

Durrant, R., & Ellis, B.J. (2003). Evolutionary Psychology. In M. Gallagher & R.J. Nelson (Eds.), *Comprehensive handbook of psychology, Vol. 3: Biological psychology* (pp. 1-33). New York: Wiley & Sons.

CHAPTER 1

Evolutionary Psychology

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Evolutionary psychology is the application of the principles and knowledge of evolutionary biology to psychological theory and research. Its central assumption is that the human brain is comprised of a large number of specialized mechanisms that were shaped by natural selection over vast periods of time to solve the recurrent information-processing problems faced by our ancestors (Symons, 1995). These problems include such things as choosing which foods to eat, negotiating social hierarchies, dividing investment among offspring, and selecting mates. The field of evolutionary psychology focuses on identifying these information-processing problems, developing models of the brain-mind mechanisms that may have evolved to solve them, and testing these models in research (Buss, 1995; Tooby & Cosmides, 1992).

The field of evolutionary psychology has emerged dramatically over the last 15 years, as indicated by exponential growth in the number of empirical and theoretical articles in the area (Table 1.1). These articles extend into all branches of psychology—from cognitive psychology (e.g., Cosmides, 1989; Shepard, 1992) to developmental psychology (e.g., Ellis, McFadyen-Ketchum, Dodge, Pettit, & Bates, 1999; Weisfeld, 1999), abnormal psychology (e.g., Mealey, 1995;

Price, Sloman, Gardner, Gilbert, & Rhode, 1994), social psychology (e.g., Daly & Wilson, 1988; Simpson & Kenrick, 1997), personality psychology (e.g., Buss, 1991; Sulloway, 1996), motivation-emotion (e.g., Nesse & Berridge, 1997; Johnston, 1999), and industrial-organizational psychology (e.g., Colarelli, 1998; Studd, 1996). The first undergraduate textbook on evolutionary psychology was published in 1999 (Buss, 1999), and since then at least three other undergraduate textbooks have been published in the area (Barrett, Dunbar, & Lycett, 2002; Cartwright, 2000; Gaulin & McBurney, 2000).

In this chapter we provide an introduction to the field of evolutionary psychology. We describe the methodology that evolutionary psychologists use to explain human cognition and behavior. This description begins at the broadest level with a review of the basic, guiding assumptions that are employed by evolutionary psychologists. We then show how evolutionary psychologists apply these assumptions to develop more specific theoretical models that are tested in research. We use examples of sex and mating to demonstrate how evolutionary psychological theories are developed and tested.

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TABLE 1.1 Growth of Publications in the Area of Evolutionary Psychology, as Indexed by the PsycINFO Database

Years of Publication	Number of Publications ^a
1985–1988	4
1989–1992	25
1993–1996	100
1997–2000	231

^aNumber of articles, books, and dissertations in the PsycINFO database that include either the phrase *evolutionary psychology* or *evolutionary psychological* in the title, in the abstract, or as a keyword. All articles from the *Journal of Evolutionary Psychology*, which is a psychoanalytic journal, were excluded.

LEVELS OF EXPLANATION IN EVOLUTIONARY PSYCHOLOGY

Why do siblings fight with each other for parental attention? Why are men more likely than women to kill sexual rivals? Why are women most likely to have extramarital sex when they are ovulating? To address such questions, evolutionary psychologists employ multiple levels of explanation ranging from broad metatheoretical assumptions, to more specific middle-level theories, to actual hypotheses and

predictions that are tested in research (Buss, 1995; Ketelaar & Ellis, 2000). These levels of explanation are ordered in a hierarchy (see Figure 1.1) and constitute the methodology that evolutionary psychologists use to address questions about human nature.

At the top of the hierarchy are the basic metatheoretical assumptions of modern evolutionary theory. This set of guiding assumptions, which together are referred to as evolutionary metatheory, provide the foundation that evolutionary scientists use to build more specific theoretical models. We begin by describing (a) the primary set of metatheoretical assumptions that are consensually held by evolutionary scientists and (b) the special set of metatheoretical assumptions that distinguish evolutionary psychology. We use the term *evolutionary psychological metatheory* to refer inclusively to this primary and special set of assumptions together.

As shown in Figure 1.1, at the next level down in the hierarchy, just below evolutionary psychological metatheory, are *middle-level evolutionary theories*. These theories elaborate the basic metatheoretical assumptions into a particular psychological domain such as mating or cooperation. In this chapter we consider two related middle-level evolutionary theories—parental investment theory and good genes sexual

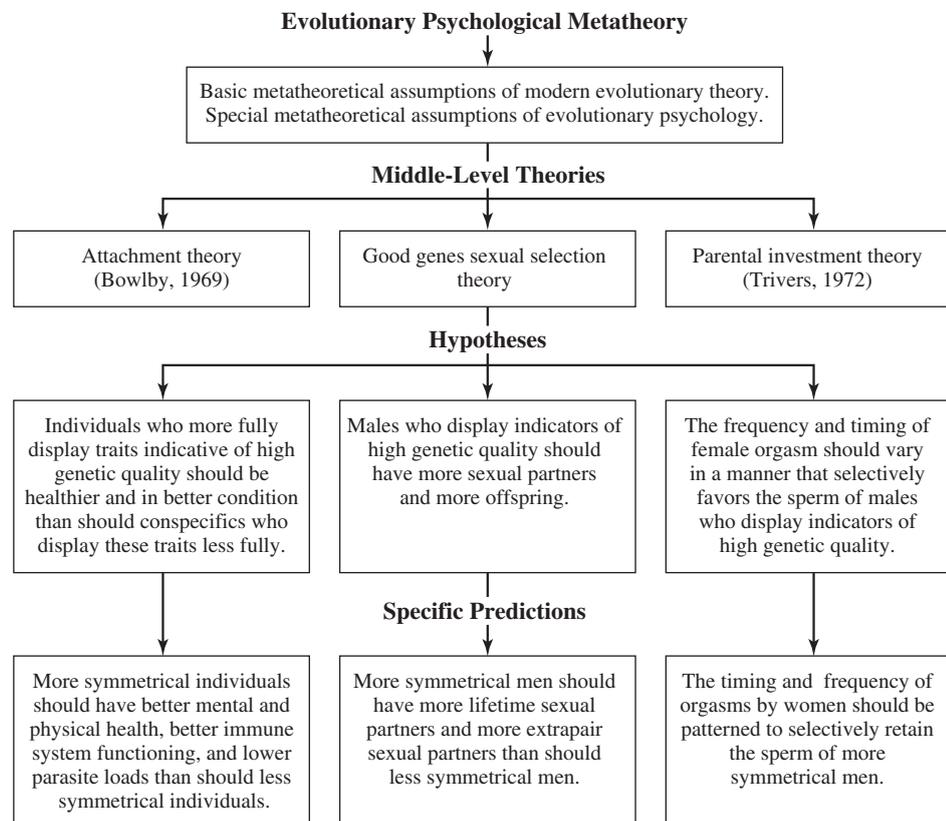


Figure 1.1 The hierarchical structure of evolutionary psychological explanations (adapted from Buss, 1995).

selection theory—each of which applies the assumptions of evolutionary psychological metatheory to the question of reproductive strategies. In different ways these middle-level theories attempt to explain differences between the sexes as well as variation within each sex in physical and psychological adaptations for mating and parenting.

At the next level down are the actual hypotheses and predictions that are drawn from middle-level evolutionary theories (Figure 1.1). A *hypothesis* is a general statement about the state of the world that one would expect to observe if the theory from which it was generated were in fact true. *Predictions* are explicit, testable instantiations of hypotheses. We conclude this chapter with an evaluation of hypotheses and specific predictions about sexual behavior that have been derived from good genes sexual selection theory. Special attention is paid to comparison of human and nonhuman animal literatures.

THE METATHEORY LEVEL OF ANALYSIS

Scientists typically rely on basic (although usually implicit) metatheoretical assumptions when they construct and evaluate theories. Evolutionary psychologists have often called on behavioral scientists to make explicit their basic assumptions about the origins and structure of the mind (see Gigerenzer, 1998). Metatheoretical assumptions shape how scientists generate, develop, and test middle-level theories and their derivative hypotheses and predictions (Ketelaar & Ellis, 2000). These basic assumptions are often not directly tested after they have been empirically established. Instead they are used as a starting point for further theory and research. Newton's laws of motion form the metatheory for classical mechanics, the principles of gradualism and plate tectonics provide a metatheory for geology, and the principles of adaptation through natural selection provide a metatheory for biology. Several scholars (e.g., Bjorklund, 1997; Richters, 1997) have argued that the greatest impediment to psychology's development as a science is the absence of a coherent, agreed-upon metatheory.

A metatheory operates like a map of a challenging conceptual terrain. It specifies both the landmarks and the boundaries of that terrain, suggesting which features are consistent and which are inconsistent with the core logic of the metatheory. In this way a metatheory provides a set of powerful methodological heuristics: "Some tell us what paths to avoid (negative heuristic), and others what paths to pursue (positive heuristic)" (Lakatos, 1970, p. 47). In the hands of a skilled researcher, a metatheory "provides a guide and prevents certain kinds of errors, raises suspicions of certain explanations or

observations, suggests lines of research to be followed, and provides a sound criterion for recognizing significant observations on natural phenomena" (Lloyd, 1979, p. 18). The ultimate contribution of a metatheory is that it synthesizes middle-level theories, allowing the empirical results of a variety of different theory-driven research programs to be explicated within a broader metatheoretical framework. This facilitates systematic cumulation of knowledge and progression toward a coherent big picture, so to speak, of the subject matter (Ketelaar & Ellis, 2000).

METATHEORETICAL ASSUMPTIONS THAT ARE CONSENSUALLY HELD BY EVOLUTIONARY SCIENTISTS

When asked what his study of the natural world had revealed about the nature of God, biologist J. B. S. Haldane is reported to have made this reply: "That he has an inordinate fondness for beetles." Haldane's retort refers to the extraordinary diversity of beetle species found throughout the world—some 290,000 species have so far been discovered (E. O. Wilson, 1992). Beetles, moreover, come in a bewildering variety of shapes and sizes, from tiny glittering scarab beetles barely visible to the naked eye to ponderous stag beetles with massive mandibles half the size of their bodies. Some beetles make a living foraging on lichen and fungi; others subsist on a diet of beetles themselves.

The richness and diversity of beetle species are mirrored throughout the biological world. Biologists estimate that anywhere from 10 to 100 million different species currently inhabit the Earth (E. O. Wilson, 1992), each one in some respect different from all others. How are we to explain this extraordinary richness of life? Why are there so many species and why do they have the particular characteristics that they do? The general principles of genetical evolution drawn from modern evolutionary theory, as outlined by W. D. Hamilton (1964) and instantiated in more contemporary so-called selfish gene theories of genetic evolution via natural and sexual selection, provide a set of core metatheoretical assumptions for answering these questions. Inclusive fitness theory conceptualizes genes or individuals as the units of selection (see Dawkins, 1976; Hamilton, 1964; Williams, 1966). In contrast, "multilevel selection theory" is based on the premise that natural selection is a hierarchical process that can operate at many levels, including genes, individuals, groups within species, or even multi-species ecosystems. Thus, multilevel selection theory is conceptualized as an elaboration of inclusive fitness theory (adding the concept of group-level adaptation) rather than an alternative to it (D. S. Wilson &

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Sober, 1994). Whereas inclusive fitness theory is consensually accepted among evolutionary scientists, multilevel selection theory is not. Thus, this review of basic metatheoretical assumptions only focuses on inclusive fitness theory.

Natural Selection

During his journey around the coastline of South America aboard the HMS *Beagle*, Charles Darwin was intrigued by the sheer diversity of animal and plant species found in the tropics, by the way that similar species were grouped together geographically, and by their apparent fit to local ecological conditions. Although the idea of biological evolution had been around for some time, what had been missing was an explanation of *how* evolution occurred—that is, what had been missing was an account of the *mechanisms* responsible for evolutionary change. Darwin's mechanism, which he labeled *natural selection*, served to explain many of the puzzling facts about the biological world: Why were there so many species? Why are current species so apparently similar in many respects both to each other and to extinct species? Why do organisms have the specific characteristics that they do?

The idea of natural selection is both elegant and simple, and can be neatly encapsulated as the result of the operation of three general principles: (a) phenotypic variation, (b) differential fitness, and (c) heritability.

As is readily apparent when we look around the biological world, organisms of the same species vary in the characteristics that they possess; that is, they have slightly different *phenotypes*. A whole branch of psychology—personality and individual differences—is devoted to documenting and understanding the nature of these kinds of differences in our own species. Some of these differences found among members of a given species will result in differences in *fitness*—that is, some members of the species will be more likely to survive and reproduce than will others as a result of the specific characteristics that they possess. For evolution to occur, however, these individual differences must be *heritable*—that is, they must be reliably passed on (via shared genes) from parents to their offspring. Over time, the characteristics of a population of organisms will change as heritable traits that enhance fitness will become more prevalent at the expense of less favorable variations.

For example, consider the evolution of bipedalism in humans. Paleoanthropological evidence suggests that upright walking (at least some of the time) was a feature of early hominids from about 3.5 million years ago (Lovejoy, 1988). Presume that there was considerable variation in the propensity to walk upright in the ancestors of this early hominid species as the result of differences in skeletal structures, relevant neural

programs, and behavioral proclivities. Some hominids did and some did not. Also presume that walking on two feet much of the time conferred some advantage in terms of survival and reproductive success. Perhaps, by freeing the hands, bipedalism allowed objects such as meat to be carried long distances (e.g., Lovejoy, 1981). Perhaps it also served to cool the body by reducing the amount of surface area exposed to the harsh tropical sun, enabling foraging throughout the hottest parts of the day (e.g., Wheeler, 1991). Finally, presume that these differences in the propensity for upright walking were heritable in nature—they were the result of specific genes that were reliably passed on from parents to offspring. The individuals who tended to walk upright would be, on average, more likely to survive (and hence, to reproduce) than would those who did not. Over time the genes responsible for bipedalism would become more prevalent in the population as the individuals who possessed them were more reproductively successful than were those who did not, and bipedalism itself would become pervasive in the population.

Several points are important to note here. First, natural selection shapes not only the physical characteristics of organisms, but also their behavioral and cognitive traits. The shift to bipedalism was not simply a matter of changes in the anatomy of early hominids; it was also the result of changes in behavioral proclivities and in the complex neural programs dedicated to the balance and coordination required for upright walking. Second, although the idea of natural selection is sometimes encapsulated in the slogan *the survival of the fittest*, ultimately it is *reproductive* fitness that counts. It doesn't matter how well an organism is able to survive. If it fails to pass on its genes, then it is an evolutionary dead end, and the traits responsible for its enhanced survival abilities will not be represented in subsequent generations. This point is somewhat gruesomely illustrated by many spider species in which the male serves as both meal and mate to the female—often at the same time. Ultimately, although one must survive to reproduce, reproductive goals take precedence.

Adaptation

Natural selection is the primary process which is responsible for evolutionary change over times as more favorable variants are retained and less favorable ones are rejected (Darwin, 1859). Through this filtering process, natural selection produces small incremental modifications in existing phenotypes, leading to an accumulation of characteristics that are organized to enhance survival and reproductive success. These characteristics that are produced by natural selection are termed *adaptations*. Adaptations are inherited and

reliably developing characteristics of species that have been selected for because of their causal role in enhancing the survival and reproductive success of the individuals that possess them (see Buss, Haselton, Shackelford, Bleske, & Wakefield, 1998; Dawkins, 1986; Sterelny & Griffiths, 1999; Williams, 1966, 1992, for definitions of adaptation).

Adaptations have biological *functions*. The immune system functions to protect organisms from microbial invasion, the heart functions as a blood pump, and the cryptic coloring of many insects has the function of preventing their detection by predators. The core idea of evolutionary psychology is that many psychological characteristics are adaptations—just as many physical characteristics are—and that the principles of evolutionary biology that are used to explain our bodies are equally applicable to our minds. Thus, various evolutionary psychological research programs have investigated psychological mechanisms—for mate selection, fear of snakes, face recognition, natural language, sexual jealousy, and so on—as biological adaptations that were selected for because of the role they played in promoting reproductive success in ancestral environments.

It is worth noting, however, that natural selection is not the only causal process responsible for evolutionary change (e.g., Gould & Lewontin, 1979). Traits may also become fixated in a population by the process of genetic drift, whereby neutral or even deleterious characteristics become more prevalent due to *chance* factors. This may occur in small populations because the fittest individuals may turn out—due to random events—not to be the ones with the greatest reproductive success. It does not matter how fit you are if you drown in a flood before you get a chance to reproduce. Moreover, some traits may become fixated in a population not because they enhance reproductive success, but because they are genetically or developmentally yoked to adaptations that do. For example, the modified wrist bone of the panda (its “thumb”) seems to be an adaptation for manipulating bamboo, but the genes responsible for this adaptation also direct the enlarged growth of the corresponding bone in the panda’s foot, a feature that serves no function at all (Gould, 1980).

There is much debate among evolutionary biologists and philosophers of biology regarding the relative importance of different evolutionary processes (see Sterelny & Griffiths, 1999, for a good introduction to these and other issues in the philosophy of biology). The details of these disputes, however, need not concern us here. What is important to note is that not all of the products of evolution will be biological adaptations with evolved functions. The evolutionary process also results in *by-products* of adaptations, as well as a residue of *noise* (Buss et al., 1998; Tooby & Cosmides,

1992). Examples of by-products are legion. The sound that hearts make when they beat, the white color of bones, and the human chin are all nonfunctional by-products of natural selection. In addition, random variation in traits—as long as this variation is selectively neutral (neither enhancing nor reducing biological fitness)—can also be maintained as residual noise in organisms.

Demarcating the different products of evolution is an especially important task for evolutionary psychologists. It has often been suggested that many of the important phenomena that psychologists study—for example, reading, writing, religion—are by-products of adaptations rather than adaptations themselves (e.g., Gould, 1991a). Of course, even by-products can be furnished with evolutionary explanations in terms of the adaptations to which they are connected (Tooby & Cosmides, 1992). Thus, for example, the whiteness of bones is a by-product of the color of calcium salts, which give bones their hardness and rigidity; the chin is a by-product of two growth fields; and reading and writing are by-products (in part) of the evolved mechanisms underlying human language (Pinker, 1994).

The important question is *how* to distinguish adaptations from nonadaptations in the biological world. Because we cannot reverse time and observe natural selection shaping adaptations, we must make inferences about evolutionary history based on the nature of the traits we see today. A variety of methods can (and should) be employed to identify adaptations (see M. R. Rose & Lauder, 1996). Evolutionary psychologists, drawing on the work of George Williams (1966), typically emphasize the importance of *special design* features such as economy, efficiency, complexity, precision, specialization, reliability, and functionality for identifying adaptations (e.g., Buss et al., 1998; Pinker, 1997; Tooby & Cosmides, 1990). One hallmark that a trait is the product of natural selection is that it demonstrates *adaptive complexity*—that is, the trait is composed of a number of interrelated parts or systems that operate in concert to generate effects that serve specific functions (Dawkins, 1986; Pinker, 1997).

Echolocation in bats is a good example of such a trait. A collection of interrelated mechanisms allows foraging bats to maneuver around obstacles in complete darkness and to pick out small rapidly moving prey on the wing. Echolocating bats have a number of *specialized* mechanisms that precisely, reliably, and efficiently enable them to achieve the *function* of nocturnal locomotion and foraging. Bats have mechanisms that allow them to produce rapid, high-frequency, short-wavelength cries that are reflected by small objects. Moreover, the frequency and rapidity of these cries are modified depending on the distance of the object being detected (low-frequency waves penetrate further but can only be used to

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detect large objects). Bats also have specialized mechanisms that protect their ears while they are emitting loud sounds, and their faces are shaped to enhance the detection of their returning echoes. It is extraordinary unlikely that such a complex array of intertwining processes could have arisen by chance or as a *by-product* of evolutionary processes. Thus, one has clear warrant in this case to assert that echolocation in bats is a biological adaptation.

Many traits, however, may not be so clearly identifiable as adaptations. Furthermore, there are often disputes about just what *function* some trait has evolved to serve, even if one can be reasonably sure that it is the product of natural selection. In adjudicating between alternative evolutionary hypotheses, one can follow the same sort of strategies that are employed when comparing alternative explanations in any domain in science—that is, one should favor the theory or hypothesis that best explains the evidence at hand (Haig & Durrant, 2000; Holcomb, 1998) and that generates novel hypotheses that lead to new knowledge (Ketelaar & Ellis, 2000).

Consider, for example, the alternative explanations that have been offered for the origin of orgasm in human females.

- Female orgasm serves no evolved function and is a by-product of selection on male orgasm, which is necessary for fertilization to occur (Gould, 1991b, pp. 124–129; Symons, 1979).
- Orgasm is an adaptation that promotes pair-bonding in the human species (Eibl-Eibesfeldt, 1989).
- Female orgasm is an adaptation that motivates females to seek multiple sexual partners, confusing males about paternity and thus reducing the probability of subsequent male infanticide (Hrdy, 1981).
- Female orgasm is an adaptation that serves to enhance sperm retention, therefore allowing females to exert some control over the paternity of their offspring via differential patterns of orgasm with specific male partners, especially those of high genetic quality (Baker & Bellis, 1993; Smith, 1984).

Although all of these models have some plausibility, it is the last suggestion that is beginning to be accepted as the best current explanation. Baker and Bellis (1993) have demonstrated that females retain more sperm if they experience copulatory orgasms up to 45 min after—or at the same time as—their male partners. Thus, depending on their timing, orgasms appear to enhance the retention of sperm via the “up-suck” from the vagina into the cervix. The selective sperm retention model predicts that women will experience more orgasms—and specifically, more high-sperm-retention orgasms—with men who have specific indicators of genetic

quality. This prediction has been supported in research on dating and married couples (Thornhill, Gangestad, & Comer, 1995). Moreover, the occurrence of high sperm retention orgasms are a significant predictor of a desire for pregnancy in women, suggesting that female orgasms are one mechanism for increasing the likelihood of conception (Singh, Meyer, Zambarano, & Hurlbert, 1998).

Although there are a number of theories of extrapair mating in human females (mating that occurs outside of a current, ongoing relationship), one prominent suggestion is that extrapair mating has evolved to enhance reproductive success by increasing selective mating with males who demonstrate high genetic quality (e.g., Gangestad, 1993; Greiling & Buss, 2000). In support of this idea, men who possess indicators of high genetic quality (as assessed by degree of symmetry of bilateral physical traits) are more likely to be chosen by women specifically as extrapair sex partners but not as partners in long-term relationships (Gangestad & Simpson, 2000). Further, Bellis and Baker (1990) found that women were most likely to copulate with extrapair partners but not with in-pair partners during the fertile phase of their menstrual cycles. Finally, as a result of the type and frequency of orgasms experienced by women, it appears that levels of sperm retention are significantly higher during extrapair copulations than during copulations with in-pair partners (Baker & Bellis, 1995).

In summary, although more research needs to be done, our best current explanation for the human female orgasm is that it is an adaptation specifically, precisely, and efficiently designed to manipulate the paternity of offspring by favoring the sperm of males of high genetic quality. This model (a) concurs with what is known about female orgasm; (b) generated specific, testable predictions about patterns of variation in female orgasm that were as yet unobserved and were not forecast by competing models; (c) generated interesting new lines of research on female orgasm that provided support for the predictions; and (d) led to acquisition of new knowledge about the timing and probability of female orgasm with different partners.

Sexual Selection

Not all adaptations can be conceptualized as adaptations for survival per se. Although the bat’s complex system of echolocation enables it to navigate and forage in darkness, the human female orgasm has no such obvious utilitarian function. As Darwin (1871) clearly recognized, many of the interesting features that plants and animals possess, such as the gaudy plumage and elaborate songs of many male birds, serve no obvious survival functions. In fact, if anything, such traits

are likely to reduce survival prospects by attracting predators, impeding movement, and so on. Darwin's explanation for such characteristics was that they were the product of a process that he labeled *sexual selection*. This kind of selection arises not from a struggle to survive, but rather from the competition that arises over mates and mating (Andersson, 1994; Andersson & Iwasa, 1996). If—for whatever reason—having elongated tail feathers or neon blue breast plumage enables one to attract more mates, then such traits will increase reproductive success. Moreover, to the extent that such traits are also heritable, they will be likely to spread in the population, even if they might diminish survival prospects.

Although there is some debate about how best to conceptualize the relationship between natural and sexual selection, sexual selection is most commonly considered a component or special case of natural selection associated with mate choice and mating. This reflects the fact that differential fitness concerns differences in both survival and reproduction. Miller (1999) notes that “both natural selection and sexual selection boil down to one principle: Some genes replicate themselves better than others. Some do it by helping their bodies survive better, and some by helping themselves reproduce better” (p. 334). Whereas the general processes underlying natural and sexual selection are the same (variation, fitness, heritability), the products of natural and sexual selection can look quite different. The later parts of this chapter review sexual selection theory and some of the exciting research it has generated on human mating behavior.

To summarize, we have introduced the ideas of natural and sexual selection and shown how these processes generate adaptations, by-products, and noise. We have also discussed ways in which adaptations can be distinguished from non-adaptations and have offered some examples drawn from recent research in evolutionary psychology. It is now time to consider an important theoretical advance in evolutionary theorizing that occurred in the 1960s—inclusive fitness theory—that changed the way biologists (and psychologists) think about the nature of evolution and natural selection. Inclusive fitness theory is the modern instantiation of Darwin's theory of adaptation through natural and sexual selection.

Inclusive Fitness Theory

Who are adaptations good for? Although the answer may seem obvious—that they are good for the organisms possessing the adaptations—this answer is only partially correct; it fails to account for the perplexing problem of altruism. As Darwin puzzled, how could behaviors evolve that conferred advantage to other organisms at the expense of the principle organism that performed the behaviors? Surely such acts of

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generosity would be eliminated by natural selection because they decreased rather than increased the individual's chances of survival and reproduction.

The solution to this thorny evolutionary problem was hinted at by J. B. S. Haldane, who, when he was asked if he would lay down his life for his brother, replied, “No, but I would for two brothers or eight cousins” (cited in Pinker, 1997, p. 400). Haldane's quip reflects the fact that we each share (on average) 50% of our genes with our full siblings and 12.5% of our genes with our first cousins. Thus, from the gene's-eye point of view, it is just as advantageous to help two of our siblings to survive and reproduce as it is to help ourselves. This insight was formalized by W. D. Hamilton (1964) and has come to be known variously as *Hamilton's rule*, *selfish-gene theory* (popularized by Dawkins, 1976), *kin-selection theory*, or *inclusive fitness theory*.

The core idea of inclusive fitness theory is that evolution works by increasing copies of genes, not copies of the individuals carrying the genes. Thus, the genetic code for a trait that reduces personal reproductive success can be selected for if the trait, on average, leads to more copies of the genetic code in the population. A genetic code for altruism, therefore, can spread through kin selection if (a) it causes an organism to help close relatives to reproduce and (b) the cost to the organism's own reproduction is offset by the reproductive benefit to those relatives (discounted by the probability that the relatives who receive the benefit have inherited the same genetic code from a common ancestor). For example, a squirrel who acts as a sentinel and emits loud alarm calls in the presence of a predator may reduce its own survival chances by directing the predator's attention to itself; however, the genes that are implicated in the development of alarm-calling behavior can spread if they are present in the group of close relatives who are benefited by the alarm calling.

SPECIAL METATHEORETICAL ASSUMPTIONS OF EVOLUTIONARY PSYCHOLOGY

In addition to employing inclusive fitness theory, evolutionary psychologists endorse a number of special metatheoretical assumptions concerning how to apply inclusive fitness theory to human psychological processes. In particular, evolutionary psychologists argue that we should primarily be concerned with how natural and sexual selection have shaped *psychological mechanisms* in our species; that a *multiplicity* of such mechanisms will exist in the human mind; and that they will have evolved to solve *specific* adaptive problems encountered in *ancestral environments*. Although these

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general points also apply to other species, they are perhaps especially pertinent in a human context and they have received much attention from evolutionary psychologists. We consider these special metatheoretical assumptions, in turn, in the following discussion.

Psychological Mechanisms as the Main Unit of Analysis

Psychological adaptations, which govern mental and behavioral processes, are referred to by evolutionary psychologists as *psychological mechanisms*. Evolutionary psychologists emphasize that genes do not cause behavior and cognition directly. Rather, genes provide blueprints for the construction of psychological mechanisms, which then interact with environmental factors to produce a range of behavioral and cognitive outputs. Most research in evolutionary psychology focuses on identifying evolved psychological mechanisms because it is at this level where invariances occur. Indeed, evolutionary psychologists assert that there is a core set of universal psychological mechanisms that comprise our shared human nature (Tooby & Cosmides, 1992).

To demonstrate the universal nature of our psychological mechanisms, a common rhetorical device used by evolutionary psychologists (e.g., Brown, 1991; Ellis, 1992; Symons, 1987) is to imagine that a heretofore unknown tribal people is suddenly discovered. Evolutionary psychologists are willing to make a array of specific predictions—in advance—about the behavior and cognition of this newly discovered people. These predictions concern criteria that determine sexual attractiveness, circumstances that lead to sexual arousal, taste preferences for sugar and fat, use of cheater detection procedures in social exchange, nepotistic bias in parental investment and child abuse, stages and timing of language development, sex differences in violence, different behavioral strategies for people high and low in dominance hierarchies, perceptual adaptations for entraining, tracking, and predicting animate motion, and so on. The only way that the behavior and cognition of an unknown people can be known in advance is if we share with those people a universal set of specific psychological mechanisms.

Buss (1999, pp. 47–49) defines an evolved psychological mechanism as a set of structures inside our heads that (a) exist in the form they do because they recurrently solved specific problems of survival and reproduction over evolutionary history; (b) are designed to take only certain kinds of information from the world as input; (c) process that information according to a specific set of rules and procedures; (d) generate output in terms of information to other psychological mechanisms and physiological activity or manifest behavior that is directed at solving specific adaptive problems

(as specified by the input that brought the psychological mechanism on-line).

Consider, for example, the psychological mechanisms underlying disgust and food aversions in humans. These psychological mechanisms, which are designed to find certain smells and tastes more aversive than others, can be said to have several features:

- They exist in the form they do because they recurrently solved specific problems of survival over evolutionary history. As an omnivorous species, humans consume a wide variety of plant and animal substances. Not all such substances, however, are safe to eat. Many plants contain natural toxins, and many animal products are loaded with parasites that can cause sickness and death. The psychological mechanisms underlying disgust and food aversions function to reduce the probability of ingesting and digesting dangerous plant and animal substances.
- These mechanisms are designed to take a specific and limited class of stimuli as input: the sight, touch, and especially taste and smell of plant and animal substances that were regularly harmful to our ancestors. Feces and animal products are especially likely to harbor lethal microorganisms and, cross-culturally, are most likely to elicit disgust (Rozin & Fallon, 1987).
- Inputs to the psychological mechanisms underlying disgust and food aversions are then processed according to a set of decision rules and procedures, such as (a) avoid plant substances that taste or smell bitter or especially pungent (indicating high concentrations of plant toxins; Profet, 1992); (b) avoid animal substances that emit smells suggestive of spoilage (indicating high levels of toxin-producing bacteria; Profet, 1992); (c) avoid foods that one has become sick after consuming in the past (Seligman & Hager, 1972); (d) and avoid foods that were not part of one's diet in the first few years of life (especially if it is an animal product; Cashdan, 1994).
- When relevant decision rules are met, behavioral output is then generated, manifested by specific facial expressions, physical withdrawal from the offending stimuli, nausea, gagging, spitting, and vomiting.
- This output is specifically directed at solving the adaptive problem of avoiding consumption of harmful substances and of expelling these substances from the body as rapidly as possible if they have been consumed.

Evolutionary psychologists assume that humans possess a large number of specific psychological mechanisms (e.g., the ones underlying food aversions and disgust) that are directed at solving specific adaptive problems. This assumption is

commonly referred to as the *domain specificity* or *modularity* of mind.

Domain Specificity of Psychological Mechanisms

Evolutionary psychologists posit that the mind comprises a large number of content-saturated (*domain-specific*) psychological mechanisms (e.g., Buss, 1995; Cosmides & Tooby, 1994; Pinker, 1997). Although evolutionary psychologists assert that the mind is *not* comprised primarily of content-free (*domain-general*) psychological mechanisms, it is likely that different mechanisms differ in their levels of specificity and that there are some higher-level executive mechanisms that function to integrate information across more specific lower-level mechanisms.

The rationale behind the domain-specificity argument is fairly straightforward: What counts as adaptive behavior differs markedly from domain to domain. The sort of adaptive problems posed by food choice, mate choice, incest avoidance, and social exchange require different kinds of solutions. As Don Symons (1992) has pointed out, there is no such thing as a general solution because there is no such thing as a general problem. The psychological mechanisms underlying disgust and food aversions, for example, are useful in solving problems of food choice but not those of mate choice. If we used the same decision rules in both domains, we would end up with some very strange mates and very strange meals indeed. Given the large array of adaptive problems faced by our ancestors, we should expect a commensurate number of domain-specific solutions to these problems.

A clear analogy can be drawn with the functional division of labor in human physiology. Different organs have evolved to serve different functions and possess properties that allow them to fulfill those functions efficiently, reliably, and economically: The heart pumps blood, the liver detoxifies poisons, the kidneys excrete urine, and so on. A super, all-purpose, domain-general internal organ—heart, liver, kidney, spleen, and pancreas rolled into one—faces the impossible task of serving multiple, incompatible functions. Analogously, a super, all-purpose, domain-general brain-mind mechanism faces the impossible task of efficiently and reliably solving the plethora of behavioral problems encountered by humans in ancestral environments. Thus, neither an all-purpose physiological organ nor an all-purpose brain-mind mechanism is likely to evolve. Evolutionary psychologists argue that the human brain-mind instead contains domain-specific information processing rules and biases.

These evolved domain-specific mechanisms are often referred to as psychological *modules*. The best way to conceptualize such modules, however, is a matter of some

contention. Jerry Fodor (1983), in his classic book *The Modularity of Mind*, suggests that modules have the properties of being domain-specific, innately specified, localized in the brain, and able to operate relatively independently from other such systems. Potentially good examples of such psychological modules in humans include language (Pinker, 1994), face recognition (Bruce, 1988), and theory of mind (Baron-Cohen, 1995). For example, the systems underlying language ability are specially designed to deal with linguistic information, emerge in development with no formal tuition, and appear to be located in specific brain regions independent from other systems, as indicated by specific language disorders (aphasias), which can arise from localized brain damage.

Not all of the evolved psychological mechanisms proposed by evolutionary psychologists, however, can be so readily characterized. Many mechanisms—such as landscape preferences, sexual jealousy, and reasoning processes—may be domain-specific in the sense of addressing specific adaptive problems, but they are neither clearly localized (neurally speaking) nor especially autonomous from other systems. It seems most plausible to suggest that there is a considerable degree of integration and interaction between different psychological mechanisms (Karmiloff-Smith, 1992). It is this feature of human cognitive organization that allows for the tremendous flexibility and creativity of human thought processes (Browne, 1996). It is also not clear whether domain specificity is best characterized by way of specific computational mechanisms or in terms of domain-specific bodies of mental representations (Samuels, 2000).

We should also expect—in addition to whatever taxonomy of specialized mechanisms that is proposed for the human mind—that there are some domain-general processes as well. The mechanisms involved in classical and operant conditioning may be good candidates for such domain-general processes. However, even these domain-general processes appear to operate in different ways, depending on the context in question. As illustrated in a series of classic studies by Garcia and colleagues (e.g., Garcia & Koelling, 1966), rats are more likely to develop some (adaptively relevant) associations than they are others, such as that between food and nausea but not between buzzers and nausea. Similar prepared learning biases have been demonstrated in monkeys (Mineka, 1992) and also in humans (Seligman & Hagar, 1972). For example, humans are overwhelmingly more likely to associate anxiety and fear with evolutionarily relevant threats such as snakes, spiders, social exclusion, and heights than with more dangerous but evolutionarily novel threats such as cars, guns, and power lines (Marks & Nesse, 1994).

In sum, although some doubt remains over the nature and number of domain-specific psychological mechanisms that

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humans (and other animals) possess, the core idea of specialized adaptive processes instantiated in psychological mechanisms remains central to evolutionary psychology. An approach to the human mind that highlights the importance of evolved domain-specific mechanisms can advance our understanding of human cognition by offering a theoretically guided taxonomy of mental processes—one that promises to better carve the mind at its natural joints.

The Environment of Evolutionary Adaptedness

The concept of biological adaptation is necessarily an historical one. When we claim that the thick insulating coat of the polar bear is as an adaptation, we are claiming that possession of that trait advanced reproductive success in *ancestral* environments. All claims about adaptation are claims about the past because natural selection is a gradual, cumulative process. The polar bear's thick coat arose through natural selection because it served to ward off the bitter-cold arctic weather during the polar bear's evolutionary history. However, traits that served adaptive functions and thus were selected for in past environments may not still be adaptive in present or future environments. In a globally warmed near-future, for example, the polar bear's lustrous pelt may become a handicap that reduces the fitness of its owner due to stress from overheating. In sum, when environments change, the conditions that proved advantageous to the evolution of a given trait may no longer exist; yet the trait often remains in place for some time because evolutionary change occurs slowly. Such vestigial traits are eventually weeded out by natural selection (if they consistently detract from fitness).

The environment in which a given trait evolved is termed its *environment of evolutionary adaptedness* (EEA). The EEA for our species is sometimes loosely characterized as the Pleistocene—the 2-million-year period that our ancestors spent as hunter-gatherers in the African savanna, prior to the emergence of agriculture some 10,000 years ago. The emphasis on the Pleistocene is perhaps reasonable given that many of the evolved human characteristics of interest to psychologists, such as language, theory of mind, sophisticated tool use, and culture, probably arose during this period. However, a number of qualifications are in order. First, the Pleistocene itself captures a large span of time, in which many changes in habitat, climate and species composition took place. Second, there were a number of different hominid species in existence during this time period, each inhabiting its own specific ecological niche. Third, many of the adaptations that humans possess have their origins in time periods that substantially predate the Pleistocene era. For example, the mechanisms underlying human attachment and

sociality have a long evolutionary history as part of our more general primate and mammalian heritage (Foley, 1996). Finally, some evolution (although of a relatively minor character) has also probably occurred in the last 10,000 years, as is reflected in population differences in disease susceptibility, skin color, and so forth (Irons, 1998).

Most important is that different adaptations will have different EEAs. Some, like language, are firmly anchored in approximately the last 2 million years; others, such as infant attachment, reflect a much lengthier evolutionary history (Hrdy, 1999). It is important, therefore, that we distinguish between the EEA of a *species* and the EEA of an *adaptation*. Although these two may overlap, they need not necessarily do so (Crawford, 1998). Tooby and Cosmides (1990) summarize these points clearly when they state that “the ‘environment of evolutionary adaptedness’ (EEA) is not a place or a habitat, or even a time period. Rather, it is a statistical composite of the adaptation-relevant properties of the ancestral environments encountered by members of ancestral populations, weighted by their frequency and fitness-consequences” (pp. 386–387). Delineating the specific features of the EEA for any given adaptation, then, requires an understanding of the evolutionary history of that trait (e.g., is it shared by other species, or is it unique?) and a detailed reconstruction of the relevant environmental features that were instrumental in its construction (Foley, 1996).

It is not uncommon to hear the idea that changes wrought by “civilization” over the last 10,000 years have radically changed our adaptive landscape as a species. After all, back on the Pleistocene savanna there were no fast food outlets, plastic surgery, antibiotics, dating advertisements, jet airliners, and the like. Given such manifest changes in our environment and ways of living, one would expect much of human behavior to prove odd and maladaptive as psychological mechanisms that evolved in ancestral conditions struggle with the many new contingencies of the modern world. An assumption of evolutionary psychology, therefore, is that mismatches between modern environments and the EEA often result in dysfunctional behavior (such as overconsumption of chocolate ice cream, television soap operas, video games, and pornography). Real-life examples of this phenomenon are easy to find. Our color constancy mechanisms, for instance, evolved under conditions of natural sunlight. These mechanisms fail, however, under some artificial lighting conditions (Shepard, 1992). Similarly, the dopamine-mediated reward mechanisms found in the mesolimbic system in the brain evolved to provide a pleasurable reward in the presence of adaptively relevant stimuli like food or sex. In contemporary environments, however, these same mechanisms are subverted by the use of psychoactive drugs such as

cocaine and amphetamines, which deliver huge dollops of pleasurable reward in the absence of the adaptively relevant stimuli—often to the users' detriment (Nesse & Berridge, 1997).

Although we can detail many ways in which contemporary and ancestral environments differ, much probably also remains the same. Humans everywhere, for example, still find and attract mates, have sex, raise families, make friends, have extramarital affairs, compete for status, consume certain kinds of food, spend time with kin, gossip, and so forth (Crawford, 1998). Indeed, Crawford (1998) argues that we should accept as our null hypothesis that current and ancestral environments do *not* differ in important and relevant respects for any given adaptation. Most important is that current and ancestral environments do not have to be identical in every respect for them to be the same in terms of the relevant details required for the normal development and expression of evolved psychological mechanisms. For example, the languages that people speak today are undoubtedly different from the ones our ancestors uttered some 100,000 years ago. However, what is necessary for the development of language is not the input of some specific language, but rather any kind of structured linguistic input. Adaptations have *reaction norms*, which are the range of environmental parameters in which they develop and function normally. For most adaptations, these norms may well encompass both current and ancestral environments (Crawford, 1998).

To summarize, in this section we have outlined three special metatheoretical assumptions that evolutionary psychologists use in applying inclusive fitness theory to human cognition and behavior. First, the appropriate unit of analysis is typically considered to be at the level of evolved psychological mechanisms, which underlie behavioral output. Second, evolutionary psychologists posit that these mechanisms are both large in number and constitute specialized information processing rules that were designed by natural selection to solve specific adaptive problems encountered during human evolutionary history. Finally, these mechanisms have evolved in ancestral conditions and are characterized by specific EEAs, which may or may not differ in important respects from contemporary environments.

THE MIDDLE-LEVEL THEORY LEVEL OF ANALYSIS

The metatheoretical assumptions employed by evolutionary psychologists are surrounded by a protective belt, so to speak, of auxiliary theories, hypotheses, and predictions (see Buss, 1995; Ketelaar & Ellis, 2000). A primary function of

the protective belt is to provide an empirically verifiable means of linking metatheoretical assumptions to observable data. In essence, the protective belt serves as the problem-solving machinery of the metatheoretical research program because it is used to provide indirect evidence in support of the metatheory's basic assumptions (Lakatos, 1970). The protective belt does more, however, than just protect the meta-theoretical assumptions: It uses these assumptions to extend our knowledge of particular domains. For example, a group of physicists who adopt a Newtonian metatheory may construct several competing middle-level theories concerning a particular physical system, but none of these theories would violate Newton's laws of mechanics. Each physicist designs his or her middle-level theory to be consistent with the basic assumptions of the metatheory, even if the middle-level theories are inconsistent with each other. Competing middle-level theories attempt to achieve the best operationalization of the core logic of the metatheory as it applies to a particular domain. The competing wave and particle theories of light (generated from quantum physics metatheory) are excellent contemporary exemplars of this process.

After a core set of metatheoretical assumptions become established among a community of scientists, the day-to-day workings of these scientists are generally characterized by the *use of*—not the *testing of*—these assumptions. Metatheoretical assumptions are used to construct plausible alternative middle-level theories. After empirical evidence has been gathered, one of the alternatives may emerge as the best available explanation of phenomena in that domain. It is this process of constructing and evaluating middle-level theories that characterizes the typical activities of scientists attempting to use a metatheory to integrate, unify, and connect their varying lines of research (Ketelaar & Ellis, 2000).

Middle-level evolutionary theories are specific theoretical models that provide a link between the broad metatheoretical assumptions used by evolutionary psychologists and the specific hypotheses and predictions that are tested in research. Middle-level evolutionary theories are consistent with and guided by evolutionary metatheory but in most cases cannot be directly deduced from it (Buss, 1995). Middle-level theories elaborate the basic assumptions of the metatheory into a particular psychological domain. For example, parental investment theory (Trivers, 1972) applies evolutionary metatheory to the question of why, when, for what traits, and to what degree selection favors *differences between the sexes* in reproductive strategies. Conversely, attachment theory (Bowlby, 1969; Simpson, 1999), life history theory (e.g., Chisholm, 1999), and good genes sexual selection theory (e.g., Gangestad & Simpson, 2000) each in different ways applies evolutionary metatheory to the question of why, when,

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for what traits, and to what degree selection favors *differences within each sex* in reproductive strategies. In this section we review parental investment theory and good genes sexual selection theory as exemplars of middle-level evolutionary theories.

Parental Investment Theory

Imagine that a man and a woman each had sexual intercourse with 100 different partners over the course of a year. The man could potentially sire 100 children, whereas the woman could potentially give birth to one or two. This huge discrepancy in the number of offspring that men and women can potentially produce reflects fundamental differences between the sexes in the costs of reproduction. Sperm, the sex cells that men produce, are small, cheap, and plentiful. Millions of sperm are produced in each ejaculate, and one act of sexual intercourse (in principle) is the minimum reproductive effort needed by a man to sire a child. By contrast, eggs, the sex cells that women produce, are large, expensive, and limited in number. Most critical is that one act of sexual intercourse *plus* 9 months gestation, potentially dangerous childbirth, and (in traditional societies) years of nursing and carrying a child are the minimum amount of reproductive effort required by a woman to successfully reproduce. These differences in what Trivers (1972) has termed *parental investment* have wide-ranging ramifications for the evolution of sex differences in body, mind, and behavior. Moreover, these differences hold true not only for humans but also for all mammalian species.

Trivers (1972) defined parental investment as “any investment by the parent in an individual offspring’s chance of surviving (and hence reproductive success) at the cost of the parent’s ability to invest in other offspring” (p. 139). Usually, but not always, the sex with the greater parental investment is the female. These differences in investment are manifest in various ways, from basic asymmetries in the size of male and female sex cells (a phenomenon known as *anisogamy*) through to differences in the propensity to rear offspring. For most viviparous species (who bear live offspring), females also shoulder the burden of gestation—and in mammals, lactation and suckling. In terms of parental investment, the sex that invests the most becomes a *limiting resource* for the other, less investing sex (Trivers, 1972). Members of the sex that invests less, therefore, should compete among themselves for breeding access to the other, more investing sex. Because males of many species contribute little more than sperm to subsequent offspring, their reproductive success is primarily constrained by the number of fertile females that they can inseminate. Females, by contrast, are constrained by

the number of eggs that they can produce and (in species with parental care) the number of viable offspring that can be raised. Selection favors males in these species who compete successfully with other males or who have qualities preferred by females that increase their mating opportunities. Conversely, selection favors females who choose mates who have good genes and (in paternally investing species) are likely to provide external resources such as food or protection to the female and her offspring (Trivers, 1972).

Parental investment theory, in combination with the metatheoretical assumptions of natural and sexual selection, generates an array of hypotheses and specific predictions about sex differences in mating and parental behavior. According to parental investment theory, the sex that invests more in offspring should be more careful and discriminating in mate selection, should be less willing to engage in opportune mating, and should be less inclined to seek multiple sexual partners. By contrast, the sex investing less in offspring should be less choosy about whom they mate with, compete more strongly among themselves for mating opportunities (i.e., take more risks and be more aggressive in pursuing sexual contacts), and be more inclined to seek multiple mating opportunities. The magnitude of these sex differences should depend on the magnitude of differences between males and females in parental investment during a species’ evolutionary history. In species in which males only contribute their sperm to offspring, males should be much more aggressive than should females in pursuing sexual contacts with multiple partners, and females should be much choosier than should males in accepting or rejecting mating opportunities. In contrast, in species such as humans in which both males and females typically make high levels of investment in offspring, sex differences in mating competition and behavior should be more muted. Nonetheless, the sex differences predicted by parental investment theory are well documented in humans as well as in many other animals. In humans, for example, men are more likely than are women to pursue casual mating opportunities and multiple sex partners, men tend to have less rigid standards than women do for selecting mates, and men tend to engage in more extreme intrasexual competition than women do (Buss, 1994; Daly & Wilson, 1988; Ellis & Symons, 1990; Symons, 1979).

Among mammalian species, human males are unusual insofar as they contribute nonnegligible amounts of investment to offspring. Geary (2000), in a review of the evolution and proximate expression of human paternal investment, has proposed that (a) over human evolutionary history fathers’ investment in families tended to improve but was not essential to the survival and reproductive success of children and (b) selection consequently favored a mixed paternal strategy,

with different men varying in the extent to which they allocated resources to care and provisioning of children. Under these conditions, selection should favor psychological mechanisms in females that are especially attuned to variation in potential for paternal investment. This hypothesis has been supported by much experimental and cross-cultural data showing that when they select mates, women tend to place relatively strong emphasis on indicators of a man's willingness and ability to provide parental investment (e.g., Buss, 1989; Ellis, 1992; Symons, 1979). These studies have typically investigated such indicators as high status, resource-acquiring potential, and dispositions toward commitment and cooperation.

The other side of the coin is that men who invest substantially in offspring at the expense of future mating opportunities should also be choosy about selecting mates. Men who provide high-quality parental investment (i.e., who provide valuable economic and nutritional resources; who offer physical protection; who engage in direct parenting activities such as teaching, nurturing, and providing social support and opportunities) are themselves a scarce resource for which women compete. Consequently, high-investing men should be as careful and discriminating as women are about entering long-term reproductive relationships. Along these lines, Kenrick, Sadalla, Groth, and Trost (1990) investigated men's and women's minimum standards for selecting both short-term and long-term mates. Consistent with many other studies (e.g., Buss & Schmitt, 1993; Symons & Ellis, 1989), men were found to have minimum standards lower than those of women for short-term sexual relationships (e.g., one-night stands); however, men elevated their standards to levels comparable to those of women when choosing long-term mates (Kenrick et al., 1990).

Mate Retention Strategies

In species with internal fertilization (all mammals, birds, reptiles, and many fish and insects), males cannot identify their offspring with certainty. In such species, males who invest paternally run the risk of devoting time and energy to offspring who are not their own. Thus, male parental investment should only evolve as a reproductive strategy when fathers have reasonably high confidence of paternity—that is, males should be selected to be high-investing fathers only to offspring who share their genes. When male parental investment does evolve, selection should concomitantly favor the evolution of male strategies designed to reduce the chance of diverting parental effort toward unrelated young (Daly, Wilson, & Weghorst, 1982; Symons, 1979). Mate retention strategies (including anatomical and behavioral adaptations) are favored

by sexual selection in paternally investing species because they increase the probability that subsequent investment made by fathers in offspring contributes to their own fitness and not to that of other males.

A fascinating array of mate retention strategies has been documented in many animal species. Male damselflies, for example, possess a dual-function penis that has special barbs that enables them to remove any sperm from prior matings before inseminating the female themselves. Furthermore, male damselflies remain physically attached to the female after mating until she has laid her eggs, thus ensuring that other males cannot fertilize them. In many species of birds with biparental care, males adjust their subsequent paternal investment (e.g., feeding of nestlings) depending on their degree of paternity certainty as determined by such factors as time spent with the mate and degree of extrapair matings in which she has engaged. The greater the likelihood that the offspring he is raising is *not* his own, the less investment is offered (e.g., Moller, 1994; Moller & Thornhill, 1998; but see Kempenaers, Lanctot, & Robertson, 1998). Sexual jealousy in humans has also been proposed as an evolved motivational system that underlies mate retention behaviors and functions to reduce the probability of relationship defection and to increase certainty of paternity in males (Buss, 2000; Daly et al., 1982). Daly et al. (1982) suggest that in men, pervasive mate retention strategies include “the emotion of sexual jealousy, the dogged inclination of men to possess and control women, and the use or threat of violence to achieve sexual exclusivity and control” (p. 11).

Females, of course, are not passive spectators to these male manipulations, but have evolved a host of strategies themselves to advance their own inclusive fitness. In many species females may try to extract investment from males through various means such as withholding sex until resources are provided, obscuring the time that they are fertile to encourage prolonged male attention, and preventing males from investing resources in multiple females. Furthermore, in some circumstances it may benefit females to extract material resources from one male while pursuing extrapair matings with other males who may be of superior genetic quality (see early discussion of the function of female orgasm; see also Buss, 1994; Greiling & Buss, 2000; for birds, see Moller & Thornhill, 1998; Petrie & Kempenaers, 1998).

Although the general pattern of greater female parental investment and less male parental investment is most common, a variety of species exhibit the opposite arrangement. For example, in a bird species called the red-necked phalarope, it is the male who takes on the burden of parental investment, both incubating and feeding subsequent offspring. As predicted by parental investment theory, it is the

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female in this species who is physically larger, who competes with other females for reproductive opportunities, and who more readily pursues and engages in multiple matings. In addition, levels of parental investment may vary *within* a species over time, with corresponding changes in mating behavior. For example, in katydids or bush crickets, males contribute to offspring by offering mating females highly nutritious sperm packages called spermatophores. When food resources are abundant, males can readily produce these spermatophores. Under these conditions, males compete with each other for mating access to females and readily pursue multiple mating opportunities. When food resources are scarce, however, spermatophores are costly to produce. Under these conditions, it is the females who compete with each other for mating access to males with the valued spermatophores, and it is females who more readily engage in multiple matings (see Andersson, 1994, pp. 100–103). These examples of so-called *sex-role reversed species* illustrate that sex differences do not arise from biological sex per se; rather, they arise from differences between the sexes in parental investment.

Parental investment theory is one of the most important middle-level theories that guides research into many aspects of human and animal behavior. Both the nature and the magnitude of sex differences in mating and parental behaviors can be explained by considering differences between the sexes in parental investment over a species' evolutionary history. A host of general hypotheses and specific predictions have been derived from considering the dynamics of parental investment and sexual selection, and much empirical evidence in both humans and other animals has been garnered in support of these hypotheses and predictions. Parental investment theory is one of the real triumphs of evolutionary biology and psychology and gives support to a host of important metatheoretical assumptions.

Good Genes Sexual Selection Theory

In order to adequately characterize the evolution of reproductive strategies, one must consider parental investment theory in conjunction with other middle-level theories of sexual selection. In this section we provide a detailed overview of good genes sexual selection theory, as well as briefly summarize the three other main theories of sexual selection (via direct phenotypic benefits, runaway processes, and sensory bias).

The male long-tailed widowbird, as its name suggests, has an extraordinarily elongated tail. Although the body of this East African bird is comparable in size to that of a sparrow, the male's tail feathers stretch to a length of up to 1.5 meters

during the mating season. These lengthy tail feathers do little to enhance the male widowbird's survival prospects: They do not aid in flight, foraging, or defense from predators. Indeed, having to haul around such a tail is likely to reduce survival prospects through increased metabolic expenditure, attraction of predators, and the like. The question that has to be asked of the male widowbird's tail is how it could possibly have evolved. The short answer is that female widow birds *prefer* males with such exaggerated traits—that is, the male widowbird's extraordinary tail has evolved by the process of *sexual selection*. That such a female preference for long tails exists was confirmed in an ingenious manipulation experiment carried out by Malte Andersson (1982). In this study, some males had their tail feathers experimentally reduced while others had their tails enhanced. The number of nests in the territories of the males with the supernormal tails significantly exceeded the number of nests in the territories of those males whose tails had been shortened. Clearly female widowbirds preferred to mate with males who possess the superlong tails.

To explain *why* the female widowbird's preference for long tails has evolved, we need to consider the various mechanisms and theories of sexual selection. The two main mechanisms of sexual selection that have been identified are mate choice (usually, but not always, by females) and contests (usually, but not always, between males). The male widowbird's elongated tail is an example of a trait that has apparently evolved via female choice. The 2.5-m tusk of the male narwhal, by contrast, is a trait that appears to have evolved in the context of male-male competition. Other, less studied mechanisms of sexual selection include scrambles for mates, sexual coercion, endurance rivalry, and sperm competition (Andersson, 1994; Andersson & Iwasa, 1996). In his exhaustive review of sexual selection in over 180 species, Andersson (1994) documents evidence of female choice in 167 studies, male choice in 30 studies, male competition in 58 studies, and other mechanisms in 15 studies. Sexual selection, as illustrated in a recent book by Geoffrey Miller (2000), has also been proposed as an important mechanism for fashioning many traits in our own species, including such characteristics as music, art, language, and humor.

Four main theories about how sexual selection operates have been advanced: via good genes, direct phenotypic benefits, runaway processes, and sensory bias. These different theories, however, are not necessarily mutually exclusive and may be used together to explain the evolution of sexually selected traits. The core idea of *good genes sexual selection* is that the outcome of mate choice and intrasexual competition will be determined by traits that indicate high genetic viability (Andersson, 1994; Williams, 1966). Males (and, to a lesser extent, females) of many bird species, for example, possess a

bewildering variety of ornaments in the form of wattles, plumes, tufts, combs, inflatable pouches, elongated tail feathers, and the like. Moreover, many male birds are often splendidly attired in a dazzling array of colors: iridescent blues, greens, reds, and yellows. Keeping such elaborate visual ornamentation in good condition is no easy task. It requires time, effort, and—critically—good health to maintain. Females who consistently choose the brightest, most ornamented males are likely to be choosing mates who are in the best condition, which reflects the males' underlying genetic quality. Even if females receive nothing more than sperm from their mates, they are likely to have healthier, more viable, and more attractive offspring if they mate with the best quality males. According to Hamilton and Zuk (1982), bright plumage and elaborate secondary sexual characteristics, such as the male peacock's resplendent tail, are accurate indicators of the relative parasite loads of different males. A heavy parasite load signals a less viable immune system and is reflected in the condition of such traits as long tail feathers and bright plumage.

Many secondary sexual characteristics therefore act as *indicators* of genetic quality. Moreover, according to the *handicap principle* developed by Amotz Zahavi (1975; Zahavi & Zahavi, 1997), such traits must be costly to produce if they are to act as reliable indicators of genetic worth. If a trait is not expensive to produce, then it cannot serve as the basis for good genes sexual selection because it will not accurately reflect the condition of its owner. However, if the trait relies on substantial investment of metabolic resources to develop—as does the male widowbird's tail—then only those individuals in the best condition will be able to produce the largest or brightest ornament. In this case, expression of the trait will accurately reflect underlying condition.

In a slightly different take on the handicap principle, Folstad and Karter (1992) have suggested that in males, high levels of testosterone, which are necessary for the expression of secondary sexual characteristics (those sex-linked traits that are the product of sexual selection), also have harmful effects on the immune system. According to this *immunocompetence handicap* model, only the fittest males will be able to develop robust secondary sexual characteristics, which accurately indicate both high levels of testosterone and a competent immune system—and therefore high genetic quality. These general hypotheses were supported in a recent meta-analysis of studies on parasite-mediated sexual selection. This meta-analysis demonstrated a strong negative relationship between parasite load and the expression of male secondary sexual characteristics. In total, the most extravagantly ornamented individuals are also the healthiest ones—and thus the most preferred as mates (Moller, Christie, & Lux, 1999). Of course in species in which there is substantial paternal

investment (including humans), males will also be choosy about whom they mate with and will also select mates with indicators of high genetic fitness. In many bird species, for example, both males *and* females are brightly colored or engage in complex courtship dances. Thus, relative levels of parental investment by males and females substantially influence the dynamics of good genes sexual selection.

Genes, of course, are not the only resources that are transferred from one mate to another in sexually reproducing species. Although the male long-tailed widowbird contributes nothing but his sperm to future offspring, in many species parental investment by both sexes can be substantial. It benefits each sex, therefore, to attend to the various resources that mates contribute to subsequent offspring; thus, one of the driving forces behind sexual selection is the *direct phenotypic benefits* that can be obtained from mates and mating. These benefits encompass many levels and types of investment—from the small nuptial gifts offered by many male insect species to the long-term care and provisioning of offspring.

Homo sapiens is a species commonly characterized by long-term pair-bonding and biparental care of offspring. Therefore, in addition to traits that indicate the presence of good genes, both males and females should be attentive to characteristics that signal the ability and willingness of potential mates to devote time and external resources to future offspring. As has been demonstrated in many studies of human mate preferences (see Buss, 1994), both males and females rate kindness and warmth as the most important attributes in long-term mates. A partner with the personality traits of kindness, honesty, and warmth is someone who is both more likely to remain in a long-term relationship and who will invest time and resources in future offspring. Women (more so than men) also rate the presence of status and resource-accruing potential as important attributes in potential mates (Buss, 1989), suggesting that males with the ability to contribute external resources to future offspring are favored.

It is important to note that some characteristics may be indicative of both good genes *and* the ability to offer direct phenotypic benefits; thus, these two different theories of sexual selection are not necessarily incompatible. For example, a male bird with bright, glossy plumage may be preferred as a mate not only because of his high genetic quality, but also because he is less likely to transmit parasites to prospective sexual partners. However, compatibility between good genes and direct benefits is often not apparent, and it is expected that the relative importance of these two mate selection criteria will vary on a species-by-species basis. We also expect variation to occur *within* species in the relative weighting of good genes versus direct phenotypic benefits in mate selection (Gangestad & Simpson, 2000; Gross, 1996). For

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example, Gangestad and Simpson (2000) have argued that human females make trade-offs between males with traits indicating good genes and males with traits signaling high likelihood of paternal investment. Some women at some times pursue a relatively unrestricted strategy of engaging in short-term sexual relationships with partners who may be high in genetic quality, whereas other women may adopt a more restricted strategy of selecting long-term partners who are likely to offer substantial paternal investment. The prevalence of extrapair mating in humans suggests that both strategies may be pursued simultaneously: Resources may be extracted from one high-investing male while extrapair matings are pursued with other males who display indicators of high genetic quality (see earlier discussion of the function of female orgasm). Men also must make trade-offs between seeking multiple sexual partners and investing substantially in only one or a few mates. Which strategies are chosen is determined in part by such factors as father absence, individual differences in mate value, and availability of mates (e.g., Draper & Harpending, 1982; Gangestad & Simpson, 2000; Kirkpatrick & Ellis, 2001).

So far we have discussed good genes and direct phenotypic benefits as ways of understanding the dynamics of sexual selection. Two other processes have also been suggested that can account for the evolution of sexually selected traits. The first of these theories—*runaway sexual selection* (Fisher, 1958)—states that preferences and traits coevolve through a feedback process that can lead to the rapid evolution of specific traits for essentially arbitrary reasons. For example, consider that females of given lizard species have a preference for males with an enlarged and elaborate head crest. This preference may have evolved initially because such males may have greater genetic viability (i.e., good genes) or because of some innate sensory bias (discussed further later in this chapter). Males with the enlarged crests will become more prevalent in the population and the female preference for the trait will also become more widespread. Males with large crests increase their inclusive fitness by enhanced mating opportunities and females advance their inclusive fitness because they are more likely to have male offspring with the enlarged crest, who will in turn be more likely to succeed in mating contexts. After the preference is in place, however, the elaborate crest may become decoupled from any indicator of health or fitness and simply spread because of the preference per se. The male crest will increase in size as the trait and the preference for the trait coevolve until the crest becomes so large and elaborate that it undermines survival.

Unlike good genes sexual selection, empirical evidence for the runaway process (in its pure form) is fairly sparse. However, Eberhard (1985, 1993) has suggested that the evolution of male genitalia may prove an instructive example of

runaway sexual selection in action. As documented in Eberhard's fascinating book, *Sexual Selection and Animal Genitalia*, male genitalia come in a bewildering variety of shapes and sizes—they are often decorated with knobs, spines, hooks, and flanges that are seemingly unrelated to the utilitarian task of sperm transfer. Eberhard (1993) argues that it is *unlikely* that variations in penis morphology are useful indicators of the ability to resist parasites or of general male vigor (i.e., they are probably not reliable markers of good genes). It seems plausible instead to suggest that female preferences, due initially to biases towards certain kinds of tactile stimulation, have coevolved with genitalia morphology in classic runaway fashion, leading to the seemingly arbitrary array of genitalia structures found in the animal world.

A key aspect of the runaway process is that traits that are preferred are arbitrarily related to fitness in the sense that such traits do not indicate genetic viability (as is the case with good genes models). However, the runaway process has to begin with a preference that is usually based on actual viability or is the result of sensory bias. The *sensory bias* model of sexual selection involves the evolution of traits via sexual selection due to preferences resulting from sensory orientations that are the product of other selective processes (Ryan & Keddy-Hector, 1992). Whereas in good genes and runaway sexual selection, preferences and traits coevolve, the sensory bias theory requires the *prior* origin of preferences and the *latter* evolution of traits that exploit those preferences. The evolution of male calls of the Tungara frog appears to be explained by this sensory-bias model of sexual selection. Females prefer male frogs with low-frequency calls. Neurophysiological evidence indicates that the auditory system of female frogs is tuned in a way that is biased toward the low-frequency component of these calls. Because bigger male frogs produce lower-frequency calls, a good genes model of sexual selection may seem indicated. However, Ryan and Rand (1990) argue that because closely related frog species also demonstrate this female bias in the *absence* of male calling, the male trait arose to exploit the preexisting sensory bias of the females, which itself has arisen as the result of other selective forces.

Good genes sexual selection is another important middle-level theory that has proven valuable in generating a number of interesting and testable hypotheses about both human and nonhuman animal behavior. As we have discussed, good genes sexual selection theory is one of a number of alternative (although often compatible) middle-level theories of sexual selection. Making predictions that distinguish between these different middle-level applications of sexual selection metatheory can sometimes be difficult. However, as reviewed in the next section, good genes sexual selection theory (often in conjunction with parental investment theory) enables us to

derive a number of general hypotheses and specific predictions that can be empirically tested.

THE HYPOTHESES LEVEL OF ANALYSIS

At the next level down in the hierarchy of explanation are the actual hypotheses drawn from middle-level evolutionary theories (see Figure 1.1). As noted earlier, a hypothesis is a general statement about the state of the world that one would expect to observe if the theory from which it was generated were in fact true. An array of hypotheses can often be derived from a single middle-level theory. These hypotheses can be considered to vary along a continuum of confidence (Ellis & Symons, 1990). At the top of the continuum are so-called firm hypotheses (such as the relation between relative parental investment and intrasexual competition for mating opportunities) that are clear and unambiguous derivations from an established middle-level evolutionary theory. As one moves down the continuum, however, firm hypotheses give way to more typical formulations—hypotheses that are inferred from a middle-level theory but not directly derived from it. This distinction can be illustrated by considering the issue of paternity uncertainty. The supposition that in species characterized by both internal female fertilization and substantial male parental investment, selection will favor the evolution of male mechanisms for reducing the probability of expending that investment on unrelated young is a firm hypothesis that can be directly derived from the theory. What form these mechanisms will take, however, cannot be directly derived from the theory because natural and sexual selection underdetermine specific evolutionary paths. Selection could favor the evolution of sexual jealousy, or it could favor the evolution of sperm plugs to block the cervix of female sexual partners following copulation (see earlier discussion of mate retention strategies). Given the universal occurrence of jealousy in humans (Daly et al., 1982), evolutionary psychologists have hypothesized that men's jealousy should be centrally triggered by cues to sexual infidelity, whereas women's jealousy should be centrally triggered by cues to loss of commitment and investment. This hypothesis is reasonably inferred from the theory but cannot be directly deduced from it. We refer to this type of hypothesis as an *expectation*. This hypothesis was originally proposed by Daly et al. (1982) and has since received considerable empirical support (Buss, Larsen, Westen, & Semmelroth, 1992; Buunk, Angleitner, Oubaid, & Buss, 1996; DeSteno & Salovey, 1996; Wiederman & Allgeier, 1993).

As one moves farther down the continuum of confidence into the area where inferences from middle-level theories are drawn farther from their core, expectations grade insensibly

into interesting questions or hunches. At this level, different interpretations of the theory can and do generate different hypotheses. For example, Buss and Shackelford (1997) have proposed two competing evolutionary hypotheses concerning the effects of unequal attractiveness between romantic partners on women's mate retention behavior. The first hypothesis suggests that individuals (both women and men) married to others who are perceived as more attractive than the self will devote *more* effort to mate retention than will individuals married to others who are perceived as equally or less attractive than the self. The logic behind this hypothesis is that individuals who are married to relatively attractive partners are at greater risk of losing them. The second hypothesis suggests the opposite, but only for females: Women married to men who are perceived as more attractive than the self will relax their mate retention efforts. The logic behind this hypothesis focuses on the greater ability of men to fractionate their reproductive investment among multiple partners. For example, a man can simultaneously beget and raise children with three different women (a phenomenon that is quite common in polygynous societies), whereas it would take a woman several years to bear and raise children with three different men. Because of the male ability to partition investment, women may face the trade-off of obtaining a fraction of the attention and resources of a highly attractive male or the full attention and resources of a less attractive male. Buss and Shackelford (1997) suggest that women in unevenly matched marriages might devote *less* effort to mate retention, an implicit acknowledgment of the potential costs involved in trying to prevent the more attractive partner from devoting some of his resources to outside relationships.

Although this type of theorizing is admittedly speculative, it is inevitable at the lower end of the continuum of confidence—in domains where there is not strong middle-level theoretical development and about which relatively little is known. Studies designed to test these hypotheses often have an exploratory quality. The data obtained from testing such hypotheses, however, can work their way back up the explanatory hierarchy to enable the development of more rigorous theoretical models (Ketelaar & Ellis, 2000). In the following section, we review hypotheses derived from good genes sexual selection theory. We number these hypotheses and note whether (in our opinion) they are firm hypotheses, expectations, or hunches.

Good Genes Sexual Selection Theory: Hypotheses

The principles of good genes sexual selection theory in combination with parental investment theory have been used to generate a number of interesting hypotheses in a variety of species, including humans. In the following discussion we

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use the term *females* to refer to the sex that invests more in offspring and *males* to refer to the sex that invests less in offspring. We recognize, of course, that these sex roles are sometimes reversed.

For a given trait to be a *reliable* indicator of genetic value, it must be costly to produce. According to the handicap principle (Zahavi & Zahavi, 1997), traits that indicate good genes can only be maintained by individuals who are the fittest in the population, as indicated by their ability to maintain steady growth rates, resist parasites, compete successfully in intrasexual contests, and so forth. Consequently, good genes indicators that are preferred by members of the opposite sex should require substantial metabolic resources to develop and maintain. It follows, therefore, that individuals who more fully display traits indicative of high genetic quality should be healthier and in better condition than should conspecifics who display these traits less fully (H1; firm hypothesis). An implication of this hypothesis is that individuals with elaborate secondary sexual characteristics should have lower levels of parasitic infection. Further, traits indicative of good genes can only be developed to their fullest potential in individuals with robust immune systems that are able to overcome the immunosuppressant effects of sex hormones such as testosterone (see earlier discussion of immunocompetence handicap theory; Folstad & Karter, 1992). Expression of traits indicative of good genes, therefore, should be positively related to effective immune system functioning.

Evidence that sexually selected traits can increase reproductive success while reducing survival prospects (i.e., handicap traits) has accumulated in a number of species, including the European barn swallow. The male barn swallow is adorned with elongated tail feathers. Males with longer tail feathers are preferred by females and sire more offspring (Moller, 1994). However, males with such long tails are less efficient at foraging and are more likely to suffer predation by birds of prey (Moller et al., 1998). Thus, female preference for males with elongated tail feathers appears to reflect good genes sexual selection in action. A recent meta-analysis of studies assessing parasite load, immune function, and the expression of secondary sexual characteristics in a diverse array of species has found that the fullest expression of sexually selected traits is positively related to immune system functioning and negatively related to parasite load (Moller et al., 1999)—that is, the brightest, largest, most ornamented individuals are also the ones with the smaller number of parasites and the most robust immune systems.

An important factor influencing the intensity of good genes sexual selection is variance in reproductive success. Two principles are relevant here. First, there tends to be greater *variance* in male than in female reproductive success;

this is because males are more able to distribute their sex cells across multiple partners. Indeed, the ability of males to inseminate a large number of females often results in a sexual lottery in which some males win big while others lose out entirely. For example, in one study of elephant seals, a total of only eight males were found to be responsible for inseminating 348 females (Le Boeuf & Reiter, 1988). Second, because of this disparity, sexual selection tends to act more strongly on males than on females in shaping intrasexual competitive abilities and producing specialized fitness signals for attracting the opposite sex (Trivers, 1972; see also Cronin, 1991).

A core premise of good genes sexual selection is that certain traits have evolved because they are reliable indicators of genetic quality—that is, these traits reliably signal viability and good condition that can be passed on to offspring through genetic inheritance. All else being equal, individuals that possess such traits should be preferred as mates (H2; firm hypothesis), be more successful in intrasexual contests (H3; firm hypothesis), or both. Parental investment theory further suggests that males will be more likely than females to possess and display indicators of genetic quality (H4; expectation), whereas females will be more likely than males to select mates on the basis of these indicators (H5; expectation). In total, then, males that possess and display indicators of genetic quality should have more sexual partners and more offspring (H6; firm hypothesis). For example, among mandrills, a primate that inhabits the rainforests of West Africa, males who possess the brightest red and blue pigmentation on the face, rump, and genitals (which presumably are indicators of good genes) are more often preferred as mates by females. Further, DNA analysis has shown that they are also more likely than their less chromatically exuberant counterparts to sire offspring (Dixson, Bossi, & Wickings, 1993).

In species in which females engage in nonreproductive, situation-dependent sexual activity (rather than strictly cyclical sexual activity), females' preferences for males who display indicators of high genetic quality should vary as a function of their phase of the reproductive cycle. Around the time of ovulation, when females are most fertile, they should express the strongest preference for males with good genes. At other times in the reproductive cycle, when females are not ovulating, this preference should be more muted (H7; expectation). Humans are the clearest example of a primate that engages in sexual activity throughout the reproductive cycle. Other primates tend to be more seasonal and cyclical in their breeding activities than humans are, although not exclusively so (see Hrdy, 1981).

We earlier discussed the selective sperm retention hypothesis for female orgasm, which suggests that females exert some control over the paternity of their offspring by differential

patterns of orgasm with specific male partners. In species characterized by female orgasm, the frequency and timing of female orgasm should vary in a manner that selectively favors the sperm of males who display indicators of high genetic quality (H8; hunch).

Good genes sexual selection theory has been used to generate hypotheses about mating effort, parental effort, and trade-offs between them. There are essentially three strategies that individuals can use to increase their reproductive success: (a) Increase the fitness of their offspring by mating with individuals of high genetic quality, (b) increase the fitness of their offspring by enhancing parental investment (by one or both parents), or (c) increase the number of offspring produced. No one strategy is inherently better than any other, and the pursuit of one strategy usually involves trade-offs with the others (see Gangestad & Simpson, 2000). For example, individuals who produce a greater number of offspring (c) tend to have lower fitness of offspring.

Consistent with (a), females can increase their reproductive success by preferentially investing in offspring that are sired by males of high genetic quality. Thus, among females there should be a positive correlation between levels of parental investment in offspring and the genetic quality of the offspring's father (H9; expectation). Peahens, for example, have been found to lay more eggs for peacocks with larger trains and more elaborate tails (Petrie & Williams, 1993).

In species characterized by long-term pair-bonding and biparental care of offspring, but in which individuals sometimes engage in short-term and extrapair mating, there should be a negative correlation between the genetic quality of males and levels of parental investment by males in offspring (H10; expectation). There are two bases for this hypothesis. First, males who possess reliable indicators of high genetic quality can afford to put less direct effort into offspring; this is because they make more valuable genetic contributions to offspring, and thus their female partners may be willing to tolerate less parental investment—devaluing (b)—in return for their good genes—enhancing (a). Second, diverting effort away from parental investment toward extrapair matings should yield greater payoffs for males of high genetic quality (because they are more popular on the mating market). Thus, males with good genes can be expected to devote proportionally more reproductive effort to mating (c) and less to parenting (b). A corollary of this hypothesis is that males who possess reliable indicators of good genes will engage in more short-term and extrapair mating (H11; expectation) and be more preferred by females as short-term and extrapair mates (H12; expectation).

Hypotheses 10–12 have been supported in an extensive series of studies on the European barn swallow. The barn

swallow is small, migratory, insect-eating bird, which is characterized by pair-bonds that last the length of the breeding season and biparental care of offspring. Male and female birds are similar in many respects except that males have much longer tails than do females, which suggests that tail length is a sexually selected characteristic (Moller, 1994). Males with longer tail feathers not only tend to spend less time incubating and feeding offspring (Moller, 1994), but also are more preferred by females as primary mates, engage in more extrapair mating, and sire more extrapair offspring than do males with shorter tails (Moller & Tegelstrom, 1997). These data suggest that (a) females are willing to trade off parental investment for good genes in their primary pair-bonds and (b) females pursue extrapair copulations with males who possess indicators of good genes. We find it interesting that the probability of females' pursuing extrapair copulations decreases as a function of the length of the tail feathers of their primary mate (Moller, 1994), suggesting females who are already receiving high-quality genetic benefits have less motivation for extrapair mating.

In sum, hypotheses derived from good genes sexual selection theory can explain the origins of a wide variety of physical and behavioral traits across a diversity of animal species, from humans to scorpion flies. The specific ways in which these hypotheses are played out, however, depends on the nature of the species being studied. Humans and barn swallows, for example, both engage in medium- to long-term pair-bonding, both have greater female parental investment, and both are characterized by relatively frequent extrapair mating. We would expect, therefore, that females in both species will preferentially seek extrapair sex partners who possess indicators of good genes. However, specific markers of good genes vary across species. Human males do not possess elongated tail feathers, bright spots on their rump, or bright red faces. Thus, although the general hypotheses derived from good genes sexual selection theory have wide applicability, the detailed predictions derived from these hypotheses depend on the species under consideration. In the next section we describe specific predictions as they apply to human mating.

THE PREDICTION LEVEL OF ANALYSIS

Because hypotheses are often too general to be tested directly, it is at the next level of explanation—the level of specific predictions—where the battles between competing theoretical models are often played out. *Predictions* correspond to specific statements about the state of the world that one would expect to observe if the hypothesis were in fact true. They represent explicit, testable instantiations of hypotheses. One

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might argue that predictions form the substance of any theory, for here is where most of the action takes place as specific predictions are either supported or refuted.

The performance of evolution-based predictions provides the basis for evaluating the more general hypotheses from which they are drawn. For example, a number of specific predictions have been derived from the evolutionary hypothesis that men (more than women) will be intensely concerned about the sexual fidelity of reproductive-aged partners. Some of these predictions include (a) sexual infidelity by wives will be a more frequent cause of divorce than will sexual infidelity by husbands (Betzig, 1989); (b) the use or threat of violence by husbands to achieve sexual exclusivity and control of wives will vary as a function of wives' reproductive value, which peaks in the late teens and declines monotonically thereafter (M. Wilson & Daly, 1996); and (c) in the context of competing for romantic partners, the tactic of spreading rumors that a same-sex rival is sexually promiscuous will be more effective when performed by women than by men (because it raises the specter of cuckoldry; see Buss & Dedden, 1990). The fact that the first two predictions have been supported by extensive cross-cultural data whereas the third prediction has not been supported factors into one's evaluation of the more general hypothesis from which these predictions were generated. That two of the three predictions garnered strong support provides indirect support for the hypothesis. That the third prediction was rejected raises questions about the hypothesis. Ultimately, the value of the more general hypothesis and theoretical model is judged by the cumulative weight of the evidence (Ketelaar & Ellis, 2000).

Good Genes Sexual Selection Theory: Predictions

A number of specific, testable predictions can be derived from the hypotheses generated by good genes sexual selection theory. Although predictions can be made about the characteristics of a wide array of animal species, we focus in this section on a discussion of predictions pertaining specifically to humans. We consider the hypotheses outlined in the preceding section ("The Hypothesis Level of Analysis") and derive predictions relating specifically to human health and reproductive behavior. For each prediction we also review studies, where relevant, that have been carried out to test these specific predictions.

Before we examine these predictions in detail, it is worth considering just what traits in humans—like elongated tail feathers in male barn swallows—might be reliable indicators of good genes. One important marker of genetic quality that has emerged in research on a diverse array of species is a phenomenon known as *fluctuating asymmetry* (Moller &

Swaddle, 1997). Fluctuating asymmetry refers to small random deviations from perfect bilateral symmetry in different parts of the body. Higher levels of fluctuating asymmetry (i.e., more asymmetry) are believed to reflect developmental instability. This developmental imprecision can arise because of a range of factors, such as food deficiency, parasites, inbreeding, and exposure to toxic chemicals. Biologists have hypothesized that individuals with good genes are better able to buffer themselves against these genetic and environmental insults and thus tend to be more symmetrical. Because fluctuating asymmetry has a heritable component, mate preference for symmetrical, developmentally stable individuals can be expected to result in more viable offspring (see Moller & Swaddle, 1997). The specific predictions reviewed in this section focus on the relations between fluctuating asymmetry and both health and reproductive behavior.

1. More symmetrical individuals should have better mental and physical health, better immune system functioning, and lower parasite loads than should less symmetrical individuals (from H1). Although these predictions have only been tested in a small number of studies using human participants, initial results have been largely supportive. In studies of American undergraduates, levels of symmetry in both men and women have been found to positively correlate with psychometric intelligence (Furrow, Armijo-Prewitt, Gangestad, & Thornhill, 1997) and negatively correlate with measures of psychological, emotional, and physiological distress (Shackelford & Larsen, 1997). In addition, more symmetrical men have been found to have greater ejaculate size and better sperm quality (Manning, Scutt, & Lewis-Jones, 1998) and lower resting metabolic rates (Manning, Koukourakis, & Brodie, 1997) than have less symmetrical men. Perceived health has also been shown to be positively correlated with symmetry and averageness of male faces (Rhodes et al., 2001). Finally, in a study of men in rural Belize, the occurrence of life-threatening illnesses was found to be significantly higher in men who were less symmetrical (Waynforth, 1998). Taken together, these findings suggest that more symmetrical individuals, as predicted, tend to be healthier and in better physical and psychological condition than do their less symmetrical counterparts.

The remaining hypotheses (H2–H12) focus on the relations between markers of genetic fitness and reproductive behavior. Because of sex differences in parental investment, these hypotheses primarily concern *female preferences* for males who possess indicators of good genes and individual differences in *male mating behavior* as a function of genetic quality. An array of specific predictions have been derived from Hypotheses 2–12. As reviewed in the following discussion, empirical tests of these predictions have generated new

lines of research that have substantially advanced our understanding of behavior in sexual and romantic relationships.

2. *More symmetrical men should have more lifetime sexual partners (from H2–H6) and more extrapair sexual partners (from H10) than should less symmetrical men.* These predictions have been tested in an initial series of studies on American undergraduates (reviewed in Gangestad & Simpson, 2000; Gangestad & Thornhill, 1997a). Symmetry was assessed by totaling right-left differences in seven bilateral traits (e.g., ankle girth, wrist girth). Consistent with the predictions, men who were more symmetrical were found to have more lifetime sexual partners (even after controlling for age and physical attractiveness) and more extrapair sexual encounters during ongoing relationships (even after controlling for relationship length, partners' extrapair sex, and both partners' physical attractiveness). In contrast, no consistent relation was found between women's symmetry and number of lifetime sexual partners or extrapair sexual relationships.

In ancestral environments, before the advent of reliable contraceptive methods, number of sexual partners can be expected to have been positively related to number of offspring. The finding that more symmetrical men in rural Belize both had more sexual partners and fathered more children lends support to this suggestion (Waynforth, 1998).

3. *More symmetrical men should be more successful in intrasexual contests than should less symmetrical men (from H2, H4).* This prediction has been tested both indirectly (by looking at the traits associated with fluctuating asymmetry) and directly (by examining behavior in experimental studies on mate competition). Men who are more symmetrical have been found to display higher levels of traits that are associated with success in intrasexual competition. Specifically, more symmetrical men tend to be bigger, to be more muscular and vigorous, to initiate more fights with other men, and to be more socially dominant than do less symmetrical men (reviewed in Gangestad & Simpson, 2000). Consistent with these correlational data, Simpson, Gangestad, Christensen, and Leck (1999) found that more symmetrical men competed more aggressively with other men for a lunch date with an attractive woman in a laboratory experiment. Each male participant was interviewed by the woman and then at the end of the interview was asked by the woman why she should choose him for the lunch date rather than the competitor (who was ostensibly in the next room). Compared with men who were less symmetrical, more symmetrical men tended to engage in competition with the rival, such as by directly comparing themselves with and belittling him. In total, the correlational and experimental data reviewed here suggest that more symmetrical men tend to display more costly traits,

such as large size and social and physical dominance, which facilitate success in direct intrasexual contests.

4. *More symmetrical men should be preferred by women as short-term and extrapair sexual partners (from H11).* Gangestad, Simpson, Cousins, and Christensen (1998) had women view videotapes of men being interviewed by an attractive woman (as described previously). The female participants then rated the male interviewee's attractiveness both as a potential long-term mate and as a short-term mate. A short-term mate was defined as either as a one-time sex partner or an extrapair sex partner. Women also completed a questionnaire that assessed their general *willingness* to have sex without commitment and emotional closeness. Women who reported more willingness to have sex without intimacy and commitment were categorized as being *inclined* toward short-term mating, whereas women who reported less willingness were categorized as being *disinclined* toward short-term mating. Among women who were inclined toward short-term mating, there was a significant positive correlation between the male interviewee's symmetry and the women's ratings of how attractive he was as a short-term mate (but not as a long-term mate). In contrast, among women who were disinclined toward short-term mating, male symmetry was uncorrelated with women's ratings of how attractive he was as either a short-term or a long-term mate. These data suggest that men who are more symmetrical are preferred as short-term mates specifically by women who are most inclined to engage in short-term mating. Moreover, Gangestad and Thornhill (1997b) found that male symmetry predicted the number of times that men were chosen by women as extrapair mates. Taken together, these data support the prediction that more symmetrical men should be more preferred by women as short-term and extrapair sexual partners.

5. *Women's preferences for symmetrical men should be heightened around the time of ovulation when women are most fertile (from H7).* This prediction has been supported in provocative new research on women's preference for the scent of symmetrical men as a function of variation in the menstrual cycle. This research employed what has been called a stinky T-shirt design, in which women sniffed shirts that had been slept in by different men and rated them on the pleasantness, sexiness, and intensity of their odors. The men who slept in these shirts were also measured on fluctuating asymmetry. The extraordinary finding was that the shirts worn by more symmetrical men were rated as smelling better than the shirts worn by less symmetrical men, but *only* by women who were likely to be in the fertile stage of their menstrual cycle (especially days 6–14). This finding was originally reported by Gangestad and Thornhill (1998a) and has since been replicated in their own lab in the United States (Thornhill & Gangestad, 1999)

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and in an independent lab in Germany (Rikowski & Grammar, 1999). These data suggest that the smell of men who are more symmetrical is preferred by women specifically when women are most likely to conceive.

6. *Women's preferences for men with masculine facial characteristics should be heightened around the time of ovulation when women are most fertile (from H7).* As discussed earlier, the immunocompetence handicap model suggests that only the fittest males will be able to develop robust secondary sexual characteristics, which accurately indicate both high levels of testosterone and a competent immune system (i.e., good genes). Exaggerated masculine facial characteristics, such as high cheekbones and a strong jaw and chin, are associated with high levels of testosterone and have been hypothesized to be reliable indicators of immunocompetence in men (see Folstad & Karter, 1992). Recent research in the United Kingdom and Japan has examined variation in women's preferences for male faces as a function of women's stage in the menstrual cycle (Penton-Voak et al., 1999; Penton-Voak & Perrett, 2000). Consistent with good genes sexual selection theory, more masculine-looking faces were preferred by women around the time of ovulation (when risk of conception is highest), especially in the context of short-term mating. In contrast, more feminine male faces, which may indicate dispositions toward increased paternal investment, were slightly preferred by women during other phases of the menstrual cycle (when risk of conception is lower). These data provide further evidence that men who display indicators of good genes are most preferred by women when they are most likely to get pregnant.

7. *The timing and frequency of orgasms by women should be patterned to selectively retain the sperm of more symmetrical males (from H8).* Thornhill et al. (1995) have conducted an initial test of this prediction on a sample of American undergraduates. The partners of more symmetrical men reported having more orgasms during sexual intercourse than did the partners of less symmetrical men (even after controlling for men's physical attractiveness). More important, levels of symmetry in male partners positively correlated with the frequency of high-sperm-retention orgasms in female partners (i.e., female orgasms occurring just prior to or after male orgasm). This effect has now been replicated in a second larger sample (Moller, Gangestad, & Thornhill, 1999). These data suggest that women increase their probability of conception when having sex with men of high genetic quality.

8. *More symmetrical men should allocate less investment to ongoing relationships (from H10).* Using the Partner-Specific Investment Inventory (Ellis, 1998), Gangestad and

Thornhill (1998b) examined levels and types of investment in long-term dating relationships. More symmetrical men, who tended to allocate less investment to their dating relationships overall, were particularly likely to be less honest with their partners, to sexualize other women more, and to spend less time with their partners. The exception to this rule was that more symmetrical men tended to provide more physical protection to their partners. Although symmetrical men apparently devote less time and energy to their relationships overall, they may compensate (reproductively speaking) for this lack of investment by providing good genes and perhaps through their greater ability to physically protect their partners.

In conclusion, specific predictions drawn from hypotheses generated by good genes sexual selection theory have been tested across a range of studies. Although research derived from good genes sexual selection theory on humans is still in its early stages, an accumulating body of evidence now supports the supposition that a collection of male traits (reflected in levels of fluctuating asymmetry) have been selected for because of their role in advertising genetic quality to prospective mates. Good genes sexual selection theory has proven valuable in guiding research in a number of ways and has led to the detection of new phenomena. It is difficult to imagine, for example, how other approaches to human mating could have predicted (let alone explained) the finding that men's symmetry is positively related to judgments of odor attractiveness by women who are most likely to be in the fertile stage of their menstrual cycle. Of course, there is much more to the dynamics of sexual and romantic relationships than can be explained by good genes sexual selection theory. This middle-level evolutionary theory has proved valuable, however, in both explaining and predicting a host of interesting phenomena relating to behavior in sexual and romantic relationships—not only in humans, but also in a wide range of animal species.

THE FUTURE OF EVOLUTIONARY PSYCHOLOGY

Evolutionary explanations have had a long—at times acrimonious—history in the behavioral sciences. Darwin's revolutionary theory of adaptation through natural selection, which explained the origins of human mental and behavioral characteristics in terms of evolution, transformed a long-standing worldview. Before Darwin, the prevailing belief was that "man" was created in God's divine image and held a special place at the center of the cosmos. Ever since Darwin, however, *Homo sapiens* has been viewed as firmly anchored in

the natural world, as one species among millions in the great tree of life.

Darwin himself saw no problem in extrapolating his evolutionary ideas beyond the realm of bees, barnacles, and baboons to embrace the human species as well (e.g., Darwin, 1871, 1872). Others too, such as Darwin's protégé George Romanes (1882), appreciated the great explanatory power of evolutionary theory. Romanes used it to launch a comparative program of research aimed at illuminating the evolutionary origins of human intelligence. In America, the great nineteenth-century psychologist and philosopher William James (1890) also characterized human consciousness in a Darwinian fashion as a mechanism that enables humans to adapt to changing environments. James's evolution-inspired ideas were to spark the short-lived but influential functionalist movement in psychology in the early part of the twentieth century. The core idea of functionalism was that mind and behavior have *functions*—they serve to adapt organisms to their environment (e.g., Angell, 1907). Functionalist thinking in psychology, however, fell out of favor with the rise of behaviorism in the early part of the twentieth century. The behaviorist paradigm, which specified that a small number of domain-general learning mechanisms accounted for the rich repertoire of human (and animal) behavior, precluded an explanatory role for the kinds of species-specific, domain-specific psychological mechanisms that are central to functionalist, evolutionary analyses.

The return of evolutionary explanations in psychology can be traced to a number of important developments. First, behaviorism declined as psychology's dominant paradigm. Animal behavior research in the 1950s and 1960s demonstrated that the content-free learning processes specified by behaviorists simply could not account for the kinds of behaviors in which animals actually engaged (e.g., Breland & Breland, 1961; Garcia & Koelling, 1966). Behaviorism in its pure form also seemed unable to satisfactorily explain the origin of complex human traits such as language, which linguists such as Chomsky (1959) argued were built on a foundation of innate cognitive processes. Second, the development of a number of important middle-level evolutionary theories in the 1960s and 1970s, such as kin selection theory (Hamilton, 1964), parental investment theory (Trivers, 1972), and reciprocal altruism (Trivers, 1971) provided the basis for important new programs of research in evolutionary biology and psychology. These middle-level theories enabled evolutionary scientists to generate myriad testable hypotheses and predictions that spanned a diversity of animal species.

The formulation of these middle-level theories was important in the emergence in the late 1970s of sociobiology, which

was defined by one of its principle architects, E. O. Wilson (1975), as “the systematic study of the biological basis of all social behavior” (p. 3). However, sociobiology proved to be a highly controversial discipline, especially when its adherents extended their ideas to explanations of human mental and behavioral characteristics. Sociobiological explanations were variously criticized as being untestable, unfalsifiable, deterministic, and ideologically unsound (e.g., S. Rose, Kamin, & Lewontin, 1984). Evolutionary psychology, as we have introduced it in this chapter, can be viewed historically as part of a long tradition of attempts to explain human psychological characteristics in evolutionary terms. The use of a coherent and powerful set of middle-level theories, the focus on evolved domain-specific psychological mechanisms, and a commitment to rigorous empirical testing, however, sets evolutionary psychology (in some respects) apart from its predecessors.

Controversy nonetheless remains over evolutionary explanations in psychology. Some critics continue to view evolutionary psychology as supporting a view of human nature that is based on genetic determinism—the idea that specific traits are caused by specific genes with a limited role for environmental factors. A glance at almost any publication by evolutionary psychologists, however, should be enough to see that this criticism is unfounded. It is almost universally agreed that *all* human traits are the result of the complex and dynamic interplay between genetic and environmental factors. Indeed, no evolutionary psychologist would argue that human behavior is rigidly fixed by virtue of our genetic inheritance; instead, much recent work in evolutionary psychology has emphasized the highly flexible and contingent nature of human psychological adaptations (e.g., Dekay & Buss, 1992; Gangestad & Simpson, 2000).

The criticism that evolutionary explanations are somehow untestable and lacking appropriate empirical rigor is still asserted by some critics of evolutionary psychology. This criticism is also unfounded (see Ketelaar & Ellis, 2000, and Ellis & Ketelaar, 2000, for detailed treatment of the issue of testability of evolutionary explanations). As demonstrated in this chapter, evolutionary psychologists employ a series of well-formulated middle-level theories that generate hypotheses and specific predictions that are testable and open to potential falsification. These empirical tests enable one to evaluate the middle-level evolutionary theories and metatheoretical assumptions from which the hypotheses and predictions are drawn. Despite the fact that human psychological characteristics are the product of evolutionary forces operating in ancestral environments, time machines are not essential methodological tools because modern humans carry around

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the legacy of ancestral adaptations that can be assessed using standard psychological methods.

The Impact of Evolutionary Psychology

Perhaps one of the most interesting questions regarding the future of evolutionary psychology concerns its scope of influence in the behavioral sciences. There is no question that evolutionary psychology has a broad range of applications. Indeed, evolutionary theory has been used to generate explanations of social behavior in all species, even those that are as yet undiscovered. Although the present chapter has focused primarily on reproductive strategies, evolutionary psychological theory and research extends into all major branches of psychology (e.g., Buss, 1999; Gaulin & McBurney, 2000). Will the endeavors of evolutionary psychologists thus serve to unify the currently fragmented discipline of psychology under the umbrella of a single metatheory? Does evolutionary psychology, as some suggest (e.g., Buss, 1995; Tooby & Cosmides, 1992), offer a radical new paradigm for psychological science?

To address this question, it is important to explicate the difference between evolutionary (*ultimate*) and nonevolutionary (*proximate*) explanations. Evolutionary psychological explanations focus on ultimate accounts of human psychological characteristics—that is, they explain *why* traits such as language or sexual jealousy exist in terms of the functions those traits served in ancestral environments. Nonevolutionary psychological explanations, by contrast, generally focus on *how* traits work in terms of proximate social, developmental, cognitive, or neural processes. Consider the phenomenon of morning sickness in pregnant women. An ultimate explanation for morning sickness is that it is an adaptation that has evolved because it helps to protect the pregnant woman and the developing fetus from the ingestion of toxic substances (Flaxman & Sherman, 2000; Profet, 1992). Proximate explanations of morning sickness focus on current physiological and psychological processes involved in food aversions during pregnancy. Proximate explanations address such questions as *What are the conditions under which morning sickness occurs, What neural circuits are involved, and What are the chemical changes that underpin increased olfactory sensitivity during the first trimester of pregnancy?* Neither type of explanation is inherently better than the other, nor does one preclude the other. Rather, ultimate and proximate explanations are complementary and mutually enriching.

Ultimate and proximate explanations, however, are not independent: They inform and influence each other. Discerning the evolved function of a psychological mechanism, for

example, should aid in discovering how the mechanism works—that is, understanding evolved function can generate hypotheses about proximate mechanisms and causation. There are various ways to conceptualize the relation between different theories in science. Using the terminology employed by Thagard (1992), we suggest that it is unlikely that the explanations offered by evolutionary psychologists will entirely replace or supplant nonevolutionary explanations. This is because the two types of explanations target different levels of analysis (ultimate vs. proximate causation). Rather, we suggest that the theories offered by evolutionary psychologists tend to *sublate* extant proximal theories—that is, evolutionary psychological theories partly incorporate and partly reject such theories. Along these lines, we suggest that there are at least three ways in which evolutionary psychological theory and research influences the larger field of psychology.

1. Evolutionary Psychology Opens New Lines of Inquiry in Psychology

The use of evolutionary psychological models sometimes generates novel hypotheses and lines of research that had not—and in many cases could not—be derived from other theoretical models. One example of this point is the research on fluctuating asymmetry and reproductive behavior that was reviewed in this chapter. Another example is theory and research on father involvement and timing of daughters' reproductive development. Draper and Harpending (1982, 1988) have proposed a middle-level evolutionary theory of the role of father involvement in the development of female reproductive strategies. This theory posits that individuals have evolved to be sensitive to specific features of their early childhood environments, and that exposure to different early environments biases individuals toward acquisition of different reproductive strategies. Specifically, Draper and Harpending proposed that an important function of early experience is to induce in girls an understanding of the quality of male-female relationships and male parental investment that they are likely to encounter later in life. According to the theory, this understanding has the effect of canalizing a developmental track that has predictable outcomes for girl's reproductive behavior at maturity. Girls whose early family experiences are characterized by father absence (where women rear their children without consistent help from a man who is father to the children) perceive that male parental investment is not crucial to reproduction; these girls are hypothesized to develop in a manner that accelerates onset of sexual activity and reproduction, reduces reticence in forming sexual relationships, and orients the individual toward relatively unstable pair-bonds

(Draper & Harpending, 1982, 1988). Belsky, Steinberg, and Draper (1991; see also Surbey, 1990) added to this theory the hypothesis that girls from paternally deprived homes should also experience earlier pubertal maturation. From an evolutionary perspective, early pubertal maturation, precocious sexuality, and unstable pair-bonds are integrated components of an accelerated reproductive strategy. During human evolution, this accelerated strategy may have promoted female reproductive success in ecological contexts in which male parental investment was not crucial to reproduction.

Although variation in the timing of pubertal maturation in girls is a socially relevant topic (i.e., early-maturing girls experience relatively high rates of breast cancer, teenage pregnancy, depression, and alcohol consumption; e.g., Vikho & Apter, 1986; Udry & Cliquet, 1982; Caspi & Moffitt, 1991; Graber, Lewinsohn, Seeley, & Brooks-Gunn, 1997), there was almost no research on the psychosocial antecedents of this variation prior to publication of the evolutionary model. This gap occurred because no other theory of socialization and child development provided a framework for studying timing of puberty. Indeed, researchers operating outside of the evolutionary umbrella had never thought to look at the relation between fathers' role in the family and daughters' maturational tempo. With the introduction of the evolutionary model of pubertal timing (see especially Belsky et al., 1991), this topic developed into a fruitful new area of research. Most studies suggest that girls reared in father-absent homes reach menarche several months earlier than do their peers reared in father-present homes (Moffitt, Caspi, Belsky, & Silva, 1992; Surbey, 1990; Wierson, Long, & Forehand, 1993). Moreover, some of these studies have found that the longer the period of father absence, the earlier the onset of daughters' menstruation (Moffitt et al., 1992; Surbey, 1990). However, not all studies (see Campbell & Udry, 1995) have found an accelerating effect for years of father absence on menarcheal age. Ellis and Garber (2000) found that years of stepfather presence, rather than years of biological father absence, best accounted for girls' pubertal timing (suggesting a possible pheromonal effect). Finally, Ellis et al. (1999) present longitudinal data showing that father-effects on daughters' pubertal timing involve more than just father-absent effects: Within father-present families, girls who had more distant relationships with their fathers during the first 5 years of life experienced earlier pubertal development in adolescence. Consistent with the original theorizing of Draper and Harpending (1982), the quality of fathers' investment in the family emerged as the most important feature of the proximal family environment in relation to daughters' reproductive development (Ellis et al., 1999).

2. Evolutionary Psychology Enriches Existing Bodies of Knowledge in Psychology

The use of an evolutionary psychological perspective may enrich existing bodies of theory and data in psychology. Evolutionary psychological metatheory, together with middle-level evolutionary theories, provide a powerful set of methodological heuristics that can provide guidance on what paths to follow (e.g., suggesting new hypotheses and providing criteria for recognizing significant observations) and what paths to avoid (e.g., raising suspicion of certain explanations or observations).

Consider, for example, theory and research on sexual jealousy in humans. Psychologists working outside of an explicitly evolutionary framework have contributed to our understanding of jealousy in numerous ways. A large body of empirical research has documented an array of cultural, developmental, and personality correlates of jealousy; detailed models of the causes of jealousy have been constructed; and the clinical management of pathological jealousy has been investigated (see Salovey, 1991; White & Mullen, 1989). Psychologists working inside an evolutionary psychological framework have also addressed the topic of jealousy, and this research has enriched the extant literature on jealousy in at least three ways.

First, the use of an evolutionary psychological framework has led to a variety of novel hypotheses about sexual and romantic jealousy that have generated fruitful new lines of research on the topic (see Buss, 2000). For example, evolutionary psychologists have hypothesized that levels of jealousy experienced by men (but not women) and amounts of time and energy expended on mate retention by men (but not women) will be negatively correlated with partner's age, regardless of one's own age. This gender-specific, age-specific hypothesis is based on the supposition that men with young, reproductive-aged partners are most at risk of being cuckolded and thus investing in offspring who are not their own. Consistent with this hypothesis, Flinn (1988) found that the amount of mate guarding engaged in by men in a Caribbean village decreased significantly when partners were pregnant or postmenopausal. Furthermore, Buss and Shackelford (1997) found that the amount of mate retention behavior engaged in by men (but not by women) was inversely related to the female partner's age, even after controlling for the male partner's age.

Second, evolutionary psychological approaches have been instrumental in correcting certain errors regarding the nature of jealousy. For example, the contention that jealousy is entirely a socially constructed emotion—essentially determined by cultural factors such as social roles and political institutions

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(e.g., Hupka, 1991; Bhugra, 1993)—has been questioned by evolutionary psychologists. Evolutionary psychologists conceptualize sexual jealousy as a biological adaptation designed by sexual selection to reduce paternity uncertainty and the threat of relationship loss (e.g., Daly et al., 1982). Sexual jealousy should be a universal emotion that is experienced in all cultures when a valued sexual relationship is threatened by a rival. Although some writers have claimed that sexual jealousy does not exist in some cultural groups such as Samoans and the Inuit, not to mention the swinging couples of the 1970s, subsequent analyses have shown that jealousy truly is a cross-cultural universal (Buss, 2000; Daly et al., 1982) and a major motive for homicide throughout the world (Daly & Wilson, 1988).

Third, an evolutionary perspective may prove valuable in integrating various middle-level theories of sexual and romantic jealousy. An extensive psychological literature has documented that feelings of jealousy are related to such factors as relationship quality, rival characteristics, partner similarity, gender, and attachment style (see White & Mullen, 1989). Various social and cognitive models, such as appraisal theory (White & Mullen, 1989) and self-evaluation maintenance theory (DeSteno & Salovey, 1996), have been suggested to account for these relations. An evolutionary psychological approach to jealousy may help integrate such models by providing overarching explanations for *why* certain patterns of appraisal occur in the specific contexts they do, and *why* jealousy is modified by such factors as relative mate value and the characteristics of rivals (Buss, 2000).

3. Evolutionary Psychology Radically Changes Certain Domains of Psychological Inquiry

In some domains, evolutionary psychology has offered more substantive changes to the kinds of explanations employed by nonevolutionary psychologists. For example, the metatheoretical assumptions of sexual selection theory, as instantiated in parental investment theory and good genes sexual selection theory, have radically changed theory and research on mate selection and intrasexual competition. Before the systematic application of evolutionary theory to human mate selection, most work in the area emphasized *proximity* (the tendency to date and marry people with whom one has regular social contact) and *matching* (the tendency to date and marry people whose value on the mating market is similar to one's own) as causal agents in mate selection (e.g., Myers, 1993). The proximity effect was explained as a function of the frequency of social interaction together with the principle that familiarity breeds fondness. The matching effect was conceptualized as an outcome of basic principles of social exchange.

Although proximity and matching are relevant to mate selection, the social models that were used to explain these phenomena have largely been supplanted by current evolutionary models of mating preferences and behavior. General principles of social exchange, familiarity, and interaction frequency simply proved inadequate to explain the facts about human mating. These principles could not account for universal differences between men and women in mate selection criteria (e.g., Buss, 1989), for systematic variation within each sex in orientation toward long-term versus short-term mating (e.g., Gangestad & Simpson, 2000), or for lawful variation across species in mating preferences and behavior (e.g., Trivers, 1985). It is just these types of questions that are addressed by parental investment theory and good genes sexual selection theory. Although some attempts have been made to integrate evolutionary and social exchange perspectives (e.g., Fletcher, in press; Kenrick, Groth, Trost, & Sadalla, 1993), the bottom line is that evolutionary psychological models have dramatically changed the nature of research on mating preferences and behavior (as reviewed in this chapter).

Future Directions

In this chapter we have introduced some of the core ideas and assumptions that comprise the field of evolutionary psychology. We have also illustrated how these ideas can be employed in the development of specific, testable hypotheses about human mind and behavior. The rapid growth in publications in the area of evolutionary psychology over the past decade suggests a growing acceptance of the importance of evolutionary ideas in the behavioral sciences. What can we expect, however, from evolutionary psychology in the twenty-first century? What are the crucial issues that need to be addressed by evolutionary psychologists, and how are evolutionary psychological ideas likely to influence the various subdisciplines of psychology?

Perhaps the most crucial task for evolutionary psychologists in the coming decades will be the identification and elucidation of psychological adaptations. As Buss (1999) notes, evolutionary psychologists have catalogued most of the obvious and plausible psychological adaptations (especially those relating to human mating), but many more remain undiscovered or inadequately characterized. The concept of biological adaptation, as George Williams (1966) has noted, is an onerous one and should only be deployed if the appropriate sorts of evidence to make such a claim are available. Because adaptations are the product of natural selection operating in ancestral environments, and because psychological traits such as jealousy, language, and self-esteem are not easily reconstructed from fossils and artifacts, direct evidence for

biological adaptations may be difficult to come by (Lewontin, 1998; Richardson, 1996). One of the challenges for evolutionary psychology, therefore, will be to develop increasingly more rigorous and systematic methods for inferring the evolutionary history of psychological characteristics (see Durrant & Haig, 2001).

How best to characterize psychological adaptations also remains an important issue for evolutionary psychology. As we have seen, evolutionary psychologists assume that the human mind comprises a large number of domain-specific psychological mechanisms that have evolved to solve specific adaptive problems in our evolutionary past. However, many important questions remain regarding the relative specificity of such mechanisms, the way that they might develop over time in response to different environmental contexts, and how these mechanisms operate in terms of proximate cognitive and neurobiological processes.

Consider, for example, the theory that self-esteem acts as an interpersonal monitor—or sociometer—that tracks the membership status of individuals in social groups (Leary & Downs, 1995; Leary, Tambor, Terdal, & Downs, 1995). Leary and colleagues approached this well-studied psychological phenomenon by asking the important question: What is the (evolutionary) function of self-esteem? Their answer is that people do not strive for self-esteem as some kind of end point or ultimate goal. Rather, self-esteem reflects one's level of relative social inclusion or acceptance in social groups. Self-esteem, therefore, functions to motivate individuals to pursue courses of action that can restore or improve their acceptance by relevant others. In short, the self-esteem system is characterized as a psychological adaptation that has evolved to solve the recurrent adaptive problem of social exclusion and the fitness costs that such rejection would have entailed in ancestral environments.

However, many important questions remain regarding the nature of the self-esteem system, even if it can be plausibly considered a psychological adaptation. For example, Kirkpatrick and Ellis (2001) have suggested that one should expect self-esteem to be carved in to multiple domains to reflect the different types of interpersonal relationships that were important during human evolutionary history. Thus, they argue that there will be a number of different sociometers that gauge relative social inclusion in such domains as mating relationships, family relationships, and instrumental coalitions. Just how many different sociometers humans possess, however, remains an open question. Furthermore, we are only beginning to understand how the mechanisms underlying self-esteem develop over time in response to different environmental contexts and how they operate at a proximate cognitive and physiological level. One of the

important challenges for evolutionary psychology, therefore, lies in fleshing out the details of putative psychological adaptations such as self-esteem.

Over the next couple of decades, we expect that the coherent body of theory developed by evolutionary psychologists will be applied more regularly to many new fields in the behavioral sciences, especially such applied domains as organizational, environmental, and clinical psychology. For example, within clinical psychology, evolutionary explanations have been recently advanced for a variety of specific disorders, such as depression (Price et al., 1994), phobias (Marks & Nesse, 1994), substance abuse (Nesse & Berridge, 1997), and autism (Baron-Cohen, 1995). Even the very basis of the classification of mental disorders has been reconceptualized from an evolutionary perspective (Murphy & Stich, 2000). Specifically, Murphy and Stich urge that we should draw a fundamental distinction between mental disorders that arise from the *malfunction* of specific evolved psychological mechanisms, on the one hand, and those that occur due to a *mismatch* between our evolved psychological architecture and contemporary environments, on the other. Thus, autism can be plausibly conceptualized as the result of a malfunctioning of the theory of mind module, which has evolved to make inferences about others' behavior on the basis of imputed mental states such as beliefs and desires (Baron-Cohen, 1995). Depression, by contrast, as conceptualized by the social-competition model (Price et al., 1994), may result from increased likelihood of drawing unfavorable comparisons with other individuals due to the enlarged size of our potential social groups, brought about by population growth and advances in information technology.

In suggesting that evolutionary psychology will expand into new domains, we do not mean to imply that extant psychological theories will be overthrown or replaced. Rather, as more is known about the evolutionary origins of the human mind, more integrated theories can be developed—ones that recognize the important role of multiple explanations drawn across different levels of analysis.

In conclusion, *Homo sapiens*, like all other species, is the product of a history of evolution. Our opposable thumb, bipedal stance, and color visual system are all testimony to the gradual process of natural selection operating over vast spans of time. Just as the anatomical and physiological features of our bodies are explicable in evolutionary terms, so too are the complex array of psychological processes that make up the human brain-mind. The rapidly growing field of evolutionary psychology—from its broad metatheoretical assumptions to the specific predictions that are tested in research—offers a coherent and progressive paradigm aimed at uncovering the origins and functions of human

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mental and behavioral characteristics. In this chapter we have offered an introduction to some of the key ideas, issues, and methods that guide applications of evolutionary theory to human cognition and behavior. Although evolutionary psychology still meets resistance on some fronts, we believe that its value and potential for investigating questions of human nature is great.

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