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The Genesis of Animal Play

Testing the Limits

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10 Does the Platypus Play?

10.1 An Informative Relic Group

When the marsupials split off from the lineage that became the eutherian mammals about 100 mya, dinosaurs dominated the terrestrial landscape. Many millions of years earlier the mammal-like reptiles evolved and perhaps about 200 mya the monotremes first appeared (figure 7.1). Today the remnants of this ancient group live only in Australia and New Guinea, although fossils have been found in South America. These mammals have retained the most primitive, that is reptilian, characteristics, and their exact relationships to other mammals are still controversial (Musser, 2003). Although I portrayed the monotremes as splitting off the lineage leading to marsupials and eutherians (figure 10.1), this is not the only hypothesis available. Unfortunately, fossil evidence for the relationships among Mesozoic mammals is quite sparse.

Four scenarios have been advanced over the past century for the relationship of monotremes with other mammals (M. Griffiths, 1978). The most radical view is that monotremes independently evolved from therapsid (''mammal-like'' reptiles) and the similarity with marsupials is convergent. Another view is that monotremes are derived from early marsupials, sharing derived characters such as the dentition of the milk teeth. A third view, based on brain case morphology, is that the monotremes are allied with extinct mammalian nontherian orders such as the Multituberculata and the Triconodonta, and with these and other groups belong in a separate subclass of mammals called the Prototheria. Other specialists would link monotremes just with the Multituberculata and place the placental mammals and marsupials in the Theria subclass. The current consensus seems to be to consider all living mammals a monophyletic group evolved from a cynodont mammal-like reptile with monotremes most closely related to the long-extinct mammalian groups, the multituberculates and triconodonts (Colbert, Morales, & Minkoff, 2001). Since there are problems with all these views, it is most conservative to divide living mammals into three subclasses for the monotremes, marsupials, and placentals. Molecular evidence may shuffle the relationships still more (Grützner et al., 2003; Zardoya & Meyer, 2004). Regardless, if play is found in monotremes, the potential for evolving play would go back at least to the earliest mammals.

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Unfortunately, only two families of monotremes exist today: the duckbilled platypus (one species) and spiny anteaters (two genera, two species). These fascinating animals have been increasingly studied in recent decades. Excellent concise overviews of anatomy, life history, reproduction, and physiology are available (Eisenberg, 1981; Grant, 1989; M. Griffiths, 1978, 1989; Nowak, 1999) along with a fascinating book on the history of the scientific controversies surrounding them (Moyal, 2001). A brief review is given here in addition to addressing the question of play in this group of mammals that might be critical in understanding the genesis of mammalian play.

The echidnas (spiny anteaters) live in New Guinea (*Zaglossus*, long-nosed echidna), where they are large (5–10 kg); and in Australia, Tasmania, and nearby islands (*Tachyglossus*, short-nosed echidna), where they are small (3–6 kg). *Tachyglossus* is highly specialized for feeding on ants and termites. *Zaglossus* feeds on earthworms and small arthropods, but is otherwise little studied, and most of our knowledge of echidnas is based on *Tachyglossus* (M. Griffiths, 1978). Both species have long tongues, no teeth, and powerful bodies covered with hedgehoglike spines. They can dig burrows with ease.

The platypus (*Ornithorhynchus anatinus*), an aquatic specialist, lives in eastern nonarid Australia and along rivers into South Australia. Its streamlined body is considerably smaller than that of echidnas (0.5–2.0 kg), but shows more sexual dimorphism; adult male mass is almost twice that of females (Grant, 1989). A fine, but dated, review of the sensory and behavioral biology of the species is available (Burrell, 1927) in addition to a later review (M. Griffiths, 1978). Platypuses, with their ducklike bill, primarily feed on soft aquatic invertebrates and crustaceans. They seem to eat prodigious amounts for their body size: a 2-pound (0.9-kg) female was recorded eating 1 3/4 pounds (0.8 kg) of washed live food in 1 day (Fleay, 1944)!

Both groups of monotremes are highly specialized animals. While retaining more reptilian characteristics than other mammals, they certainly are not living fossils in the narrow sense. Although monotremes do have some ancestral traits, they also have many derived specialized traits. However, for the echidna, ''the overall skeletal characteristics do suggest a living species that might represent the ancestral mammalian condition'' (Jerison, 1973: 7), while Musser (2003) argues that platypuses are the much older family. The monotreme reproductive mode of laying eggs, the structure of their sperm, their possession of internal testes, and the structure of their pectoral girdles all show strong reptilian affinities. The name Monotremata derives from the fact that like all reptiles, a single orifice, the cloaca, is used for passing urine, digestive wastes, and gametes. Marsupials also share this trait.

Monotremes maintain lower body temperatures than most other mammals, about 30–32°C. Monotremes, especially the echidna, do not regulate their body temperature as precisely as most eutherian mammals and thus they have been termed heterothermic (M. Griffiths, 1989). However, some placental mammals, such as sloths, also

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show less than precise thermoregulatory abilities. The neonates of many placental species that have altricial young lacking insulation (hair and fur) also have a limited ability to thermoregulate. It is possible that the heterothermic tendencies of sloths may have been secondarily developed as an evolutionary response to a slow-paced life-style relying on a low-energy diet (leaves). The situation with the platypus is similar. The platypus is able to maintain a stable body temperature of 32°C until an ambient temperature of 30°C is reached. However, in cool weather the extremities may only be 1 or 2°C above ambient air or water temperature (Grant, 1989). Since the ability of ancestral monotremes to thermoregulate is not known, the extant, highly derived forms may also be showing a secondary response.

All monotremes are relatively long lived (close to 20 years) and reproduce slowly, having clutches of only one or two offspring yearly. Being long lived, it might pay to benefit from experience. In fact, a feature of monotremes that is not primitive is that they possess very large and differentiated brains compared with some basal groups of placental mammals (insectivores such as the hedgehog) and marsupials (didelphids such as the opossum) (Jerison, 1973). The purpose of these brains has been the subject of a debate that is still unresolved.

Little is known about the natural behavior of monotremes, but play does not appear prominent. Fagen (1981), summarizing the types and distribution of mammalian play, does not report observations on the spiny anteaters. Echidnas have a very large and convoluted brain (Butler & Hodos, 1996) and can learn some tasks as quickly as laboratory rats (M. Griffiths, 1989). The behavior patterns recorded for the echidna may preclude typical play. Their antipredator strategy is to roll up into a spine-protected ball, thus obviating the need for the active defensive maneuvers often seen in play. Similarly, the forelegs of the animals are modified so much for digging that the use of the forepaws in manipulation or grooming is limited (Eisenberg, 1981). Sometimes these two traits operate in concert, as when the echidna digs an escape burrow while its spines protect its exposed dorsum. Echidnas have highly specialized food habits.

Clearly, we need to know more, but all the above features, combined with their low-energy diet, which demands a high rate of intake, suggest that play would not be conspicuous in these animals. Brattstrom (1973), a scientist specializing in reptiles and their behavior, described the social and maintenance behavior of *Tachyglossus* in detail, listing more than sixty postures, feeding and defensive behaviors, locomotion, bodily maintenance, and investigative responses such as sniffing. He reported nothing resembling play and concluded that the echidnas' behavior was quite simple and less complex than that found in many lizards. They are primarily solitary as adults.

In the platypus, the brain is smooth (it has an unconvoluted cortex, like that of a laboratory rat) but relatively large. Although no formal learning studies appear to have been performed on the platypus, there are considerably more behavioral observations

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available than in the echidnas. The animals occupy a semiaquatic niche in Australia that is not occupied by any marsupials. They are quite active at times and when not in the water remain in burrow retreats. Platypuses seem to possess a richer array of foraging and defensive behavior patterns than do echidnas, although I am not aware of any comparative ethograms. Foraging on a wide array of aquatic animals, they also have almost twice as high a metabolic rate as echidnas and an even larger brain, almost at the eutherian mammalian average for their body size (Eisenberg, 1981).

10.2 Play in Monotremes

Play has not been noted in echidnas, and all evidence for play in the platypus is anecdotal (Fagen, 1981); given the importance of this group, I will review what we know.

The classic description is from Bennett (1835), who had a captive pair in his room in Sydney. ''One evening both the animals came out about dusk, went as usual and ate food from the saucer, and then commenced playing one with the other like two puppies, attacking with their mandibles and raising the fore paws against each other. In the struggle one would get thrust down, and at the moment when the spectator would expect it to rise again and renew the combat, it would commence scratching itself, its antagonist looking on and waiting for the sport to be renewed'' (1835: 256).

Later he writes: ''Sometimes I have been able to enter into play with them, by scratching and tickling them with my finger; they seemed to enjoy it exceedingly, opening their mandibles, biting playfully at the finger, and moving about like puppies indulged with similar treatment'' (Bennett, 1835: 256). After providing them with a pan of shallow water ''with a turf of grass in a corner, they enjoyed it exceedingly. They would sport together, attacking one another with their mandibles, and roll over in the water in the midst of their gambols; and would afterwards retire, when tired, to the turf, where they would lie combing themselves. It was most ludicrous to observe these uncouth-looking little beasts running about, overturning and seizing one another with their mandibles, and then in the midst of their fun and frolic coolly inclining to one side and scratching themselves in the gentlest manner imaginable'' (Bennett, 1835: 256–257).

Although this certainly sounds like social play, Burrell (1927) was skeptical and, aware of the enormous appetite of these animals, thought that the responses Bennett observed were the death agonies of starving animals. Moreover, many of Bennett's observations were of animals on land, on which they are apparently quite awkward (Burrell, 1927). However, supporting Bennett's observations, apparently independently, were those of Fleay (1944), who was the first to breed the platypus in captivity. After about 5 months of age, the single young female behaved somewhat similarly to the animals that Bennett observed a century earlier. ''Feeding vigorously whenever the occasion presented itself, rolling on her back and playfully scratching herself, clinging

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Table 10.1
Application of the play criteria to the anecdotal reports of play in the platypus

Play Criteria	Social Play	Sensorimotor Play
Incompletely functional	Yes	Yes
Endogenous component	Yes	Yes
Structural or temporal difference	?	?
Repeated performance	Yes	Yes?
Relaxed field	Yes	Yes

with all four feet to any hand that approaches her, or playing ''chasie'' by holding on to her mother's tail with her beak, or even pursuing her own tail like a pup, Corrie at the end of March, 1944, had become the most frolicsome, fat, and engaging little duckbill one could imagine'' (Fleay, 1944: 43).

More recent captive observations and observations in the field are rare concerning play in the platypus, although an authoritative review of monotreme biology accepted Bennett's conclusions and noted the accuracy of his many other observations on platypuses (M. Griffiths, 1978). Moreover, a few years later a leading monotreme biologist (Grant, 1983) did note the following, which suggests locomotor play: ''During the crisp early mornings and evenings of this season [Autumn], the newly emerged juveniles can be seen 'playing' in the water with much more splashing than is normally seen when adults are going about the daily business of obtaining their food. For the young this playfulness is shortlived and is soon replaced by normal feeding behaviour and the behaviour that ensures their future survival'' (1983: 55).

How do these sparse observations stack up against the five criteria (table 10.1)? The main problem is that the observations are limited and anecdotal. The similarity with puppies claimed by both Bennett and Fleay could be due to their own familiarity with dog play and their desire to convey some idea of the behavior seen to readers who presumably are also familiar with dogs.

Surplus resource theory would predict that under benign conditions play might indeed be seen in these aquatic animals. Platypuses eat aquatic invertebrates in the wild and will eat earthworms, grubs, and small shrimp in captivity. However, their need for food is enormous, up to or equal to their body weight each day. Although one might expect a generalist feeding on hidden prey to show some foraging-related play, it may be virtually impossible for these animals to reach satiation in the wild. Could their physiology be such that although they attained endothermy, they did it at the expense of not having any spare time, especially in the wild? Could Spencer, without even knowing about them, have had the platypus in mind as an ''inferior animal''? Too little is known about their social system to be more precise than that. We do know that platypuses have the aquatic specializations, brain size, and ecological niche that might

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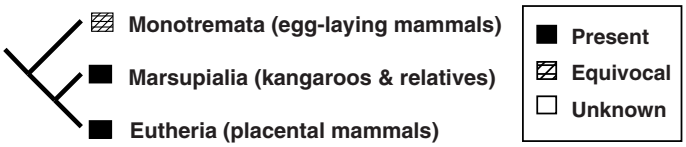

Figure 10.1
Phylogeny of the major mammalian groups and occurrence of play.

be conducive to the occurrence of play. Young animals do have a period during development when they are protected and provided for by the mother. Burrow observations would be most informative. However, growth rates are quite rapid, and available energy may be channeled to growth, as in most reptiles.

An apparent paradox here is that many marsupials seem to have relatively smaller brains than monotremes, and yet many are socially playful. Again, we see that the relationship of play to brain size is murky indeed. According to SRT, it would be predicted that the platypus would be more playful and more diverse in its play than the echidna. Eisenberg (1981) has related brain size (encephalization quotient) in many mammals to the kind of antipredator strategy used (passive or active) and locomotion dimensionality (two or three dimensions). In both cases, relatively larger brains should be found in the latter categories. The platypus has a more active escape strategy than the echidna and operates in a three-dimensional environment; it also has a larger, if less convoluted, brain. Since arguments have been made that the most basic play may be locomotor and be related to antipredator tactics (Byers, 1984), then to this extent the observation of more play in the platypus makes sense.

Recently a new wrinkle has developed. Both the platypus and at least one species of echidna have been shown to be electroreceptive (Moller, 1995; Proske & Gregory, 2003). This means that they can perceive weak electric fields, as can many fish and some amphibians. They may use this information to locate food. However, their detection threshold is much higher than in fish (Moller, 1995). Monotreme electroreception is passive, however, while many fishes possess an active electrosensitivity system. In active mode, fish produce weak electrical signals that can be used to detect prey and other environmental features in a way similar to that of bats employing ultrasonic sounds that reflect from objects and convey information on distance, size, and movement. Those fish species with the most advanced electrosensory abilities have brains far larger than is typical for fish, by a factor of 100 or more. Electrophysiological investigations have shown that the large brain of some fish is related to their electrosensitivity (Moller, 1995). Early neurophysiology investigations of the echidna brain showed that much of the large association cortex was ''silent.'' Could the larger brain of the monotremes be related to possession of this sensory modality?

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10.3 Evolution and Mammalian Play

A chapter has been devoted to these enigmatic animals, in spite of the weak evidence for play, because they may be central to the issue of origins. If we accept that some play or very playlike behavior may occur in the platypus, then play might be plesiomorphic in mammals, and found in their common ancestor. Conversely, the appearance of play in eutherians, marsupials, and monotremes might be due to a suite of traits involving energetics, ecology, life history, and brain development that favor behavior meeting the five play criteria (figure 10.1).

As even earlier radiations of animals are covered in the following chapters, even more time will be expended on questionable data concerning the occurrence and form of play in nonmammalian taxa. Given the occurrence of play in all subclasses of mammals, however, such exploration is essential in the quest for its origins.

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