Darwin's Legacy to Comparative Psychology and Ethology

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Charles Darwin made numerous seminal contributions to the study of animal behavior over his long career. This essay places these contributions in the context of Darwin's life, showing his long-standing interest in psychological and behavioral issues encompassing all species, including humans. Ten areas are highlighted: natural history; communication; sexual selection and courtship; comparative cognition; emotion; instinct and behavioral development; inheritance of behavior; phylogeny of behavior; sociobiology and behavioral ecology; and applied animal behavior, animal welfare, and conservation. Several newer emphases that Darwin anticipated are briefly discussed. Darwin, while not always correct by current standards, crucially aided the process of firmly embedding psychological phenomena in a naturalistic scientific ethos.

Keywords: Darwin, ethology, comparative psychology, animal behavior, behavioral evolution

If you want new ideas, read old books. This is certainly the case with Charles Darwin's writings in the field of animal behavior. In no other area of psychology did Darwin have a more immediate and profound effect than in the study of the behavior of animals. Although humans are also animals, here I use *animal* to exclude our own species, since Darwin's influence on the direct study of human behavior and psychology, though of signal importance today, had relatively little effect in the decades following the publication of *On the Origin of Species* (Darwin, 1859/1967). His later treatises that dealt centrally with evolutionary aspects of human behavior, cognition, and emotion (e.g., Darwin, 1871, 1872) initially elicited more theological and philosophical reaction than scientific study. This was largely because there were virtually no human fossil remains and the relevant social sciences were less advanced empirically than natural history, given the complexity, diversity, and controversy the study of our own species has always entailed.

Even limiting this essay largely to Darwin's role in the emergence of animal behavior as a focus of scientific study in the late 19th century down to the present is a formidable challenge. There are literally thousands of research articles and hundreds of books available derived from Darwin's behavioral theories and empirical writings. Many of these contributions offer intriguing, elevating, sad, deplorable, and inspiring stories of increasing knowledge, methodological advances, unfortunate misunderstandings, bitter controversies, fascinating characters, intellectual dead ends, and resuscitations of ideas once deemed untenable. This roller coaster ride is what makes the history of science so fascinating for some of us and so crucially important for all researchers who want to be more than a spoke in the wheels of the current scientific enterprise. In Darwin we can find sources relevant to many of the debates of the last 150 years on the directions the study of animal behavior and psychology should take. How we view the behavior of other species strikes close to our image of our own species more than does, say, the structure of our internal organs.

Darwin's contributions to animal behavior and psychology are typically ignored by biologists, who want to claim Darwin as exclusively one of their own. For example, Padian (2008) listed 10 areas in which he claimed Darwin's legacy is most apparent. Most of these are obviously seminal such as natural selection, classification informed by genealogy, the tree of life, an ancient earth, and biogeography. The interrelatedness of all life (ecology) is also listed along with gradual evolutionary change, extinction, and co-evolution. The only largely behavioral contribution listed is sexual selection, but Padian only pointed out that processes of mate choice can help to explain physical differences between the sexes. I find this bowdlerizing of Darwin quite unfortunate.

Arguably, when one gets beyond atavistic creationist debates on whether evolution exists, public and general intellectual concern with Darwin today is actually not focused on any of the 10 issues listed above, except for sexual selection, which is increasingly being viewed as central to much of human psychology and the current instantiation of evolutionary psychology (see Buss, 2009, this issue). Interestingly, sexual selection was either ignored or misunderstood by most early writers, including prominent biologists (e.g., Delage & Goldsmith, 1912; Geddes & Thomson, 1890). Dewsbury (2009, this issue) notes that eminent psychologists were originally more accepting of sexual selection than were biologists. Nonetheless, sexual selection was barely mentioned in the three edited volumes resulting from the major conference celebrating the 100th anniversary of the publication of *On the Origin of Species* held at the University of Chicago in 1959 (Tax, 1960).

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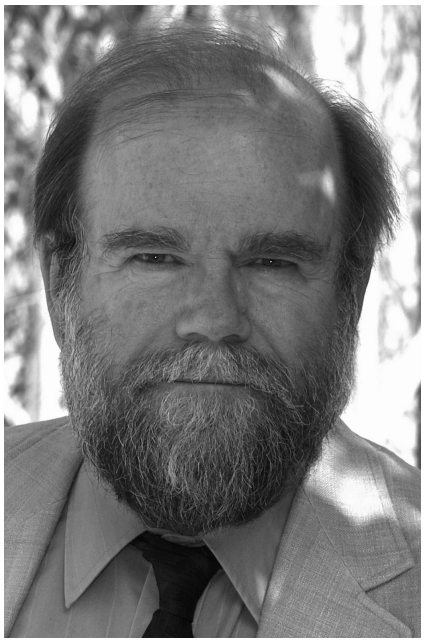

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The moral and ethical implications of the claims by the highly respected Darwin that the roots of virtually all our behavior derive from natural processes operating on ancestral species, rather than gods or angels, was and still is at the center of the controversy over Darwinian science. Beyond this we need to recognize the dichotomy, still present today, between those studying animal behavior largely as a tool for exploring the topics listed by Padian and those who were interested in animal behavior for its own sake or to gain insight into our own behavior. In the latter group there was a further split between those who wanted to make a direct assault on the comparison of animal with human behavior (many comparative psychologists) and those who, though motivated initially by an interest in the behavior, natural history, and general biology of animals, be they ants, geese, wolves, or monkeys, could not resist applying their findings and approaches to understanding human behavior as well (many ethologists and zoologists). This tension is long-standing and still with us. Much behavioral neuroscience research using animals is justified in a biomedical context, for example. Regardless, Darwin's continuing relevance is due to the protean sweep and revolutionary impact of his ideas. The indubitable fact is that the universal acid of his ideas (Dennett, 1995) eats away at differing parts of the protective ideological veneer with which all people, scientists included, cover themselves.

Darwin's Odyssey

In the beginning, Darwin was a boy who loved nature, dogs, and the outdoor life. Later, at university, he collected beetles and gravitated toward the leading naturalists in England. This led to the defining event in his career: the opportunity to travel around the world as naturalist aboard the H.M.S. *Beagle.* He was prepared to be a magnificent observer, and his book based on the journal he kept during his voyage (Darwin, 1845) is full of wonderful descriptions of not only all aspects of natural history, including geography, geology, and fossils, but behavioral observations on and interpretations of the animals and peoples of the areas he visited. His genuine interest in culture and human psychology also permeate the book, as does his aversion to slavery, poverty, and human degradation. Dewsbury (2009, this issue) provides useful detailed biographical sources on Darwin's life.

Upon his return from the trip around the world, Darwin's main scientific tasks were preparing the scientific reports of the various collections made and data recorded. This involved working with leading specialists, and the publication of these reports made his reputation as a rising scientific star. During this period he also kept a series of notebooks that allow the evolution of his ideas to be reconstructed. It is in these writings that we can see how interested he was in animal behavior, people, and psychology. The view that Darwin only began applying his ideas to psychology after the publication of *On the Origin of Species* in 1859 is erroneous and misrepresents the motivational scope underpinning Darwin's corpus (Burghardt, 1992).

Darwin and the Study of Animal Behavior

Since Darwin's work has influenced so much of animal behavior, it is not possible to discuss all the current research extending or correcting Darwin's insights. Because of the depth of his contributions, I first briefly discuss how Darwin developed his ideas, next look at 10 influential research areas in which Darwin's contributions were integral and continuing, and then mention some developing research topics reflecting Darwin's passions that earlier scientists found a bit embarrassing. My goal is really to encourage readers from all areas of psychology to explore the rich and ongoing legacy bequeathed to us by Darwin.

Darwin's writings encompass virtually all the major areas in animal behavior, although neuroscience and genetics were in the future. It is helpful to use, as an intellectual scaffolding, Niko Tinbergen's (1963) famous analysis of the four aims of ethology, which I later extended to five (Burghardt, 1997), to organize Darwin's work in all areas of behavior and psychology. These five areas involve the study of (a) causal or mechanistic processes, (b) function or adaptiveness, (c) evolutionary patterns and processes, (d) individual development, and (e) private and subjective experiences. Keeping these five aims in mind will also help us understand how comparative psychology and the more zoologically derived ethology split in their application of the Darwinian legacy to the understanding of behavior. It also aids in appreciating some of the pitfalls that have confronted the emerging fields of human ethology, sociobiology, evolutionary psychology, and comparative cognition as well as earlier fields such as behaviorism, physio-

logical psychology, perception, learning, motivation, behavior genetics, and ethology.

Darwin's main published writings on animal behavior include the chapter on instinct in *On the Origin of Species* (Darwin, 1859/1967), significant parts of *The Expression of the Emotions in Man and Animals* (Darwin, 1872), and large sections of *The Descent of Man, and Selection in Relation to Sex* (Darwin, 1871). His other writings, especially his books on climbing plants, pollination, domestication, and earthworms also included much behavioral information and actually more of the details of the clever and creative experiments that Darwin performed to test his numerous hypotheses. Besides his original descriptive observations and experiments, he also relied on the published literature and information relayed by his many correspondents around the world. Unfortunately, his use of anecdotes, often unverified, led to dismissal of many of his more provocative behavioral claims as laid out in the early chapters of *The Descent of Man,* where he made his most forceful case for mental continuity across species. After looking over his entire body of work, however, I came up with the following list of 10 behavioral fields that Darwin most directly influenced.

1. Natural History

The ethological emphasis on behavioral description in naturalistic contexts would have been welcomed by Darwin. He was awed by the diversity and complexity of behavioral phenomena his entire life. His curiosity was unbounded. When he developed his theory of natural selection, he found it necessary to show that behavior—for Darwin no less a part of the biology of a species than physical traits—could be interpreted in light of natural selection. Thus he extended observations of others by watching ant colonies, for example. There were many other famous (mostly tropical) 19th-century naturalists, including Alexander von Humboldt, Alfred Russel Wallace, and William Bates, who accumulated more extensive natural history collections (cf. Beddall, 1969), but it was Darwin's theory of natural selection (also arrived at by Wallace) that incorporated them into a coherent story of the workings of nature.

The greatest challenge any new theory faces is the extent and accuracy of the predictions that it engenders. At a time when so many traits of animals seemed bizarre and superfluous, Darwin looked closely and watched ants, honeybees, birds, and earthworms. He knew there had to be a reason flowers had so many complex structures, perfumes, and beautiful coloration. These were there not for our pleasure but to serve adaptive functions, often reproductive ones involving animals. It was up to naturalists to discover what these were, how they worked, and why they came to be. From flower structures Darwin predicted with accuracy what kinds of structures and behavior their unknown pollinators would be found to possess.

Darwin was not only a great naturalist; he recognized, supported, and nurtured many others throughout his life. Unfortunately, in both biology and psychology, descriptive and natural history studies have been marginalized unless carried out as part of large-scale comparative or theoretically sophisticated projects. The exceptions are often in behavior, such as when a mystery as to how an animal accomplishes some remarkable feat is solved or a remarkable ability is uncovered. A recent example is the discovery that when nematode parasites infest a Neotropical ant, the ant develops an enlarged bright red gaster (rear end), which it then elevates when walking. This appears like a ripe berry to us and presumably to the birds who, after ingesting the "berries," pass the nematodes in their feces, which the ants then unwittingly collect to feed their brood, maintaining the cycle (Yanoviak, Kaspari, Dudley, & Poiner, 2008). Here we have a parasite modifying the appearance and behavior of the host! Fascinating observations such as these are essential in keeping the field of animal behavior vital, exciting, and tied to the context in which behavior functions and evolves. The consequences can be profound for understanding the behavioral evolution of our own species as well. For example, Boesch (2007) recently claimed that most captive studies of ape cognition are flawed because they eliminate the richness of an unfettered life and are even tainted by using human, rather than conspecific, experimenters! This has led to a vigorous debate on research strategies in comparative cognition (Boesch, 2008; Tomasello & Call, 2008).

2. Communication

A perennial and popular area of animal behavior concerns how animals communicate. Such communication is often through the strange and unusual body postures, movements, dances, sounds, and chemical signals animals use in courtship, fighting, threatening, and even deceiving predators. Darwin described many examples, and although he was not the first to be deeply interested in how animals communicate "ideas" or emotions to others (e.g., Thompson, 1851), his writings on sexual selection (Darwin, 1871) used such observations freely. His book on the expression of emotions (Darwin, 1872), which attempted to develop a causal and evolutionary theory of emotional expression, was a major step forward in the understanding of communication (Burghardt, 1973; Marler & Hamilton, 1966). Darwin outlined three principles that removed much of the mystery from the study of communication. The principle of *serviceable associated habits* was an explicit associationist concept anticipating Pavlovian conditioning. The principle of *antithesis* noted that emotions generate behavioral postures and signals in such a way that extreme opposite "states of mind" produce incompatible postures and movements that foster clear communication, including intentions. The principle of the *direct action of the nervous system* noted that extreme fear, for example, would lead almost automatically to perspiring, defecation, urination, piloerection, and changes in breathing. These behavioral "by-products" could also lead to signal systems. Darwin's ideas were later developed by researchers in animal learning, ethology, and physiological psychology as well as in human emotion (Hess & Thibault, 2009, this issue).

Animal communication studies have come a long way since Darwin's time. Photography was in its infancy then, and movies and video technology were in the future, as were the abilities to record and analyze animal vocalizations and songs, to collect, isolate, and identify chemical cues (pheromones), to record responses in the brain, and to quantitatively characterize the complexity of social interactions. There have been numerous treatises on animal communication that delineate the elegant mechanisms that have been uncovered on how and why animals communicate information about mates, predators, and even deceptive information to conspecifics as well as predators. Darwin, with all his imagination, could not have anticipated the 1973 Nobel Prize-winning studies of bee language dancing (von Frisch, 1967), the imprinting and phylogeny of communication in birds (Lorenz, 1981), or the evolutionary process of ritualization of communication signals (Tinbergen, 1951). But even these accomplishments pale in comparison with the technical sophistication of recent studies. For example, a special issue of the *Journal of Comparative Psychology* (Schwartz, Freeberg, & Simmons, 2008) is devoted to auditory communication in noisy environments across a host of species, the intricacies of which would have amazed and delighted Darwin.

3. Sexual Selection and Courtship

Darwin's companion book to the emotions (Darwin, 1871) considered animal communication from a different perspective, that of sexual selection. Sexual selection is emphasized in the Buss (2009) essay in this issue and is thus not explained here except for the reminder that animals within a species compete for mates. Members of the same sex compete for resources and opportunities that facilitate mating with members of the other sex. While male–male competition is most evident and dramatic, competition among females is also recognized. Similarly, members of one sex often compete for the behavioral and physical features that best attract members of the opposite sex, perhaps as markers of fertility, health, social status, and parenting skills. Obviously, communication is involved here, although sometimes males overpower females. Sexual selection did not really come into its own until the publication of a seminal volume (Campbell, 1972) at the 100th anniversary of Darwin's book. Robert Trivers (1972) wrote a pathbreaking paper on parental investment for this volume that modeled predictions derived from sexual selection theory on parental care in monogamous and polygynous species; this paper is one of the foundation documents of current evolutionary psychology, sociobiology, and behavioral ecology.

4. Comparative Cognition

The modern field of comparative cognition was not identified as such until recently. However, comparative psychology, a broader field that covers many other topics such as sensory processes, orientation, reproductive behavior, as well as traditional learning processes and comparative intelligence, was well established by the 1920s (Dewsbury, 1984). The area of comparative mentality or mental processes was central to Darwin's (1871) *The Descent of Man* and the books by his protégé G. J. Romanes and also C. Lloyd Morgan (e.g., Morgan, 1894; Romanes, 1883). Darwin strove in *The Descent of Man* to show that not only were there aspects of the behavior of human beings only explicable as originating in our nonhuman ancestors (e.g., facial expressions) but also that many of the behavioral traits we deem so unique to humans are found in rudimentary form in other species as well. This latter side of Darwin was not emphasized until the 1950s, and when it was, the reaction from human chauvinists in biology, the social sciences, and the humanities was swift and often brutal. A prime example of a leading intellectual being threatened by the work on chimpanzee "language" and honey bee dancing was Mortimer J. Adler, who was moved to give a series of lectures (Adler, 1967) that I heard while teaching at the University of Chicago. In spite of intellectuals accepting biological evolution, Darwin was way ahead of his time in proposing a serious science of mental continuity. Buss (2009, this issue) recounts some of this history.

The modern field of comparative psychology can be traced to Darwin's focus on mental continuity in *The Descent of Man*, which led to attempts to gather information on animal intelligence and other psychological traits largely through experimental studies of captive, often domesticated, animals such as white rats, inbred mice, dogs, and pigeons, although a wide range of species were at least sampled. By the 1930s, a massive corpus of information on animals could be published (Maier & Schneirla, 1935; Warden, Jenkins, & Warner, 1935, 1936, 1940). However, the subsequent rise of Hullian and Skinnerian animal conditioning studies led to the demise of interest in species diversity except for some primates. Dewsbury (1984, 1985) and Boakes (1984) have provided excellent histories of comparative psychology and animal learning.

Today, studies of cognitive processes in animals have uncovered language-like behaviors, symbolic communication, construction and use of tools, use of numbers (numerosity), planning for the future, reliving the past, social learning, cultural transmission, visual illusions, and so on (e.g., see the 50-plus short essays by leading contemporary researchers in Bekoff, Allen, & Burghardt, 2002). Closely related species are increasingly being studied for nuanced differences in cognitive capacities in order to trace evolutionary trajectories of mind. A neat example is serial reversal learning differences in three species of corvid birds (crow relatives) that are providing testable hypotheses on the evolution of behavioral plasticity or flexibility (Bond, Kamil, & Balda, 2007).

5. Emotion

Emotion in animals is an area of rapidly growing interest in neuroscience (Panksepp, 1998), although for many years emotion studies in animals were limited to fear, rage, and sexual lust, with a bit of maternal affection thrown in. Actually, most mainline psychology ignored Darwin's contribution to emotions until the work of Ekman and Izard

(see Hess & Thibault, 2009, this issue). The role of emotion in communication was also downplayed until the 1970s. In recent years, the view among scientists is beginning to approach that of many pet owners: Animals do experience a wide range of emotions, not just those related to fighting and fear (Balcombe, 2006). New methods of assessing preferences, of measuring stress and aggressivity (including noninvasive cortisol and sex hormone methods), and brain imaging make it increasingly difficult to assert that the emotional experiences underlying emotional expression can never be studied in other species. Affective neuroscience is a Darwinian legacy (Panksepp, 1998), and it seems imperative that the "new" evolutionary psychology should not largely ignore the emotional, communicative brain and its intricate evolutionary history (Nesse & Elsworth, 2009, this issue; Panksepp & Panksepp, 2000).

6. Instinct and Behavioral Development

The modern field of comparative ethology can be traced back to the *Origin of Species* and a concern with instinctive, rather than learned or intelligent, behavior and the value of an evolutionary approach in understanding how behavior evolved into its myriad forms through natural selection. Darwin clearly subscribed to the view that much animal behavior was instinctive and that patterns of behavior could be studied in a fashion similar to that with regard to other evolved traits, an idea embraced by ethologists. Learning and fairly remarkable cognitive accomplishments and the awareness that behavior had an ontogeny were not ruled out. Darwin, ever the naturalist, closely observed the development of behavior in one of his children in 1840; although only published much later (Darwin, 1877), these observations constituted one of the first baby biographies and influenced the nascent field of developmental psychology as well as many of its practitioners (see Wozniak, 2009, this issue).

The ethologists did effectively resuscitate the study of instinctive behavior and its motivational and neural correlates, however, and it was arguably their most substantive, as well as notorious, contribution (Lorenz, 1981; Tinbergen, 1951). Their job was not easy in psychology since instinct and innateness had been largely abandoned as scientifically worthless concepts. It is impossible to recount the "instinct wars" here, but key papers can be found in several collections (Burghardt, 1985b; Dewsbury, 1985; Houck & Drickamer, 1996) and historical overviews in Burghardt (1973) and Dewsbury (1984). Today we understand much more clearly how environments can turn gene action on and off, how genetic adaptations influence how much and in what ways experience can alter behavior, and the sophisticated neural systems underlying instinctive responses. Instincts, not always carefully deployed, are again fashionable topics in leading journals (e.g., Jones, 2008). Still, Darwin was right on the money as to their importance.

Play behavior is one area where instinct and development seem to come together. Darwin wrote on play from a comparative perspective, even accepting observations of play in ants. But by the mid-20th century, play was considered the provenance of mammals, and, by the 1970s, of a few birds. Today we know that more careful characterizations of play show that it can also be identified in lizards, turtles, fishes, octopuses, and insects (Burghardt, 2005). Understanding play, long a conundrum, needed the sundering of the apparent necessary connection between large brains and intelligence. The early practice, recapitulation, and surplus energy theories of animal (and human) play developed in a Darwinian context in the late 19th century together contain most aspects of a genuinely evolutionary view of play.

But many other areas of development are also showing promise, and in some sense we can trace them back to Darwin's Lamarckian bent and the attraction it had for many of his followers. Lamarck postulated that the behavior and experiences of an adult animal could be passed on to his or her offspring. In the absence of any knowledge of genetics, this was not too outrageous. Many leading and committed Darwinians were Lamarckians into the 20th century. Today, ideas of behavioral change mechanisms that superficially resemble Lamarckian inheritance but are products of natural selection, such as the Baldwin effect, are again being raised, modeled, and seriously discussed (Wozniak, 2009, this issue).

7. Inheritance of Behavior

As noted above, Darwin, while most known for the theory of natural selection, did not rule out Lamarckian inheritance of acquired characteristics entirely. In fact, in the face of criticism of the early editions of the *Origin of Species* he became more Lamarckian. At the time Darwin wrote and throughout his life, Mendelian (particulate) inheritance was not recognized. Still, Darwin had examples of natural selection that could exclude inheritance of acquired traits, as in his brilliant explanation for the evolution of sterile casts in social insects. In truth, the nature–nurture issue is still with us, though in ever-changing guises.

Behavioral differences among breeds of dogs bred for different abilities such as pointing, herding, and retrieving were used by Darwin to show that behavioral traits or tendencies could be inherited and differ even within a species. Current work documents that natural selection has led to many geographic differences in behavior as well as in coloration, size, and physiological adaptation to different climates (Foster & Endler, 1999) and that the study of such differences is key to understanding speciation and other evolutionary processes. The well-traveled Darwin logically extended his understanding of natural selection and inheritance to differences among human racial and ethnic groups living in different environments (Darwin, 1871; Dewsbury, 2009, this issue). Although the topic is not popular in psychology today, increasing evidence is supporting a genetic aspect to population differences in susceptibility to diseases, physiology underlying behavioral performance, processing of different foods, and other features that have psychological relevance, and refined methods of analysis may mean renewed study would be useful.

Evidence is also accumulating that single genes can influence behavior quite dramatically, although for most behavioral traits it is felt that several to many genes may

also be involved. Today genetic sequencing and molecular methods are rapidly developing and show that behavior may be influenced greatly by gene expression (the turning on or off of genes via experience) and that experience can channel major behavioral changes even in animals with identical genes at the relevant sites. There can also be significant genetic components to the ability to profit by experience (Bekoff et al., 2002). Studies on the genetics of behavior promise to lead to major changes in how mental disorders are conceptualized, described, and treated, especially if their evolutionary origins are also explored.

8. Phylogeny of Behavior

Certainly one of Darwin's major contributions to psychology was the evidence he arrayed to support the claim that instincts evolved in a fashion similar to that for morphological traits of organisms and that this history could be traced through comparing the behavior patterns of living species and inferring from these the putative behavior and evolutionary history of extinct ancestors. These homologies are used to support the common ancestral behavioral traits, just as can be done with morphological traits. This evidence was used in Chapter 6 of the first edition of *On the Origin of Species* in 1859. Darwin traced the evolutionary steps for the construction of beehives and the trait of capturing and using as "slaves" ants of one species by another.

One of the major emphases of the early ethologists was using behavior to trace the evolution of behavior. This method was pioneered by Oskar Heinroth, Charles Otis Whitman, Konrad Lorenz, and many others (Burghardt, 1985b). As ethology developed in the 1970s and 1980s, this phylogenetic aspect was downplayed, but with the development of modern computerized phylogenetic (cladistic) methods, interest in behavioral evolution reemerged (e.g., Brooks & McLennan, 1991). Today, molecular genetic methods of determining the most probable phylogenetic relationships are being used with careful behavior descriptions to determine the nature and extent of behavioral homologies. Often behavioral traits are more robust and informative than physical traits.

9. Sociobiology and Behavioral Ecology

William Hamilton (1964a, 1964b) made explicit the notion put forth by Darwin that it is not only one's direct descendents that contribute to one's reproductive success but the relative survival of other relatives and their offspring. This *inclusive fitness* is not only a major aspect of calculating selection, natural and sexual, across individuals, but it helps to explain altruism toward individuals who are not one's own offspring. The critical measure here is the coefficient of relatedness, *r*, used to develop what became known as Hamilton's rule. Hamilton's rule states that if an animal aids a relative at a cost to itself, it will be selectively advantageous only if the fitness benefit of the behavior to the recipient, multiplied by the level of relatedness (1/4 in the case of a niece), is more than the fitness cost to the donor or altruist. This was a major innovation in how science looks at helping behavior and altruism in general.

E. O. Wilson, renowned for his studies of ant behavior, pheromones, and biogeography, combined his acceptance of the ethologists' view that behavior should be studied phylogenetically just as any other trait of an organism with the contributions of Hamilton and others to develop sociobiology (E. O. Wilson, 1975), a field that attempted to apply a more explicit and predictive evolutionary theory to the understanding of the diverse social and sexual arrangements found in the natural world, knowledge that may also help promote understanding of human behavior and its diversity as well. Contentious implications of the methods and findings of this approach to animal behavior led to the "sociobiology wars" of the 1970s and 1980s, which replaced the "instinct wars" of the 1950s and 1960s. Wilson's use of inclusive fitness to show how homosexuality can be a stable trait in a population was a major controversy, as he advanced a plausible mechanism (aiding nondirect kin).

Richard Dawkins, a student of Tinbergen's, moved the debate on evolution from the survival of individual organisms to the survival of genes themselves (Dawkins, 1976). The view that the organism is just a vehicle manipulated by genes for the latter's survival was unsettling to many and has reinvigorated still-ongoing debates on the levels of selection (genes, gene complexes, organisms, families, groups, communities, societies, and ecosystems). An informative exchange can be found in an article by D. S. Wilson and Sober (1994) and the resulting commentaries. *Behavioral ecology* is more often seen as the preferred term for this field today. Sociobiology still has negative implications in some quarters; it also can be viewed as too limited to social behavior when, in fact, the theoretical apparatus can encompass foraging, antipredator responses, deception, mimicry, and other aspects of behavior.

10. Applied Animal Behavior, Animal Welfare, and Conservation

There is now an active area of interest in what may be called applied animal behavior which focuses on domesticated species in agriculture and laboratories, companion animals, and veterinary medicine. Much of this interest has to do with ameliorating captive conditions that lead to poor breeding, physical illness, malnutrition, abnormal and even dangerous behavior, and so on.

Darwin was not the first to be interested in the behavior of domesticated species, but he made it a prime topic. Since natural selection could not be observed in nature in historical time with the tools then available, Darwin looked to human-induced artificial selection to obtain insights into the power and processes of natural selection in wild populations. Darwin, with his knowledge of domesticated animals such as sheep, dogs, cattle, chickens, and pigeons, was well aware of how the breeds differed behaviorally and that these differences were often related to the use of animals by people.

These behavioral differences Darwin felt were the result, often, of unconscious or inadvertent selection of animals that best showed the trait of most interest. The animals (or plants) that exemplified the traits desired by

their owners or breeders were more likely to be mated, and again the breeders would be selected from the best ones. Today, selection for racehorses is an extreme example, but sperm collection and storage has revolutionized the cattle-breeding industry, among others. Changes of traits, including behavior, could be noticed in several generations under such intense selection, and Darwin used that insight to extrapolate to lower selection pressures operating over thousands of generations.

Darwin was not unaware of the plight of animals in research, and in *The Descent of Man* he made a prescient statement: "Everyone has heard of the dog suffering under vivisection, who licked the hand of the operator; this man, unless he had a heart of stone, must have felt remorse to the last hour of his life" (Darwin, 1871). In the second edition, Darwin added that such work could be justified in terms of increasing knowledge, but one must also remember that anesthetics were not used in such surgeries then and the studies that sickened Darwin in 1871 would never pass muster today in most countries. Again, Darwin's sentiments as well as intellect were ahead of his time. Darwin would thus be very comfortable with the current concerns with animal treatment in research laboratories, a topic that has been one of great interest, sometimes controversially, within the American Psychological Association.

Finally, although the conservation crisis was not then looming, Darwin was concerned about the long-term implications of human actions and would be gratified at how behavior is now becoming essential knowledge to conservation biology and the breeding of endangered species (Gibbons, Durrant, & Demarest, 1995).

Darwin and the Future of the Study of Animal Behavior

Given the many aspects of the study of comparative psychology and ethology informed by almost 50 years of Darwin's contributions, and the 150 years since the publication of *On the Origin of Species*, will Darwin have a continuing role in the future directions of these fields? Do scientists and students still need to read Darwin, not just to see why and how these fields have developed and to understand current science, but to develop insights and ideas to be explored in the future? I very much think so. Certainly the best minds in evolution science in 1959 made many wrong moves. We are lucky that others went back to Darwin with fresh eyes. Here are several issues that I think will be seriously explored in future years much more than they are now.

Language and Culture

It is unfortunate in some ways that psychology is endemically anthropocentric. It results in our species being the pinnacle by which the psychological accomplishments of all other species are measured. But it is understandable that we are most concerned about our origins and how and why we came to be what we are. Two areas still often considered beyond the pale for meaningful comparisons are language and culture. Still, debates on human-language-like skills in other animals are ongoing in the face of evidence in parrots and chimpanzees (e.g., see the papers in Bekoff et al., 2002), and similar issues are current in terms of the transmission of behavioral traits by nongenetic means. We know that dialects in birdsong, foraging methods in nonhuman primates, and other traits can endure for generations, though their evolutionary importance is still debatable, as is their similarity to our cultural transmission methods. Still, there are some intriguing data that need to be confronted (e.g., McGrew, 1992).

Consciousness

Consciousness may be the final frontier in terms of making the link between human and nonhuman behavior. Studies of consciousness and subjective states in animals were rampant in comparative psychology until the rise of behaviorism. With but a few exceptions (vitalists and European protophenomenologists; Burghardt, 1985a), these disappeared from scientific discourse by 1940. How can we ever know what is going on in the mind of an individual from another species? Is this not beyond science? However, all science is based on probabilities, inferences, and predictions, and this certainly holds true in claims about the extent and qualities of animal sentience (Burghardt, 1997). The emergence of cognitive psychology in the 1960s, cognitive ethology in the 1970s (Griffin, 1976), comparative cognition in the 1980s, and cognitive and affective neuroscience in the 1990s, along with the powerful tools of brain imaging, have made it much more likely that we can identify and partially characterize the subjective states of other species. Still, the definitional and conceptual issues are complex (cf. Merker, 2007; Terrace & Metcalfe, 2005).

Morality

In the immediate aftermath of Darwin's writings on human behavior in the early 1870s, religious, philosophical, political, and other writers were concerned about the general acceptance of evolution, especially human evolution, and the implications for morals and virtue (Cooper, 1878; Dawson, 1875; Graham, 1884). Thus, although many religious and political thinkers welcomed Darwinism, the concerns of biblical literalists soon became vociferous and continue to resonate with those in today's creationist and intelligent design movements.

Darwin had no problem seeing rudiments of moral behavior, such as loyalty and helping behavior, in other species, especially his beloved dogs. Recent work is showing traits such as fairness and equity aversion in some primates (de Waal, 2006). Although controversial in its details, this area of research, which includes but goes beyond altruism, has been embraced by respected scientists. Books by respected scientists have confronted once again the sources of morality, if not religion, in our ancestors (de Waal, 2006; Hauser, 2006; cf. Seton, 1907). Religion, so varied yet ubiquitous in all known human societies, is an ancient trait, much more so than agriculture, writing, and the construction of shelters and boats. This also suggests that some other species may have "spiritual" or emotional responses to nature or the death of offspring

and group members that could have led to the sophisticated theologies of today. In any event, morality can clearly be sundered from religion, even if one function of modern religion is to refine and enhance ethical behavior among conspecifics.

Aesthetics and Beauty

Darwin proposed that female choice of mates involved aesthetics, because the extravagant plumage and other secondary sexual characteristics of many males seemed not to be very useful in fighting and actually made males more conspicuous and perhaps more vulnerable to predators. The reverse could also be true; males may, as in our species, gauge females on various traits of beauty, traits such as symmetry that we now postulate are attractive since they signal health, fertility, and so forth. Traits that we view as cute are often derived from those associated with human and animal infants and children (Lorenz, 1981). Dissanayeke (1992) extended the origins of artistic expression beyond beauty to a more general notion of making things or the self "special." Artistic expression may turn out to be another seminal area in which Darwin made his mark on animal behavior.

Summing Up

Darwin will need to be read closely and sympathetically for a good deal longer. Time has shown that scientists and scholars in the decades following Darwin ignored topics he discussed that they did not deem relevant. Perhaps in no other area has Darwin been more selectively read than in behavior, both human and animal. But it is in behavior and psychology that, as Darwin predicted, an evolutionary perspective will be most long-lasting and important. Although some of us are far more comfortable being labeled Darwinians than others, the fact is that Darwin's work continually raises provocative new perspectives for each new generation or school. Darwin's "remains" cannot be poured into an urn and put on a shelf while the world moves on. They will continue to fertilize science in unexpected and controversial ways for years to come.

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