

Evolution and Human Behavior

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In the distant future I see open fields for far more important researches. Psychology will be based on a new foundation, that of the necessary acquirement of each mental power and capacity by gradation. Light will be thrown on the origin of man and his history.

—Darwin 1859

As foretold by Darwin (1859), scientists across multiple disciplines including anthropology, biology, and psychology have started to apply the same evolutionary principles (e.g., sexual selection, parental investment, parent-offspring and intra-genomic conflict, kin selection, reciprocal altruism, and life history theory) used to understand the behavior of nonhuman species to explain human behavior, cognition, and culture. Currently, a handful of overlapping fields of research—evolutionary psychology, human behavioral ecology, evolutionary developmental biology, and gene-culture coevolutionary perspectives—share this common goal. Though there is great diversity in methodological approach and the particular focus of investigation, together the human evolutionary behavioral sciences have taken great strides in uncovering the elements of human nature.

Our aim in this chapter is to provide an overview of two major avenues of research: human behavioral ecology and evolutionary psychology. Both approaches share the central tenets of evolutionary biology and an appreciation of the distinction between ultimate and proximate questions of causality as outlined by Tinbergen (1963) and Mayr (1976b). They differ mainly according to the types of research questions they ask and the data viewed as appropriate to answering these questions. To illustrate the strengths of each approach and how they complement the work being done on nonhumans, we provide examples of active

research in each discipline: in human behavioral ecology, patterns of food production in the Hadza; in evolutionary psychology, investigations into the architecture of human kin detection; and how women's sexuality changes across the menstrual cycle. Although advancements in research and theory on these and other topics in humans arise from principles grounded in evolutionary biology, work on humans now has the potential to contribute novel insights to behavioral ecology and evolutionary biology by providing key tests of ideas within the field and by contributing to important comparative perspectives. Throughout our discussion we point out ways this might occur. In addition, we touch on current debates and conclude with our thoughts on future directions of the field.

APPROACHES TO STUDYING HUMAN BEHAVIOR

Approaches to studying human behavior parallel that of nonhuman behavioral ecology in many respects. Both human behavioral ecology and evolutionary psychology maintain that human nature, just like wasp, finch, or mole-rat nature, is a product of historical selective forces. Accordingly, these fields apply evolutionary principles to derive empirically testable predictions regarding the selection pressures that may have shaped human cognition and behavior. For example, selection pressures

relating to the differential parental investments by men and women guide research on human mate choice; selection pressures posed by deleterious recessive mutations and pathogens guide investigations of inbreeding avoidance in humans; life history theory informs the study of human maturation rates and senescence; and kin selection and reciprocal altruism yield predictions about the nature of various forms of human cooperation. Thus, human behavioral ecology and evolutionary psychology draw upon the same pool of theoretical tools to study human nature.

Despite a shared focus on the same species, human behavioral ecology and evolutionary psychology nevertheless differ in the kinds of research questions they emphasize and, as a result, the kinds of data they collect. We address each discipline next but wish to point out that, rather than existing as two entirely separate fields, human behavioral ecology and evolutionary psychology complement one another and, in our view, represent two sides of the same Darwinian coin—one focusing primarily on the structure of our evolved psychological adaptations (evolutionary psychology), and the other primarily on their behavioral outputs (human behavioral ecology)—both sharing an emphasis on function.

Human Behavioral Ecology: A Focus on Behavior

Human behavioral ecologists apply the same approach as nonhuman behavioral ecologists, investigating how ecological and social variation within and between populations account for the variation of particular behavioral strategies and resulting individual reproductive success (for a more in-depth discussion, see chapters 1 and 2). In this way, human behavioral ecology attempts to model the selection pressures that existed throughout human evolution and that played a role patterning modern human behavior. Tools used by behavioral ecologists to generate predictions about and interpret data on humans mirror those used to study non-humans. They include quantitative modeling for identifying optimal behavioral and reproductive strategies within a certain socioecological context and the assessment of the trade-offs humans make, not only in the behavioral strategies employed, but also in the investment in various physiological processes. For instance, increased levels of testosterone

might facilitate mating effort at the expense of parenting effort or immunocompetence (e.g., Ellison 2003).

Human behavioral ecologists investigate social and ecological selection pressures by collecting data on the fitness consequences of human behavior in purportedly “natural” contexts, that is, contexts similar in key ways to those experienced by human ancestors dating back at least thousands of years. This approach, however, has not been without controversy. For instance, there has been much discussion regarding the utility of measuring current reproductive success to identify ancestral selection pressures (e.g., Borgerhoff Mulder 2007; Symons 1992; see also chapter 2, of this volume). These discussions have helped clarify the strengths and weaknesses of the behavioral ecology approach in humans. In general, we point out that human behavioral ecology and the conceptual tools they employ have shed light on many patterns of human behavior (e.g., see Smith & Winterhalder 1992). For example, calories returned to camp provide insights on foraging and hunting strategies. Similarly, allocation of these calories to others in the group sheds light on patterns of cooperation, mating effort, and parenting effort (see below). Finally, indices of health such as fluctuating asymmetry and body mass index have been used to investigate mating behavior (e.g., Sherry & Marlowe 2007).

Evolutionary Psychology: A Focus on Psychological Mechanisms

Though exceptions exist, typically human behavioral ecologists are less focused on identifying the proximate mechanisms that govern decision making and regulate behavior. As was pointed out in chapters 8–10, however, natural selection shapes behavior by shaping developmental and psychological processes that, in turn, generate behavior. Evolutionary psychologists are interested in understanding the architecture of these processes (Tooby & Cosmides 1992). More specifically, the aim of evolutionary psychology is to identify and detail the structure of human cognitive adaptations based on evidence of functional design. The brain, however, is not as straightforward a structure to reverse engineer as the heart, eye, or wing; its form does not provide obvious clues to function. To uncover the nature of our psychological adaptations,

evolutionary psychologists employ a set of guiding principles. These include the notion that our neural circuits were designed by natural selection to solve *adaptive problems*—conditions generating long enduring selection pressures whose successful navigation impacted survival and reproductive success, however distally. Examples of adaptive problems (with associated selection pressures in parentheses) include avoiding predators (various predators in the environment), avoiding sex with close genetic relatives (deleterious recessive mutations), finding nutritious food (nutritional requirements for growth and development and variation in available nutrients), caring for offspring (kin selection), and selecting a mate (differential parental investments by the sexes and sexual selection).

A second guiding principle is that of functional specialization. Evolutionary psychologists posit that different neural circuits likely exist to solve different adaptive problems. This is because psychological mechanisms well designed to perform one task are unlikely to perform additional diverse tasks equally well. This principle is seen throughout the human body: bodily functions are carried out by dedicated organs, not one general-purpose organ. The same logic applies to psychological adaptations. A system for avoiding the ingestion of pathogens is unlikely to process information regarding reciprocal altruism or govern kin detection. For this reason, evolutionary psychologists expect the human neuro-computational architecture to contain a constellation of integrated, functionally specialized psychological mechanisms. Much debate has occurred over the degree of functional specialization (often framed as modularity), especially in the human brain given the broad scope of human intellectual capacities (e.g., Buller 2005; Elman et al. 1996; Panksepp & Panksepp 2000). We address this topic in more depth in box 31.1.

In general, the concepts of adaptive problem and functional specialization help generate hypotheses regarding evolved behaviors as well as our brain's information-processing architecture. To investigate the information-processing systems that natural selection shaped to enable a particular ability, evolutionary psychologists start with the question of what a well-engineered system designed to perform a particular function might look like. It is not expected that natural selection shaped systems to perform perfectly, because evolutionary responses always are subject to trade-offs and historical

constraints (e.g., take the existence of a blind spot in our visual system). Nevertheless, models of the cognitive procedures required to perform a task can sharpen predictions and reveal new relationships.

Information-processing models of psychological adaptations bear much similarity to those developed for animals (see chapter 10). They include a description of ancestrally available cues, both external (e.g., social information) and internal (e.g., physiological states), that would have provided information about a particular recurring state. For instance, seeing one's mother breast-feeding a newborn provides information regarding probable siblingship; the detection of one's mate in bed with someone else provides information regarding infidelity; and low blood glucose levels signal the need for additional food. Models also postulate how these cues are transformed into internal representations and they specify the decision-making and motivational systems that use these representations to regulate behavior (Tooby, Cosmides, Sell, Lieberman & Sznycer 2008). Empirical investigations in the laboratory and in the field can help refine proposed computational models—for example, by integrating additional mechanisms that compute newly discovered or hypothesized cost-benefit trade-offs—which, in turn, can generate new lines of inquiry. Importantly, information-processing models and associated findings in humans can inform investigations in nonhuman species that faced similar adaptive problems and therefore might employ similar cognitive solutions.

In summary, according to evolutionary psychologists, psychological adaptations can be viewed as a set of information-processing systems that were designed by natural selection in response to the various adaptive problems faced by our ancestors. Taking advantage of the empirical techniques employed across the psychological sciences including those found within social and cognitive psychology, neuropsychology, and neuroscience, this approach has shed light on a wide range of human behaviors and cognitive abilities such as those relating to mate choice, social exchange, aggression, human face recognition, social categorization, theory of mind, intuitive physics, and various emotions (e.g., see Buss 2005). Below, we illustrate how evolutionary psychologists approach human behavior and cognition, using two examples: human kin detection and female mating preferences across the menstrual cycle.

BOX 31.1 Modularity in Human Psychology

Much debate surrounds the topic of modularity, especially as it relates to human psychology. The notion of modularity is of particular concern for those interested in the computational theory of mind, which, based on the work of philosophers such as Turing, proposes that mental *outputs* (thoughts, perceptions, behaviors) derive from computations or algorithmic operations on information. The philosopher Jerry Fodor (1983) highlighted the idea that certain computations require operations that are *modular*. However, Fodor had a particular conception of modularity in mind and suggested that only computations possessing the following features could be considered modular:

1. Modules are domain specific, that is, they process only a select type of information (e.g., linguistic or visual information).
2. Modules operate in a mandatory fashion, that is, they automatically process information specific to their domain. For instance, when your eyes are directed toward a flower, you cannot help but see the flower—the visual information is necessarily taken as input.
3. Modules do not generate representations that are accessible to central (i.e., conscious) processes, but instead generate lower level representations of which we have no conscious awareness.
4. Modules are informationally encapsulated. This means that of the range of information that could, in principle, contribute to a particular analysis, only a small proportion is in fact accessed. Put another way, computations that modules perform are likely not affected by feedback from higher level processes (e.g., ones that generate representations regarding expectations or beliefs). For instance, visual processes that create the Muller-Lyre illusion (lines with different arrow ends that appear to be different lengths, yet are in fact identical) do not have access to outputs of higher level feedback processes. Subjects can know that the lines are identical (by measuring them), but this does not affect the way the lines are perceived. This is one example of how visual processes draw upon limited, encapsulated, lower level information to generate percepts.
5. Modules are associated with a fixed neural architecture.
6. Modules exhibit characteristic breakdown patterns.
7. Modules follow an innately specified developmental trajectory.

Importantly, Fodor proposed that modularity characterizes perceptual input systems including vision, audition, olfaction, and language, but not more *central* cognitive processes such as those governing judgment and decision making (*higher cognition*). For instance, our visual system contains various computational procedures that are modular, including those that permit us to see color or infer objects from two dimensional arrays of stimulation on our retinas. They are modular because, for example, we cannot help but see color, and our perceptions of color are not influenced by higher level decisions. Fodor's criteria, more central systems cannot qualify as modular. This is because, among other things, central systems have access to a wide range of inputs and do not necessarily operate in a mandatory fashion.

As discussed in this chapter, evolutionary psychologists also argue that psychological systems are modular. Contrary to Fodor, however, evolutionary psychologists argue that even computational procedures downstream of perceptual processes are governed by modules (e.g., those guiding judgment, decision making, and emotions). For instance, evolutionary psychologists have proposed that kin detection mechanisms are evolved

modules. But the information processed by these modules (e.g., duration of coresidence) is downstream to perceptual input systems and available to more central systems.

So do evolutionary psychologists argue against Fodor that central processing can be modular? In fact, not in any straightforward sense: Fodor and evolutionary psychologists have used the terms *module* and *modularity* in different ways. Fodor's modules are defined by structural criteria (e.g., information encapsulation and limited access to more central mental representations). By contrast, evolutionary psychologists define modules in terms of *functional specialization* (Barrett & Kurzban 2006). Using kin detection as an example, kin detection mechanisms take as input information relevant to the task of categorizing according to kinship (and not just any input). These inputs, far from being shallow perceptual inputs, are likely higher level representations. For instance, receiving care from the same caregivers throughout childhood has been proposed as one cue to siblingship that is taken as input by kin detection mechanisms. Assessments of sharing the same caregivers (typically one's mother and father) likely rely on a suite of complex higher level systems. The system is specialized, because it relies on specific information from which it yields a specific decision (the reliability of an inference that a particular individual is a sibling). But the system is not modular in a strict Fodorian sense.

In general, rather than using *a priori* criteria for generating predictions regarding likely structures of cognitive systems, evolutionary psychologists maintain it is more useful to consider functionality, as a system's function will, to a large extent, dictate its information processing structure (Sperber 2005). Thus, evolutionary psychologists do not primarily concern themselves with whether functionally specialized processing of information is modular in a strict Fodorian sense. Rather, they see that many decisions must rely on functionally specialized systems. For example, incest aversion appears to be a function of specific cues such as coresidence duration and seeing one's mother caring for a newborn, and women's attraction to men's masculine features appears to depend on their ovulatory status in ways that other decisions are not. It is difficult to see how these computations could be the result of a highly general processing system (e.g., one system that took as input both kinship cues and ovulatory status and generated appropriate behavior toward kin and potential mates).

This is not to say that evolutionary psychologists do not concern themselves with issues of how cognitive systems are structured. Indeed, they are interested in coming to understand how, in general, computational systems can be functionally specialized without being limited by the structural criteria set forth by Fodor, and how their structure is instantiated in our neural networks. Barrett (2005), for instance, proposes one perspective on this topic.

Once functional specialization is taken as the key concept and not Fodor's strict criteria for modularity, other related issues become easier to dissect. Take, for instance, debates about cognitive flexibility. It would seem that the greater the number of Fodor-type modules we relied upon, the less flexible and adaptable our decision making would be. That's because many of our decisions would rely on automatic, encapsulated procedures, with no opportunity for modification based on our experiences or reflection, and no ability to deal with anything more than a very narrow range of information. Given humans' ability to learn from experiences and, through careful reflection, to solve a vast array of novel problems never before encountered in ancestral or modern environments, it may seem a natural conclusion that our minds are not characterized by massive modularity.

Again, however, evolutionary psychologists do not claim that functional specialization is modular in Fodor's sense. Rather, the adaptationist principle of functional specialization provides a starting point for understanding the flexibility generated from our evolved cognitive mechanisms. Cognitive mechanisms may be specialized to take particular subsets of information as input (consider the paralyzing alternative of taking any and all information as input continuously). Flexibility may arise because some information may be distinct from that which played a role in the mechanism's evolution, but be sufficiently similar to

(continued)

BOX 31.1 (cont.)

be processed. For instance, as discussed by Sperber (2005), given that cognitive mechanisms evolved to process information in a particular domain, one can distinguish between that mechanism's *proper domain*, the set of inputs the system evolved to process, and that mechanism's *actual domain*, the set of inputs the system actually processes, regardless of whether they played a causal role in the evolution of that mechanism. It is therefore possible that evolved mechanisms process a wider range of inputs than what they were originally selected to process, leading to a wider range of behavioral outputs. A similar point may be made with regard to nonpsychological adaptations. The human hand may have been modified by selection to manipulate tools using materials available in ancestral environments, but it may now be used to manipulate a much larger range of modern objects, for example, to open refrigerator doors.

Importantly, some human capacities involve abilities to learn and innovate solutions, in instances across a wide array of specific content domains (e.g., *improvisational intelligence*; Barrett et al. 2007). These capacities, too, however, possess specialized information-processing structure as reflected, for instance, in psychological theories of various kinds of learning (Gallistel 2000). Hence, in theory they can be characterized in ways similar to other psychological adaptations.

In sum, evolutionary psychologists bypass the debate on modularity by deemphasizing structural criteria as typified by Fodor's concept of modularity, and stressing evolved functional specialization. This allows them to ask questions such as, what would the information-processing structure of a system well-designed to perform function X look like? In this way, evolutionary psychologists are able to generate new hypotheses regarding a wide array of cognitive processes underlying human behavior.

EXAMPLES OF CURRENT RESEARCH IN HUMAN EVOLUTIONARY BEHAVIORAL SCIENCE

Human behavioral ecology and evolutionary psychology emphasize different sequelae of historical selection pressures, namely, the association of adaptive behavioral strategies with particular socioecologies versus the existence of functionally specialized information-processing procedures, respectively. However, these approaches complement one another. Together they provide the methods for detailing many aspects of human nature. Next, we highlight three examples of recent research within the human behavioral sciences. Though we discuss each example as originating with researchers identified as either human behavioral ecologists or evolutionary psychologists, questions pertinent to the goals of both disciplines should be applied to each, a topic we return to in our conclusions.

Patterns of Food Production in Human Foragers

Most human foraging groups rely substantially on the production of meat through hunting or fishing. In most of these groups, men hunt and fish more than do women. Accordingly, men tend to produce more calories than women. Marlowe (2001) reported that, on average, across 95 foraging groups, men produced 64% of all calories. In 9 groups on which careful food-weighing techniques were applied, men's production accounted for, on average, 66% of all calories (Kaplan et al. 2000). Notable exceptions do exist. In particular, in many groups within the matrilineal belt of Africa and in the insular Pacific, women produce as many or more calories as men. In these areas, hunting of large game is relatively uncommon, and horticulture, an activity women commonly engage in, is relatively common (e.g., Schlegel & Barry 1986).

A critical question that behavioral ecologists have asked is, why do men hunt? That is, what ancestral

fitness benefits led men to generate, through hunting, calories that exceed what they consume?

Hunting in the Hadza

The Study Population The Hadza of Tanzania is one group whose foraging activities have been investigated extensively through research by Nick Blurton-Jones, Kristen Hawkes, and their colleagues and students (notably, Frank Marlowe). The Hadza number about 1,000 and live a nomadic lifestyle in a savanna-woodland habitat. They live in small groups, averaging about 30 individuals per group, with migration between groups common. Typically, groups move to a new location every month or two. Women dig tubers, gather berries, and collect other fruits. Men collect honey and fruit and hunt mammals and birds with bows and arrows. Children's diets are subsidized by the efforts of men and postreproductive women (though the Hadza are at the low end of the cross-cultural distribution of men's contributions to subsistence, with men producing only about 40% of the calories overall). At age 10, children produce about half of the calories they consume through gathering of fruit (Hawkes et al. 1995).

The Paternal Care Hypothesis One view of men's hunting is that it functions as paternal care—that is, it benefits men's fitness through increased offspring survival or quality. According to this view, men and women have evolved to cooperatively raise offspring. In so doing, they divide their labor efforts, with women in traditional societies performing most of the direct child care, and men supplying food through activities that women cannot readily do while caring for children, primarily hunting. Kaplan et al. (2000) argue that biparental care and a sexual division of labor evolved in humans as part of a larger coadapted complex of features, including extractive foraging of high-quality foods, a long period of juvenile dependency, intensive learning in childhood, and a long productive life span that renders skill-intensive means of production (which requires many years to acquire to peak levels) worth pursuing.

The Show-Off Hypothesis Hadza hunters share meat across the band instead of giving it directly to their nuclear families, particularly when the captured game is large. Hunters have greater control

over the consumption of small game and can direct larger shares to their own families. In a series of papers in the 1990s, Hawkes and colleagues argued that men's hunting, especially large-game hunting, has been selected to advertise (show off) a male's mate value because successful hunting results in benefits in the currency of mating opportunities (Hawkes 2004). Put otherwise, hunting functions (largely) as mating effort, especially hunting of large game. In support, good hunters are more likely to remate following the death of a spouse and are more likely to take a second wife when a first wife reaches menopause (Marlowe 2000). Good hunters in the Ache, another widely studied foraging group, have more extra-pair mates than do less successful hunters. In addition, Hadza men purportedly allocate greater time on hunting large game than is profitable, given relative rates of return from hunting large game and smaller game, respectively (see Hawkes 2004; though see also Marlowe 2003). Second, although children's nutritional status is predicted by their mothers' food production, it is not predicted by the rate of food produced by fathers (Hawkes 2004).

Hawkes and colleagues accept that men's hunting does subsidize the diets of women and children. However, they argue that men have not been selected to hunt because hunting large game resulted in greater offspring fitness through direct nutritional benefits. The benefits of men's surplus production are a fortuitous side effect for women and children, not benefits that directly shaped men's hunting efforts. Hawkes et al. essentially suggest that female preferences for good hunters may have both direct and possibly indirect effects for females (see chapter 24). For example, Marlowe (2005) found that Hadza women rate hunting prowess as more important in potential mates than any other feature. Thus, Hawkes and colleagues argue that men's hunting is a sexually selected trait via female preference (see Hawkes 2004).

A Blended View The male-hunting-as-parental-effort and the male-hunting-as-mating-effort theories sometimes are presented in extreme forms, if not by their proponents, then by their critics. But good hunting may have both natural and sexually selected effects on men. Historically, men's hunting may have yielded reproductive benefits by enhancing parental investment as well as mate attraction. Accordingly, the modulation of hunting

behavior may arise from psychological adaptations with two different functions—parental effort and mating effort—served at least partly by distinct adaptations.

Under a mixed model, different hunting endeavors may differentially benefit men through parental investment and mating effort. Hawkes et al. (2001) emphasize that men's large game hunting is not an effective or efficient means of provisioning offspring. Large-game hunting may hence benefit men substantially in the form of mating effort (though, we note, alternative explanations, such as benefits achieved through building of social alliances, are possible). By contrast, men in foraging societies have much more control of the distribution of captured small game and may preferentially direct it toward primary partners and offspring. Thus the hunting of small game may function as an effective means by which men exert parental investment.

Marlowe (2003) presents data on the Hadza that are consistent with a blended view. Overall, married Hadza women produce as many calories as do married Hadza men. Women with small offspring, however, produce far fewer calories than produced by women without young offspring. Compared to all other married women, women whose youngest child is 3 years of age or younger harvest fewer calories, and women with an infant 1 year of age or younger harvest only about half as many calories as other married women. These outcomes are consistent with the argument that women's child care interferes with effective foraging. When women have young children, however, their husbands' production of calories increases, and substantially exceeds that of their wives. Hence, whereas in couples without a child 3 years of age or younger, wives produce more calories than husbands do, in couples with an infant younger than 1 year of age, men produce almost 70% of the calories (see figure 31.1). These increases in production by Hadza men presumably function to make up for deficits in the harvesting of calories by wives with small children.

Hadza men, then, appear to facultatively adjust their work efforts (and perhaps the prey items they target) in response to the direct food production of wives, as it varies with the presence or absence of young children. This pattern is not well explained by the idea that men's work functions solely as mating effort (see Marlowe 2003 for a discussion of possible alternative explanations). Moreover, separation of men into fathers and stepfathers provides additional evidence that men's production functions

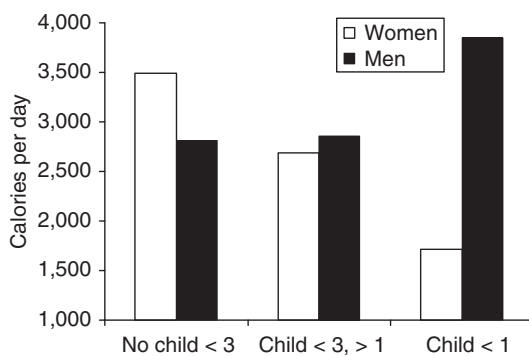


FIGURE 31.1 Hadza male and female caloric production as a function of a couple having no child under age 3, a child older than 1 but younger than 3, and a child younger than 1 year old. Adapted from Marlowe (2003).

partly as parental effort. Approximately 30% of Hadza children have stepfathers. Stepfathers do not show the same pattern of enhanced food production in response to the presence of young children in the household that children's genetic fathers demonstrate.

Summary of Human Foraging

In sum, human behavioral ecologists have studied patterns of men's and women's foraging in considerable detail. Of particular interest are the evolved functions of men's hunting. Sharp debate has led to focused investigation of when and how men decide to allocate their foraging efforts. At this time, it appears likely that men's hunting does partly function as parental effort, and hence benefits of food production for offspring have at least partly shaped the decision processes that underlie men's foraging efforts. Nonetheless, men's hunting may also function to attract mates. Additional research into the psychological systems responsible for foraging decisions—an evolutionary psychological approach—may sharpen our understanding of the forces of selection that shaped them. (For further discussion, see Smith 2004.)

Kin Detection and Kin-Directed Behavior

Another area of active research within the human evolutionary behavioral sciences is the investigation

of the cognitive mechanisms governing kin detection and kin-directed behavior. As in other species that regularly encountered close genetic relatives across the life span, mechanisms for detecting kin are expected to exist in humans for at least two reasons: to avoid choosing a close genetic relative as a sexual partner, thereby avoiding the deleterious consequences associated with inbreeding, and to regulate altruistic and competitive effort according to the probability of genetic relatedness as indicated by inclusive fitness theory. But how might evolution have engineered a psychological system to discriminate according to genetic relatedness and then regulate sexual aversions and altruistic motivations accordingly?

An evolutionary psychological approach to this question involves developing models of our evolved computational architecture. At minimum, a system designed to avoid inbreeding and to allocate assistance according to genetic relatedness would need a way to assess relatedness and systems governing sexual attraction and altruism. One recently proposed model of kin detection and kin-directed behaviors suggests the following components: (1) procedures that monitor for and take as input the particular cues signaling relatedness, (2) a *kinship estimator* that takes as input the detected cues and, based on these cues, computes for each individual, *i*, an estimate of relatedness, or *kinship index* (KI), and (3) procedures that feed the KI into two separate motivational systems: one regulating sexual attraction/avoidance and one regulating altruistic/competitive behavior (see figure 31.2; adapted from Lieberman et al. 2007). Thus, according to this model, the same kin detection procedures can regulate two distinct classes of behavior.

Cues Used to Assess Genetic Relatedness

There are a number of constraints that confine the set of cues selection might have favored to engineer kin detection systems. For instance, barring recent medical technology, we are not able to directly compare genomes to assess kinship. However, other possible kinship cues exist. One possibility includes the use of more evolutionarily novel cultural information such as linguistic kin terms. But these are unlikely to be the primary cues used to detect kin because kin terms can blur genetic boundaries (e.g., *aunt* in our culture refers to a parent’s sister, a blood relative, and a parent’s brother’s wife, a nonblood

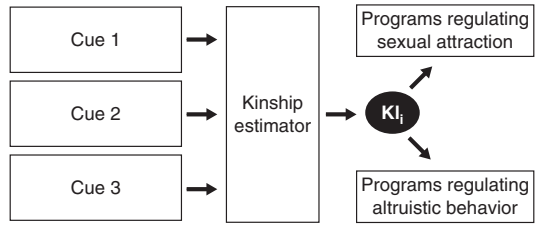


FIGURE 31.2 A model of the information-processing architecture of human kin detection. Cues that correlated with relatedness throughout our species’ evolutionary history are taken as input by a *kinship estimator* that computes for each individual, *i*, an estimate of kinship or *kinship index* (KI). The KI is then taken as input by two distinct motivational systems: one regulating sexual attraction and one regulating altruistic motivations. Specifically, the computed KI is capable of having multiple effects: as KI increases (i.e., as the probability an individual is likely to be kin increases), programs guiding sexual attraction can be downregulated and those guiding sexual avoidance upregulated. With respect to helping behavior, as KI increases, programs guiding altruistic motivations can be upregulated and programs guiding competitive motivations downregulated. Thus, according to this model, the same kin detection procedures can regulate two distinct classes of behavior. Redrawn from Lieberman et al. (2007).

relative). Furthermore, it is unlikely that phylogenetically prior kin detection mechanisms that functioned in the absence of linguistic information were overwritten by more variable and potentially less reliable cultural information.

Rather, it is likely we rely on ecologically valid cues that correlated with genetic relatedness in human ancestral environments. Importantly, the cues mediating kin detection might differ depending on the type of kin in question. To the extent that different cues signaled an individual was a specific type of close genetic relative (e.g., mother, father, offspring, or sibling), different detection mechanisms are likely to exist. Additionally, males and females might use distinct cues to identify the same type of kin. For example, because men can never be fully certain of their relatedness to offspring, the cues signaling that an infant is indeed one’s own are likely to differ for men and women.

A range of kinship cues have been identified by evolutionary biologists investigating inbreeding

avoidance and altruism in nonhuman species (for review, see Hepper 1991). For instance, early association, a spatial cue that identifies likely siblings in species in which offspring require extended maternal care, predicts patterns of social preferences and mate choice in species such as voles, mice, macaques, and chimps. In some species, chemical cues guide kin detection and associated kin-directed behaviors. Studies on house mice, for example, show that mate preferences are guided by assessments of similarity at loci controlling the major histocompatibility complex (MHC). That is, males and females prefer to mate with individuals who are MHC dissimilar from themselves, a preference thought to protect against the negative effects of pathogens. For MHC disassortative mating to occur, however, individuals require a referent, either themselves or a close relative, to determine what counts as MHC dissimilar. A series of cross-fostering experiments in which individuals were raised by MHC-dissimilar parents showed that individuals preferred to mate with others who were dissimilar from their foster parent's MHC composition. Thus MHC-guided mate preferences appear to use parental phenotypes as referents of one's own genetic composition (e.g., Penn & Potts 1999).

In the human evolutionary literature, the majority of research has focused on the detection of siblings and the associated development of sexual aversions and sibling-directed altruism. Next, we briefly discuss some recent findings from this literature.

Sibling Detection: Exposure to Mother-Infant Association and Coresidence Duration

The ancestral social environment of humans was such that a likely reliable cue to siblingship would have been seeing one's own mother caring for (e.g., breast-feeding) a newborn. Indeed, the intense mother-child association that typically occurs surrounding the natal period and continues throughout the first few years of life would have served as a stable anchor point for others to infer relatedness. Thus, if an individual observed an infant receiving care from the individual's own mother (at least the female categorized as one's own mother), then it was highly probable that that infant was the individual's sibling. Further, exposure to this cue would have signaled genetic relatedness regardless of coresidence (or association)

duration. That is, regardless of whether one was 5, 10, or 15 years old, maternal-infant directed care would have cued probable genetic relatedness. However, as potent a cue as mother-infant association might be, it is available only to older siblings already present in the social environment; the arrow of time forbids a younger sibling from having seen his or her older sibling born and cared for as an infant. For younger siblings, then, what cue or cues might evolution have used to identify probable older siblings?

One solution is to track the flow of parental effort. Any child regularly receiving care from one's own mother and father had a higher probability of being kin than children receiving care from other individuals. Moreover, the longer the care, the more likely the individual would have been a sibling. This cue, operationalized as childhood coresidence duration, was first proposed by Edward Westermarck, a Finnish social scientist who noted that children reared in close physical proximity during childhood tend to develop a sexual aversion toward one another later in adulthood (Westermarck 1891/1921). This idea, known as the *Westermarck hypothesis* (WH), has received support from various anthropological and psychological investigations (see review in Lieberman et al. 2003). Perhaps most notable are the cases of the Israeli kibbutzim and Taiwanese minor marriages, two natural experiments inadvertently created by cultural institutions in which unrelated children were reared in close physical proximity throughout childhood. As the WH predicts, children reared together throughout childhood rarely marry one another (Israeli kibbutzim: Shepher 1983), and if forced to marry suffer decreased rates of fertility and increased rates of divorce and extramarital affairs (Taiwanese minor marriages: Wolf 1995). Together, these studies point to early coresidence as one cue our mind uses to assess relatedness and to dampen sexual desires. However, they raise many questions. For example, does coresidence duration predict sexual aversions differently for the younger and older sibling in a sib-pair? As suggested above, older siblings might rely on a different cue to identify probable younger siblings, one that operates independent of coresidence duration. Also, do the same kinship cues that regulate inbreeding avoidance also regulate kin-directed altruism, the other suite of behaviors relying on assessments of relatedness? These and other questions are being addressed in the psychological sciences.

Psychological Investigation of Kinship Cues

It is not ethical to subject humans to the life-altering experiments used by evolutionary biologists to study kin recognition in nonhuman animals. For this reason, scientists have either had to look for natural experiments, such as those mentioned above, or take advantage of the natural variation that exists in families composed of actual genetic relatives. To investigate whether a proposed cue serves as a signal of relatedness, it is possible to match individual variation in exposure to the specific cue (e.g., coresidence duration, maternal-infant association) to behaviors and reactions relating to sexual behaviors with family members. Converging lines of evidence that we use a particular cue to categorize individuals according to genetic relatedness can be found through investigations of altruism. If the same kin detection mechanism serves to regulate both sexual avoidance and altruism, then a cue to kinship should show parallel effects across these two distinct motivational systems.

Recently, a team of researchers set out to investigate whether our mind evolved to use coresidence duration and maternal-infant association as separate cues for detecting older siblings and younger siblings, respectively. Using surveys to collect information, Lieberman et al. (2007) found that individuals not exposed to their mother caring for their sibling as a newborn (as it is typically for the younger sibling in a sib-pair), their duration of coresidence with an opposite sex sibling predicted aversions to sibling incest, as measured by disgust at imagining sex with one's own sibling and moral sentiments relating to third-party sibling incest. By contrast, for individuals exposed to their mother caring for their sibling as an infant (the older siblings in a sib-pair), coresidence duration with an opposite sex sibling *did not* predict aversion to incest. When measures of altruistic attitudes and behavior were analyzed, the same pattern emerged. That is, coresidence duration with a sibling predicted altruism more strongly for individuals without access to the more potent cue of seeing their mother caring for their sibling as a newborn (see figure 31.3). These data provide compelling evidence that the mind uses two different cues for identifying older versus younger siblings and for regulating sexual aversions and altruistic motivations.

Upon inspecting the levels of aversions and altruistic inclinations reported, Lieberman et al.

(2007) found that older siblings exposed to the cue of seeing their mother care for a younger sibling as a newborn reported intense levels of disgust toward sexual acts with that sibling as well as increased levels of altruism across all durations of coresidence. That is, regardless of whether a subject resided for 15 or only 3 years with their younger sibling, the level of sexual aversion reported in response to sibling incest and altruistic inclinations were close to the maximum. In contrast, for subjects for whom this cue was not available and who relied on coresidence duration as a cue to siblingship (the younger siblings in the dataset), disgust at sexual acts with their older sibling and sibling-directed altruism were low for shorter periods of coresidence and gradually increased with extended periods of coresidence. In fact, data suggest it takes approximately 14–15 years of coresidence for younger siblings to reach the same level of sexual aversions and altruistic effort reported by older siblings who were exposed to the cue of seeing their mother care for their sibling as a newborn.

Taken together, these data provide a first glimpse into the cognitive procedures governing kin detection and kin-directed behavior in humans. The findings indicate that the mind uses at least two cues to detect siblings and mediate inbreeding avoidance and kin-directed altruism: exposure to maternal investments in a newborn (used by older siblings to detect younger siblings) and duration of coresidence throughout periods of shared parental investment (typically used by younger siblings to detect older siblings). Because these same cues were found to regulate aversions and altruism in the same way, it suggests the existence of a single set of kinship-estimating procedures that feed motivational systems guiding mate choice and, separately, altruistic effort.

Additional Lines of Inquiry

Cues aside from coresidence duration and exposure to maternal-infant association may also play a role in sibling detection. For example, facial resemblance has been found to predict trustworthiness as well as attractiveness (DeBruine 2005). And olfactory cues such as those derived from the major histocompatibility complex (MHC) have been found to influence mate choice (e.g., Wedekind & Furi 1997; it should be noted here that MHC similarity may not function to cue kinship in this context but rather may cue compatible MHC alleles). No matter what the cues, if the model of kin detection

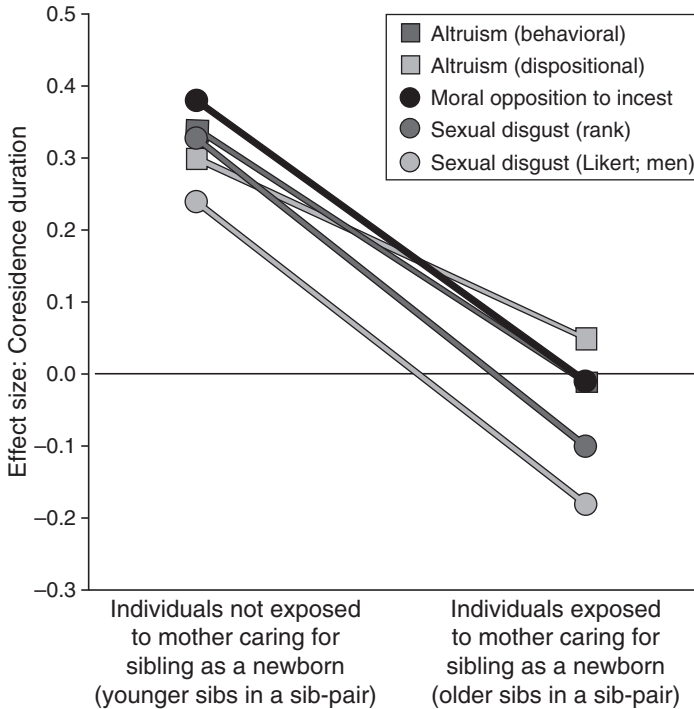


FIGURE 31.3 Two different cues to siblingship, exposure to maternal-neonate association and coresidence, regulate sexual aversions and sibling-directed altruism in the same manner. For individuals not exposed to the potent cue of seeing their mothers caring for a younger sibling as a newborn (typically the younger siblings in a sib-pair), coresidence duration is used as the cue to siblingship and, as the left-hand points on the chart show, significantly predicts disgust toward engaging in sexual acts with that sibling (two different measures), moral opposition to third-party sibling incest, and sibling-directed altruism (two different measures). By contrast, individuals exposed to their mother caring for their sibling as a newborn (typically the older sibling in a sib-pair), coresidence duration does not predict sexual aversions, moral opposition to incest, or altruism (right-hand points on the chart that hover around an effect size of zero). These data suggest that the detection of older and younger siblings relies on different types of cues. Redrawn from Lieberman et al. (2007).

and kin-directed behaviors outlined above is correct, these cues should regulate both sexual aversions and altruism.

Of course, many questions remain unanswered. For example, if coresidence duration mediates sibling detection, is a specific period of coresidence (e.g., ages <5) required, as some have suggested (Shepher 1983; Wolf 1995)? Or does each year of coresidence contribute in equal increments to a computed kinship estimate as research by Lieberman et al. (2007) suggests? Furthermore, what cues might distinguish a full biological sibling from maternal and paternal half siblings? Are there specific neural circuits associated with kin detection procedures? Do impairments in these regions explain certain psychopathologies underlying, for

instance, incestuous interests? These questions can be addressed through interdisciplinary collaborations within the human evolutionary behavioral sciences but also with researchers interested in kin recognition mechanisms in animals (e.g., Holmes & Sherman 1983; Gerlach et al. 2008). In this way, we can develop a more complete picture of the psychological adaptations governing human kin detection and kin-directed behaviors.

Implications for Inquiry into Kin Detection Mechanisms in Nonhuman Species

The application of evolutionary psychological approaches to human kin recognition can inform

investigations of similar processes in nonhuman species (Rendall 2004; Hepper 1991). For instance, in species that regularly encountered close kin over the life cycle, inbreeding avoidance mechanisms are expected to exist. Thus, computational procedures that estimate relatedness based on the cues that would have carved kin from nonkin over that species' evolutionary history should also exist. But kin detection doesn't buy inbreeding avoidance. Motivational systems must exist that use estimates of relatedness to regulate behavior. This view can be helpful in understanding the processes governing the behavior of nonhuman animals observed in natural and laboratory environments.

For example, there has been discussion in the animal literature regarding the extent to which dispersal of one or both sexes serves as an evolved mechanism for inbreeding avoidance. Some researchers have suggested that dispersal patterns evolved specifically to decrease the probability of close kin matings (Cockburn et al. 1985; Costello et al. 2008; Wolff 1992). From this point of view, dispersal patterns are behaviors that evolved to solve the problem of inbreeding avoidance. Alternately, others have suggested that dispersal patterns do not function as an adaptation for inbreeding avoidance per se, but instead are a result of intrasexual competition and territory choice that achieve inbreeding avoidance as a by-product (Moore & Ali 1984). Although these latter forces may indeed influence dispersal patterns in species of birds and mammals, in those species in which fertile close genetic relatives had a high probability of encountering one another during maturity and choosing one another as mates, systems for kin detection and sexual inhibition are expected to exist. The operation of systems producing a sexual aversion, or otherwise rendering those individuals categorized as close kin as unacceptable mates, could result in the dispersal of individuals of either sex (or both sexes) to seek alternate mates. That is, dispersal behaviors may, at least in part, be a consequence of cognitive systems inhibiting the choice of close kin as sexual partners, not the evolved function per se. In this case and in other areas of joint interest, we suggest that considerations of the computational architecture underlying a particular set of behaviors can provide additional hypotheses for investigating evolved adaptations in human and nonhuman species alike.

Changes in Women's Sexuality across the Cycle

A final example of how evolutionary approaches to humans are stimulating new ideas concerns patterns of female sexuality. Similar to many other species, human females are fertile during a brief window of their cycles, from a few days prior to the day of ovulation up until the day of ovulation itself (e.g., Wilcox et al. 1995). Based on this fact, what has become known as the *ovulatory shift hypothesis* was proposed (see Gangestad & Thornhill 2008; for a first statement of the basis for this idea, see Grammer 1993). If ancestral females benefited from multiple matings to obtain genetic benefits for offspring, but at some potential cost of losing social mates, selection may have shaped female preferences for male features indicative of those benefits to vary as a function of fertility status: to be maximal at peak fertility and less pronounced outside the fertile period. The logic is that of conflicting demands (see chapter 8): if the costs of multiply mating (e.g., losing a partner) exceed benefits at that point in time (e.g., whenever fertilization is not possible), then females should avoid extra-pair partners at those times. Cycle shifts in preferences should also be more extreme when women evaluate men along dimensions relating to genetic benefits (e.g., their sexiness) rather than dimensions related to long-term mateship compatibility (Penton-Voak et al. 1999).

Over a dozen studies in the past few years show that female preferences clearly do shift. At mid-cycle, normally ovulating, nonpill-using women particularly prefer a number of male traits perceived through a variety of sensory modalities: the scents associated with male symmetry and social dominance, facial and bodily masculinity, taller height, masculine vocal qualities, and masculine behavioral displays. Symmetry, masculine facial, body, and vocal qualities, intrasexual competitiveness, and various forms of talent ancestrally may have been indicators of intrinsic good genes. (Intrinsic good genes are those that have additive effects on fitness and hence could benefit the offspring of any female; see Jennions & Petrie 2000 and chapter 24 of this volume). Not all positive traits are sexier mid-cycle, however. Traits particularly valued in long-term mates (e.g., promise of material benefits) appear to be preferred as strongly by infertile women as by fertile women. In one study, Gangestad et al. (2007) had women rate the attractiveness of men shown

on videotapes. Independent samples of women rated men on a variety of qualities desirable in mates. Whereas women were particularly sexually attracted to men seen to be arrogant, intrasexually competitive, muscular, and physically attractive when they were in a fertile phase of their cycles, no cycle shifts were observed in women's attraction to men seen to be successful financially, intelligent, or kind and warm. Interestingly, men who appeared to be sexually faithful were less sexually attractive when women were fertile.

Shifts in Women's Sexual Interests

Patterns of women's sexual interests also shift across the cycle. In one study, normally ovulating women reported thoughts and feelings over the previous 2 days twice: once when fertile (as confirmed by a luteinizing hormone surge, 1–2 days before ovulation) and once when infertile. When fertile, women reported greater sexual attraction to and fantasy about men other than primary partners—but not primary partners (for reviews, see Gangestad & Thornhill 2008; Thornhill & Gangestad 2008). The study was not able to examine what kinds of men women were attracted to, but the studies on shifts of female preferences provide good reason to think that these men tended to possess masculine faces, voices, scents, and behavioral displays.

In fact, however, the ovulatory shift hypothesis expects a more finely textured pattern. On average, ancestral women could have garnered genetic benefits through extra-pair mating, but those women whose primary partners had good genes could not. Selection thus should have shaped interest in extra-pair men mid-cycle to itself depend on partner features; only women with men who, relatively speaking, lack purported indicators of genetic benefits should be particularly attracted to extra-pair men when fertile. Findings support this prediction. In one study, for instance, women with asymmetrical partners were more attracted to extra-pair men when fertile; not so of women with symmetrical partners, who were more attracted to their partner mid-cycle (see Gangestad et al. 2005).

Though most work on the ovulatory shift hypothesis has examined women's preferences for men who vary with respect to features thought to possibly have been associated with “intrinsic” good genes ancestrally, women may also particularly prefer men who possess another form of good

genes when mid-cycle: compatible genes, genes that work well together with genes women possess and thereby enhance offspring fitness. It has been conjectured that men who possess alleles at major histocompatibility complex (MHC) loci that differ from women's own MHC alleles possess a form of compatible genes (e.g., Penn & Potts 1999). Indeed, women appear to be particularly attracted to the scent of men who possess MHC alleles dissimilar to their own (see review in Garver-Apgar et al. 2006). A recent study showed that women who share MHC alleles with romantic partners, and thereby have partners with incompatible genes, were less sexually responsive to their partners and more likely to have had sex with a man other than their partners while romantically involved with their partners. They furthermore reported particularly enhanced sexual attraction to men other than partners when fertile in their cycles (Garver-Apgar et al. 2006; see figure 31.4).

Male Counterstrategies across the Cycle

If women have been under selection to seek good genes mid-cycle, men should have been under selection to take additional steps to prevent them from seeking extra-pair sex at this time (see chapters 22 and 23). Multiple studies indicate that they do so by being more vigilant, proprietary, or monopolizing of mates' time (see Gangestad & Thornhill 2008; Thornhill & Gangestad 2008).

Men might use one or more of several candidate cues of fertility status. Men find the scent of ovulating women particularly attractive, judge women's faces more attractive mid-cycle, and may detect subtle behavioral changes (see Thornhill & Gangestad 2008). Whatever the cues, the view that women are not benefited by men detecting their cycle-related fertility status suggests that women are unlikely to have been designed through selection to send them (see Thornhill & Gangestad 2008; this general view, however, may be subject to debate). Men, nonetheless, should be selected to detect by-products of fertility status that women do not fully suppress, and apparently can detect at least one. Consistent with this idea, men are particularly vigilant of their partner during mid-cycle when they are paired with women who should least want them to be vigilant—those particularly attracted to extra-pair men mid-cycle (see Thornhill & Gangestad 2008).

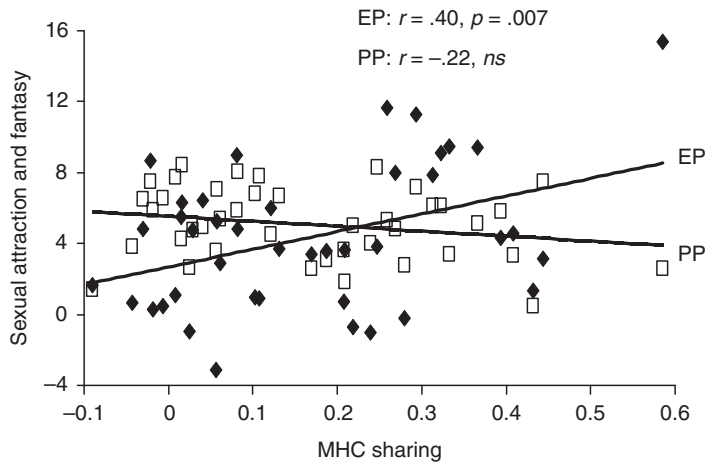


FIGURE 31.4 Women’s reported sexual attraction to and fantasy about men other than primary partners and primary partners during the fertile phase as a function of proportion of MHC alleles shared across partners. MHC loci assessed were the A, B, and DR β loci. Age and relationship status were statistically controlled, such that plotted values are residuals (with these variables controlled) plus the sample mean. *Solid line*: Attraction to extra-pair men. *Dashed line*: Attraction to primary partners. Interaction $F_{1,36} = 11.1$, $P < 0.002$. Redrawn from Garver-Apgar et al. (2006).

Do Women Possess Estrus? A Comparative Perspective

A long-standing conclusion about the evolution of human sexuality is that the lack of estrus (a distinctive fertile phase of the ovarian cycle characterized by intensified sexual receptivity and proceptivity) is a derived feature. Indeed, a key issue that scholars pursued through the 1970s and 1980s is what insights the evolutionary loss of women’s estrus reveals about the evolution of human sociality more generally. For instance, some scholars proposed that loss of estrus and its replacement with continuous sexual receptivity across the cycle promoted pair-bonding, a crucial evolutionary novelty in the hominid lineage (e.g., Symons 1979).

The recent findings about changes in women’s sexuality across the cycle led Thornhill and Gangestad (2008) to revisit the claim that women lost estrus. Women’s fertile-phase sexuality, they argued, is estrus—that is, it shares homologies with fertile-phase sexuality in close relatives and mammals in general. Though women’s estrous sexuality may have been modified in the context of pair-bonding, it was never evolutionarily lost.

At the same time, Thornhill and Gangestad (2008) proposed that reproductive biologists’ understanding of the functions of female estrus

must be sharpened in light of both comparative data and evolutionary theory. A common conception of estrous sexual proceptivity (“heat”) and attractivity is that they function to obtain sperm from males in general, permitting conception. Thornhill and Gangestad (2008) argue that, in fact, because sexual selection operates strongly on males to find and inseminate fertile females, females typically need not pay the costs for such adaptations designed to arouse male sexual interest. Accordingly, they propose, female estrous behavior is discriminating sexuality; it at least partly functions to attract females to males who can provide genetic benefits to offspring when females may conceive.

Women’s fertile-phase sexuality can be understood in this context. During estrus, women are particularly attracted to men who display purported ancestral indicators of genetic benefits to offspring (e.g., masculinity). Women are not more attracted to men in general during this phase. Outside of estrus, women retain sexual interests, but this interest is not characterized by precisely the same pattern of attraction. This extended sexuality (sexual receptivity during nonconceptive periods) functions differently from estrus; that is, it evolved because it enhanced reproductive success in other ways. Arguably, according to Rodriguez-Girones and Enquist

(2001), it functions to obtain direct benefits, largely from long-term male partners.

Findings on other species, however, can also be interpreted in light of these claims. An illustration is provided by common chimpanzees. Females are actually more sexually receptive and initiate sex with more males outside of the period of peak fertility than during the most fertile period (Stumpf & Boesch 2005). Sex during the period of infertility appears to function to reduce male aggression toward offspring by confusing paternity, which females do by having sex with most any resident male. At peak fertility, by contrast, females are actually choosier and their preferences tend to converge on the same males, ones that may offer the best genes for offspring.

More generally, Thornhill and Gangestad (2008) conjecture, women's estrus possesses homologies not only with other female mammals, but with female vertebrates in general. All vertebrates possess receptors for estrogen, named for it being the "gen" (or generator) of estrus. Estrogen's effects on female sexuality may be homologous across (nearly) all vertebrates and function, in some ways, similarly (which is not to deny that other reproductive hormones, such as progesterone and testosterone, phylogenetically almost as old as estrogen, also play important roles in modulating female sexuality in these species). For instance, females of many bird species exhibit different mating preferences during their fertile period than during the period preceding peak fertility. Do these changes across their fertile periods possess homologies with women's estrus? According to Thornhill and Gangestad's (2008) proposals, they do.

Full evaluation of these claims obviously requires much more research. Claims about the function of estrus illustrate, however, how research on human behavior may not only be inspired by evolutionary, reproductive, and comparative biology, but may also, through comparative and phylogenetic considerations, lead to broad evolutionary perspectives.

FUTURE DIRECTIONS IN HUMAN BEHAVIORAL EVOLUTIONARY SCIENCE

As we have emphasized, human behavioral ecologists rely heavily on optimality models of how selection pressures affect behavioral strategies, models rooted in the recognition that organisms possess

limited budgets of time and energy. They focus on trying to understand the behavioral outcomes of implicit allocation decisions. Evolutionary psychologists, by contrast, are fundamentally concerned with identifying the proximate mechanisms that were shaped by selection and that guide decision making and behavior. They often discuss selection pressures and the adaptive problems they created and predict the form of the behaviors and cognitive mechanisms that evolved in response. And, they rely heavily on arguments relating to functional design to assess claims about adaptation.

In the coming years, we foresee increasing cross-fertilization and, ultimately, integration of approaches. Increasingly, human behavioral ecologists appear to be interested in specific physiological mechanisms through which resource allocations are made. One topic of interest is the hormonal regulation of resource allocation. Testosterone, for instance, may be conceptualized as a messenger in a distributed communication system, one that can simultaneously upregulate and downregulate specific activities (e.g., energy dedicated to muscle growth, the neural underpinnings of status competition). Increases in male testosterone and its utilization lead to increases in broadly conceived mating effort, but at the expense of somatic maintenance and parental effort. Guided by this model, behavioral and reproductive ecologists have investigated the conditions that lead to decreases (e.g., fatherhood) and increases (e.g., divorce) in men's testosterone levels (for a review, see Ellison 2003). Based on similar thinking, factors that affect women's estrogen levels across their cycles (which reflect allocations to reproductive effort) have been explored (e.g., Ellison 2003). Some behavioral ecologists have also become interested in the psychological adaptations responsible for allocation decisions (e.g., Marlowe 2003, 2005; Cashdan 1993).

At the same time, evolutionary psychologists increasingly utilize optimality models and concepts of trade-offs in their thinking about selection (e.g., see DeScioli & Kurzban 2007). For instance, evolutionary psychologists interested in understanding adaptations that regulate mating effort recognize that they should be sensitive not only to the benefits of mating effort but also to the opportunity costs of lost parental or somatic effort (e.g., Ellison 2003). Examples such as this suggest a growing overlap and synergy between human behavioral ecology and evolutionary

psychology. We foresee increased attention to a variety of other phenomena by the human evolutionary sciences, many that will benefit from similar conceptual cross-fertilization.

Phenomena of Culture

Thirty years ago, discussions of evolution and culture typically pitted them as alternative influences on human behavior. Today, evolutionary scientists are more interested in understanding how various cultural phenomena reflect ancestral selection. What selection pressures shaped human abilities involved in the horizontal and vertical transmission of information? What selection pressures are responsible for traits leading to the importance of regulation of behavior through group norms? What led to human abilities to innovate, and how, precisely, can we characterize these abilities? Behavioral ecologists, as well as evolutionary psychologists, have addressed these issues (see, for instance, readings in Gangestad & Simpson 2007).

One conceptual approach emphasizes the coevolution of genetic information and culture (e.g., Richerson & Boyd 2005). For instance, selection may give rise to adaptations that solve a particular social problem. In turn, the behavior generated by these adaptations may alter, as a by-product, group-level socioecologies, which then set the stage for new selection. A complete understanding of the evolved bases of culture requires not only an understanding of adaptations that give rise to culture (see, e.g., Sperber 2005), it also requires an understanding of human adaptations *to* cultural phenomena. This enterprise demands an understanding of how individual-level “strategies” generate group-level phenomena, which may require agent-based modeling and simulation (e.g., Aktipis 2004).

Multilevel Selection. A related topic concerns levels of selection. Many evolutionary behavioral scientists have focused on understanding adaptations produced by selection on individuals. Others have suggested that selection on groups of individuals may be responsible for a variety of human social characteristics (e.g., Sober & Wilson 1998; box 14.3 of this volume). The processes through which multilevel selection can occur are now understood analytically (e.g., Price 1970). Nevertheless, questions concerning whether selection other than that on the genic and individual level explains adaptations remain (for more on group level selection, see Richerson & Boyd 2005; Sober & Wilson 1998).

Development and Phylogeny

Tinbergen famously identified four levels at which behavioral phenomena can be explained (see chapters 1 and 29). Human evolutionary behavioral scientists have primarily focused on understanding two levels of explanation: function and proximate mechanism. The processes through which adaptations develop and the phylogenetic history of the evolution of adaptations and their by-products have received much less attention to date. We foresee increased attention to these phenomena in the future.

SUMMARY

The evolution-based behavioral and cognitive science of Darwin’s premonition has been born, and has fledged into a multidisciplinary effort. The field of human evolutionary behavioral science is still in its youth, but great progress has been made in the few decades scientists have applied evolutionary principles to human nature. We anticipate the coming years will see continued growth, maturity, and enhanced productivity.

SUGGESTIONS FOR FURTHER READING

Laland and Brown (2002) have written a valuable introduction to major approaches to the study of human behavior from evolutionary perspectives: sociobiology, behavioral ecology, evolutionary psychology, and gene-culture coevolutionary theory. Barkow et al.’s (1992) book contains classic statements of the perspective of evolutionary psychology—a melding of adaptationist thinking and a computational theory of mind. A number of handbooks of evolutionary psychology that provide overviews of theory and empirical findings on humans generated by the perspective have recently appeared, including those by Buss (2005), Crawford and Krebs (2007), and Dunbar and Barrett (2007). All are important summaries of the current state of the field. Gangestad and Simpson (2007) posed 10 specific questions that remain debated to key contributors to the field. The essays that resulted address major methodological and metatheoretical issues including reconstructing the evolution of the human mind, measuring reproductive success, modularity

of mind, development, group selection, intelligence, and culture. Hirschfeld and Gelman's (1994) edited collection illustrates why and how evolutionary psychologists identify functional specialization.

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