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Introduction: Going Beyond Primates

People often wonder if some nonhuman animal beings (hereafter animals) have codes of social conduct that regulate their behaviour in terms of what is permissible and what is not permissible during social encounters. In a recent issue of this journal (Volume 7, No. 1-2, 2000), researchers from many disciplines debated the evolutionary origins of morality. Essentially, they 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, namely that behavioural, cognitive, and emotional variations among different species are differences in *degree* rather than difference in *kind,* are often invoked in such exercises.

Evolutionary reconstructions of social behaviour often depend on educated guesses (some good and some not so good) about the past social (and other) environments in which ancestral beings lived. 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 is very 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 (2000) concern that 'morality in animals might lie outside of the realm of measurement techniques available to science' (p. 34) needs to be taken seriously. Nonetheless, it seems clear that detailed comparative analyses of social behaviour 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.

Many discussions of the evolution of morality centre on the development of various sorts of models (e.g. Axelrod, 1984; Ridley, 1996; Skyrms, 1996; Dugatkin, 1997; Sober and Wilson, 1998; 2000; various authors' essays in *Journal of Consciousness Studies,* 2000, volume 7, No. 1- 2). 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).

Here I briefly discuss some comparative data on social play behaviour in hope of broadening the array of species in which researchers attempt to study animal morality. I am specifically concerned with the notion of 'behaving fairly'. In the term '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 will cash this out below in my discussion of social play behaviour.

It is important not to be a cognitive or a moral speciesist, for currently we simply do not have enough data to make hard and fast claims about the taxonomic distribution of cognitive skills and emotional capacities necessary for being able to empathize with others or to behave fairly (Allen and Bekoff, 1997; Bekoff, 2000a,b). Recently, Marler (1996, p. 22) 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.' Tomasello and Call (1997, pp. 399-400) 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.' 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 behaviour by studying social carnivores (Schaller and Lowther, 1969; Tinbergen, 1972; Thompson, 1975), species whose social behaviour and organization resemble that of early hominids in a number of ways (divisions of labour, food sharing, care of young, and inter- and intrasexual dominance hierarchies).

Social Play, Communication, and Cooperation: Behaving Fairly

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). Many mammals, especially youngsters, engage in social play, relentlessly seeking out play and expressing joy as they run about and wrestle, chase, and bite others (Bekoff and Byers, 1981 ; 1998; Fagen, 1981). In his book *The Descent of Man and Selection in Relation to Sex,* Charles Darwin wrote: 'Happiness is never better exhibited than by young animals, such as puppies, kittens, lambs, &c., when playing together, like our own children' (Darwin, 1871/1936, p. 448).

When individuals play they typically use action patterns that are also used in other contexts, such as predatory behaviour, antipredatory behaviour, 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 behaviour 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 behaviour 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 behaviour 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). Bekoff (1995) found that play signals in infant canids (domestic dogs, wolves, and coyotes) were used nonrandomly, especially when biting accompanied by rapid side-to-side shaking of the head was performed. 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. There also is little evidence that play signals are used to deceive others in canids or other species. Cheaters are unlikely to be chosen as play partners because others can simply refuse to play with them[1] and choose others, and limited data on infant coyotes do 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.)

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) 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 behaviour 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 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 not voluntarily roll-over on his back during fighting, but would do so while playing. In some instances role-reversing and self-handicapping and 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 behavioural sequences, might serve to signal an individual's intention to continue to play.

Fine-Tuning Play: Why Cooperate and Play Fairly?

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 (1993, p. 192) noted that, 'Levels of cooperation in play of juvenile primates may exceed those predicted by simple evolutionary arguments…' The highly cooperative nature of play has evolved in many other species (Fagen, 1981; Bekoff, 1995; Bekoff and Allen, 1998; Power, 2000). 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; Dugatkin, 1997; various authors' essays in this journal, Volume 7, No. 1- 2, 2000 and references therein), none has considered 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 on-going play sequences to maintain a play mood and to prevent play from escalating into real aggression. Detailed analyses of film show that there are subtle and fleeting movements and rapid exchanges of eye contact that suggest that players are exchanging information on the run, from moment-to-moment, to make certain everything is all right - that this is still play. Why might they do this? 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 *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-terms 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).

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.

Social Play and Social Morality: Some Possible Connections

I suggest 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 what is permissible and what is not permissible, and the existence of these codes might have something to say about 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. (Social morality does not mean other animals are behaving unfairly when they kill for food, for example, for they have evolved to do this.)

To stimulate further comparative research 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. A focus on social cooperation is needed to balance the plethora of research that is devoted to social competition (for further discussion, see Boehm, 1999, and Singer, 1999). Behaving fairly evolved because it helped young animals acquire social (and other) skills needed as they mature into adults.

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 behaviour. Individuals coordinate their behaviour -- 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,* 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 consequentially packs, broke down when there were too many wolves. Whether or not the dissolution of packs was due to individuals not behaving fairly is unknown, but this would be a valuable topic for future research in wolves and other social animals.

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 behaviour. At any given moment individuals know their 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).

Following the lines of Sober and Wilson's (1998, pp. 135-7) 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).

Neurobiological Bases of Sharing Intentions and Mind-Reading

How might a play bow (or other action) serve to provide information to its recipient about the sender's intentions? 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). 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 between individuals engaged in an on-going social interaction such as play. Neuro-imaging studies will also be useful.

Keeping Open Minds About Social Morality in Animals: Employing the Precautionary Principle

In summary, I argue that mammalian social play is a useful behavioural 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 behavioural 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 others animals reaction to unfairness. He suggests that perhaps behaving fairly pays off in the long run.

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 (or disconfirm) 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 data base is scant. 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.[2] Learning about the taxonomic distribution of animal morality involves answering numerous and often difficult questions. Perhaps it will

tum -out that the best explanation for existing data in some taxa is that some individuals do indeed on some occasions modify their behaviour to play fairly.

Ecologists and environmentalists have developed what they call the 'precautionary principle' (Applegate, 2000) that is used for making decisions about environmental problems. Essentially, 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 well 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. As Whiten (2000) points out in his discussion of whether or not animals read other's emotions, we should not ignore available observations and insights if we want them to serve as heuristics for further systematic research.

Play may be a unique category of behaviour 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 behaviour (e.g. hunting, care-giving). This sort of egalitarianism is thought to be a precondition for the evolution of social morality in humans. From where did it arise? Truth be told, we really do not know much about the origins of egalitarianism or social morality in animals. And, arm-chair 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 in behavioral scientists face. We need to rise to the task before us rather than dismiss summarily and unfairly, in a speciesistic manner, the moral lives of other animals. Fair is fair.

Notes

[1] I thank David Sloan Wilson for making these points in his detailed review of an earlier draft of this essay.

[2] At a meeting in Chicago, Illinois (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.

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References

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

Applegate, J.S. (2000), 'The precautionary preference: An American perspective on the precautionary principle', *Human and Ecological Risk Assessment,* **6,** pp. 413-43.

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

Aviles, L. (1999), 'Cooperation and non-linear dynamics: An ecological perspective on the evolution of sociality', *Evolutionary Ecology Research,* **1,** pp. 459- 77.

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

Bekoff, M. (1975), 'The communication of play intention: Are play signals functional?' *Semiotica,* 15, pp. 231- 9.

Bekoff, M. (1977a), 'Social communication in canids: Evidence for the evolution of a stereotyped mammalian display', *Science,* **197,** pp. 1097-9.

Bekoff, M. (1977b), 'Mammalian dispersal and the ontogeny of individual behavioral phenotypes', *American Naturalist,* **111,** pp, 715- 32.

Bekoff, M. (1995), 'Play signals as punctuation: The structure of social play in canids', *Behaviour,* **132,** pp. 419-29.

Bekoff, M. (ed. 2000a), *The Smile of a Dolphin: Remarkable Accounts of Animal Emotions* (New York, Discovery Books/Random House).

Bekoff, M. (2000b), 'Animal emotions: exploring passionate natures', *BioScience,* **50,** pp. 861- 70.

Bekoff, M. and Allen, C. (1992), ' Intentional icons: towards an evolutionary cognitive ethology', *Ethology,* **91,** pp. 1-16.

Bekoff, M. and Allen, C. (1998), ' Intentional communication and social play: How and why animals negotiate and agree to play', in *Animal Play: Evolutionary, Comparative, and Ecological Perspectives,* ed. M. Bekoff and J.A. Byers (Cambridge and New York: Cambridge University Press).

Bekoff, M. and Byers, J.A. (1981), 'A critical reanalysis of the ontogeny of mammalian social and locomotor play: An ethological hornet's nest', in *Behavioral Development: The Bielefeld Interdisciplinary Project,* ed. K. Immelmann, G.W. Barlow, L. Petrinovich and M. Main (New York: Cambridge University Press).

Bekoff, M. and Byers, J.A. (ed. 1998), *Animal Play: Evolutionary, Comparative, and Ecological Approaches* (New York: Cambridge University Press).

Bernstein, I.S. (2000), 'The law of parsimony prevails: Missing premises allow any conclusion', *Journal of Consciousness Studies,* **7** (1 - 2), pp. 31-4.

Boehm, C. (1999), *Hierarchy in the Forest: The Evolution of Egalitarian Behavior* (Cambridge, MA: Harvard University Press).

Bradley, B.J. (1999), 'Levels of selection, altruism, and primate behavior', *Quarterly Review of Biology,* 74, pp. 171- 94.

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,* Third edition with an Introduction, Afterword, and Commentaries by Paul Ekman (New York: Oxford University Press).

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

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

Fagen, R. (1993), 'Primate juveniles and primate play', in *Juvenile Primates: Life History, Development, and Behavior,* ed. M.E. Pereira and L.A. Fairbanks (New York: Oxford University Press).

Flack, J.C. and de Waal, F. (2000), 'Any animal whatever: Darwinian building blocks of morality in monkeys and apes' , *Journal of Consciousness Studies,* 7 (1 - 2), pp, 1-29.

Frith, C.D. and Frith, U. (1999), 'Interacting minds- a biological basis ', *Science,* **286,** pp. 1692- 5.

Gallese, V. (1998), 'Mirror neurons: from grasping to language', *Consciousness Bulletin,* Fall, pp. 3-4.

Gallese, V. and Goldman, A. (1998), 'Mirror neurons and the simulation theory of mind-reading' , *Trends in Cognitive Science,* 2, pp. 493- 501.

Gould, S.J. and Lloyd, E.A. (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, pp. 11904-9.

Hill, H.L. and Bekoff, M. (1977), 'The variability of some motor components of social play and agonistic behaviour in Eastern coyotes, *Canis latrans* var. *',Animal Behaviour,* 25, pp. 907- 9.

Kitchen, D.M. and Packer, C. (1999), 'Complexity in vertebrate societies', in *Levels of Selection in Evolution,* ed. L. Keller (Princeton, NJ: Princeton University Press).

Leigh, Jr., E.G. (1999), 'Levels of selection, potential conflicts, and their resolution: Role of the "common good"', in *Levels of Selection in Evolution,* ed. L. Keller (Princeton: Princeton University Press).

Marler, P. (1996), 'Social cognition: Are primates smarter than birds?', in *Current Ornithology,* Volume 13, ed. V. Nolan, Jr. and E.D. Ketterson (New York: Plenum Press).

Mayr, E. (2000), 'Darwin's influence on modem thought', *Scientific American,* 283, pp. 67- 71.

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

Power, T. G. (2000), *Play and Exploration in Children and Animals* (Hillsdale, NJ: Lawrence Erlbaum Associates)

Ridley, M. (1996), *The Origins of Virtue: Human Instincts and the Evolution of Cooperation* (New York, Viking).

Schaller, G.B. and Lowther, G.R. (1969), 'The relevance of carnivore behavior to the study of early hominids', *Southwestern Journal of Anthropology,* 25, pp, 307-41.

Scott, J.P. and Fuller, J.L. (1965), *Genetics and the Social Behavior of the Dog* (Chicago, IL: University of Chicago Press).

Skyrms, B. (1996), *Evolution of the Social Contract* (New York, NY: Cambridge University Press).

Singer, P. (1999), *A Darwinian Left: Politics, Evolution, and Cooperation* (New Haven, CT: Yale University Press)

Sober, E. and Wilson, D.S. (1998), *Unto Others: The Evolution and Psychology of Unselfish Behavior* (Cambridge, MA: Harvard University Press).

Sober, E. and Wilson, D.S. (2000), 'Summary of: *Unto Others: The Evolution and Psychology of Unselfish Behavior', Journal of Consciousness Studies,* 7 (1 - 2), pp. 185- 206.

Spinka, M., Newberry, R.C. and Bekoff, M. (2001), 'Mammalian play: Can training for the unexpected be fun?', *Quarterly Review of Biology* (in press).

Thompson, P.R. (1975), 'A cross-species analysis of carnivore, primate, and hominid behavior', *Journal of Human Evolution,* 4, pp. 113- 24.

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

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

Watson, D.M. and Croft, D.B. (1996), 'Age-related differences in playfighting strategies of captive male red-necked wallabies *(Macropus rufogriseus banksianus)', Ethology,* **102,** pp. 333-46.

Whiten, A. (2000), 'Walking in another's shoes', in *The Smile of a Dolphin: Remarkable Accounts of Animal Emotions,* ed. M. Bekoff (New York: Discovery Books/Random House).