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Animal Play and the Evolution of Morality: An Ethological Approach

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ABSTRACT: In this paper we argue that there is much to learn about "wild justice" and the evolutionary origins of morality – behaving fairly – by studying social play behavior in group-living mammals. Because of its relatively wide distribution among the mammals, ethological investigation of play, informed by interdisciplinary cooperation, can provide a comparative perspective on the evolution of ethical behavior that is broader than is provided by the usual focus on primate sociality. Careful analysis of social play reveals rules of engagement that guide animals in their social encounters. Because of its significance in development, play may provide a foundation of fairness for other forms of cooperation that are advantageous to group living. Questions about the evolutionary roots of cooperation, fairness, trust, forgiveness, and morality are best answered by attention to the details of what animals do when they engage in social play – how they negotiate agreements to cooperate, to forgive, to behave fairly, and to develop trust. We consider questions such as why play fairly? Why did play evolve as it has? Does "being fair" mean being more fit? Do individual variations in play influence an individual's reproductive fitness? Can we use information about the foundations of moral behavior in animals to help us understand ourselves? We conclude that there is likely to be strong selection for cooperative fair play because there are mutual benefits when individuals adopt this strategy and group stability may also be fostered. Numerous mechanisms have evolved to facilitate the initiation and maintenance of social play, to keep others engaged, so that agreeing to play fairly and the resulting benefits of doing so can be readily achieved.

1. Social play: A foundation of fairness

Helping behaviors, food sharing, and turn-taking during play are all examples of animal behavior that have some features in common with human moral behavior. In this paper we focus specifically on what an ethological approach to turn-taking during social play might reveal about the evolution of morality, or what Bekoff (2004) labels "wild justice". Except among relatively large-brained mammals and birds, social play is not widespread in the animal kingdom. Because of the apparent cognitive demands involved in social play, it provides a fascinating context for studying the evolution of cooperation and fairness. Players must cooperate to prevent play from turning into fighting or mating. The social dynamics of play require on-going negotiations of cooperation and agreements to behave fairly, and animals appear to have evolved signals for this specific purpose which can be usefully understood as "intentional icons" in Millikan's (1984) sense (Bekoff and Allen, 1992).

There are several terms in the preceding paragraph that are likely to give critical readers pause. For example, what do we mean when we say that animals negotiate or that they behave fairly? We are not in a position to offer final definitions of these terms, but neither, we believe, is anyone else. However, in the context of social play we think of fairness as the tendency to maintain mutually the implicitly agreed upon rules of this sort of social interaction during which players undertake not to dominate, prey on, or mate with their playmates. Thus, animals who could otherwise exploit an advantage due to their social rank, or their size, do not do so, and the benefits of social play are distributed more equitably than might otherwise be predicted. (We will return to these important points later when we discuss the various mechanisms by which social play is maintained.)

At its current stage, the comparative, evolutionary study of animal behavior requires full consideration of both similarities and differences among species, and by using terms like these we especially draw attention to similarities. Thus our use of the term "negotiation" is intended to capture the extent to which the joint maintenance of a play bout is a continuous, dynamic process between players. As a working guide to what we mean by "behave fairly"

we use the notion that animals often have social expectations when they engage in various sorts of social encounters, and the violation of these expectations constitutes being treated unfairly.

Despite the apparent looseness of such talk, by carefully studying the dynamics of cooperative social play behavior one can, in fact, test ideas about the cognitive requirements for successful play. Tied into the notion of expectation is the element of surprise. Often, animals seem surprised by what happens to them in a given social interaction. For example, a dog or wolf may cock her head from side-to-side and squint, as if she is wondering what went "wrong" when a play-mate becomes too assertive or too aggressive. By analyzing play interactions, one can test hypotheses about the causes and functions of these behaviors. A more difficult task is to assess the emotions involved, such as whether animals may feel indignant or betrayed when they are wronged, when their expectations or sense of justice are violated, or when they are not being treated "right". The difficulty of answering questions about the nature of emotions in other animals is no reason to abandon attempts to answer them. Gruen (2002) points out that there are still many gaps in our knowledge of the cognitive and emotional capacities operating when humans perform various moral actions (but see Greene et al., 2001 for progress on this issue), and she argues that we need to study animals to determine if they share these capacities or some variation of them.

Because of the pivotal role of social play in the development of young animals, we argue that it may provide a "foundation of fairness" for other forms of social cooperation allowing groups (communities) to be built from individuals working in harmony with other individuals. Further, based on recent research on the neurobiology of human cooperation, we argue that "being fair" may feel good for animals as well. Lastly, we stress that in our efforts to learn more about the evolution of morality there is a need to broaden comparative research to include animals other than nonhuman primates, and to consider specific activities in which appropriately limited ethical principles might apply. Although there are many avenues for research, in this paper we wish to illustrate the value of taking an ethological, and specifically a cognitive ethological, approach to social play.

2. Cognitive ethology: A philosophical history

The origins of classical ethology lie in a passion for watching the spontaneous behavior of animals, often under natural or unconfined conditions. The central figures of classical ethology are Konrad Lorenz and Niko Tinbergen, who shared the Nobel prize for medicine in 1973 with Karl von Frisch. Lorenz and Tinbergen viewed ethology as an integrative science, combining different kinds of question about animal behavior. Tinbergen (1963) identified four overlapping areas with which ethological investigations should be concerned, namely, evolution (phylogeny), adaptation (function), causation, and development (ontogeny). Thus ethologists aimed to understand the various aspects of behavior within a Darwinian framework. European ethologists were often suspicious of the aims and methods of contemporary American psychologists who preferred to study the behavior of animals (usually rats and pigeons) under relatively austere laboratory conditions. Although some aspects of the dispute between lab psychologists and classical ethologists had political overtones, there was a core philosophical disagreement about scientific methodology and the nature of nonhuman animals as research subjects. Since behavioral abilities have evolved in response to natural selection pressures, ethologists favor observations and experiments on animals in conditions that are as close as possible to the natural environment where selection occurred. Behavioristic psychologists charge in response that the complexities of natural observation make it impossible to have enough experimental control to rule out competing hypotheses.

Classical ethology arose in an era when the scientific pendulum had swung hard against theorizing about the mental states of nonhuman animals. Darwin had maintained that there is continuity of mental powers between humans and other species, but by the early part of the 20th Century, the Darwinian program of mentalistic comparative psychology was largely regarded as far too anecdotal and anthropomorphic to meet the canons of scientific enquiry. Behavioristic psychology promised to turn psychology into a rigorous science, but it did so by mechanizing much of the study of animal behavior and limiting the methods of investigating animal learning to a few standard conditioning procedures in

standardized environments such as mazes and Skinner boxes. One of the achievements of Lorenz and, particularly, Tinbergen, was to turn naturalistic observation into repeatable science. Nevertheless, the framework in which they interpreted animal behavior was one of instincts and drives rather than the thoughts and emotions attributed by Darwin.

The last three decades have seen the pendulum swing back in the other direction, to where it is now common to find both field biologists and laboratory psychologists attempting to delineate the cognitive capacities of nonhuman animals (Bekoff et al., 2002). Tinbergen's (1963) framework is also useful for those interested in animal cognition (Jamieson and Bekoff, 1993; Allen and Bekoff, 1997; Smuts, 2001). Much of this work goes under the description "cognitive ethology" which was coined by Griffin (1978). However, many of those who take a cognitive approach to animals reject Griffin's label because they associate it with his more controversial views about the centrality of questions about animal consciousness to the proper study of animal behavior. But Burghardt (1997) embraces Griffin's approach by suggesting the addition of a fifth area, private experience, to Tinbergen's scheme. Burghardt notes that

> The fifth aim is nothing less than a deliberate attempt to understand the private experience, including the perceptual world and mental states, of other organisms. The term private experience is advanced as a preferred label that is most inclusive of the full range of phenomena that have been identified without prejudging any particular theoretical or methodological approach (Burghardt, 1997: p. 276).

The study of the evolutionary origins of morality asks ethologists to consider questions of emotion, empathy, and other private aspects of experience.

Although there are still many skirmishes between scientists schooled in the behaviorist tradition and those schooled in the ethological tradition, there is also increasing convergence on the need to combine field and laboratory approaches to the study of animal cognition in a wide variety of taxonomic groups (Bekoff et al., 2002). There is much interdisciplinary interest in questions about animal behavior – what available data mean, what methods are the best for answering questions that are frequently at once important, challenging and frustrating, and what role representatives of different disciplines play in helping us to gain a better understanding of the behavior of our nonhuman kin. It is important to consider all sources of information – even anecdotes can drive further empirical research. Philosophers also can play a role in helping to identify the presuppositions underlying disputes, and in helping to place ethological approaches to behavior in the general context of scientific reasoning and discovery. In return, ethological approaches to behavior have the potential to revolutionize philosophical thinking about alleged differences between humans and other animals, placing our appreciation for similarities and differences on a firmer evolutionary basis, helping us to understand the origins of human behavior (Dennett, 1983; see also Allen and Bekoff, 1997 for further discussion).

3. An ethological approach to morality

A range of approaches to questions about the evolutionary origins of morality is being pursued within a variety of disciplines. Grounded as it is in the specific details of animal behavior, the ethological approach lies at the most concrete end of the range of approaches. At the other end of the range lie the mathematical abstractions of game theorists, who wrestle with the problem of constructing models for the selection and maintenance of cooperative behavior in a competitive environment. The diverse contributions to a recent volume on the evolution of morality (Katz, 2000) reflect this range, beginning with the Flack and de Waal's investigation of what they call the "building blocks for morality" among the social relationships of nonhuman primates (Flack and de Waal, 2000), and ending with Skyrms' synthesis of game theory and adaptation in constructing models for the evolution of morality (Skyrms, 2000).

In commentary published alongside Flack and de Waal (2000), some of the critics rejected the idea that the behavior of nonhuman primates is "genuinely" moral in the same sense as human moral behavior. Human moral behavior spans a range of capacities from performing specific behaviors to theoretical reasoning. Other animals don't theorize at the level of the Kantian categorical imperative, but for that matter, neither do all humans. Of course, humans generally are capable of reasoning theoretically about their morality in ways that most animals almost certainly are not. Nevertheless, human morality also involves some very basic emotional responses and

tendencies towards distributing resources fairly. These moral responses, we believe, have analogues in animal behavior (see also Brosnan and de Waal, 2003, 2004). It is important to note, however, that to say that the roots of morality can be found in animal behavior is not necessarily to say that morality itself is a characteristic of those animals (any more than the fact that the roots of Christianity lie in Judaism entails the false conclusion that Jews are Christians). Nevertheless, better understanding of human morality can be expected from studying its roots, even if those roots are themselves non-moral.

But it is also possible that the behavior of some nonhuman animals is best understood as a genuine form of moral behavior, albeit not identical to human moral behavior. Some animals appear to have codes of social conduct that regulate their behavior in terms of what is permissible and what is not permissible during social encounters (for references see Bekoff, 2004). Such regulation need not be identical to human morality, and it is a separate question whether any nonhuman animals are themselves moral agents with a moral sense who are able to live in moral communities. Nevertheless, the question is worth broaching. Bernstein's (2000, p. 34) concern that "morality in animals might lie outside of the realm of measurement techniques available to science" needs to be taken seriously, but our view is that detailed comparative analyses of social behavior in animals can indeed provide insights into the evolution of morality, and perhaps even reveal unsuspected similarities between the behavior of humans and other animals.

4. Animal play and social contracts: Lessons in cooperation, justice, fairness, and trust

Whereas the existence of animal morality is not obvious, animal play is obvious. Social play in animals is an exhilarating activity in which to engage and to observe. The rhythm, dance, and spirit of animals at play is incredibly contagious. Of course we all know that dogs and cats love to play. So do many other mammals. Buffaloes will follow one another and playfully run onto and slide across ice, excitedly bellowing "Gwaaa" as they do so. Birds also playfully soar across the sky chasing, diving here and there, apparently frolicking with one another. There are rather evident emotions associated with play – joy and happiness – that drive animals into it. One way to get animals (including humans) to do something is to make it fun. Studies of the neurochemistry of play in animals support the claim that play is fun. Play in rodents is associated with and regulated by neurotransmitters that are known to play roles in other pleasurable activities (Siviy, 1998; Panksepp, 1998, 2000).

To learn about the dynamics of play from behavioral studies, it is essential to pay attention to subtle details that are otherwise lost in superficial analyses. During play there are continuous rapid exchanges of information. Dogs and other animals keep track of what is happening when they play so we also need to pay attention to details. Ethological studies of play need to be based on careful observation and analyses of video-tape. For example, Bekoff and his students watch tapes of play one frame at a time to see what the animals are doing and how they exchange information about their intentions and desires to play. This is tedious work (not play at all!), but it is also the only way of noticing the more subtle and fleeting behavioral patterns that occur during social play.

When individuals play they typically use action patterns that are also used in other contexts, such as predatory behavior, antipredatory behavior, and mating activities. Behavior patterns that are observed in mating may be intermixed in flexible kaleidoscopic sequences with actions that are used during fighting, looking for prey, and avoiding being eaten. These actions may not vary much across different contexts, or they may be hard to discriminate even for the participants. So, the following questions have driven our research. How do animals know that they are playing? How do they communicate their desires or intentions to play or to continue to play? How is the play mood maintained?

Because there is a chance that various behavior patterns that are performed during on-going social play can be misinterpreted, individuals need to tell others "I want to play", "this is still play no matter what I am going to do to you", or "this is still play regardless of what I just did to you". An agreement to play, rather than to fight, mate, or engage in predatory activities, can be negotiated in various ways. Individuals may use various behavior patterns – play markers – to initiate play or to maintain (prevent termination of) a play mood (Bekoff, 1975; Flack et al., 2004) by punctuating play sequences with these

actions when it is likely that a particular behavior may have been, or will be, misinterpreted (it is also possible that there are auditory, olfactory, and tactile play markers). The idea that there is "communication about communication" during social play is an extension of Bateson's (1955) notion of metacommunication (for discussion see Bekoff, 1972).

One action that is very common in play among canids (members of the dog family) is the "bow". Bows occur almost exclusively in the context of social play. Bows are a highly ritualized and stereotyped movement (the animal crouches on her forelimbs and elevates her hindlimbs) that seems to function to stimulate recipients to engage (or to continue to engage) in social play. Bows have been extensively studied in various canids in this context. Bows occur throughout play sequences, but most commonly at the beginning or towards the middle of playful encounters. In a detailed analysis of the form and duration of play bows, Bekoff (1977a) discovered that duration was more variable than form, and that play bows were always less variable when performed at the beginning rather than in the middle of ongoing play sequences. Three possible explanations for this change in variability include: (1) fatigue, (2) the fact that animals are performing them from a wide variety of preceding postures, and (3) there is less of a need to communicate that "this is still play" than there is when trying to initiate a new interaction. These explanations are not exclusive alternatives.

In a long-term and continuing study of social play Bekoff also found that play signals in infant canids (domestic dogs, wolves, and coyotes) were used non-randomly, especially when biting accompanied by rapid side-to-side shaking of the head was performed (Bekoff 1995). Biting accompanied by rapid side-to-side shaking of the head is performed during serious aggressive and predatory encounters and can easily be misinterpreted if its meaning is not modified by a play signal.

Play signals are an example of what ethologists call "honest signals". There is little evidence that social play is a manipulative or "Machiavellian" activity. Play signals are rarely used to deceive others in canids or other species. There are no studies of which we are aware that actually look at the relative frequencies of occurrence of honest and deceptive play signaling, but Bekoff's own long-term observations indicate that deceptive signaling is so rare that he cannot remember more than a few occurrences in thousands of play sequences. Cheaters, individuals who invite another individual to play and then attempt to dominate them, are unlikely to be chosen as play partners because others can simply refuse to play with them and choose others. Limited data on infant coyotes show that cheaters have difficulty getting other young coyotes to play (Bekoff's personal observations). It is not known if individuals select play partners based on what they have observed during play by others.

In domestic dogs, one expectation may be that play is by invitation only. Those who violate this expectation may be avoided or chased from play groups. There is no direct evidence for this claim, but the following example suggests, at least, that play in dogs resists distraction from dogs who have not gone through the typical communicative processes of soliciting play. While studying dog play on a beach in San Diego, California, Horowitz (2002) observed a dog she called Up-ears enter into a play group and interrupt the play of two other dogs, Blackie and Roxy, without a play bow. Up-ears was chased out of the group and when she returned Blackie and Roxy stopped playing and looked off toward a distant sound. Roxy began moving in the direction of the sound and Up-ears ran off following their line of sight. Roxy and Blackie immediately began playing once again. (The appearance of deception in this case is interesting but beside the point we wish to make about the cooperative conditions for play.)

Playing individuals also engage in role-reversing and self-handicapping to maintain social play (Bekoff and Allen, 1998; Bauer and Smuts, 2002; Horowitz, 2002). Each can serve to reduce asymmetries between the interacting animals and foster the reciprocity that is needed for play to occur. Self-handicapping happens when an individual performs a behavior pattern that might compromise herself. For example, a coyote might not bite her play partner as hard as she can, or she might not play as vigorously as she can. Watson and Croft (1996) found that red-neck wallabies adjusted their play to the age of their partner. When a partner was younger, the older animal adopted a defensive, flat-footed posture, and pawing rather than sparring occurred. In addition, the older player was more tolerant of its partner's tactics and took the initiative in prolonging interactions.

Role-reversing occurs when a dominant animal performs an action during play that would not

normally occur during real aggression. For example, a dominant animal would not voluntarily roll-over on his back during fighting, but might do so while playing. In some instances role-reversing and self-handicapping can occur together. For example, a dominant individual might roll over while playing with a subordinate animal and inhibit the intensity of a bite.

From a functional perspective, self-handicapping and role-reversing, similar to using specific play invitation signals and gestures, or altering behavioral sequences, might serve to signal an individual's intention to continue to play. In this way there can be mutual benefits (as discussed below) to each individual player because of their agreeing to play and not fight or mate. This might differentiate cooperative play from more altruistic actions such as the situation in which a male Diana's monkey helped a female get food when she could not learn the task that would bring her food (Markowitz, 1982). There seemed to be no benefit to the male doing so. (We thank Jan Nystrom for marking this distinction).

5. Fine-tuning play: Why cooperate and play fairly?

It is important to ask why animals carefully use play signals to tell others that they really want to play and not try to dominate them and why they engage in self-handicapping and role-reversing. During social play, while individuals are having fun in a relatively safe environment, they learn ground rules that are acceptable to others – how hard can they bite? how roughly can they interact? – and how to resolve conflicts. There is a premium on playing fairly and trusting others to do so as well. There are codes of social conduct that regulate actions that are and are not permissible, and the existence of these codes likely speaks to the evolution of morality. Individuals might also generalize the implicit rules of interaction ("codes of conduct") learned in playing with specific individuals to other group members and to other situations such as food sharing, defending resources, grooming, and giving care.

We suggest that cooperation and fairness evolve because they are important in the formation and maintenance of social relationships (Solomon 1995 also forcefully argues this point) and that these relationships, in turn, improve the fitness of both individuals and groups. If behaving fairly is a common adaptation among social animals, then the combative Hobbesian world in which individuals are constantly at one another's throats is not the natural state of affairs. Nature may not be always red in tooth and claw, and altruism need not be conceived of as selfishness disguised. In fact, it is likely that at a certain level of sophistication, fairness itself becomes a social goal and that animals monitor each other for violations of expectations involving social cooperation (e.g., Hauser and Marler, 1993; de Waal, 1996; Horowitz, 2002). An ethological approach to fairness thus has much potential to provide an alternative view of the evolution of morality.

Playtime generally is safe time. Transgressions and mistakes are forgiven and apologies are accepted by others especially when one player is a youngster who is not yet a competitor for social status, food, or mates. Fagen (1993, p. 192) noted that "Levels of cooperation in play of juvenile primates may exceed those predicted by simple evolutionary arguments...". Detailed studies of play in various species indicate that individuals trust others to maintain the rules of the game (Bekoff and Byers, 1998). While there have been numerous discussions of cooperative behavior in animals (e.g., Axelrod, 1984; de Waal, 1996; Ridley, 1996; Dugatkin, 1997; Hauser, 2000; Sober and Wilson, 2000; essays in Katz, 2000 and references therein), none has considered the details of social play, the requirement for cooperation and reciprocity and its possible role in the evolution of morality, namely behaving fairly. Although Flack and de Waal (2000) did not feature play, they have more recently analyzed play in juvenile chimpanzees as a test bed for ideas about social rules (Flack et al., 2004).

Individuals of different species seem to fine-tune on-going play sequences to maintain a play mood and to prevent play from escalating into real aggression. Detailed analyses of film show that in canids there are subtle and fleeting movements and rapid exchanges of eye contact that suggest that players are exchanging information from moment-to-moment, to make certain everything is all right, that this is still play. Aldis (1975) suggested that in play fighting, there is a 50:50 rule so that each player "wins" about 50% of their play bouts by adjusting their behavior to accomplish this (for further discussion and details on rodent play, see Pellis, 2002). A "win" is identified by comparing the behavioral outcome of a mock contest to the behaviors exhibited by winners of serious contests,

(e.g., pinning an opponent to the ground or standing over him).

Why might animals fine-tune play? While play in most species does not take up much time and energy (Bekoff and Byers, 1998; Power, 2000), and in some species only minimal amounts of social play during short windows of time early in development are necessary to produce socialized individuals (two 20 min play sessions with another dog, twice a week, are sufficient for domestic dogs from three to seven weeks of age; cf., Scott and Fuller 1965), researchers agree that play is very important in social, cognitive, and/or physical development, and may also be important for training youngsters for unexpected circumstances (Sutton-Smith 1997; Spinka et al. 2001). While there are few data concerning the actual benefits of social play in terms of survival and reproductive success, it generally is assumed that short-term and long-term functions (benefits) vary from species to species and among different age groups and between the sexes within a species. No matter what the functions of play may be, experts agree that there is little doubt that play has some benefits and that the absence of play can have devastating effects on social development (Power, 2000; Spinka et al., 2001; Burghardt, 2004).

During early development there is a small time window when individuals can play without being responsible for their own well-being. This time period is generally referred to as the "socialization period" for this is when species-typical social skills are learned most rapidly. It is important for individuals to engage in at least some play. All individuals need to play and there is a premium for playing fairly if one is to be able to play at all. If individuals do not play fairly they may not be able to find willing play partners. In coyotes, for example, youngsters are hesitant to play with an individual who does not play fairly or with an individual whom they fear (Bekoff, 1977b). In many species individuals also show play partner preferences and it is possible that these preferences are based on the trust that individuals place in one another.

Of interest to biologists is how differences in the performance of a given behavior influences an individual's reproductive success. It is extremely difficult to show with great certainty that the performance of a specific behavior is directly and causally coupled to reproductive success, especially under field conditions, so in many instances we have to rely on indirectly justified answers to this question.

In a field study of coyotes, Bekoff (1977b) found evidence to suggest that individuals might suffer some decline in his or her reproductive fitness if they do not play by the expected and accepted rules of the game. Coyote pups who don't play as much as others because they are avoided by others, or because they themselves avoid others, are less tightly bonded to other members of their group and more likely to strike out on their own. But life outside the group is much more risky than within it. In a seven year study of coyotes living in the Grand Teton National Park outside Moose, Wyoming, Bekoff and Wells (1986) found that more than 55% of yearlings who drifted away from their social group died, whereas fewer than 20% of their stay-at-home peers did. Was it directly because of play? We are not sure, but information collected on captive coyotes suggested that the lack of play was a major factor in individuals spending more time alone, away from their littermates and other group members.

Dugatkin and Bekoff (2003) constructed a game-theoretical model to analyze four possible strategies that an individual could adopt over time (for species in which fairness can be expressed during two different developmental stages), namely, being fair (F) and at a later date being fair (F/F), being fair and then not fair (F/NF), being not fair and then fair (NF/F), and being not fair and then not fair (NF/NF). Of these, only F/F was an Evolutionarily Stable Strategy (ESS) that could evolve under the conditions of the model. None of the other three strategies were ESSs, and when no strategy was an ESS all four could coexist. There are two clear predictions from these results. First, always acting fairly should be more common than never acting fairly in species in which fairness can be expressed during two different developmental stages. Second, there should be many more cases in which none of the strategies modeled would be an ESS, but all four could coexist at significant frequencies. That F/NF is not an ESS is of interest because this strategy could be conceived as a form of deceit. This finding fits in well with what is known about play signals, for, as mentioned above, there is little evidence that play signals are used to deceive others at any stage of development. The predictions of the model are also testable in principle by following identified individuals and recording how they distribute fairness across different activities as they mature. To the best of our knowledge this line of research is not being currently

pursued nor are there any data that can be used to assess the validity of this prediction.

We are confident that close scrutiny of social animals will reveal more evidence that individuals benefit from being able to evaluate the basic fairness of situations they encounter (i.e., the mutual maintenance of implicitly agreed upon rules). We fully realize that at this time our predictions are little more than a promissory note, but in reality just about all discussions of the fitness consequences of various behavior patterns are better or worse "just-so stories". However, this is not to claim that we will never be able to make more forceful claims about the likely fitness consequences of different behavioral patterns when more data are in (Bekoff 2002). This is, perhaps, one of the greatest challenges faced by ethological research, cognitive and otherwise. To get beyond "just-so" stories, what is needed is genuinely comparative work, comparing behavioral adaptations of different species as a consequence of social and environmental differences. This makes the task of investigating the roots of morality in non-human species all the more important for a proper evolutionary understanding of human morality.

Even more controversial is a possible role for group selection in the evolution of moral behavior. It seems plausible that a more generalized moral sense, or the roots of such a moral sense, developed during play could benefit groups as a whole as a result of group members learning rules of engagement that influence their decisions about what is acceptable behavior when dealing with each other in a variety of contexts. At an advanced stage, such an understanding would be essential if individuals are to work in harmony to create a successful group able to out-compete other groups. In social groups, individuals often learn what they can and cannot do, and the group's integrity depends upon individuals conforming to certain rules. As a result of lessons in social cognition and empathy that are offered in social play, individuals may learn what is "right" or "wrong" – what is acceptable to others – the result of which is the development and maintenance of a social group that operates efficiently. Following the lines of Sober and Wilson's (1998, p. 135ff) discussion concerning the choice of social partners, it may be that behaving fairly is a group adaptation – or group fitness advantage (Lisa Lloyd, personal communication) – but once a social norm evolves it becomes individually advantageous to behave fairly for there are costs to not doing so (Elliott Sober, personal communication).

Mammalian social play is a useful behavioral phenotype on which to concentrate in order to learn more about the evolution of fairness and morality. While birds and individuals of other species engage in social play, there are too few data from which to draw detailed conclusions about the nature of their play, although such data would be welcome. In light of recent work showing an important role for emotions in human moral decisions (Greene et al., 2001) we can also ask what role emotions play in the evolution of morality. At this time, we really need long-term field studies of social animals for which it would be reasonable to hypothesize that emotions and morality (or its precursors) have played a role in the evolution of sociality, that emotions and morality are important in the development and maintenance of social bonds that allow individuals to work together for the benefit of all group members (see also Gruen, 2002). To stimulate further comparative research (and the development of models) on a wider array of species than has previously been studied, we offer the hypothesis that morality, in this case behaving fairly, is an adaptation that is shared by many mammals, not only by non-human and human primates. Behaving fairly evolved because it helped young animals acquire social (and other) skills needed as they mature into adults. A focus on social cooperation is needed to balance the plethora of research that is devoted to social competition and selfishness (for further discussion see Boehm, 1999; Singer, 1999; Wilson, 2002; and especially Adams and Burnett, 1991 for discussion of the different emphasis placed on cooperation by female ethologists).

Let us stress that we are not arguing that there is a gene for fair or moral behavior. As with any behavioral trait, the underlying genetics is bound to be complex, and environmental influences may be large and difficult to pin down. Nonetheless, provided there is variation in levels of morality among individuals, and provided virtue is rewarded by a greater number of offspring, then genes associated with good behavior are likely to accumulate in subsequent generations. The observation that play is rarely unfair or uncooperative is perhaps the strongest indication that natural selection acts to weed out those individuals who do not play by the rules.

6. Morality and human nature: The precautionary principle

Just how central is morality to "human nature"? We do not really know despite strong claims to the contrary. However, arguments appealing to evolutionary continuity that emphasize the brutal side of human nature by using animal models to rationalize cruelty, divisiveness, warfare, territoriality, and selfishness present a disingenuous use of much available information on animal social behavior. While animals surely can be nasty, this does not explain much of the behavior that is expressed to other individuals. Animals do make choices to be nice and to be fair.

Ecologists and environmentalists have developed what they call the "precautionary principle" that is used for making decisions about environmental problems. This principle states that a lack of full scientific certainty should not be used as an excuse to delay taking action on some issue. For example, according to this principle, uncertainty about global warming should not be used to delay efforts to reduce carbon emissions. The precautionary principle can also be easily applied in studies of the evolution of morality. To wit, we claim that enough is known to warrant further comparative studies of the evolution of morality in animals other than nonhuman primates, and that until these data are available we should keep an open mind about what individuals of other taxa can and cannot do.

It is important for us to learn more about the evolution of morality and how this information can be used to give us hope for the future rather than our accepting a doomsday view of where we are all heading "because it's in our nature". Accepting that competition, selfishness, and cheating are what drives human and animal behavior leaves out a lot of the puzzle of how we came to be who we are. Cooperation and fairness can also be driving forces in the evolution of sociality.

The importance of interdisciplinary collaboration and cooperation in studies of animal cognition, cooperation, and moral behavior cannot be emphasized too strongly. It seems likely that the origins of virtue, egalitarianism, and morality are more ancient than our own species. While fair play in animals may be a rudimentary form of morality, it still could be a forerunner of more complex and more sophisticated human moral systems. Only an ethological approach can provide the concrete details that are necessary to properly evaluate hypotheses about the evolutionary roots of morality. In this paper, we have focused on turn-taking during social play as a behavioral indicator of rudimentary morality. The full investigation of the origins of morality will require careful attention to the development of other behavioral indicators. Only with the involvement of philosophers, ethicists, anthropologists, geneticists, evolutionary biologists, neurobiologists, and psychologists can the concrete details of animal behavior be properly understood in the context of the broader discussion about the nature of human morality.

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