03ch 12/5/03 11:28 AM Page 53
Aldine/Sussman/169329

3

Wild Justice, Cooperation, and Fair Play

Minding Manners, Being Nice, and Feeling Good

Marc Bekoff

SOCIAL MORALITY, MANNERS, AND COOPERATION IN ANIMALS: DOING WHAT COMES NATURALLY

> Those communities which included the greatest number of the most sympathetic members would flourish best and rear the greatest number of offspring.
>
> (Charles Darwin [1871]1936:163)

> I believe that at the most fundamental level our nature is compassionate, and that cooperation, not conflict, lies at the heart of the basic principles that govern our human existence. . . . By living a way of life that expresses our basic goodness, we fulfill our humanity and give our actions dignity, worth, and meaning.
>
> (His Holiness the Dalai Lama 2002:68)

> My thesis is that justice is first of all a natural sentiment, an inborn sense of our connectedness with others and our shared interests and concerns.
>
> (Solomon 1995:153)

There are many areas in which researchers and nonresearchers can pursue interesting, important, challenging, and interdisciplinary questions that center on the interface of science, religion, ethics, and the place of humans in the world. One such area concerns the evolution of social

03ch 12/5/03 11:28 AM Page 54
Aldine/Sussman/169329

Aldi

morality, manners if you will, and the negotiation and enforcement of cooperation, fairness, social norms, and etiquette (for wide-ranging discussion see Solomon 1995; de Waal 1996; Ridley 1996, 2001; Mitchell 1998; Field 2001; Hinde 2002; Wilson 2002; de Waal and Tyack 2003). Recently there has been a resurgence of interest in the notion of fairness in humans (Douglas 2001; Riolo, Cohen, and Axelrod 2001; Sigmund and Nowak 2001; Bowles and Gintis 2002; Fehr and Gächter 2002; Sigmund, Fehr, and Nowak 2002; Bewley 2003; Fehr and Rockenbach 2003). Researchers are interested in learning about how individuals from different cultures share resources, and if they share them equitably even if they are not compelled to do so. Much research shows that human beings are more generous and more fair than game-theory and other models predict. There seems to be a set of core values that are learned through social interactions with others, and these values influence moral decisions. There also is evidence that people will punish free-riders in the absence of personal gain, and that cooperation is sustained by such "altruistic punishment" (Bowles and Gintis 2002; Fehr and Gächter 2002). Taken together, cross-cultural data suggest that there may well be an innate drive to be fair.

But what about nonhuman animal beings (hereafter animals)? Many animals live in fairly stable social groups that resemble those of ancestral humans. There are divisions of labor, food sharing, communal care of young, and inter- and intrasexual dominance hierarchies. Many animals, especially mammals, also share with humans neuroanatomical structures in the amygdala and hypothalamus and neurochemicals (dopamine, serotonin, oxytocin) that form the neural bases for the expression and experience of emotions and empathy (Panksepp 1998; Preston and de Waal 2002). A wide variety of social behavior patterns in animals have also been influenced by living in small groups. If one is a good Darwinian, it seems premature to claim that *only* humans can be empathic and moral beings. As animals share their emotions with us it becomes increasingly difficult to deny their existence.

In this chapter I consider various aspects of the evolution of cooperation and fairness using social play behavior in animals, especially mammals, as my exemplar of an activity in which one would expect to see ongoing negotiations of cooperation and agreements to behave fairly because the social dynamics of play require that players agree to play and not to fight or to mate with one another. I am specifically concerned with the notion of "behaving fairly." By "behaving fairly" I use as a working guide the notion that animals often have social expectations when they engage in various sorts of social encounters the violation of which constitutes being treated unfairly because of a lapse in social etiquette. I conclude that social play might be a "foundation of fairness." I also argue that it is through social cooperation that groups (communities) are built from individuals agree-

03ch 12/5/03 11:28 AM Page 55
Aldine/Sussman/169329

ing to work in harmony with other individuals. Whether or not individuals lose various "freedoms" when balanced against the benefits that accrue when they work for the "good of a group" is unknown and needs to be studied more carefully in various species. Further, based on recent research on the neurobiology of human cooperation, I argue that "being fair" may feel good for animals as well. Lastly, I stress that in our efforts to learn more about the evolution of social morality we need to broaden our comparative research to include animals other than nonhuman primates.

Researchers from many disciplines have debated the evolutionary origins of social morality, asking if some animals have codes of social conduct that regulate their behavior in terms of what is permissible and what is not permissible during social encounters. They want to know just what are the moral capacities of animals, are they moral agents with a moral sense who are able to live in moral communities? In a recent issue of the *Journal of Consciousness Studies* [7(1/2), 2000], researchers from many disciplines debated the evolutionary origins of morality. These scholars were interested in discussing animal roots on which human morality might be built, even if it is not identical to animal morality. Charles Darwin's (1859, [1872] 1998) ideas about evolutionary continuity, that behavioral, cognitive, emotional, and moral variations among different species are differences in *degree* rather than differences in *kind*, are often invoked in such exercises. This view argues that there are shades of gray among different animals and between nonhumans and humans, that the differences are not black and white with no transition stages or inexplicable jumps (Gruen 2002; Güzeldere and Nahmias 2002; see also many other essays in Bekoff, Allen, and Burghardt 2002). Current work in evolutionary biology and anthropology suggests that linear scales of evolution in which there are large gaps between humans and at least some animals are simplistic views of the evolutionary process. Further, as I will discuss below, models and explanations that exclude group-selection in deference to individual selection also need to be revisited.

THE EVOLUTION OF SOCIAL MORALITY: CONTINUITY, PROTOMORALITY, AND QUESTIONS OF HUMAN UNIQUENESS

> Different as they are from language-using human beings, they are able to form relationships not only with members of their own species, but also with human beings, while giving expression to their own intentions and purposes. So that the relationships are far more clearly analogous to human relationships than some of the philosophical theorizing that I have discussed would allow. Some human beings indeed

03ch 12/5/03 11:28 AM Page 56
Aldine/Sussman/169329

> and some nonhuman animals pursue their respective goods in company with and in cooperation with each other. And what we mean by 'goods' in saying this is precisely the same, whether we are speaking of human or dolphin or gorilla.
>
> (Macintyre 1999:61)

Evolutionary reconstructions of social behavior often depend on educated guesses (some better than others) about the past social (and other) environments in which ancestral beings lived. In the same sense that other's minds are private, so is evolution. Often it is difficult to know with a great deal of certainty very much about these variables and how they may have figured into evolutionary scenarios. It is an understatement to note that it is extremely difficult to study the evolution of morality in any animal species, and the very notion of animal morality itself often makes for heated discussions. Bernstein's concern that "morality in animals might lie outside of the realm of measurement techniques available to science" (2000:34) needs to be taken seriously. *Nonetheless, it seems clear that detailed comparative analyses of social behavior in animals can indeed provide insights into the evolution of social morality.* To be sure, these sorts of studies are extremely challenging, but the knowledge that is gained is essential in our efforts to learn more about the evolution of sociality and social morality and to learn more about human nature and perhaps human uniqueness.

Many discussions of the evolution of morality center on the development of various sorts of models (e.g., Axelrod 1984; Ridley 1996, 2001; Skyrms 1996; Dugatkin 1997; Sober and Wilson 1998, 2000; *Journal of Consciousness Studies* 2000). While these models are very useful for stimulating discussion and further research, they do not substitute for available data (however few) that may bear on animal morality [see, for example, some essays in Aureli and de Waal (2000) for additional comparative information].

The study of the evolution of morality, specifically cooperation and fairness, is closely linked to science, religion, theology, spirituality, and perhaps even different notions of God, in that ideas about continuity and discontinuity (the possible uniqueness of humans and other species), individuality, and freedom need to be considered in detail. Furthermore, it is important to discuss relationships among science, religion, and God because spirituality and the notion of one form of God or another had strong influences on the evolution of our ancestors, their cognitive, emotional, and moral lives.

Recently, Peterson (2000; see also Peterson 1999) has pondered the evolutionary roots of morality (stages that he refers to as "quasi-morality" and "proto-morality" in animals) and religion in relation to the roles played by cognition and culture. He also stresses the importance of recognizing con-

03ch 12/5/03 11:28 AM Page 57
Aldine/Sussman/169329

tinuities and discontinuities with other animals, arguing ultimately (and speciesistically) that while some animals might possess protomorality [they are able "to rationally deliberate actions and their consequences" (2000:475)] none other than humans is "genuinely moral" because to be able to be genuinely moral requires higher emergent levels of cognition as well as culture and the world view that culture provides, namely, religion. Peterson claims that

> quasi-moral and proto-moral systems do not require a global framework that guides decision making. They are always proximate and pragmatic. In these systems, there is no long-term goal or ideal state to be achieved. Yet, genuine morality is virtually inconceivable without such conceptions. (ibid.:478)

Peterson also claims that any sociobiological account (based on selfishness or combativeness) of human morality is incomplete. I agree and also argue that this is so for some nonhuman animals as well. To be sure, Peterson's views are very stimulating. I cannot go into detail here but suffice it to say, and I hope that it becomes clear later on, when animals are studied in their own worlds they may indeed have their own form of genuine morality, there might indeed be long-term goals and ideal states to be achieved. Our anthropocentric view of other animals, in which humans are so taken with themselves, is far too narrow. The worlds and lives of other animals are not identical to those of humans and may vary from species-to-species and even within species. The same problems arise in the study of emotions (Bekoff 2002a) if we believe that emotions in animals are going to be identical to or even recognizably similar among different species. There is also variability among humans in what some might view as long-term goals and ideal states, and it would of course be premature to conclude that there is one set of long-term goals and ideal states that characterize, or are essential to, the capacity to be genuinely moral. We really are not experts about ourselves. To cash out stages of moral evolution as does Peterson, it looks like quasi-morality and protomorality are less than genuine morality. This view could lead to linear hierarchical views of evolution, whether or not it is Peterson's intent to go this route.

COOPERATION AND FAIRNESS ARE NOT BY-PRODUCTS OF AGGRESSION AND SELFISHNESS

In my view, cooperation is not merely always a by-product of tempering aggressive and selfish tendencies [combating Richard Dawkins' (1976) selfish genes] and attempts at reconciliation. Rather, cooperation and fairness can evolve on their own because they are important in the formation

03ch 12/5/03 11:28 AM Page 58
Aldine/Sussman/169329

and maintenance of social relationships. This view, in which nature is sanitized, contrasts with those who see aggression, cheating, selfishness, and perhaps amorality as driving the evolution of sociality. The combative Hobbesian world in which individuals are constantly at one another's throats is not the natural state of affairs, nature is not always red in tooth and claw, and altruism is not always simply selfishness disguised. Dawkins (2001), himself, has been quoted as saying "A pretty good definition of the kind of society in which I don't want to live is a society founded on the principles of Darwinism."

DOES IT FEEL GOOD TO BE FAIR?

Are some animals capable of the emotions and empathy that underlie morality? Watching animals in action has convinced many researchers, including myself, that they possess various emotions upon which a moral sense is built. We know that in humans these feelings are located in the brain's amygdala and hypothalamus and mediated by neurotransmitters such as dopamine, serotonin, and oxytocin. We also know that many animals, especially mammals, share with humans the same neurological structures and chemicals (Panksepp 1998; Bekoff 2002a). Of course, this does not necessarily mean that animals share our feelings, but careful observation of individuals during social encounters suggests that at least some of them do. And, their feelings are not necessarily identical to ours but this is of little or no concern because it is unlikely that they should be the same as ours. Indeed, it is unlikely that any two humans share precisely the same feelings when a given emotion is expressed.

In a recent review Preston and de Waal (2002) reported that empathy is more widespread among animals than has previously been recognized (see also Kuczaj, Tranel, Trone, and Hill 2001). In one classic study, Wechlin, Masserman, and Terris (1964) showed that a hungry rhesus monkey would not take food if doing so subjected another monkey to an electric shock. In similar situations rats will also hold back when they know their actions would cause pain to another individual. In another study, Diana monkeys were trained to insert a token into a slot to obtain food (Markowitz 1982). A male was observed helping the oldest female who had failed to learn the task. On three occasions he picked up the tokens she had dropped, put them into the machine, and allowed her to have the food. His behavior seemed to have no benefits for him at all; there did not seem to be any hidden agenda.

Elephants also may show concern for others. Joyce Poole (1998), who has studied African elephants for decades, was told a story about a teenage female who was suffering from a withered leg on which she could put no weight. When a young male from another group began attacking

03ch 12/5/03 11:28 AM Page 59
Aldine/Sussman/169329

the injured female, a large adult female chased the attacking male, returned to the young female, and touched her crippled leg with her trunk. Poole argues that the adult female was showing empathy and sympathy.

While good stories are not enough to make a compelling argument, there are so many such anecdotes that can be used to provide a solid basis for further detailed empirical research. Ignoring them is to ignore a rich database. I have argued elsewhere that the plural of anecdote is data (Bekoff 2002a).

We will probably never know whether these rats, monkeys, and elephants were feeling empathy as we do. But there are ways in which we can start comparing what is going on in animal brains to what happens in our own. Neuroimaging techniques are shedding new light on human emotions, and it likely will not be long before we start doing similar studies with other animals.

It is important to consider the possibility that it feels good to be fair to others, to cooperate with them and to treat them fairly, to forgive them for their mistakes and shortcomings. Recent neural imaging research on humans by Rilling and his colleagues (2002) has shown that the brain's pleasure centers are strongly activated when people cooperate with one another, that we might be wired to be fair or nice to one another. (I do not want to argue here that "being fair" always means "being nice.") This is extremely significant research for it posits that there is a strong neural basis for human cooperation and that it feels good to cooperate, that being nice is rewarding in social interactions and might be a stimulus for fostering cooperation and fairness. This sort of noninvasive research is precisely what is needed on other animals. Studies of the evolution of social morality need to consider seriously the rich cognitive ("intellectual") and deep emotional lives of other animals (Bekoff 2000, 2002a, 2002b) and how these capacities and a sense of self figure into a moral sensibility and the ability to make moral judgments. Truth be told, we really do not know much about these capacities even in our primate relatives despite claims that we do (Bekoff 2002c, 2003).

ANIMAL PLAY: LESSONS IN COOPERATION, FAIRNESS, AND TRUST

"Happiness is never better exhibited than by young animals, such as puppies, kittens, lambs, &c., when playing together, like our own children." So wrote Charles Darwin in his book *The Descent of Man and Selection in Relation to Sex*.

Animal play is obvious, but animal social morality is not (for definitions of social play see Bekoff and Byers 1981, 1998; Fagen 1981; Power 2000; Burghardt 2002). Social play in animals is an exhilarating activity in which

03ch 12/5/03 11:28 AM Page 60
Aldine/Sussman/169329

to engage and to observe. The rhythm, dance, and spirit of animals at play is incredibly contagious. Not only do their animal friends want to join in or find others with whom to romp, but I also want to play when I see animals chasing one another, playing hide-and-seek, and wresting with reckless abandon. My body once tingled with delight as I watched a young elk in Rocky Mountain National Park, Colorado, running across a snow field, jumping in the air and twisting his body while in flight, stopping to catch his breath, and then jumping and twisting over and over and again. There was plenty of grassy terrain around but he chose the snow field. Buffaloes will also follow one another and playfully run onto and slide across ice, excitedly bellowing "Gwaaa" as they do so. And, of course, we all know that dogs and cats love to play, as do many other mammals. Birds also playfully soar across the sky chasing, diving here and there, and frolicking with one another.

I think of play as being characterized by what I call the "five s's of play," its spirit, symmetry, synchrony, sacredness, and soulfulness. The spirit of play is laid bare for all to see as animals prodigally run about, wrestle, and knock one another over. The symmetry and synchrony of play are reflected in the harmony of the mutual agreements to trust one another—individuals share intentions to cooperate with one another to prevent play from spilling over into fighting. This trust is sacred. Finally, there is a deepness to animal play in that the players are so immersed in play that they are the play. Play is thus a soulful activity, perhaps the essence of the individual's being at the moment as they play from deep in their hearts. As Aquinas noted, play is about being, there are no why's in play.

There is also a feeling of incredible freedom and creativity in the flow of play. So it is important also to keep in mind the six f's of play, its flexibility, freedom, friendship, frolic, fun, and flow. As they run about, jump on one another, somersault, and bite one another animals create mind-boggling scenarios. Behavior patterns that are observed in mating are intermixed in flexible kaleidoscopic sequences with actions that are used during fighting, looking for prey, and avoiding being eaten.

The unmistakable emotions associated with play—joy and happiness—drive animals into becoming at one with the activity. One way to get animals (including humans) to do something is to make it fun, and there is no doubt that animals enjoy playing. Studies of the chemistry of play support the claim that play is fun. Dopamine (and perhaps serotonin and norepinephrine) are important in the regulation of play. Rats show an increase in dopamine activity when anticipating the opportunity to play (Siviy 1998) and enjoy being playfully tickled (Panksepp 1998, 2000). There is also a close association between opiates and play (Panksepp 1998).

Neurobiological data are essential for learning more about whether play truly is a subjectively pleasurable activity for animals as it seems to

03ch 12/5/03 11:28 AM Page 61
Aldine/Sussman/169329

be for humans. Siviy's and Panksepp's findings suggest that it is. In light of these neurobiological ("hard") data concerning possible neurochemical bases for various moods, in this case joy and pleasure, skeptics who claim that animals do not feel emotions might be more likely to accept the idea that enjoyment could well be a motivator for play behavior.

IT BEGINS WITH AN HONEST "BOW": "I WANT TO PLAY WITH YOU"

"Would you care to play?" asks one wolf of another. "Yes, I would." After each individual agrees to play and not to fight, prey on, or mate with the other, there are ongoing rapid and subtle exchanges of information so that their cooperative agreement can be fine-tuned and negotiated on the run, so that the activity remains playful. Incorporated into explanations of social play are such notions as trusting, behaving fairly, forgiving, apologizing, and perhaps justice, behavioral attributes that underlie social morality and moral agency. Recent research by Okamoto and Matsumara (2000) suggests that punishment and apology play a role in maintaining cooperation between individual nonhuman primates.

When individuals play they typically use action patterns that are also used in other contexts, such as predatory behavior, antipredatory behavior, and mating. These actions may not vary much across different contexts, or they may be hard to discriminate even for the participants. 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 ongoing 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 a play mood (Bekoff 1975, 1977a, 1995; Bekoff and Allen 1992, 1998; Allen and Bekoff 1997) 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; Bekoff and Byers 1981; Fagen 1981). I found that play signals in infant canids (domestic dogs, wolves, and coyotes) were used nonrandomly, especially when biting was accompanied by rapid side-to-side shaking of the head (Bekoff 1995). Biting accompanied by rapid side-to-side shaking of the head is performed during serious aggressive and

03ch 12/5/03 11:28 AM Page 62
Aldine/Sussman/169329

predatory encounters and can easily be misinterpreted if its meaning is not modified by a play signal. There also is little evidence that play signals are used to deceive others in canids or other species.

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 I am aware that actually look at the relative frequencies of occurrence of honest and deceptive play signaling, but my own long-term observations indicate that deceptive signaling is so rare that I cannot remember more than a few occurrences in thousands of play sequences. Cheaters 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 (personal observations). It is not known if individuals select play partners based on what they have observed during play by others.

In domestic dogs there is little tolerance for noncooperative cheaters. Cheaters may be avoided or chased from play groups. There seems to a sense of what is right, wrong, and fair. While studying dog play on a beach in San Diego, California, Alexandra 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. 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. Even in rats fairness and trust are important in the dynamics of playful interactions. Sergio Pellis (2002), a psychologist at the University of Lethbridge in Canada, discovered that sequences of rat play consist of individuals assessing and monitoring one another and then fine-tuning and changing their own behavior to maintain the play mood. When the rules of play are violated, when fairness breaks down, so does play.

Individuals might also know that they are playing because the actions that are performed differ when they are performed during play when compared to other contexts (Hill and Bekoff 1977), or the order in which motor patterns are performed differs from, and might be more variable than, the order in which they are performed during the performance of, for example, serious aggressive, predatory, or reproductive activities (Bekoff and Byers 1981).

Individuals also engage in role-reversing and self-handicapping (Bekoff and Allen 1998; Bauer and Smuts 2002; Horowitz 2002) to maintain social play. 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

03ch 12/5/03 11:28 AM Page 63
Aldine/Sussman/169329

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 partners 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 might voluntarily not roll over on his back during fighting, but would do so while playing. In some instances role-reversing and self-handicapping might 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 or altering behavioral sequences, might serve to signal an individual's intention to continue to play. In this way there can be mutual benefits to each individual player because of their agreeing to play and not fight or mate. This might differentiate cooperative play from the situation described above in which a male Diana monkey helped a female get food when she could not learn the task that would bring her food. There seemed to be no benefit to the male to do so. (I thank Jan Nystrom for marking this distinction.)

CAN ANIMALS FORGIVE?

Even for the behavior of forgiving, which is often attributed solely to humans, the renowned evolutionary biologist David Sloan Wilson shows that forgiveness is a complex biological adaptation. In his book *Darwin's Cathedral: Evolution, Religion, and the Nature of Society,* Wilson concludes that "forgiveness has a biological foundation that extends throughout the animal kingdom" (2002:195). And further, "Forgiveness has many faces—*and needs to*—in order to function adaptively in so many different contexts" (ibid.:212). While Wilson concentrates mainly on human societies, his views can easily be extended—and responsibly so—to nonhuman animals. Indeed, Wilson points out that adaptive traits such as forgiveness might not require as much brain power as once thought. This is not to say that animals aren't smart, but rather that forgiveness might be a trait that is basic to many animals even if they don't have especially big and active brains. Perhaps if we try to learn more about forgiveness in animals and how it functions in play, we will also learn to live more compassionately and cooperatively with one another.

03ch 12/5/03 11:28 AM Page 64
Aldine/Sussman/169329

FINE-TUNING PLAY: WHY COOPERATE AND PLAY FAIRLY?

For years I tried to figure out why play evolved as it did. Why do animals carefully use play signals to tell others that they really want to play and not try to dominate them, why do they engage in self-handicapping and role-reversing? One morning, while hiking with my companion dog, Jethro, I had one of those infamous "aha" experiences and the puzzle was solved. It dawned on me that during social play, while individuals are having fun in a relatively safe environment, they learn ground rules that are acceptable to others—how hard they can bite, how roughly they can 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 speak to the evolution of social morality. What could be a better atmosphere in which to learn social skills than during social play, where there are few penalties for transgressions? Individuals might also generalize codes of conduct learned in playing with specific individuals to other group members and to other situations such as sharing food, defending resources, grooming, and giving care. (Social morality does not mean other animals are behaving unfairly when they kill for food, for example, for they have evolved to do this.)

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. There is a certain innocence or ingenuousness in play. Individuals must cooperate with one another when they play—they must negotiate agreements to play (Bekoff 1995). Fagen noted that "levels of cooperation in play of juvenile primates may exceed those predicted by simple evolutionary arguments" (1993:192). The highly cooperative nature of play has evolved in many other species (Fagen 1981; Bekoff 1995; Bekoff and Allen 1998; Power 2000; Burghardt 2002). 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; Ridley 1996; de Waal 1996; Dugatkin 1997; Hauser 2000; *Journal of Consciousness Studies* 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 social morality, namely behaving fairly.

Individuals of different species seem to fine-tune ongoing 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 on the run, from

03ch 12/5/03 11:28 AM Page 65
Aldine/Sussman/169329

moment-to-moment, to make certain everything is all right—that this is still play. Aldis (1975) suggested that in play, there is a 50:50 rule so that each player "wins" about 50 percent of its play bouts by adjusting its behavior to accomplish this (for further discussion and details on rodent play, see Pellis 2002).

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-minute play sessions with another dog, twice a week, are sufficient for domestic dogs from three to seven weeks of age (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 (Spinka, Newberry, and Bekoff 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- 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, there seems to be little doubt that play has *some* benefits and that the absence of play can have devastating effects on social development (Power 2000; Burghardt 2002).

In canids and many other mammals (and some birds) there is a small time window during early development 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.

FAIRNESS AND FITNESS

I believe that a sense of fairness is common to many animals, because without it there could be no social play, and without social play individual animals and entire groups would be at a disadvantage. If I am correct, morality evolved because it is adaptive in its own right, and not because it is merely an antidote to competition or aggression. Behaving fairly helps

03ch 12/5/03 11:28 AM Page 66
Aldine/Sussman/169329
Aldi

many animals, including humans, to survive and flourish in their particular social environment. I fully realize that this may sound like a radical idea, particularly if one views morality as uniquely human and a sort of mystical quality that sets us apart from other animals. But if you accept my argument that play and fairness are inextricably linked then it is just a short move to showing that individual animals might well benefit from these behaviors.

My own fieldwork on coyotes has revealed one direct cost paid by animals that fail to engage fully in play. I have found that coyote pups who do not play much are less tightly bonded to other members of their group and are more likely to strike out on their own (Bekoff 1977b). 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, we found that more than 55 percent of yearlings who drifted away from their social group died, whereas fewer than 20 percent of their stay-at-home peers did (Bekoff and Wells 1986).

THE EVOLUTION OF FAIRNESS: A GAME-THEORETICAL MODEL

Much research on the evolution of cooperation has been modeled using game-theoretic approaches. Lee Dugatkin and I (Dugatkin and Bekoff 2003) used a similar technique 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 our 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 we 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 I mentioned above, there is little evidence that play signals are used to deceive others at any stage of development (Bekoff 1977a; Bekoff and Allen 1998). Our ideas are certainly testable in principle by following identified individuals and recording how they distribute fairness across different activities as they mature.

03ch 12/5/03 11:28 AM Page 67
Aldine/Sussman/169329

NEUROBIOLOGICAL BASES OF SHARING INTENTIONS AND MIND-READING: SOME POSSIBLE CONNECTIONS AMONG ACTING, SEEING, FEELING, AND FEELING/KNOWING

How might a play bow (or other action) serve to provide information to its recipient about the sender's intentions? Is there a relationship among acting, feeling, seeing, and feeling/knowing? Perhaps one's own experiences with play can promote learning about the intentions of others. Perhaps the recipient shares the intentions (beliefs, desires) of the sender based on the recipient's own prior experiences of situations in which she performed play bows. Recent research suggests a neurobiological basis for sharing intentions. "Mirror neurons," found in macaques, fire when a monkey executes an action and also when the monkey observes the same action performed by another monkey (Gallese 1998; Gallese and Goldman 1998; Motluk 2001).

Research on mirror neurons is truly exciting and the results of these efforts will be very helpful for answering questions about which species of animals may have "theories of mind" or "cognitive empathy" about the mental and emotional states of others. Gallese and the philosopher Alvin Goldman suggest that mirror neurons might "enable an organism to detect certain mental states of observed conspecifics . . . as part of, or a precursor to, a more general mind-reading ability" (1998:493). Laurie Carr and her colleagues at the University of California at Los Angeles discovered, by using neuroimaging in humans, similar patterns of neural activation both when individuals observed a facial expression depicting an emotion and when they imitated the facial expression. This research suggests a neurobiological underpinning of empathy (Laurie Carr, personal communication). Frith and Frith (1999) report the results of neural imaging studies in humans that suggest a neural basis for one form of "social intelligence," understanding others' mental states (mental state attribution).

More comparative data are needed to determine if mirror neurons (or functional equivalents) are found in other taxa and if they might actually play a role in the sharing of intentions or feelings—perhaps keys to empathy—between individuals engaged in an ongoing social interaction such as play. Neuroimaging studies will also be especially useful.

LEVELS OF SELECTION

I am sure that close scrutiny of social animals will reveal more evidence that having a sense of fairness benefits individuals. More controversially, I also believe that a moral sense benefits groups as a whole because during social play group members learn rules of engagement that influence their

03ch 12/5/03 11:28 AM Page 68
Aldine/Sussman/169329

decisions about what is acceptable behavior when dealing with each other. Such an understanding is essential if individuals are to work in harmony to create a successful group able to outcompete other groups. Following the lines of Sober and Wilson's (1998:135ff.) discussion concerning the choice of social partners, it may be that behaving fairly is a group adaptation, 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). We still need somehow to figure out how to test rigorously extant ideas about levels of selection—group selection "versus" individual selection—and studies of the evolution of social morality are good places to focus for expanding our views (e.g., Boehm 1999; Leigh 1999; see also Aviles 1999; Bradley 1999; Gould and Lloyd 1999; Kitchen and Packer 1999; Mayr 2000).

SPECIESISM AND THE TAXONOMIC DISTRIBUTION OF MORAL CAPACITY: THE IMPORTANCE OF STUDYING SOCIAL CARNIVORES

We simply do not have enough data to make hard and fast claims about the taxonomic distribution among different species of the cognitive skills and emotional capacities necessary for being able to empathize with others, to behave fairly, or to be moral agents. Recently, Marler concluded his review of social cognition in nonhuman primates and birds as follows: "I am driven to conclude, at least provisionally, that there are more similarities than differences between birds and primates. Each taxon has significant advantages that the other lacks" (1996:22). Tomasello and Call summarized their comprehensive review of primate cognition by noting that "the experimental foundation for claims that apes are 'more intelligent' than monkeys is not a solid one, and there are few if any naturalistic observations that would substantiate such broad-based, species-general claims" (1997:399–400). While Flack and de Waal's (2000) and others' focus is on nonhuman primates as the most likely animals to show precursors to human morality, others have argued that we might learn as much or more about the evolution of human social behavior by studying social carnivores (Schaller and Lowther 1969; Tinbergen 1972; Thompson 1975; Drea and Frank 2003), species whose social behavior and organization resemble that of early hominids in a number of ways (divisions of labor, food sharing, care of young, and inter- and intrasexual dominance hierarchies).

What we really need are long-term field studies of social animals for which it would be reasonable to hypothesize that emotions and morality have played a role in the evolution of sociality, that emotions and morality are important in the development and maintenance of social bonds that

03ch 12/5/03 11:28 AM Page 69
Aldine/Sussman/169329

allow individuals to work together for the benefit of all group members (see also Gruen 2002).

IMPORTANCE OF PREDICTION: A LITMUS TEST FOR KNOWING?

The ability to make accurate predictions about what an individual is likely to do in a given social situation may be closely linked with one's having extensive experience with specific individuals. Of course, extensive formal ("scientific") experience watching animals is not necessary for being able to make accurate predictions. Also, while I cannot know with absolute certainty that any of the animals about whom I have written (or others) have beliefs, desires, or intentions, I also cannot know with absolute certainty if they have a sense of "right" or "wrong" or if they are merely acting "as if" they are moral beings. They perform what can be called "moral behavior" but it might have no bearing on what they are thinking or feeling. However, the inescapable uncertainty associated with these claims does not mean that I do not know quite a lot about what is happening in their minds. It seems fair to ask skeptics to do more than say "'as if' is not enough" and to assume some responsibility for studying these questions in more rigorous ways.

In *Species of Mind*, Colin Allen and I (1997) argued that there are a number of reasons that cognitive explanations that entail beliefs, desires, or intentions may be the best explanations to which to appeal because they help us come to terms with questions centering on the comparative and evolutionary study of animal minds. First, the explanatory power of our theorizing is increased. Second, it is obvious that a cognitive approach can generate new ideas that can be tested empirically, help in evaluations of extant explanations, lead to the development of new predictive models, and, perhaps, lead to the reconsideration of old data, some of which might have resisted explanation without a cognitive perspective. Third, cognitive explanations account for observed flexibility in behavior better than do less flexible stimulus-response accounts that stipulate do "this" in "this" situation or "that" in "that" situation (Bekoff 1996). Fourth, cognitive explanations might help scientists come to terms with larger sets of available data that are difficult to understand. Fifth, cognitive explanations may also be more parsimonious and less cumbersome than explanations that require numerous and diverse stimulus-response contingencies (Bekoff 1996; Allen and Bekoff 1997; Bekoff and Allen 1997; see also de Waal 1991).

The ability to predict what an individual is likely to do next in a social encounter might be a useful litmus test for what is happening in that individual's brain. This is not to say that the ability to predict ongoing

03ch 12/5/03 11:28 AM Page 70
Aldine/Sussman/169329

behavior will ever be as accurate as, say, astronomical predictions concerning the position of stars in the sky. Nonetheless, researchers and others who have spent much time watching individual animals are rather good at predicting their behavior, and many of these predictions are tied in with attributions of beliefs, desires, or intentions. This is the case for my own extensive experience of watching canids signal their intentions to engage in and to maintain social play. Intentional or representational explanations are important to my making accurate predictions about future behavior.

All I want to put out on the table here is the idea that the ability to predict behavior with a high degree of accuracy might also be a good reason to favor cognitive explanations in certain situations. Accurate prediction might be used as one measure of what a human observer "knows" about the behavior of the animals he or she is studying. So, before skeptics adamantly claim that prediction is not a viable candidate for accepting, in some cases, that intentional or representational explanations can be reliable accounts of what animals might believe, desire, or intend, they should pay attention to the veracity (and parsimony) of the predictions that are offered.

WILD JUSTICE, SOCIAL PLAY, AND SOCIAL MORALITY: WHERE TO FROM HERE?

> Justice presumes a personal concern for others. It is first of all a sense, not a rational or social construction, and I want to argue that this sense is, in an important sense, natural. (Solomon 1995:102)
>
> It is not difficult to imagine the emergence of justice and honor out of the practices of cooperation. (Damasio 2003:162)

To stimulate further comparative research (and the development of models) on a wider array of species than has previously been studied, I offer the hypothesis that social morality, in this case behaving fairly, is an adaptation that is shared by many mammals, not only by nonhuman and human primates. Behaving fairly evolved because it helped young animals acquire social (and other) skills needed as they matured 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). I often wonder if our view of the world would have been different had Charles Darwin been a female, if some or many of the instances in which competition is invoked were

03ch 12/5/03 11:28 AM Page 71
Aldine/Sussman/169329

viewed as cooperation. Women tend to "see" more cooperation in nature than do men. Adams and Burnett (1991) discovered that female ethologists working in East Africa use a substantially different descriptive vocabulary than do male ethologists. Of the nine variables they studied, those concerning cooperation and female gender were the most important in discriminating women's and men's word use. They concluded that "The variable COOPERATION demonstrates the appropriateness of feminist claims to connection and cooperation as women's models for behaviour, as divergent from the traditional competitive model" (ibid.:558). Why women and men approach the same subject from a different perspective remains largely unanswered.

Group-living animals may provide many insights into animal morality. In many social groups individuals develop and maintain tight social bonds that help to regulate social behavior. Individuals coordinate their behavior—some mate, some hunt, some defend resources, some accept subordinate status—to achieve common goals and to maintain social stability. Consider, briefly, pack-living wolves. For a long time researchers thought pack size was regulated by available food resources. Wolves typically feed on such prey as elk and moose, each of which is larger than an individual wolf. Hunting such large ungulates successfully takes more than one wolf, so it made sense to postulate that wolf packs evolved because of the size of wolves' prey. Defending food might also be associated with pack-living. However, long-term research by Mech (1970) showed that pack size in wolves was regulated by *social* and not food-related factors. Mech discovered that the number of wolves who could live together in a coordinated pack was governed by the number of wolves with whom individuals could closely bond ("social attraction factor") balanced against the number of individuals from whom an individual could tolerate competition ("social competition factor"). Codes of conduct and packs broke down when there were too many wolves. Whether or not the dissolution of packs was due to individuals behaving unfairly is unknown, but this would be a valuable topic for future research in wolves and other social animals. Solomon (1995:143) contends that "A wolf who is generous can expect generosity in return. A wolf who violates another's ownership zone can expect to be punished, perhaps ferociously, by others." These claims can easily be studied empirically. [For interesting studies of the "social complexity hypothesis," which claims "that animals living in large social groups should display enhanced cognitive abilities" when compared to those who do not, see Bond, Kamil, and Balda (2003:479) and Drea and Frank (2003)].

In social groups, individuals often learn what they can and cannot do, and the group's integrity depends upon individuals agreeing that certain rules regulate their behavior. At any given moment individuals know their

03ch 12/5/03 11:28 AM Page 72
Aldine/Sussman/169329
Aldi

place or role and that of other group members. As a result of lessons in social cognition and empathy that are offered in social play, individuals 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. The absence of social structure and boundaries can produce gaps in morality that lead to the dissolution of a group (Bruce Gottlieb, personal communication).

In summary, I argue that mammalian social play is a useful behavioral phenotype on which to concentrate in order to learn more about the evolution of fairness and social 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.) There is strong selection for playing fairly because most if not all individuals benefit from adopting this behavioral strategy (and group stability may be also be fostered). Numerous mechanisms (play invitation signals, variations in the sequencing of actions performed during play when compared to other contexts, self-handicapping, role-reversing) have evolved to facilitate the initiation and maintenance of social play in numerous mammals—to keep others engaged—so that agreeing to play fairly and the resulting benefits of doing so can be readily achieved.

Ridley (1996) points out that humans seem to be inordinately upset about unfairness, but we do not know much about other animals' reaction to unfairness. He suggests that perhaps behaving fairly pays off in the long run. Dugatkin's and my model of the development and evolution of cooperation and fairness (Dugatkin and Bekoff 2003) suggests it might. Hauser (2000) concluded that there is no evidence that animals can evaluate whether an act of reciprocation is fair. However, he did not consider social play in his discussion of animal morality and moral agency. De Waal (1996) remains skeptical about the widespread taxonomic distribution of cognitive empathy after briefly considering social play, but he remains open to the possibility that cognitive empathy might be found in animals other than the great apes (see Preston and de Waal 2002). It is premature to dismiss the possibility that social play plays some role in the evolution of fairness and social morality or that animals other than primates are unable intentionally to choose to behave fairly because they lack the necessary cognitive skills or emotional capacities. We really have very little information that bears on these questions.

Let me stress that I am 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. No matter. Provided there is variation in levels of morality among individuals, and provided virtue is rewarded by a greater number of offspring, then any genes associated with good behavior are likely to accumulate in subsequent gen-

03ch 12/5/03 11:28 AM Page 73
Aldine/Sussman/169329

erations. And the observation that play is rarely unfair or uncooperative is surely an indication that natural selection acts to weed out those who do not play by the rules.

Future comparative research that considers the nature and details of the social exchanges that are needed for animals to engage in play—reciprocity and cooperation—will undoubtedly produce data that bear on the questions that I raise in this brief essay and also help to "operationalize" the notion of behaving fairly by informing us about what sorts of evidence confirm that animals are behaving with some sense of fairness. In the absence of this information it is premature to dismiss the possibility that social play plays some role in the evolution of fairness and social morality or that animals other than primates are unable intentionally to choose to behave fairly because they lack the necessary cognitive skills or emotional capacities. These are empirical questions for which the comparative database is scant.

Gruen (2002) also rightfully points out that we still need to come to terms with what it means to be moral. She also suggests that we need to find out what cognitive and emotional capacities operate when humans perform various moral actions, and to study animals to determine if they share these capacities or some variation of them. Even if it were the case that available data suggested that nonhuman primates do not seem to behave in a specific way, for example, playing fairly, in the absence of comparative data this does not justify the claim that individuals of other taxa cannot play fairly. [At a meeting in Chicago in August 2000 dealing with social organization and social complexity, it was hinted to me that while my ideas about social morality are interesting, there really is no way that social carnivores could be said to be so decent—to behave (play) fairly—because it was unlikely that even nonhuman primates were this virtuous.]

Learning about the taxonomic distribution of animal morality involves answering numerous and often difficult questions. Perhaps it will turn out that the best explanation for existing data in some taxa is that some individuals do indeed on some occasions modify their behavior to play fairly.

Play may be a unique category of behavior in that asymmetries are tolerated more so than in other social contexts. Play cannot occur if the individuals choose not to engage in the activity and the equality (or symmetry) needed for play to continue makes it different from other forms of seemingly cooperative behavior (e.g., hunting, caregiving). This sort of egalitarianism is thought to be a precondition for the evolution of social morality in humans. Whence did it arise? Truth be told, we really do not know much about the origins of egalitarianism. Armchair discussions, while important, will do little in comparison to our having direct experiences with other animals. In my view, studies of the evolution of social morality are among the most exciting and challenging projects that

03ch 12/5/03 11:28 AM Page 74
Aldine/Sussman/169329

behavioral scientists (ethologists, geneticists, evolutionary biologists, neurobiologists, psychologists, anthropologists), theologians, and religious scholars face. We need to rise to the *extremely* challenging (and frustrating) task before us rather than dismiss summarily and unfairly, in a speciesistic manner, the moral lives of other animals. *Fair is fair*.

There is no doubt that studying and learning about animal play can teach us to live more compassionately with heart and love. Keep in mind the spirit, symmetry, synchrony, sacredness, and soul of play. Learning about the evolution of cooperation, fairness, trust, and social morality goes well beyond traditional science and can be linked to religion, theology, and perhaps even different notions of God because ideas about continuity and discontinuity (the possible uniqueness of humans and other species) and individuality have to be taken into account. I cannot think of a more exciting field of inquiry, and I feel lucky that I am able to pursue the daunting questions that are concerned with the evolution of social morality.

MORALITY AND HUMAN NATURE: THE PRECAUTIONARY PRINCIPLE

Just what role does human morality play in defining "human nature"? We do not really know despite strong claims to the contrary. Using animal models to rationalize cruelty, divisiveness, warfare, territoriality, and selfishness is 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," which 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. The precautionary principle can be easily applied in studies of the evolution of social morality. To wit, I claim that we know enough to warrant further comparative studies of the evolution of social 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 social morality and how this information can be used to give us hope for the future rather than 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.

03ch 12/5/03 11:28 AM Page 75
Aldine/Sussman/169329

The importance of interdisciplinary collaboration and cooperation in studies of animal cognition, cooperation, and moral behavior cannot be emphasized too strongly. There really *is* a paradigm shift in our studies of the evolution of morality. It is clear that morality and virtue didn't suddenly appear in the evolutionary epic beginning with humans. While fair play in animals may be a rudimentary form of social morality, it still could be a forerunner of more complex and more sophisticated human moral systems. It is self-serving, anthropocentric speciesism to claim that we are the *only* moral beings in the animal kingdom. It is also a simplistic and misleading view to assume that humans are merely naked apes.

The origins of virtue, egalitarianism, and morality are more ancient than our own species. Humans also aren't necessarily morally superior to other animals. Indeed, it might just be that animal morality is purer than human morality because animals likely don't have as sophisticated notions of right and wrong. Wouldn't that be something? But, we will never learn about animal morality if we close the door on the possibility that it exists. It is still far too early to draw the uncompromising conclusion that human morality is different in *kind* from animal morality and walk away smugly in victory, fooling ourselves along the way.

ACKNOWLEDGMENTS

Much of this discussion appeared in two of my previous papers (Bekoff 2001a, 2001b) and has been updated where possible. I thank Bob Sussman for comments on an earlier draft of this paper and all of the people at the meeting at which this paper was discussed for their valuable and interdisciplinary insights.

REFERENCES

Adams, E. R. and G. W. Burnett. 1991. "Scientific Vocabulary Divergence among Female Primatologists Working in East Africa." *Social Studies of Science* 21:547–60.

Aldis, O. 1975. *Play-Fighting*. New York: Academic Press.

Allen, C. and M. Bekoff. 1997. *Species of Mind: The Philosophy and Biology of Cognitive Ethology*. Cambridge, MA: MIT Press.

Aureli, F. and F. B. M. de Waal (Eds.). 2000. *Natural Conflict Resolution*. Berkeley: University of California Press.

Aviles, L. 1999. "Cooperation and Non-Linear Dynamics: An Ecological Perspective on the Evolution of Sociality." *Evolutionary Ecology Research* 1:459–77.

Axelrod, R. 1984. *The Evolution of Cooperation*. New York: Basic Books.

Bauer, E. B. and B. B. Smuts. 2002. "Role Reversal and Self-Handicapping during Playfighting in Domestic Dogs, *Canis familiaris*." Paper presented at the meetings of the Animal Behavior Society, University of Indiana.

03ch 12/5/03 11:28 AM Page 76
Aldine/Sussman/169329

Bekoff, M. 1975. "The Communication of Play Intention: Are Play Signals Functional?" *Semiotica* 15:231–39.
Bekoff, M. 1977a. "Social Communication in Canids: Evidence for the Evolution of a Stereotyped Mammalian Display." *Science* 197:1097–99.
Bekoff, M. 1977b. "Mammalian Dispersal and the Ontogeny of Individual Behavioral Phenotypes." *American Naturalist* 111:715–32.
Bekoff, M. 1995. "Play Signals as Punctuation: The Structure of Social Play in Canids." *Behaviour* 132:419–29.
Bekoff, M. 1996. "Cognitive Ethology, Vigilance, Information Gathering, and Representation: Who Might Know What and Why?" *Behavioural Processes* 35:225–37.
Bekoff, M. (Ed.). 2000. *The Smile of a Dolphin: Remarkable Accounts of Animal Emotions.* New York: Discovery Books/Random House.
Bekoff, M. 2001a. "Social Play Behaviour, Cooperation, Fairness, Trust and the Evolution of Morality." *Journal of Consciousness Studies* 8(2):81–90.
Bekoff, M. 2001b. "The Evolution of Animal Play, Emotions, and Social Morality: On Science, Theology, Spirituality, Personhood, and Love." *Zygon* 36:615–55.
Bekoff, M. 2002a. *Minding Animals: Awareness, Emotions, and Heart.* New York: Oxford University Press.
Bekoff, M. 2002b. "Virtuous Nature." *New Scientist* (13 July):34–37.
Bekoff, M. 2002c. "Self-Awareness." *Nature* 419:255.
Bekoff, M. 2003. "Consciousness and Self in Animals: Some Reflections." *Zygon* 38:229–45.
Bekoff, M. and C. Allen. 1992. "Intentional Icons: Towards an Evolutionary Cognitive Ethology." *Ethology* 91:1–16.
Bekoff, M. and C. Allen. 1997. "Cognitive Ethology: Slayers, Skeptics, and Proponents." Pp. 313–34 in *Anthropomorphism, Anecdote, and Animals: The Emperor's New Clothes?* edited by R. W. Mitchell, N. Thompson, and L. Miles. Albany, NY: SUNY Press.
Bekoff, M. and C. Allen. 1998. "Intentional Communication and Social Play: How and Why Animals Negotiate and Agree to Play." Pp. 97–114 in *Animal Play: Evolutionary, Comparative, and Ecological Perspectives,* edited by M. Bekoff and J. A. Byers. Cambridge and New York: Cambridge University Press.
Bekoff, M., C. Allen, and G. M. Burghardt (Eds.). 2002. *The Cognitive Animal.* Cambridge, MA: MIT Press.
Bekoff, M. and J. A. Byers. 1981. "A Critical Reanalysis of the Ontogeny of Mammalian Social and Locomotor Play: An Ethological Hornet's Nest." Pp. 296–337 in *Behavioral Development: The Bielefeld Interdisciplinary Project,* edited by K. Immelmann, G. W. Barlow, L. Petrinovich, and M. Main. New York: Cambridge University Press.
Bekoff, M. and J. A. Byers (Eds.). 1998. *Animal Play: Evolutionary, Comparative, and Ecological Approaches.* New York: Cambridge University Press.
Bekoff, M. and M. C. Wells. 1986. "Social Behavior and Ecology of Coyotes." *Advances in the Study of Behavior* 16:251–338.
Bernstein, I. S. 2000. "The Law of Parsimony Prevails: Missing Premises Allow Any Conclusion." *Journal of Consciousness Studies* 7:31–34.
Bewley, T. 2003. "Fair's Fair." *Nature* 422:125–26.
Boehm, C. 1999. *Hierarchy in the Forest: The Evolution of Egalitarian Behavior.* Cambridge, MA: Harvard University Press.

03ch 12/5/03 11:28 AM Page 77
Aldine/Sussman/169329

Bond, A., A. C. Kamil, and R. P. Balda. 2003. "Social Complexity and Transitive Inference in Corvids." *Animal Behaviour* 65:479–87.

Bowles, S. and H. Gintis. 2002. *"Home reciprocans." Nature* 415:125–28.

Bradley, B. J. 1999. "Levels of Selection, Altruism, and Primate Behavior." *Quarterly Review of Biology* 74:171–94.

Burghardt, G. M. 2002. *The Genesis of Play.* Cambridge, MA: MIT Press.

Damasio, A. 2003. *Looking for Spinoza: Joy, Sorrow, and the Feeling Brain.* New York: Harcourt.

Darwin C. 1859. *On the Origin of Species by Means of Natural Selection.* London: Murray.

Darwin, C. [1871] 1936. *The Descent of Man and Selection in Relation to Sex*. New York: Random House.

Darwin, C. [1872] 1998. *The Expression of the Emotions in Man and Animals,* 3rd edition (with an Introduction, Afterword, and Commentaries by Paul Ekman). New York: Oxford University Press.

Dawkins, R. 1976. *The Selfish Gene.* New York: Oxford University Press.

Dawkins, R. 2001. "Sustainability Doesn't Come Naturally: A Darwinian Perspective on Values." <www.environmentfoundation.net/richard-dawkins.htm>.

de Waal, F. 1991. "Complementary Methods and Convergent Evidence in the Study of Primate Social Cognition." *Behaviour* 18:297–320.

de Waal, F. 1996. *Good-Natured: The Origins of Right and Wrong in Humans and Other Animals.* Cambridge, MA: Harvard University Press.

de Waal, F. and P. L. Tyack (Eds.). 2003. *Animal Social Complexity: Intelligence, Culture, and Individualized Societies.* Cambridge, MA: Harvard University Press.

Douglas, K. 2001. "Playing Fair." *New Scientist* (2281, 10 March):38–42.

Drea, C. M. and L. G. Frank. 2003. "The Social Complexity of Spotted Hyenas." Pp. 121–48 in *Animal Social Complexity: Intelligence, Culture, and Individualized Societies,* edited by F. de Waal and P. L. Tyack. Cambridge, MA: Harvard University Press.

Dugatkin, L. A. 1997. *Cooperation among Animals: An Evolutionary Perspective.* New York: Oxford University Press.

Dugatkin, L. A. and M. Bekoff. 2003. "Play and the Evolution of Fairness: A Game Theory Model." *Behavioural Processes* 60:209–14.

Fagen, R. 1981. *Animal Play Behavior*. New York: Oxford University Press.

Fagen, R. 1993. "Primate Juveniles and Primate Play." Pp. 183–96 in *Juvenile Primates: Life History, Development, and Behavior,* edited by M. E. Pereira and L. A. Fairbanks. New York: Oxford University Press.

Fehr, E. and S. Gächter. 2002. "Altruistic Punishment in Humans." *Nature* 415: 137–40.

Fehr, E. and B. Rockenbach. 2003. "Detrimental Effect of Sanctions on Human Altruism." *Nature* 422:137–40.

Field, A. 2001. *Altruistically Inclined? The Behavioral Sciences, Evolutionary Theory, and the Origins of Reciprocity.* Ann Arbor: University of Michigan Press.

Flack, J. C. and F. de Waal. 2000. "Any Animal Whatever: Darwinian Building Blocks of Morality in Monkeys and Apes." *Journal of Consciousness Studies* 7:1–29.

Frith, C. D. and U. Frith. 1999. "Interacting Minds: A Biological Basis." *Science* 286:1692–95.

03ch 12/5/03 11:28 AM Page 78
Aldine/Sussman/169329

Gallese, V. 1998. "Mirror Neurons: From Grasping to Language." *Consciousness Bulletin* (Fall):3–4.

Gallese, V. and A. Goldman. 1998. "Mirror Neurons and the Simulation Theory of Mind-Reading." *Trends in Cognitive Science* 2:493–501.

Gould, S. J. and E. A. Lloyd. 1999. "Individuality and Adaptation across Levels of Selection: How Shall We Name and Generalize the Unit of Darwinism." *Proceedings of the National Academy of Sciences* 96:11904–09.

Gruen, L. 2002. "The Morals of Animal Minds." Pp. 437–42 in *The Cognitive Animal,* edited by M. Bekoff, C. Allen, and G. M. Burghardt. Cambridge, MA: MIT Press.

Güzeldere, G. and E. Nahmias. 2002. "Darwin's Continuum and the Building Blocks of Deception." Pp. 353–62 in *The Cognitive Animal,* edited by M. Bekoff, C. Allen, and G. M. Burghardt. Cambridge, MA: MIT Press.

Hauser, M. 2000. *Wild Minds.* New York: Henry Holt.

Hill, H. L. and M. Bekoff. 1977. "The Variability of Some Motor Components of Social Play and Agonistic Behaviour in Eastern Coyotes, *Canis latrans* var." *Animal Behaviour* 25:907–9.

Hinde, R. A. 2002. *Why Good Is Good: The Sources of Morality.* New York: Routledge.

His Holiness the Dalai Lama. 2002. "Understanding Our Fundamental Nature." Pp. 66–80 in *Visions of Compassion: Western Scientists and Tibetan Buddhists Examine Human Nature,* edited by R. J. Davidson and A. Harrington. New York: Oxford University Press.

Horowitz, A. C. 2002. "The Behaviors of Theories of Mind, and a Case Study of Dogs at Play." Ph.D. dissertation, University of California, San Diego.

Journal of Consciousness Studies. 2000. Volume 7(1/2).

Kitchen, D. M. and C. Packer. 1999. "Complexity in Vertebrate Societies." Pp. 176–96 in *Levels of Selection in Evolution,* edited by L. Keller. Princeton, NJ: Princeton University Press.

Kuczaj, S., K. Tranel, M. Trone, and H. Hill. 2001. "Are Animals Capable of Deception or Empathy? Implications for Animal Consciousness and Animal Welfare." *Animal Welfare* 10:S161–73.

Leigh, E. G., Jr. 1999. "Levels of Selection, Potential Conflicts, and Their Resolution: Role of the 'Common good.'" Pp. 15–30 in *Levels of Selection in Evolution,* edited by L. Keller. Princeton, NJ: Princeton University Press.

Macintyre, A. 1999. *Dependent Rational Animals: Why Human Beings Need the Virtues.* Chicago: Open Court.

Markowitz, H. 1982. *Behavioral Enrichment in the Zoo*. New York: Van Reinhold.

Marler, P. 1996. "Social Cognition: Are Primates Smarter Than Birds?" Pp. 1–32 in *Current Ornithology,* Volume 13, edited by V. Nolan, Jr., and E. D. Ketterson. New York: Plenum.

Mayr, E. 2000. "Darwin's Influence on Modern Thought." *Scientific American* 283:67–71.

Mech, L. D. 1970. *The Wolf.* Garden City, NY: Doubleday.

Mitchell, L. E. 1998. *Stacked Deck: A Story of Selfishness in America*. Philadelphia: Temple University Press.

Motluk, A. 2001. "Read My Mind." *New Scientist* 169:22–26.

Okamoto, K. and S. Matsumara. 2000. "The Evolution of Punishment and Apology: An Iterated Prisoner's Dilemma Model." *Evolutionary Ecology* 14:703–20.

03ch 12/5/03 11:28 AM Page 79
Aldine/Sussman/169329

Panksepp, J. 1998. *Affective Neuroscience*. New York: Oxford University Press.
Panksepp, J. 2000. "The Rat Will Play." Pp. 146–47 in *The Smile of a Dolphin: Remarkable Accounts of Animal Emotions,* edited by M. Bekoff. New York: Random House/Discovery.
Pellis, S. 2002. "Keeping in Touch: Play Fighting and Social Knowledge." Pp. 421–27 in *The Cognitive Animal,* edited by M. Bekoff, C. Allen, and G. M. Burghardt. Cambridge, MA: MIT Press.
Peterson, G. R. 1999. "The Evolution of Consciousness and the Theology of Nature." *Zygon* 34:283–306.
Peterson, G. R. 2000. "God, Genes, and Cognizing Agents." *Zygon* 35:469–80.
Poole, J. 1998. "An Exploration of a Commonality between Ourselves and Elephants." *Etica & Animali* 9:85–110.
Power, T. G. 2000. *Play and Exploration in Children and Animals.* Hillsdale, NJ: Lawrence Erlbaum Associates.
Preston, S. D. and F. B. M. de Waal. 2002. "Empathy: Its Ultimate and Proximate Bases." *Behavioral and Brain Sciences* 25:1–72.
Ridley, M. 1996. *The Origins of Virtue: Human Instincts and the Evolution of Cooperation.* New York: Viking.
Ridley, M. 2001. *The Cooperative Gene*. New York: Free Press.
Rilling, J. K., D. A. Gutman, T. R. Zeh, G. Pagnoni, G. S. Berns, and C. D. Kitts. 2002. "A Neural Basis for Cooperation." *Neuron* 36:395–405.
Riolo, R. L., M. D. Cohen, and R. Axelrod. 2001. "Evolution of Cooperation without Reciprocity." *Nature* 414:441–43.
Schaller, G. B. and G. R. Lowther. 1969. "The Relevance of Carnivore Behavior to the Study of Early Hominids." *Southwestern Journal of Anthropology* 25: 307–41.
Scott, J. P. and J. L. Fuller. 1965. *Genetics and the Social Behavior of the Dog*. Chicago: University of Chicago Press.
Sigmund, K. and M. A. Nowak. 2001. "Evolution: Tides of Tolerance." *Nature* 414:403–5.
Sigmund, K., E. Fehr, and M. A. Nowak. 2002. "The Economics of Fair Play." *Scientific American* 286(1):83–87.
Singer, P. 1999. *A Darwinian Left: Politics, Evolution, and Cooperation*. New Haven, CT: Yale University Press.
Siviy, S. 1998. "Neurobiological Substrates of Play Behavior: Glimpses into the Structure and Function of Mammalian Playfulness." Pp. 221–42 in *Animal Play: Evolutionary, Comparative, and Ecological Perspectives,* edited by M. Bekoff and J. A. Byers. New York: Cambridge University Press.
Skyrms, B. 1996. *Evolution of the Social Contract.* New York: Cambridge University Press.
Sober, E. and D. S. Wilson. 1998. *Unto Others: The Evolution and Psychology of Unselfish Behavior.* Cambridge, MA: Harvard University Press.
Sober, E. and D. S. Wilson. 2000. Summary of *Unto Others: The Evolution and Psychology of Unselfish Behavior*. *Journal of Consciousness Studies* 7:185–206.
Solomon, R. 1995. *A Passion for Justice: Emotions and the Origins of the Social Contract.* Lanham, MD: Rowan & Littlefield.
Spinka, M., R. C. Newberry, and M. Bekoff. 2001. "Mammalian Play: Training for the Unexpected." *Quarterly Review of Biology* 76:141–68.

03ch 12/5/03 11:28 AM Page 80
Aldine/Sussman/169329

Thompson, P. R. 1975. "A Cross-Species Analysis of Carnivore, Primate, and Hominid Behavior." *Journal of Human Evolution* 4:113–24.

Tinbergen, N. 1972. *Introduction to Hans Kruuk, The Spotted Hyena.* Chicago: University of Chicago Press.

Tomasello, M. and J. Call. 1997. *Primate Cognition.* New York: Oxford University Press.

Watson, D. M. and D. B. Croft. 1996. "Age-Related Differences in Playfighting Strategies of Captive Male Red-Necked Wallabies (*Macropus rufogriseus banksianus*)." *Ethology* 102:333–46.

Wechlin, S., J. H. Masserman, and W. Terris, Jr. 1964. "Shock to a Conspecific as an Aversive Stimulus." *Psychonomic Science* 1:17–18.

Wilson, D. S. 2002. *Darwin's Cathedral: Evolution, Religion, and the Nature of Society.* Chicago: University of Chicago Press.