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Testing the Limits

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9   The Alternate Radiation: Play in Marsupials

9.1   Introduction

Most of our comparative knowledge of play is necessarily based on the familiar mammals of the world: cats, dogs, monkeys, rats, and horses. These are the animals studied by most scientists exploring the mysterious world of animal play. In an earlier chapter, I used a comparison of ectothermic reptiles with typical (eutherian or placental) mammals as a way of developing some understanding of what may be involved in the occurrence of playfulness. Differences from reptiles were related to the evolution of mammalian characteristics such as endothermy, parental care, high metabolic rates, and large brains. Within mammals, preliminary attempts are being made to systematically catalog variations in playfulness and relate such variation to differences in these same characteristics within and across mammalian groups (Iwaniuk, Nelson, & Pellis, 2001). Going further, I used the mammal–reptile contrast to outline an evolutionary scenario to help understand some of the diversity within placental mammals (chapter 6). However, the relationships are only correlational and have not yet been rigorously analyzed; alternative explanations abound. For example, any comparisons among the various radiations of eutherian mammals (primates, canids, rodents) could really be viewed as only one radiation (placental mammals). Controversy about the independence of taxa in comparative testing of hypotheses (Felsenstein, 1985) has made conclusions suspect if all animals compared share the same trait. Rather than argue about the quality, independence, and appropriateness of making comparisons among eutherian mammals in order to understand the processes underlying play, it would be useful to have another comparison group that is independent from the eutherians. Since play is found in almost every placental mammalian order, it is plausible to postulate that play occurred in the earliest mammals and was lost in some lineages. Thus play did not originate in eutherian mammals and only secondary, not primary, factors can be identified.

We are left with two hypotheses. One is that the variation among mammalian groups in ''reptilian'' traits and the positive correlation with playfulness is more than

just a singular relationship existing only in one group, placental mammals. The second hypothesis is that play arose once in mammalian evolution. It would be a useful test of these ideas to have another mammalian radiation with comparable traits to study. Fortunately, we do.

As the world of play description and theory that emerged at the end of the nineteenth century was being formulated and debated, an independently evolved, and evolving, mammalian radiation was being uncovered. These are the marsupials, the now-familiar kangaroos, wallabies, koalas, and opossums, along with dozens of other species about which we still know little. It is only with the rapid development of world-class science in Australia that the details of a wide range of marsupials are becoming known. An excellent, well-illustrated volume by Walton and Richardson (1989) summarizes this work.

The Marsupialia split off from the eutherian line at least 100 mya, in the Cretaceous (see figure 7.1; Clemons, 1989). Based on amino acid substitutions, these dates may be pushed back a bit farther (Clemons, Richardson, & Baverstock, 1989).

Marsupials are members of the Metatheria. It is often thought that with the exception of the domesticated dingo and the monotremes, the marsupials are the sole native mammals of Australia. This is not true. Australia has an extensive representation of bats and rodents, including many endemic species. Bats have been in Australia for upward of 50 million years, while rodents have been there no more than 4 million years (Strahan, 1995). In contrast, humans probably introduced the dingo less than 10,000 years ago. Many marsupials are also found on other nearby South Pacific islands, especially New Guinea, which has a number of endemic species. One order, the Didelphimorphia (opossums), has an extensive radiation in South America, with one species, the Virginia opossum (*Didelphis virginiana*) being very common in North America. It is so successful that its range is still expanding northward. There are many other families of marsupials, with thirteen being found in Australia alone (Walton & Richardson, 1989). The taxonomy of the entire Metatheria is in flux, and the phylogenetic relationships of many families are in dispute (Nowak, 1999). I follow Nowak (1999) in recognizing seven orders of marsupials. Table 9.1 provides a nested taxonomy down to the level of the family.

Do the types of play seen in marsupials vary along the same dimensions as in comparable eutherian groups? To claim that the Metatheria are a useful control group for testing hypotheses derived from placental mammals, one needs to show comparable ecological and behavioral diversity in the two groups. That there is. Marsupials can be carnivores, granivores, frugivores, omnivores, and folivores. There are species that specialize in eating termites or just nectar and pollen. Although no marsupials are truly aquatic, there are arboreal leapers and gliders as well as burrowing molelike forms. Other marsupials hop, climb, and swim.

Marsupials do not reach the great body mass of many eutherians or reptiles, but they do range from a mouselike form (Dasyuridae) weighing less than 5 g as an adult to large kangaroos weighing 85 kg, a range of 1 to 17,000! Although it has not been well studied, antipredator behavior in marsupials is similar to much of that in placental mammals (Coulson, 1996). However, predation on macropods (kangaroos and wallabies) may be less than that on ecologically similar placentals (Croft, 1989). Marsupials and placental mammals often converge in physical appearance and behavior, as shown by the similarities between Australasian possums and Madagascan lemurs (Winter, 1996). The macropods are herbivorous mammals generally viewed as the ecological equivalents to the ungulates (Croft & Ganslosser, 1996). The total number of marsupial species is rather small, about 300. More than 25 percent of these are South American opossums, the oldest and most conservative living marsupials. Didelphids were presumably already present in South America when the continents separated and have speciated extensively since then.

Although the invasion of Australia by placental mammals (rabbits, foxes, cats, deer, and goats among others) and the resulting impact on native marsupials is well known, several members of the kangaroo family (macropods) have themselves become established outside of Australia and the southeast Pacific islands.

9.2   Play in the Metatheria

Until recent years, the research on play in marsupials was limited. Fagen (1981) only reviewed work in two families of marsupials, and this was in less than three pages. His tables (1981: 221–222) include reports on four of the twenty-one currently recognized families (in three of the seven currently recognized orders). Nonetheless, Fagen clearly recognized the importance of marsupials for a comparative study of the evolution of play by looking at convergent processes, although this was funneled through his reliance on brain size: ''Whether marsupial play is less elaborate, less frequent, or less stable than the play of corresponding mammals (as the brain-size hypothesis might predict) is not known'' (Fagen, 1981: 81).

The situation is better today. Play has been documented in more marsupial species, families, and orders. Detailed studies of several species are also now available. The current situation for research on marsupial play is summarized by Lissowsky (1996), who reviewed play in marsupials, and Watson (1998), who reviewed play in the Macropodoidea, the superfamily that includes the Macropodidae (kangaroos and wallabies) and Potoridae (rat kangaroos). Both authors cite recent and unpublished observations and theses. The marsupial species accounts in Strahan (1995) also added taxa to the list of animals studied (e.g., the Myrmecobiidae; see also Friend & Burrows, 1983). Among other references consulted, Grzimek (1972) contains considerable anecdotal

Table 9.1
Nested taxonomy and play occurrence in the Metatheria (marsupials)

Order/Suborder/Superfamily/Family	Genera/Number of Species	Loco-motor Play	Object Play	Social Play	Byers play index	Iwaniuk, Nelson, & Pellis play index	EI	Selected Common Names
South American Radiation								
Order Didelphimorphia								
Marmosidae	8/53	?		Yes		2/3	116	Pouchless mouse opossums
Caluromyidae	2/4							Woolly opossums
Gironiidae	1/1							Bushy-tailed opossums
Didelphidae	4/8							Pouched opossums
Order Microbiotheria	1/1							High-altitude Monito del Monte
Order Paucituberculata	2/7							Shrew opossums
Australasian Radiation								
Order Notoryctemorphia	1/1							Marsupial mole
Order Dasyuromorphia								
Dasyuridae	17/62	Yes	Yes	Yes	1–3	1–3	100	"Mice," "cats," Tasmanian devil
Thylacinidae	1/1						148	Tasmanian wolf
Myrmecobiidae	1/1	Yes		Yes	3	3		Numbat or banded anteater
Order Peramelemorphia								
Peramelidae	4/11	Yes		?	1	1–2	99	Dry-country bandicoots, bilbies
Peroryctidae	4/11						128	Rainforest bandicoots
Order Diprotodontia								
Suborder Vombatiformes								
Phascolarctidae	1/1			Yes	2	2		Koala
Vombatidae	2/3	Yes		Yes	3	3		Wombats

Table 9.1
(continued)

Order/Suborder/ Superfamily/Family	Genera/ Number of Species	Loco-motor Play	Object Play	Social Play	Byers play index	Iwaniuk, Nelson, & Pellis play index	EI	Selected Common Names
Suborder Phalangerida								
Petauroidea							156	
Petauridae	3/10	Yes		Yes	?	1–3		Gliders, striped possums
Pseudocheiridae	6/16	Yes			1/2	1–2		Ringtailed, greater gliding possums
Tarsipedoidea								
Tarsipedidae	1/1	Yes		Yes	2	2		Honey possum
Acrobatidae	2/2				1	1		Feather-tailed possums
Macropodoidea								
Macropodidae	12/61	Yes	Yes	Yes	3	2–3	142	Kangaroos, wallabies
Potoroidae	5/10	Yes		Yes	3	2–3	166	Rat kangaroos
Phalangeroidea								
Phalangeridae	6/22	Yes			2	2	130	Phalangers, possums, cuscuses
Burramyoidea								
Burramyidae	2/5				1	1	98	Pygmy possums
Total species	~295							

information. Two recent papers based on comparative analyses of degree of play and brain development in marsupials offer additional information (Byers, 1999a; Iwaniuk, Nelson, & Pellis, 2001).

For comparative purposes, the marsupials can be divided into several groups. Here I emphasize those for which some data on play are available (table 9.1). This arrangement is derived from Walton and Richardson (1989) and chapters therein, especially Clemons (1989), and from Nowak (1999).

Lissowsky (1996) begins her review of marsupial play by stating that her ''aim is to demonstrate that play behaviour occurs in very similar ways in both subclasses, and that marsupial play is neither less frequent nor less diverse than play in placentals'' (1996: 187). This claim may be overstated, but given the lack of behavioral research on marsupials, it still may be a question of insufficient study. Watson (1998) also points out that the view of marsupials as inferior (see later discussion) may have biased observers against interpreting some of their behavior as play. He makes a good case that such misinterpretation has in fact taken place.

9.2.1 Locomotor Play

Locomotor play is found in all families for which any play has been recorded. Southern hairy-nosed wombats (*Lasiorhinus latifrons*) are heavy bodied and highly social. They are arid country grazers living in large underground warrens and have long life-spans, living up to 17 years in captivity (R. T. Wells, 1989). They engage in leaping and bipedal jumping play, as well as extensive social play with a keeper (Fagen, 1981; Lissowsky, 1996). The carnivorous dasyurids show running play as well. All the larger dasyurids engage in locomotor and other forms of play, while the smaller species show virtually none (Croft, 1982). One of the smallest dasyurids, the fat-tailed dunnart (*Sminthopsis crassicaudata*), showed no clear play, but at 11 weeks of age the young engage in a period of short, quick runs with no apparent external stimulus, a phenomenon termed incipient locomotor play (Ewer, 1968b). Bandicoots (*Isoodon obesulus*) perform a variety of nonagonistic behaviors that were considered play by Fagen (1981): leaping, burrowing, climbing, and chasing. Lissowsky (1996) lists this species as engaging in play chasing, but omits it from the list of species that engage in locomotor play. Winter (1996) reports that the arboreal phalanger (*Trichosaurus vulpecula*) plays at climbing. Rat kangaroo (*Potorous tridactylus*) juveniles move extremely fast during play (Lissowsky, 1996). All these phenomena are also common in placental mammal play.

The greatest amount of locomotor play is shown by the macropods, where it seems largely, but not always, related to simulations of predator avoidance behavior (Watson, 1998). Locomotor play seems to decline rapidly with age in macropods. Sex differences exist in some species in the frequency and duration of locomotor play. For example, juvenile male red kangaroos (*Macropus rufus*) played more than juvenile females, but eastern gray kangaroo (*Macropus fulginosus*) females played more than males (Lissowsky, 1996; Watson, 1998).

9.2.2   Object Play

Object manipulation of all kinds seems rather undeveloped in marsupials, and play with objects has been reported only for the dasyurids (Croft, 1982) and macropods. Among the dasyurids, object play in the large carnivorous Tasmanian devil (*Sarcophilus harrisii*) is most documented. A captive individual seized various toys in its mouth and vigorously shook them (Ewer, 1968a). Another captive devil incorporated objects such as water troughs and hollow logs into social and locomotor play (Fagen, 1981). Lissowsky (1996), commenting on a species of broad-footed marsupial mice (*Antechinus stuartii*) suggests that tail-pulling by siblings is a form of predatory object play. These animals also play with twigs, leaves, and small harmless insects by catching, releasing, nipping, patting, or tossing them.

   Macropods are almost exclusively herbivorous, but still show object play (Lissowsky, 1996; Watson, 1998). Watson describes this in some detail; unfortunately, all reports are anecdotal. Some macropods use their dexterous forelimbs and mouth to bite, grab, and manipulate items such as sticks, bark, grass, leaves, food, paper, feathers, and novel objects left in their enclosures. They may also wrestle with bushes and throw sticks against their chest. Red kangaroo males engage in more object play than females (Lissowsky, 1996). However, only juvenile macropods have ever been reported responding to objects with play. It is interesting that the much smaller omnivorous rat kangaroos (potorids), the other family in the Macropoidea and the sister group of the macropods, have never been recorded to engage in object play. In other marsupial families, species that manipulate food and other objects do not appear to do so in accord with the definition of play used here.

9.2.3   Social Play

Social play in marsupials is sufficiently well known in some species that it can be grouped into various kinds of play (also see chapter 4).

Parallel Play   In this type of play, two individuals engage in the same play behavior, but do not directly interact. This is usually locomotor or object play. Lissowsky (1996) lists three species of macropods and one potoroid (rat kangaroo) as engaging in parallel play.

Contact Play   Lissowsky (1996) has described this type of play as being the earliest play behavior seen in *Dasyurus maculatus*. It occurs in preweaning individuals where the young of both sexes climb on the back of the mother; the behavior does not seem to be related to predatory, defensive, or courtship behavior (Settle, 1978), although given the theories from Groos (1898) to Pellis (1993), the latter should not be dismissed without further study. One macropod has been reported to engage in ''pouch play'' in which the young lies on its back and tries to catch hold of the mother's forelimb or fur.

Play Chasing   This behavior, which occurs in marsupial herbivores, seems similar to that seen in eutherian herbivores. It may involve subadults or adults and juveniles (Lissowsky, 1996). In addition to the three families she mentions (dry-forest bandicoots, dasyurids, and macropods), it also has been reported in the sole members of the Tarsipedidae, the honey possum (Russell, 1986), and the Myrmecobiidae, the numbat (Byers, 1999a; Friend & Burrows, 1983).

Play Fighting   This is the most common form of social play in marsupials, as it is in placentals. Although widely studied in marsupials, especially in macropods, we still know less about it than in placental mammals (Lissowsky, 1996; Watson, 1998).

Until recently, play of any type had not been recorded in the American marsupial radiation (didelphids), but this has now been rectified in a description of play fighting in the gray short-tailed opossum (*Monodelphis domestica*) (Fadem & Corbett, 1997). In this species, both climbing over the back of another animal and bipedal boxing with the front paws is recorded in juveniles of both sexes. Play wrestling occurs in the honey possum (Russell, 1986). Young animals chase each other, followed by wrestling and huddling together "amicably."

Play fighting has been reported in several of the largest carnivorous marsupials, but not the smaller species (Croft, 1982; Iwaniuk, Nelson, & Pellis, 2001; Lissowsky, 1996; Morton, Dickman, & Fletcher, 1989). For example, the largest Australian dasyurid, the tiger quoll (*Dasyurus maculatus*), begins wrestling play as soon as its eyes open at 61–63 days of age, while aggression is not seen until a week or more later. By 90 days of age, social play is well developed and the young chase, stalk, and wrestle with each other. These opportunistic carnivores eat insects and mammals supplied by the parents, but do not kill and eat their own prey until later and are not weaned until 120 days of age or older (Settle, 1978). Play fighting is also well developed in the southern hairy-nosed wombat (Fagen, 1981). It is recorded in virtually all macropods (Lissowsky, 1996; Watson, 1998) and there are several reports for many species. Some of these studies rival the most detailed studies of primate and carnivore play in placental mammals. Play fighting in macropods is thus the aspect of marsupial play that I will present in depth.

There are several thorough ethograms of play fighting in macropods (figure 9.1). Probably the most thorough published studies are the series of papers by Watson and colleagues (Watson, 1993; Watson & Croft, 1993, 1996) on red-necked wallabies (*Macropus rufogriseus banksianus*). Based on observations of captives in naturalistic settings, these workers set forth a meticulous ethogram; traced the ontogeny of play fighting, sex differences, and partner preferences; and made inferences as to whether there is support for the theory that play fighting serves as motor training or whether it enhances socialization.
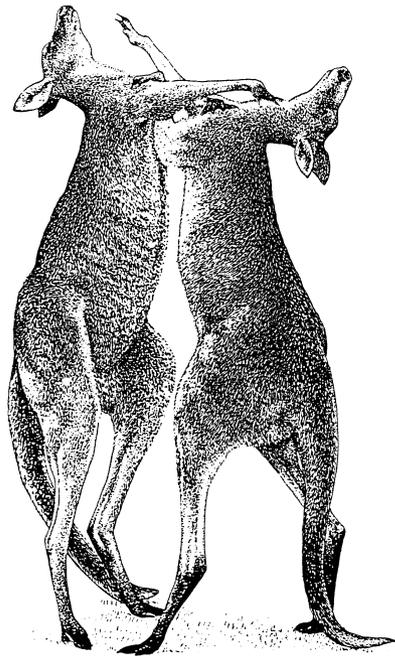
Figure 9.1
Play fighting as stylized boxing in kangaroos, *Macropus giganteus*. (From Russell, Lee, & Wilson, 1989)

Red-necked wallabies are sexually dimorphic, with males larger than females. Sexual competition seemed more important to males than females. Furthermore, males, but not females, disperse from their natal area upon reaching sexual maturity.

Play fighting in red-necked wallabies involved twenty-one actions that can be placed in five categories (Watson & Croft, 1993): play initiation (approach and orient toward), fighting (skip, grab, spar, paw, push/hit, attack, kick, and defend or break contact), affiliative/sexual (sniff, touch, hold, allogroom, mount), acts during pauses (feed, autogroom, shake, head arch), and acts associated with terminating bouts (orient away, leave). Play fights could be high or low intensity. They were repetitive and had a definite, but not rigid, structure. Play fighting was noted to be ''relaxed,'' and potentially dangerous acts such as kicks were inhibited. Skipping was seen only during play and thus is viewed as a good candidate for a play signal. Other acts were exaggerated or differed from their typical context, such as autogrooming and shaking. Play fights were also characterized by the absence of the following acts seen during serious fighting in macropods: stiff-legged walking, grass-pulling displays, and agonistic vocalizations

Figure 9.2
Play fight sparring in mother and young kangaroos. (From Russell, Lee, and Wilson, 1989)

(Watson, 1993). Furthermore, no resource was identifiable as the object of competition (e.g., food, water, resting sites, sexual partner). All these characteristics of play fighting in red-necked wallabies show that the behavior easily meets the five play criteria.

Males play fought almost thirty times more than females, although the three females that did fight had bout durations as long as those of males. Play fighting began as early as 7 months after birth, which was soon after the young began to leave the pouch and 2 months before permanent emergence (figure 9.2). Following weaning at about 16 months of age, the duration of play fights decreased, but the frequency increased. It declined sharply at 20–22 months of age, which is the onset of sexual maturity in males.

Watson and Croft (1993) subdivided the development of play fighting in male wallabies into three stages in which different patterns of play fighting predominated. The first involved high-intensity fights that increased with age from prepouch emergence to weaning. The second lasted from weaning to sexual maturity. As this stage progressed, play fights were shorter and play initiations and solicitations were increasingly rebuffed. Peak instability took place at sexual maturity. During this time, true agonistic behavior increased and partner relationships became unstable. The third stage was found among older adult males and was characterized by low-intensity play fights.

More than 90 percent of the play groups were dyadic. Male wallabies preferred play partners of the same sex and comparable age and dominance status. Females initiated

play bouts with younger males as well as with their male offspring. No play between females was ever recorded. Play partnerships developed among males, but these were only weakly related to affiliative behaviors outside the play context (Watson, 1993). A further study established that wallabies adjusted their play tactics to the age of their partner. Older partners seemed to self-handicap when they played with younger and smaller wallabies. They did this by standing flat-footed, pawing rather than sparring, and not using the strength and power they were capable of deploying. Younger animals were more likely to spar and take on a high stance posture (Watson & Croft, 1996). Shaking apparently functions as an appeasement or metacommunication (''it is only play'') signal.

The presence of some of the more advanced features of play fighting, especially self-handicapping and play signals, has been established in several species of marsupials. No exclusive and necessary play signals have been documented for any marsupial, however (Watson, 1998), and are rare in placental mammals as well (Pellis & Pellis, 1996); self-handicapping seems more common (Watson, 1998). Role reversals are frequent in red-necked wallabies (Watson & Croft, 1996) and red kangaroos (Croft & Snaith, 1991), and probably occur in other macropods as well (Watson, personal communication, 1997).

Watson and Croft (1993) and Watson (1998) make a strong case that many reports of adult ritualized fights in macropods are misclassified play fights. The basic argument is that the agonistic elements described above (as in red-necked wallabies) are absent and no resource is ever identified as the reason for serious competition. If this view is sustained, then macropods show more frequent adult play than that found in many placental mammals.

Sex Play   Sexual behaviors such as sniffing, tail pawing, mounting, thrusting, and other precocial sexual activity may occur in juveniles. Adult females may also take on the male role (Watson, 1998). Such behavior may occur alone or in the context of play fighting, much as we have seen in rodents; this is even true of a didelphid (Fadem & Corbett, 1997).

Interspecific Social Play   This form of play has been recorded in several species, primarily in hand-reared animals in response to their caregivers (Watson, 1998, personal communication, 1997) and in wombats as mentioned earlier.

A similarity with eutherian mammals is the greater frequency of play in well cared-for captive marsupials compared with animals in the field (Watson, personal communication, 1997). Red-necked wallabies are rather solitary and when they were observed in the field during a severe drought, no play of any type was seen, although it has been reported in the field (Watson, personal communication, 1997).

9.3   Phylogeny of Play in Marsupials

Fagen (1981) noted (in his table 3.2) that play was recorded in four families, the carnivorous Dasyuridae (five species), the bandicoot family (Peramelidae), wombats (Vombatidae), and kangaroos and wallabies (Macropodidae). From the more recent literature we can add examples from one of the three American orders of marsupials (opossums) as well as the Potoroidae (rat kangaroos), Phalangeridae (possums), Myrmecobiidae (numbat), and in fact members of eleven of fifteen families in the Australasian radiation. New marsupials are still being discovered or even rediscovered. Three of the four families in which play has not been observed consist of only one to five species, most little studied. These include small marsupials such as pygmy possums and the marsupial mole. The Virginia opossum has been studied for years without any references to play that I could locate (cf. Fagen, 1981; Lissowsky, 1996). This is of interest because the Virginia opossum is a foraging generalist and perhaps the most successful marsupial in competition with placental mammals. Play must not be currently important to its success. Although play may not be at all prominent in opossums, Glickman and Sroges (1966) noted that in their brief curiosity tests, Virginia opossums did grab and manipulate small objects. This was not a study of play, however, and the five play criteria are not met.

In table 9.1, I list the types of play that have been found by family. Note that by far the most diverse play is found in the Dasyuridae and the macropods. These are, except for the little-studied neotropical mouse opossums, the most speciose (i.e., rich in species) extant families. Furthermore, the most diverse play has been recorded for these species, especially the macropods (Lissowsky, 1996; Watson, 1998). As we have seen, play in macropods is rather common and highly developed, while in the dasyurids, it is limited to the larger species. Dasyurids can be very small, whereas macropods are all at least several hundred grams as adults. The one large family in which play has not been reported until recently is the superfamily Petauroidea, the gliders. Based on ecology (it is an extractive forager) and brain size, it might be expected to play, and this has now been confirmed (Iwaniuk, Nelson, & Pellis, 2001; Russell, Lee, & Wilson, 1989).

The conclusion that locomotor play is the earliest-appearing type of play (Byers, 1984) is supported by the findings in marsupials. Ten families show this behavior. Five of them show play chasing, which seems easily derived from locomotor play when a conspecific, especially a sibling, is present. Play fighting and play signals are reported for three families (wombats, dasyurids, and macropods), but sexual play and object play are reported only in the latter two. However, in macropods, play fighting is even more common than locomotor play in animals that have permanently left the pouch. In red-necked wallabies, play by pouch young is more often locomotor. Adult females never play fight and rarely perform locomotor play; young adult males do both (Watson, personal communication, 1997).

A problem in comparing marsupials with placental mammals now needs to be pointed out. Until recently, all 300 or so marsupials were placed in a single order, the Marsupialia, while living placental mammals are currently organized into 16 (Novacek, 1992) or 19 (Nowak, 1999) orders. There are also about fifteen times as many placental species as marsupial species. Thus comparing orders of eutherians with the approximately same number of families of marsupials could be considered an apples-and-oranges error. Maybe not. The higher taxonomic levels are always somewhat problematic, and what constitutes genera, families, orders, and the many intermediate groups often seems arbitrary across groups of animals. The number of species involved and our anthropomorphic determination of what makes for useful categories are important considerations. The diversity among marsupials certainly is apparently beyond that seen in any single eutherian order, both in amount and type of play. With the recognition that marsupials are best viewed as consisting of at least seven orders, the diversity between placental and marsupial orders is not inordinately extreme. That there are fewer orders and species in the marsupials could be related to the more limited geographic areas where most of their modern evolution has taken place (i.e., Australia).

Play, often very complex, has been found in most of the eutherian orders. Play is sometimes rare or simple in very small mammals, mammals with very low metabolic rates, and mammals feeding on low-nutrient diets. Marsupials do have lower metabolic rates than placentals and have a smaller average body size. These limitations, especially body size, do not apply to many marsupials, yet marsupial play, outside of macropods, seems rather simple and undeveloped in all but a few species, in spite of the enthusiasm of Lissowsky (1996). The macropods include the largest marsupials and they are rather long lived. Even compared with comparable placental species, however, macropods are not as energetically and continually playful as are many large herbivorous eutherian mammals, such as deer and horses. However, as described for reptiles in chapter 11, play does not have to be the frenetic, vigorous activity seen in many placental mammals to be true play.

Thus in spite of macropod social play being both common and complex, it may seem that play is not nearly as common in marsupials as in eutherian mammals, at least at the family level. Object play and manipulation seem particularly undeveloped. With the possible exception of social play in some macropods, there do not appear to be any marsupial player equivalents of otters, bears, or monkeys, all of whom have stages in their life in which play is very prevalent. Perhaps this is a bit unfair. Many placental mammalian families have not been reported to play, but the three groups mentioned (aquatic carnivores, terrestrial carnivores, and primates) have larger brains and higher metabolic rates than other groups.

The South American opossums have been little studied as a group. The finding of quite well-developed social play fighting in the gray short-tailed opossum led to the authors claiming that since didelphids are one of the oldest marsupial orders, play is

very ancient (Fadem & Corbett, 1997). Indeed, this mouse opossum, which has been shown to play, is so primitive it has no pouch. Other South American marsupials, so little known, need to be studied. One likely candidate for playing, based on SRT, is the little-known yapok or water opossum (*Chironectes minimus*) found throughout much of Central and South America, although it is seemingly rare (Nowak, 1999). An adult weighs up to a kilogram or more. The yapok is an excellent swimmer, has webbed feet, and is carnivorous on small aquatic animals that it locates with its forefeet. The sole member of the Microbiotheria, the Monito del Monte (South American high-altitude opossum), should be studied as well, since it is considered the most primitive of living marsupials, even retaining some monotreme traits not found in any other marsupials (Nowak, 1999).

9.4   Why Do Marsupials Differ from Placental Mammals?

When first discovered, marsupials were considered clearly inferior in brain development, intelligence, and behavioral complexity compared with eutherians (Grzimek, 1972). Nonetheless, the brains of marsupials are in many respects similar to those of eutherian mammals (Butler & Hodos, 1996; Rowe, 1996). They vary in amount of cortex (encephalization) and cortical convolutions, as do eutherian mammals. There are some differences in the connections between the two hemispheres, with the marsupials being more similar to monotremes. Despite the similarities, it has been shown that the relative brain mass of marsupials, controlling for body mass, is generally less than in comparable placental mammals (Eisenberg, 1981; Jerison, 1973). For example, the didelphids (opossums) seem to have the lowest brain development and the macropods (kangaroos and relatives) the highest within the marsupials (Dawson et al., 1989). The didelphids are considered among the oldest groups of living marsupials, and an opossum the size of a cat has a brain less than 20 percent the size of the cat's (Hoffman, 1982). On the other hand, the tammar wallaby (*Macropus eugenii*) has a larger brain for its body size than diverse placental mammals such as a laboratory mouse, rat, guinea pig, or pig, and the brain is nearly equivalent in size to that of sheep (Renfree et al., 1982). Still, as a group marsupials are less brain laden than placental mammals. If play is related to brain size, then marsupials should play, but less frequently and with less complexity, as Fagen (1981) suggested. But brain size is also related to metabolic rate and this is generally lower in marsupials. Furthermore, adult altricial mammals have smaller brains for their body size than adult precocial mammals (Harvey & Bennett, 1983), and marsupials are the ultimate altricial species if birth, rather than emergence from the pouch, is considered. Is brain size, metabolic rate, or neither related to play variation in marsupials?

   The eutherian-marsupial behavior comparison has been revisited with more data and insight than have been hitherto available (Croft & Ganslosser, 1996). Based on more

recent data, marsupials are about at the relative brain size level of advanced insectivores and some prosimians, but have relatively smaller and less complex brains than all monkeys and apes (Rowe, 1996).

The brain size data are worth exploring further. Since larger species have relatively smaller brains in terms of body mass than smaller species, an allometric relationship has been established between body size and brain size that allows species of different sizes to be compared (Jerison, 1973). As indicated in chapter 8, this ratio is called the EQ (encephalization quotient). Rowe (1996) adjusted the EQ to 100 for values based on dasyurids (and called it the encephalization index or EI). Using this index, opossums in the genus *Didelphis* (including the Virginia opossum) have a value of 75, the lowest yet found in a marsupial (but see Iwaniuk, Nelson, & Pellis, 2001, for lower values in some other marsupials using a different measure). The EI values reported by family are listed in table 9.1. Note that the families reported to play have generally larger values. Since these values vary so much within families, a better approach would be to compare playful and nonplayful species within each family as well as the mean level of play, using some play metric, and mean brain size by family or even genus.

Table 9.1 lists the play values, by family, for Australasian groups as used in brain size and play analyses by Byers (1999a) and Iwaniuk, Nelson, and Pellis (2001). Comparing these values with placentals, it appears that the basal insectivore EI is 60 and that for the entire order about 100; prosimians average 256 and monkeys and apes 543. The highest EI for a marsupial seems to be an arboreal possum in the Petauridae (*Dactylopsila trivirgata*). The one individual measured had a value of 224, but has not been reported to play (Iwaniuk, Nelson, & Pellis, 2001). This species has forelimb digits specialized for foraging and extracting ants from crevices in tree bark (Nowak, 1999; Rowe, 1996). This "outlier" species is not represented in the table. The mean of 156 is for the genus *Petaurus* itself. I have talked to people who have had sugar gliders (*Petaurus breviceps*), another member of this family, as pets and they have mentioned play with objects. Thus these animals are included in the table with a question mark.

Studies on the cortical representations in the brains of placentals, monotremes, and marsupials cannot tell us which features, or which species, reflect the ancestral mammalian form (Rowe, 1996). Even the similarities that exist "may reflect parallel evolution rather than the retention of attributes characteristic of an ancestral form of cerebral cortex" (Rowe, 1996: 33). In spite of their having somewhat smaller brains than eutherians, the amount of neocortex in marsupials, contrary to earlier reports, is about the same. Learning abilities in the marsupials studied have not been found to be inferior to those of ecologically similar placental mammals when their ecological and behavioral adaptations are considered, although their intellectual inferiority is often assumed. This may not be entirely appropriate. For example, the dasyurid *Sminthopsis crassicaudata* weighs only about 10 g as an adult, which is much smaller than a house mouse, and has a very small brain with little neocortex for its body size (Bonney &

Wynne, 2002; Jerison, 1973). Yet it is the first marsupial to be shown to have the ''win stay, lose shift'' learning strategy found in many eutherian mammals (Bonney & Wynne, 2002).

Marsupials are born in a more altricial state than eutherian mammals. Consider the tammar wallaby, which at birth weighs about 0.5 g, whereas the adult weight is around 5 kg, a difference of 10,000 (Rowe, 1996)! Full brain development is not reached until more than 6 months after birth (Renfree et al., 1982). During the first 180 days after birth, the brain increases from 4.5 to 60 percent of the adult weight. At emergence from the pouch at 250 days, the brain is about 70 percent of the adult weight. This provides a great opportunity to not only follow neural and sensory development but to observe the details of behavioral ontogeny. However, just as placental mammals are born at different stages of development, as in the altricial–precocial dichotomy, so are marsupials born with different levels of cortical development (Rowe, 1996). Some marsupials are born with less developed brains than others (Rowe, 1996), but all are much more altricial than any placental mammal.

If we consider emergence from the pouch comparable to placental birth, then the precocial–altricial range is more similar to that seen in eutherian mammals. It also has been argued that a better equivalent to placental mammal birth is when the young become endothermic and insulated with fur (Russell, 1982). Macropods are more likely to have extensive parental care after leaving the pouch and may have brains that are less fully developed (Renfree et al., 1982) than other marsupials from other families or species. Thus postpouch parental care may indicate less behavioral precocity and be reflected in more play. This extreme initial altriciality, with most neural development taking place in the womb in placentals, but after birth in marsupials and monotremes, also suggests that the latter are the animals of choice to test the suggested relationship and continuity between prenatal spontaneous movements and play (Bekoff, Byers, & Bekoff, 1980).

Metabolic rates in marsupials are significantly lower than those of placental mammals (McNab, 1988). They also do not vary as much as in placental mammals. Marsupials may have evolved in tropical forest environments and many macropods (e.g., tree kangaroos) and the potorids still live in these environments in Australia, as do all three South American orders of marsupials. However, tree kangaroos appear to have secondarily invaded arboreal habitats and adapted the macropod locomotor style to living in trees. Low metabolic rates may have facilitated the success of so many diurnal marsupials in the hot, arid areas of Australia as the continent dried out beginning in the Miocene; high metabolic rates could have mitigated their success. Lizards, for example, are more successful (in biomass) in deserts than many mammals and birds because they can endure food shortages and wait for highly seasonal food resources. The lower metabolic rate in marsupials suggests a constrained life in the ectotherm direction, and thus may dampen the expression of play in spite of other favorable factors.

In the first formal study of brain size in Australian marsupials and play, Byers (1999a) found a significant relationship at the family level, correcting for body size, with all four of his most playful families (numbat, potorids, macropods, and wombats) above the regression line. According to Byers, only these families, and some dasyurids, have juvenile play. On the other hand, there was no relationship with metabolic rate, leading to the comment that we find here ''mind over metabolism'' (Byers, 1999b: 40) and the claim that young playful marsupials ''are directing their own brain assembly'' (Byers, 1999b: 45). The latter statement reflects Byers's view that play may be important in developing the brain at certain critical stages in life (Burghardt, 2001; Byers & Walker, 1995). In addition, according to SRT, play should be related to energetic, ecological, and behavioral factors. The koala has a restricted behavioral repertoire, a low metabolic rate, a sedentary way of life (it is inactive 20 hours a day), a specialized plant diet, a slow rate of locomotion (although it is capable of quick bursts of speed), and a smooth-surfaced brain that is much smaller than its brain cavity (Byers, 1999a; Strahan, 1995). The wombats, closest relatives to the koala, are at the opposite of the koala in almost every dimension. Wombats are playful, koalas far less so.

It should be pointed out that Byers (1999a) used only a measure of play frequency on a three-point scale: (1) no play, (2) play bouts of less than 5 seconds occurring less than once every 45 minutes over fewer than 3 days after leaving the pouch, or (3) play occurring for bouts of at least 20 seconds on most days after leaving the pouch. I assume that there were no species in between categories 2 and 3.

A more recent study (Iwaniuk, Nelson, & Pellis, 2001) pointed out some problems in Byers's analysis and added more species. Byers averaged play across families using his three-point scale (see table 9.1); one or two playful species in a larger family could skew the results. In addition, the relatedness of the families was not considered, resulting in comparisons that were confounded by the degree of relationship among the families. For example, almost all the playful species except for the dasyurids are in one order, the Diprotodontia.

Iwaniuk and colleagues (2001) used the same play scale as Byers did, but included more species. They used an accepted phylogeny for the relationships among the forty-five species for which they had data. Overall brain size (EQ) was significantly correlated with both play frequency (replicating Byers, 1999a) and play wrestling (play fighting); the results were attenuated by using the method of independent contrasts. Although positive correlations between overall brain size (EQ) and neocortical size were found for both play frequency and play wrestling, only the relationship between play frequency and neocortex size ($r = 0.59$) approached statistical significance at the family level, and only that of play frequency and overall brain size ($r = 0.26$) approached significance using the full data set. In a study of eighteen diverse marsupials, forelimb dexterity (wrist, paw, digits) was also significantly related to cortex size, not total brain size (Iwaniuk, Nelson, & Whishaw, 2000). Relating forelimb dexterity and play holding

brain/cortex size constant would help test more of the foraging mode hypotheses in chapter 6 and could be carried out across all terrestrial vertebrates (Iwaniuk & Whishaw, 2000).

In placental mammals, play, especially social play, is somewhat related to social organization. Among marsupials, even the large macropods show far less diversity and complexity in social systems than eutherians. Beyond mother-infant bonds, there is no complex social network and there are no instances of hierarchical control of mating opportunities as extreme as that found in wolves and chimps (Hendrichs, 1996). On the other hand, the kinds of choices made by females are similar for marsupials and placental mammals (Walker, 1996). Also, as in many lizards, birds, and eutherian mammals, male size-based dominance hierarchies that enhance access to females have been documented in many kangaroos (Croft, 1989).

When contrasting two distinct stocks of animals in order to "detect the influence of phylogenetic constraints we need to show consistent differences (a patterning of differences) between two phylogenetically distinct arrays when faced with similar sets of niche opportunities" (Jarman & Kruuk, 1996: 80). To evaluate sociality, these authors classified female spatial-social organization into six categories of style as shown in table 9.2.

All but two of the thirteen families of marsupials Jarman and Kruuk evaluated had 100 percent of all species studied in category D. The exceptions were six of sixty-three macropod species, categorized as E, and all of the Petauridae, whose species fall into categories A, B, or C, many of which carry out group defense. The latter group consists of small arboreal nectar and sap specialists comparable to small marmosets and galagos. Since they show convergence with these placentals in niche and social system, marsupials can evolve more complex social systems, although most have not.

The authors argue that style D is the original and ancient mammalian style of adult female sociality and that all other styles can be derived from it. "There seems to be no general adaptive reasons for the metatherian failure to evolve sociality or defence of

Table 9.2
Styles of spatial-social organization in adult female mammals

Range Defense	Sociality	Style
Defended by female	Forages solitarily	A
Defended by group	Forages solitarily	B
Defended by group	Forages socially	C
Undefended range	Forages solitarily	D
Undefended range	Forages in ephemeral groups	E
Undefended range	Forages in persistent groups	F

Source: Jarman & Kruuk (1996)

range. On the evidence, the Metatheria either have not met the same evolutionary challenges as some Eutheria, or they are relatively behaviorally plesiomorphic, perhaps the victims of phylogenetic constraints'' (Jarman & Kruuk, 1996: 96). Thus social organization, at least the female style looked at here, is not of value in understanding the distribution of play among marsupials. That territorial defense can occur in marsupials is shown by Bennett's tree kangaroo (*Dendrolagus bennettianus*) in Australia (Strahan, 1995). Males of this species defend discrete territories and are intolerant of each other. Their polygynous system is similar to that in many eutherian mammals as well as many lizards. When the radiation of tree kangaroos in New Guinea is studied, we may find much more complex social organization. Two other members of the genus *Dendrolagus* that have been studied have high play frequency scores and play fighting (Iwaniuk, Nelson, & Pellis, 2001).

No dasyurids, which include the carnivorous marsupials, show social foraging or social range defense. This is in contrast with eutherian carnivores and insectivores. In terms of predatory behavior, the typical view is that marsupial carnivores are less flexible in response to prey than are eutherians (Pellis & Officer, 1987). In a comparative study of both the attack strategy predators used prior to prey contact and how they performed head shaking after grasping prey, Pellis and Officer (1987) compared four carnivorous dasyurid marsupials from three genera with the well-studied domestic cat. Responses to prey such as mice, rats, chickens, guinea pigs, and invertebrates were filmed. There were differences among the marsupials with one species, *Dasyuroides brynei*, having the only frontal attack tactic. Head shaking was found in all species, but might be modified by habitat constraints (e.g., arboreality). Having only a highly domesticated placental mammal for comparison, they judiciously drew no conclusions about the relative plasticity of marsupial and eutherian predators. In a later study (Ben-David, Pellis, & Pellis, 1991), the predatory tactics of the marbled polecat (*Vormela peregusna syriaca*) were described in which the location of bites was related to the size of prey and whether the prey were fleeing or defending themselves. This variability was interpreted as related to the opportunistic and nonspecialized nature of the prey this species eats. However, the authors pointed out that many placental mammalian predators are also quite stereotyped in their predatory tactics. These include species that are considered highly playful, such as mongooses (Rasa, 1984). More detailed comparisons of predatory tactical diversity among placental and marsupial lineages would be most useful in establishing the relative degree of flexibility shown both across taxa and within individuals and whether such flexibility is at all related to amount or type of play. Object play, so common in predatory placentals, is present, but does not seem highly developed even in the carnivorous marsupials. It is too soon to relate generalized predatory behavior to amount of object play, although predators clearly engage in object play in ways that resemble aspects of real predation.

Does the lessened social complexity in marsupials explain the lessened variability in their behavior? Hendrichs (1996) closely compared marsupial and placental mammal sociality. Although there is indeed overlap with some eutherian species, he also recognized that marsupials nonetheless differ from eutherians in body size (smaller), metabolic rate (lower), hemispheric connections (fewer), sociality (less complex), and cognitive competence (less), among other differences. He evaluated sociality in light of four factors: social, physiological, mental, and behavioral. In all domains marsupials, even macropods, seem to function on an overall lower level than their eutherian counterparts. Hendrichs concluded that cognitive and behavioral competence requires physiological complexity, but not social complexity. On the other hand, complex social organization requires physiological (varying stress and coping reactions) and behavioral (varying social and reproductive roles) differentiation, but not necessarily high mental competence. He thus concluded that the lower average mental competence of marsupials is not due to lack of more complex sociality, but may be the result of less pronounced physiological and behavioral differentiations. Nevertheless, the "less pronounced physiological and behavioural differentiations possibly do not favour the quick and precise—and therefore costly—activations and regulations necessary for efficiency in complex mammalian systems" (Hendrichs, 1996: 131). This conclusion bears a close, and apparently independent, resemblance to the arguments I previously made in comparing mammals and nonavian reptiles in general (Burghardt, 1988b). On the other hand, the exceptions are often the most illuminating. A comparison of different groups of marsupials and eutherian mammals of similar size, diet, and microhabitat would allow more precise understanding of the exact methods being employed, including the role of any playfulness.

In summation, many of the more complex patterns of social play seen in placental mammals (play fighting, play signals, role reversal, self-handicapping) can be found in at least some marsupials. However, is it also safe to conclude that play is not as ubiquitous in the families with smaller marsupials as it is in those with larger-bodied species? Could the fact that play is more common in larger-bodied and more speciose families of marsupials be related to their relative success? We cannot yet answer this question.

Nevertheless, we can give tentative answers to the two questions posed at the beginning of this chapter. The absence of play in the families of marsupials with relatively small brains, such as the didelphids, the oldest known lineage of marsupials with the exception of the one extant member of the Microbiotheriidae (the South American high-altitude opossum, about which little is known), suggests that brain size is involved. It also suggests that the earliest marsupials did not play, at least complexly, and thus play is not homologous in metatherian and eutherian mammals. As for the other issue, whether the ectotherm–endotherm contrasts used with eutherian mammals can be also used with marsupials, the answer is a tentative yes. Degree of

altriciality, body size, metabolic rate, captivity effects, all seem to vary in marsupials according to SRT, but the data are still very sparse. The macropods are a critical group for this evaluation, but most of the smaller and more cryptic kangaroos, wallabies, and their relatives have not yet been studied. Since macropods are so often compared with ungulates as their placental ecological equivalents, more formal analysis should be carried out here as well, using comparable methods and data gathering so quantitative, not just qualitative, comparisons can be made.