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Animal Behavior

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Few areas of scientific investigation have spawned more alternative approaches than animal behavior: comparative psychology, ethology, behavioral ecology, sociobiology, behavioral endocrinology, behavioral neuroscience, neuroethology, behavioral genetics, cognitive ethology, developmental psychobiology—the list goes on. Add in the behavioral sciences focused on the human animal, and you can continue the list with ethnography, biological anthropology, political science, sociology, psychology (cognitive, social, developmental, evolutionary, etc.), and even that dismal science, economics. Clearly, no reasonable-length chapter can do justice to such a varied collection. We have opted therefore to focus on three of these subdisciplines and to provide a somewhat historical tour of them, mentioning along the way the philosophical points that are of particular interest to us, but allowing the development of these points to be limited only by the imaginations of our readers. For readers seeking a more-traditional historical survey, see Dewsbury (1984a, b) and Burghardt (1985a).

Our chosen brief is to write about comparative psychology, ethology, and cognitive ethology, although other approaches, especially neuroscience, will be mentioned where appropriate. These sciences are philosophically significant because they are enmeshed in ancient philosophical questions about the nature of mind and purposeful action and about the differences between humans and other animals. These sciences are also clustered because of their attention to mechanistic explanations of individual animal behavior as opposed to attempting to capture regularities at a population level, such as the game-theoretic strategic models popular among behavioral ecologists.

Ancient beginnings

From a certain vantage point, it can seem that scientists and philosophers today are discussing the same old questions raised by ancient Greeks: Do animals have a language? Do they reason? Can all nonhuman animal behavior be explained in terms of instinct? What is the nature of animal consciousness and emotions? To a first approximation, this is correct. But scientists now know a lot more about animal behavior than did Aristotle, Descartes, or even Darwin. Consequently, even though the questions may appear to be the same, the terms in which they are posed and the range of possible answers have changed. The philosophical problems take on different complexions as science proceeds.

The nuances cannot be appreciated without a historical approach to understanding the different scientific contexts of the three branches of science that are our main focus. These three sciences only emerged as such during the past 150 years. But they emerged in the context of a discussion that has ancient roots. Thus, we begin with Aristotle, who famously maintained that only humans are rational animals. According to Sorabji (1995), Aristotle created a crisis for Greek thought by denying reason to animals, thus requiring a

“wholesale reanalysis” (7) of the nature of mental capacities and a revision in thinking about “man and his place in nature above the animals” (ibid.). The debate about reasoning and self-knowledge in animals proceeded on the basis of some widely repeated anecdotes, such as the tale of a hunting dog told by Chrysippus. The dog, reaching a crossroads in pursuit of another animal, was said to have sniffed two of the roads leading away and immediately set off down the third without sniffing. Sorabji (1995) reports that Chrysippus did not take this to show that the dog really reasons, but only that it “virtually” goes through a syllogism: “The animal went either this way, or that way, or the other way. But not this way, or that way. So that way” (Sorabji 1995, 26). Nevertheless, the argument about what is reasoning, and whether animals display it, remains with us to this day, as evidenced by a recent volume titled *Rational Animals?* (Hurley & Nudds 2006).

Another important Aristotelian influence on early scientific thinking about animal behavior is the great chain of being, which is derived from early Christian interpretation of his scale of nature (Lovejoy 1936). European exploration during the seventeenth and eighteenth centuries resulted in many stories and eventually some actual specimens of the anthropoid apes reaching Europe (see contributions to Corbey & Theunissen 1995). Many of the stories were quite fantastical, and the individuals that reached Europe were generally short-lived if they didn’t arrive dead in the first place, so sources of information about their behavior were poor. Nonetheless, it was clear that these apes were anatomically and behaviorally similar to humans, and thus they threatened the sharp distinction between humans and other animals. It is important to mention that European ideas about these apes also served to reinforce racial ideas about the inferiority of African “pygmies” and other “savage races,” conceived as lying intermediate between the apes and “civilized” Europeans.

As portrayed by Sorabji, and as indicated by the legacy just described, Aristotle’s reasons for interest in animal behavior seem more concerned with the desire to fully understand human nature than concerned with interest in animal behavior for its own sake (but see Steiner 2005, ch. 3, for a more-balanced account of Aristotle’s motivations). These distinct motivations for studying animal behavior also persist to this day. For instance, a widely used comparative psychology textbook (Domjan & Burkhard 1992) emphasizes in its introduction the idea that animals provide models for investigating human psychology, whereas a more biology-oriented introductory textbook on animal behavior (Manning & Dawkins 1998) emphasizes in its introduction the direct satisfaction of understanding why animals do what they do. Of course, these motivations for studying animal behavior are not necessarily exclusive, but different emphases affect the kind of science that gets done, as illustrated in what follows.

First steps

Getting science done at all with respect to animal behavior took a surprisingly long time. The ancient Greek approach was heavily anecdotal, and there are few glimmers of systematic approaches to studying animal behavior until the nineteenth century, some two centuries after the initiation of the scientific revolution. An early glimmer is provided

by late eighteenth-century attempts to record birdsong systematically using musical notation (Barrington 1773; see also White [1789]1939). Other precursors to the science of animal behavior include the work of Frédéric Cuvier, who from 1804 until his death in 1838 investigated the development of captive mammals and their sexual and social behavior. Also notable is the work of Alfred Russel Wallace who in 1867 wrote a paper called “The Philosophy of Birds’ Nests,” arguing that an experimental investigation of the role of instincts for nest building in birds was necessary. His paper is perhaps the earliest we know to argue explicitly for an experimental approach to animal behavior. A noteworthy contribution to the early experimental literature is Douglas Spalding’s 1872 paper on instinctual feeding behaviors in chicks. Human interest in bird behavior seems to have often played a crucial role in the development of the sciences of animal behavior.

Although experimentation is the paradigmatic notion of systematic investigation, carefully documented observation also plays an important role in the development of many sciences. In 1868, Lewis Henry Morgan, better known for his pioneering work in ethnography, published what is widely regarded as the first monograph on a single species, the American beaver. Morgan’s measurements and detailed sketches of beaver dams and his measurements of the physical dimensions of beaver specimens show that a quantitative approach to the physical features of animals and their behavioral products was not beyond imagination. In many ways, his ethnographic work foreshadows the ethological approach to animal behavior that arose in the twentieth century. But in Morgan’s beaver work, the collection of data on the animals’ actual, real-time behavior is all but absent, and his section on their perceptual capacities provides only anecdotes to illustrate his claims.

Morgan, in 1857, had also written an essay on animal psychology (Johnston 2002), which appeared in a much-abbreviated form as the final chapter of his beaver book. In his original paper, he took on the ancient question of instinct versus reason and argued that all extant definitions of instinct are unintelligible, save one. This one, which he adopts ironically at the very end of his paper, he attributes to William Hamilton: “An instinct is an agent which performs blindly and ignorantly a work of intelligence and knowledge.” In other words, Morgan insinuates that instinct is nothing other than a label that is used to deny reason to animals by asserting instead that they act “as if rationally,” and that is postulated for no better reason than to provide a difference between humans and animals. We have already seen the idea that animals are “as if” rational in Chrysippus’s dog’s virtual syllogism, and the idea crops up in comparative psychology again and again. (Compare, also, Evans & Marler’s 1995 discussion of “functional reference” as a way of avoiding the question of whether animal alarm vocalizations actually refer to the predators that evoke them.)

Although Morgan was a theistic antievolutionist, his ideas about animal intelligence were very congenial to Darwin’s theory. He even notes that the intellectual gap between the “highest” and “lowest” humans is as great or greater than that between the “lowest” humans and the “highest” animals (Johnston 2002, 342), thus anticipating a very similar claim by Darwin made years later: “We must . . . admit that there is a much wider interval in mental power between one of the lowest fishes, as a lamprey or lancelet,

and one of the higher apes, than between an ape and a man” (Darwin 1871, 445).

Darwin devoted considerable portions in both *The Origin of Species* and *The Descent of Man* to animal behavior, with the obvious goal of demonstrating mental continuity among the species. To make his case, Darwin relied heavily on anecdotes provided by his correspondents. His protégé George Romanes is nowadays the poster boy (or whipping boy) for embracing the anecdotal approach (Romanes 1882). (Although to be fair to Romanes, which the critics rarely are, his published collection of anecdotes was intended as a preliminary for direct, systematic investigation.) Darwin himself made numerous observations of animal behavior, and his final work, on earthworms, describes his experiments on the flexibility of their behavior in manipulating leaves, which he took to show considerable intelligence (Crist 2002). But there were also those who argued against the suitability of experimental methods for phenomena as complex as animal behavior (LeConte 1875; Johnston 2003). Joseph LeConte, a geologist who started as a creationist but was converted to Darwin’s evolutionary views, also wrote on instinct and intelligence, arguing contra Morgan that beaver dams are the product of instinct (1875, 658) and contra both Morgan and Darwin for a big gap between animal intelligence and human intelligence.

Neither systematic observation nor experimentation really took hold until the twentieth century. We think that the late arrival of experimentation to animal behavior studies poses something of a puzzle. One hypothesis for why it took so long is technological: Field observation of animals in natural conditions requires access to cheap field glasses (Adriaan Kortlandt, personal communication) and improved means of capturing images (Nemes 2005). But while this suggestion has some merit for ethology, with its predilection for observation in natural environments, it doesn’t really explain why behavioral experiments on captive animals were slow to come. Physiologists, after all, had conducted experiments on animals for a long time, and going back to Descartes, the notion of a reflex was importantly derived from animal experimentation, including vivisection.

Descartes had argued that animals are automata—reflex-driven machines with no intellect or other thinking capacities. T. H. Huxley (1874) traces the philosophical development of the idea that animals are automata. Huxley reports a series of experiments on a frog, showing very similar reflexive behavior even when it had its spinal cord severed or large portions of its brain removed. From this he argues that, with the brain gone, the frog can’t be conscious, but since it can still do the same sorts of things that it could do before the brain removal, there is no need to assume consciousness even in the presence of the entire brain. (Curiously, or conveniently, he ignores the fact that the brain-damaged frog is clearly less reactive to its environment than it was before.) Huxley goes on to argue that consciousness is, at best, superfluous. (This idea, that consciousness is epiphenomenal, remains popular among many scientists and philosophers today.) Regardless of the status of consciousness, the general effect of reflexive physiology seems to have been to make these scientists less inclined to search for and investigate more-sophisticated forms of animal behavior.

Thus, on top of Aristotle’s division between instinct and reason, we have the

Cartesian distinction between mechanical reflex and conscious thought. It's tempting to map the one distinction onto the other, and Descartes certainly made the capacity for reason central to his argument that only humans have conscious thought. But it would be a mistake to assimilate the two. First, a number of authors before and after Darwin have assumed that some sort of conscious experience accompanies instinctive and reflexive actions. Second, there are various senses of consciousness in play (Allen 2005), and different senses are taken by different authors to track different aspects of animal behavior. That phenomenal consciousness is uniquely attached to fully reflective thought is a strong and highly doubted claim, even though it has current defenders among philosophers, such as Carruthers (2000). In sum, though, the kinds of physiological experimentation on animal reflexes, combined with the demotion of animal behavior to the categories of the unconscious, reflexive, and instinctual, were not conducive to the kinds of experimental and observation work on sophisticated animal behavior that characterizes the comparative psychology and ethology that emerged in the twentieth century.

Perhaps a related reason that the experimental approach was late coming to animal behavior is that the Aristotelian and Cartesian divisions push learning and memory into the background. Reflexes and instincts are conceptually fixed, whereas reason and thought, despite using learned or remembered facts, say nothing about the process of learning or memorization itself. It took Ivan Pavlov, a physiologist, to discover the conditioned reflex and to adapt his experimental methods from physiology to the study of associative conditioning during the 1890s (Pavlov 1927; Yerkes & Morgulis 1909). Physiologist Jacques Loeb's book *Comparative Physiology of the Brain and Comparative Psychology* (Loeb 1900) was also an influential source of ideas about associative learning and instinct (see also Brigandt 2005).

There were glimmers of an understanding of learning as an important aspect of animal behavior in earlier, nineteenth-century works. One interesting figure is John Bascom (Johnston 2003), who wrote on instinct in 1871 and published textbooks on psychology (1869) and comparative psychology (1878). Bascom, a philosopher and antievolutionary theologian, is now largely forgotten, but in his 1869 book, he advances several possible alternative explanations for "as if rational" behavior in animals. He uses associationist principles (widespread among psychologists of his day) to explain animal behavior without appealing to reason (1869, 220). Bascom defends his position on purely theoretical grounds; he does mention some anecdotes but in a very pro forma fashion, and he explicitly says that it doesn't matter if they are true or not because something like them will be. He also accuses those who treat animals and humans the same as guilty of poor reasoning (an early charge of "anthropomorphism") and deliberately attempts to explain away anecdotes apparently supporting animal rationality. Bascom defends associationist explanations by pointing out the kind of foresightless, trial-and-error learning that animals use, although he also deems some animal learning, e.g., spatial learning, to be too fast to be attributed to reason. According to Johnston (2003), Bascom even anticipated the extremely influential Morgan's canon (see below) when he argued that an associative explanation of animal behavior is preferable to attributing reason because it's a weaker hypothesis (Bascom 1869, 223). Bascom's associationism is not

quite the same as is found in the behavioristic psychology that comes out of Thorndike's and Pavlov's later work because the former relies heavily on an explicitly cognitive conception of memory. Bascom's arguments against animal reasoning on the grounds that the capacity to make one inference would entail the ability to make many and his emphasis on the importance of language relate him back to Descartes and also forward to Davidson's arguments against the rationality of animals (Davidson 1982). Although Bascom uses the term "comparative psychology" in his 1878 title, Johnston (2003) argues that this work along with that of L. H. Morgan and LeConte (discussed above) do not add up to a comparative psychology as we now understand that term because no institutions or unifying intellectual frameworks resulted from the efforts of these thinkers.

Establishing such a science using the framework of Darwin's theory of evolution was Romanes' expressed intention in his 1882 book, *Animal Intelligence*. In *The Origin of Species*, Darwin gives an account of instinct as different from reason or habit, and then notes that some evidence of reason seems to appear in the behavior of most creatures, quoting Pierre Huber's (1810) observations of ants (Darwin [1859]1985, 70). Darwin goes on to compare behaviors to anatomical traits, arguing that instincts have the same sort of properties that other traits need for selection to work, specifically variability and heritability. Still focusing on insects, he provides an account of the selection of traits in ants, using terms such as "bravery," which seem stunningly anthropomorphic from our present vantage point. He then turns to a discussion of hive making, displaying the brilliant imagination that went into his subtle experiments using colored wax to show how the hexagonal structure of the hive is optimal and can be understood as a produce of selection. This experimental approach is less evident in the *Descent*. There, Darwin's case for the claim that humans have no special behavioral capacities (or "mental powers," as Darwin calls them) consists of listing various powers which he attributes to nonhuman animals. Thus, curiosity, imitation, attention, memory, tool use, etc., are attributed on the basis of numerous accounts of incidents where animals were alleged to have displayed these properties, which were previously held to be the preserve of humans alone. The cases are all overdescribed and crudely anthropomorphized. Thus, for example, Huber is cited again as having seen ants "gamboling" at play, and this is taken to be a "demonstration" of emotion (1871, 70). Darwin takes great pains to praise the reliability and credibility of his witnesses—a form of evidential support whose status in other parts of science was abandoned as soon as methods for obtaining replicable results were developed. This suggests the backward state of this form of investigation at the time, and it also looks forward to the challenges with which Romanes had to deal.

Despite its problems, the *Descent* contains many interesting ideas. There is Darwin's suggestion, for instance, that association of ideas (following Hume) could provide a third way to act, between instinct and reason, and he exploits this suggestion to sketch a general learning theory. Also, his discussion of tool use and language prefigures much that is in the current literature and, in some respects, only recently rediscovered. In the end, however, Darwin ends up saying a lot of things in the *Descent* that suggest a hierarchical view of intelligence, which he had so carefully avoided in the discussion of evolution in the *Origin*.

Perhaps there is something about cognitive or mental traits that makes ranking them from low to high more seductive. But why is this? One problem may be that we have mostly functional standards for the identification of such traits. Take memory as an example. Even though we know much more about memory than Darwin did, still we individuate types of memory largely in functional ways (short-term, long-term, semantic, episodic), and this tends to impose an ordering (good short-term memory is necessary for long-term memory, for example). Furthermore, the adaptiveness of capacities thus identified owes more to the way in which they are identified than to their actual evolutionary history in the sense that, when we have to identify structure by function, we tend to use functions that make sense to us, but this move makes such ersatz structures functionally optimal by definition or, more precisely, by construction (Crowley 2006). As a result, the attempt to give evolutionary explanations of these structures is much less informative than evolutionary explanations of anatomical and physiological structures, which can be identified in a more-independent fashion.

It is in the context of uncertainty about what the basic phenomena even are that Romanes proposed to collect as much information as he could from all sources, including anecdotes, before embarking on the task of systematizing the field of comparative psychology. Although he starts off by stating firm criteria for inclusion in his compendium, in the end it seems that almost any story will do because, he suggests, sticking to his original criteria would omit some of the most-interesting phenomena. It's not just that the anecdotes describe singular events, but that they are described in the most anthropomorphic terms. The questionably anthropomorphic descriptions (for example, a story of ants "rescuing" another ant) even have the effect of calling into question whether the events took place at all. In any case, Romanes' more-systematic project never materialized, and so the putative phenomena never received the full theoretical treatment that he had promised. The result is that Romanes' legacy is primarily negative, as his anecdotal, anthropomorphic approach was widely rejected.

Comparative psychology

The problem of unwarranted anthropomorphism was a major impetus for Conwy Lloyd Morgan's attempts to develop a new methodology in his 1894 *Introduction to Comparative Psychology*. Lloyd Morgan believed that scientific understanding of the mental states of animals depends on a "double inductive" process, combining inductive inferences based on observation of animal behavior with introspective knowledge of our own minds. He recognized that this method contained an anthropomorphic bias, which he sought to counter with his "basal principle," now known as Morgan's canon: "[I]n no case may we interpret an action as the outcome of the exercise of a higher psychical faculty, if it can be interpreted as the outcome of the exercise of one which stands lower in the psychological scale" (Lloyd Morgan 1894, 53). The introspectionist component of Lloyd Morgan's methodology did not survive the general purge of explicitly introspective methods from human psychology at the beginning of the twentieth century (Boakes 1984), but the canon lived on; it has been called "possibly the most important single sentence in the history of the study of animal behavior" (Galef 1996, 9).

Quite what Morgan's canon means and how to justify it are active topics of historical and philosophical investigation (e.g., Burghardt 1985b; Sober 1998, 2005; Radick 2000; Thomas 2001). Questions about it include what Lloyd Morgan means by "higher" and "lower," to what extent the principle can or should be justified by evolutionary considerations, and whether the canon collapses to a principle of parsimony, a version of Ockham's razor, or some general principles of empirical justification. Despite current uncertainty about what it really means, Morgan's canon, interpreted (or, perhaps, misinterpreted; Thomas 2001) as a strong parsimony principle, served a central rhetorical role for behavioristic psychologists, who sought to eliminate mentalistic talk from comparative psychology, and despite the decline of strict behaviorism, it continues to survive as a pedagogically useful reminder that mentalistic (anthropomorphic) interpretations of animal behavior need to be carefully justified.

Although Morgan's canon played a central rhetorical role in the development of a fully experimental comparative psychology, the credit for truly launching the experimental discipline must go to Edward L. Thorndike. He measured the time taken by his animal subjects, including cats and dogs, to escape from various "puzzle boxes" that he constructed in his laboratory. As trial and error gave way to a learned response, the time to escape decreased. In Thorndike's report of these results (Thorndike 1911), we see some of the first uses of graphs to display quantitative results obtained from multiple subjects, prefiguring the explosion of methods of statistical analysis that were to have an enormous influence on psychology. Lloyd Morgan, whom Thorndike met as a student of William James in 1896 when the former visited Harvard (Burkhardt 2005), had discussed a similar case of his dog learning to bump his head against the latch of a garden gate in order to open the gate. Lloyd Morgan describes trying to teach the dog to use his nose instead of the top of his head to open the gate, and concluding from his failure to do so that the dog had learned only an association between his specific behavior and the outcome and had no insight into the mechanism (Lloyd Morgan 1930). The contrast between Lloyd Morgan's work at the bottom of his garden and Thorndike's elaborate apparatus designed for laboratory investigation speaks volumes about the methodological shift that Thorndike's work signaled.

Thorndike also characterized his task as the discovery of general laws of learning. His law of effect is still widely regarded as a major contribution to comparative psychology:

Of several responses made to the same situation, those which are accompanied or closely followed by satisfaction to the animal will, other things being equal, be more firmly connected with the situation, so that, when it recurs, they will be more likely to recur; those which are accompanied or closely followed by discomfort to the animal will, other things being equal, have their connections with that situation weakened, so that, when it recurs, they will be less likely to occur. The greater the satisfaction or discomfort, the greater the strengthening or weakening of the bond. (Thorndike 1911, 244)

The idea that there are general laws of learning, applicable across species, is a major point of difference between comparative psychologists and ethologists. Both sides

appeal to Darwin's legacy to justify their positions. To comparative psychologists, common descent justifies the claim that there should be a high degree of similarity in learning mechanisms among the species (see Domjan & Burkhard 1992). To ethologists, the process of natural selection suggests that differences will arise due to phylogenetic diversification (e.g., adaptation to specific niches; Manning & Dawkins 1998). We can also add that the psychologists' quest for laws is sometimes mentioned as evidence for "physics envy." Whether physics is an appropriate general model for science is a long-standing debate which we can only mention here. Nevertheless, the new scientific discipline of laboratory-based, experimental comparative psychology, centered around the discovery and investigation of principles of associative learning, was truly established by Thorndike's work, which came shortly after Yerkes and Morgulis (1909) introduced Pavlov's results to English-speaking scientists.

A major development out of these influences was the radically antimentalist behaviorism of John B. Watson (1928), who was influenced by Pavlov, and B. F. Skinner (1953), who was influenced by Thorndike. Despite their differences, both scientific and philosophical, the generally radical orientation of Watson's and Skinner's behaviorism was enormously important and influential. They both strongly rejected any attempts to explain animal behavior in terms of unobservable mental states. An important modification of this approach was the work of Clark Hull (1943) who appealed to fully-operationalized intervening variables as explanatory constructs while accepting the general antimentalism of the radical behaviorists. As these psychologists and their students retreated into the laboratory and pursued more and more arcane investigations of the fine details of reinforcement schedules in less than a handful of species, they became increasingly distanced from biologists who wanted to understand the relevance to reproductive fitness of animal behavior in all of its enormous variety. Although there are numerous philosophical issues that arise in strict behaviorism, these have been extensively discussed elsewhere (see Graham 2005 for an overview), and they would take us too far afield for this chapter in a handbook on the philosophy of biology.

It would also be a mistake to think that all comparative psychologists went down pathways that were antimentalist or unconcerned with biology. On the first point, comparative psychology always included more approaches than strict behaviorism, e.g., Tolman's psychologist notion of intervening variables (Tolman 1948). Primatologists in particular continued to try new ways to get their subjects to demonstrate reasoning capacities, language use, insight learning, and a variety of other "higher" capacities. Second, even strict behaviorism found its own way of accommodating the relationship of learning to evolution without actually acknowledging it (Timberlake 2002). Timberlake and Lucas (1989) note that, in "tuning" their laboratory apparatuses so that they produced replicable results, even the Skinnerians were implicitly adjusting their equipment to the evolved characteristics of the particular species under study.

Classical ethology

Lacking the space to pursue the issues arising from behaviorism in any more detail, we

turn now to the roots of ethology. Although the use of the term “ethology” to describe the biological study of animal behavior can be traced back to at least 1859 (Jaynes 1969), it was not until the twentieth century that a recognizable community of ethologists began to emerge. (For the “prehistory” of classical ethology, and the influence of figures such as Oskar Heinroth and Wallace Craig on Konrad Lorenz, see Burkhardt 2005.)

Ethology is a hard science to classify. Part natural history with an emphasis on fieldwork, part experimental science conducted on captive animals, this diversity owes much to the different styles of its two seminal figures, Konrad Lorenz and Niko Tinbergen (see Burkhardt 2005). Initially, innate behaviors were the central focus of Lorenz’s work. According to Lorenz, it is the investigation of innate behaviors in related species that puts the study of animal behavior on a par with other branches of evolutionary biology, and he demonstrated that it was possible to derive the phylogenetic relations among species by comparing their instinctive behavioral repertoires (Lorenz 1971a). In pursuing this direction, Lorenz and Tinbergen explicitly sought to distance ethology from the purposive, mentalistic animal psychology of Bierens de Haan and the lack of biological concern they detected in American comparative psychology (see Brigandt 2005).

Much of the earliest ethological work concentrated on nonmammalian species, especially birds, but also insects and fish. Paul Griffiths (personal communication) suggests that the Lorenzian account looks more plausible to those who work on these taxa because they display more stereotypical (and hence plausibly innate) behavior than do mammals. The fact that ethologists were interested in relatively rigid behaviors, which they took to be inherited, perhaps explains why the investigation of learning had little appeal for them.

Like Lloyd Morgan, the ethologists rejected Romanes’ anecdotal approach, but they also criticized Lloyd Morgan’s subjectivist approach. Of considerable importance in making ethological observations systematic was the development of the notion of an ethogram—a catalog of repeated behavioral elements which allows different observers to coordinate and agree upon their observations. This more-regimented approach to reporting observations goes a considerable way toward eliminating the problems associated with anthropomorphism, although disputes remain about whether the labels chosen for the different behavioral elements might illicitly smuggle in subjective ideas, such as intention or purpose. (Should, for example, a chimpanzee with its hand out be described as begging?) Issues of gender bias can also be raised in light of early (male) ethologists’ concentration on classifying behaviors in terms of dominance, aggression, etc. (Gruen 1995).

Central to Lorenz’s ideas about the epistemology of ethology is the importance of extensive “presuppositionless” observation of animals by scientists as a necessary preparatory phase for experiment (Lorenz 1981; Brigandt 2003; Allen 2004). Lorenz developed a theory of the process of going from observation to experiment, according to which extensive observation leads through gestalt processes to a kind of knowledge or expertise that enables the scientist to design experiments that will justify conclusions drawn through inductive methods. Unraveling this would take more space than we have

available here (see Brigandt 2003; the literature on evolutionary epistemology is also relevant, e.g., Lorenz 1973; Callebaut & Pinxten 1987). We believe the topic is ripe for further investigation by philosophers of science. For one thing, the suggestion that ethological expertise and knowledge precede the experimental work seems to make Lorenz's view supportive of the idea that philosophers of science need to pay more attention to the context of discovery (Reichenbach 1938) rather than limiting attention to the context of justification. Lorenz seems to have had much more interest in discovery than justification, besides which, he recognized that Tinbergen was the better experimentalist anyway. Experimental work in the context of classical ethology served a couple of purposes. One was to identify the conditions under which innate behaviors are "released." The other was in "deprivation" experiments, where the goal was to determine whether a particular behavioral trait will appear even if the animal is deprived of some condition that might be thought to be crucial for its development.

A pivotal event in the development of ethology was Daniel Lehrman's (1953) critique of Lorenz's concept of instinct. Lorenz insisted on treating the learned and innate causes of behavior completely independently (Brigandt 2005). Lehrman argues forcefully that Lorenz and his followers were too quick to label behaviors as instinctual because they failed to consider the role of development or learning sufficiently and confused different levels of organization in the organism, too quickly relating instincts to hypothetical physiological mechanisms. Lehrman's concern is not merely that the ethologists have miscategorized certain behaviors, but that "instinct" (or "innate" or "species-typical") can mean different things, some of which are compatible with development and learning. For example, rat nest-building behavior is species-typical and innate in the sense that it will emerge under a wide variety of environmental conditions, even when nest material is absent during development, yet this behavior also has a developmental component because it will not emerge if young rats are deprived of any opportunity to carry objects.

Tinbergen took Lehrman's criticisms more seriously than did Lorenz (see, also, Griffiths 2004 on the reception of the concept of instinct in Britain in the 1950s). Tinbergen's consideration of Lehrman's critique eventuated in his 1963 paper, "On Aims and Methods of Ethology." In this paper, Tinbergen proposes to identify ethology by its methods and the questions it asks rather than its theories, thus distancing ethology from commitment to any specific view on the nature of instinct, and Lorenz's in particular. He proposes that ethology is the application of generally scientific and specifically biological methods to four questions (the first three he credits to Huxley): causation, survival value, evolution, and ontogeny. The addition of ontogeny is clearly a response to Lehrman's critique, but arguably this was part of Tinbergen's last-ditch attempt to try to keep together the ethological approach to animal behavior that Tinbergen himself had referred to as a "ragbag" (Burkhardt 2005, 5) and that was beginning to drift apart as the study of different aspects of behavior were becoming increasingly specialized and new approaches emerged. Among these new approaches were behavioral ecology and sociobiology which, through their use of optimality models, greatly reduced the significance of questions about causation or development. Even though behavioral ecology uses rational choice models,

such as those derived from game theory, it explicitly denies that these models provide an account of the actual psychological processes of animals “choosing” among alternative strategies.

Cognitive ethology

Not all animal-behavior scientists gave up on the Darwinian idea of mental continuity, however. Donald Griffin, who made his reputation on the basis of very rigorous work that involved careful physical measurements to prove that bats use echolocation, aimed to restore questions about animal minds, and specifically animal consciousness, to central position (Griffin 1976). Griffin (1978) coined the term “cognitive ethology” to describe this research program. Although this term suggests a marriage between cognitive science and classical ethology, Griffin’s approach bore little direct resemblance to either. Even so, the term is still apt insofar as Griffin, like cognitive scientists, rejected behaviorist strictures against theorizing about mental states and, like ethologists, emphasized observation and experiments conducted under naturalistic conditions. The association with ethology is also apt because the scientists receptive to Griffin’s method were much more likely to be ethologists than psychologists (although fierce criticism emerged from both directions). But rather than exploiting the computational and information-processing ideas driving cognitive science or focusing on the inheritable behavioral traits that are the domain of ethologists, Griffin emphasized behavioral flexibility and versatility as the chief source of evidence for consciousness, which he defined as “the subjective state of feeling or thinking about objects and events” (Griffin & Speck 2004, 6). In seeing subjectivity, at least in simple forms, as a widespread phenomenon in the animal kingdom, Griffin’s position also bears considerable resemblance to Lloyd Morgan’s. Burghardt reports that “considerable discomfort with subjectivism” (Burghardt 1985b, 907) arose during the Dahlem conference that Griffin convened in an early discipline-building exercise (Griffin 1981). Griffin’s subjectivist position, and the suggestion that even insects such as honeybees are conscious, seemed to many scientists to represent a lamentable return to the anthropomorphic overinterpretation of anecdotes seen in Darwin and Romanes. To be fair, although there may be some merit to the charge of overinterpretation of the available data, the anecdotalist charge is probably not warranted because Griffin does not repeat the “friend-of-a-farmer” kind of story collected by Romanes, but bases his interpretations on results from the much more sophisticated scientific literature that had accumulated more than a century after Darwin. It is also important to note the role played by neurological evidence in his argument, when he concludes that the intensive search for the neural correlates of consciousness has not revealed “any structure or process necessary for consciousness that is found only in human brains” (Griffin & Speck 2004).

Even though a number of researchers adopted the mantle of cognitive ethology (Dennett 1983; Cheney & Seyfarth 1990; Ristau 1991; Burghardt 1985b; Bekoff & Jamieson 1993; Allen & Bekoff 1997), they tended to focus less on consciousness per se and more on other aspects of animal cognition, such as communication, concepts, meaning, planning, and deception. There are exceptions, of course, such as Burghardt (1997), who proposed adding the study of private experiences as a fifth aim for ethology.

Nonetheless, Griffin continued to lament the fact that the specific topic of animal consciousness was receiving inadequate attention (Griffin 2002). At Griffin's Dahlem conference, Dennett offered his intentional stance as the framework for experimental design and interpretation in cognitive ethology, arguing that it is possible to design experiments that test among different levels of intentional explanation: At the first level, an animal has beliefs about nonmental features of the world; at the second level, the animal is capable of beliefs about first-order mental states; and so on (Dennett 1983). This too also has little to do with subjective awareness, particularly in light of Dennett's skepticism about qualia (Dennett 1991). Regardless of how the intentional stance relates to consciousness (or not), a serious issue for Dennett's methodology concerns the rationality assumption required for drawing inferences about experiments, which he characterizes as a version of the general adaptationist strategy in biology (Dennett 1983). When pressed for more precision on just what the assumption of rationality entails, Dennett (personal communication) describes it as a heuristic that allows researchers to make predictions about what animals will do by projecting their own reasoning abilities into the circumstances. This feature of Dennett's view makes it seem like a version of Lloyd Morgan's introspective method. Given his instrumentalism about mental state attributions, Dennett has principled reasons to resist demands for greater precision about the notion of rationality. But it is unclear whether this provides a sufficiently precise methodology for the more-realist ambitions of many cognitive ethologists.

Lorenz and Tinbergen held opposing views about the tractability of questions about the role of emotion in animal behavior, with Lorenz citing Heinroth's view that "animals are highly emotional people of very limited intelligence" (Lorenz 1971b, 334). Much of the work in cognitive ethology has proceeded without much consideration of emotion. For instance, it warrants only one brief mention by Griffin and Speck (2004, 12), when they consider the possibility that emotion plays a role in goal-directed behavior. Burghardt (1985b) conducted a survey in which he found that people are generally much more willing to attribute human-like emotions to animals than they are to attribute human-like cognitive capacities. One might well wonder, therefore, why theorists seem much more drawn to cognition as evidence for consciousness. A collection of anecdotes from scientists is one of the few attempts to reintroduce the topic to ethology (Bekoff 2000).

From ragbag to quilt, and beyond

Among physiologists, emotion in animal behavior seems to have played a much more significant role, although they are not arguing for or about animal consciousness. Dror (1999) explains how the emotional state of animals was considered to be a source of noise in physiological experiments in the early twentieth century, and researchers took steps to ensure that animals were calm before their experiments. Dror also explains how the need to control such affective noise was used to justify the idea that the laboratory was the ideal place to do this work (cf. Timberlake & Lucas 1989 on tuning the apparatus). Without the necessary conditions, physiological measurements were hard to replicate. The resulting conception of emotional affect as something that needs to be eliminated in

order to get at the “truth” of an animal’s physiology seems odd if affect itself is a physiological state; the calm and the aroused versions of the system should, presumably, both be of interest to the physiologist. Dror points out that, although physiologists were forced to deal with the problem of emotional noise, attempts to treat emotion as a subject of study in its own right never crystallized to the extent of generating a journal or other institutional features (Dror 1999, 219).

More recently, Jaak Panksepp has been arguing for a research program that he calls “affective neuroscience” (2004). Responding to the worry that affect can’t be measured directly, Panksepp and Burgdorf (2003) point out that indirect measurements are common in science, so the skepticism about emotions is unwarranted. Whether this burden-shifting strategy is effective requires more analysis using the tools of the philosophy of science. Panksepp faces the challenge that attributing emotional states to animals is unwarranted anthropomorphism. Philosophical discussions of just how much of a “sin” anthropomorphism is (Fisher 1995; Keeley 2004) have focused on the logical form of the inference, but, while technically correct, this may miss what is of most concern to scientists. Attempts by scientists to take a balanced approach to anthropomorphic reasoning (e.g., the “critical anthropomorphism” of Burghardt 1991) emphasize the need for detailed knowledge of the animal (species) before it can be safely employed. Panksepp also suggests that degree of homology reduces the worry about anthropomorphism. Rather than thinking of anthropomorphism abstractly, philosophers of science need to consider how it actually functions (or malfunctions) in the science (see contributions to Mitchell et al. 1997). This will also require taking into account the possibility that there is a cultural or religious dimension to Western concern about anthropomorphism that is not a universal scientific concern (Asquith 1984, 1995; de Waal 2003; Steiner 2005).

Panksepp (2005) sees a role for ethology in identifying the neurological structures of interest to affective neuroscience. But Panksepp and Burgdorf assert that their work on rat laughter will highlight “general principles” of positive affect and motivation in mammal brains (2003, 545). This concern with general principles seems to align them more with the psychologists than the ethologists in their general scientific objectives. Nevertheless, it is clear that Panksepp is striving toward an integrative approach. He also writes (2005, 59): “The field of learning is also littered with hard to interpret findings, because changes in emotions could easily masquerade as learning effects. Motivational changes often produce effects similar to learning changes.” These comments remind us of the more-general issue arising in the science of animal behavior concerning the importance and the difficulty of unifying the different perspectives provided by functional, adaptive, neurological, developmental, genetic, physiological, and psychological approaches.

There have been various attempts over the years to try to develop a fully integrative approach to animal behavior, but the study of behavior continues to be pulled in different directions, with scientists taking potshots at the perceived limitations of those working in different traditions. Lehrman was the founding director of the Institute of Animal Behavior at Rutgers University in Newark, New Jersey, and oversaw a very interdisciplinary group. His death in 1972 prompted Colin Beer (1975) to ask the

question: “Was Professor Lehrman an ethologist?” Beer answers yes. Tinbergen’s famous 1963 paper was, of course, an attempt to provide a framework for integration. Yet, despite this, we have seen continuing reasons for worry about the tendency of ethologists to spin off in different directions. Ethologists are not the only ones to be worried about spin-off, as the standard behavioristic learning paradigms have become standardized tools for other kinds of investigation, such as behavioral pharmacology and behavioral neuroscience. Traditional learning theorists fear that the paradigms that get adopted in these related fields represent a dumbed-down version of learning theory, and a feared outcome is extinction by hybridization (a term we are metaphorically extending from conservation biology). Extinction is not necessarily a bad thing if something better is available. Grau and Joynes (2005), for example, point out that the traditional classification of learning into classical conditioning and instrumental/operant conditioning is based on experimental protocols rather than mapping onto the underlying systems, and they argue that this classificatory scheme has become an impediment to the scientific investigation of the neural mechanisms of learning.

The study of birdsong is one area where neural and behavioral approaches have been combined with some success since the 1960s. The challenge of finding ways to combine multiple perspectives in a sophisticated way will continue to make animal behavior a dynamic corner of the life sciences, with plenty of scope for philosophers to contribute to the development and analysis of new frameworks. For example, Timberlake and Lucas (1989) propose to analyze animal behavior using the modular notion of a “behavior system,” which they describe as “a complex control structure related to a particular function or need of the organism” (24). The relevant functions and needs are identified in evolutionary terms. Because their abstract characterization of how the various system modules interact provides few constraints on actual mechanisms, it is tempting to think that this is a problem for unifying the different levels at which behavior can be explained. But this flexibility may be an advantage if one regards behavior systems theory as an example of Elisabeth Lloyd’s idea that a “theory” in biology is best thought of as a set of model “templates” (Lloyd 1994).

Circling or spiraling?

The devil is in the details, of course, and this chapter has barely scratched the surface of those details. We have given short shrift to whole areas of behavioral biology, especially behavioral ecology, sociobiology, behavioral neuroscience, and behavioral genetics. We have focused on animal behavior rather than on the behavior of the one species that we cannot avoid, namely, ourselves. We have failed to provide details of many ongoing controversies, such as whether dolphins really recognize themselves in mirrors, whether starlings can identify recursive syntax violations, whether chimpanzees or dogs know what others can see, and what to make of crows fashioning tools, monkeys rejecting unfair rewards, fish rubbing inflamed lips, and rats laughing when tickled (see Bekoff 2004).

From a cursory inspection of the debates going on in these areas, it can seem as though the same old topics and views in animal behavior get revisited time after time.

Darwin, for example, talked about tool use, and this topic is now back in fashion (e.g., Whiten et al. 2005). Questions about animal language and reasoning continually resurface, as do worries about anthropomorphism. But we don't think this is purely a reinvention of the wheel. Rather, each revisitation occurs as a result of better investigatory techniques and theoretical ideas. The discussions of animal cognitive capacities found, say, in Griffin and Speck (2004) or the edited collection by Bekoff, Allen, and Burghardt (2002) are based on a far richer data set than Romanes could have imagined. The character of the debate is thereby changed. Similarly, as our appreciation grows for the enormously complex interactions among genes and environment during development (Stotz & Griffiths 2004), the old disputes about instinct and learning take on new forms. Indeed, it even becomes questionable whether a clear distinction can be drawn between learning and development. To this, one can add the concept of neural plasticity and wonder how it relates to older categories of learning (Grau & Joynes 2005).

There are philosophical issues to be grappled with at many levels. Under the major headings of philosophy of science, the study of animal behavior can contribute to our thinking about explanation, evidence, theory, unification, function, causation, the status of laws in biology, and the effects of gender and cultural bias. Some of the issues are particularly acute for animal behavior because of the hybrid status of animal-behavior studies on the margins of both biology and psychology. This, as we have seen, also raises particular issues of concern when a biological perspective on animal behavior is generalized to humans. Philosophical progress in understanding these issues depends on having a firm grasp of the scientific and historical details.

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