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The Genesis of Animal Play

Testing the Limits

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6 The Genesis of Play: An Integrative Approach

There are many factors influencing play, and chapter 5 considered those dealing with establishing the adaptive function of play; some costs of play; the development and genetics of play; and motivational, emotional, and neural substrates of play. All these topics could only be touched on, but it was important to present some findings relevant to understanding the true complexity of play, while not, I hope, signaling the impossibility of gaining some understanding of play as an evolutionary phenomenon. In this chapter, life history, social, and ecological factors underlying play will be covered, along with the difficult issues of energy and physiology that together help us predict in what species and contexts play should be found. It thus expands on conclusions reached in my first theoretical play foray.

The frequent observation that play occurs only when animals are in a “relaxed field,” sated, warm, content, and so forth supports the view that play of various kinds originated in animals with (1) sufficient metabolic resources; (2) an efficient aerobic system; (3) a relatively familiar and often risk-free juvenile environment; (4) the ability to accumulate more energy than can be shunted to growth; (5) escape from the need to behaviourally thermoregulate to bring the body to the optimum for vigorous behavior; (6) innate precocial exploratory and arousal mechanisms; (7) specific motivational and behavioural systems; and (8) relatively high survival rate of offspring (Burghardt, 1984: 31).

6.1 Parsing the Problem of Energy and Play

The concepts of energy and excess (surplus) energy have been used in the analysis of play. However, the energy concept has been used to refer to quite different aspects of animals and their behavior, leading to considerable confusion. Four of these uses are outlined in table 6.1. For example, Spencer used energy in his surplus energy model to refer to stored nutritional reserves such as fat (use 2) that would be expressed in vigorous behavior (use 1), tapping into instinctive behavior patterns organized in neural motivational systems centers (use 3). The possible role of play in enhancing the arousal level of animals to an “optimal” state represents a fourth use. Throughout this book we

Table 6.1Various connotations of the terms *energy* and *surplus* in reference to play

Meaning of Energy	Manifestation of Surplus
1. Vigorous (energetic) behavior	1. Elevated activity level (hyperactivity, fidgety, persistent, rambunctious)
2. Metabolic potential (i.e., from food)	2. Excess available metabolic reserves (e.g., fat)
3. Derived from specific behavior system(s) (e.g., motivation, drive, or instinct)	3. Extreme accumulated specific motivation, drive state, or action-specific energy (e.g., predatory, sexual)
4. Level of general behavioral arousal or responsiveness	4. High level of alertness

Source: Based on Burghardt (1984)

have seen application of all four energy concepts to play, and it is time to differentiate them.

The brain uses much of an animal's energy expenditure, up to 20 percent or more, even when it is only 2 percent of the body mass (S. T. Parker, 1990). Thus brain size and metabolic rate seem to be closely related (Burghardt, 1984). Endothermy (warm-bloodedness) is a trait that demands considerable energy and is also related to metabolic rate. I have discussed the details of this relationship elsewhere and noted that animals with very low metabolic rates and those relying on anaerobic metabolism (table 6.2), play less (Burghardt, 1984, 1988b). Very small mammals, such as shrews, have high metabolic rates and high thermoregulatory costs because of their large surface-to-mass ratio. These attributes may preclude having sufficient metabolic energy available to expend in playlike behavior that may not efficiently serve immediate survival needs. Very small (< 10 g) endotherms are rarely recorded as engaging in play. For example, many studies have experimentally determined the serious constraints on small hummingbird behavior (e.g., López-Calleja & Bozinovic, 2003). Likewise, nutritionally and energetically rich diets may foster play by providing both "excess" metabolic resources and the time for play. Time spent foraging may reduce or eliminate the time for play. Consider the parallel with laborers who work long, physically exhausting shifts for minimal pay. Such laborers are not the ones traveling the world searching for exciting adventurous play, such as trying to travel around the world by balloon, building a faster yacht, or climbing the highest mountains. Similar time constraints could explain why play in adult harbor seals (*Phoca vitulina*), generally solitary and locomotor, is more common outside the breeding season (Renouf, 1993).

Metabolic rates in animals are not easily measured. Basal metabolic rate (BMR), resting metabolic rate (RMR), and maximum metabolic rate (MMR) all have different measurement demands (see A. F. Bennett, 1982; Burghardt, 1984; Nagy, 1982, 2000) and different implications for the ability of animals to express the energetic behavior

Table 6.2

Metabolic terms related to behavioral performance in animals

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1. *Basal metabolic rate* (BMR). Minimal metabolic rate when fasting under optimal environmental conditions. All metabolic rates may be measured indirectly (by oxygen consumption) or directly (by heat production).
 2. *Standard metabolic rate* (SMR). Minimum metabolic rate at a given temperature in an ectotherm (no heat production).
 3. *Resting metabolic rate* (RMR). The level of oxygen consumption or heat production when an animal is not engaged in any overt activity.
 4. *Field metabolic rate* (FMR). Daily total energy costs of animals in the field engaged in all normal activities. Often measured by estimating CO₂ production using the doubly labeled "heavy" water method.
 5. *Aerobic metabolism*. Release of metabolic energy by use of external (gaseous) oxygen, generally obtained through breathing, lungs, and associated systems.
 6. *Aerobic scope*. The range of oxygen consumption rate between minimum and maximum aerobic oxygen utilization.
 7. *Anaerobic metabolism*. Release of metabolic energy by the breakdown of stored glycogen to lactic acid. This occurs when insufficient molecular oxygen is available through ordinary respiration.
 8. *Anaerobic scope*. Rate of lactic acid formation during the onset of vigorous activity (usually the first 30 seconds).
 9. *Anaerobic capacity*. The amount of lactic acid formed during longer activity bouts, usually those preceding exhaustion.
 10. *Maximum sustainable activity*. The amount of exertion (often measured in duration or rate of locomotion) an animal can carry out continuously without building up an oxygen deficit.
 11. *Energy costs of activity*. Amount of energy (joules or calories) needed to perform a given behavior. Should be measured as a *rate* of energy output, as in metabolic rate (i.e., watts = joules/second) (P. Martin, 1984). The net cost of activity is the difference between the total energy expenditure rate during activity minus the RMR.
 12. *Total metabolic scope*. The difference between BMR and maximum combined contributions of aerobic and anaerobic metabolism.
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we are predisposed to label as play (table 6.2). Brain size in mammals appears to be more related to factors such as arborality and patchily distributed diets than metabolic rate (McNab & Eisenberg, 1989). Thus arboreal hunters have bigger brains than terrestrial counterparts. For example, a rather arboreal jaguar (*Panther onca*) has a relatively larger brain, but lower metabolic rate, than lions (*Panthera leo*) or tigers (*Panthera tigris*). Metabolic rate may thus be influenced by physiological demands that have little effect on brain size. Metabolic and brain size processes and measures will be invoked later in interpreting play diversity and play origins. For now it is sufficient to state that the complex relationships among brain size, metabolic rate, body size, endothermy, and thermoregulation argue against any simple relationships between play type or amount of play with any of these factors.

It is, however, germane to ask how energetically costly play is in the more playful mammals in which it has been measured. In cats, play seems to add about 4 percent to the energy budget (P. Martin, 1984b) and this has been used to argue that play is not very costly (and also perhaps not very important). This may not be a generalized conclusion because some species, such as pronghorn antelope, may expend so much energy in play that if the energy went into growth, it would produce 7 percent more growth at 12 weeks of age; play consumes about 20 percent more energy than that used at rest (Miller & Byers, 1991). Thus, allocation of time and energy in play is not a simple matter and warrants careful analysis (Bekoff & Byers, 1992). Such allocation has been a focus of optimization theory in recent animal behavior, including optimal foraging theory, where energy intake and time and energy expenditures, sometimes accompanied by risk, are central considerations.

One consequence of an energy constraint on behavior is that the energy costs of locomotion vary with the medium in which the animal operates. All things being equal, swimming consumes the least energy, flying is next in energetic cost, and terrestrial running or walking the most costly (McNab, 2002). These differences can be considerable. A 10 g mouse expends almost 30 times more energy walking than a 10 g bird does as it covers the same distance (McNab, 2002). Since swimming is less costly than terrestrial locomotion, play may be more common in aquatic animals, and in animals operating in both aquatic and terrestrial media, play should be more common and less energetically constrained in water. This is a robust prediction from an energetics perspective that has received support (Burghardt, 1988b). For example, marine mammals such as seals and dolphins are perhaps the most playful of all mammals (Fagen, 1981).

Although up to this point only stored metabolic energy and stored excess energy (fat) have been discussed, it is clear that metabolic energy is essential but not sufficient for play. For example, some species may have much stored energy and be fat, such as sloths, yet do not engage in vigorous behavior (use 1 in table 6.1) because of physiological constraints. One would not expect a fat tortoise to rapidly chase a sibling and wrestle with it. Vigorous behavior, which is often viewed as essential to play, may be an anthropocentric conceit based on the time scale of our own behavior. Thus gentle or slow-motion play might be ignored or viewed as not “real” play. This bias must be put aside when a comparative approach is taken. The nature of play and its “vigorous” execution must be viewed from the perspective of the performer, not the observer.

Play as a response to activity in specific neural centers or, more generally, the activation of specific behavioral systems, is another aspect of energy that has led to confusion (use 3 in table 6.1). The concept of energy accumulation as a driving force for the amount and intensity of behavior is an old idea easily transferred to the play context. Thus, as described earlier, Lorenz and other early ethologists advocated an action-specific energy (Lorenz, 1956, 1981) or action-specific potential (Thorpe, 1956) underlying the performance of species-specific behavior patterns (instincts). These were more

molecular versions of the more general basic “drives” of the experimental psychologists (Mook, 1996). The application of such ideas to play goes back to other advocates of both instinctive energetics and surplus energy theory. The prolific and influential psychologist William McDougall (1924) described an energy model of instinct very similar to Lorenz’s and also was an advocate of surplus energy. Spencer himself advocated a somewhat mentalistic neural center model in his surplus energy theory. In all these models, lowering of the stimulus threshold needed to elicit behavior, owing to deprivation (e.g., hunger) or lack of opportunity to engage in specific behavior patterns, was a key factor in both instinctive behavior and play (e.g., hunting).

Play as a consequence of a general arousal process (use 4) is invoked in models in which play is viewed as a way of self-stimulation or relieving boredom. Play may be a means of achieving optimal arousal for proper neural and physical development. For example, it has been argued that the exaggerated locomotor and rotational play in harbor seals promotes vestibular stimulation (Renouf & Lawson, 1986), which may be reinforcing or pleasurable. In the general arousal view, play is of interest primarily as an activation process that gets the animal “up and going” and is controlled more by internal endogenous factors (see play criterion two) than external stimuli, although the latter may induce or facilitate play, as when objects or partners are made available (Spinka, Newberry, & Bekoff, 2001). In young rats, postsuckling arousal leads to increasing behavioral activation so that at weaning the pups leave the nest (Gerrish & Alberts, 1997). These authors argue that play is activated at this time. There are considerable observations showing that play in young animals is more prevalent after feeding (e.g., Burghardt & Burghardt, 1972). Human infants, after feeding, initiate and maintain play with the mother, not vice versa (E. Blass, personal communication, 2002). Blass writes: “In order for the brain to develop, it requires punctate stimulation—what better time or way to get it than after a meal.”

An old relationship in psychology may be relevant here: the Yerkes-Dodson law. In this relationship, task learning is viewed as influenced by arousal level (Mook, 1996). Easy tasks are most quickly learned and performed when the animal is highly aroused, whereas difficult tasks are most easily learned and performed when the animal is rather relaxed and not highly stressed or too “motivated.” In other words, if you are starving when you are in a class on a difficult subject or taking a difficult test, you are not likely to do well, which is why there are recommendations to get a good night’s sleep and have a nutritious breakfast before an important exam, meeting, or performance. For most tasks, however, research suggests that moderate arousal or anxiety may be most effective. The Yerkes-Dodson law has two implications for the study of play. First, it suggests that there is no single optimal set point of arousal, but that it is contingent on the behavior being performed and the state of the animal. Second, play might be a sensitive indicator of how an individual perceives a task or function. Thus the arousal level seen in play devoted to physical tasks such as simple locomotion may be quite

different from that underlying more cognitively demanding play. Some graylag goslings (*Anser anser*) were more innovative than others in that they learned to trigger a food dispenser at 8–11 months of age while siblings in the social group never did learn and could only scrounge food dispensed by the “producers.” These innovative geese were quicker at learning to uncover hidden food at 4–6 weeks of age and also had higher fecal corticosterone levels at 2 weeks of age (Pfeffer, Fritz, & Kotrschal, 2002). The authors note the research indicating that corticosterone is an arousal response to stress. The moderate levels seen in the goslings may be associated with enhancement of neural synapse reorganization and dendritic growth as well as priming memory formation and consolidation. Nevertheless, the response repertoire of the species, its metabolic and physiological capacities, and individual differences in arousal need to be considered in any comparisons.

In sum, the different and often subtle and indirect ways in which energy concepts are used in studying play need to be distinguished and the relationships among the uses recognized.

6.2 Ecology and Play

A variety of ecological factors seem to influence the type and amount of play seen in natural settings. These factors can be divided into two types: those involving the evolutionary adaptations of the species (e.g., typical diet and habitat) and those related to the changing circumstances in which the animal finds itself (e.g., food shortages). There is a wide range of evidence supporting the conclusions drawn here that will not be presented in detail. It is the implications of the conclusions that are important for the working model to be used in evaluating the comparative evidence. The “ecology” of the juvenile animal during development was considered previously. As is evident, however, brain size and metabolic rate covary with ecological relationships, and so determining causal pathways is not straightforward at all.

6.2.1 Some Species Attributes and Play

Body size within an animal lineage is often related to the complexity of behavior shown, although this is often related to brain size (K. R. Gibson, 1990). It is also possible that in larger endothermic animals, the metabolic costs of thermoregulation are reduced and thus more metabolic resources are available for behaviors that are less essential for immediate survival than in smaller species in a lineage (Burghardt, 1988b). Furthermore, larger species generally have longer life-spans, including longer juvenile periods in which behavior patterns and skills preparatory for adulthood can be developed, rehearsed, and consolidated, as well as longer adult periods during which continuing and changing social and ecological circumstances need to be accommodated (S. T. Parker & Gibson, 1990).

Within mammals, brain size, metabolic rate, and perhaps intelligence, are related to dietary niche. Carnivores, omnivores, and frugivores that forage widely for dispersed food resources have larger brains than more specialized species or those foraging on widely available food such as leaves (K. R. Gibson, 1990; McNab, 1980). In a modeling approach to the evolution of generalists, specialists, and plasticity, van Tienderen (1997) concluded that specialists only evolved when “selection within habitats was severe and optimal phenotypes for different habitats were widely different” (p. 1372). In contrast to such “hard selection,” in all other contexts varied levels of generalists evolved. In other words, resources were more abundant and risks lower.

Active pursuit of prey or cooperative hunting is also associated with large brains and high metabolic rates (Jerison, 1973; McNab, 1980), as in dolphins and otters. These are often mammals in which play is quite common (Fagen, 1981; Iwaniuk, Nelson, & Pellis, 2001).

Among the animals reported to engage in considerable object play, extractive foragers (animals needing to search in leaf litter or under rocks for small animals, in flowers for nectar, in tree trunks for insects) are prominent (Fagen, 1981). Raccoons (*Procyon lotor*) and cebus monkeys are typical examples. Scavengers, such as condors (*Vultur gryphus*) and other vultures, are also highly playful, as I discovered at the Knoxville zoo (Burghardt, 1996). Why might this be? Such animals need a complex repertoire of motor actions, object recognition skills, learning abilities (for various food items and appropriate search and capture responses), and the capability to apply them in diverse settings. Quantitative studies on evaluating the complexity of various behavior patterns and the variability needed in their effective deployment should, by this perspective, be related to the amount of play seen. Methods used to assess the complexity of a seemingly trivial task, such as how gorillas eat thistles (Byrne, Corp, & Byrne, 2001), could be used to obtain empirical data to test this idea.

Furthermore, foraging typically takes up much of the daily routine of extractive foragers in the wild. In captivity, the need to engage in serious foraging is typically reduced because of the high-energy and easily obtained nutrition that is provided. Thus manipulating objects in a playful manner might be a consequence of time, energy, response availability, and exploratory motives.

6.2.2 Ecological Conditions and Play

In a class study of a captive group of nine baboons (*Papio hamadryas*) at the Knoxville zoo, play was recorded along with weather and temperature. Temperature varied little and did not affect play, but weather did (Lori Taylor, unpubl. ms, 1992). Play was more frequent on sunny than cloudy or rainy days for most of the nine play behaviors recorded. Considerable studies confirm that play of all types is readily curtailed in both the wild and captivity in times of food shortage, climatic adversity, social upheaval, and chronic stress (Burghardt, 1984; Caro, 1988; Sommer & Mendoza-Granados, 1995).

John Robinson carried out an extensive field study of seasonal variation in time budgets in capuchin monkeys (*Cebus olivaceus*) but did not publish data on play (Robinson, 1986). However, when he heard me speak about this phenomenon he looked up his data based on 14 months of intensive sampling of more than 15,000 intervals. Sure enough, during the 5 month (Dec. to Apr.) foraging stressed dry season, play was 18 times less frequent than during the following 5 wetter months (0.32 percent and 5.88 percent respectively) (John Robinson, personal communication, 2001). Exposing young rats to just several cat hairs (Panksepp, 1998a) suppressed play fighting dramatically (figure 6.1). Exposing pregnant rats to a cat greatly reduced pup survival and those that did survive grew more slowly, explored less, and had memory deficits (Lordi et al., 2000). Although play was not measured, it is likely that this would have been affected as well.

Play appears, then, to be a low-priority behavior that is readily curtailed when issues of more immediate survival are at stake. Recent work continues to support this conclusion, which is one of the most robust findings in the play literature. The effects of this phenomenon are shown in diverse ways, however. The amount of play seen in wild populations can be used as a measure of habitat quality in Hanuman langur monkeys (*Presbytis entellus*). A population with food and water shortages that is forced to eat low-quality leaves rather than energetically rich fruits played only about 15 percent as often as animals in a high-quality habitat, and the bouts of play were shorter (Sommer & Mendoza-Granados, 1995). Similar population differences in social play in rich and poor habitats have been reported in other species, such as squirrel monkeys (J. D. Baldwin & Baldwin, 1974). In this species, laboratory experiments in which food was reduced decreased play and replicated the field findings (J. D. Baldwin & Baldwin, 1976). Conversely, supplementing food to free-living Belding's ground squirrels increased social play in litters as compared to unprovisioned controls (Nunes et al., 1999). Comparable results were found with meerkats (Sharpe et al., 2002). Thus, measures of play might be useful in assessing the effects of captive environments as well.

Two experiments on the role of food restriction on social play in rats came to conclusions that might seem to contradict the role of food shortage in reducing play. In the first, rat pups were undernourished by removing them from the mother for 12 hours a day and placed in an incubator. This went on for the first 23 days of life, after which the pups were weaned and they, along with normally reared rats, were given unlimited rat chow (Loranca, Torrero, & Salas, 1999). Both male and female pups were significantly lighter than the controls, but from days 20 to 60 (puberty is at day 40) the undernourished rats played more! However, the authors noted that the incubator environment led to sensory deprivation, the mother-infant bond was altered, and overall, females played more than males, reversing typical findings. Thus interpretation is difficult. Another experiment was more transparent and was done on the same strain (Wistar) of rats (Almeida & de Araújo, 2001). During the lactation period, moms and

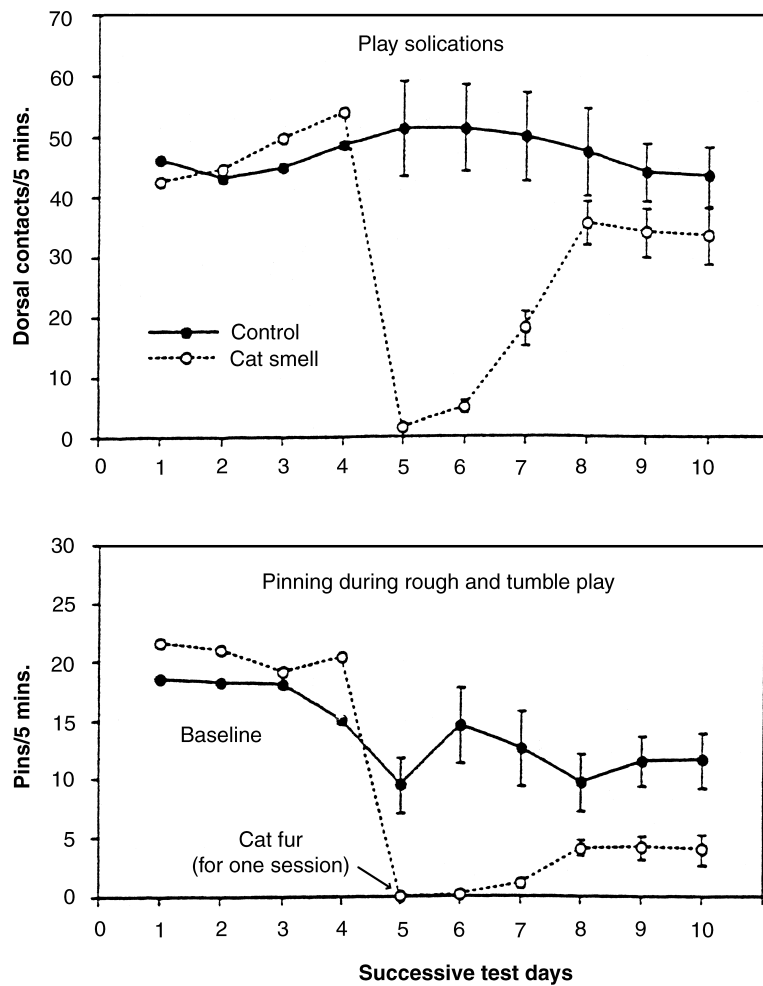


Figure 6.1

Exposure to cat hair on test day 5 abolished social play in rats for several days. (From Panksepp, 1998a)

pups were given either a diet with normal protein (16 percent) or low protein (6 percent), weaned at 21 days, and play observed during week 5. Half the low protein reared rats were switched to the normal diet and half stayed on the low protein diet. The results were clear. Rats continually malnourished played less than the controls and previously malnourished rats played more, replicating the previous study. The authors found the increased play in the now normally fed rats to be a compensation effect. They concluded by referring to studies showing “that chronic malnutrition causes less social involvement, less happy affect and greater timidity in free play in children during the first four years of age.” (p. 50).

Marine mammals have high basal metabolic rates that are thought to be due to the high rate of heat loss in cold aquatic environments (S. D. Thompson et al., 1987). California sea lions (*Zalophus californianus*) show this feature particularly clearly, and young pups have very high metabolic rates along with a high growth rate (S. D. Thompson et al., 1987). Sea lion behavior, then, should be particularly sensitive to the availability of metabolic resources. A remarkable test of the relationship between nutritional resources available to pups and various measures of behavior in a wild population occurred when an ongoing study of maternal investment in sea lions was “interrupted” by an El Niño event in 1983 (Ono, Boness, & Oftedal, 1987). During an El Niño year, the major fish species eaten by sea lions decrease, and the adverse effect of this food shortage was reflected by the increased time mothers spent foraging and their higher metabolic costs during this period. This unusual “natural experiment” is described here in some detail.

Mother sea lions give birth to a single pup on land, where they nurse the pup periodically after extensive foraging trips. Pups are not active until after 3 weeks of age, at which time they associate in groups and begin to explore, swim, and play in tide pools and coves. Individual pups and mothers were marked and monitored, the pups being weighed shortly after birth and after about 2 months of age. Milk intake was measured using a deuterium-labeled “heavy water” method. Pup behavior was recorded and included such categories as resting, suckling, on-land social and object play, swimming, and aggression.

The study took place over several years, with the El Niño event in the middle. The authors expected that pups born during the El Niño year would maximize energy reserves by suckling more, resting more, and engaging in less high-energy behavior patterns. An exception was aggression, which they thought would be increased owing to stress and competition. Comparisons were made during the year preceding El Niño (PRE), during El Niño (EN), and for the 2 years following El Niño (POST1 and POST2). The PRE period was a good year for food resources, as was the preceding year. The POST1 period was a good year preceded by a poor food-resource year (EN). Differences between the PRE and POST years could then be attributed to the effect of El Niño in the year before the POST1 period.

The results were many, but in terms of play they were clear. Pup weight gain was significantly lower in the EN year compared with all other years, and infant mortality was also much higher in the EN year. The number of pups born was lower in both the EN and POST1 years. The POST1 effect was due to the poorer condition of females in the year following the EN. Pup behavior changes across the PRE, EN, and POST1 years were revealing. Active behavior significantly decreased between PRE (32 percent of observations) and EN (25 percent) and POST1 (22 percent). This category was further broken down into aquatic activity (including social play in water), aggression, and play on land. Neither aquatic activity nor aggression changed at all over the 3 years. Play on land, however, declined sharply and significantly between PRE (9.1 percent) and EN (5.2 percent). Furthermore, a significant further reduction occurred in the POST1 year (3.0 percent). The authors, in explaining their unexpected results concerning play, interpreted them as follows: The decline in terrestrial play was due to the effects of long-term food deprivation. The absence of a decline in swimming and aquatic play was due to the importance of learning swimming skills for later survival. The fact that play on land is energetically more costly than aquatic locomotion may be a more proximate reason why terrestrial play declined and fits the comparative findings more satisfactorily.

6.3 Social Factors and Play

6.3.1 Social Organization and Play

Except for some differences in male and female play fighting, the role of social organization beyond that of the family unit does not seem to be a major factor in the kind of play exhibited. Certainly locomotor and object play are not highly related, as would be expected. More social imitation in play might be expected in species where there are opportunities for observing conspecifics in nonamicable circumstances (Miklosi, 1999). Similarly, adult social play outside of courtship contexts should be more common in species that live in social groups, although many highly social animals, including primates, show little adult social play.

My skepticism about claims for play being more prevalent in highly social species is based on the fact that black bears we studied and orangutans both engage in intense play fighting as juveniles, although both are highly solitary species as adults (outside of the mother-infant bonds) and adult-adult play is rare. Thus the argument that play fighting in bears and orangutans is preparation for dealing with adult social life did not appear valid (Burghardt, 1982). In short, while the complexity of adult social organization may have some influence on the secondary features of play, it appears to have little to do with the occurrence of play itself.

Recently this paradox was at least partially resolved in a comparative analysis of adult-adult play in primates. Pellis and Iwaniuk (1999a, 2000a) found that such play

in primates, both in sexual and nonsexual contexts, is more prevalent in primates with loose, even somewhat solitary, social organization in which unfamiliar animals interact, than in primates with more rigidly hierarchical or nuclear family types of social organization. Similarly, in a comparative analysis of sixteen macaque monkeys (*Macaca*), the type of social organization seemed related to the duration and nature of play fighting, with hierarchical species having briefer and more asymmetrical play fighting than the more loosely organized and more socially tolerant species (Thierry, Iwaniuk, & Pellis, 2000). Data were not available for many species; studies such as these suggest where additional data are needed.

6.3.2 Male and Female Play

Sex differences in play are common, especially in social play, and have been much reviewed (Power, 2000). In fact, being able to explain sex differences in play fighting (amount and type of play fighting and choice of partners) is considered one of the greatest accomplishments of modern animal play research (Caro, 1988; Pereira & Fairbanks, 1993; P. K. Smith, 1982). That is, males typically play fight more than females, do it more roughly, and prefer to play with other males. As discussed earlier (Biben, 1986), squirrel monkey males engage in directional (winner-loser) play fights more than females, who engage in nondirectional play fights. Hormones are involved in sex differences (Beatty, 1984), but the nature of the differences needs to be understood through a more contextual approach than merely a causal physiological one.

The extent of the differences in male and female play seem related to the importance of fighting among males in polygynous societies, with more male play fighting in polygynous species, or species in which males disperse and have to establish themselves in new groups. For example, it has been claimed that in gorillas, vervet monkeys (*Cercopithecus* sp.), and galagos (Galaginae) males fight more than females and also prefer male play partners that are equal or older in age, whereas females play fight less and preferentially choose younger play partners. On the other hand, ringtailed lemur females and males play fight equally. This difference was attributed to the fact that in the first three species male reproductive success is directly tied to fighting ability (Fairbanks & Pereira, 1993). Although the relationship seems to hold over a diversity of primates, only a few have been looked at and the pattern needs to be studied much more closely. For example, Richardson's ground squirrel is highly polygynous, with much male-male fighting during the breeding season; however, there is no difference between males and females in aggressive play fighting (Pasztor et al., 2001). The role of phylogeny and sociality in play fighting is thus complex and perhaps quite evolutionarily labile, as shown by a comparative analysis of muroid rodents (Pellis & Iwaniuk, 1999b).

One of the most intriguing studies of sex differences in play involves the spotted hyena, in which females are dominant to males, larger than males, and have external

genitalia that look like the male scrotum and phallus. Females also have higher levels of circulating androgens (testosterone) relative to males than is typical in female mammals. What about play in this species? Juvenile hyenas have been observed for locomotor, object, and social play (Pedersen et al., 1990). Females were markedly more playful than males in several measures of locomotor and social play, but did not differ in object play. In no context did males play more than females. Although this reversal of the typical male-female difference may suggest that androgens play a causal role, gonadectomized hyenas did not differ from intact animals in playfulness. Circulating hormones were not measured, however.

Sex differences in morphology and behavior are undoubtedly related to hormones, hormone levels, and development, but the ways in which hormones function in different species need much more research, and the story seems to be getting less, not more, clear (Forger, 2001). For example, the development of attack and defensive moves in rat play fighting differs for males and females, with the former becoming rougher at puberty (Foroud & Pellis, 2003). For this to occur, males need neonatal androgens. However, while ovariectomy at either birth or weaning led to females adopting the male type of rough behavior, neonatal testosterone had no effect on females (Pellis, 2001). On this last point there are conflicting results (Hotchkiss et al., in press) both in rats and other species (e.g., sheep; Orgeur, 1995) in that androgenized (testosterone loaded) female fetuses become masculinized, including in play.

Hormones may be particularly important in restructuring neural circuits and behavior at puberty in rodents and other species (Romeo, Richardson, & Sisk, 2002), the time during which male social play often begins to differ from that of females. A recent, and disturbing, study highlights the value social play may have as a marker of proper development (Hotchkiss et al., in press). A commonly used fungicide, vinclozolin, is an environmental endocrine-disrupting chemical. To assess its possible role in mammalian sexual differentiation, neonatal rats were injected with vinclozolin and play and other behaviors recorded. Although general activities were not affected, at 7 weeks males showed female-style play. The incorporation of play into standardized behavioral measures (Rohlman et al., 2001), may prove useful in assessing the effects on children of neurotoxic environmental chemicals, which are becoming increasingly prevalent across the world.

Sex differences in object and locomotor play exist in some species, but are typically less marked. In young kittens, the increase in object play from weeks 8 to 12 is much greater in males than females (P. Bateson, 1981). If this object play is practice for effective predation, then such a difference cannot easily be explained, since both sexes need to be effective predators, females perhaps more so since they need to feed their litters. It is interesting that females from mixed-sex litters showed as much object play as their brothers. This could be due to prenatal hormonal influences ameliorating sex differences that may have no functional role in play at all. In fact, object play in cats

has been shown to be unrelated to adult predatory efficiency (Caro, 1980). Individual and sex differences in play have not been looked at in terms of either learning ability, innovativeness, or production of novel behavior, although this seems a worthwhile issue. For example, in some species females and in others males, are the most innovative (Pfeffer, Fritz, & Kotrschal, 2002).

Human beings are somewhat of an exception in that gender differences in physical and locomotor play, object play, sociodramatic play, games and sports, where play occurs, and other aspects of play have been extensively documented (Pellegrini & Smith, 1998; Power, 2000). Although it was controversial in the past (e.g., Harper & Huie, 1978), the view that there are evolved male-female differences in human play that interact with social training and culture can no longer be doubted. The fact that male vervet monkeys (*Cercopithecus aethiops sabaesus*) prefer to play with “boy” toys (car and ball) and female monkeys with “girl” toys (doll and a pot) suggest that human object play may also been shaped by sexually differentiated selection pressures (Alexander & Hines, 2002). However, as with play fighting, sex differences in play are most likely derived secondary processes.

Insofar as male and female animals have different foraging, social, reproductive, habitat, and predatory avoidance behavior based on genetic predispositions, hormones, and neural connections, sex differences are to be expected (Burghardt, 1988b). The existence of differences between the sexes does not prove that some behaviors are designed for training or practice or that they originated for such purposes. The fact that play fighting may have diverse roles in behavioral development speaks to the evolutionary ease with which it can gain or lose functions (Pellis & Iwaniuk, 1999b). The increase in risky play and risk-taking behavior in human adolescents, especially males, may have a hormonal basis in postpuberty changes (Spear, 2000). A note of caution on hormonally mediated sex differences needs to be added. In mammals with multiple offspring in litters, males and females may be influenced by hormones produced by their intrauterine siblings or, more specifically, by the position of a fetus to neighboring fetuses. Many effects have been noted, particularly masculinized behavior (Ryan & Vandenberg, 2002). Such effects are also found in human multiple births and effects on sex typical play may prove of considerable interest.

6.3.3 Play as a Signal

Play is often studied only from its consequences for the player, but perhaps play is also a signal to others (Chiszar, 1985). Play may have been selected for in social species and in those with parental care as a sign that offspring and other conspecifics are healthy, adequately nourished, and ready to learn or even obtain their independence in various behavioral realms as they move toward weaning or other forms of adult independence. In addition, playful animals may be socially more friendly with one another.

Another twist is found in squirrel monkeys, which play in peer groups somewhat removed from adults. Although the monkeys are rather unattentive to predators while engaged in their vigorous games, they also emit loud play vocalizations during this time, vocalizations that do not seem to have any role in the play itself (Biben & Symmes, 1986). The function of this signal appears to be to alert adults, who are now more vigilant themselves while the play bouts occur (Biben, Symmes & Bernard, 1989). Many mothers know that when the rambunctious sounds of play cease, it is time to check what mischief or danger might be afoot.

The actual form of the play may be less important since it has been co-opted for another use. Ghiselin may have an important point when he writes: “many of our educational practices may be seriously misguided as a result of folk psychology. Little boys playing soldier are not practicing to slaughter their fellow men, but furthering peaceful life in their own society. The way to make a killer out of a child is to put him into a genuinely competitive situation—such as Little League baseball” (1974: 261).

The next extension of this idea is to sexual selection. Males and females both want friendly, helpful mates, and a sense of humor is often high on the list of desired traits (Buss, 1999). If such qualifications also include a playful attitude toward life, then play can be a force in sexual selection (Chick, 2001). This possibility moves play into the realm of artificial selection. If true, it may also lend plausibility to H. G. Wells’s view about the future of human evolution (chapter 1)! Nonetheless, play as used as either a propensity, an attitude toward life, or as an approach to life is a fascinating proposition and could explain the enigma of adult play. Play is indeed used in courtship in some primates (Pellis & Iwaniuk, 1999a), in other species as claimed by Groos (1898), and may underlie precocial play in other animals as well.

6.4 An Instructive Comparison: Mammals and Ectothermic Reptiles

Why has play been historically most described in and attributed to mammals? Several processes have been suggested earlier favoring play in animals and these may be the very factors most likely to be found in combination in mammals. They are listed in table 6.3 as a contrast between “typical” mammals and their closest sister taxa, nonavian reptiles. These factors have been incorporated in an evolutionary-developmental perspective called the surplus resource theory, or SRT. Developed earlier in Burghardt (1984, 1988), some of the core ideas have been extended and elaborated by Coppinger and Smith (1989) and Nigel Barber (1991). Surplus resource theory incorporates physiology (e.g., activity metabolism, thermoregulation), life history (e.g., parental care, altriciality, food niche, ontogenetic shifts), behavioral repertoire (complex movements, behavioral diversity, social organization), and psychological factors (stimulus deprivation, habituation, exploration). It is focused on the origins of primary process

Table 6.3

Contrasts between typical mammals and ectothermic reptiles relevant to the occurrence of play

Mammals	Reptiles
<i>Metabolic and physiological contrasts</i>	<i>Metabolic and physiological contrasts</i>
High basal and resting metabolic rates	Low basal and resting metabolic rates
Rich vascular system and highly oxygenated blood	Fewer capillaries and less efficient blood-transport system; blood capable of carrying far less oxygen
Capable of sustained, vigorous activity (aerobic metabolism)	Vigorous behavior sporadic and short lived; reliance on anaerobic metabolism for sustained vigorous activity
Endothermy provides high resting metabolism, allowing rapid onset of vigorous play. Costs of overcoming inertia increase with weight	Ectothermy allows a low-energy (conservation) life-style; the behaviors needed to raise body temperature to aerobic optimum are often incompatible with play
Young, growing animals typically have higher basal metabolic rates than adults	Young, growing animals do not have basal metabolic rates different from those of adults
Rapid recuperation after sustained activity; short period of vulnerability to predators	Recuperation from sustained activity (to normal lactic acid levels) measured in hours; extended period of vulnerability to predators
Exercise increases cardiovascular and endurance functions	Little evidence of physiological benefits of exercise; exercise may even be harmful
<i>Developmental contrasts</i>	<i>Developmental contrasts</i>
Young often enter world with incompletely functional sensory and motor systems	Young enter world with highly functional sensory and motor systems
Neonates have food, heat, shelter, and protection provided by parent	Neonates must provide most, if not all, their own resources
Neonates have many motor and perceptual systems restricted to juvenile period (e.g., sucking)	Most neonatal behaviors show clear continuities with adult motor and perceptual systems
Neonatal/juvenile period available to develop or perfect functional social, feeding, locomotor, or antipredator skills	Most behaviors necessary for adult survival are highly functional at birth; however, skill improvement can occur
Young typically interact with, and individually recognize, siblings, parents, or other colony members	Young often have little opportunity for social interaction and learning involving siblings, parents, or other colony members
Relatively determinate juvenile growth allows for excess metabolic energy in "good times"	Relatively indeterminate juvenile growth leads to most energy intake being channeled into growth
Neonates capable of sustained activity	Even well-fed neonates have less endurance than adults
"Relaxed field" common in juveniles	"Relaxed field" rare in juveniles

Table 6.3
(continued)

Mammals	Reptiles
<i>Behavioral and ecological contrasts</i>	<i>Behavioral and ecological contrasts</i>
Play occurs most frequently when juveniles are well fed, often after feeding	Postingestion behavior in reptiles is characterized by lethargy, distended stomachs, and basking or holing up out of harm's way, often due to greatly elevated metabolic rates needed for digestion
Relatively few offspring, especially in the more "playful" families	Relatively more offspring, with higher mortality, over equivalent adult life-spans
Almost universal highly developed parental care with social bonding between parents and offspring and among siblings	Typically only rudimentary parental care or none, with little development of social bonds with offspring
Large brains with extensive neocortex needing more energy and allowing more variable and flexible behavior	Smaller brains with less neocortex needing less energy, but constraining behavioral complexity and flexibility
Limbs and faces allowing more complex manipulatory and communicative responses	Limbs (or none at all) and faces with more limited motor and expressive capacities
Often extensive integration within and across perceptual and motor systems	Often limited integration within and across various perceptual and motor systems

play as well as the conditions in which derived process play will flourish. The most important of these are classified and depicted in figure 6.2.

6.4.1 Energetic Differences

The first suite of traits affecting play involves energetic differences between ectothermic reptiles and mammals. Reptiles typically are metabolically constrained from performing vigorous, energetically expensive behaviors, especially those of any substantial duration (A. F. Bennett, 1982; McNab, 2002). This constraint is due to their low resting and maximal metabolic rates, limited aerobic capacity, and long recovery times after anaerobic expenditures. Reptiles have about 10 percent of the metabolic rate of a comparably sized mammal (although most reptiles are much smaller than mammals). Both metabolic rates and typical body sizes are further reduced in amphibians. It is difficult to deduce the vigor and endurance of animals at the dawn of tetrapod vertebrate evolution since atmospheric oxygen may have reached 35 percent in the Late Paleozoic (Graham et al., 1995), and possibly fostered radiation of many groups, gigantism, and novel behavioral phenotypes. Small body size leads to greater heat loss and expenditures of time and energy to maintain body temperature by moving back and forth from cool to warm locations to behaviorally thermoregulate (ectotherms) or to obtain calories to maintain body temperature (endotherms). It is relevant

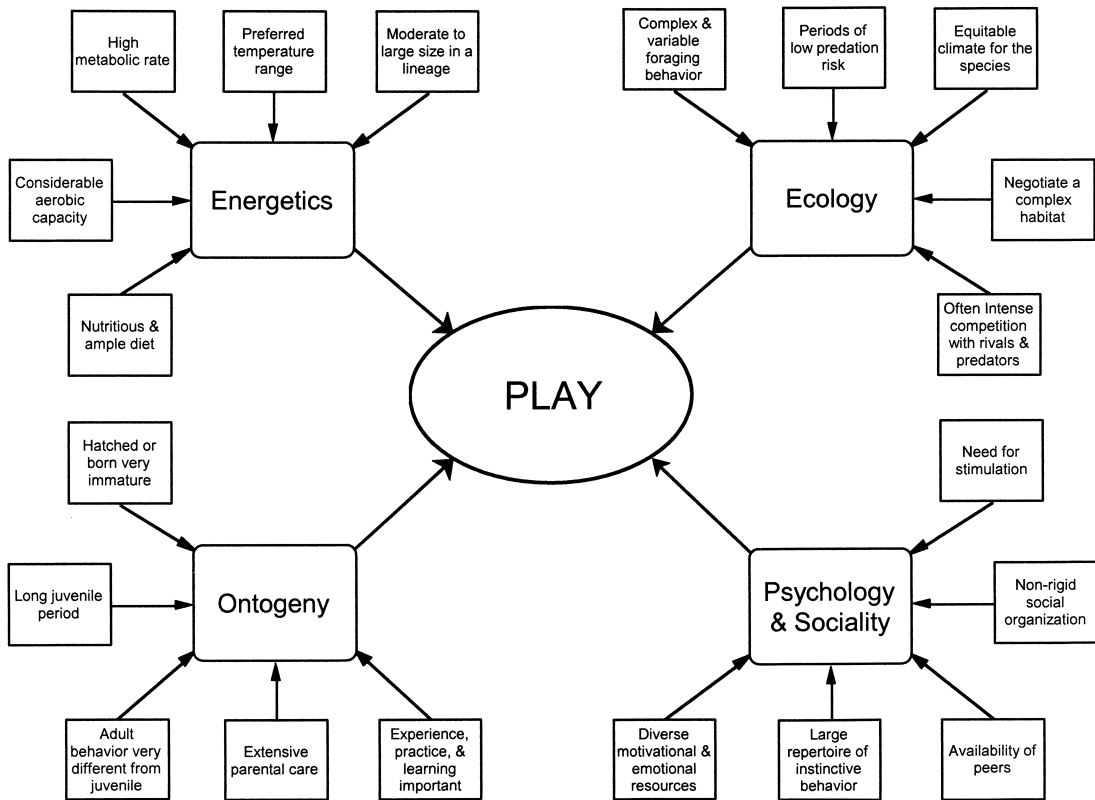


Figure 6.2

The surplus resource theory model of play indicating the major factors underlying playfulness.

to note that the traditional theory that endothermy evolved via increasing metabolic rate has been questioned through experiments that increased the metabolic rate of *Varanus* lizards to the mammalian level with no substantial increase in metabolically produced heat or thermogenesis (Bennett, Hicks, & Cullum, 2000). Taken together, in ectotherms these factors inhibit the performance of, and selection for, costly, vigorous, playlike behavior that has limited utility or none.

Very small mammals also appear to play less than larger species in a lineage (Burgardt, 1988b). Countering this trend is the fact that play occurs more often, at least in mammals, in juveniles that have not yet reached adult size. In these cases the animals, such as rodent pups, have grown fur and become better able to thermoregulate, and secondary derived processes may underlie playful behavior.

Phylogenetic factors and other traits such as type of parental care and quality of diet complicate the role of metabolism in play. Among primates, folivorous species

(animals that eat leaves) with diets containing few calories play less than frugivorous (animals that eat sugar-laden fruit) or omnivorous species that eat diets containing more energy (Fagen, 1981). They also typically have lower metabolic rates and such relationships with diet hold across many species (McNab, 1980; Burghardt, 1988b).

Studies also suggest that the endurance of young reptiles, such as snakes, is less than that of adults and this may be related to lowered blood oxygen-carrying capacity (Pough, 1977, 1978). Furthermore, studies on a diverse set of lizards and a turtle show that growing neonatal ectothermic reptiles do not have higher basal metabolic rates than adults, whereas the energy costs of growth are considerable in mammals and birds and thus these young animals have higher metabolic rates than adults (Nagy, 2000). These differences also make the costs of vigorous behavior such as play much higher for ectothermic reptiles. On the other hand, feeding induces greatly increased metabolic costs in reptiles (Secor & Phillips, 1997; Wang, Busk, & Overgaard, 2001), often tenfold over resting BMR, that mitigate the propensity to vigorously play after feeding found in many mammals. Furthermore, the necessity for reptiles to use anaerobic metabolism for vigorous activity greatly increases post-exercise metabolic costs and recovery (Hancock, Adolph, & Gleeson, 2001), which probably increases the risk of predation. In fact, reptiles rarely ever perform at maximal capacity and do so “only in situations that have a critical impact on fitness” (Hertz, Huey, & Garland, 1988: 927). Still, they incur the high behavioral costs of thermoregulation in order to “be prepared” for emergencies and thus, as the authors suggest, are “more like Boy Scouts than Olympians” (Hertz, Huey, & Garland, 1988: 934).

6.4.2 Life History Factors

The second suite of characteristics involves developmental factors, almost all of which revolve around the limited parental care and attendant precocity of juvenile nonavian reptiles. With the exception of all crocodylians, most neonatal reptiles are not cared for by their parents (Shine, 1988). Consequently, immediately upon birth or hatching, they must devote their activities to obtaining food, finding shelter, avoiding predation, and growing rapidly. This limits the safe time or opportunity for practicing or perfecting behaviors (motor abilities, perceptual-motor coordination, and social skills) to be used in an uncertain future. Most young reptiles are very small, and selection will have shaped abilities that enhance juvenile survival, such as remaining quiet and inconspicuous. Such behaviors are, of course, incompatible with vigorous play. There is also no source of high-fat, high-protein nourishment available at little cost, as in juvenile birds and mammals.

Although nonavian reptiles are highly precocial and superficially resemble and behave like miniature adults, they nonetheless may learn many things as they go about their serious activities. Reptiles also grow as rapidly as food resources allow; unlike

mammals and birds, there is no necessary age-defined period of youth. Young reptiles, unlike young mammals, typically do not get fat; again, they just grow as fast as food resources permit. This characteristic of reptiles is termed indeterminate growth. Reptiles convert a higher percentage of assimilated energy to biomass and thus can grow on a smaller ration than a mammal.

Given plentiful food, however, endotherms can add weight at a higher rate than an ectotherm amniote; this might be a major benefit of endotherm parental care. N. Barber (1991) has advanced a "brown fat" hypothesis in which vigorous play is a means for well-provisioned young mammals to avoid obesity through increased heat production (thermogenesis), a view very akin to Spencer's surplus energy theory. Although there is no supportive play data, thermogenesis could be a primary play process. Thermogenesis can be induced by high-fat diets (Bachman et al., 2002) as a means of obesity resistance. More controversial evidence also implicates fidgeting and related activities as a major factor in thermogenic resistance to obesity in humans (Levine, Eberhardt, & Jensen, 1999). In any event, obesity is not a problem for wild reptiles, although many captive reptiles of the larger species are often fed excessively rich or abundant food, leading to overweight, lethargic adult animals. How could a mechanism to reduce fat through play evolve when, for example, simply reducing caloric intake would seem to be simpler? We know that there is a complex Lipostatic (fat-sensing) system that aids in regulating fat storage in mammals, though rather loosely in humans (Mercer & Speakman, 2001). "Some mammals appear able to cope with excess energy by burning it off" (p. 102). Why not just eat less? Well, consider fruit-eating animals that must take in lots of food (and energy) to meet their protein requirements. "Rather than store the excess as fat they burn it off by flying" (p. 102). Thus mammals, as compared to reptiles, have many more mechanisms to produce surplus activity that could lead to play. Interestingly leptin, a hormone regulating body mass and energy output in mammals, has been shown to increase preferred body temperature, activity, and metabolic rate in fence lizards (*Sceloporus undulatus*); at the same time they ate less but did not differ in weight gain from controls (Niewiarowski, Balk, & Londrville, 2000).

The last life history characteristic I will mention is that reptiles typically have large litter and clutch sizes, with both smaller neonates and higher juvenile mortality than endotherms. Thus, any delayed benefits of play would be less important than current risks.

Since reptiles have a low-energy life-style and a limited capacity for extensive, vigorous movement, they also may not suffer the adverse consequences of not moving or being otherwise unstimulated for extended periods. Parental care may have led to animals being kept in protected, but often boring (nonstimulating) burrows and nests. Performing activities or responding to siblings may have been a means to increase arousal and consequent neural and muscular activity during the active development

of the neural and morphological systems that are more precocially developed in reptiles. Ancestral mammals would have used various instinctive behavioral repertoires available to them, not because they needed to be practiced, but because they were the legacies of a more precocial ancestry and were a means to increase arousal and sensorimotor stimulation.

6.4.3 Behavioral and Ecological Factors

Certain kinds of complex ecological and social interactions and operations upon the environment seem to characterize the more playful species. For example, object play is found most often in active predators, scavengers, extractive foragers, and generalist feeders that rely on manipulation by limbs and mouth. Reptiles do not have the rich repertoire of possible movements of limbs and face seen in many mammals. The lack of parental care may have prevented the evolution of social bonding and affiliation in reptiles to the extent that it is seen in birds and mammals (MacLean, 1985), and thus social play is less likely than object and locomotor play. It is interesting that it is in those reptiles with more variable diets and active foraging techniques, such as soft-shelled turtles (Burghardt, 1998a; Burghardt, Ward, & Rosscoe, 1996), that more exploration, curiosity, and sometimes play are found. The same probably holds in fish (part II).

6.4.4 Surplus Resources and Play

The various kinds of differences (metabolic, developmental, neural, behavioral, and ecological) help explain why some groups of animals play and others do not. As a guide to identifying behavior in nonavian reptiles that could be candidates for traditional-appearing play, I have used the above and related physiological, psychological, and life history contrasts to predict that mammalian or avianlike play in reptiles should be rare and occur only in specific contexts in which those factors facilitating play in mammals and birds are also present. This exercise also provided suggestions of mammalian groups in which we would expect to find the most complex play and the most time spent in play (Burghardt, 1988b). A series of predictions was supported that suggest that many of the factors listed earlier are associated with the occurrence of play and may in fact have facilitated its evolutionary origin. For example, as indicated earlier, since less energy is needed for locomotion in water than on land, aquatic mammals should be particularly playful—and they are. The first play we confirmed in reptiles was in aquatic turtles (Burghardt, Ward, & Rosscoe, 1996; M. Kramer & Burghardt, 1998), supporting predictions made a decade earlier (Burghardt, 1988b).

Thus metabolic, behavioral, and ontogenetic (e.g., available time) resources are involved in incipient play and may have been the basis for the first inklings of playlike behavior, only some of which, through natural selection, were elaborated into complex and functional play.

6.5 The Surplus Resource Theory of Play

6.5.1 Four Important Processes Underlying Play

The preceding sections have shown that a simple or unitary functional, neural, developmental, or ecological explanation of play is improbable. The fact that social play is most prevalent in some animals, object play in others, and locomotor play in still other species, along with varying degrees of overlap, underscores the complexity in behavior that meets the five play criteria. The many subdivisions of these general play types and the elaborations found, especially in apes and humans, also are consequences of evolutionary processes and biological properties that vary among animals, even within placental mammals. This makes it likely that the initial advantages of incipient playlike behavior did not involve any particular functions, such as perfecting later behavior, increasing endurance, or facilitating behavioral flexibility.

Four main factors appear to underlie play in animals and some of these may be necessary, although not sufficient, for play to occur: (1) There is sufficient metabolic energy (both energy stores and the capacity for sustained vigorous activity). (2) The animals are buffered from serious stress and food shortages, which is especially important in species with a prolonged development until reproductive age (e.g., young animals are well cared for by parents). (3) There is a need for stimulation to elicit species-typical behavioral systems or to reach an optimal level of arousal for physiological functioning (e.g., there is susceptibility to boredom). (4) There is a life-style that involves complex sequences of behavior in varying conditions, including diverse and unpredictable environmental and/or social resources (e.g., generalist species should play more with objects than those with more rigid, specialized behavioral repertoires).

Play in all species, then, including human beings, will be most prevalent when there are excess resources along with appropriate evolved motivational, physiological, and ecological systems. Play can evolve independently whenever physiological (including neural), life history, metabolic, ecological, and psychological conditions, in conjunction with a species' behavioral repertoire, reach a threshold level. Play then appears, and its fate depends on its consequences in the lives of animals. As seen in later chapters, specific types of play are beginning to be mapped on evolutionary trees to trace their path, just as other traits of animals have been tracked through time.

6.5.2 Parental Care, Relaxed Selection, and Play

The evolutionary processes that led to the extensive parental care found in mammals and birds are, like the evolution of endothermy, little understood. Although ectothermic reptiles, specifically lizards and snakes, have evolved some parental behavior toward eggs and offspring multiple times (Shine, 1988), it was not till the advent of endothermy that parental care reached the high levels of complexity seen in birds and mammals. Ted Case (1978) argued that while postnatal care occurred before endo-

thermy evolved, endothermy was necessary for its radiation. Furthermore, care of precocial young preceded the evolution of small, helpless altricial young and may have originated from larger reptilian ancestors, which were longer lived and better able to defend their offspring. Also, as we have seen, larger endotherms are less energetically constrained and thus could devote more "excess" energy to offspring care. In addition, as Case (1978) points out, they are more energetically able to have relatively large precocial young. The scenario that Case (1978) advocates is the following: early mammals were shrew or mouse sized. Being energetically constrained, they could only produce small eggs relative to body size as do reptiles, but unlike reptiles, they could only afford to produce undeveloped altricial young that needed extensive postnatal care. The main constraint here was the larger, more complex nervous system in endotherms. Although dated in many ways, Case's scenario raises questions that the study of play may help answer.

However it occurred, it is in the transition to extensive parental care that the need to distinguish between primary and secondary processes in play becomes critical. More specifically, I propose that the advent of parental care led to the deterioration of some aspects of neonatal response systems through less precise functional motor patterns, the lowering of the stimulus thresholds necessary to elicit such responses, and the broadening of the range of effective stimuli inducing such ethotypic behavior. In addition, the increased aerobic metabolic capacities resulting from endothermy modified or even reorganized developmental processes so that incipient play and other experiential avenues were not only available to some species, but may well have had to be exploited by them for continued survival to replace lost, suppressed, or maturationally delayed response systems.

In this way, new response patterns could arise that would themselves be retained by natural selection if they had an advantage over animals with different modes of response. For example, if natural selection is continually honing predatory skills so that less successful juvenile predators starve or are otherwise less fit than more skilled predators, once selection is removed, the mechanisms for capturing prey should show a reverse process and become less precise. Individual developmental processes involving both maturation and experience may become necessary and animals able to be developmentally flexible should have an advantage over those that are not.

A prediction would be that domesticated cats removed for generations from preying on live animals would be less competent hunters as juveniles than nondomesticated small cats. Among gartersnakes (*Thamnophis*), we have shown that species specializing in aquatic prey capture fish more efficiently than those that are prey generalists or earthworm specialists. Experience, however, can make up for some of the deficits in terrestrial prey specialists (Burghardt & Krause, 1999; Halloy & Burghardt, 1990). In fact, experience-altered prey preferences are themselves heritable in snakes (Burghardt, Layne, & Konigsberg, 2000), so natural selection could act upon such plasticity rather

than the behavior and preferences themselves. Indeed, the importance of practice and repetition in all sorts of behaviors, including the most “hard-wired” or “innate” behavior in animals from flies and frogs to birds and mammals, is becoming increasingly documented in developmental psychobiology (DeVoogd & Lauay, 2001; Fentress & Gadbois, 2001; Hirsch et al., 2001; Oppenheim, 2001). The effectiveness of such practice and experience will often prove to be heritable and thus open to selection. Since natural selection operates less intensely on neonatal behavior after the evolution of parental care, play may evolve some role in refining behavioral performance and capability and become itself a heritable trait. This removal of the operation of selection on the original role of a behavior also provides an opportunity for it to operate on different aspects of behavioral phenotypes.

The longer the developmental period before effective adult action, the less need there is for rapid maturation of behavioral systems and the more drawn out the process can be. A secondary process of play derived from the primary processes outlined earlier would be supported if research showed that vigorous rough-and-tumble play of young rats and dogs enhances adult performance, promotes socialization, or increases behavioral flexibility. However, it is precisely because the more primary processes of play have been ignored that predictions made from secondary processes have fared poorly. An example of an important primary process derived from SRT would be the role of metabolic rate or parental care in production of “surplus” behavioral “mutants” that could in turn be selected ontogenetically and phylogenetically. An apparent secondary process derived from a detailed consideration of primary processes is based on the claim by Byers and Walker (1995) that there is a correlation between the onset of vigorous motor play and the age at which permanent long-term changes occur in the muscular and cerebellar systems of several species of domesticated animals. If play is essential or even useful in establishing these permanent physiological systems, then a secondary process has been established. If the play behavior is a mere accompaniment to this developmental process, with no causal role, then it is but another primary process.

6.5.3 Play as a Joint Outcome of Genetics, Experience, and Selection

Today we know that phenotypic expression of behavior patterns is a complex epigenetic outcome of interactions and feedback occurring at many levels from allele to protein synthesis (gene expression) to behavioral performance and social experience. Selection can operate on all these levels and more, at least indirectly. Therefore, play may have a subtle yet profound role in behavioral ontogeny and phylogeny that we are only beginning to appreciate.

The study of the role of play in development should initially focus on the primary processes leading to behavior satisfying the five criteria for play. Increased endurance, functional endothermy, parental care, major developmental changes during early

ontogeny, and lack of sufficient external stimulation facilitated incipient playlike behavior. As the trends favoring this incipient play expanded, play acquired secondary functions, including those underlying greater behavioral, social, and cognitive complexity through the evolution of secondary processes. Animals that are initially more precocial in their behavior systems will have less opportunity for primary playlike processes to occur because of their great need to engage in highly functional behavior early in life. The contrast between the “efficient” mouse and the less efficient neurodevelopmental course of the more slowly maturing laboratory rat (Whishaw et al., 2001) may be reflected in the fact that laboratory rats are among the most playful rodents, and mice are among the least. Such developmental processes underlying the probability of low-cost inefficiencies could reflect the model that G. C. Williams (1991) suggested.

Could play be a “random process generator” or a means of creating “adaptive variability” (Sutton-Smith, 1999)? Fagen (1974) compared the variability seen in play with that found in genetic systems. Play shows similarities to chromosomal inheritance in that play sequences may display recombination, fragmentation, translocation, and duplication. Such variation, heritable, can provide raw material for natural selection to operate upon. Perhaps play also produces behavioral mutants. Recent molecular genetics methods that produce overexpressed alleles, add genes, or eliminate loci (gene knockouts) allow further genetic metaphors. Similar genetic processes may be involved in the ancestral stages of primary process play as well the production of novel behavioral phenotypes that, if adaptive, can become secondary or tertiary play. Such processes may involve surplus resources producing dispersal phenotypes that not only expand their ecological niche but also produce novel adaptations for surviving in new habitats (Geist, 1978).

However, much play is far from random, is species-typical, and seems to operate within tight boundaries. Pellis (1993) has shown how play fighting can differ among closely related species with little or no overlap. This suggests that play in these species may have become secondary process play and genetically fixed, whereas primary process play may be the source of more nonadaptive mutants. There is virtually no support for any of this speculation. Thus the challenge is not just to state that play creates novel behavioral phenotypes but to uncover the actual processes underlying such behavioral variation.

Neural and physiological changes resulting from experienced-based learning and plasticity may have opened up new possibilities for cognitive and emotional complexity in many mammals and some birds as compared to nonavian reptiles. For example, play among littermates in Belding’s ground squirrels (*Spermophilus beldingi*) (figure 6.3) may help establish or consolidate kin recognition cues that later facilitate recruitment to aid in defense against predators in social mobbing species (Holmes, 2001). In this species littermates live in underground burrows until they are weaned and emerge on day 27, at which time social play is a prominent activity involving both littermates and

Social play in cross-fostered juvenile ground squirrels

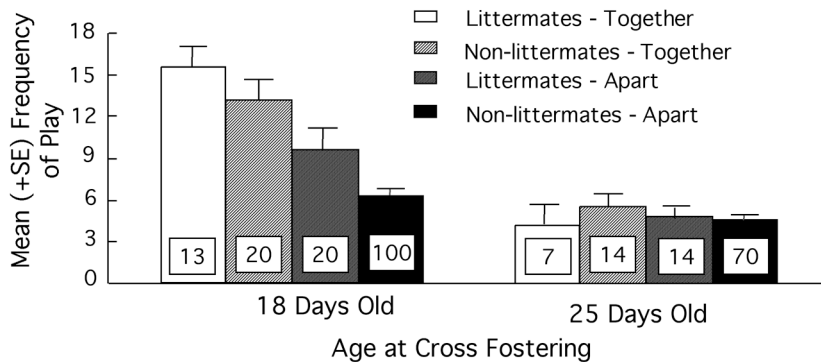


Figure 6.3

Play partner preferences in Belding's ground squirrels are influenced by kinship and familiarity. Animals were cross-fostered at 2 or 9 days before typical emergence from natal burrows. Mean play frequencies among pairs during the first 20 days above ground. Number of pairs of juveniles in boxes inside bars. (From Holmes, 2001)

other juveniles. Both genetic (kinship) and age-specific early experience (familiarity) influence the amount of play seen after pups emerge from nest burrows. How might these more advanced secondary processes have operated? Were they in fact tertiary processes? Could they have jump started a cognitive revolution? Such extensions are not the issue here since the focus is on the initial origins of play, but the consequences of such behavior may, as this question suggests, have important ramifications for studies of behavior, evolution, and neuroscience.

Even if play is more frequent and diverse in animals with larger telencephalons (or parts thereof), we still have to decide whether this is a circumstance supporting enhanced mental abilities, maintaining instinctive responses that are now far more plastic than ancestral states, or is a currently epiphenomenal or atavistic phenomenon, as suggested by the original surplus energy and recapitulation play theories.

According to SRT, play originated through nonadaptive indirect means (primary process), but could also have incorporated secondary processes that allowed behavioral and psychological abilities to shape new behavior and capacities, perhaps through positive feedback. A hallmark of mammalian behavioral evolution is the rapid diversification of behavior, the genome and the size of the telencephalon in a relatively short time span (geologically speaking) compared with many ectothermic vertebrates and invertebrates, whose core behavior patterns and abilities may have changed little over millennia in spite of often rapid microevolutionary adaptation. The persistence of core perceptual and behavioral systems as legacies from the past needs to be incorporated

into our thinking more than it has been (Coss, 1991, 1999; Coss & Goldthwaite, 1995; Panksepp, 1998a).

But are mammals not vastly different from other vertebrates? Consider that physical and behavioral adaptations involving milk production and its delivery and ingestion are restricted to modern mammals. Facial expressions and vocal repertoire are also much more complex in all mammals than in the extant reptilian sister groups (squamates, tuatara, and turtles). The fine motor control of many parts of the body (limbs, digits, tail, snout, mouth, ears) almost simultaneously is probably more developed in many mammals (and some birds) than in ectothermic reptiles and amphibians. True, but the mechanisms underlying these differences may be more superficial than we typically think (Burghardt, 1988b). For example, play gets animals doing things, and doing things may cause rapid changes in dendritic spines (Coss & Perkel, 1985) as well as activating chemical changes and brain areas (Gordon et al., 2002). Animals capable of being more active and active in diverse ways are going to have many more opportunities for these brain changes to take place and lead to even more behavioral change in a positive feedback manner (see Petersen, 1988, for a provocative but little-known non-neural feedback model of play and Baldwin, 1896, for a recently resuscitated “organic selection” model).

6.5.4 Domestication as a Model of the Evolutionary Consequences of Parental Care

A parallel model for testing the evolutionary scenario of surplus resource theory is the course of domestication. Many of the processes postulated here as having occurred in juvenile mammals with the onset of parental care and the consequent buffering from the demands of life are also found in domesticated species. The match is remarkable. Price (1984) documented these processes completely independently of the theory outlined here. Domesticated species, such as dogs, are much more playful than their wild counterparts, even taking into account captive conditions. Many behavioral skills found in wild populations (wolves) show deterioration in domesticated forms (dogs). Domesticated dogs have larger litters and considerably smaller brains (Coppinger & Coppinger, 1998). In fact, it has been argued that most changes in the physical structure of domesticated dogs compared with their wolf ancestors are due to changes in rate of development, specifically the retention of juvenile traits or neoteny (paedomorphism). There is now evidence that those dog breeds most physically different from wolves also have the smallest and most juvenile visual signaling repertoire (D. Goodwin, Bradshaw, & Wickens, 1997). But studies of dogs in one category, working sheep dogs, provide a glimpse of the actual processes involved in relation to play (Coppinger et al., 1987). One type of sheep dog herds and moves sheep from place to place while the other type guards and protects sheep. These two types are behaviorally quite distinct and were bred separately in similar habitats for many generations. Adults of both breeds were observed. The herding dogs never exhibited social play approach

behavior toward sheep but guard dogs did so frequently. Conversely, the herding dogs, but not guard dogs, approached sheep with the stalking behavior seen in early stages of predation. Furthermore guard dogs would not even hunt, let alone kill and eat, either live or anesthetized chickens, while wolves and herd dogs would. Thus guard dogs, through domestication, have lost the predatory sequence. The authors argue that during domestication the guard dogs were selected for a prepredatory developmental stage and treat sheep more as social playmates while herding dogs “retained at least a segment of the full ancestral predatory sequence” (Coppinger et al., 1987: 105).

The pattern of increasing playfulness as brain size decreases may be quite common. Kruska (1987a,b) has shown that in many mammals, domestic populations have brain sizes 5 percent smaller than wild populations after only a few generations. This is shown in both a rodent (bank vole, *Clethrionomys glareolus*) and carnivore (polecat). Ferrets were domesticated from wild polecats 2500 years ago and now have brain sizes 30 percent smaller than wild animals. The effects of domestication on brains result in a relatively greater decrease in neocortex and those brain areas involved in planning and problem solving as well as inhibiting impulsive, emotional, and instinctive behavior. Relaxed selection in farm or hatchery-reared animals can be rapid and dramatic and affect not only overall brain size but specific brain areas involved in various types of behavior (see Marchetti & Nevitt, 2003).

In chapter 5 behavioral genetic studies of domestic species showing changes that are due to selection in play and exploration were discussed. A careful study of play behavior in wild animals undergoing domestication might be a most useful method to see how buffering animals from the harsher aspects of existence may change the amount, type, and frequency of play as well as cognitive capacities. Similarly, studies of feral animals undergoing the reverse process would also be useful. In any event, it is important to be critically anthropomorphic, because it is all too easy to conclude that the more affectionate or compliant dog is smarter than the more elusive, unpredictable, high-strung wolf or devious coyote. In fact, hand-reared wolves are more insightful and better at problem solving and observational learning than dogs (Frank et al., 1989). Frank (1980) argues that wolves also have more stimulus boundness in the sense that selection has honed components of a behavioral system “responsive to only a narrow bandwidth of cues and releases highly stereotyped behaviors” (Frank, 1980: 394).

Perhaps only less smart animals were actively selected for domestication by human beings and thus they were selected to have smaller brains. This appears unlikely, as in the most careful study of the process of domestication by Belyaev and Russian colleagues (Trut, 1999). Merely selecting silver foxes (*Vulpes vulpes*) for tameness alone led, after 10–35 generations, to animals that showed marked changes in coat color, ear

and tail morphology, more rapid sensory development (e.g., eyes opened earlier), and delayed onset of fear and the plasma corticosteroid surge. The foxes thus had a longer period for bonding with humans and other animals and showed much more interest and “friendliness” to people (which seems to include playful interactions) than the initial stock population. Although I could not find any data on brain size, cranial height and width were both reduced in the selected foxes (Trut, 1999) and brain measurements are planned (Trut, personal communication, 2001).

A nice statement of how domestication may have facilitated play and altered behavioral organization is provided by Coppinger et al. (1987: 104) in regard to the guarding sheep dogs where “play-bites and play-chases were apparently separable motor units of their behavior system that may be combined at any opportunity with other motor units to produce non-functional, non-systematic sequences of mixed social behaviors that strung together are commonly referred to as ‘play’ behavior.”

Similarly, the initial forms of play in vertebrates are most likely derived from instinctive behavior patterns whose form and motivation are controlled by the basal ganglia and limbic system of the telencephalon and structures in the diencephalon. The rapid rate of evolutionary changes in endothermic animals, especially mammals, in brain size and behavioral complexity are remarkable and still little understood. One consequence may have been increased amounts of primary process play during periods of rapid speciation and diversification of mammalian lineages beginning about 65 million years ago. Surplus resource theory suggests that primary processes involved in play may have been a major engine in this rapid cascade of evolutionary change that led to increased behavioral diversity and later to cognitive complexity in endothermic animals (chapter 15). This may have occurred by natural selection for behavioral play variants that were then incorporated into serious endeavors and functions, so that the once playful behavior was eventually transformed and fixed so that it shifted to being outside the realm of play defined according to the criteria developed earlier.

The thesis here, then, is that after a period of evolutionary reorganization in behavioral ontogeny accentuated by the lengthening of parental care (Burghardt, 1988b), play came to facilitate rapid behavioral and mental development by providing altered phenotypes for natural selection to prune and shape. The motivational and emotional concomitants of play are probably, as neurological findings suggest, more conservative than the behavioral expressions, and so motivational and emotional concomitants of play will need to be studied along with play behavior. Ethologists, behavioral ecologists, and physiologists will need to consider the experience of play, ethology’s fifth aim. To speak metaphorically, play is on a leash, yearning to be free.

In chapter 1 it was established that play is paradoxical, not to say ambiguous (Sutton-Smith, 1997), in many ways. We are on the path to understanding it, but the trail is still tangled with vines and hidden in mist. This chapter has ranged widely in

the search for processes that may underlie playful behavior in order to at least help orient the directions that explorers of play might take using more rigorous methods. The view of play and its origins outlined here suggests that playlike behavior evolved episodically throughout animal evolution under suitable ecological and physiological conditions. Play, in this approach, is both evolutionary detritus and an evolutionary pump. Using the five criteria for play and the general features of surplus resource theory as a compass, it is now appropriate to explore and evaluate evidence on the diversity and radiation of animals and their many types of playful behavior.