The Great Struggles of Life

Darwin and the Emergence of Evolutionary Psychology

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Darwin envisioned a scientific revolution for psychology. His theories of natural and sexual selection identified two classes of struggles—the struggle for existence and the struggle for mates. The emergence of evolutionary psychology and related disciplines signals the fulfillment of Darwin's vision. Natural selection theory guides scientists to discover adaptations for survival. Sexual selection theory illuminates the sexual struggle, highlighting mate choice and same-sex competition adaptations. Theoretical developments since publication of On the Origin of Species identify important struggles unknown to Darwin, notably, within-families conflicts and conflict between the sexes. Evolutionary psychology synthesizes modern evolutionary biology and psychology to penetrate some of life's deep mysteries: Why do many struggles center around sex? Why is social conflict pervasive? And what are the mechanisms of mind that define human nature?

Keywords: Darwin, evolutionary psychology, great struggles of life, sexual selection, sexual conflict

harles Darwin may be considered the first evolutionary psychologist. At the end of *On the Origin* of Species, Darwin predicted, "In the distant future ... psychology will be based on a new foundation, that of the necessary acquirement of each mental power and capacity by gradation. Much light will be thrown on the origin of man and his history" (Darwin, 1859, p. 488).

Darwin outlined several core tenets for the scientific realization of this vision. He used the concept of *struggle* to convey the logic of selection. Struggles could be literal, as when two canines fight over food to stay alive. Darwinian struggles were also metaphorical, as when "a plant on the edge of a desert is said to struggle for life against the drought" (Darwin, 1859, p. 62).

Darwin's theories of natural and sexual selection provided the light and the way for understanding struggles for existence and struggles for mates. At the same time, Darwin failed to identify several key evolutionary struggles revealed by successive scientific revolutions within evolutionary biology. This article traces Darwin's influence on evolutionary psychology and outlines the field's development beyond Darwin's vision.

The Struggle for Existence

A key to Darwin's insight was the Malthusian insight that species produce more individuals than can actually survive. Darwin estimated that if there were no causes of early death, it would take a mere thousand years before the earth literally would run out of standing room for humans! Clearly, some causal forces prevent species from experiencing geometric rates of increase.

Darwin articulated the theory of natural selection syllogistically:

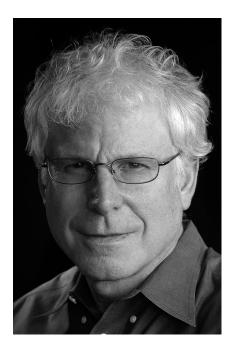
If under changing conditions of life organic beings present individual differences in almost every part of their structure, and this cannot be disputed; if there be, owing to their geometric rate of increase, a severe struggle for life at some age, season, or year, and this certainly cannot be disputed; then . . . it would be a most extraordinary fact if no variations had ever occurred useful to each being's own welfare . . . But if variations useful to any organic being ever do occur, assuredly individuals thus characterized will have the best chance of being preserved in the struggle for life; and from the strong principle of inheritance, these will tend to produce offspring similarly characterized. (Darwin, 1859, pp. 126–127)

The theory of natural selection made four important contributions. First, it explained change over time in organic design, "descent with modification." Second, it furnished the causal process by which different species originate. Third, it explained the seemingly purposive quality of the component parts—their adaptive functions, or the particular ways in which these characteristics aid survival. Fourth, natural selection unified all species past and present, including humans, into one grand tree of descent. We knew for the first time in history our true place in nature.

Darwin identified three classes of survival struggles that form the core of important research in evolutionary psychology today: "As more individuals are produced than can possibly survive, there must in every case be a struggle for existence, either one individual with another of the same species, or with individuals of different species, or

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with the physical conditions of life" (Darwin, 1859, p. 63). These struggles have spawned discoveries in modern evolutionary psychology (see Table 1).

Struggles With the Natural Conditions of Life

The hostile forces of nature against which organisms struggle come in many forms—extremes of weather and climate, food shortages, falls from trees or cliffs, drowning, and natural disasters such as earthquakes or landslides. Evolutionary psychologists have discovered plausible candidate adaptations produced by some of these hostile forces. The empirical discovery of female superiority in spatial location memory (particularly for immobile food objects), for example, was not made until Silverman and Eals (1992) hypothesized it as an adaptation to food gathering. This discovery contrasted sharply with previously documented male superiority in other forms of spatial ability, such as mental rotation and vector integration (dead reckoning)—abilities that solve navigational problems central to hunting (New, Krasnow, Truxaw, & Gaulin, 2007).

On the basis of the savanna hypothesis, researchers discovered cross-cultural evidence for adaptive landscape preferences for lush environments abundant with resources and distastes for environments lacking resources and posing risks to survival (Orians & Heerwagen, 1992). People's evolved sense of aesthetics includes fondness for lush foliage, blooming berries, and fresh water. Humans gravitate toward sheltered places where they can see without being seen. Many modern humans are currently shielded from these ancestral struggles with the forces of nature. Nonetheless, naturally selected adaptations continue to be activated in the modern world in our patterns of food consumption and our habitat preferences. Our evolved fondness for fat, for example, so scarce and valuable for survival in ancestral times, now leads to overeating, obesity, Type II diabetes, clogged arteries, and premature heart disease. Although many modern humans no longer struggle with the harsh conditions of life that confronted our ancestors, they struggle with some of the adaptations that are activated in a modern environment that differs profoundly from ancestral environments.

Struggles With Other Species

Humans battle with other species upon whom they prey and who prey upon them. Even after a hunter has successfully killed an animal for his family's dinner, he must compete for the meat with insects, vultures, microorganisms, and other mammalian carnivores. Humans even struggle with plants. Some plants, especially cabbage, cauliflower, broccoli, and Brussels sprouts, contain allylisothiocynate, which humans find bitter and unpleasant—a defensive adaptation in plants that helps them to avoid being consumed. Children's distaste for these vegetables has an adaptive logic. Consuming too much allylisothiocynate can actually be toxic to children.

What about predators? Barrett (2005) provided empirical evidence for the early childhood emergence of predator and antipredator adaptations. These include the conceptual primatives of *predator* and *prey*; rules for understanding when predators detect and approach prey; and specialized asymmetries of inference regarding animals. Young children, for example, understand that whereas lions are inclined to eat zebras, zebras are not disposed to eat lions.

The most common human fears and phobias include snakes and spiders. To many, these are vestigial adaptations, designed for an environment long forgotten. Countries such as Sri Lanka, however, have high rates of snake bites. Roughly 1,140 Sri Lankans die of snake bite annually, which suggests that snakes remain a hostile force in some parts of the world. Evidence also supports the hypothesis that humans have evolved specialized spider-detection adaptations that emerge in infancy (Rakison & Derringer, 2008).

Although most modern humans no longer struggle with dangerous species, the adaptations that evolved from those former struggles continue to be expressed in the modern world. People do not seek psychological treatment for car phobias, since they rarely occur, despite the fact that modern deaths by car accidents greatly exceed deaths by snake bite and falls from heights. Psychological and pharmacological treatments of snake and flying phobias, though, remain booming businesses today.

Struggles With Members of One's Own Species

Darwin recognized that humans posed dangers to other humans. The most dramatic battles occur in warfare, the life-and-death struggles that take the lives of dozens, hundreds, and sometimes thousands. Darwin displayed a keen awareness that men used warfare as a means of capturing women and reproductively relevant resources such as food, tools, and territory (Darwin, 1871). Modern evolutionary psychologists have documented specialized psychological

Struggle	Discovery/phenomenon	Authors		
Struggle for existence				
The conditions of life	Spatial location memory Habitat preferences	Silverman & Eals, 1992 Orians & Heerwagen, 1992		
Other species	Disgust adaptations Anti-predator adaptations Snake and spider fears Fessler et al., 2005 Barrett, 2005 Nesse, 2005; Rakison & Derringer			
Own species	Warfare adaptations Tooby & Cosmides, 1988 Anti-homicide defenses Duntley, 2005			
Struggle for mates				
Male same-sex struggles	Physical aggressiveness Steep future discounting	ressiveness Daly & Wilson, 1988 discounting Wilson & Daly, 2004		
Female mate choice	Preference for resources Preference for protection	Buss, 1989b Buss & Schmitt, 1993		
Male mate choice	Preference for low waist-to-hip ratio Universal standards of beauty	Singh, 1993 Sugiyama, 2005		
Female same-sex struggles	Derogation of competitors Appearance enhancement	Buss & Dedden, 1990 Symons, 1979		
Mutual mate choice	Cross-character assortment	Buss & Barnes, 1986		
Additiona	al within-species struggles highlighted by mod	dern evolutionary theory		
Struggles within families		, ,		
Parent–offspring conflict	Conflict over weaning	Trivers, 1974		
1 0	Context-specific infanticide	Daly & Wilson, 1988		
Sibling rivalry	High among full siblings	Michalski & Euler, 2008		
Conflict within stepfamilies Battle of the sexes	Step-child abuse and murder	Daly & Wilson, 2005		
Intersexual deception	Commitment deception Sexual deception	Haselton et al., 2005 Haselton et al., 2005		
Sexual coercion	Specialized rape fears Risk avoidance at ovulation Thornhill & Thornhill, 1989 Gallup & Chavanne, 2003			

The Great Struggles	of Life and	Corresponding	Empirical	Discoveries

Table 1

adaptations for warfare in men (Buss, 2005; Tooby & Cosmides, 1988; van der Dennen, 1995). Successful warriors in traditional tribal cultures attain higher social status, attract more wives, and have more children than do less successful warriors (Buss, 2005; Chagnon, 1988; Patton, 2000).

DNA studies of genetic signatures reveal that warriors who vanquished other groups of men sired many progeny. In a study of blood samples from 16 populations near the former Mongolian empire, geneticists discovered that 8% of men bore a chromosomal signature characteristic of the Mongol rulers (Zerjal et al., 2003). An astonishing 16 million men in that region alive today are likely descendants of the ruthless conqueror Genghis Kahn. Similar genetic traces of our warlike past have been discovered in Great Britain. Evidence from paleontological, archeological, and ethnographic records, as well as recent psychological studies, supports the hypothesis that humans have evolved adaptations for killing other humans, along with evolved defenses for preventing getting killed (Buss, 2005; Duntley, 2005).

The close connection between warfare and reproduction reveals that the great struggles of life are sometimes closely connected. Those who succeed in the struggle for existence face a second Darwinian struggle—the battle for mates.

The Struggle for Mates

Darwin agonized over facts that seemed inexplicable according to his theory of natural selection, such as the brilliant plumage of peacocks. How could luminescent plumage possibly have conferred a survival advantage? The peacock's plumage, metabolically costly and a lure to predators, appeared to contradict the theory of natural selection. Darwin noted that "the sight of a feather in a peacock's tail, whenever I gaze at it, makes me sick!" (Darwin in a letter to Asa Gray, April 3, 1860, printed in Burkhardt, Porter, Browne, & Richmond, 1993). Also perplexing were pervasive sex differences. Why would the sexes differ given that both have faced the same struggles for existence?

To address these puzzles, Darwin developed a second evolutionary theory, the theory of *sexual selection*. Sexual selection "depends on the advantage which certain individuals have over others of the same sex and species, in exclusive relation to reproduction" (Darwin, 1871, p. 256).

Sexual selection encompasses two component processes. The first centers on *same-sex competition*. If males compete, and the victors gain preferential sexual access to females, then evolution occurs because the victorious males reproduce more successfully and consequently pass on genes that contributed to the development of qualities that led to their successes.

The second process centers around *mate preferences*. The female "exerts some choice and accepts one male in preference to others. Or she may accept . . . not the male which is the most attractive to her, but the one which is the least distasteful" (Darwin, 1871, p. 273). Female mate choice also produces a struggle among males who "display their charms before the female" (p. 272). Although Darwin focused on female choice and female competition, we now know that male choice and female competition also are prevalent, especially among humans (Buss, 1994, 2003).

Both processes of sexual selection, same-sex competition and preferential mate choice, produce sex differences and explained why peacocks have brilliant plumage while peahens do not. As Darwin put it, "The males have acquired their present structure, not from being better fitted to survive in the struggle for existence, but from having gained an advantage over other males, and from having transmitted this advantage to their male offspring alone" (Darwin, 1871, p. 257). Peahens prefer to mate with males showing the most brilliant plumage, likely an honest health indicator that signals a low parasite load.

Sexual selection theory made little impact on biologists at the time and languished for roughly a century. Within the past several decades, however, it has emerged as one of the most important theories in modern evolutionary biology, inspiring theoretical refinements (Kokko, Jennions, & Brooks, 2006; Trivers, 1972) and launching hundreds of empirical studies in evolutionary psychology (Buss, 2008).

Competition Among Males

Whereas physical contests among males are relatively rare in the modern industrial world, they are not absent. Physical contests such as boxing, sumo wrestling, professional football, and "ultimate fighting" are almost exclusively male activities. Physical contests were almost surely more prevalent in ancestral times. Darwin quoted an anthropological informant's observations of North American Indians:

It has ever been the custom among these people for the men to wrestle for any woman to whom they are attached; and, of course, the strongest party always carries off the prize. A weak man, unless he be a good hunter, and well-beloved, is seldom permitted to keep a wife that a stronger man thinks worth his notice. (Darwin, 1871, p. 341)

The club fights, ax fights, wrestling matches, and chest-beating contests among traditional cultures attest to the importance of men's physical battles (e.g., Chagnon, 1983; Hill & Hurtado, 1996).

Men's contests did not merely affect body morphology. They affected the nature of male psychology: Mere bodily strength and size would do little for victory, unless associated with courage, perseverance, and determined energy. With social animals, the young males have to pass through many a contest before they win a female, and the older males have to retain their females by renewed battles. (Darwin, 1871, p. 344)

The man who "has higher energy, perseverance, and courage . . . will generally become more eminent in every pursuit, and will gain the ascendancy" (Darwin, 1882, p. 587). Darwin observed that these qualities emerge during development primarily when males enter reproductive competition—the "mental faculties" as he called them "no-toriously undergo a considerable change at puberty" (p. 588).

The logic of male intrasexual competition, of course, is more general than physical contests. If position in status hierarchies influences preferential access to mates, for example, then men can compete with each other for rank and status without a physical contest, and sometimes without interacting with each other at all. Men devote more effort to status striving than do women, for example, which is almost certainly a product of adaptations that evolved over deep time as a result of recurrent male intrasexual struggles (Buss, 2008).

Competition to attract women defines another struggle predicted by sexual selection theory. Evolutionary psychological research has identified dozens of tactics of attraction men use to compete for mates (Buss, 1988; Miller, 2000; Schmitt & Buss, 1996). These include displaying a good sense of humor, showing good manners, being wellgroomed, offering help, keeping physically fit to create a healthy appearance, wearing stylish outfits, giving gifts, cooking a woman a gourmet meal, taking her out to a restaurant, showing signs of commitment, declaring their undying love, and expressing self-confidence.

Men also sabotage their sexual rivals, another strategy in the struggle, as studies of derogation of competitors have documented (Buss & Dedden, 1990; Schmitt & Buss, 1996). These tactics include denigrating a rival's financial resources, impugning his physical prowess, scoffing at his achievements, making dire prognostications about his future job prospects, calling him selfish and exploitative, and saying that he likes to "use" women. Research also shows that some men physically dominate the rival in front of the woman they are attempting to attract, a form of public humiliation in which the victim's social status suffers.

Wilson and Daly (2004) provided evidence that men possess a specialized adaptation for "discounting the future," valuing immediate goods over future goods. When given a choice between a smaller sum of money tomorrow versus a larger sum of money at a later date, men more than women tend to choose the immediate resource. The discounting function became especially steep after men viewed images of physically attractive women. This shift in the steepness of future discounting did not occur after men viewed images of unattractive women, nor did it occur for women viewing either attractive or unattractive male faces. The male-specific shift in future discounting, rather than reflecting maladaptive impulsivity, reflects an adaptation designed to obtain immediate reproductive benefits when future opportunities are uncertain.

The specifics of male battles hinge on a subtle conceptual link between the two components of sexual selection inherent in sexual selection theory—that the tactics of competition among men, the dimensions along which they compete, should be dictated by the mate preferences of females (Buss, 1988).

Female Mate Choice

Darwin proved prescient in highlighting female choice. Women universally prefer men with economic resources, as well as the qualities that lead to economic resources, such as ambition, industriousness, social status, self-confidence, and slightly older age (Buss, 1989a; Kenrick & Keefe, 1992). Women also have well-articulated desires for masculine faces, scents of symmetrical men, and other health cues. They also prize bravery, athletic prowess, and a high shoulder-to-hip ratio—indicators of the physical ability to protect them and their children.

Darwin recognized that women were far from passive in the game of mating: "Women have more power in choosing, rejecting, and tempting their lovers, or of afterwards changing their husbands, than might have been expected" (Darwin, 1871, p. 389). This insight paved the way for modern evolutionary psychologists to explore additional complexities of female sexual psychology. A woman's mate preferences shift according to whether she is pursuing a casual sex partner or a husband (Buss & Schmitt, 1993); whether she is ovulating or not (Thornhill & Gangestad, 2008); her mate value (Buss & Shackelford, 2008); and her age, life stage, and other personal circumstances (Buss, 2008). Darwin's insights into the importance of female choice, in short, provided the foundation for much modern research on female mating psychology.

Male Mate Choice

Darwin also recognized male mate choice and anticipated research on the importance of physical attractiveness: "Man is largely, but by no means exclusively, influenced in the choice of his wife by external appearance" (Darwin, 1871, p. 355). Darwin, however, did not know why.

For most of psychology's history, the dominant view has held that standards of physical attractiveness were arbitrary and almost infinitely culturally variable, a point on which Darwin concurred. He pointed to cultural practices such as tattoos, bodily adornments, and mutilations that some cultures found to enhance a woman's attractiveness but which Westerners found physically repulsive.

Darwin's emphasis on cultural variability in standards of beauty was partly strategic. He sought to highlight the role of sexual selection in creating divergences within species and hence to add sexual selection to natural selection as a potential causal force in the origin of new species. This theoretical focus led Darwin to overlook what evolutionary psychologists later demonstrated empirically—that some standards of beauty are truly universal. Universal standards of female beauty, we now know, correspond to two classes of variables—cues to youth and cues to health, both of which are ultimately cues to fertility (Sugiyama, 2005; Symons, 1979). A low waist-to-hip ratio (WHR), for example, has been documented across cultures as a key criterion for female body beauty (Singh, 1993; Sugiyama, 2005). A low WHR signals youth, health, and nonpregnancy status. Other universal standards of beauty include clear skin, lustrous hair, full lips, good muscle tone, sprightly gait, and absence of sores or lesions—all key cues to youth, health, and fertility (Sugiyama, 2005).

If males, like females, had evolved specific mate preferences, it logically follows that females will compete with each other to embody what men want (Buss, 1988). Evolutionary psychologists have documented empirically the ways in which women compete with other women.

Competition Among Females

Research verifies that women across all known cultures compete vigorously with other women to enhance their physical appearance. They use appearance enhancement as a tactic of mate attraction (Buss, 1988; Schmitt & Buss, 1996) as well as a tactic of mate retention (Buss & Shackelford, 1997). Women, more than men, denigrate their sexual rivals on appearance. Using gossip, they convey to targeted males that their rivals are fat, unattractive, and have unsightly wrinkles (Buss & Dedden, 1990).

Women's same-sex battles hinge on whether they are pursuing a man for a long-term committed mateship or a short-term sexual encounter. Because men value sexual fidelity as a paternity confidence cue, for example, women's derogation tactics focus on impugning their rival's sexual conduct—calling the rival promiscuous, loose, easy to get into bed, and wanton (Buss & Dedden, 1990). These tactics backfire if the man is seeking a short-term mate, since they indicate to the man a higher probability of gaining sexual access. Thus, women adjust their derogation tactics according to mating context (Schmitt & Buss, 1996). The key point is that sexual selection theory predicts that when males exert mate preferences, the competition among females for access to desirable males can be as ferocious as the analogous competition among males.

Mutual Mate Choice and Mate Value Theory

Although Darwin stressed the ubiquity of female mate choice and male competition, he was also correct that humans engage in mutual mate choice, or "selection on both sides" (Darwin, 1871, p. 903). Similarly, some early seeds of "mate value theory" (Buss, 1994, 2003) can be discerned in his writings. Those higher in mate value are better able to fulfill their mate preferences and enact preferred mating strategies (Buss, 1994, 2003). Individuals lower in mate value have fewer options and must "settle." Darwin noted, "The most powerful and able males would succeed best in obtaining attractive females. They would succeed best in the general struggle for life, and in defending their females, as well as their offspring, from enemies of all kinds" (Darwin, 1882, p. 617). Similarly, women high in mate value "want it all" and are more exacting in their mate preferences for indicators of good genes, abundant resources, and parenting proclivities (Buss & Shackelford, 2008).

Darwin thus anticipated "cross-character assortment," where males and females couple with each other based on congruent elevation on different, but similarly valued, characteristics, resulting in assortment for overall mate value (Buss & Barnes, 1986). The mating of physically attractive women with men high in status and resources is the most well-documented modern example of cross-character assortment (Buss, 1994, 2003).

Although Darwin did not elaborate on the emotion of love, he hinted at its importance in the great struggles of life by quoting Schopenhauer: "The final aim of all love intrigues, be they comic or tragic, is really of more importance than all other ends in human life. What it all turns upon is nothing less than the composition of the next generation" (quoted in Darwin, 1882, p. 609). Evolutionary scientists have shown that love, far from being a Western cultural phenomenon, is the universal emotion in long-term mutual mate choice (Buss et al., 1990; H. Fisher, 2004; Symons, 1979). Love functions as a commitment device and bonding adaptation, signaling the long-term devotion of reproductively relevant resources to one partner (Buss, 2006; Frank, 1988).

Monumental Struggles of Life Missed by Darwin

Although natural and sexual selection identified critical struggles of life, theoretical developments after Darwin resulted in the discovery of unforeseen domains of conflict. These started with the discovery of genes and particulate inheritance (Mendel, 1866). Next came the "modern synthesis" that integrated particulate inheritance and population genetics with Darwin's theories of selection (e.g., R. A. Fisher, 1930). Finally, the theory of inclusive fitness (Hamilton, 1964) and the working out of the logical implications of genic selection (Dawkins, 1976, 1989; Trivers, 1974) illuminated important and previously missed struggles, notably, conflicts within families and the battle of the sexes.

Conflicts Within Families

Genetic relatedness often produces abundant acts of helping toward kin (Burnstein, Crandall, & Kitayama, 1994; Jeon & Buss, 2007). Nonetheless, the 50% difference in genetic relatedness between parents and their children predicts that they will sometimes conflict-an insight first elaborated in Trivers's (1974) theory of parent-offspring conflict. The optimal allocation of parental resources from a parent's perspective differs from the optimal allocation of resources from the child's perspective. Selection favors adaptations in children to extract more resources from parents than is optimal from the parent's perspective. This leads to predictable conflict over the timing of weaning, which parents typically want to enact sooner than does the child. Even behaviors such as suicide attempts by adolescents are sometimes motivated by attempts to extract extra investment from parents (Andrews, 2006).

Although parent-offspring conflict theory was a century in the future, Darwin astutely observed the widespread phenomenon of infanticide (Darwin, 1871, p. 381). Darwin even presaged research conducted more than 100 years later by identifying some of the key circumstances in which women kill their own infants, such as lack of resources needed to raise the child (Daly & Wilson, 1988) and desire to retain their mate value (Buss, 2005). This implied, much to Darwin's horror, that humans might possess contextcontingent adaptations to commit infanticide. Evolutionary psychologists subsequently showed that these contexts include (a) when the woman lacks a mate willing to invest resources in the child, (b) when the woman is young and hence has many years of reproductive potential ahead of her, and (c) when the infant is deformed, which suggests a low likelihood of surviving (Daly & Wilson, 1988).

Sibling rivalry defines another struggle that follows from parent–offspring conflict theory (Mock & Parker, 1998). Siblings often amplify their levels of begging and exaggerate their needs in order to secure more resources from parents, at the expense of their siblings (Michalski & Euler, 2008).

An especially poignant example of within-family conflict occurs within stepfamilies. Having a stepparent in the home is the most powerful predictor of child abuse and homicide of children (Daly & Wilson, 2005). Rates of these crimes are between 40 and 100 times greater within stepfamilies than among nonstepfamilies. Lack of genetic relatedness, in short, portends family conflict.

Sexual Conflict

Conflict between females and males is another type of struggle that follows from a deep understanding of genic selection (Parker, 1979, 2006). Conflicts of evolutionary interests between individual males and females set the stage for one of the most robust and rapid evolutionary processes yet discovered-sexually antagonistic co-evolution. Antagonistic co-evolution can occur whenever the fitness optimum for each sex differs. Consequently, both optima cannot be achieved simultaneously. Consider a simple example, one likely to characterize humans: the optimal amount of investment, or its key psychological indicator, emotional involvement, by a potential mate before consenting to sexual intercourse. If the optimum emotional involvement is higher for women than for men, sexual conflict can ensue. A woman cannot attain her (higher) optimum investment prior to sex without simultaneously preventing the man from attaining his (lower) optimum investment.

Evolutionary psychologists have used sexual conflict theory to discover an array of sex-differentiated mating adaptations. One class centers on deception. Women and men deceive each other in distinct ways. Men, for example, deceive women about the depths of their feelings, commitment, and love in order to secure sexual access to women (Haselton, Buss, Oubaid, & Angleitner, 2005). One study found that 71% admitted to deceiving a woman in these ways, compared to only 39% of women when asked a parallel question. Women, in turn, have evolved defenses against these forms of deception, such as prolonging courtship before consenting to sex to provide a wider window for assessing a man's mating intention (Buss, 1994, 2003). The emotions of anger and upset, triggered by experiencing these forms of deception, function to encode these forms of strategic interference for storage in memory and ultimately motivate women to avoid future deception by men (Buss, 1989a; Haselton et al., 2005).

Women, in turn, sometimes deceive men about the likelihood of sexual access in order to secure material benefits, to evoke jealousy in existing mates, or to increase their perceived mate value (Buss, 2003). Some women smile, flirt, and emit other ambiguous signals to exploit men's sexual psychology. Men, more than women, report experiencing these forms of sexual deception. And men, more than women, report that they experience greater anger and emotional upset when deceived in these sexually exploitative ways (Haselton et al., 2005).

Another key form of sexual conflict involves sexual coercion (Lalumiere, Harris, Quinsey, & Rice, 2005). Empirical studies point to women's defenses against sexual coercion, such as specialized fears of rape, the formation of female–female coalitions, avoidance of risky activities, selection of male friends and mates who function as "body-guards," and concern with collateral damage to social reputation when sexual coercion occurs (Buss, 2003).

Sexual conflict also occurs within mateships. Sexual infidelity by one partner diverts reproductively relevant resources to a same-sex rival of the other partner. Jointly held resources can be diverted to one partner's kin at the expense of the other partner's kin. Sexual conflict even occurs after breakups. Spurned mates sometimes stalk expartners, often interfering with the ex's efforts to remate with other men in order to get her back (Buss, 2000).

The battle of the sexes, in short, defines one of the momentous struggles unknown to Darwin, a battleground that follows logically from the modern "gene's eye" view of selection.

Discussion

Although considered controversial by some, modern evolutionary psychology signals the actualization of Darwin's prediction that psychology would be based on a new foundation. His theories of natural and sexual selection identified core processes by which functional psychological mechanisms evolve—the struggle for existence and the struggle for mates. Natural and sexual selection serve important functions that characterize the best scientific theories—they guide investigators to important domains of inquiry, generate novel predictions, provide cogent explanations for known facts, and produce empirical discoveries that would not otherwise have been made.

The importance of human mating, so close to the engine of the evolutionary process of differential reproductive success, remained largely unrecognized for most of the history of psychology. Once evolutionary psychologists began to use the theory of sexual selection, research and theory on human mating mushroomed. It exists today as one of evolutionary psychology's first "success stories." Dozens of important mating phenomena, ranging from patterns of partner selection to patterns of partner expulsion, from the hidden rhythms of ovulation to the functions of extra-pair mating, never would have been discovered without an evolutionary lens.

Darwin's theory of sexual selection also furnished the most cogent theory in psychology for identifying sex differences (Buss, 1995). In Darwin's words, "sexual selection apparently has acted on man, both on the male and female side, causing the two sexes to differ in body and mind." (Darwin, 1871, p. 419). Darwin's insight provided the groundwork for a cogent meta-theory of psychological sex differences-women and men are expected to differ psychologically primarily in those domains in which they have recurrently faced different adaptive problems over deep time (Buss, 1995). Those different adaptive problems occur primarily in the mating arena. Perhaps ironically for those who prefer to minimize the existence of sex differences, the evolutionary meta-theory also provides a cogent explanation for the vast similarities between the sexes. Men and women are predicted to be psychologically similar in all domains in which they have recurrently faced similar adaptive problems (Buss, 1995).

Evolutionary psychology has advanced beyond Darwin's vision in several ways. The first stems from theoretical developments in evolutionary theory that occurred after Darwin's day—the discovery of particulate inheritance, the modern synthesis, the theory of inclusive fitness, and the understanding of the logical implications of genic selection. The second was fashioned by the cognitive revolution—the view that psychological adaptations can be conceptualized as information-processing devices instantiated in the brain (Tooby & Cosmides, 2005). The third followed from exploring new domains, such as sexual conflict and within-family conflict, that are being illuminated by modern evolutionary theory.

Despite some successes, the fulfillment of Darwin's vision remains unfinished. This article has focused attention on the many social conflicts and struggles illuminated by evolutionary theory. Highlighting these darker sides of human nature may inadvertently create resistance to evolutionary psychology among those who prefer to focus on the rosier aspects of human psychology. A useful corrective would be greater exploration of understudied topics such as cooperative friendships, coalitions, and kin alliances. Recent theoretical and empirical work on the evolution of cooperation offers a promising sign that these gaps are beginning to be filled (e.g., Tooby, Cosmides, & Price, 2006). It is no contradiction to depict the human mind as containing evolved mechanisms for altruism, helping, and cooperation, as well as for conflict, competition, and treachery.

Coverage of evolutionary psychology in introductory psychology textbooks has expanded dramatically over the past two decades (Cornwell, Palmer, Guinther, & Davis, 2005). Unfortunately, many psychologists remain misinformed about modern evolutionary theory and the theoretical foundations of evolutionary psychology. One recent article, for example, reviewed 10 major undergraduate textbooks in social psychology and found that every one of them contained at least one fundamental misunderstanding of inclusive fitness theory (Park, 2007).

Despite these scholarly lapses, there are promising signs that every branch of psychology is becoming more deeply informed by evolutionary psychology. In the field of perception, for example, researchers have documented an adaptive auditory looming bias, a perceptual overestimation of the nearness of approaching compared to receding sounds-a perceptual bias that alerts humans to potential dangers associated with looming acoustical sources, such as predators or aggressive humans (Neuhoff, 2001). Vision researchers, guided by evolved navigation theory, have documented a descent illusion (Jackson & Cormack, 2007). Owing to the dangers associated with falling from heights, humans appear to have evolved a bias such that they perceive distances viewed from the top to be 32% greater than the same distances when viewed from the bottom. Both perceptual biases, one in audition and one in vision, derive from error management theory, which posits that selection will fashion adaptive biases designed to avoid the more costly error in judgment under conditions of uncertainty (Haselton & Buss, 2000).

Evolutionary cognitive psychologists also have discovered adaptive biases in the domains of attention, memory, and judgment under uncertainty (Todd, Hertwig, & Hoffrage, 2005). The evolutionary framework of life history theory is opening theoretical doors for unifying theories of psychological development (Kaplan & Gangestad, 2005). The growth of evolutionary social psychology has been exponential over the past decade (Buss, 2008). To paraphrase one eminent scholar, evolutionary psychology provides the most cogent theories we have in the domains of mating, sexuality, relationships, families, friendship, cooperation, altruism, social conflict, status hierarchies, coalition formation, aggression, and morality (Pinker, 2002).

Clinical psychology too is beginning to become infused with evolutionary analyses. Evolutionary psychology provides a nonarbitrary definition of psychological disorders, called the "harmful dysfunction" definition: "A disorder exists only when an internal mechanism is incapable of performing one of its natural [evolved] functions" (Wakefield, 2005, p. 894). Evolutionary clinical psychologists have also provided insights into many of the more common psychological problems—depression, anxiety disorders, eating disorders, sexual disorders, and personality disorders (Nesse, 2005).

Evolutionary psychology illuminates important connections among many of the traditional subfields of psychology. Perceptual and cognitive mechanisms, for example, are closely integrated with social psychological mechanisms of mating. Key components of mate value are assessed through the senses of sight, smell, and touch, providing input into mechanisms of mate attraction and mate selection. All psychological adaptations have developmental trajectories, often coming online at puberty, when individuals enter reproductive competition. Individuals differ in stable ways in the mating strategies pursued. Mating mechanisms also can go awry, as when mating anxiety maladaptively inhibits appropriate mating effort. In short, evolutionary psychology provides a unifying meta-theoretical framework that justifies why seemingly disparate phenomena from perceptual biases to psychological disorders truly belong within the covers of the same introductory psychology textbook.

In 1859, Darwin provided a vision of a distant future in which psychology would be based on the new foundation. The distant future that Darwin envisioned is upon us. Modern psychologists are privileged to experience a scientific revolution that signals the realization of that vision.

REFERENCES

- Andrews, P. W. (2006). Parent–offspring conflict and cost–benefit analysis in adolescent suicidal behavior. *Human Nature*, 17, 190–211.
- Barrett, H. C. (2005). Adaptations to predators and prey. In D. M. Buss (Ed.), *The handbook of evolutionary psychology* (pp. 200–223). New York: Wiley.
- Burkhardt, F., Porter, D. M., Browne, J., & Richmond, M. (Eds.). (1993). *The correspondence of Charles Darwin, Volume 8, 1860.* Cambridge, England: Cambridge University Press.
- Burnstein, E., Crandall, C., & Kitayama, S. (1994). Some neo-Darwinian decision rules for altruism: Weighing cues for inclusive fitness as a function of the biological importance of the decision. *Journal of Per*sonality and Social Psychology, 67, 773–789.
- Buss, D. M. (1988). The evolution of human intrasexual competition: Tactics of mate attraction. *Journal of Personality and Social Psychology*, 54, 616–628.
- Buss, D. M. (1989a). Conflict between the sexes: Strategic interference and the evocation of anger and upset. *Journal of Personality and Social Psychology*, 56, 735–747.
- Buss, D. M. (1989b). Sex differences in human mate preferences: Evolutionary hypotheses tested in 37 cultures. *Behavioral and Brain Sciences*, 12, 1–49.
- Buss, D. M. (1994). *The evolution of desire: Strategies of human mating*. New York: Basic Books.
- Buss, D. M. (1995). Psychological sex differences: Origins through sexual selection. American Psychologist, 50, 164–168.
- Buss, D. M. (2000). *The dangerous passion: Why jealousy is as necessary as love and sex.* New York: Free Press.
- Buss, D. M. (2003). The evolution of desire: Strategies of human mating (2nd ed.). New York: Basic Books.
- Buss, D. M. (2005). *The murderer next door: Why the mind is designed to kill*. New York: Penguin Press.
- Buss, D. M. (2006). The evolution of love. In R. J. Sternberg & K. Weis (Eds.), *The new psychology of love* (pp. 65–86). New Haven, CT: Yale University Press.
- Buss, D. M. (2008). Evolutionary psychology: The new science of the mind (3rd ed.). Boston: Allyn & Bacon.
- Buss, D. M., Abbott, M., Angleitner, A., Biaggio, A., Blanco-Villasenor, A., Bruchon-Schweitzer, M., et al. (1990). International preferences in selecting mates: A study of 37 societies. *Journal of Cross-Cultural Psychology*, 21, 5–47.
- Buss, D. M., & Barnes, M. L. (1986). Preferences in human mate selection. Journal of Personality and Social Psychology, 50, 559–570.
- Buss, D. M., & Dedden, L. (1990). Derogation of competitors. Journal of Social and Personal Relationships, 7, 395–422.
- Buss, D. M., & Schmitt, D. P. (1993). Sexual strategies theory: An evolutionary perspective on human mating. *Psychological Review*, 100, 204–232.
- Buss, D. M., & Shackelford, T. K. (1997). From vigilance to violence: Mate retention tactics in married couples. *Journal of Personality and Social Psychology*, 72, 346–361.
- Buss, D. M., & Shackelford, T. K. (2008). Attractive women want it all: Good genes, economic investment, parenting proclivities, and emotional commitment. *Evolutionary Psychology*, *6*, 134–146.
- Chagnon, N. (1983). *Yanomamö: The fierce people* (3rd ed.). New York: Holt, Rinehart, & Winston.

- Chagnon, N. (1988). Life histories, blood revenge, and warfare in a tribal population. *Science*, 239, 985–992.
- Cornwell, R. E., Palmer, C., Guinther, P. M., & Davis, H. P. (2005). Introductory psychology texts as a view of sociobiology/evolutionary psychology's role in psychology. *Evolutionary Psychology*, *3*, 355–374.
- Daly, M., & Wilson, M. (1988). Homicide. Hawthorne, NY: Aldine.
- Daly, M., & Wilson, M. (2005). The "Cinderella effect" is no fairy tale. *Trends in Cognitive Science*, 9, 507–508.
- Darwin, C. (1859). On the origin of the species by means of natural selection. London: John Murray.
- Darwin, C. (1871). *The descent of man, and selection in relation to sex*. London: John Murray.
- Darwin, C. (1882). *The descent of man, and selection in relation to sex* (2nd ed.) London: John Murray.
- Dawkins, R. (1976). The selfish gene. New York: Oxford University Press.
- Dawkins, R. (1989). *The selfish gene* (2nd ed.). New York: Oxford University Press.
- Duntley, J. D. (2005). Adaptations to dangers from humans. In D. M. Buss (Ed.), *The handbook of evolutionary psychology* (pp. 224–249). New York: Wiley.
- Fessler, D. M. T., Eng, S. J., & Navarrete, C. D. (2005), Elevated disgust sensitivity in the first trimester of pregnancy: Evidence supporting the compensatory prophylaxis hypothesis. *Evolution and Human Behavior*, 26, 344–351.
- Fisher, H. (2004). Why we love. New York: Henry Holt.
- Fisher, R. A. (1930). *The genetical theory of natural selection*. New York: Dover.
- Frank, R. (1988). Passions within reason. New York: Norton.
- Gallup, G. G., & Chavanne, T. J. (2003). Variations in risk taking behavior over the menstrual cycle: An improved replication. *Evolution and Human Behavior*, *24*, 391–398.
- Hamilton, W. D. (1964). The genetical evolution of social behavior. I and II. *Journal of Theoretical Biology*, 7, 1–52.
- Haselton, M. G., & Buss, D. M. (2000). Error management theory: A new perspective on biases in cross-sex mind reading. *Journal of Personality* and Social Psychology, 78, 81–91.
- Haselton, M., Buss, D. M., Oubaid, V., & Angleitner, A. (2005). Sex, lies, and strategic interference: The psychology of deception between the sexes. *Personality and Social Psychology Bulletin*, 31, 3–23.
- Hill, K., & Hurtado, A. M. (1996). Ache life history. New York: Aldine De Gruyter.
- Jackson, R. E., & Cormack, L. K. (2007). Evolved navigation theory and the descent illusion. *Perception & Psychophysics*, 69, 353–362.
- Jeon, J., & Buss, D. M. (2007). Altruism toward cousins. Proceedings of the Royal Society B: Biological Sciences, 274, 1181–1187.
- Kaplan, H. S., & Gangestad, S. W. (2005). Life history theory and evolutionary psychology. In D. M. Buss (Ed.), *The handbook of evolutionary psychology* (pp. 68–95). New York: Wiley.
- Kenrick, D. T., & Keefe, R. C. (1992). Age preferences in mates reflect sex differences in reproductive strategies. *Behavioral and Brain Sciences*, 15, 75–133.
- Kokko, H., Jennions, M. D., & Brooks, R. (2006). Unifying and testing models of sexual selection. *Annual Reviews of Ecology, Evolution and Systematics*, 37, 43–66.
- Lalumiere, M. L., Harris, G. T., Quinsey, V. L., & Rice, M. E. (2005). *The causes of rape*. Washington, DC: American Psychological Association.
- Mendel, G. (1866). Versuche über Pflanzenhybriden [Experiments on plant hybrids]. Verhandlungen des Naturforschenden Vereins in Brünn, 4, 3–47.
- Michalski, R. L., & Euler, H. A. (2008). Evolutionary perspectives on sibling relationships. In C. A. Salmon & T. K. Shackelford (Eds.), *Family relationships: An evolutionary perspective* (pp. 185–204). New York: Oxford University Press.
- Miller, G. (2000). The mating mind. New York: Penguin.
- Mock, D. W., & Parker, G. A. (1998). *The evolution of sibling rivalry*. New York: Oxford University Press.
- Nesse, R. M. (2005). Evolutionary psychology and mental health. In D. M. Buss (Ed.), *The handbook of evolutionary psychology* (pp. 903–927). New York: Wiley.
- Neuhoff, J. G. (2001). An adaptive bias in the perception of looming auditory motion. *Ecological Psychology*, 13, 87–110.
- New, J., Krasnow, M. M., Truxaw, D., & Gaulin, S. J. C. (2007). Spatial

adaptations for plant foraging: Women excel and calories count. Proceedings of the Royal Society B: Biological Sciences, 274, 2679–2684.

- Orians, G. H., & Heerwagen, J. H. (1992). Evolved responses to landscapes. In J. Barkow, L. Cosmides, & J. Tooby (Eds.), *The adapted mind* (pp. 555–579). New York: Oxford University Press.
- Park, J. H. (2007). Persistent misunderstandings of inclusive fitness and kin selection: Their ubiquitous appearance in social psychology textbooks. *Evolutionary Psychology*, 5, 860–873.
- Parker, G. A. (1979). Sexual selection and sexual conflict. In M. S. Blum & A. N. Blum (Eds.), *Sexual selection and reproductive competition among insects* (pp. 123–166). London: Academic Press.
- Parker, G. A. (2006). Sexual conflict over mating and fertilization: An overview. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 361, 235–259.
- Patton, J. Q. (2000). Reciprocal altruism and warfare: A case from the Ecuadorian Amazon. In L. Cronk, N. A. Chagnon, & W. Irons (Eds.), Adaptation and human behavior: An anthropological perspective (pp. 417–436). New York: Aldine de Gruyter.
- Pinker, S. (2002). *The blank slate: The modern denial of human nature*. New York: Penguin.
- Rakison, D. H., & Derringer, J. L. (2008). Do infants possess an evolved spider-detection mechanism? *Cognition*, 107, 381–393.
- Schmitt, D. P., & Buss, D. M. (1996). Mate attraction and competitor derogation: Context effects on perceived effectiveness. *Journal of Per*sonality and Social Psychology, 70, 1185–1204.
- Silverman, I., & Eals, M. (1992). Sex differences in spatial abilities: Evolutionary theory and data. In J. H. Barkow, L. Cosmides, & J. Tooby (Eds.), *The adapted mind* (pp. 533–549). New York: Oxford University Press.
- Singh, D. (1993). Adaptive significance of waist-to-hip ratio and female physical attractiveness. *Journal of Personality and Social Psychology*, 65, 293–307.
- Sugiyama, L. (2005). Physical attractiveness in adaptationist perspective. In D. M. Buss (Ed.), *The handbook of evolutionary psychology* (pp. 292–342). New York: Wiley.
- Symons, D. (1979). The evolution of human sexuality. New York: Oxford University Press.
- Thornhill, R., & Gangestad, S. W. (2008). The evolutionary biology of human female sexuality. New York: Oxford University Press.
- Thornhill, R., & Thornhill, N. W. (1989). The evolution of psychological pain. In R. Bell (Ed.), *Sociobiology and the social sciences* (pp. 73– 103). Lubbock, TX: Texas Tech University Press.
- Todd, P. M., Hertwig, R., & Hoffrage, U. (2005). Evolutionary cognitive psychology. In D. M. Buss (Ed.), *The handbook of evolutionary psychology* (pp. 776–802). New York: Wiley.
- Tooby, J., & Cosmides, L. (1988, April). The evolution of war and its cognitive foundations (Institute for Evolutionary Studies Technical Report 88–1). Paper presented at the Evolution and Human Behavior Meetings, Ann Arbor, MI.
- Tooby, J., & Cosmides, L. (2005). Conceptual foundations of evolutionary psychology. In D. M. Buss (Ed.), *The handbook of evolutionary psychology* (pp. 5–67). New York: Wiley.
- Tooby, J., Cosmides, L., & Price, M. E. (2006). Cognitive adaptations for n-person exchange: The evolutionary roots of organizational behavior. *Managerial and Decision Economics*, 27, 103–129.
- Trivers, R. L. (1972). Parental investment and sexual selection. In B. Campbell (Ed.), *Sexual selection and the descent of man: 1871–1971* (pp. 136–179). Chicago: Aldine.
- Trivers, R. (1974). Parent-offspring conflict. American Zoologist, 14, 249-264.
- van der Dennen, J. M. G. (1995). *The origins of war*. Groningen, The Netherlands: Rigin Press.
- Wakefield, J. C. (2005). Biological function and dysfunction. In D. M. Buss (Ed.), *The handbook of evolutionary psychology* (pp. 878–902). New York: Wiley.
- Wilson, M., & Daly, M. (2004). Do pretty women inspire men to discount the future? *Proceedings of the Royal Society B: Biological Sciences*, 271(Suppl. 4), S177–S179.
- Zerjal, T., Xue, Y., Bertorelle, G., Wells, R. S., Bao, W., Zhu, S., et al. (2003). The genetic legacy of the Mongols. *American Journal of Human Genetics*, 72, 717–721.