to $b = D_L/f$. In either case, LRS cannot have a local maximum.

Corollary 4: Critical values of offspring dependency μ promoting the transition from SEQ to SIM can be calculated analytically from Eq. (5) for any parameter combination:

$$\mu_{crit}(D_L, D_P, s, f) = \frac{L}{s^{D_L + D_P}K + L} \quad (12)$$

with $K = \frac{1}{1 - s^f} - \frac{D_L}{1 - s^{fD_L}}$ and $L = \frac{D_L s^{fD_L}}{1 - s^{fD_L}} - \frac{s^f}{1 - s^f}$.

This directly follows from A3. A transition between SEQ and SIM as optimal strategies will occur when

$$R(1) = R\left(D_L / f\right)$$

This can be used to determine threshold values for any parameter in dependence of the others.

Corollary 5:

$$\lim_{s \to 1} \mu_{crit}(D_L, D_P, s, f) = 1/2$$

This limit can easily been calculated by applying the Limit[] function of the computer algebra system Mathematica (Wolfram Research Inc. 2016) to Eq. (12).

Proposition 4: Worker number W_{max} at the beginning of sexual production affects final cumulative sexual number $S(T)$ at time $t = T$ after the beginning of sexual production as a linear multiplicative factor in the colony model provided by Oster and Wilson (1978): $S(T) \sim W_{max}$

Proof: The dynamic equation for the number of sexuals $S(t)$ at time t after the onset of sexual production is

$$\frac{\partial S(t)}{\partial t} = cW_{max}e^{-\mu t} - \nu S(t) \qquad (13)$$

with worker efficiency rate c, worker mortality rate μ, and sexual mortality rate ν. The solution to this equation is

$$S(t) = \frac{cW_{max}}{\mu - \nu}\left(e^{-\nu t} - e^{-\mu t}\right)$$

resulting in

$$S(T) \sim W_{max}$$

at the end of the season when $t = T$. Calculation has been checked with computer algebra system Mathematica (Wolfram Research Inc. 2016).

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