

## **Cognitive ethology and the empirical analysis of nonhuman social behavior\***

M. Bekoff\*\*

Department of Environmental, Population and Organismic Biology, University of Colorado  
Boulder, Colorado 80309-0334 USA

**ABSTRACT.** *Cognitive ethology and the empirical analysis of nonhuman social behavior*.- As a relatively new interdisciplinary science, cognitive ethology is under attack with respect to its scientific status. However, there also are many supporters of cognitive ethological research. In this paper I consider (1) the sorts of topics in which cognitive ethologists are interested, (2) some connections between cognitive analyses of social behavior and philosophical concepts including intentionality, representation, and folk psychology, (3) different views of cognitive ethology, (4) recent work on social play and antipredator vigilance that seem to benefit from taking a cognitive perspective, and (5) what is gained by taking a cognitive approach to the study of social behavior and what is lost by not doing so. Cognitive ethology has a bright future, and has much to gain from a broad interdisciplinary perspective.

**KEY WORDS:** Cognitive ethology, Animal cognition, Animal minds, Social play, Vigilance

### **Cognitive ethology: a preliminary agenda**

There is a lot of interest in cognitive ethology by people who come to their views from vastly different perspectives. Many examples and/or detailed arguments can be found in Griffin (1976, 1984, 1992), Wyers (1985), Byrne & Whiten (1988), Cheney & Seyfarth (1990, 1992), Burghardt (1991), deWaal (1991), Ristau (1991a), Allen

(1992, 1993a, b), Beer (1992), Caro & Hauser (1992), Whiten & Ham (1992), Allen & Hauser (1991, 1993), Bekoff (1993a, b), Jamieson & Bekoff (1993), Heyes (1993a, b), Wemelsfelder (1993), and Bekoff & Allen (1994). Renewed interest in cognitive ethology has signified a return to many of the ideas of Charles Darwin and early anecdotal cognitivists (Jamieson & Bekoff, 1983), especially their appeals to evolutionary theory, their close association with natural history, and their reliance on anecdote and anthropomorphism to

\*Parts of this paper were presented in the plenary session on comparative cognition at the XXIII International Ethological Conference held in Torremolinos, Spain, September 1993

\*\*Mailing address: 296 Canyonside Drive, Boulder, Colorado 80302 USA  
Telephone: 303-443-6857; Fax: 303-443-2275; e-mail: bekoffm@spot.colorado.edu

inform and motivate more rigorous study. Comparative cognitive ethology is also an important extension of classical ethology because it explicitly licenses hypotheses about the internal states of animals in the tradition of Tinbergen (1951, 1963) and Lorenz (1981).

In the present essay, research on non primates will primarily be considered. Many people inform their views of cognitive ethology by using the same studies over and over again --most are on nonhuman primates-- and they often forget that there are many other nonhuman animals (hereafter animals) who also show interesting patterns of behavior that lend themselves to cognitive analyses (Beck, 1982). Furthermore, people often fail to recognize that in many instances sweeping generalizations about the cognitive skills (or lack thereof) of species of primates (and not of individuals) are based on small data sets from a limited number of individuals representing few taxa (Platt, et al., 1991; Swartz & Evans, 1991; Bekoff, et al., 1993; Heyes, 1993a; Wemelsfelder, 1993).

Although I am enthusiastic about the field of cognitive ethology, I do not believe that all behavior patterns will benefit from a cognitive analysis, but I feel that some surely will benefit. It is narrow-minded both to think that no analyses of behavior will benefit or that all analyses will benefit from a cognitive approach. I also strongly favor empirical research and the careful use of anecdotal data --anecdotes are data-- to inform these endeavors.

### **What are cognitive ethologists interested in?**

Cognitive ethologists (1) are interested in comparing thought processes, consciousness, beliefs, and rationality in animals, (2) are concerned with claims about the evolution of cognitive processes in animals, (3) emphasize broad taxonomic comparisons and do not focus on a few

select representatives of limited taxa, (4) favor observations and experiments (only those that meet the strictest guidelines for animal welfare) in conditions that are as close as possible to the natural environment where selection has occurred, and (5) maintain that field studies of animals that include careful observation and experimentation can inform studies of animal cognition, and that cognitive ethology will not have to be brought into the laboratory to make it respectable. While some are of the opinion that advanced cognition is confined to the laboratory (e.g. Premack, 1988, pp. 171-172), those who have studied animals in the wild disagree (e.g. de Waal, 1991, p. 311; McGrew, 1992, pp. 83ff).

Two notions to which cognitive ethologists pay a lot of attention are the needs of individual organisms in the habitats in which they evolved or in which they currently reside, and also the animals' perceptual worlds, or *umwelts*. A concentration on individuals and not on species should form an important part of the agenda for future research in cognitive ethology. There is a lot of individual variation in behavior within species and sweeping generalizations about what an individual ought to do because she belongs to a given species must be taken with great caution. In contrast to cognitive ethologists, cognitive psychologists typically work on related topics in laboratory settings, and do not emphasize comparative or evolutionary aspects of animal cognition. When cognitive psychologists do make cross-species comparisons, they are usually interested in explaining different behavior patterns in terms of common underlying mechanisms; ethologists, in common with other biologists, are often more concerned with the diversity of solutions that living organisms have found for common problems.

Given their interest in the evolution of cognition, cognitive ethologists also pay attention to mental continuity between humans and other animals. They note that evolutionary biologists talk about the evolution of hearts, lungs, kidneys, and

stomachs, and even brains, and cognitive ethologists recognize that if brains are associated in some way with minds and thinking then there is something to be gained by looking at possible continuity between human and nonhuman animals. Of course, this view does not mean that there is continuity between all taxa, but it does mean that it would be wrong to look at continuity between structure and function in some systems and not in others.

### **Some philosophical underpinnings of cognitive ethology**

Cognitive studies lead us to consider questions such as "What does it mean to claim that Jethro (my companion dog) behaves intentionally? "What does it mean to claim that he has a belief?" "What does it mean to have a representation of something?" For example, in my work on social play I am interested in questions such as "Does Jethro want Henrietta to play with him?" Does Jethro believe that Henrietta wants to play with him?" "Does Jethro believe that Henrietta believes that he wants to play with her?" And, in my work on antipredatory vigilance I am interested in questions that center on if and how birds represent their individuals in their flocks to themselves. These are questions for empirical cognitive studies to answer.

Three major areas in philosophy of mind are important to cognitive ethology, namely, intentionality, representation, and folk psychology (Millikan, 1984, 1993; Brand & Harnish, 1986; Bogdan, 1986; Sterelny, 1990; Godfrey-Smith, 1991; Clark, 1993; Goldman, 1993). One major question in philosophy of mind concerns "how thoughts and other mental states get their intentional or representational character" (Goldman, 1993, p. 76). Intentionality, in the limited philosophical sense, means that mental states have content; they are *about* things, and may be noted as *x* believes *that* *p*. Thus, an individual can be said to

behave intentionally when she has propositional attitudes such as beliefs about something, or desires of something. One of the major problems and challenges in cognitive ethology and the study of cognition in general is getting from behavior to mental content (Allen, 1992, 1993a).

While Lorenz, Tinbergen, and others have used terms such as "intention movements," they are used quite differently than in the philosophical sense. Lorenz and Tinbergen were referring more to preparatory movements that might communicate what individuals were likely to do next, and not necessarily their beliefs and desires, although one might suppose that the individuals did indeed want to fly and believed that if they moved their wings, they would fly. This distinction is important to mark because the use of these terms do not necessarily add a cognitive dimension to classical ethological notions, although they could.

Representation is generally is taken to mean that something stands for something as being in a certain way (for detailed discussions see Sterelny, 1990 and Perner, 1991). Thus, in a cognitive ethological inquiry about antipredatory vigilance, we can ask if a bird represents his flock to himself as being in a certain geometric distribution or as being of a certain size (see below).

Finally, folk psychology can be thought of as a common sense theory of mind embedded in the wisdom of the common folk. Folk psychological explanations appeal to intentionality-beliefs and desires.

While there is some concern about the shortcomings of folk psychological explanations and how these may influence research in cognitive ethology (Beer, 1992), there are more and more of those who feel very comfortable using folk psychological explanations as aids to understanding (Cling, 1991; Saidel, 1992; Christensen & Turner, 1993; Goldman, 1993). Eliminativists, who deny that there are any propositional attitudes, provide the hardest line against folk psychology. These individuals take the stand that neural events and

neural properties are all there is. However, those who have studied not only philosophy of mind but also animal behavior disagree with their position. For example, Bennett (1993, p. 385) notes that "attributions of beliefs and desires are nothing unless they help us to explain behavior. The intentional concepts that we ordinarily use, the ones that are defined by folk psychology, simply are explanatory, and attempts to analyze them come to grief if they don't give a central place to that fact." Kim Sterelny (personal communication) has suggested that perhaps we should concentrate on the mental lives of the animals themselves, and not try to apply human-based folk psychology to nonhumans; rather, for example, we might try to characterize the folk psychology of dogs.

Saidel (1992) also points out that in many instances, a folk psychological explanation does the work it is supposed to do, whereas an appeal to neural events does not. For example, it is unlikely that Eric and Marc are in the same neural state when they are running out of a burning building, but it is highly likely that they will give the same explanation of why they ran out of the burning building--they didn't want to get burned; This argument that it is highly improbable that a given mental property has the same neural form in all organisms is called the argument from multiple realizability (Goldman, 1993).

Of course, there are many other points of connection between cognitive ethology and philosophy of mind. For example, I have not said anything about consciousness or information processing. These will be considered below, but only briefly and indirectly.

### **Some different views on animal minds: slayers, skeptics, and proponents**

"Probably a majority of animal behaviour workers

would now accept that, no matter how difficult they may be to study, it is no longer possible to deny the existence of true thought processes and even consciousness of some type in some mammals and birds." (Manning & Dawkins, 1992, p. 143)

The major problems that cognitive ethology faces are those that center on methods of data collection and analysis, and on the description, interpretation, and explanation of behavior (Bekoff & Jamieson, 1990a, b; Jamieson & Bekoff, 1993). It is of interest to note that while some people feel very comfortable with evolutionary or adaptationist explanations that can be rather tenuous or vague, they also feel comfortable rejecting outright cognitive explanations that are not necessarily any more questionable. In a recent attempt to analyze how cognitive ethology is viewed, we have identified three major groups whose members have different perspectives of cognitive ethology (but also among some of whom there are blurred distinctions), namely, slayers, skeptics, and proponents (for discussion see Bekoff & Allen, 1994). The positions that members of each of these categories usually take can be summarized as follows:

*Slayers:* Slayers deny any possibility of success in cognitive ethology. Sometimes slayers conflate the difficulty of doing rigorous cognitive ethological investigations with the impossibility of doing so. Slayers also often ignore specific details of work by cognitive ethologists and frequently mount philosophically motivated objections to the possibility of learning anything about animal cognition. Slayers do not believe that cognitive ethological approaches can lead, or have lead, to new and testable hypotheses. They often pick out the most difficult and least accessible phenomena to study (e.g. consciousness) and then conclude that because we can gain little detailed knowledge about this subject, we cannot do better in other areas. Slayers also appeal to parsimony in explanations of animal behavior, but they dismiss the possibility that cognitive explanations can be more

parsimonious than noncognitive alternatives, and they deny the utility of cognitive hypotheses for directing empirical research. Slayers are also troubled by folk psychological, anthropomorphic, and cognitive explanations.

*Skeptics:* Skeptics are often difficult to categorize. They are a bit more open-minded than slayers, and there seems to be greater variation among skeptical views of cognitive ethology than among slayers' opinions. However, some skeptics recognize some past and present successes in cognitive ethology, and remain cautiously optimistic about future successes; in these instances they resemble moderate proponents. Many skeptics appeal to the future of neuroscience, and claim that when we know all there is to know about nervous systems, cognitive ethology will be superfluous. Like slayers, skeptics frequently conflate the difficulty of doing rigorous cognitive ethological investigations with the impossibility of doing so. Skeptics also find folk psychological, anthropomorphic, and cognitive explanations to be problematic.

*Proponents:* Proponents recognize the utility of cognitive ethological investigations. They claim that there are already many successes and they see that cognitive ethological approaches have provided new and interesting data that also can inform and motivate further study. Proponents also accept the cautious use of folk psychological and cognitive explanations to build a systematic explanatory framework in conjunction with empirical studies, and do not find anecdotes or anthropomorphism to be thoroughly off-putting. Some proponents are as extreme in their advocacy of cognitive ethology as some slayers are in their opposition. But most proponents are willing to be critical of cognitive ethological research without dooming the field prematurely; if cognitive ethology is to die, it will be of natural causes and not as a result of hasty slayings.

Representative views of people who have been placed in each group are discussed in detail by

Bekoff & Allen (1994). Two examples of the slayer's position that are of interest to cognitive ethologists are Heyes's (1987) and Wasserman's (1993) positions. Heyes, who is a laboratory psychologist, denies that evidence gained by observing animals in natural settings is particularly relevant to understanding animal minds. She advises cognitive ethologists to hang up their field glasses and turn to laboratory research if they want to understand animal cognition. She writes:

"It is perhaps at this moment that the cognitive ethologist decides to hang up his field glasses, become a cognitive psychologist, and have nothing further to do with talk about consciousness or intention." (Heyes, 1987, p. 124)

Heyes (1993c), in a well-argued paper, has extended some of her claims more forcefully. Not only does she believe "that there is still no convincing evidence of mental state attribution in non-human animals," but she also maintains "that most current methods of investigation do not have the potential to provide such evidence" (p. 177). Her latest paper is a challenge that should be accepted with open arms by those who embrace cognitive ethology. In her criticisms, Heyes concentrates heavily on laboratory studies. One possibility that Heyes needs to consider in more detail is that there are events that occur in the wild, that while difficult to study, may help to provide some of the sorts of evidence that she claims is lacking.

Wasserman's (1993) position on cognitive ethology is poorly argued and ill-informed when compared to Heyes's. Wasserman makes no attempt to discuss critically current literature and feels comfortable with the claim that "Griffin's (1978) call for a cognitive ethology *appears to* be a throwback to a prescientific analysis of behavior in terms of conscious experience" (p. 223; my emphasis). Furthermore, Wasserman concludes that "There is simply no clear or necessary role for subjective experience to play in behavior ..." (p. 223) and that the study of mental experience "*might*

not be a fitting topic for scientific inquiry.." (p. 223; my emphasis). While there is equivocation in these claims, Wasserman does not tell us about the sources underlying this uncertainty. Nonetheless, cognitive ethology is dismissed as an unsuitable candidate for a viable field of scientific inquiry. Other slayers, like Williams (1992), argue against the study of animal cognition on the basis of a philosophical view about the privacy of the mental or by the related "other minds" problem. These critics typically do not give specific critiques of actual empirical investigations carried out by cognitive ethologists; rather they try to dismiss such investigations on philosophical grounds alone. Still others, such as Rosenberg (1990), pay careful attention to actual work in behavioral biology, specifically the study of play, but they belittle the idea that it might be possible to attribute human concepts to nonhumans. Rosenberg's argument against a science of intentionality is based on considerations that seem to conflate the difficulty of specifying the content of intentional states with the impossibility of doing so (Allen, 1992; Allen & Bekoff, 1993). Specifically, Rosenberg appeals to his inability to imagine what organisms could do to allow the attribution of certain concepts; the difficulty of thinking of suitable experiments is a challenge, not necessarily a barrier to concept attribution (Allen & Hauser, 1991).

In general, skeptics are a bit more open-minded than slayers. With respect to the sorts of explanations that are offered in studies of animal cognition, many slayers and some skeptics favor noncognitive explanations because they believe them more parsimonious and more accurate than cognitive alternatives, and less off-putting to others who do not hold the field of cognitive ethology in high esteem. For example, Snowdon (1991, p. 814) claims that:

"It is possible to explore the cognitive capacities of nonhuman animals without recourse to mentalistic concepts such as consciousness, intentionality, and deception. Studies that avoid mentalistic terminology

are likely to be more effective in convincing other scientists of the significance of the abilities of nonhuman animals."

Proponents are more optimistic in their views about the contributions that the field of cognitive ethology and its reliance on field work and on comparative ecological and evolutionary studies can make to the study of animal cognition in terms of opening up new areas of research (e.g., Ristau, 1991b, p. 102) and reconsidering old data. A summary of their views is as follows:

"At this point, however, cognitive ethologists can console themselves with the knowledge that their discipline is an aspect of the broader field of cognitive studies and conceptually may not be in any worse shape than highly regarded, related fields such as cognitive psychology. We are a long way from understanding the natural history of the mind, but in our view this amounts to a scientific challenge rather than grounds for depression or dismissal." (Jamieson & Bekoff 1992a, p. 81)

### **Social play and antipredatory vigilance: what might individuals know about themselves and others?**

Social play and antipredatory vigilance are two very different behavior patterns that lend themselves to cognitive studies. Both areas lend themselves to empirical analysis, and both are connected to different notions such as intentionality and representation. Furthermore, in studies of social play and vigilance, folk psychological explanations have been useful for informing and motivating further research, and these sorts of explanations have also turned out to be very good predictors of behavior.

### **The communication of play intention**

Some believe that play may provide more

promising evidence of animal minds than many other behavior patterns, and analyses of play present a great challenge to researchers (Mitchell, 1990; Bekoff & Allen, 1992; Allen & Bekoff, 1993; Wemelsfelder, 1993). It would have been unfortunate if people decided that just because play was difficult to study, it was impossible to study.

When animals play, they typically use action patterns that are also used in other contexts such as predatory behavior, antipredatory behavior, and mating (Bekoff & Byers, 1981; Fagen, 1981). Because play is typically composed of motor patterns that are also used in a variety of other contexts, an individual needs to be able to communicate to potential play partners that he is not trying to dominate them, eat them, or mate with them.

In most species in which play has been described, play-soliciting signals appear to foster some sort of cooperation between players so that each responds to the other in a way consistent with play and different from the responses the same actions would elicit in other contexts. For example, in coyotes, the response to a threat gesture after a play bow had immediately preceded the threat or a play signal had been performed in the beginning of an interaction, is different from the response to threat in the absence of any preceding play signal (Bekoff, 1975). The play bow somehow altered the meaning of a threat signal by establishing (or maintaining) a "play mood." There is much room here for a theory for mental attribution and explanations that appeal to intentionality (Bekoff, 1993a; Jamieson & Bekoff, 1993).

Let's consider in more detail the question of whether or not signals that appear to be used to communicate play-intention could foster the cooperation among participants that is necessary for play to occur. It generally is assumed that such play-soliciting signals transmit messages such as "what follows is play," "this is still play," or "let's play again." In canids, play bows also occur throughout play sequences, but usually at the

beginning or towards the middle of playful encounters. Thus, the latter two messages--"this is still play," or "let's play again"--may be sent after a very short break or after rough play has occurred. Supporting evidence concerning the importance of play signals for allowing cooperative social play to occur comes from studies in which it is shown that play-soliciting signals show little variability in form or temporal characteristics, and that they are used almost solely in the context of play (Bekoff, 1977). These features of bows can be related to the fact that when engaging in social play, canids typically use action patterns that are also used in other contexts such as predatory behavior, agonistic encounters, or mating, where misinterpretation of play intention could be injurious.

Analyses of play sequences may also inform future studies of social play. For example, in intraspecific comparisons, it has been found that sequences of social play are usually more variable than sequences of nonplay behavior (Bekoff & Byers, 1981). Is it possible that animals read differences in behavioral sequences that are performed during play and in other contexts? Might increased (or consistent variations in) variability in sequences also (along with play signals) that convey the message "this is play" and enable individuals to predict what is likely to occur or to understand what has already occurred. We can also ask if there are differences in the variability and structure of play sequences that are preceded by a play signal when compared to play bouts that are not?

There might also be important species differences, especially when comparing wild canids. For example, the play sequences of infant coyotes were considerably more variable than those of infant wolves, and one wonders if this is because infant coyotes are more aggressive towards one another than are infant wolves. What is also very interesting is that the coefficients of variation for duration and form for play bows performed at the beginning of play sequences are also lower for infant coyotes when compared to infant wolves, young dogs, and

adult dogs, and the coefficient of variation for the form of the play bow is also lower for bows performed during a play bout for infant coyotes when compared to other canids for which there are similar data. The difference between infant coyotes and the next closest group (infant wolves) is also larger than the difference between the other groups. Recall also that the play sequences of infant coyotes were much more variable than the play sequences for the infant wolves.

Here then, at least, is some compelling evidence that play bows might actually influence on-going play, so that it remains play. Young coyotes, being more aggressive than other young canids, use play bows to keep a cap on aggressive tendencies so that they can engage in social play. Colin Allen (personal communication) has suggested that as animals become fatigued, they may have lower thresholds for certain sorts of play spilling over into serious aggressive encounters.

### **Future research**

A cognitive perspective will be very useful in future analyses of social play. Comparative observations strongly suggest that individuals expect that play will ensue if they perform a bow; they act as if they want play to occur. On many occasions it looks as if animals are frustrated or surprised when their bow is not reciprocated in a way that is consistent with their belief about what is most likely to occur, namely, social play. Frustration also may be inferred from the common observation that canids and other mammals are very persistent in their attempts to get others to play with them and they often engage in some sort of self-play such as tail-chasing, after a bow or other play invitation signal is ignored, or they rapidly run over to another individual and try to get them to play.

Surprise is more difficult to deal with, but often

dogs or coyotes looked surprised when, on a very rare occasion, a bow resulted in the recipient attacking the signaler. The soliciting animal's eyes opened widely, her tail dropped, and she rapidly turned away from the noncooperating animal to whom she directed a play-soliciting signal, as if what happened was totally unexpected and perhaps confusing. After moving away the surprised animal often looked at the other individual, cocked her head to one side, squinted, and furrowed her brow, and seemed to be saying "I want to play, this is not what I wanted to happen."

With respect to the solicitor's beliefs about the future, detailed analyses of movie film also show that on some occasions, a soliciting animal begins to perform another behavior before the recipient commits himself. The solicitor behaves as if she expects that something specific will happen and commits herself to this course of action. A major question, then, is how to operationalize these questions; what would be convincing data? How do we know when we have an instance of a given behavior(s)? Thus, we need to ask what is frustrated, what is the goal, and what is the belief about? In attempts to answer these and other questions, there simply is no substitute for detailed descriptions of subtle behavior patterns (Bekoff, 1992; Golani, 1992).

### **Antipredatory vigilance: the importance of failure**

In studies of vigilance it generally is assumed, for simplicity's sake, that individuals compromise their ability to detect predators when feeding with their heads down, and compromise their food intake when scanning for predators with their heads up. Thus, it has been argued that there are good reasons for individuals to live, or at least to forage for food, in groups, if doing so increases the probability of detecting a predator or reduces the time spent

scanning for predators, thus permitting more time to be spent doing other things.

A very popular question in the comparative study of vigilance is "How does the behavior of individuals vary in groups of different sizes?" Another, and perhaps more important question to which very little attention has been directed, is "Why does the relationship between group size and scanning rates where it is not expected to fail?" These data should not be viewed as negative data or noise. Rather, they should be used to inform and motivate new research as well as reanalyses of old data. Generally, it has been found that there is a negative relationship between group size and rates of scanning by individuals and a positive relationship between group size and the probability of predator detection. This is because there are more eyes and perhaps other sense organs (e.g., Sullivan, 1984) that can be used to scan for or to detect predators. Elgar (1989) notes that although the negative relationship between group size and individual scanning rate is quite robust and is approaching the status of dogma (Lima, 1990), few studies have actually controlled for confounding variables, such as variation in the density and type of food resources, group composition, ambient temperature and time of day, proximity to a safe place and to the observer, visibility within the habitat, and group composition (see also Lima, 1990 and Lima & Dill, 1991). With respect to whether or not an individual is really being vigilant, Lazarus (1990, p. 65) notes that "... researchers have simply assumed that the behaviour in question is vigilance, and have then sought its function" (see also Valone, 1989, 1993). Lima (1990) also claims that there seem to be no studies that have directly examined the question of whether foragers pay any attention to the behavior of other group members. He also concludes that very little is known about the perceptions of the animals being studied and that many models of vigilance reflect mainly the perceptions of the modelers themselves (p. 262).

A cognitive analysis of vigilance in which we

are concerned with what an individual might know about himself and others would involve asking at least the following questions, all of which are interconnected and all of which lend themselves to empirical study. While some of the following questions are not directly related to cognitive inquiry, all can inform and motivate such an approach. Some are also very basic, but this return to basics is necessary.

(1) What is a group? What does it mean to say that an individual is a member of a group and is our conception of group the same as that of the animals? In studies of vigilance, variations in group size are often used to explain variations in other patterns of behavior, and precise measurements of group size are essential. Questions that inform the conception of group membership include "Is there a critical distance between individuals below which we can say with some degree of certainty that they are members of the same group?" and "Do individuals have to spend a certain amount of time together within a certain distance to justify calling them a group? With respect to studies of vigilance, Elgar, Burren, & Posen (1984) found that a house sparrow who was in visual contact with other house sparrows but separated by 1.2 meters scanned as if she was alone.

(2) Does the size of a group or the geometric distribution or orientation of individuals influence individual vigilance?

It is important to keep in mind that there are confounding variables such as the geometric relationships among group members and how individuals are oriented in space--in a circle, a triangle, or in a straight line, for example--that might influence scanning rates of individuals. Little attention has been paid to group geometry. Some authors write about visual obstructions but do not consider the actual geometry of the group. For example, Elgar (1989) does not directly refer to geometry as a variable influencing scanning for predators, but he does write about visual obstructions, in terms of how they might influence

vigilance and risk of predation. Likewise, in his review of vigilance in mammals, Quenette (1991) writes about visual obstructions and their effect on vigilance because they influence how information is received from the environment. Elgar et al. (1984, p. 221) report data that strongly suggest that in house sparrows, "it is necessary for them to be able to continuously see their flockmates." Further, they review literature that shows that in general, scanning rates in small passerines do not decrease significantly with flocks larger than eight or nine birds. They write: "It is possible that sparrows simply cannot estimate the number of birds in larger flocks... " Of course, it also is possible that birds and other animals cannot estimate the number of birds in flocks that are organized in a way such that visual inspection is difficult or impossible. There is a lot of work still to be done.

One important point about which I could find very little information involves how the geometry of the flock of potential prey influences predator detection. There may well be trade-offs such that although it is easier to see what other flock members are doing when the birds are arranged in a specific geometric array, it also is easier for potential predators to see them.

Answers to the question "How does the geometric distribution of individuals influence individual vigilance?" will likely have something to say about animal cognitive abilities. Thus, while it is known that the location of an individual in her group (center or periphery) can influence her pattern of vigilance, it remains to be studied how the geometry of the whole group influences the ease with which an individual is able to assess what others are doing by seeing or hearing them. For example, it seems that it would be easier to see what others are doing if individuals were organized in a circle rather than in a straight line, but this is not known. My working hypotheses are that in flocks of birds (including mixed flocks containing house finches, steller's jays, juncos, cowbirds, evening and black-headed grosbeaks; composition

varies seasonally), as it becomes more difficult (at least on my view) for a bird to see other members of a flock, (1) the birds move their bodies more to orient themselves to other birds, (2) they change their relative positions more frequently, (3) their head movements are more random, and (4) they spend a greater percentage of time being vigilant.

Questions such as "How does a bird or other nonhuman assess group geometry?" also need to be considered; it is not known if and how individuals actually assess the geometry of the group in which they are a member.

(3) Do changes in group size or geometry influence patterns of social interactions? It is possible that as group size and geometry change, either singly or together, there is also a change in how individuals interact. If this is the case, then it might be possible for an individual to gain information about these variations from changes in encounter patterns without having to read them directly, as has been suggested for ants (Gordon, Paul, & Thorpe, 1993). To the best of my knowledge, there are no data for birds or mammals that can be used to answer these questions with any degree of certainty.

### **Future research**

Some other interesting questions that may be informed by a cognitive approach include: "Do individuals change their relative position in a group to make it more likely that they could feed more efficiently and/or detect potential predators more easily?"

"Is this a cooperative endeavor; do individuals move synchronously?" Also, "Does one's position in a group influence whether he can assess changes in group size or geometry?" Here I am asking if and how the location of an individual in a group makes it easier or more difficult to know how many other individuals are there and how they are

distributed in space. It might be very useful for an individual to be able to see what others are doing, for while scanning, an individual might also pick up and store information about what individuals in a particular part of the group are most likely to be doing, or she might generalize from her own previous experience in that part of the group to what others are most likely to be doing when they are in that position. If we can get answers to these sorts of questions, we might be able to assess if it is possible that the inverse relationship between group size and individual scanning rate levels off or fails because of the inability of individuals to monitor the behavior of "too many other animals" who might also be difficult to see. If there are "too many animals," it is possible that large groups may break up into smaller subgroups (Valone, 1993). Furthermore, it is possible that birds may also be using auditory (or other) cues to obtain information about other flock members (Sullivan, 1984).

### **The advantages of an evolutionary, comparative, and ecological cognitive ethology?**

Two important questions need to be given serious attention. These are "What is gained by appealing to the possibility of cognitive explanations?" and "What is lost by dismissing the possibility of cognitive explanations?" Answering the second question first, it seems clear that we would lose a lot of information about the possible richness of animals' lives if we ignored the possibilities that they behaved intentionally on some occasions. Even if we discover that some animals do not appear all that cognitive, this does not mean that they are not cognitive at all. Perhaps, because of their relatively impoverished cognitive abilities, the few skills that they have are more important to them than many of the cognitive skills

that we possess, many of which are not used very often at all.

Now, what are some reasons for advocating cognitive analyses and explanations of animal behavior? Why might cognitive explanations be the best explanations to which we can appeal to help us come to terms with the study of animal minds. There are many reasons why people are interested in the study of animal cognition. That the explanatory power of our theorizing is increased applies without question. Further, it is obvious that a cognitive approach will allow for the generating and testing of new ideas, and perhaps, the reviewing and reanalyzing of old data.

While each of the following reasons does not necessarily warrant a cognitive approach, taken together they justify the current interest in cognitive ethology. Further, these are not the only reasons that one might offer, just some suggestions that take into account a number of factors. These include the following (in no order of importance).

(1) Many models in ethology and behavioral ecology presuppose cognition. Thus, it would be especially useful to have informed ideas about the types of knowledge that nonhumans have about their social and nonsocial environments and how they use this information (Allen & Hauser, 1991).

(2) It may be more economical or parsimonious to assume that not everything that an individual needs to be able to do in all situations in which he finds himself is preprogrammed. While general rules of thumb may be laid down genetically during evolution, specific rules of conduct that account for all possible contingencies are too numerous to be hard-wired (Griffin, 1984). Behavioristic learning schemes can account for some flexibility in organisms, but learning at high degrees of abstraction from sensory stimulation seems less amenable to behavioristic analysis (Allen & Hauser, 1991). Cognitive models of learning provide explanatory schemes for such cases. We can also add that it might actually be more parsimonious to appeal to cognitive explanations in terms of

accounting for complex patterns of behavior with fewer explanations.

(3) The assumption of animal minds leads to more rigorous empirical analyses of behavioral plasticity and flexibility in the many and diverse situations--both social and nonsocial--that many nonhumans regularly encounter. Further, Yoerg (1991) argues that considerations of cognitive function can lead to original ideas about behavioral adaptation.

(4) By providing different perspectives on behavior, cognitive ethology can raise new questions that may be approached from other levels of analysis. For example, appeals to detailed descriptive information about subtle behavior patterns (Bekoff, 1992; Golani, 1992) and to neuroethological data (e.g. Dennett, 1991; Dusenbery, 1992; Griffin, 1992; Bullock, 1993; Hauser, 1993; Lahav, 1993; Stein & Meredith, 1993; Wemelsfelder, 1993) may be important for informing further studies in animal cognition, and might also be useful for explaining data that are already available. Such analyses will not make cognitive ethological investigations superfluous (as some eliminativists think), because behavioral evidence is primary over anatomical or physiological data in assessments of cognitive abilities (Allen, 1990).

(5) Welfare issues are tightly connected to views on the cognitive abilities of nonhumans (Bekoff & Jamieson, 1991; Jamieson & Bekoff, 1992b; Bekoff, 1994) and humans (Dresser, 1993).

To these we can also add that we will be able to test Charles Darwin's and others' ideas about mental continuity.

Interdisciplinary efforts are essential in our quest for knowledge about animal minds. In these joint efforts, keeping an open mind would also be useful at this stage of the game. Philosophers need to be clear when they tell us about what they think about animal minds and those who carefully study the behavior of nonhumans need to tell philosophers what we know, what we are able to do, and how we

go about doing our research. If it is because philosophers do not have the experience with empirical work that allows them to make realistic suggestions for experimental design, then it would be useful for philosophers to watch ethologists at work (Dennett, 1987, 1988). This experience might allow philosophers to gain a better understanding of what cognitive ethology is all about. Even then, it may be the case that ethologists are ill-advised to look to philosophers for a crisp and empirically rigorous definition of intentionality (for example), even if some philosophers promise to provide one (Colin Allen, personal communication). Philosophical theories are only starting points for empirical investigation, so no one should be too wedded to any particular theory. Nonetheless, starting points are necessary, so the philosophical theories are useful (Allen, 1993b).

Obviously, taking a strong cognitive stance will not be a deterrent to learning more about animal behavior and animal minds. Detailed observational and experimental research in cognitive ethology is possible and should be encouraged; field work should be pursued wherever possible. Cognitive ethologists should not hang up their field glasses and have nothing to do with talk about nonhuman intentional behavior. Rather, cognitive ethologists should welcome the fact that they are dealing with difficult and important questions. Subjectivity, indeterminacy, and intractability present stumbling blocks, but not impenetrable barriers. As Lawrence Shapiro (personal communication) points out, the "privacy" of mental states does not necessarily present more or less of a problem for cognitive ethology than the invisibility of electrons does for chemistry. Claims about minds and electrons are posited abductively because they make the most sense of the data that have been collected. To allow such posits in chemistry but not in cognitive ethology is to adopt a double standard, which is unfair to cognitive ethology. Shapiro recommends that cognitive ethologists no longer worry about subjectivity, because this characterization serves to

stigmatize their subject matter, distinguishing it in a way that leads to an undeserved skepticism.

In conclusion, while many of the problems facing cognitive ethologists are difficult and do not submit to easy answers, they are not necessarily impossible problems with which to deal. The challenges put forth by slayers and skeptics should be accepted by proponents of cognitive ethology. In the future, cognitive ethologists most likely will be pursuing the challenging questions that confront them, rather than looking for other work.

### Resumen

*Etología cognitiva y el análisis empírico del comportamiento social no humano.*

La etología cognitiva, como ciencia interdisciplinaria relativamente nueva, está siendo atacada con respecto a su estatus científico. Sin embargo, existen también muchos apoyos a la investigación cognitiva etológica. En este trabajo se consideran (1) los tipos de problemas en los que están interesados los etólogos cognitivos, (2) algunas conexiones entre análisis cognitivo del comportamiento social y conceptos filosóficos incluyendo intencionalidad, representación y psicología popular, (3) visiones diferentes de la etología cognitiva, (4) trabajos recientes sobre juego social y vigilancia antidepredadora que parece se benefician de la perspectiva cognitiva, y (5) qué se gana considerando una aproximación cognitiva al estudio del comportamiento social y qué se pierde no haciéndolo. La etología cognitiva tiene un brillante futuro y mucho que ganar desde una amplia perspectiva interdisciplinaria.

### Acknowledgements

I thank Dale Jamieson, Larry Shapiro, Eric Saidel, David Rosenthal, Kim Sterelny, Ruth

Millikan, Susan Townsend, John Lazarus, Cecelia Heyes, Daniel Dennett, Gordon Burghardt, Charles Snowdon, and especially Thomas Valone and Colin Allen for discussing many of these issues with me. Thomas Valone and Colin Allen provided useful comments on an ancestral version of this essay.

### References

- Allen, C., 1990. *Animal consciousness*. Paper presented at the Central Division of the American Philosophical Association.
- Allen, C., 1992. Mental content and evolutionary explanation. *Bio. Phil.*, 7:1-12.
- Allen, C., 1993a. Mental content. *Brit. J. Phil. Sci.*, 43:537-553.
- Allen, C., 1993b. Intentionality: Natural and artificial. In: *Comparative Approaches to Cognitive Science*. (J.-A. Meyer & H. Roitblat, Eds.), Cambridge: MIT Press.
- Allen, C. & Bekoff, M. 1993. Intentionality, social play, and definition. *Bio. Phil.*, In press.
- Allen, C. & Hauser, M.D., 1991. Concept attribution in nonhuman animals: Theoretical and methodological problems in ascribing complex mental processes. *Phil. Sci.*, 58:221-240.
- Allen, C. & Hauser, M.D., 1993. Communication and cognition: Is information the connection? *Philosophy of Science Association*, 2: In press.
- Beck, B.B., 1982. Chimpocentrism: Bias in cognitive ethology. *J. Human Evol.*, 11:3-17.
- Beer, C., 1992. Conceptual issues in cognitive ethology. *Adv. Study Behav.*, 21: 69-109
- Bekoff, M., 1975. The communication of play intention: Are play signals functional? *Semiotica*, 15:231-239.
- Bekoff, M., 1977. Social communication in canids: Evidence for the evolution of a stereotyped mammalian display. *Science*, 197:1097-1099.
- Bekoff, M., 1992. Description and explanation: A

- plea for plurality. *Behav. Brain Sci.*, 15:269-270.
- Bekoff, M., 1993a. Cognitive ethology and the explanation of nonhuman animal behavior. In: *Comparative Approaches to Cognitive Science*. (J.-A. Meyer & H. Roitblat, Eds.), Cambridge: MIT Press.
- Bekoff, M., 1993b. Review of Griffin 1992. *Ethology*, In press.
- Bekoff, M. 1994. Cognitive ethology and the treatment of nonhuman animals: How matters of mind inform matters of welfare. Submitted.
- Bekoff, M. & Allen, C., 1992. Intentional icons: towards an evolutionary cognitive ethology. *Ethology*, 91:1-16.
- Bekoff, M. & Allen, C., 1994 Cognitive ethology: Slayers, skeptics, and proponents. In: *Anthropomorphism, Anecdote, and Animals: The Emperor's New Clothes?* (R.W. Mitchell, N. Thompson & L. Miles, Eds.). University of Nebraska Press: Lincoln
- Bekoff, M. & Byers, J.A., 1981. A critical reanalysis of the ontogeny of mammalian social and locomotor play: An ethological hornet's nest. In: *Behavioral Development: The Bielefeld Interdisciplinary Project: 296-337* (K. Immelmann, G.W. Barlow, L. Petrinovich & M. Main, Eds.). New York: Cambridge University Press.
- Bekoff, M. & Jamieson, D., 1990a. (Eds.) *Interpretation and explanation in the study of animal behavior: Vol. 1, Interpretation, intentionality, and communication*. Boulder, Colorado: Westview Press.
- Bekoff, M. & Jamieson, D., 1990b. (Eds.) *Interpretation and explanation in the study of animal behavior: Vol. 2, Explanation, evolution, and adaptation*. Boulder, Colorado: Westview Press.
- Bekoff, M. & Jamieson, D., 1991. Reflective ethology, applied philosophy, and the moral status of animals. *Persp. Ethol.*, 9:1-47.
- Bekoff, M., Townsend, S.E. & Jamieson, D., 1993. Beyond monkey minds: Towards a richer cognitive ethology. *Behav. Brain Sci.*, In press.
- Bennett, J., 1993. Comments on Dennett from a cautious ally. *Behav. Brain Sci.*, 16:381- 385.
- Bogdan, R.J. (Ed.), 1986. *Belief: Form, content and function*. New York: Oxford University Press.
- Brand, M. & R.M. Harnish (Eds.), 1986. *The representation of knowledge and belief*. Tucson: University of Arizona Press.
- Bullock, T.H., 1993. How are more complex brains different? *Brain Behav. Evol.*, 41:88-96.
- Burghardt, G.M., 1991. Cognitive ethology and critical anthropomorphism: a snake with two heads and hognose snakes that play dead. In: *Cognitive ethology: The minds of other animals. Essays in honor of Donald R. Griffin: 53-90* (C.A. Ristau, Ed.). Hillsdale, New Jersey: Lawrence Erlbaum.
- Byrne, R. & Whiten, A. (Eds.), 1988. *Machiavellian intelligence: Social expertise and the evolution of intellect in monkeys, apes, and humans*. New York: Oxford University Press.
- Caro, T.M. & Hauser, M.D., 1992. Is there teaching in nonhuman animals? *Q. Rev. Biol.*, 67:151-174.
- Cheney, D.L. & Seyfarth, R.M., 1990. *How monkeys see the world: Inside the mind of another species*. Chicago: University of Chicago Press.
- Cheney, D.L. & Seyfarth, R.M., 1992. Précis of How monkeys see the world: Inside the mind of another species. *Behav. Brain Sci.*, 15:135-182.
- Christensen, S.M. & Turner, D.R. (Eds.), 1993. *Folk psychology and the philosophy of mind*. Hillsdale, New Jersey: Lawrence Erlbaum.
- Clark, A., 1993. Mice, shrews, and misrepresentation. *J. Phil.*, 90:290-310.
- Cling, A.D., 1991. The empirical virtues of beliefs. *Phil. Psychol.*, 4:303-323.
- Dennett, D.C., 1983. Intentional systems in cognitive ethology: The "Panglossian paradigm" defended. *Behav. Brain Sci.*, 6:343-390.
- Dennett, D.C., 1987. Reflections: Interpreting monkeys, theorists, and genes. In: *The*

- intentional stance*: pp. 269-286. Cambridge: MIT Press.
- Dennett, D. C., 1988. Out of the armchair and into the field. *Poetics Today*, 9:205-221.
- Dennett, D.C., 1991. *Consciousness explained*. Boston: Little, Brown.
- Dresser, R., 1993. Culpability and other minds. *Southern California Law J.*, 2:41-88.
- Dusenbery, D.B., 1992. *Sensory ecology: How organisms acquire and respond to information*. San Francisco: W. H. Freeman.
- Elgar, M.A., 1989. Predator vigilance and group size in mammals and birds: A critical review of the empirical evidence. *Biol. Reviews*, 64:13-33.
- Elgar, M.A., Burren, P.J. & Posen, M., 1984. Vigilance and perception of flock size in foraging house sparrows *Passer domesticus* L. *Behaviour*, 90:215-223.
- Fagen, R., 1981. *Animal Play Behavior*. New York: Oxford University Press.
- Godfrey-Smith, P., 1991. Signal, decision, action. *J. Phil.*, 88:709-722.
- Golani, I., 1992. A mobility gradient in the organization of vertebrate movement: The perception of movement through symbolic language. *Behav. Brain Sci.*, 15:249-308.
- Goldman, A., 1993. *Philosophical Applications of Cognitive Science*. Boulder, Colorado: Westview Press.
- Gordon, D.M.; Paul, R.E. & Thorpe, K., 19 What is the function of encounter patterns in ant colonies? *Anim. Behav.*, 45:1083-1100.
- Griffin, D.R., 1976. *The question of animal awareness: Evolutionary continuity of mental experience*. New York: The Rockefeller University Press.
- Griffin, D.R., 1984. *Animal thinking*. Cambridge: Harvard University Press.
- Griffin, D.R., 1992. *Animal minds*. Chicago: University of Chicago Press.
- Hauser, M.D., 1993. Right hemisphere dominance for the production of facial expression in monkeys. *Science*, 261:475-477.
- Heyes, C.M., 1987. Cognisance of consciousness in the study of animal knowledge. In: *Evolutionary Epistemology*:105-135 (Callebaut W & Pinxten R, Eds). D. Reidel: Boston.
- Heyes, C.M., 1993a. Reflections on self-recognition in primates. *Anim. Behav.*, In press.
- Heyes, C.M., 1993b. Imitation, culture, and cognition. *Anim. Behav.*, In press.
- Heyes, C.M., 1993c. Anecdotes, training, trapping and triangulating. Do animals attribute mental states? *Anim. Behav.*, 46:177-188.
- Jamieson, D. & Bekoff, M., 1992a. Some problems and prospects for cognitive ethology. *Between The Species*, 8:80-82.
- Jamieson, D. & Bekoff, M., 1992b. Carruthers on nonconscious experience. , 52:23-28.
- Jamieson, D. & Bekoff, M., 1993. On aims and methods of cognitive ethology. *Philosophy of Science Association*, 2: In press.
- Lahav, R., 1993. What neuropsychology tells us about consciousness. *Phil. Sci.*, 60:67-85.
- Lazarus, J., 1990. Looking for trouble. *New Scientist*, 125:62-65.
- Lima, S.L., 1990. The influence of models on the interpretation of vigilance. In: *Interpretation and Explanation in the Study of Animal Behavior: Vol. II, Explanation, Evolution, and Adaptation*: 246-267 (M. Bekoff & D. Jamieson, Eds.). Boulder, Colorado: Westview Press.
- Lima, S.L. & Dill, L.M., 1990. Behavioral decisions made under the risk of predation: A review and prospectus., 68:619-640.
- Lorenz, K.Z., 1981. New York: Springer-Verlag.
- Manning, A. & Dawkins, M.S., 1992. *Animal behaviour*. New York: Cambridge University Press.
- McGrew, W.C., 1992. *Chimpanzee material culture: Implications for human Evolution*. New York: Cambridge University Press.
- Metcalfe, N.B., 1984a. The effects of habitat on the vigilance of shorebirds: Is visibility important? *Anim. Behav.*, 32:981-985.
- Metcalfe, N.B., 1984b. The effects of mixed-species

- flocking on the vigilance of shorebirds: Who do they trust? *Anim. Behav.*, 32:986-993.
- Millikan, R.G., 1984. *Language, thought, and other biological categories*. Cambridge: MIT Press.
- Millikan, R.G., 1993. *White queen psychology and other essays for Alice*. Cambridge: MIT Press.
- Mitchell, R.W., 1990: A theory of play. In: *Interpretation and Explanation in the Study of Animal Behavior: Vol. I, Interpretation, Intentionality, and Communication*: 197-227 (M. Bekoff & D. Jamieson, Eds.). Boulder, Colorado: Westview Press.
- Perner, J., 1991. *Understanding the representational mind*. Cambridge: MIT Press.
- Platt, M.M., Thompson, R.L. & Boatright, S.L., 1991. Monkeys and mirrors: Questions of methodology. In: *The monkeys of Arashiyama* (L.M. Fedigan & P.J. Asquith, Eds.). Albany, New York: SUNY Press.
- Premack, D., 1988. "Does the chimpanzee have a theory of mind?" revisited. In: *Machiavellian Intelligence: Social Expertise and the Evolution of Intellect in Monkeys, Apes, and Humans*: 160-179 (R. Byrne & A. Whiten, Eds.). New York: Oxford University Press.
- Quenette, P.-Y., 1990. Functions of vigilance behaviour in mammals: A review. *Acta Oecologica*, 11:801-818.
- Ristau, C. (Ed.), 1991a. *Cognitive ethology: The minds of other animals. essays in honor of Donald R. Griffin*. Hillsdale, New Jersey: Lawrence Erlbaum.
- Ristau, C., 1991b. Aspects of the cognitive ethology of an injury-feigning bird, the piping plovers. In: *Cognitive ethology: The minds of other animals. Essays in honor of Donald R. Griffin*: 91-126 (C.A. Ristau, Ed.). Hillsdale, New Jersey: Lawrence Erlbaum.
- Rosenberg, A., 1990. Is there an evolutionary biology of play? In: *Interpretation and explanation in the study of animal behavior: Vol. 1, Interpretation, intentionality, and communication*: 180-196 (M. Bekoff & D. Jamieson, Eds.). Boulder, Colorado: Westview Press.
- Saidel, E., 1992. What price neurophilosophy? *Philosophy of Science Association*, 1:461-468.
- Snowdon, C.T., 1991. Review of Ristau 1991. *Science*, 251:813-814.
- Stein, B.E. & Alexander, M.A., 1993. *The merging of the senses*. Cambridge: MIT Press.
- Sterelny, K., 1990. *The representational theory of mind: An introduction*. Cambridge: Basil Blackwell.
- Sullivan, K.A., 1984. Information exploitation by downy woodpeckers in mixed-species flocks. *Behaviour*, 91:294-311.
- Swartz, K.B. & Evans, S., 1991. Not all chimpanzees (*Pan troglodytes*) show self-recognition. *Primates*, 32:483-496.
- Tinbergen, N., 1951. *The study of instinct*. Oxford: Oxford Univ. Press.
- Tinbergen, N., 1963. On aims and methods of ethology. *Z. Tierpsychol.*, 20:410-429.
- Valone, T.J., 1989. Group foraging, public information, and patch estimation. *Oikos*, 56:357-363.
- Valone, T.J., 1993. Patch information and estimation: A cost of group living. *Oikos*, In press.
- Waal, de F.B., 1991. Complementary methods and convergent evidence in the study of primate social cognition. *Behaviour*, 118:297-320.
- Wasserman, E.A., (1993). Comparative cognition: Beginning the second century of the study of animal intelligence. *Psychol. Bull.*, 113:211-228.
- Wemelsfelder, F., 1993. Animal boredom: Towards an empirical approach of animal subjectivity. Doctoral Thesis, Rijksuniversiteit te Leiden.
- Whiten, A. & Ham, R., 1992. On the nature and evolution of imitation in the animal kingdom: Reappraisal of a century of research. *Adv. Study Behav.*, 21:239-283
- Williams, G.C., 1992. *Natural Selection: Domains, levels, and challenges*. New York: Oxford

University Press.

Wyers, E.J., 1985. Cognitive-behavior in sticklebacks. *Behaviour*, 95:1-10.

Yoerg, S. I. 1991. Ecological frames of mind: the role of cognition in behavioral ecology. *Q. Rev. Biol.*, 66:287-301.

(Recibido: agosto 1993)