

Tree Thinking: A New Paradigm for Integrating Comparative Data in Psychology

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ABSTRACT. Over the past 15 years, several important theoretical and methodological developments have emerged from evolutionary biology. These developments—collectively dubbed *tree thinking*—are now well known in evolutionary biology but have yet to be incorporated into mainstream psychology. Tree thinking has revolutionized evolutionary biology and has the potential to do the same for how comparative data are integrated into psychology. Tree thinking holds that explanations (or narratives) for adaptations must be based on an understanding of the adaptations' history (or chronicle) over evolutionary time. This tenet of tree thinking requires researchers to consider hitherto neglected patterns of data. The authors present the ideas and methods behind tree thinking, examining their implications for psychology.

Key words: animal studies, comparative psychology, evolutionary psychology, research methods or methodology

RESEARCHERS NOW WIDELY ACCEPT that to understand the nature of the human species, or any other biological taxon,¹ it is critical to understand the role of evolutionary processes, such as natural selection, mutation, and genetic drift. One of the most prominent evolutionary principles is of course Darwin's (1859/1964) theory of natural selection, which holds that traits that confer a fitness advantage are more likely to survive into future generations than are neutral or detrimental traits. With a focus on *Homo sapiens*, evolutionary psychologists

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aim to explain the function of traits in terms of natural selection, especially in the so-called *ancestral environment* of human evolution.²

Therefore, one crucial challenge to understanding the function of a trait requires identifying the conditions that characterized the ancestral environment that helped to shape that trait. There are two common approaches to meeting this challenge. One approach is to base explanations for psychological traits on the selection pressures that were likely present in relatively recent times, most typically the Pleistocene epoch, which ran from about 1.7 million years ago to about 11,000 years ago (e.g., Buss, 1991; Tooby & Cosmides 1990, 1992). For example, Silverman and Eals (1992) developed predictions about the different spatial abilities of men and women on the basis of the sexual division of labor between hunting and gathering during hominid evolution. A second approach is to draw on comparative data, showing how traits are associated with other traits or features of the ecology. For example, Miller, Putcha-Bhagavatula, and Pederson (2002) used data from several primate species to identify the correlates of different mating strategies.

However, there are problems with each of these approaches. The problem with explanations based on the Pleistocene era is that researchers usually assume that a trait evolved in that era without first establishing that it did indeed emerge then. Clearly, an explanation that is based on the conditions that characterize the Pleistocene era would make little sense if the trait predated this period. The problem with many comparative analyses is that the data are rarely organized in a systematic fashion. As we will explain later in this article, this lack of framework means that the comparative data are often a lot less compelling than they may first appear. The solution to both of these problems lies in timing: identifying the point when a trait (or *character*, as it is usually called in phylogenetic systematics) developed.

Many evolutionary thinkers in psychology have yet to appreciate the importance of determining the timing of evolutionary events. Evolutionary biology suffered for years under this burden, and the consequences were numerous. By explaining character evolution without first establishing the timing of these changes, biologists were not making the most effective use of their data. Moreover, the biologists built their classification systems (and all of the work involved in entering new taxa into them) on unsound principles, and the research questions that developed from them were fundamentally flawed. For example, researcher after researcher made too much of strong correlations between traits. However, many of these researchers did not appreciate that the nature of the evolutionary relatedness among the species violates a basic statistical assumption (i.e., that the taxa exhibiting the traits should be independent sources of data, not dependent as if multiple species shared a trait by virtue of descent from a common ancestor; Felsenstein, 1985). Evolutionary biologists have begun to appreciate these issues only relatively recently.

In this article, we suggest that like the field of evolutionary biology, areas of psychology that rely on comparative data would benefit from pinpointing the

emergence and disappearance of traits in historical, evolutionary time. Fortunately, theoretical and methodological techniques are now available in the field of evolutionary biology to implement an approach that incorporates the timing of when traits emerged (Brooks & McLennan, 1991; Felsenstein, 2003; Harvey & Pagel, 1991). These techniques and principles provide a framework that will enable psychologists to incorporate the first 600 million years of human evolutionary history. One of the most helpful articles on the topic appeared in 1988, when Robert O'Hara heralded the importance of this new approach and named it *tree thinking*.

Tree Thinking and Evolutionary Explanations

To explain tree thinking, the ornithologist and evolutionary biologist Robert O'Hara (1988) drew an analogy with the study of history. In that field, a distinction is made between the chronicle and the narrative. The *chronicle* is a chronological list of historical events. For example, one 20th century chronicle is the following: Germany invaded Poland, and then England declared war on Germany. In contrast, the *narrative* is the story or explanation of how and why those events occurred. Thus, for example, the corresponding narrative may be the following: England declared war on Germany because Germany had invaded Poland. The narrative depends on the chronicle and must be consistent with it. It would make no sense to say that England declared war on Germany because Germany had invaded Poland if in fact Germany had not invaded Poland.

O'Hara (1988) took this concept and applied it to the field of evolutionary biology. He argued that the explanations or stories that we tell about organisms and their traits are the narratives of evolutionary biology. As in the field of history, these explanatory narratives depend on an underlying chronicle. In the case of organismal evolution, he argued that the chronicle takes the form of a *phylogenetic tree*, a diagram depicting the evolutionary descent relationships among taxa. Thus, evolutionary explanations must rely on phylogenetic trees. Such trees provide the record of evolutionary events and thus provide the backbone for evolutionary narratives. There are two major types of evolutionary events depicted on trees: *speciation events*, when one species splits into two; and *evolutionary novelties*, the appearance of new or modified traits.

Tree thinking is critical to evolutionary studies because it provides a falsifiable set of hypotheses about evolutionary history that becomes, in turn, the grounding upon which all evolutionary stories may be based. To the extent that any hypothesis about the function of a trait involves an explanatory narrative for that trait (e.g., women evolved to be choosier about their mates than did men *because* they invested so much more energy in their offspring than did men), that narrative must be based on knowledge of the described events (e.g., that human females did in fact evolve this trait). As O'Hara (1988) said, "trivial as it may sound, before giving an explanation of a change from A to B, one ordinarily needs

to know A” (p. 150). This simple step prevents people from building a narrative on the basis of a false chronicle.

Tree thinking recognizes that species are not independent replicates within a class (as earlier thinkers had tended to see them), but are instead interconnected parts of an evolutionary tree (Felsenstein, 1985). It emphasizes the explanation of evolutionary events in the context of a tree and it portrays evolutionary history as a story of divergence (O’Hara, 1997).

At a broad theoretical level, the basic points underlying tree thinking have long been recognized by psychologists (Hodos & Campbell, 1969; Tooby & Cosmides, 1989). However, it is only in the past decade or so, with the major conceptual and methodological advances in evolutionary biology, that researchers have cleared the path to apply these theoretical models in research contexts (Brooks & McLennan, 1991; Harvey & Pagel, 1991).

To take advantage of tree thinking, one must become familiar with some of the principles of the subdiscipline within evolutionary biology that is known as phylogenetic systematics. *Phylogenetic systematics* (also known variously, and with slightly different connotations, as *systematics*, *phylogenetics*, and *cladistics*) is a set of theories and methods for deriving falsifiable hypotheses about the evolutionary descent relationships among organisms and for studying the evolution of the various traits of those organisms over time. These relationships can be depicted in a tree-like diagram. The next section will provide a brief introduction to these concepts.

Primer on Phylogenetic Systematics

The main goal of the field of systematics is to derive the phylogenetic relationships among species. Because these relationships developed through the process of descent, the result of such an analysis is a tree depicting both the evolutionary relationships among the taxa of interest and the relative timing of the divergences among them. Figure 1 shows a tree representing the phylogenetic relationships among a subset of primate taxa. Taxa are positioned at the endpoints of branches, and the junctions of the branches represent the evolutionary relationships among them. For example, because the branches leading to the two species of chimpanzees (*Pan paniscus* and *Pan troglodytes*) connect to each other before either of them connects to any other branches, the diagram indicates that these two species are more closely related to each other than either is to any other taxon shown. The fact that their common branch next connects to that of humans indicates that in turn, chimpanzees and humans are more closely related to each other than either is to any of the other primate species.

As with any scientific hypothesis, researchers can never know phylogenetic relationships such as those in Figure 1 with absolute certainty. Instead, they make inferences about them that are more, or less, supported by evidence that is related to the process of evolutionary descent. This evidence consists primarily of the

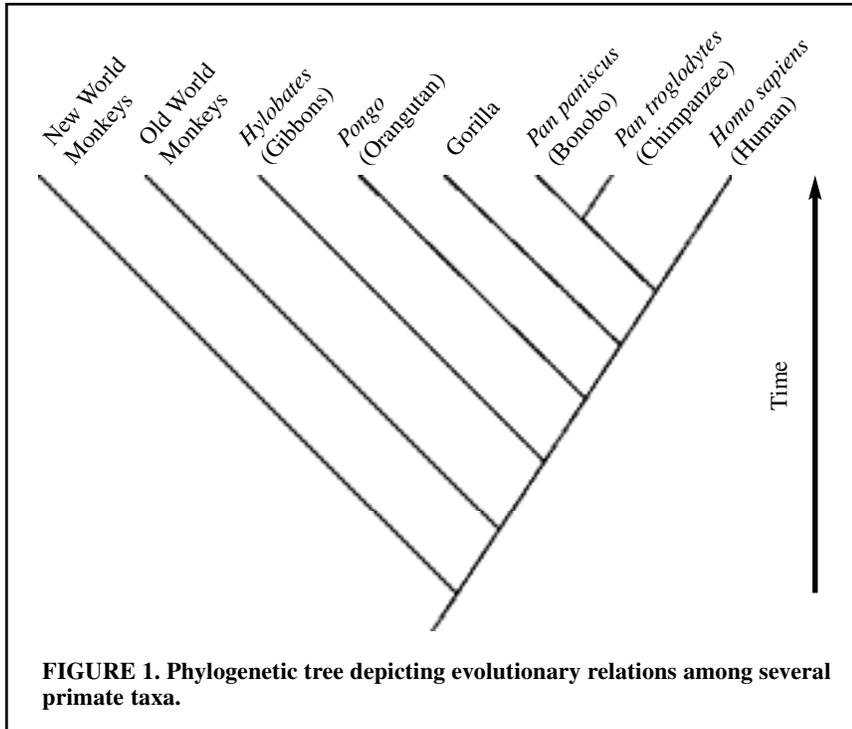
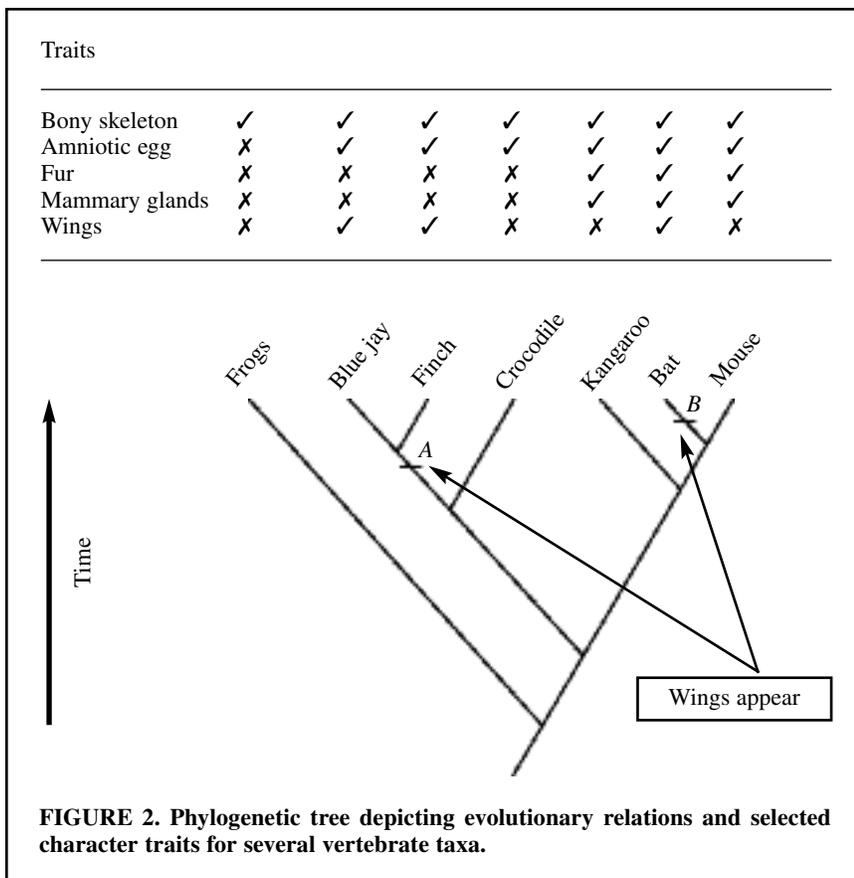


FIGURE 1. Phylogenetic tree depicting evolutionary relations among several primate taxa.

pattern of distribution of inherited traits among the taxa of interest. Any trait that descendants inherit from ancestors can potentially provide information about evolutionary relatedness. Thus, morphological characteristics (e.g., presence or absence of a particular bone or shape of a particular muscle), behavioral characteristics (e.g., propensity to build hanging nests, aggression toward territorial intruders), genetic characteristics (DNA sequence of a particular gene, molecular weight of a particular protein), and others are all valid sources of information about evolutionary relationships (Hillis, Moritz, & Mable, 1996). Even with all this information, it is sometimes difficult to pinpoint with certainty the timing and order of speciation events.

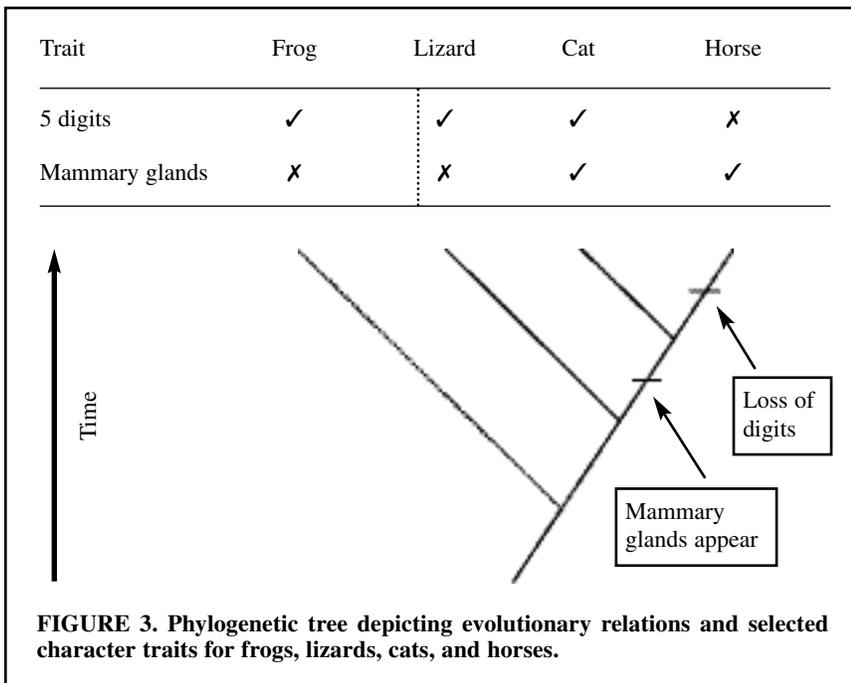
Unfortunately, not every similarity or difference among organisms accurately reflects the evolutionary history of those organisms because, although descendants do inherit traits from their ancestors, change often occurs as well. Consider three of the taxa shown in Figure 2—blue jays, finches, and bats—all of which have the heritable trait of wings. The preponderance of evidence suggests that blue jays and finches share the trait by virtue of *evolutionary relatedness* (i.e., that they share an ancestor that evolved wings, represented by point A in Figure 2). But the fact that the bird species share the trait of wings with bats is an example of *evolutionary convergence* (i.e., the ancestors of birds and bats



evolved wings independently; points A and B in Figure 2) and is misleading about their phylogenetic relationships. The question thus becomes one of separating the revealing from the misleading, and therein lies much of the work for systematists.

Since the 1960s, researchers have made great advances in both the theory and the practice of this work. In 1966, a German biologist named Willi Hennig made the profound realization that not only are some similarities misleading about evolutionary relationships, similarities of the unevolved (primitive) form are totally uninformative. For example, let us say one wants to work out the relationships among a lizard, a cat, and a horse. The first step is to pick an outgroup taxon—that is, one which, on the basis of a preponderance of other evidence, is known a priori to be more distantly related to all three ingroup taxa than any ingroup taxon is to the others. Given these three taxa, one appropriate outgroup taxon we might choose is a frog (the amphibian lineage diverged from

that leading to reptiles, birds, and mammals approximately 325–350 million years ago). The second step is to examine traits in both the ingroup and outgroup species and compare them (see Figure 3). One trait that a person could consider is the number of digits on the foot, and for these taxa we would find that the frog, the lizard, and the cat all have five digits on their feet, whereas the horse has only one. According to strict similarity alone, this trait would imply that the cat and lizard are more closely related to each other than either is to the horse. The frog, according to its a priori designation as the outgroup, is by definition the most distantly related to all of them. Hennig observed that this obvious error makes it clear that we should avoid using overall similarity of primitive traits alone as our measure of phylogenetic relationship. Instead, he showed that researchers should focus on similarity on the basis of derived traits. For example, by comparison with the outgroup, one discovers that having five digits is the primitive condition for our ingroup (because the frog has the five-digit condition), whereas having one digit is derived within the ingroup (i.e., it evolved during the evolutionary history of the ingroup after its divergence from the outgroup). Therefore, researchers should not use the shared occurrence of five digits in the lizard and the cat as evidence of a close relationship between these two species. Instead, researchers should use derived characteristics. In this example, one such characteristic would be the presence



of mammary glands. Because the frog does not have mammary glands, one can decide that these glands are derived within our ingroup and thus the shared presence of mammary glands in both the cat and the horse is presumed to have been derived in their common ancestral lineage after its divergence from the lizard, thus accurately indicating the phylogenetic relationships among these three species.

With hindsight, one can see that tree-thinking had begun: Hennig's (1966) brilliant insight that only traits that evolved during the divergences of interest contain a record of those divergences opened the way to a new approach to systematics and, indeed, to evolutionary biology as a whole.

Implications of Tree Thinking for Psychologists

Tree thinking consists of explicitly using the principles of evolutionary descent and applying them in scientific thought and research to living organisms, including humans. Tree thinking is a crucial tool for any psychologist who is interested in gaining evolutionary insight into humans because it provides the chronicle on which the psychological narratives must be based. Therefore, it will provide information about when particular traits arose, the identity and characteristics of the organisms that evolved those traits, and the nature of the environment in which those organisms lived.

Researchers may construct with varying degrees of certainty all patterns of trait evolution—no matter how complex—by using computer programs that have been developed by evolutionary biologists (e.g., MacClade, Version 3.0, Maddison & Maddison, 1992; Phylogenetic Analysis Using Parsimony [PAUP], Version 4, Swofford, 2001). Numerous programs for doing phylogenetic analyses are now widely available (see http://en.wikipedia.org/wiki/Phylogenetics_software for an up-to-date list), as are several useful practical guides (e.g., Skelton, Smith, & Monks, 2002) and primers (Lipscomb, 1998). Although most of these programs and methods were originally developed for use with morphological and genetic traits, they can easily be applied to behavioral and psychological traits. In fact, behavioral traits have been shown to be as useful as morphological traits in constructing phylogenetic trees (de Queiroz & Wimberger, 1993). The evolutionary biological literature is full of such behavior-based phylogenetic analyses, often in taxa that typically evade the attention of psychologists.

In the next section, we will outline five implications of tree thinking for psychology. We will illustrate them with reference to several studies, drawing most heavily on an exemplary series of phylogenetic analyses, in which Fraley, Brumbaugh, and Marks (2005) mapped the traits of pair bonding, neoteny, and paternal care onto a known phylogenetic tree of 44 mammalian species. We will focus on that study because it shows how tree thinking can be used to answer questions about the evolution of human psychological traits.

Tree Thinking Provides a Theoretical Framework for Organizing Comparative Data

Psychologists have long drawn on examples from the nonhuman literature. Indeed, the basic principle underlying comparative psychology is that knowledge about one species can inform us about other species. In most comparative studies, research is performed on nonhuman animals with the ultimate goal of learning about humans. Researchers have examined a vast range of phenomena using the comparative method. Indeed, so much of psychology has been based on animal research that animal studies are often taken for granted (Domjan & Purdy, 1995). However, comparative psychologists have not always been sufficiently concerned with understanding how the phylogenetic relations among species can affect cross-species generalizations (Hodos & Campbell, 1969). Later in the article, we will use examples to show how tree thinking provides an integrative framework for organizing and understanding findings from comparative psychology by placing research findings within an evolutionary historical context (although there are some circumstances in which phylogenetic methods are not needed; Losos, 1999).

Some comparative studies focus on identifying co-occurrences of traits across taxa. To illustrate, imagine that we want to investigate the co-occurrence patterns of the physical traits in Figure 2. At first glance, it may seem that our sample size should be seven, corresponding to the seven taxa in the figure. A tree-thinking approach indicates that the effective sample size of independent cases is rarely as large as the number of taxa (Felsenstein, 1985). Our tree shows that the trait of having amniotic eggs evolved only once. That is, blue jays, finches, crocodiles, kangaroos, bats, and mice all have amniotic eggs by virtue of inheritance from a common ancestor. To count this pattern as seven cases would be counting the same (ancient) event seven times. Similarly, for the fur trait, there is one case—not three—because the modern kangaroo, bat, and mouse species all have this trait as a result of a single evolutionary event that was shared by their ancestor. Wings appeared twice (at Figure 2, Points A and B). Thus, for the trait of wings, the number of cases is two (corresponding to evolutionary Events A and B)—not three (the number of species with wings). It should be clear that this important consideration about how to understand comparative data falls directly out of tree thinking.

In the context of discussing the evolution of long- versus short-term mating preferences, Miller et al. (2002) marshalled evidence of various mating strategies in several primate species. However, they did not organize the data in a phylogenetic tree, and the reader is not able to determine whether the species represent several independent evolutionary events (e.g., the emergence of a copulatory plug) or just one. In contrast, a tree-thinking analysis of mating strategies in primates would provide a chronicle on which narratives about trait evolution could be based. For example, Lindenfors and Tullberg (1998) showed

how the emergence of mating strategies was tied to the emergence of size and size dimorphism.

Fraley et al.'s (2005) article on pair bonding, neoteny, and paternal care undertook two kinds of analysis. The first analysis was a standard comparative analysis correlating pair bonding with a number of other species-level characteristics such as the degree of paternal care, the size of the groups, the size of the individuals, and the degree of neoteny (developmental immaturity). Although these analyses identified some correlates (e.g., neoteny, paternal care) of pair-bonding, the meaning of these associations was ambiguous because it was not known how attributable they were to common ancestry. In contrast, analyses that took into account the phylogenetic relationships among the species could show which traits were correlated over and above the effects of having a common ancestor. Fraley et al.'s analyses showed that the association between paternal care and pair bonding could be attributed to convergent evolution (i.e., emerging multiple times independently), whereas the association between neoteny and pair bonding could be attributed to homology (i.e., species sharing an ancestor). As we shall explain later, this kind of data is much more informative for testing and building theories than traditional forms of comparative data.

Another tree-thinking approach is to examine the evolution of gene sequences already associated with traits. Lesch et al. (1997) examined genetic information across a range of mammals, including tree shrews, rhesus monkeys, chimpanzees, and humans. This information, along with the known phylogenetic relations among the species, indicated that the gene sequence that is associated with anxiety (the serotonin transporter gene-linked polymorphic region known as 5-HTTLPR) probably arose in the genome about 40 million years ago.

Tree Thinking Shows Us When and How Many Times Particular Traits Evolved

The tree thinker's approach to studying the history of a trait is to map the distribution of that trait on a phylogenetic tree and reconstruct the evolutionary events in that trait's history. The result of this analysis is often intuitively obvious when the trait's evolution has been very simple. For example, all mammals have mammary glands but all nonmammals do not; therefore, it is easy to infer that mammary glands arose once, in the common ancestor of all mammals, and were passed down to all of that ancestor's descendants. However, when a trait has evolved multiple times and been secondarily lost in some—but not all—descendants, the trait's evolutionary history is more difficult to infer. In these situations, it also becomes easier for researchers to forget that history may be relevant to studying the trait in a particular species of interest. For example, pair bonding is a trait that humans share with some other mammals as well as other nonmammalian vertebrates (e.g., some fish and birds). Fraley et al.'s (2005) analysis of pair bonding showed how the current distribution of this trait across species

almost certainly reflects several independent originations, plus trait retention, in descendant lineages. In addition, their analyses indicated that paternal care appears to have earlier evolutionary origins than does pair bonding. As noted below, these data can be used to develop and test theories about the preconditions that facilitated the emergence of pair bonding.

Tree Thinking Sheds Light on the Nature of the Environment That Shaped a Particular Trait

Once researchers reconstruct the evolutionary history of a human trait on a tree, they not only realize that it may have evolved long before humans appeared, but also gain information about the nature of the *environment of evolutionary adaptedness* (EEA; Symons, 1990) for that trait. This information is invaluable for understanding the forces that contributed to the trait's evolution. For example, knowing that the human trait of preferring fatty foods evolved when such foods were scarce helps us understand why that preference creates problems in our current environment with its easy access to fatty foods.

Evolutionary psychologists are familiar with this argument when it is applied to recent human evolutionary history. For example, researchers explain the fact that it is much more common to see phobias to snakes or spiders than to objectively more dangerous items such as guns or cars by noting that there has not been enough time for humans to adapt to all aspects of the current technologically rich environment (Buss, 1999a). Tree thinking offers additional levels of precision about the specific EEA for each particular trait. For example, if researchers can pinpoint the evolution of human sociality to the ancestor of all the great apes except the orangutan (i.e., the branch leading exclusively to gorillas, chimpanzees, and humans), then the knowledge of this environment's (approximately 15–18 million years ago; Arnason, Xu, Gullberg, & Graur, 1996; Napier & Napier, 1985) climatic patterns, geographic location, habitat status, and presence of other extant species will gain additional information to use in forming hypotheses about the trait's adaptive value.

Also, hypotheses about the forces driving adaptations have implications for when the adaptation arose. Consider one hypothesis that has been proposed to explain the emergence of jealousy. According to one line of reasoning, sex differences in reproductive biology account for the fact that men are more sensitive than are women to sexual infidelity and women are more sensitive than are men to emotional infidelity (e.g., Buss, 1995a, 1995b, 2000). Specifically, fertilization takes place inside women's bodies but not men's, with the result that women can be sure that they are the mother of their children, but men cannot be so certain of their paternity. If this biological feature is what drives jealousy, and if some form of jealousy helps to solve the problem of paternity uncertainty, then we should expect to find some form of jealousy emerging any time after internal reproduction emerged. The logic provided for the emergence of jealousy (i.e., as an adap-

tation to the selection pressures associated with internal reproduction) compels the psychologist to place the possible emergence of jealousy within a specific window in evolutionary history. The beginning of this particular window is marked by the appearance of internal reproduction, which emerged with the reptiles in the Carboniferous period of the Paleozoic era about 325 million years ago. This suggests the possibility of finding evidence for jealousy across a wide range of mammal, bird, lizard, turtle, and crocodile taxa.

If one finds it unlikely that jealousy could evolve in turtles or lizards, then he or she must abandon or modify the hypothesized explanation. For example, researchers might hypothesize that jealousy arises when there is internal fertilization and internal gestation or when there is internal fertilization and pair bonding or when there is internal fertilization, internal gestation, and pair bonding. Each of the modified hypotheses suggests new sets of analyses to determine the point at which these conditions arose and therefore the taxa in which one could find evidence of jealousy. Thus, phylogenetic analyses provide a way of testing evolutionary hypotheses, furnishing clear predictions about where investigators should look for evidence of a trait. Similarly, Fraley et al.'s (2005) analyses of pair bonding direct attention to likely ancestral candidates for when this trait emerged, paving the way for more focused phylogenetic analyses to home in on the conditions shaping the trait's evolution.

Tree Thinking Guides the Search For Causal Mechanisms

Tree thinking sheds new light on psychological phenomena, providing important clues to the likely causal mechanisms that could not be identified by other means. The information furnished by Fraley et al.'s (2005) analyses of pair bonding, which showed when the trait evolved and what other social features pre-existed when it did evolve (e.g., paternal care), can direct theory building about the processes underlying pair bonding. For example, Fraley et al.'s data inform the question of whether pair-bonding may lead male parents to care for offspring or whether male care for offspring leads to pair bonding. Their results show that, for the 44 species examined, paternal care evolved long before pair bonding, ruling out the possibility that pair bonding leads to paternal care. Nonetheless, the traits were related, indicating that paternal care may have provided the preconditions for the emergence of pair bonding. In contrast, although the presence of neoteny or developmental immaturity was also associated with the presence of pair bonding, Fraley et al. suggested "that neoteny did not play a role in the evolution of pair bonding or vice versa" (p. 11) posing serious problems for Fraley and Shaver's (2000) neoteny hypothesis (i.e., that attachment among human adults is a by-product of humans' prolonged neotenus state).

Fraley et al.'s (2005) study is important because it demonstrates how tree thinking can be applied to answer fundamental questions concerning the evolution of human psychological traits. It is worth noting that, like many phylogenetic

analyses, the data on which Fraley et al. based their analyses were all readily available in articles, books, and research Web sites. Thus, it was by bringing tree thinking to currently available data that such important strides were made.

The importance of using tree thinking to determine the timing of trait evolution is primarily that we have a more accurate understanding of what happened during evolutionary history. Rather than making a general statement about human adaptations to a range of problems, we can propose a precise hypothesis about the ancient origin of a trait that humans now demonstrate (as well as other animals). Furthermore, this understanding and knowledge pave the way for additional questions to improve our understanding of actual evolutionary events.

Tree Thinking Shows Us Which Traits May Belong Uniquely to Humans

The reconstruction of trait evolution is important for psychologists who are interested in understanding the nature of human nature, that is, who aim to explain the traits that make us uniquely human (Buss, 1999a, 1999b). These reconstructions determine the timing of all human traits and thus show both which human traits actually evolved in the lineage leading directly to modern humans and which traits may have evolved earlier in our evolutionary history.

Of course, psychologists are well aware that most traits evolved before the emergence of modern man, but it is recent evolutionary history, especially the Pleistocene, that has a favored status in evolutionary psychological explanations of selection pressures. Cosmides and Tooby (1997) suggest, "Our ancestors spent well over 99% of our species' evolutionary history living in hunter-gatherer societies. That means that our forebears lived in small, nomadic bands of a few dozen individuals who got all of their food each day by gathering plants or by hunting animals." A tree thinker would argue that this statement relies on a rather narrow definition of what constitutes a human ancestor. Nonetheless, many evolutionary psychological thinkers agree that humans have what Cosmides and Tooby called a "stone age mind." Washburn and Moore wrote, "Most of human evolution took place before the advent of agriculture when men lived in small groups, on a face-to-face basis" (as cited in Gladwell, 2002, p. 177). Symons (1992) stated that the Pleistocene is the "environment in which the overwhelming majority of human evolution occurred" (p. 143). Indeed, Cosmides, Tooby, and Barkow (1992) noted that a common assumption that most of the contributors to their landmark book, *The Adapted Mind*, was that "the evolved structure of the human mind is adapted to the way of life of Pleistocene hunter-gatherers" (p. 5). As Miller et al. (2002) observed, "When scientists search for evolutionary adaptations, they typically consider what humans were like during the Pleistocene era" (p. 93).

A tree thinker would agree about the importance of understanding the ecological conditions under which our ancestors lived but would not be tied a priori to any particular time period. Many organisms qualify as human ancestors, but most of them lived long before the last few million years, were not very humanoid,

and did not live on grassy savannahs. A vast number of the problems faced by humans' Pleistocene ancestors were also faced by ancestors that predated the Pleistocene era. These problems might include many, if not all, the challenges sometimes characterized as human survival problems, such as food shortages, toxins, predators, parasites, diseases, and extremes of climate (Buss, 1999a).

To understand the evolution of any particular trait, the tree thinker aims to identify the appropriate chronicle. To illustrate, consider one supposedly human adaptation for survival: the negative response to the ingestion of substances that contain toxic components (Buss, 1999a). When, during evolutionary time, did this trait evolve? A survey of the literature reveals that a wide array of species spanning a vast evolutionary history has negative responses to toxic substances. A phylogenetic reconstruction of the trait's evolutionary history would show that, because of its wide distribution in living animals, avoidance of toxic foods most likely evolved in the ancestor of all living animals (Maddison & Maddison, 1992). Of course, since the trait first appeared, there have been plenty of additional selections shaping the specific form of antitoxin mechanism in each extant species. Nonetheless, although humans do indeed have mechanisms to deal with the problem of ingesting toxic foods, it is almost certain that they did not originate in humans within the past 2 million years. Instead, humans inherited the mechanisms from their species' ancestors, and in this case, the ancestor was one that lived as much as 1500 million years ago (Wang, Kumar, & Hedges, 1999), far back in the Precambrian period, and the trait has remained present out of phylogenetic inertia and stabilizing selection.

Of course, humans are a unique species in many ways. A benefit of tree thinking is that it helps researchers derive a more accurate understanding of just how humans differ from other animals. A complete chronicle would pinpoint the timing of the evolution of every human trait, and thus reveal precisely which of the traits evolved along the lineage leading to modern humans after our lineage split from that of chimpanzees (or, in some cases, after the split from our even closer relatives, such as *Australopithecus* and the Neanderthals; e.g., Dean, Leakey, Reid, Schrenk, & Schwartz, 2001).

Some human traits appear to be unique in the world. Such traits include the capacity to mentally represent a host of causal forces (Povinelli & Bering, 2002) and the capacity for complex language (Diamond, 1992; Pinker, 1994). For uniquely human traits, it is difficult to use tree thinking techniques in the traditional sense, because without a point of comparison (i.e., other species), we cannot learn much about the trait's evolution. Furthermore, with no living organisms to represent the variation of interest (e.g., early humans without language), it is difficult to make inferences about the adaptive significance of the trait back in time (e.g., Haig & Durrant, 2000). Nonetheless, psychologists can make creative use of anatomical and cultural archeological evidence to shed light on the likely emergence of behavioral traits, even within hominid taxa. Moreover, researchers in evolutionary biology are developing new ways to use some of the basic prin-

ciples of tree thinking within species, and it is becoming possible to study the evolution of intraspecifically variable traits from a tree-based perspective (e.g., Cavalli-Sforza & Cavalli-Sforza, 1995; Pagel, 2001).

Limitations

Tree thinking can offer researchers a new outlook on how comparative data are used to inform theories about the timing and thence the function of traits. However, it is important for researchers to have a clear idea of what tree thinking cannot explain. Knowing where its limits lie will help evolutionary psychologists combine tree thinking with the other available methods.

One important distinction to draw is that between the origin of a trait and the maintenance of a trait. As developmental systems theorists have recently argued (e.g., Lickliter & Honeycutt, 2003), natural selection cannot be responsible for the origin of a trait because selection is not generative. Rather, new traits emerge because of novelties in developmental outcomes, which are often due to novel mutations. Phylogenetic analyses are useful because they can help pinpoint the timing of evolutionary novelties. However, the maintenance (or initial spread) of a trait once it emerged is a separate process and one that can involve multiple phenomena. Selection is surely one important evolutionary force enabling traits to spread. So too, however, is random drift, which presumably is responsible for the spread of selectively neutral gene sequences. Phylogenetic analyses can be useful for understanding trait maintenance and spread, but they are not the only means of doing so. For example, design features can tell much about the adaptive value of traits.³ One need not know the precise evolutionary history of bird wings to understand that it involved their selection for flight. Indeed, evidence of design is needed to make a good argument for selection no matter how much comparative data are involved (e.g., see Andrews, Gangestad, & Matthews, 2002). So, although tree thinking is useful, it is not the only tool that is useful to evolutionary biologists. Thus, tree thinking will often be only one of several methods that are used to unravel the evolutionary puzzles, and sometimes it may not offer much information over and above purely functional explanations.

The distinction between the origins of a trait and its maintenance has an important implication for how researchers use tree thinking to test functional theories of traits. Tree thinking can be combined with functional arguments to direct researchers to look for the possible window of time during which a trait emerged, but the failure to find that trait at the beginning of that window does not count as evidence against the functional argument. As we noted earlier, the functional argument that internal fertilization drove the evolution of jealousy would direct the tree thinker to search for jealousy across a wide range of mammal, bird, lizard, turtle, and crocodile taxa. However, selection cannot lead to the emergence of a trait in the first place (only to the spread and maintenance of a trait once it has

emerged), so a failure to find jealousy in lizards would not refute the internal-fertilization functional argument: The existence of conditions that may prove advantageous for a trait does not guarantee that the trait will emerge. Tree thinking may guide researchers to where to look for the first evidence of a trait, but the logic of tree thinking does not imply that a trait will emerge as soon as conditions favor its selection.

On a related note, researchers should bear in mind that identifying the conditions under which a trait evolved could turn out to be uninformative about the function of the trait. A functional trait may have emerged largely independently of the unique features of a particular set of conditions; if eyes first evolved in marine organisms, then it may be useful to consider the properties of light transmission in water when theorizing about how eyes evolved. However, eyes continued to be adaptive on terrestrial environments so the selective pressures were not unique to marine environments. The fact that eyes continued in a wide variety of niches informs our understanding of selection because traits that no longer benefit their beholders often degrade as a result of the effects of mutation.

Conclusion

In this article, we proposed that functional explanations would be most useful to researchers when explanations are explicitly based on evolutionary chronicles. Although the superficial consequences of this new emphasis may seem trivial, its deeper contingency is groundbreaking. We highlighted the value of considering the human chronicle as just one twig on an enormous evolutionary tree. Such a step raises the possibility that a trait could be shared by many species, and it provides a clear roadmap for where researchers should search for comparative data. Ideally, articles on the evolutionary origin and significance of psychological traits would include phylogenetic trees, as is standard practice in phylogenetic journals (e.g., *Biological Journal of the Linnean Society*). As in other domains that use cladistic analyses, psychological researchers need to define very carefully the traits that they are examining and to operationalize the traits in terms of observable behaviors.

Our primary message is that researchers trying to understand the evolutionary history of organisms or their traits would benefit from having the most complete understanding possible of the phylogenetic relationships of the relevant species. In some ways, our point is merely an extension of what most psychologists already accept: that our full evolutionary history and comparative data are relevant to the discipline. With the present article, our goal is to bring this background assumption to the forefront, placing tree thinking right at the heart of evolutionary arguments. We suggest that the explicit use of tree thinking represents (to many psychologists) a new way of interpreting organismal data that is fundamentally more faithful to the evolutionary process than traditional approaches. The shift in thinking that it produces—however subtle it may initially

seem—lights the way to a more intuitive path to understanding true evolutionary narratives. In doing so, tree thinking shows the way to a fully integrated understanding of human evolution in all of its length and depth.

AUTHOR NOTE

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NOTES

1. A *taxon* is any group of biological organisms that researchers have given a name in the classification system, including single species (e.g., *Homo sapiens*) and larger, more inclusive groups (e.g., the genus *Homo*, the class *Mammalia*, the phylum *Chordata*, etc.).
2. At a proximal level, traits are determined by genetic and environmental influences and an interaction between the two. For phylogenetic analyses to be relevant, it is necessary only that the traits have a genetic component.
3. The use of “design” refers to shaping by the process of natural selection and does not imply any higher-level designer, such as God.

REFERENCES

- Andrews, P. W., Gangestad, S. W., & Matthews, D. (2002). Adaptationism: How to carry out an exaptationist program. *Behavioral and Brain Sciences*, 25, 489–553.
- Arnason, U., Xu, X., Gullberg, A., & Graur, D. (1996). The Phoca Standard: An external molecular reference for calibrating recent evolutionary divergences. *Journal of Molecular Evolution*, 43, 41–45.
- Brooks, D. R., & McLennan, D. A. (1991). *Phylogeny, ecology, and behavior: A research program in comparative biology*. Chicago: University of Chicago Press.
- Buss, D. M. (1991). Evolutionary personality psychology. *Annual Review of Psychology*, 42, 459–491.
- Buss, D. M. (1995a). Evolutionary psychology: A new paradigm for psychological science. *Psychological Inquiry*, 6, 1–30.
- Buss, D. M. (1995b). Psychological sex differences: Origins through sexual selection. *American Psychologist*, 50, 164–168.
- Buss, D. M. (1999a). *Evolutionary psychology: The new science of the mind*. Boston: Allyn & Bacon.
- Buss, D. M. (1999b). Human nature and individual differences: The evolution of human personality. In L. A. Pervin & O. P. John (Eds.), *Handbook of personality: Theory and research* (pp. 31–56). New York: Guilford.
- Buss, D. M. (2000). *The dangerous passion*. New York: Free Press.
- Cavalli-Sforza, L. L., & Cavalli-Sforza, F. (1995). *The great human diasporas: The history of diversity and evolution*. Reading, MA: Addison-Wesley.

- Cosmides, L., & Tooby, J., (1997). *Evolutionary psychology: A primer*. Retrieved March 18, 2004, from University of California, Santa Barbara, Department of Psychology Web site: <http://www.psych.ucsb.edu/research/cep/primer.html>
- Cosmides, L., Tooby, J., & Barkow, J. H. (1992). Introduction: Evolutionary psychology and conceptual integration. In J. H. Barkow, L. Cosmides, & J. Tooby (Eds.), *The adapted mind: Evolutionary psychology and the generation of culture* (pp. 3–15). New York: Oxford University Press.
- Darwin, C. (1964). *On the origin of species*. Cambridge, MA: Harvard University Press. (Original work published 1859)
- Dean, C., Leakey, M. G., Reid, D., Schrenk, F., Schwartz, C. B. (2001, December 6). Growth processes in teeth distinguish modern humans from *Homo erectus* and earlier hominins. *Nature*, *414*, 628–631.
- de Queiroz, A., & Wimberger, P. H. (1993). The usefulness of behavior for phylogeny estimation: Levels of homoplasy in behavioral and morphological characters. *Evolution*, *47*, 46–60.
- Diamond, J. (1992). *The third chimpanzee: The evolution and future of the human animal*. New York: Harper Perennial.
- Domjan, M., & Purdy, J. E. (1995). Animal research in psychology: More than meets the eye of the general psychology student. *American Psychologist*, *50*, 496–503.
- Felsenstein, J. (1985). Phylogenies and the comparative method. *American Naturalist*, *125*, 1–15.
- Felsenstein, J. (2003). *Inferring phylogenies*. Sunderland, MA: Sinauer Associates.
- Fraley, R. C., Brumbaugh, C. C., & Marks, M. J. (2005). The evolution and function of adult attachment: A comparative and phylogenetic analysis. *Journal of Personality and Social Psychology*, *89*, 808–822.
- Fraley, R. C., & Shaver, P. R. (2000). Adult romantic attachment: Theoretical developments, emerging controversies, and unanswered questions. *Review of General Psychology*, *4*, 132–254.
- Gladwell, M. (2002). *The tipping point*. Boston, MA: Back Bay.
- Haig, B. D., & Durrant, R. (2000). Theory evaluation in evolutionary psychology. *Psychological Inquiry*, *11*, 34–38.
- Harvey, P. H., & Pagel, M. D. (1991). *The comparative method in evolutionary biology*. Oxford, England: Oxford University Press.
- Hennig, W. (1966). *Phylogenetic systematics*. Urbana: University of Illinois Press.
- Hillis, D. M., Moritz, C., & Mable, B. K. (1996). *Molecular systematics* (2nd ed.). Sunderland, MA: Sinauer.
- Hodos, W., & Campbell, C. B. G. (1969). Scala naturae: Why there is no theory in comparative psychology. *Psychological Review*, *76*, 337–350.
- Lesch, K. P., Meyer, J., Glatz, K., Flügge, G., Hinney, A., Hebebrand, J., et al. (1997). The 5-HT transporter gene-linked polymorphic region (5-HTTLPR) in evolutionary perspective: Alternative biallelic variation in rhesus monkeys. *Journal of Neural Transmission*, *104*, 1259–1266.
- Lickliter, R., & Honeycutt, H. (2003). Developmental dynamics: Toward a biologically plausible evolutionary psychology. *Psychological Bulletin*, *129*, 819–835.
- Lindenfors, P., & Tullberg, B. S. (1998). Phylogenetic analyses of primate size evolution: The consequences of sexual selection. *Biological Journal of the Linnean Society*, *64*, 413–447.
- Lipscomb, D. (1998). Basics of cladistic analysis. Diana Leigh Lipscomb's Web site at George Washington University. Retrieved January 30, 2007, from <http://www.gwu.edu/~clade/faculty/lipscomb/Cladistics.pdf>
- Losos, J. B. (1999). Uncertainty in the reconstruction of ancestral character states and lim-

- itations on the use of phylogenetic comparative methods. *Animal Behavior*, 58, 1319–1324.
- Maddison, W. P., & Maddison, D. R. (1992). *MacClade: Analysis of phylogeny and character evolution*. (Version 3.0 [Computer Software]). Sunderland, MA: Sinauer Associates.
- Miller, L. C., Putcha-Bhagavatula, A., & Pederson, W. C. (2002). Men's and women's mating preferences: Distinct evolutionary mechanisms? *Current Directions in Psychological Science*, 11, 88–93.
- Napier, J. R., & Napier, P. H. (1985). *The natural history of the primates*. Cambridge, MA: MIT.
- O'Hara, R. J. (1988). Homage to Clio, or, toward an historical philosophy for evolutionary biology. *Systematic Zoology*, 37, 142–155.
- O'Hara, R. J. (1997). Population thinking and tree thinking in systematics. *Zoologica Scripta*, 26, 323–329.
- Pagel, M. (2001). Accounting for phylogenetic and genealogical uncertainty in comparative studies. Talk presented at the Annual Meeting of the Human Behavior and Evolution Society, London, England.
- Pinker, S. (1994). *The language instinct*. London: Penguin.
- Povinelli, D. J., & Bering, J. M. (2002). The mentality of apes revisited. *Current Directions in Psychological Science*, 11, 115–119.
- Silverman, I., & Eals, M. (1992). Sex differences in spatial abilities: Evolutionary theory and data. In J. H. Barkow, L. Cosmides, & J. Tooby (Eds.), *The adapted mind: Evolutionary psychology and the generation of culture* (pp. 533–549). New York: Oxford.
- Skelton, P., Smith, A., & Monks, N. (2002). *Cladistics: A practical primer on CD-ROM*. Cambridge, England: Cambridge University Press.
- Swofford, D. L. (2001). *PAUP: Phylogenetic analysis using parsimony (and other methods)* (Version 4 [Computer Software]). Sunderland, MA: Sinauer Associates.
- Symons, D. (1990). Adaptiveness and adaptation. *Ethology and Sociobiology*, 11, 427–444.
- Symons, D. (1992). On the use and misuse of Darwinism in the study of human behavior. In J. H. Barkow, L. Cosmides, & J. Tooby (Eds.), *The adapted mind: Evolutionary psychology and the generation of culture* (pp. 137–159). New York: Oxford University Press.
- Tooby, J., & Cosmides, L. (1989). Adaptation versus phylogeny: The role of animal psychology in the study of human behavior. *International Journal of Comparative Psychology*, 2, 175–188.
- Tooby, J., & Cosmides, L. (1990). The past explains the present: Emotional adaptations and the structure of ancestral environments. *Ethology and Sociobiology*, 11, 375–424.
- Tooby, J., & Cosmides, L. (1992). The psychological foundations of culture. In J. H. Barkow, L. Cosmides, & J. Tooby (Eds.), *The adapted mind: Evolutionary psychology and the generation of culture* (pp. 19–136). New York: Oxford University Press.
- Wang, D. Y. C., Kumar, S., & Hedges, S. B. (1999). Divergence time estimates for the early history of animal phyla and the origin of plants, animals, and fungi. *Proceedings of the Royal Society London Series B*, 266, 163–171.

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