This PDF includes a chapter from the following book:

The Genesis of Animal Play
Testing the Limits

The title-level DOI for this work is:

doi:10.7551/mitpress/3229.001.0001

8   Play in the Placental Mammals

8.1   Is Play Ubiquitous among Placental Mammals?

Play is generally considered the province of the placental (eutherian) mammals (Bekoff & Byers, 1981; Fagen, 1981). These mammals include the great majority, over 80 percent, of all mammals. A thorough treatment of play in placental mammals would be longer than the treatment of all other groups of animals combined. This chapter presents examples of play in some of the less familiar mammalian groups and then gives some recent findings on the evolution of play diversity within selected groups of placental mammals: canids, rodents, ungulates, and primates. Extensive treatments of play in many groups of mammals are found in Fagen (1981), Power (2000), and Bekoff and Byers (1998), and in thousands of primary sources.

As discussed earlier, the challenge faced in this book is to explore with an objective approach and broad sweep the entire realm of phenomena that can be considered playful. If play is not the sole province of placental mammals, its appearance must depend on variables other than those associated with the biology and phylogeny of these mammals. However, if play is an ancient placental mammalian trait rather than a derived trait, then it should be found in all orders of mammals and be homologous. Some authors have claimed that this is the case (e.g., Fagen, 1981; Spinka, Newberry, & Bekoff, 2001). The truth, however, is more complex.

The living placental mammals are divided into nineteen orders (Nowak, 1999) that vary in number of families, genera, and species (table 8.1). More than two-thirds of all mammals are either rodents or bats. All major groups of mammals differentiated by the late Cretaceous, before the extinction of the dinosaurs, more than 65 mya (Lillegraven et al., 1987) and the earliest placental mammals may have lived more than 100 mya (million years ago). The phylogenetic relationship among mammalian orders is still controversial or unresolved, and a consensus tree is presented here with the major categories of play (locomotor, object, social) mapped onto the tree (figure 8.1). Although carnivores, primates, rodents, and hoofed animals dominate the literature on

Table 8.1
Prevalence of play in the orders of living placental mammals

| Order	Number of Families/ Genera/Species	Locomotor Play	Object Play	Social Play	Play Rating	Selected Common Names
Xenartha	4/13/29	Yes?	Yes?	Yes	1.5	Armadillos, anteaters, sloths
Pholidota	1/1/7			Yes	1.5	Pangolins
Lagomorpha	2/13/81	Yes	Yes?	Yes	1.5	Pikas, rabbits, hares
Rodentia	29/468/2052	Yes	Yes	Yes	2.0	Mice, rats, squirrels, gerbils, beaver, porcupines, pacas
Macroscelidea	1/4/15	Yes			1.0	Elephant shrews
Insectivora	7/68/440		Yes	Yes?	1.0	Tenrecs, hedgehogs, shrews, moles
Carnivora	8/97/246	Yes	Yes	Yes	3.0	Cats, dogs, bears, raccoons, hyenas, mongooses, weasels
Pinnipedia	3/18/34	Yes	Yes	Yes	3.0	Sea lions, seals, walrus
Scandentia	1/5/16	Yes	Yes	Yes	2.5	Tree shrews
Primates	13/66/279	Yes	Yes	Yes	3.0	Lemurs, galagos, marmosets, monkeys, apes, humans
Dermoptera	1/1/2				1.0	Flying lemurs
Chiroptera	18/192/977		Yes?	Yes?	1.5	Bats (fruit and vampire)
Tubulidentata	1/1/1				1.0	Aardvark
Artiodactyla	10/86/221	Yes	Yes	Yes	2.0	Hogs, hippos, camels, deer, giraffes, antelope, cattle, sheep
Cetacea	13/41/78	Yes	Yes	Yes	3.0	Dolphins, whales, porpoises
Perissodactyla	3/6/17	Yes	Yes	Yes	2.5	Horses, zebras, tapirs, rhinos, hoofed ungulates
Hyracoidea	1/3/7			Yes	2.5	Hyraxes
Proboscidea	1/2/2	Yes	Yes	Yes	3.0	Elephants
Sirenia	2/2/4	Yes		Yes	1.5	Manatees, dugongs
Total species	4508					
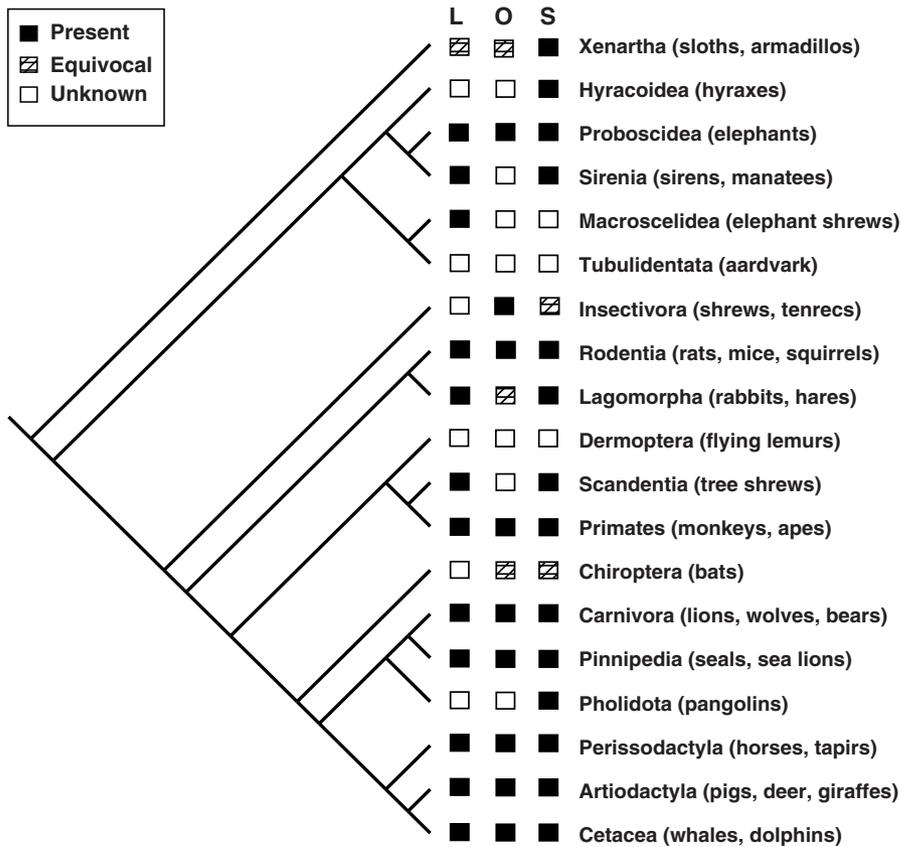
Figure 8.1
Phylogeny of eutherian mammal orders and occurrence of different kinds of play. L, locomotor play; O, object play; S, social play.

play in eutherian mammals, the emphasis here is on animals in which play is subtle, doubtful, or nonexistent.

The distribution of mammalian play given in table 8.1 shows that most groups exhibit play in all three major categories. In terms of distribution across orders, social play is most common, followed by locomotor and then object play. If only two play types occur, they are usually locomotor and social play. This reinforces the view that object play may have a different set of facilitating factors than the other two forms. Social play is typically rather active and involves locomotion, so the link between these two is not surprising.

Another consideration in evaluating table 8.1 is that some of the orders in which evidence for play is absent or questionable are also orders containing either only a

few species or species whose behavior has been little studied (Eisenberg, 1981; Fagen, 1981; Nowak, 1999). The prominent exception is the bats. Even within the bats, however, detailed behavioral ethograms and behavioral development have not been major areas of research. Furthermore, many species, even in orders in which play seems prevalent, have not been studied, so the phylogenetic distribution of play reflects, to some extent, a sampling bias. Some orders have been studied much more than others, irrespective of number of species. For example, the order that contains the two species of elephants has been much studied, and play is common in both species. On the other hand, insectivores are rather little studied, although there are several families and quite a few species. At this point, the focus is on whether play occurs in an order, what types of play occur, the relative prevalence of types of play, and how these findings relate to the factors outlined in chapter 6 as important in the occurrence of play.

Although the distribution shown in figure 8.1 suggests that play was an ancestral character found in the earliest placental mammals, the wide variation in the ubiquity and complexity of play within these orders suggests that play evolved and was later lost or greatly modified repeatedly during the evolution of placental mammals. Our comparative database is still too limited to draw final conclusions within orders, but the overall outline of the course of play diversity in mammals suggests that there are major differences in the types and extent of play in different orders of placental mammals. A brief look at some of the more problematic orders precedes a more careful look at play variation within selected orders containing highly playful species. Unless noted in the text, the information in sections 8.2 and 8.3 is based on Nowak (1999).

The topic of the formal comparison of play in mammalian orders was addressed recently by Iwaniuk and co-workers (Iwaniuk, Nelson, & Pellis, 2001). They largely limited themselves to using Fagen (1981) as a primary resource and rated play complexity on a scale of 1.0 (very limited play or none) to 3.0 (much complex play), as did Byers (1999a). Table 8.1 shows the ratings modified from Iwaniuk et al. for placental mammals. The benchmark for play complexity was the occurrence of long sequences incorporating many behavioral elements, as found in primates and carnivores. In social play, play wrestling (physical contact) was rated as more highly developed than play chasing. Given the paucity of the comparative database, the prevalence of play was not included in their scale. Nonetheless, play is common in virtually all primates and carnivores, and eventually a more quantitative approach will be necessary. Here I have discounted groups in which fairly complete study of some species shows that play is rare, even if it is found in fairly complex form in one or two species. However, such cases are key targets for analyzing the conditions under which play emerged from a phylogenetic backdrop of limited play or none, assuming that the nonplaying majority represent the ancestral condition.

8.2 Do These Mammalian Groups Play?

8.2.1 Xenartha

The xenartha (formerly called edentates in the order Edentata) are eutherian mammals with perhaps the most conservative traits, along with specializations such as few teeth or none. They have low metabolic rates, often well below typical eutherian levels. They include the families containing sloths, anteaters, and armadillos. Since there are ten times as many fossil as living genera, they are a relic group dating to before the Cretaceous. Sociality seems very undeveloped by mammalian standards and solitary living is the rule (Eisenberg, 1981). Aggressiveness to conspecifics is generally low. They are typically long lived and develop slowly. All current families evolved in South America.

There are brief reports on social play in two-toed sloths (*Choloepus didactylus* and *C. hoffmanni*) and social, locomotor, and object play in giant anteaters (*Myrmecophaga tridactyla*) (Fagen, 1981; Kawata & Elsen, 1994). These species represent the largest living sloths and anteaters, respectively, and are the most active members of their groups. There are no reports of play in armadillos, although the twenty species and eight genera provide a good diversity in habits and size (up to 60 kg). Armadillos are generalist predators on many small vertebrates and invertebrates. One species is reported to throw itself on snakes and dispatch them by slicing them with its sharp plates. The species most common in the United States, the long-nosed armadillo (*Dasypus novemcinctus*), can show considerable aggression toward conspecifics and this can include chasing and stand-up "boxing" fights. It is not known whether play fighting is seen in juveniles (McDonough, 1994). Armadillos are typically weaned at several weeks of age, and all species, including the largest, reach sexual maturity within a year. Xenartha are rated 2.0 in play complexity (Iwaniuk, Nelson, & Pellis, 2001), but this seems to be based largely on the giant anteater. My estimate would be closer to 1.5.

8.2.2 Pholidota

The pangolins are scaly-appearing mammals that have converged with the Xenartha anteaters in also specializing on ants. They have a similar small elongated head and snout and also lack teeth. They are strictly Old World, being limited to Asia and Africa. At one time they were considered to be closely related to or even part of the Xenartha, but now their relationship with other mammals is uncertain. There are only one or two young at a time and the mother-infant bond seems well developed. There is some evidence for mother-offspring and subadult social play fighting (Fagen, 1981). Iwaniuk and colleagues (2001) did not separate these taxa from the Xenartha; I would also rank them as 1.5 on their play scale.

8.2.3   Insectivora

These relatively small animals, which include the shrews, hedgehogs, and tenrecs, have relatively small brains and play is rarely mentioned, even in descriptions of well-studied species such as the tenrec (*Solenedon paradoxus*). Other reports are problematic anecdotes with perhaps the exception of several reports on hedgehogs (*Erinsceus europaeus*). These latter have been reported to exhibit inhibited play bites, play invitations, and perhaps some object play (Fagen, 1981), although the descriptions are not detailed or convincing using the five criteria (i.e., Dimelow, 1963). This species is now a popular pet and yet play is not mentioned in the pet trade manuals that I have consulted and thus may not be very common. The following unpublished description of object play in an adult dwarf hedgehog (*Hemiechinus albiventris*) provided by Andrew Iwaniuk seems to meet the five play criteria:

The hedgehog, while in a large open area (kitchen floor) was provided with the cardboard cylinder from a roll of toilet paper. She approached the cylinder and after investigating it, she wedged her head into one end. The cylinder fitted snuggly around her head and remained in place while the hedgehog walked forward waving her head around, mostly in the vertical domain. When she bumped into a wall, the cylinder fell off. She re-oriented so that she was face-on with an open end and once again wedged her head into the cylinder. This sequence of actions was repeated many times. Interspersed with these sequences of forward movement, she walked backwards and waved her head more forcefully. If the cylinder fell off, she re-oriented and again wedged her head into the open end. On this particular evening these repeated interactions with the cylinder went on for over 15 minutes. During the interactions with the cylinder the hedgehog seemed relaxed and did not emit either fear-typical or agonism-typical vocalizations. Also noteworthy was that the hedgehog engaged in such interactions with a cardboard cylinder on many separate occasions. That is, this behaviour was repeated many times on the same day and on many different days. Overall, the behaviour seemed playful, as it was voluntary, repeated and seemed enjoyable. (Iwaniuk, personal communication, 2002)

Play is ranked 1.0 in this group (Iwaniuk, Nelson, & Pellis, 2001). Still, that might be low.

8.2.4   Macroscelidea

Elephant shrews were once considered part of the insectivores, but are now considered a completely separate order that is perhaps phylogenetically close to the lagomorphs (rabbits and hares). A few highly precocious young are born and development is rapid, with the young attaining sexual maturity in 6 weeks or less. These animals are considered to be highly nervous and alert. Thus the interpretation of short dashes and leaps reported in unpublished observations on unidentified species (quoted by Fagen, 1981) as locomotor play is suspect. They are not separated from insectivores by Iwaniuk, Nelson, and Pellis (2001) and I rank them as 1.0.

8.2.5   Scandentia

Tree shrews are small squirrel-like animals once considered an early offshoot of primates and thus were the focus of considerable research, especially in neuroscience. This faded when their status as a ''primitive'' primate diminished (Nowak, 1999). They have been variously considered an advanced insectivore, allied to the elephant shrews, or most commonly today, in a separate order closely related to the primates, bats, and flying lemurs. Their brain size is about midway between that of insectivores and primates (Iwaniuk, Nelson, & Pellis, 2001). One unusual feature of the development of baby tree shrews is that the mother visits them and provides milk only once every 48 hours. Adults are essentially solitary. Individual locomotor (running, rolling) and social (chasing, mounting, boxing) play have been reported, along with role reversals, but not play wrestling (Fagen, 1981). Adult play has not been reported. Play has been described in the most-studied species, but the absence of object play and play wrestling led Iwaniuk and colleagues (2001) to rank them as 2.0.

8.2.6   Lagomorpha

Rabbits and hares, even adults, show some social play (Fagen, 1981), although this has not been systematically studied. Fagen did not report object play, but a student studying enrichment in a research colony of laboratory rabbits at the University of Tennessee documented object use in adult rabbits that appeared playlike. Play complexity was rated 1.5 by Iwaniuk and colleagues (2001). It could be that since lagomorphs, unlike rodents, rely on cryptic, motionless (freezing) behavior for avoiding predation, the more active behavior leading to play is selected against in juveniles as well as in adults in this group.

8.2.7   Tubulidentata

The single species in this order, the aardvark or ant-bear, is another species that has converged on a largely ant and termite-eating life-style, with great tooth reduction. They are often considered part of the Afrotiera, the first major radiation of mammals that took place in Africa, and may be among the most ancient living placental mammals. The young are relatively large and precocial at birth. Their behavior is largely unstudied and play has not been reported. I would rate them 1.0 based on current information.

8.2.8   Dermoptera

The Dermoptera are another small order, found only in Southeast Asia, that includes two species of flying lemurs, neither of which have been reported to play. Then again, little is known behaviorally about these largely nocturnal animals variously considered closely related to insectivores, bats, and primates. They are largely folivorous, although they may also eat flowers and fruits. I would give them a 1.0 based on the lack of current information.

8.2.9   Chiroptera

Bats are numerous, second only to rodents in number of species (almost 1000). Yet play has been described in only a few of these highly successful but very specialized mammals. Bats are divided into two suborders: the small insectivorous Microchiroptera and the generally larger fruit-eating Megachiroptera. The latter do not echolocate.

Vampire bats have highly developed social behavior that may involve reciprocal altruism; some social play has been reported in them and in fruit bats (Fagen, 1981). The milling about of neonates in crèches containing tens of thousands of young Mexican free-tailed bats in caves could involve play (Fagen, 1981), but more basic descriptive information on the behavior of the young is needed. A mother bat has only one offspring at a time but all babies are born at the same time and are crowded together on cave walls and ceilings. All the mothers leave at dusk to hunt insects and return hours later to nurse their babies; they seem quite able to find their own offspring even as they move about (McCracken, 1984). Studies of the babies in the absence of mothers are needed to see if the play criteria are met in this situation.

Object play has not been specifically described in bats, although food enrichment devices have been employed. A film of several species of fruit bats given to me by the Lubee Foundation (which carries out studies on captive fruit bats and supports much valuable research on all bats, as well as conservation and education efforts on their behalf) provided suggestive evidence for object play. The bats displayed some intriguing puzzle-solving behavior as well as manipulation of nonfood objects that could be classified as play using the five criteria. The importance of providing novel objects to maintain interest was demonstrated. Play in Chiroptera was rated as 1.0 by Iwaniuk and colleagues (2001). I would tentatively raise the ranking to 1.5, based on vampire and fruit bat behavior.

8.2.10   Hyracoidea

The vegetarian hyraxes live in Africa and Southwest Asia. Vocal communication is well developed. Some species of hyraxes live in large social groups and it is in those species that play has been most well documented. Social play in the gray hyrax (*Heterohyrax brucei*) has been especially well described (Caro & Alawi, 1985). This is one of the orders for which Fagen (1981) could report no evidence of play but for which good evidence now exists. Play complexity is rated a high 2.5 by Iwaniuk and colleagues (2001). However, this may be premature given that solitary locomotor and object play have yet to be documented.

8.2.11   Sirenia

This small group of relatively slow-moving, herbivorous aquatic mammals has been described as engaging in locomotor and gentle social play, although Fagen (1981) is skeptical because some of the behavior described as play could actually be social

grooming. Locomotor play consisting of twisting and tumbling seems to be better verified. The Sirenia are often considered to be closely related to the elephants (Proboscidae), which are highly playful. This again points out that the complexity and amount of play can differ greatly across related orders. They were not rated by Iwaniuk and colleagues (2001); I would rate them as 1.5.

8.2.12 Conclusions

These eleven orders illustrate the difficulties in any claims for the ubiquity of play, and certainly common, sustained, or complex play, in many groups of mammals. Except for the tree shrews and hyraxes, play seems quite uncommon in these orders. This is especially true of object play. Seven of the orders show no object play, and the evidence for the other four (Xenarthra, Insectivora, Lagomorpha, and Chiroptera) is sparse or anecdotal. What can we conclude? All these orders, with the possible exception of many bats, are born in an advanced state of precocity or rapidly develop to behavioral independence.

Relative brain size is often measured by the encephalization quotient (EQ), which is the ratio of the brain size expected for an animal of a given size to the value actually measured. The mean EQ for the six orders included in Iwaniuk et al. (2001) is 0.876. Lagomorphs and insectivores had the smallest mean EQ (0.592 and 0.681, respectively). Without the tree shrews, which have a large EQ (1.369) and the only one over 1.000, the mean is 0.778. Omnivores, carnivores, frugivores, and other dietary modes are represented in these orders. Scavengers and extractive foragers except for anteaters are rare or absent and these two apparent feeding modes are found in some of the species showing the most complex and common object play. Those groups with complex social lives, such as hyraxes, show considerable social play, but so do the tree shrews, which live solitary lives and have minimal contact with offspring. These orders need to be studied much more completely using the play criteria developed in chapter 3 and then classified according to the hierarchical schemes in chapter 4. However, the overall picture of playfulness in these orders will probably not change much, although it is much more likely that nocturnal species or those that raise young in burrows will harbor more surprises.

8.3 The Most Playful Orders of Placental Mammals

The remaining eight placental orders contain a large percentage of very playful species according to virtually all experts on mammals (Bekoff & Byers, 1981; Eisenberg, 1981; Ewer, 1968a; Fagen, 1981; Iwaniuk, Nelson, & Pellis, 2001; Spinka, Newberry, & Bekoff, 2001). Power (2000) has collated the details of play in about sixty representative species of these mammals (from six orders) in many useful tables. Many examples of play in part I were based on these species, particularly Rodentia (rodents),

Carnivora (cats and canids), Pinnipedia (seals and sea lions), Primates, Artiodactyla (deer, antelope, bovines, pigs), and Perissodactyla (horses). Proboscidea (elephants) and Cetacea (whales, dolphins) are well known for play as well. For example, there is evidence that killer whales (*Orcinus orca*) may teach their offspring techniques of beaching and escaping (entering and leaving shallows to capture seals) through play, and animals with this training appear to become better hunters at an earlier age (Rendell & Whitehead, 2001). Imitation of both motor and vocal behavior may also occur in cetaceans, and all this evidence is used to support true cultural transmission in this group (Rendell & Whitehead, 2001). Since imitation can also occur through play (Miklosi, 1999), play could be a major factor in the generation of novel behavior (tertiary process play) as well as in the refinement of essential basic behaviors such as prey capture (secondary process play).

Virtually all these groups contain animals with large brains and high metabolic rates, although there can be significant variation and, as discussed earlier, large brains and high metabolic rates may be dissociated. Relative brain size is generally larger in these orders than in the less playful ones, but comparative analysis shows that the relationship is weak (chapter 5; Iwaniuk, Nelson, & Pellis, 2001) and may represent a threshold that allows, but does not ensure, high levels of play (Burghardt, 1984; Iwaniuk, Nelson, & Pellis, 2001). Nevertheless, a comparison of brain size data across orders is suggestive and it is easy to see how brain size and play have been considered causally related through rough correlational analysis (chapter 5). Using the review already cited (Iwaniuk, Nelson, & Pellis, 2001), the mean EQ of these eight playful orders is 1.400. Since these authors combined the Pinnipedia with the Carnivora, the mean for orders might have been even higher. Of these more playful orders, the Artiodactyla had the smallest EQ with 0.775, and the Primates had the highest (2.151), followed closely by the Cetacea (2.071). These numbers are significantly different, although, as discussed in chapter 5, such a comparison is highly suspect.

If, however, we add the hyraxes and tree shrews to these eight orders and compare all groups scoring 2.0 or above in play complexity with those scoring 1.0 or 1.5 (Iwaniuk, Nelson, & Pellis, 2001), the mean decreases to 1.210 for the more playful orders and to 0.745 for the less playful orders. Using the play complexity criteria, Cetacea, Primates, Proboscidea, and Carnivora (and Pinnipedia) are the only orders scoring 3.0, and the mean EQ of these four orders is 1.768. It might be tempting, then, to see a causal relationship between brain size and play. Many other factors enter in, however, such as body size, feeding habits, metabolic rate, and degree of parental care, which is lengthy in most species in these orders except for some of the smaller carnivores, such as weasels.

In the better-studied orders of playful animals, it is possible to look more closely at the differences and similarities among species in the nature and extent of play behavior. This can give us insight into the ways in which play has evolved as animals have

adapted to different ecological and social niches. In all eight playful orders, all three types of play are commonly seen, and social play in many members of these orders involves the more complex attributes of wrestling, role reversal, play signals, and self-handicapping.

8.3.1   Play in Nonhuman Primates

Play has been recorded in every species of primate from all twelve families (excluding humans) for which even marginal descriptive data are available. Primates range in size from tiny mouse lemurs to gorillas and live in almost all habitats except arctic and very cold temperate areas. They can be dietary generalists or specialists, arboreal (most) or terrestrial, and have social organizations that vary from adult solitary living (orangutans), to monogamy (gibbons), to cohesive and rigid dominance hierarchies with single or multimale harems (some baboons), or looser "fission-fusion" structures (chimpanzees). Diets can range from omnivory to a focus on fruits, leaves, tree sap, invertebrates, and vertebrates, including other primates.

Play in juvenile primates is very common, although locomotor and object play may be somewhat less ubiquitous than social play. Even the former, however, is more common and more complex than that seen in almost all other groups of mammals. Tool use, which is often linked to play in primates (Power, 2000), is most common in this order as well.

Unfortunately, although there is much information on play in primates, including comparative studies (Kawata, 1980; S. T. Parker & Gibson, 1990; Pereira & Fairbanks, 1993; Power, 2000; E. O. Smith, 1978; P. K. Smith, 1982; Symons, 1978), it has not been until recently that we could begin to identify major phylogenetic patterns and relate them to diet, sociality, brain size, or other factors in any detail. There does seem to be, within primates, significant relationships of social play with the size of cerebellum, amygdala, neocortex, and striatam (Lewis, 2003; Lewis & Barton, 2004) (see figure 8.2).

Complex social play in adult primates may be one area where the growing impact of comparative evolutionary analysis may be useful in understanding variation across species (Pellis & Iwaniuk, 1999a). A recent analysis of patterns of social play among adult primates based on the published literature reached some important conclusions (Pellis & Iwaniuk, 2000a). The questions asked in this analysis derive from the fact that play is used in both sexual and nonsexual contexts. Usable play data were available for seventy-one primate species from all thirteen families, and a consensus phylogeny based on both molecular and morphological data was employed (Purvis, 1995), along with the method of independent contrasts (Felsenstein, 1985). Unlike juvenile social play, adult social play is absent in some primates and very common in others. Thus the data used for each type of social play (sexual or nonsexual) were a simple ranking on a three-part scale.

A

B

C
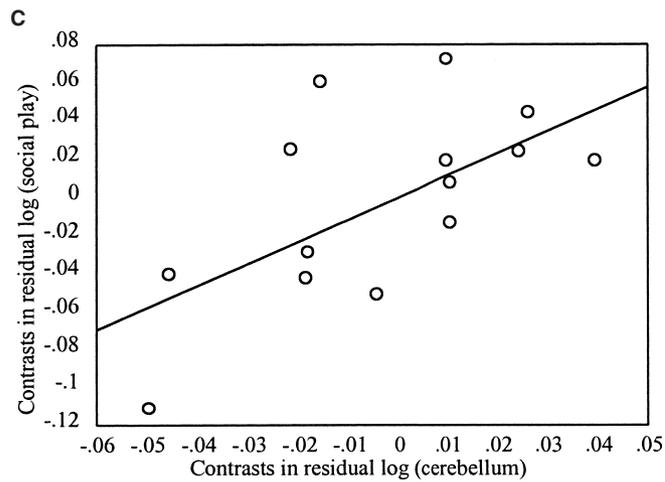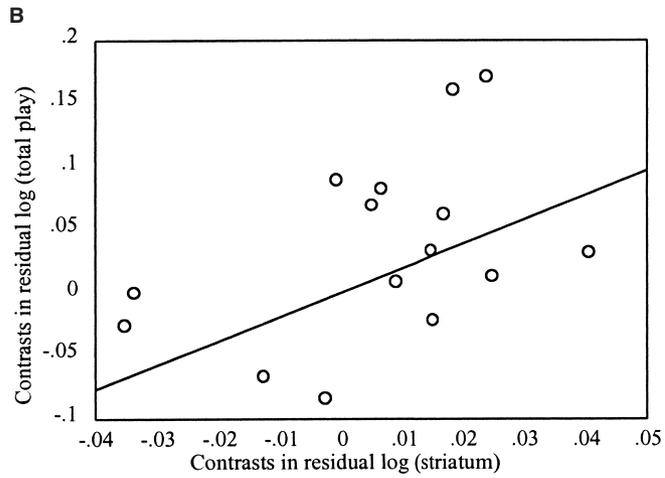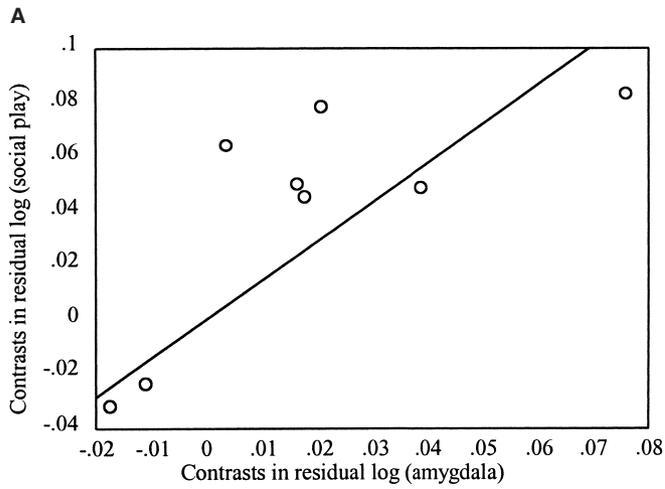
Play in sexual contexts explained a significant amount of the variation in play in nonsexual contexts. More interesting was the finding that reduced social familiarity among adults accounted for even more (30–40 percent) of the variation in play in nonsexual adult-adult play. Overall, play among adults was more frequent in primates living in social settings that had reduced contact between the sexes and other group members. Both sexual and nonsexual play was mapped onto a phylogeny of primates (figure 8.3). Rare to moderate levels of play in nonsexual contexts was the most likely ancestral state, with play becoming more or less prominent in various taxa. The functional interpretation of these phylogenetic patterns in terms of social organization and nocturnal habits has been discussed earlier (chapter 6). What is evident from the phylogenetic tree is that even at the coarse level at which play was rated in this most universally playful order of mammals, play has repeatedly changed and evolved. Thus ''deep'' phylogeny, or preprimate evolutionary history, has little effect on the nature of play across species in primates. This suggests that complex social play has important functional consequences and responds to social demands. These most likely relate to social affiliation and assessment (Pellis & Iwaniuk, 2000a). However, the measure of play used was very simple, which suggests that a more refined comparative analysis would show even more variation among closely related taxa. In any event, the multiple origins of complex play are certainly supported by this analysis.

8.3.2   Play in Rodents

Unlike primates, rodents are classified as only moderately playful as a group (Fagen, 1981), although some species, such as gray squirrels, are very playful, live in three-dimensional habitats as do many primates, and have large brains in relation to body size (Horwich, 1972). Prairie dogs (*Cynomys ludovicianus*) are ground squirrels that live in large colonies and are very social. They have an extremely complex communication system that seems to encode information that includes the type, direction, and distance of human and other intruders (Slobodchikoff, 2002). They are also extremely social and playful within the group (coterie). Fathers are especially playful with offspring, and the young have elaborate means of enticing play (Masson, 1999). Beavers (*Castor* sps), large semiaquatic rodents that live long and have complex social lives, also play frequently, including ''dancing,'' and several authors mention the inhibitions on biting and other consummatory aggressive responses that may facilitate social play (Wilsson, 1971; Ryden, 1997). Holmes has shown that play is the most common social behavior among groups of young Belding's ground squirrels and results from a complex interaction of kinship relatedness and familiarity (Holmes, 2001; figure 6.3).

◄ **Figure 8.2**

The relationship between play and the size of three noncortical brain components across a sample of representative diverse primates. (*a*) Social play and the amygdala, (*b*) total play and the striatum, and (*c*) social play and the cerebellum. (From Lewis, 2003)

Sex Play

☐ None
⬛ Moderate (gray)
⬛ Complex (black)
？ Unknown

Nonsex Social Play

☐ None
⊠ Moderate (some spp.)
⬛ Moderate (gray)
⬛ Complex (black)

	Sex	Nonsex
Eulemur (lemurs)	☐	⊠
Lemur (ring-tailed lemur)	☐	⬛
Varecia (ruffed lemur)	☐	⬛
Propithecus (sifakas)	☐	⬛
Avahi (woolly lemur)	☐	☐
Daubentonia (aye-ayes)	⬛	☐
Lepilemur (weasel lemurs)	⬛	⬛
Mirza (greater mouse lemur)	⬛	⬛
Microcebus (mouse lemurs)	☐	☐
Phaner (fork-marked dwarf lemur)	？	⬛
Nycticebus (slow lorises)	⬛	⬛
Loris (slender loris)	⬛	⬛
Perodicticus (potto)	⬛	⬛
Otolemur (greater bushbabies)	☐	⬛
Galago (bushbabies)	☐	⬛
Galagoides (dwarf galagos)	⬛	⬛
Tarsius (tarsiers)	☐	⬛
Brachyteles (woolly spider monkey)	☐	☐
Ateles (spider monkeys)	⬛	⬛
Lagothrix (woolly monkey)	☐	⬛
Alouatta (howler monkeys)	☐	⬛
Pithecia (sakis)	☐	⬛
Cacajao (ukaris)	？	⬛
Aotus (night monkeys)	☐	⬛
Callicebus (titi monkeys)	☐	☐
Cebus (capuchins)	☐	⬛
Saimiri (squirrel monkeys)	⬛	⬛
Callimico (Goeldi's monkey)	☐	☐
Saguinus (long-tusked tamarins)	⊠	☐
Leontopithecus (lion tamarins)	☐	☐
Cebuella (pygmy marmoset)	☐	☐
Callithrix (marmosets)	⬛	⬛
Theropithecus (gelada baboon)	☐	☐
Papio (baboons)	☐	☐
Cercocebus (mangabeys)	☐	☐
Mandrillus (drill and mandrill)	☐	☐
Macaca (macaques)	☐	☐
Cercopithecus (guenons)	☐	☐
Erythrocebus (patas monkey)	☐	☐
Presbytis (languers)	☐	☐
Pygathrix (Douc languer)	⬛	⬛
Colobus (black & white colobus monkeys)	☐	⊠
Hylobates (gibbons)	☐	⬛
Pongo (orangutan)	⬛	☐
Gorilla (gorillas)	☐	⬛
Pan (chimpanzees and bonobo)	⬛	⬛
Homo (humans)	⬛	⬛

Rodents are promising subjects for a phylogenetic analysis of play because variation in play is so much greater in rodents than in primates, even within the same family (Pellis et al., 1991; Poole & Fish, 1975). The Muridae comprise the largest family by far of the 29 rodent families. About two thirds of the more than 2000 rodent species are members of this single and most successful (in terms of species and distribution) of all mammalian families. There are some interesting little-known phenomena in these animals that are poorly understood but that provide opportunities for comparative study. For example, there is a radiation of mice (*Pseudemys*) in Australia that manipulate pebbles and other objects into rather elaborate mounds that may have some defensive, thermoregulatory, or visual marking function, although the development and details of the behavior seem to be little known (Cermak, 1996).

Although laboratory rats are the species most studied for social play, the comparative data on play are far less systematic and comprehensive in rodents than in primates. Thus a phylogenetic study of social play fighting in rodents was limited to thirteen species, although these ranged over eleven genera and five subfamilies of muroid rodents (Pellis & Iwaniuk, 1999b). For comparison, it should be noted that there are sixteen recognized subfamilies (Nowak, 1999). Even in this limited sample, however, the range of social play is great (Pellis, 1993). Pellis and Iwaniuk carried out a comparative analysis of social play in these thirteen species similar to that performed with primates. Instead of adult-adult play, they used juvenile play fighting but a similar rating scale. Remarkably, they found that phylogeny explained little of the diversity that they found (figure 8.4). However, differences in sociality also explained little of the variation. The presumptive ancestral state was low to moderate play, which then increased or declined in various lineages. Clearly much more work needs to be done, but these results strongly suggest that more complex social play has roots in recent, rather than ancient, evolutionary history. Furthermore, using the kinds of functional analyses listed in chapter 5, such differences among play styles almost certainly are due to either important functional roles or are by-products of other behavioral differences having functional, and ultimately adaptive, roles.

8.3.3 Play in Canids

All members of the canid line of carnivore evolution (wolves, foxes, bears, raccoons, weasels) are playful in all respects. Many of these carnivores, especially bears and weasels, are born in a highly altricial state (hairless, eyes closed, no mobility). Some, such as the highly intelligent bears, also have very large brains. These findings are exceptions to claims that the more altricial species are cognitively inferior to precocial ones

◀ **Figure 8.3**
Phylogeny of sexual and nonsexual social play in adult primates. Cross-hatching depicts genera in which only some species show nonsexual adult social play. (From Pellis & Iwaniuk, 2000a)
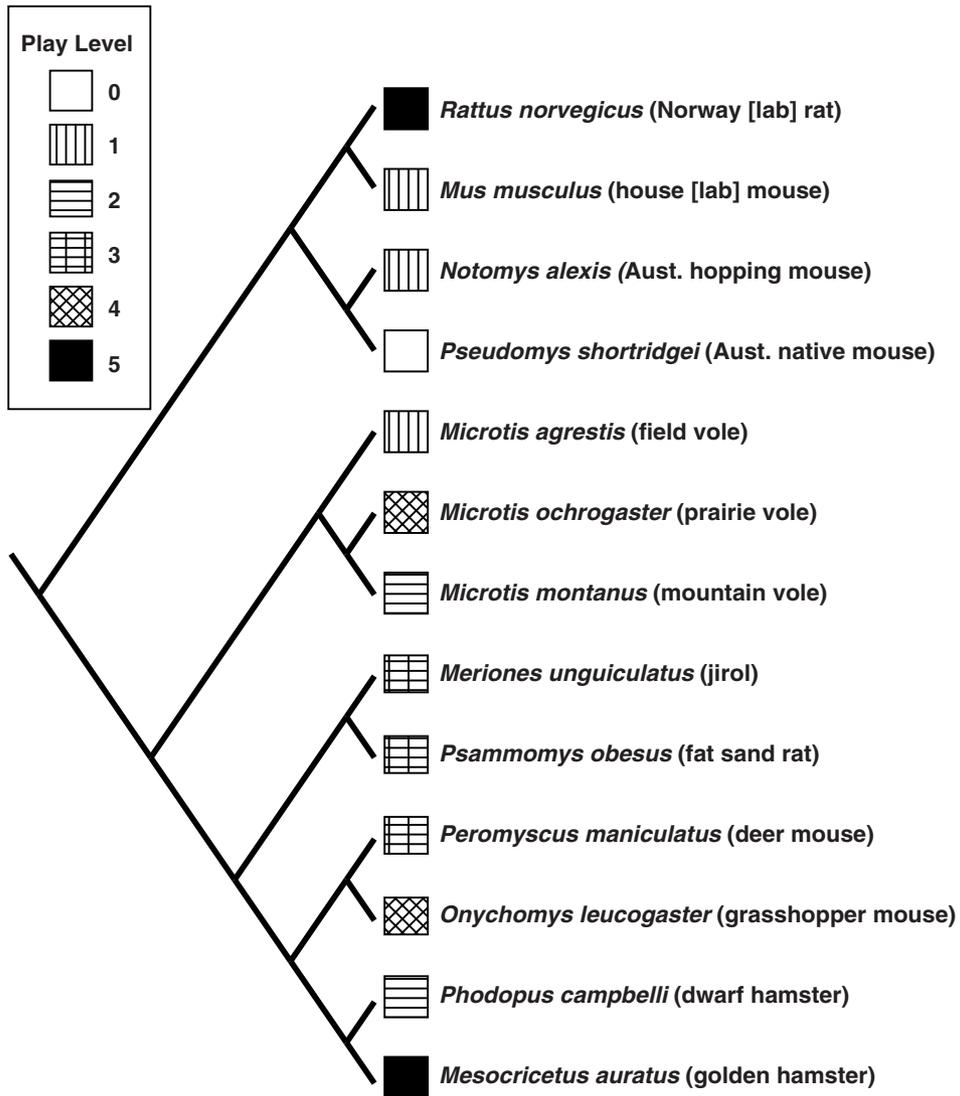
Figure 8.4

Phylogeny of social play in juvenile muroid rodents. Note that the most complex play is found only in the two species most distantly related to each other. (From Pellis & Iwaniuk, 1999b)

(S. T. Parker & McKinney, 1999; Portmann, 1990). Furthermore, bears are not very social but still have elaborate play behavior (Burghardt, 1982). One spectacled bear (*Tremarctos ornatus*) (Kawata, 1990) outdid by far any American black bear that I ever studied in his use of objects in escapes as well as his dexterity in twirling broomsticks in one hand, picking up a small metal feed pan and carrying it to a water trough, where he ''floated and pushed the pan as a child would do'' (Kawata, 1990: 13), and other spontaneous and untaught behaviors (although imitation cannot be completely ruled out).

Although play has been documented in many species of carnivores of all families (Fagen, 1981), comparative work has been most intensive on a portion of the sixteen genera and thirty-six species of the family Canidae (wolves, dogs, foxes, jackals), and a few of these comparisons are mentioned here to show the nature of differences among these often familiar animals and how such differences have been interpreted.

Canids show enormous diversity in levels of adult sociality and social organization. Even within the single genus *Canis*, there is great variation, from the social hunting packs of the gray wolf (*Canis lupus*) to the family units typical of jackals and coyotes (*Canis latrans*). The controversial red wolf (*Canis rufus*) is considered intermediate, if not a hybrid, between the gray wolf and coyote (Wagener, 1998). Social play differs in wolves and coyotes in several respects, although there are no sex differences (Bekoff, 1974, 1978a, 1995; Fox et al., 1976). Play in the red wolf is somewhat intermediate. For example, the red wolf shows the extensive parent-offspring play and exaggerated double leaping of gray wolves, along with the absence of vocalizations during play fighting. Like coyotes, however, young red wolves do not engage in sexual play and show infrequent submissive behavior; social play first appears after serious agonistic behavior has developed. Thus data on play may be useful in resolving questions concerning the relationships of closely related animals and is consistent with, but does not prove, the hybrid origin hypothesis of the red wolf.

The play behavior of three other canids, all from South America, has also been compared (Biben, 1983): the maned wolf (*Chrysocyon brachyurus*), the crab-eating fox (*Cerdocyon thous*), and the bush dog (*Speothos venaticus*). All three are the sole members of their genus and have different kinds of social organization. The maned wolf is generally solitary and monogamous during the mating season; the crab-eating fox forms long-lasting monogamous bonds, and mated pairs travel together but hunt individually. The bush dog is highly social, monogamous, lives in packs up to ten, and hunts cooperatively. All can live in wet savannahs, but the maned wolf favors grasslands while the other two species are more woodland adapted.

All three species displayed virtually the same behavior patterns in play, such as chasing, pawing, rolling over, biting, gaping, and muzzle wrestling. It is interesting that the highly social bush dogs did not engage in grappling (bipedal wrestling) or play bows (as seen in dogs, wolves, and coyotes), but they did vocalize much more during play than the other two species. Bush dog play was also less variable. In all three

species, there were no sex differences in social play, nor are the species sexually dimorphic in size. Although the ontogeny of play was roughly similar, social interactions were more frequent and peaked later in life in bush dogs than in the other two species.

Biben suggests that the bush dog retains more juvenile morphological and behavioral features than more ancestral species. For example, the adult bush dog has the short muzzle, large head, and short legs typical of young canid pups. On the other hand, the bush dog had ''a less rich and varied repertoire during interactions and had showed a higher frequency of behaviours considered aggressive (e.g., biting, growling)'' (Biben, 1983: 824). In bush dogs, the typical limits on play fighting that keep it from escalating to serious fighting were absent. Submissive behavior patterns were more common. This difference might be related to the role of social organization in patterns of social play as reported earlier for primates. Species with a looser social structure showed the richer and more complex play. In spite of the maned wolf and crab-eating fox having different levels of sociality, there were few differences between them. Biben concludes that standard predictions that more social species should have more complex play, be less aggressive, and have a dominance hierarchy are not supported.

Biben also studied object play in both the crab-eating fox and the bush dog (Biben, 1982, 1983). Pups of both species brought objects into the den beginning at about 5–7 weeks. Bush dogs chose larger objects and they hunted larger prey relative to their body size than the foxes. Foxes, but not bush dogs, maintained a hoard of ''toys.'' Much object play was social, involving tug-of-wars and chasing in foxes, but the bush dogs, although biting on objects together and carrying them around, did not engage in tug-of war (figure 8.5). Unlike social play, object play differences among the two species seem more readily understood. Bush dogs hunt cooperatively while foxes do
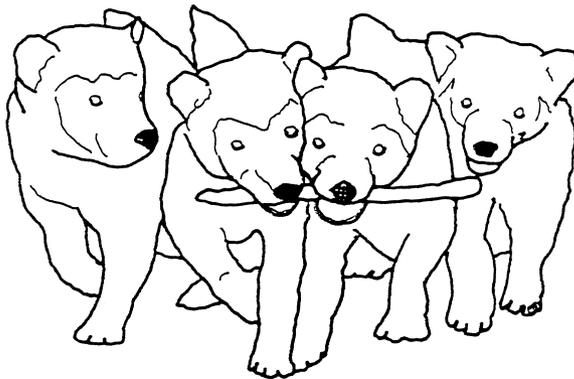

Figure 8.5
Group object play in bush dogs. (From Biben, 1982)

not. Apparently, although they group hunt and kill prey, bush dog methods are quite unsophisticated; they surround prey and bite at it repeatedly. Foxes, on the other hand, use a variety of attack modes to capture prey and thus may need more complex and acquired skills. Thus the smaller repertoire of bush dog object play may be related to their later less complex predatory behavior.

The less competitive nature of bush dog object play also is congruent with the social and food-sharing characteristics of the species. In bush dogs, 77 percent of social object play bouts were amicable compared with only 13 percent for crab-eating foxes (Biben, 1982). The type of predatory object play witnessed in the foxes was similar to that seen in other individual hunting carnivores, such as domestic cats and dogs. It is interesting that ''hunting play,'' defined as stabbing with one or both forepaws at an apparently imaginary prey item in the grass, was common in the maned wolf, rare in the fox, and absent in the bush dog.

These comparative studies on canid species support Fagen's (1981) prediction that there will be few play differences between the sexes in carnivores because of their similar roles in hunting, territorial defense, and parental care. This was also predicted in a more general form from SRT (Burghardt, 1988b). There is recent evidence relating the level of play in selected carnivores to neocortex size, excluding domestic dogs (Lewis, 2003)

8.3.4 Play in Deer

Young ungulates are quite playful, and comparative reviews document the basic patterns in many species (Byers, 1984; Fagen, 1981). Although no phylogenetic studies are available, considerable data exist on play in field or naturalistic settings in Artiodactyla, as well as on the domesticated species. Unlike many species of mammals, which are often small, nocturnal, or live in dense habitats in which observation is difficult, many ungulates are easily observed in the field and there are several fine field studies of social and locomotor play in these species, especially those found in North America (e.g., Byers, 1997; Miller & Byers, 1998; Power, 2000). Here just one comparative study is presented.

A comparison of the behavior of three species of North American Cervidae is available (Müller-Schwarze, 1984). Caribou (*Rangifer tardanus*) live in arctic and subarctic terrain, where they may seasonally migrate hundreds of kilometers. Caribou have a quite open social system; they can aggregate in the hundreds. Mothers stay with their fawns for about a year and leave before calving occurs. However, both family units (mothers and offspring) and male pairs may travel together for years. The other two species studied were the white-tailed deer (*Odocoileus virginianus*) and mule (or black-tailed) deer (*Odocoileus hemionus*). Mule deer stay with their mothers for only 3 months before weaning and are ''hiders.'' That is, they stay motionless under cover for long periods while the mother forages. Social groups are smaller and more stable than

in caribou, and intergroup and even fawn-fawn, aggression is frequent. Whitetail deer have a somewhat more open social system than do mule deer, although the basic social unit consists of the female, fawns, and yearlings from the previous year.

Play behavior in all three species contains similar elements, primarily motor patterns involved in escape behavior, with some also derived from fighting and mounting but not courtship or threat (Müller-Schwarze, 1984). Indeed, after listing all the motor patterns involved in threat and courtship, Müller-Schwarze stated that ''None of these motor patterns occur in play, although they are precisely the ones whose practising, especially in various pattern combinations, would confer benefits to the individual'' (1984: 156).

There were differences among the three species, however. The usually single caribou offspring is ''remarkably precocious. It is able to follow its mother after 1 hour of life and can outrun a human when 1 day old'' (Nowak, 1999: 1130). Play behavior begins on the second day of age and the amount and complexity of play increase over the next 9 days. Although over 90 percent of play is running, ''leaping, butting, striking, mounting, and pawing'' (Müller-Schwarze, 1984: 153) also occur. Play occupied a little over 1 percent of total activity time on average, but was more frequent on better quality range.

The kinds of play and their ontogeny in white-tailed and mule deer were very similar and only data for the latter are given. In mule deer play began later than in caribou, at 6 days of age, and peaked at 2.5 months, after which it declined, but could still occur in intense bouts. Play not only included social running (following, chasing, intercepting) but also ''head jerks, leaping, running, butting, striking, mounting, pushing, neck-craning, neck-twisting, head-shaking, and reclining'' (Müller-Schwarze, 1984: 154–155). Besides this additional complexity and the longer period of juvenile life during which play occurred, play was much more frequent than in caribou, taking up 8.9 percent of total activity time in 2–4-month-old fawns. The greater amount of agonistic behavior in mule and white-tailed deer play was interpreted by the author as being related to their greater aggressive and competitive behavior as adults. Although these results are consistent with both the developmental and ecological predictions from SRT, more detailed comparative work with more species is needed for rigorous comparative analyses.

8.3.5 Conclusions

Although a thorough phylogenetic review of play in the most playful orders of mammals is lacking, this section has shown that there is sufficient variation within orders and families to test hypotheses about the relationship of play to variation in a number of life history, social, physiological, and ecological factors. As emphasized in chapter 5, a particular relationship may not be either causal or functional, but its study is certainly necessary in order to test the generality of conclusions about play derived from

intensive experimental research on a single species such as laboratory rats or rhesus monkeys. Social play, in particular, may be rather evolutionarily labile in its complexity, frequency, and association with the factors listed above. Although play is more or less highly developed, especially in the rodents and ungulates, the basic primary and even secondary sources of play were undoubtedly present in the ancestors of all these groups. Play has flowered in many ways.

The limits of comparative analysis across orders or even species must also be recognized. Different populations of the same species must be studied carefully and population differences assessed. Indeed, current and recent selection pressures as well as the role of current ecological factors must be considered in studies of behavioral evolution (Foster & Endler, 1999). The amount of food available and group size are both positively related to the amount of play found in squirrel monkeys (J. D. Baldwin & Baldwin, 1974).

Another example of the importance of ecology is apparent in work on behavioral development and play in populations of bighorn sheep (*Ovis canadensis*) inhabiting desert and mountain environments (Berger, 1979). In these sheep many components of sexual, threat, contact, and locomotor-rotational behavior are incorporated into play shortly after birth. Berger studied three populations of sheep—a Canadian mountain population, a desert population in California, and a mountain population in Oregon derived from animals transplanted from the Canadian population about 20 years previously. Although the behavioral repertoires of all populations were similar, the desert animals played less, matured faster, and lived in smaller social groups. Both lambs and adults had lower behavioral diversities in the desert. However, the desert population appeared better nourished than the mountain population. So, why did they play less when well-nourished squirrel monkeys played more? Berger suggested that food in the desert, although more plentiful, is more dispersed and this would lead to smaller group sizes. His data showed that social play was more frequent in groups of three or more lambs, and that desert animals were more often isolated from their peers, with less opportunity for social facilitation of play. In addition, animals in desert areas achieved independence more quickly than those found in the other two habitats. Furthermore, there were more hazards in the physical environment in the desert. Thus these ecological, physical, and social factors could underlie the difference between desert and mountain populations in playfulness.

Although genetic differences might partially underlie the differences, as shown in the transplant population along with other data (Berger, 1979), later maturity in the mountain population, larger social groups of peers, and a physical environment more conducive to play were all involved in the greater play in mountain animals. Bighorn sheep living in a very arid desert environment such as that of Death Valley, California, might be a good test of the relationships among resources, group size, and play. Berger (1979) predicted that social play would be very infrequent. These studies, by

demonstrating the lability of play even within species, teach us that intensive and costly detailed studies of wild populations are needed, not just species-level descriptions and measures such as brain size, typical habitat, and diet.

8.4 More Questions than Answers

If play is not ubiquitous in all placental mammals, it is certainly widespread. Furthermore, it has been found in almost every order to at least some, albeit minimal, degree. Play is not as complex or common in some groups as in others. For example, play seems rare or absent in almost all insectivores and uncommon in bats, lagomorphs, and elephant shrews. Taking play as a single measure, simple associations of play with brain size, metabolic rate, body size, intelligence, ecology, sociality, altriciality, and other factors are modest at best. It is only when several of these factors are taken together or play is broken down into subtypes that relationships appear, as in rodents and primates. At this point, the data necessary to do multiple regression and other integrative analyses are not available.

In any event, although play appears less complex, energetic, and frequent in mammals from older or more archaic groups (e.g., Insectivora, Macroscelidea), it does occur in some species, and an effort to study these groups in closer detail is definitely needed because so many species appear to show no play at all. A formal application of objective criteria is seldom discernable in the literature, in spite of the heroic and insightful analysis of this literature by Fagen (1981). Since then, little new comparative data have accrued for most of the orders reviewed in section 8.2. Nonetheless, the ubiquity of play in mammals (Bekoff & Byers, 1981; Fagen, 1981) means that play in some form occurred in the earliest mammals, and it is to other groups that we must look to critically assess the place of placental mammalian biology in the origin of play. Do other vertebrates have play behavior and is it comparable in diversity and complexity?