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The cognitive ethology of an "injury-feigning" plover: a beginning

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ABSTRACT. *The cognitive ethology of an "injury-feigning" plover: a beginning.*- Interest in the cognitive capacities of animals has led me to study antipredator behavior of birds, specifically plovers, through observations and experiments in natural environments. I asked: 1) Do injury-feigning parent plovers want to lead an intruder/ predator away from the nest? What data could provide pertinent evidence? 2) Are plovers responsive to an intruder's attention to their nest? 3) Can plovers learn to discriminate between a potentially "dangerous" intruder and a "safe" one? Results support positive answers to these questions. To progress in the difficult endeavor of experimentally investigating purposeful and other cognitive behavior of animals, we need the efforts of many related disciplines including philosophy, biology and psychology.

KEY WORDS. Purposeful behavior, Intentionality, Injury-feigning, Antipredator behavior, Plovers, Cognitive ethology

Introduction and some philosophical problems

Donald Griffin (1976, 1992) has been particularly influential in rekindling interest in the possibility that animals may have mental experiences, including awareness, purposes, and consciousness and that such experiences are amenable to scientific investigation. "Cognitive ethology" (Griffin, 1976) is a beginning exploration of the mental experiences of animals, particularly as they behave in their natural environment in the course of theirnormal lives. Many, but not all, studies in cognitive ethology have, to date, emphasized the importance of observations of naturally occurring behavior and of experimentally based field studies.

Cognitive ethology differs from most previous studies of animal cognition, interpreted broadly to include animal learning and discrimination studies, in its emphasis on possible animal mental states and interest in matters such as deception and communication.

The major philosophical problem in cognitive ethology is, as Bennett (seminar, 1985) has phrased it, drawing conclusions about the minds of animals from premises about behavior in the circumstances in which the animals are behaving. We, and any study of mental processes, need a conceptual theory that relates mentalistic terms to patterns of behavior. And then there is the problem of awareness. It is a hotly disputed matter whether animals, to whom one might apply concepts of intentions, of belief and desire are aware of those beliefs, or say some, whether they even experience beliefs or desires, as opposed to the terms being a useful, functionalist stance for an experimenter to assume.

Though solid theories do not exist, useful approaches do. One is the intentional stance, proferred by philosophers such as Bennett (1976, Dennett (1978, 1983, 1987), and Searle (1980) and discussed by Beer (1983, 1991, 1992). "Intentional" is a philosophical term meaning "aboutness," reference. It does not mean "on purpose," though "wants it to be the case that" is an intentional phrase. Some other intentional terms are "thinks that," "believes that," "wants it to be the case that." Conventional scientific explanation is phrased at the zero order of intentional analysis without recourse to any mental state. Among possible first order intentional analyses is a description in terms of purpose, e.g. "An organism wants it to be the case that x", where x could be a response such as "organism B to follow." A second order analysis might be phrased, "Organism A wants Organism B to believe that z"; ie organism A is concerned about the mental state of B, as opposed merely to B's behavior. Given the difficulties in finding persuasive evidence for second order intentional statements, my research focusses on first order intentional analysis, specifically on an organism's purposes. I do not, however, mean to imply that a non-human animal's purposive behavior is like the very flexible, fully cognitive, full conscious, purposeful beahavior we humans sometimes have. Indeed, the philosopher Bennett (1976) and others have noted the importance of a transition among various species from rudimentary "registrations" and "goals" to full-fledged "beliefs" and "desires" characteristics of at least some human activity.

What might be, if not criteria, then descriptive properties of purposeful behavior? The psychologist Tolman (1932) has stressed persistence to the goal, especially that requiring variations in behavior, should the path to the goal be obstructed. Griffin (1985, p.37) also suggests that one criterion of conscious awareness in animals is "versatile adaptability of behavior to changing circumstances and challenges." This facet of behavior is also stressed by Boden (1983) from the vantage point of Artificial Intelligence.

I will draw upon these ideas in proposing an interpretation of distraction behavior exhibited by various species of ground nesting birds when intruders approach the eggs or young as purposive (Ristau, 1983a). I particularly chose to study birds, because we are less likely to empathize with their mental states than we do with our pets or fellow primates. This objectivity may help us to carefully specify the evidence for such an interpretation and to suggest possible levels in the transition from rudimentary to more full fledged knowledge and purposes (or beliefs and desires as termed by many philosophers). I have chosen to study a behavior which, like many behaviors, human and otherwise, is a mixture of some fixed, genetically transmitted elements and more flexible behaviors.

The "injury-feigning" plover

A. The plovers' behaviors toward intruders

I shall concentrate on the Piping Plover, *Charadrius melodus* and shall include data from Wilson's plover, C. Wilsonia, although I am also doing comparative studies of the Semipalmated Plover (*C. semipalmatus*), the Lesser Golden Plover (also known as the American Golden Plover) (*Pluvialis dominica*) and the Black-Bellied Plover (*Pluvialis apricaria*). In all these species, both parents incubate the eggs for about 3 1/2 - 4 weeks. At this point precocial young hatch which can run freely and feed themselves on their first day. The young fly in about another 3 weeks.

The nest, eggs, young and adult are all very well camouflaged. The nest, like that of many birds which perform distraction displays, is simply a scrape on the ground. Since the nest is easily accessible to predators, protection of the eggs depends on camouflage, preventing potential predators' knowledge of the nest's location, and keeping them out of the nest's vicinity.

For a plover to be conspicuous requires special behaviors or vocalizations. During incubation and before the young can fly, both parents of both species perform distraction displays to intruders which move along the ground. (See review of various species' behavior in Gochfeld, 1984.)

The Piping and Wilson's Plover are two shorebirds which typically nest on beaches or sand dunes of Eastern United States. In these two species, there are several different kinds of distraction behaviors. The bird, especially a Piping Plover, may peep loudly while walking and keeping apace or ahead of the intruder. Or the bird may fly conspicuously and slowly in a large circle, exposing its underside and bright wing stripes. As it flies or as it walks at a distance from its young, it can be heard to vocalize a "peep." This sound is often what first attracts the human's attention to the cryptically colored bird against the sandy beach. Sometimes the plover may engage in false brooding, sitting down with feathers slightly fluffed and wriggling as though it were on a nest - but doing so in the wrong location, where there are no eggs. Or it may merely pace back and forth in the general vicinity of a human, seeming to eye the presumed predator as it does so.

On some approaches of an intruder, the bird may do a gradation of broken-wing displays (BWD), perhaps beginning with a fanning tail and gradually increasing the awkwardness of walk until it has one, then both wings widely arched, fluttering and dragging. It may then vocalize loud, raucous squawks as well. To a human the sense is strong that the bird is injured, and one finds oneself trudging even hundreds of meters after the bird, only to see it suddenly fly away with agility. By that point one is far from the nest or young.

Note that the plover does not always make a broken wing display when its offspring are approached by a ground moving object. For instance, during one season's experiments, parents gave broken wing displays during approximately 40% of the close approaches to the nest. Sometimes, instead, the plover leaves the nest cryptically with a silent, low run. It may hide in hollows, tail towards the intruder, thus being very difficult to detect.

Yet another kind of variability occurs in a related species, the Killdeer *C. vociferous*. Only rarely does the killdeer perform broken wing displays to cattle, which do not eat the eggs, but may accidentally trample the eggs. Sitting tight on its nest, the killdeer is reported to lunge at the last moment in the face of cow, causing it to veer (Armstrong,1947; Walker, 1955; Graul, 1975). A somewhat similar set of reactions to mammals occurs among southern lapwings in Africa (Walters, 1980). In short, at least some species which perform broken wing displays exhibit flexibility in their use of the behavior.

But precisely what is it that the bird is doing? Is this a Fixed Action Pattern, or possibly a disorganized "hysterical" behavior as some have termed it? (Skutch, 1976, p. 403). Does the bird have to do it? Can it control initiation or stopping of the BWD? Can the behavior be construed as intentional? What is evidence for the existence of an intention?

B. What are some possible hypotheses about the plover's behavior?

Note that the following hypotheses are not mutually exclusive; it is quite possible that some combination may finally prove to be the most satisfactory.

1. Fixed action pattern (FAP):

The bird's behavior is an FAP which occurs when the parent bird is in a certain hormonal condition and in the presence of an intruder and the plover's nest or young. A Fixed Action Pattern, a concept developed by the ethologists Lorenz and Tinbergen (1951), is described in a recent textbook as follows:

"The distinguishing characteristics of the behavior are the innate and stereotyped coordination and patterning of several muscle movements which, when released, proceed to completion without requiring further sensory input. In terms of its almost total independence of feedback, the fixed-action pattern represents an extreme class of prewired behavioral performances which have come to be known as `motor programs.'" (Gould, 1982, p. 37)

If the behavior is an FAP, there are several possible predictions about the direction in which the plover makes a broken-wing display. a) The BWD should be made in random directions; thus the bird should be just as likely to display toward the nest or young as away. b) The displaying bird merely goes away from the nest/young, c) merely goes away from the intruder, d) moves away from both the nest or young and the intruder. This hypothesis requires that the plover must know the location and movements or trajectories of the young and the intruders in order to respond appropriately. That is no small feat. (And difficult to conceive of as simply an FAP.)

2. Conflict behavior:

Earlier investigators often interpreted thebroken-wing display to be the result of conflicting motivations. The displaying bird's behavior was thought to be "convulsive", "deliriously excited," and "its behavior patterns were more or less disorganized" (Skutch, 1976, p. 403). If the bird's behavior were indeed so disorganized, one would predict random directions of display or at least not consistent "leading away from the nest or young."

3. Approach/withdrawal tendencies:

This point of view, espoused by Tinbergen (1952), students of Schneirla (1959), and others is similar to the conflict hypothesis, but emphasizes more orderly behaviors by the bird than those predicted by a simple conflict hypothesis. It is predicted that the bird would make a BWD at the point of conflict of approach motivations (aggression and brooding) and withdrawal tendencies (escape). None of the possible predicted behaviors suffices to account for the complexity of the observed behaviors. Test of this model, in which a human directly approached incubating Golden Plovers, did not support the hypothesis (Bjerkjedal, 1991).

4. Pre-programmmed sequence of behavior:

By this hypothesis, the bird behaves according to a programmed sequence of behavior, in which stimuli such as direction of movement of the intruder, size of intruder, nearness to nest,and so forth determine the response of the parent bird. At least for the piping and Wilson's plovers, the variability observed in their behavior does not lend itself to an interpretation of a rigidly programmed sequence of behavior. If we allow for great flexibility in that programming, we are including the possibility of learning (Hypothesis #5), and if we allow reprogramming, we might well be talking about purposeful behaviors. Recognize, however, no program yet exists that adequately accounts for the behavior of a whole animal in the real world, so the kind of "super" program that could include descriptions of intentional behavior is not plausibly included as part of the hypothesis of "pre-programmed behavior.

5. Learning:

Plovers might be able to learn about various aspects of the situation, including which intruders are potential predators and should be dealt with more warily than others which are not. We have investigated that aspect in work I shall discuss (section IV; Ristau, 1991). The possibility of learning is not precluded by any other hypothesis.

6. Intentional or purposeful behavior:

The plover **wants** to lead the intruder away from the nest or young. It behaves so as to achieve this objective, including a broken-wing display. This hypothesis requires that the plover know the location and movements of young and intruders. I do not mean to imply that every plover has independently thought of or learned to make a BWD, since the BWD is undoubtedly an evolved, genetically transmitted behavior. However, strategies for its effective use may well be learned, both directly and by observation. The fact that a behavior or some aspect of it is learned or genetically pre-wired does not preclude the possibility of conscious thinking associated with it (see Griffin, 1984, 1985). In the next section, this hypothesis is discussed more fully.

C. Evidence needed to evaluate hypotheses about purposeful behavior, specifically re: "the plover wants to lead the intruder away from nest/young"

As already noted, drawing conclusions about mind from behavior is the major philosophical problem for cognitive ethology. Determining methods to investigate an animal's purpose is part of that formidable task. Based on the previous discussion concerning descriptive characteristics of intentional behavior, I propose the following observable behaviors as providing suggestive evidence in support of the hypothesis. I can make no claim that these are necessary and sufficient conditions for intentional behavior. I have not succeeded where centuries of philosophical thought have failed.

The outline of my argument, an attempt at a fairly general one for inferring purposeful behavior in an interactive situation is as follows:

1. The behavior exhibited should accomplish the presumed goal, though not neccessarily in every case. Thus the direction in which a parent bird moves while making a BWD should usually be adequate to lead the intruder away from the nest/young. There is, however, no requirement that the behavior be optimal. Furthermore completely accurate performance might well be suspect. In the interaction, the communicator should act so as to maximize attention to it. Thus the bird should position itself where it can readily be observed.
2. The organism should exhibit monitoring of progress towards the presumed goal. Thus the displaying plover should ascertain the intruder's attention, location and behavior. It may, however, be very difficult to obtain good evidence that an organism is doing this.
3. If progress towards the presumed goal is disrupted, the organism should be able to modify its behavior so as to again proceed towards the goal.
4. Flexibility achieved in one domain suggests that the organism may have such capacities in other domains as well.

D. Specific methods

To gather the kinds of eveidence just noted, my assistants and I conducted experiments on a barrier island off the coast of Virginia, southeast USA, interacting with Piping and Wilson's Plovers which had nests or young. We initally attempted to use a stuffed natural predator, a raccoon, mounted on a radio-controlled miniature dune buggy. Encountering too many logistical problems, we switched to a human intruder whose actions were directed by me over a walkie talkie. Essentially, the humans' behavior was designed to be unpredictable to the birds, to that extent simulating the behavior of a natural predator. Thus directions of the intruder's initial approach and changes in movements were varied. The human intruder approached the nest or young, walked in the area of offspring, stopping at the nest and at other locations and either followed or did not follow the displaying adult.

We used audio and videotape to record our observations of the birds' and human behavior, including locations and directions of movement (i.e. compass points such as north northeast). There were two sets of simultaneous observations, that of the intruder and the observer, synchronized by reporting time to the nearest second. Occasionally both observers were the intruders.

E. Results (further details in Ristau, 1991)

The reported data are drawn only from interactions in which the locations and directions of intruder, displaying birds and nest or all chicks could be determined. Data have been combined for stages with eggs and unfledged chicks. In 45 instances of broken wing displays, the data were sufficiently detailed for analysis.

1. Evidence that the plovers make broken wing displays in a direction "appropriate" to lead intruders away from the nest or young

There are actually several possible definitions of "appropriate direction", but whatever the defintion, the data support the hypothesis that the plover is attempting to get an intruder further away from the nest/young. For example, we can ask if the intruder went to the location of the displaying bird, would it be further from the nest at the end of the period of dsiplaying than at the beginning. The answer is yes, in 98% of the cases. Using the most stringent definition, we ask, would an intruder who may eventually get far from the nest, nevertheless, in the course of following the displaying adult, pass closer to the offspring? This could happen if the displaying adult and the intrtuder were on appoiste sides of the nest. Even by that stringent criterion, in 87% of the instances, a path that followed the parent plvoer would never bring the intruder closer to the nest or young. In short, yes, the birds' direction of display is adequate to get an intruder further from offspring.

Where in the intruder's visual field does the bird make broken-wing displays? If the bird is displaying in order to attract the intruder's attention, one would expect the bird to be selective about where it displays; it should display where the intruder will see it. In fact, 44 of the 45 BWDs were made to the front of the intruder rather than behind, that is, within a 180 degree arc of the intruder's visual field. The one possible exception occurred when an intruder was searching for young, was actually very near them, and moving in a zig-zag fashion, facing one way, then another. The parent made a BWD to the side of the intruder, directed away from the young, and headed opposite to the general trend of the intruder's movement toward the chicks.

Note that these data do not determine which intruder characteristics the bird was responding to, because the intruder was moving in most cases of BWDs. Thus, direction of movement as well as orientation of the intruder's eyes, head or body could be cues.

Positioning by the bird before making a BWD: Another question examined in detail was the location of the bird when it began its broken-wing displays. If this behavior is a reflex that is elicited

whenever an intruder approaches closely enough, one might expect the display to occur wherever the bird is located. However, the bird always moves before displaying. Sometimes the bird moves by flying which is an easily and accurately observable form of locomotion. One can argue that by flying to get to a location, rather than walking, a slower form of locomotion, it is probably important to the plover to get to that location rapidly. In all the cases of flying, namely 13, the bird's new position was closer to the intruder than was its position before flight. One would not expect such positioning if, as some have suggested, the bird were attempting to get away from the intruder.

Furthermore, in 11 of those 13 cases, not only was the bird closer to the intruder, but it was closer to the front of the intruder than it had been, i.e. more directly in the center of the intruder's visual field and/or the path of the moving intruder.

2. Evidence that birds making a broken-wing display monitor the intruder's behavior: To engage in these various behaviors strongly suggests the birds are monitoring the intruders. But how can one determine what a plover is monitoring? Plovers have laterally placed eyes, so they see over a wide field. It would be difficult to specify exactly what they are attending to within that field. They cannot, however, see behind them. Observations, photographs and videotapes show that as a plover is making a BWD, it often turns its head sharply back over its shoulder, its eye toward the intruder. This orientation strongly suggests monitoring of the intruder.

3. Modification of displays in response to changing intruder behavior: Suppose an intruder does not follow a displaying bird? What does the parent do then? Such occurrences were part of the experimental protocol. In short, if the intruder did follow the displaying bird, the bird did not reapproach (come closer to) the intruder. If the intruder did not follow, the bird engaged in any of a variety of behaviors. In over half of the occurrences, the bird stopped what it was doing and reapproached the intruder by either flying or walking closer. In nine instances (29%), the bird either continued to make a BWD, or increased the intensity of the display, for example, by flapping its wings more vigorously or vocalizing raucously while displaying. Of the remaining five cases, after displaying, the bird flew to the location of the young (three cases), flew away (one case), and in one other case, did not reapproach or fly.

F. Summary

The use of intense distraction displays, at least by the plovers in this study, indicates they usually perform the displays in a direction that would cause an intruder following them to get further away from the threatened nest or young. Furthermore, the birds monitor the intruder's approach and modify their behavior in response to changes in intruder locomotion. I have interpreted the data as providing at least suggestive evidence for the purposive nature (or first order intentional analysis) of the birds' behavior. As noted earlier, I do not claim that it is comparable to the fully cognitive, fully conscious plans we humans sometimes make.

To those that will have none of attempts to study "consciousness" in animals, recognize that even taking the stance of purposeful, or even intentional behavior, implying nothing of consciousness, is a fruitful enterprise. The stance led me to design experiments which I had not otherwise thought to do, which no one else had done, and which revealed complexities in the behavior of the Piping Plover predator distraction behavior not heretofore appreciated. I invite readers to adopt the stance of intentional behavior and to help delineate the levels and kinds of knowledge and purposiveness an organism might have.

The gaze experiments

In other experiments I asked whether piping plovers might be responsive to the attention of an intruder. Specifically, did the plover differentiate between an intruder who looked towards its nest region, scanning the dunes where its nest was located vs. one who looked in the opposite direction, scanning towards the ocean. As he or she was scanning, each intruder walked past the nest along the same paths at a considerable distance from the nest (15-25) meters. The birds did discriminate between the two intruders, remaining off the nest longer when an intruder looking twards it nest walked by than when one looking in the opposite direction passed.

Other work has also indicated that animals can differentiate between direction of gaze, hognosed snakes (Burhardt 1991), chickens (Gallup, 1972) and anoles (Hennig, 1977) engaging in "death feigning" for longer periods of time when confronted with a nearby human intruder staring at them as compared to an intruder averting his eyes. (review by Arduino and Gould, 1984). Important differences between my work and these other studies is both the greater distance of the intruder from the organism and, instead of staring directly at the bird, the intruder in my studies is scanning the bird's nest region, which, depending on the bird's movement, may or may not include the bird.

Can birds discriminate between "safe" and "dangerous" intruders?

In another series of experiments, I asked how plovers might come to know which intruders are potentially dangerous predators and which are more likely to be benign? They could be innately equipped to respond to sign stimuli of predators or could be learning to discriminate potential predators from benign intruders, possibly guided by innate constraints.

There is information from the laboratory and the field that suggests a significant role for learning. Such work includes birds , namely stilts, (*Himanoptus himanoptus*) mobbing egg-eating Laughing gulls (*Larus atricilla*) in one geographic region, while stilts in another region do not mob the largely insectivorous, but very similar looking, Franklin's gulls (*L. pipixcan*).(Dinsmoor, 1977) In the lab, by observing blackbirds apparently mobbing an innocuous honey-eater, other blackbirds learned to do the same (Curio et al, 1978). In other lab experiments, pigeons (*Columba livia*) learned many distinctions between between various classes of objects (both natural and man-made) and living organisms which were displayed on photographic slides (review in Watanabe, in press), including a particular person in a variety of poses and attire from other people (Herrnstein et al., 1976)

We conducted experiments to determine if piping plovers could learn to distinguish between two different intruders, one of whom had acted "safely" towards the eggs and the other more "dangerously." The essence of the experiment: Two distinctively dressed humans each walked "safely" by a nest containing eggs, at a considerable distance from the nest (12-32 meters away), not paying attention to the nest or to the parent bird. These Pre-Tests were conducted to verify that the plovers did not initially react differentially to the two intruders. One intruder then closely approached the nest approximately twice, acting in a way towards the eggs that we hoped would appear to the parent bird to be dangerous or threatening; ie pausing and hovering over the nest (these are the "dangerous" approaches). Then in the Post-Test trials, each intruder once again walked "safely" by the nest several times, at a considerable distance from the nest and not paying attention to the nest or parent. Would the parent birds now react differently to the previously "dangerous" intruder as compared to the intruder who had acted only "safely?" If the plovers can learn to discriminate between human intruders, it is most probable that they normally are able to learn an even simpler discrimination, that between different species of non-human intruders which have behaved in differentially threatening ways towards the plovers' nest or young.

In brief, the plovers did make that discrimination between the two humans, exhibiting higher levels of arousal to an intruder who had *previously* walked close to the nest and acted dangerously as compared to their reaction to the "safe" intruder. Remember, the different reactions of the plovers are tested during Post-Test trials when each intruder is walking "safely" by the nest, looking straight ahead and not paying attention to the nest or the parent. Some of the differences in behavior are the following: in slightly over half the trials when the bird made a correct discrimination, the bird got off its nest during the tangential walk of the "dangerous" intruder" while remaining on the nest for the tangential walk of the "safe intruder". Some of the other discriminating behaviors included the distance of the intruder from the nest when the bird opted to leave (leaving when the "dangerous" intruder was far away but only when the "safe" intruder was close), the distance and duration the bird got off the nest, and its posture, i.e. craning its neck up high in an alert neck posture vs. not.

Of the 13 birds with sufficient data to use in the analysis, 11 birds made correct discriminations, ie during Post-Test trials, they were more aroused by the previously "dangerous" intruder than they were by the "safe" intruder. For one bird there was no particular difference in response and one bird made a reverse discrimination.

The single incident of a reverse discrimination is particularly interesting. In that experiment, the intruder's roles had been reversed such that the person now in the role of the "safe" intruder had been the "dangerous" intruder in two previous aborted attempts to conduct the experiment and vice-versa. This atypical procedure was necessitated by a temporary lack of enough different persons to function as intruders. Under these unusual circumstances, one bird made a reverse discrimination, although its mate was correct.

Discussion

The results indicate that Piping Plovers can very rapidly learn to discriminate between a previously "dangerous" human intruder and a "safe" one, typically after only two close ("dangerous") approaches to the nest. Yet one must consider whether it is appropriate to label intruders as safe" and "dangerous". It is not clear whether a plover can form such concepts. However, in their natural world the plovers must react to some set of animals (and possibly humans) as potential predators and others as non threatening.

What mechanism might underlie the plovers' discrimination? Classical, that is, Pavlovian conditioning might be occuring, such that the plover becomes more highly aroused when an intruder is close to the nest. That "dangerous" intruder, even at a distance, becomes a conditioned stimulus for arousal. Simultaneously, the plover could be habituating to the "safe" intruder who does not come close to the nest on repeated walks past the nest.

For future work, it would be interesting to consider which aspects of the intruders' behavior are most critical to the plover's reacting in a more aroused way to the "dangerous" intruder. That intruder not only approached the nest area much more closely than did the "safe" intruder, it could also be considered as "knowing" the location of the nest and possibly of having an "intention" to cause harm, while the "safe" intruder did not. Alternatively one could argue that the "dangerous" intruder was actually not very dangerous at all; although right at the nest, it did not smash or remove any eggs. Other more straightforward manipulations to examine perceived "dangerousness" of an intruder, include varying its size, speed of approach, and direction of approach, this last being of greater theoretical significance.

General discussion

Finally I would like to make some general statements about possibly useful methods to explore purposeful behavior or intentionality in general.

1. Flexibility of behavior: An important criteria in evaluating purposeful behavior is the ability of an organism to modify its behavior when progress towards the presumed goal is obstructed in some way. Note that some of the organism's modifications may be innate or hard-wired adaptations, while others may be flexible, even novel. Comparative studies of other species might help elucidate evolutionary origins of apparently "novel" behaviors. We might also detect species in different stages of evolution of anti-predator behavior, or subject to different evolutionary or learning history with different ecological conditions or predation pressures. Predators' intelligence or specific sensory/ motoric capacities could be such a pressure. Likewise comparative work can help reveal the limits of prey species capacities and flexibility.

2. The use of one or few time occurrences of behavior: Extensive observations of naturally occurring events, in this case of predator-prey interactions, can permit one to observe rare behavioral sequences and strategies. This is a most important point. If we consider the possibility that the species we are studying are intelligent, a mark of that intelligence will be a novel response to an unusual or unsuccessful interaction. Thus part of our data set with intelligent species is likely to include one or few time occurrences. They should not be ignored. They can suggest fruitful experimentation. Furthermore, though any one event by itself is likely to be uninterpretable, a class of events can be more persuasive.

3. The "quadrangle"

This leads me to a third point, how one determines an organism's presumed goal, or in philosophical terms, its "belief/desire." To place constraints on the number of possible belief/desire pairs that could be held by an organism, Bennett (1991) suggests determining a quadrangle, the "sensory-input/belief/desire/behavior quadrangle." Rather than a single event, one finds a class of events which constitute the range of sensory inputs. To make the strongest case that explanation in terms of mental states, specifically beliefs/desires, is required (rather than a stimulus trigger for the observed behavior), one tries to determine a wide range of events/conditions quite different from one another, which are made sense of, characterized by, the animal's beliefs. The class of events could consist of typical occurrences as well as infrequent events, the latter being either naturally occurring or staged in an experiment. The animal's associated belief might be, for instance, that doing any of a variety of behaviors in these contexts will lead to the same goal, such as access to food, or getting an intruder away from the nest/young.

But these suggestions are only a beginning in the formidable task of delineating the kinds of knowledge and purposes an organism might have. I hope many scientists and philosophers will join together in this fruitful, but difficult enterprise.

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For more complete description of the work and ideas presented here, please refer to *Cognitive Ethology: The Minds of Other Animals*, 1991, edited by myself and published by Lawrence Erlbaum Associates.

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Summary

Interest in the cognitive capacities of animals has been rekindled, perhaps especially since Donald R. Griffin's book in 1974, The Question of Animal Awareness. My field observations and experiments about injury-feigning and other antipredator behavior of plovers is a development from that point of view. In my research, I asked the following questions about the birds:

1. Do parent plovers (*Charadrius melodus* and *C. wilsonia*) want to lead an intruder/predator away from the nest/young? What kinds of data could provide evidence for a purposive interpretation of behavior? Some of the data gathered from interactions of the plovers with human intruders were: Is the direction of a broken-wing display adequate to cause an intruder following them to get further away from the offspring? Where in the intruder's visual field does the parent plover usually make a broken-wing display (BWD)? (Answer: frontal plane) When the plover flies to a different position before displaying, where does it go? (Answer: closer to the intruder and typically closer to the center of the intruder's visual field/direction of locomotion) Does the displaying bird monitor the intruder's behavior? Does the displaying bird modify its behavior in response to changing intruder interactions? Specifically, if the intruder does not following the injury-feigning bird, the bird engaged in any of a variety of behaviors. In over half the occurrences, the bird stopped what it was doing and reapproached the intruder by either flying or walking closer. In less than a third of the instances the bird either continued to make a BWD or increased the intensity of the display.
2. Are plovers responsive to an intruder's attention to their nest, interpreted as direction of a human intruder's eye gaze?
3. Can plovers learn to discriminate between a potentially "dangerous" intruder and a "safe" one, defined respectively as a human which has previously approached closely to the nest and another which has not.

Results support positive answers to the questions posed.

These findings do not support a number of alternative hypotheses, for example that injury feigning is proximately governed by conflicts

between escape, aggressive and brooding drives, hypotheses termed "conflict" and "approach/withdrawal." They do begin to support a purposive interpretation of the use of displays by these species of plovers.

To identify purposive behavior experimentally and to investigate other possible mental states of animals is a most difficult task. To progress in this endeavor, we need and invite the efforts of many related disciplines including philosophy, biology, comparative, experimental, developmental and social psychology and, of course, ethology.

Resumen

La etología cognitiva de "simulación de lesiones" de un Charadridae: un comienzo.

El interés en las capacidades cognitivas de los animales ha vuelto a suscitarse, quizás especialmente desde la aparición del libro de Donald R. Griffin en 1974, *The question of animal awareness*. Mis observaciones de campo y experimentos sobre la simulación de lesiones y otros comportamientos antidepredadores en *Charadrius* es un desarrollo desde este punto de vista. En mi investigación me planteé las siguientes cuestiones sobre aves:

1. ¿Quieren los padres de *Charadrius melodus* y *Ch. wilsonia* alejar al intruso/depredador del nido/joven? ¿Que clase de datos podrían poner de manifiesto una interpretación a propósito de este comportamiento? Algunos de los datos obtenidos de las interacciones de los *Charadius* con intrusos humanos fueron: ¿Es la dirección del comportamiento de distracción de ala rota adecuado para causar que el intruso le siga para alejarlo de las crías? ¿Donde, con respecto al campo visual del intruso, los padres de *Charadrius* realizan el comportamiento de ala rota (BWD)? (respuesta: plano frontal) Cuando vuelan a una posicion diferente antes de hacer el comportamiento, ¿donde van? (respuesta: hacia el intruso y normalmente hacia el centro del campo visual o de la dirección de desplazamiento de éste) ¿Vigila el actor el comportamiento del intruso? ¿Modifica su comportamiento en respuesta a los cambios de las interacciones del intruso? Específicamente, si el intruso no sigue al ave que finge el daño realiza varios tipos de comportamiento. Aproximadamente la mitad de las veces se para y se aproxima al intruso para o bien volar o caminar cerca. En menos de un tercio de las veces continua haciendo el comportamiento BWD o bien incrementa la intensidad del mismo.
2. ¿Responden los *Charadrius* a la atención del intruso a su nido interpretado como mirar fijamente un intruso humano?
3. ¿Pueden los *Charadrius* aprender a discrimiar entre un intruso potencialmente "peligroso" y uno "seguro", definidos respectivamente como un humano que previamente se había aproximado mucho al nido y otro que no?

Los resultados apoyan positivamente las preguntas planteadas.

Estos resultados no apoyan varias hipótesis alternativas, por ejemplo que fingir el daño es gobernado próximamente por conflictos entre motivaciones de escape, agresión y cuidado de las crías, hipótesis denominadas "de conflicto" y "aproximación/alejamiento". Estas comienzan a apoyar una interpretación de intencionalidad del uso de los comportamientos por estas especies de *Charadrius*.

Identificar experimentalmente el propósito del comportamiento e investigar otros posibles estados mentales de los animales es una tarea muy difícil. Para progresar en este empeño, necesitamos y solicitamos los esfuerzos de muchas disciplinas relacionadas incluyendo filosofía, biología, psicología comparada, experimental, de desarrollo y social, y por supuesto, etología.

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