THE QUARTERLY REVIEW *of* BIOLOGY

❧❦❧

CURRENT PERSPECTIVES ON THE BIOLOGICAL STUDY OF PLAY: SIGNS OF PROGRESS

KERRIE LEWIS GRAHAM

Department of Anthropology, Texas State University-San Marcos, San Marcos, Texas 78666 USA

E-MAIL: KPLEWIS@TXSTATE.EDU

GORDON M. BURGHARDT

Departments of Psychology and Ecology and Evolutionary Biology, University of Tennessee, Knoxville, Tennessee 37996 USA

E-MAIL: GBURGHAR@UTK.EDU

ABSTRACT

There has been a recent resurgence of interest in the study of play behavior, marked by much empirical research and theoretical review. These efforts suggest that play may be of greater biological significance than most scientists realize. Here we present a brief synopsis of current play research covering issues of adaptive function, phylogeny, causal mechanisms, and development. Our goal is to selectively highlight contemporary areas of research in which the underlying processes and consequences of play should not be ignored. We elucidate some of the new and burgeoning areas of play research and interpret them from an integrative biological theoretical perspective that highlights areas in need of further experimental, comparative, and field research.

INTRODUCTION

PLAY BEHAVIOR is a paradox in humans and animals, being ubiquitous yet ambiguous (Sutton-Smith 1997; Burghardt 2005).

Play has often been ignored in biology because it is difficult to define, and its importance seems far from obvious. Although we intuitively recognize when companion an-

imals and children are playing, it is sometimes difficult, even among children, to distinguish play-fighting from aggression (Dolhinow 1999; Smith et al. 2004; Pellis and Pellis 2009). Indeed, identifying the components that make play *playful*, especially in animals or in contexts not already viewed as playful, can be challenging. Furthermore, while play is relevant to various disciplines, there are differences and discrepancies with how the term "play" is perceived among these fields, and this has led to misunderstandings of play's form and function (Pellegrini 2009). Recently, Burghardt (2001, 2005, 2010b) updated the working definitions of play by setting out five categorical criteria for recognizing it in all species, including humans. Briefly, these criteria state that play is (1) incompletely functional in the context in which it appears; (2) spontaneous, pleasurable, rewarding, or voluntary; (3) differs from other more serious behaviors in form (e.g., exaggerated) or timing (e.g., occurring early in life before the more serious version is needed); (4) is repeated, but not in abnormal and unvarying stereotypic form (e.g., rocking or pacing); and (5) is initiated in the absence of severe stress. Various and diverse researchers (e.g., Pellegrini 2009; Pellis and Pellis 2009) recognize this approach as useful, because if all five criteria are met, play can be confidently identified in any species or behavior system.

The young of most mammals play (Fagen 1981), and increasing numbers of reports also document play in non-mammals, such as birds, fishes, insects, and cephalopods (Mather and Anderson 1999; Gamble and Cristol 2002; Burghardt 2005; Dapporto et al. 2006). Such reports are crucial to a broad comparative understanding of play and are vital in addressing the evolutionary origins of play and its associated functions. By identifying play in extant species representative of ancestral forms, we can more critically infer the earliest forms and functions of play.

Categories of Play

Play behavior is generally grouped into three primary categories: (1) solitary locomotor-rotational play; (2) object play;

and (3) social play (Fagen 1981). Despite distinct terms, the boundaries of two or more play categories are often blurred, and individual categories are often subdivided.

Briefly, solitary locomotor-rotational play consists of vigorous motor acts that are typically performed alone. These include playful running and twisting in ungulates, and somersaulting in monkeys (Müller-Schwarze 1984; Sommer and Mendoza-Granados 1995). Such motor patterns often mimic, but exaggerate, normal locomotor patterns. For example, locomotor play in deer borrows elements from anti-predator flight behavior (Power 2000). Solitary locomotor-rotational play was once considered the earliest form of play, both developmentally and evolutionarily (e.g., Byers 1984), although, currently, no clear phylogenetic patterns are evident for the three categories of play in mammals and birds (Burghardt 2005).

Object play can be solitary or social (Tanner and Byrne 2010), and involves the playful use or manipulation of inanimate objects, such as a dog retrieving a stick or a cat batting a ball. For predatory and scavenging animals, object play is perhaps the most prevalent play category, borrowing sequences from hunting behavior (Biben 1986). Object play may provide opportunities to practice hand-eye (or paw-eye) coordination, although Caro (1980) found that, in kittens, direct experience better predicted how adult cats interacted with prey items than did object play with toy mice. Richard-Hansen et al. (1998) reported that a wild red howler monkey (*Alouatta seniculus*) repeatedly, but gently, used a stick to hit a sloth (*Choloepus didactylus*) resting in the same tree; this may either be an example of play or of agonistic behavior. Captive gorillas (*Gorilla gorilla*) engage in playful competition over balls and bags (Tanner and Byrne 2010). Captive octopuses (*Octopus vulgaris*) play with plastic bricks by passing them from arm to arm (Kuba et al. 2006), and kookaburras (*Dacelo novaeguineae*) playfully smack stones against trees (Watson 1992). Japanese macaques (*Macaca fuscata*) also play with stones, repeatedly clacking them together to create a loud noise (Nahallage and Huffman 2007). Indeed, it is likely that play with objects is a

developmental precursor to most, if not all, complex and cognitively flexible tool use. Parra (2007) recently described sponge use by humpback dolphins (*Sousa plumbea*) as either object play behavior or a possible foraging tool behavior.

Social play involves two or more players that are usually, but not always, conspecifics. Typical movement patterns involve chasing, wrestling, and tail-pulling, and even a form of peek-a-boo (Bekoff 1974; Sommer and Mendoza-Granados 1995; Russon et al. 2002). Of all social play patterns, rough-and-tumble play (R&T), or play-fighting, is most frequently studied in animals (Pellis and Pellis 2009). R&T has been the focus of renewed research (e.g., Pellegrini and Smith 1998; Pellegrini 2008) even in children, where it is suppressed during ever-dwindling recess time in schools. Other forms of social play include sexual play (Vankova and Bartos 2002) and play-mothering (Lancaster 1971). Maintaining social play requires that players be highly attuned to the rapidly changing nature of the play bout. Players must read social cues appropriately, react swiftly and accurately to movements, and anticipate responses. Hence, play signals have evolved in many species that act as behavioral cues or honest reassurances that the behavior is playful. Typical play signals include play bows in canids and open-mouthed play faces in primates and carnivorans (Bekoff 1975; Pellis and Pellis 1996).

The identification of types or categories of play is important to our understanding of the nature of play. However, to address play from a biological perspective, it is crucial to consider both ultimate and proximate explanations. In doing so, Tinbergen's four ethological aims are especially useful (Tinbergen 1963); thus, we consider play in terms of adaptive function and evolution (distal), and causation and development (proximate). There are two large bodies of research on play: nonhuman animals and humans, primarily children. While we emphasize animals, the human literature is highly relevant both conceptually and methodologically. Research on children's play emphasizes socio-

dramatic play, construction play, and other activities. These may have counterparts in animal play, but are more controversial and may only involve a limited range of species (Tomasello and Call 1997; Johnson et al. 2004; Burghardt 2005, 2010b; Pellegrini 2009). Furthermore, although we emphasize behavioral processes of play, we will also briefly discuss mental processes.

A Brief Excursion into Theory

Although we will emphasize recent empirical research, an understanding of some of the historical concepts that have framed much of the literature and current theory is necessary first. Historically, there are three key theories of play behavior: surplus energy, instinct-practice, and recapitulation. Each theory has been rejected, resurrected, and restructured by different researchers at different times, and all have been reviewed in detail recently (Burghardt 2005). Briefly, the surplus energy theory (Spencer 1872) focused on proximal mechanisms and posited that "higher" animals (e.g., mammals) played when they had a surfeit of good nutrition and a physiology that allowed for vigorous activity and exuberance. Groos's (1898, 1901) functional theory of play incorporated both instinct and experience as preparation for adulthood. Indeed, Groos regarded the perfection of instincts through playful practice to be the main evolutionary role of prolonged juvenile periods and parental care. Although play as practice does not explain why adult animals play, Groos (1898) suggested that play may continue into adulthood due to conditioning-like processes. Hall's (1904) recapitulation theory viewed play as a residual, even vestigial, behavior from the evolutionary past, but one nonetheless developmentally essential, even if its importance was no longer as "urgent" (Hall 1904:206). Thus, humans may find many sports satisfying because similar actions were once necessary for survival. Recapitulation forms the kernel of some modern views on play and mental development in nonhuman primates, especially those deriving from a Piagetian theoretical framework, which has greatly influenced developmental psychol-

ogy (Parker and Gibson 1979; Parker and McKinney 1999).

These three historical viewpoints were united in their view of play as a biologically-based phenomenon, important to the developing phenotype. Despite progress in recording and interpreting play, subsequent research primarily emphasized function—particularly delayed benefits—over a broader ethological approach incorporating issues of development, mechanisms, and phylogeny. In short, in both human and animal play research, variants of Groos's practice theory prevailed (Fagen 1981; Elkind 2007). The main problem is that these three theories focused separately on different aspects of Tinbergen's aims, yet each was viewed as a mutually exclusive explanation, which thus precluded their integration into a meaningful exposition on play. For example, despite the widespread rejection of Spencer's surplus energy theory, energy and physiology remained important potential parameters in the evolution of play behavior (Burghardt 1982, 1984, 2001, 2005; Barber 1991). Burghardt's (1984, 2005) surplus resource theory (SRT) posited that underlying correlates of play behavior (e.g., prolonged development, parental care, large brains, high resting metabolic rates) may facilitate selection for the broad range of behavioral and cognitive complexities prominent in endothermic (i.e., warm-blooded) animals (Burghardt 1984, 1988, 2005). Nunes et al. (1999) and Sharpe et al. (2002) notably demonstrated the causality of the relationship between nutrition and play in wild populations; Sharpe et al. (2002) found that it was nutrition, rather than changes to time budgets, that resulted in increased play behavior. Human children may also play more actively when they have an adequate diet (Espinosa et al. 1992).

ADAPTIVE FUNCTIONS OF PLAY BEHAVIOR

The predominant emphasis on play's adaptive functions has recently been tempered by increased evaluation of the phylogenetic aspects of play. We will first discuss functional questions because these seem most relevant for encouraging biolo-

gists to consider play seriously. Although play research has disproportionately assessed the functions and adaptive value of play, there remains a lack of consensus in this area (Martin and Caro 1985). If play has no benefits, any costs incurred through play should lead to selection against it. However, because play is so ubiquitous and prominent in many species, play researchers generally assert that the adaptive significance of play behavior is simply less well-understood than behaviors such as sex, grooming, or fighting (Fagen 1981). Dozens of possible functions of play have been proposed (e.g., Baldwin and Baldwin 1977; Bateson 1981; Bekoff and Byers 1981; Fagen 1981; Smith 1982; Martin and Caro 1985; Paquette 1994; Soderquist and Serena 2000; Burghardt 2005; Palagi 2006), but, although often plausible, virtually none are fully supported by empirical data (e.g., Pellis and Pellis 2009). Play likely serves multiple overlapping functions (e.g., Bateson 1981), but, until recently, tests of the adaptive functions of play in animals have been limited to variants of the motor training, practice, and socialization models. Typically, only one putative benefit is assessed, but, when several are, the results are seldom encouraging. For example, a field study on meerkats (*Suricata suricatta*)—highly social and playful carnivorans—showed no positive relationship between social play (including play-fighting), various play measures, and a range of possible functional outcomes including reduced aggression, the forging of dispersal partnerships, social cohesion, and fighting success (Sharpe and Cherry 2003; Sharpe 2005a,b,c).

Below, we outline some commonly cited functions of play and briefly review the evidence for them. Although often termed "theories," these functional views generally do not address broader issues of ontogeny, mechanisms, or evolution.

MOTOR TRAINING

Play behavior is often vigorous. An early view was that play served as physical exercise or to develop and maintain physical skills (Brownlee 1954). Play may indeed

enhance physical fitness (i.e., increase endurance and strength through improved cardiovascular capacity and muscle development); however, it appears that play provides less exercise than is needed to maintain physical fitness, and thus it cannot be solely for "getting into shape" (Byers 1998). Similarly, most effects of physical exercise are not lasting, and training improves physical fitness at any age, which suggests that adults should also play. An alternative explanation is that play modifies the young animal's developing neuromuscular system (Bekoff and Byers 1981; Byers and Walker 1995). Byers and Walker (1995) noted that the timing of play corresponds to peaks in cerebellar synaptogenesis in rats, cats, and mice. They suggest that play during sensitive developmental periods may facilitate the development of appropriate skeletal muscle fiber types and enhance cerebellar synaptogenesis. Although moderate physical activity benefits most animals (especially endotherms with high metabolic rates), the specific developmental links identified by Byers and Walker have yet to be the focus of other experimental physiological studies. While it is known that motor activity during early postnatal development can affect cerebellar synapse formation (Floeter and Greenough 1979; Pysh and Weiss 1979; Brown et al. 1991), at least 80% of cerebellar synapses are already complete prior to the appearance of play (Byers and Walker 1995), and, in many species, play persists well beyond the "sensitive period" for synaptogenesis. There is no evidence to support the hypothesis that play facilitates the development of appropriate muscle fiber types (i.e., the ratio of slow to fast fibers in a muscle). In vitro studies suggest that muscle fiber type is fixed early in neonatal development (Bandman et al. 1982; Miller and Stockdale 1986; Schafer et al. 1987), and, if postnatal changes are possible, they are determined by the pattern of innervation in the muscle (Buller et al. 1960; Armstrong 1980; Baldwin 1984). However, neither rats nor mice undertake play during the period when muscle fiber innervation is fixed (Byers and

Walker 1995). Also, experimental research shows that extensive physical exercise is detrimental to some ectothermic reptiles (Burghardt 1984).

TRAINING FOR UNEXPECTED EVENTS

Špinka et al. (2001) proposed that mammalian play can be explained in terms of training for unexpected events by allowing an animal to develop flexible kinematic and emotional responses to events that involve stress and loss of control. By pushing themselves to the brink of uncontrolled movements, playing animals practice behavioral sequences that may ultimately be used in unpredictable emergency situations (e.g., misjudging a branch high in a tree). Thus, the benefits of play are reaped primarily when animals behave near the limits of their prowess. Špinka et al.'s (2001) model is specific to mammals; they argue that the neurological bases of play are comparable across all types of play and across all species. This is unlikely even within mammals, however, because diverse brain mechanisms underlie different aspects of play (e.g., play fighting, object play), and it is definitely improbable for other taxa, especially invertebrates. This hypothesis posits that play should occur most frequently in changing environments because an animal must learn to cope with new situations, but it cannot explain why play is less frequent in poorer environments (e.g., squirrel monkeys *Saimiri sciureus*; Baldwin and Baldwin 1976) or during seasonal food shortages (e.g., Sommer and Mendoza-Granados 1995). Indeed, preparation for risks should even be more adaptive in challenging and stressful environments. Additionally, play training that pushes animals to the limits of their competence may have more direct motivational roles as well as affective proximate roles in normal behavioral development. For example, toddlers learning to walk test their limits and have fun doing so, but this usually occurs in safe contexts. The same may be true of many sports and other examples of mastery or self-assessment play (Thompson 1998), where animals also challenge themselves to reach higher plateaux of performance.

Play at the brink increases risk of injury and death, thus future research needs to examine how risks and safety are balanced. Nonetheless, formulating this hypothesis systematically and clearly in a comparative and evaluative framework makes Špinka et al.'s research (2001) a model for developing functional hypotheses about play.

PRACTICE

It has long been argued that the adaptive function of play is to practice adult skills or "instincts" (Groos 1898). Under the auspices of parental care, young animals could use play to practice and hone skills such as mating and fighting in relative safety (e.g., Smith 1982). However, studies show that mammals deprived of the opportunity to play still develop these adult skills relatively normally. For example, Caro (1980) found that kittens prevented from undertaking object play did not differ in predatory skill from kittens raised in a toy-enriched environment. Similarly, Sharpe (2005c) found that in wild meerkats, rates of play fighting and the ability to win play fights was unrelated to the ability to win serious fights in adulthood. Hård and Larsson (1971) found that when male rats were reared in isolation they exhibited subsequent incompetence in sexual performance, demonstrating difficulty in achieving the appropriate orientation during mounting behavior. This behavioral deficiency was not rectified by raising juveniles with non-playful (drugged) partners (Einon et al. 1978), suggesting that certain orientation skills require social play rather than simply social contact. However, Pellis and Pellis (1998a) argue that play fighting in rats does not include the evasive maneuver normally exhibited by female rats during mating, rendering play an inadequate means of practicing mating skills for males. Moreover, play rarely mimics serious behaviors like predation or fighting completely. In rats, the specific targets of attack and defense used in play fighting differ from those used in real fighting (Pellis 1988, 1993; Pellis and Pellis 2009; Pellis et al. 2010), and, since a motor skill can only be practiced effectively if the exact same motor pattern is undertaken (Byers 1998), play fighting will not assist in the refinement of fighting maneuvers. Further research is needed to establish why and how play borrows actions from other contexts, such as courtship and aggression.

Perhaps play occurs not as a means of practicing specific skills, but rather to induce animals to engage in vigorous complex actions that give their perceptual, neural, and motor systems experience in developing and maintaining biological and behavioral competencies. The nature of these effects may have little to do with play-specific ethotypic behaviors as compared to more general, and perhaps more evolutionarily significant, physiological and behavioral consequences. For example, Nunes et al. (2004) showed that in Belding's ground squirrels (*Spermophilus beldingi*), improvement in general motor ability was greater for juveniles that engaged in high rates of social play as compared to those that engaged in low rates, and that these elevated motor abilities were associated with early dispersal in males and with yearling breeding success in females.

SOCIAL BENEFITS

Social play is studied more than any other play category, and it has been the focus of most of the recent tests of adaptive hypotheses. Numerous social benefits to play have been suggested, including enhancing social skills, strengthening social bonds, reducing aggression, refining social assessment, learning and promoting cooperative behavior, and even encouraging sharing, reciprocity, altruism, and fairness (Fagen 1981; Lee 1983; Bekoff 2001; Sussman et al. 2005; Bekoff and Pierce 2009; Pellis and Pellis 2009). Unfortunately, there is only limited evidence to support any of these hypotheses, and it appears that mammals deprived of the opportunity to play still develop normal social relationships (e.g., Baldwin and Baldwin 1974). At best, lack of play experience may lessen an individual's ability to deal appropriately with social stressors, reacting with hypo- or hyper-defensiveness toward conspecifics, relative to individuals who engaged in play as juveniles (Hol et al. 1999). Pellegrini

(e.g., 1993) showed that children who engage in lots of R&T are more socially competent in non-play situations; the same is true for rats (Pellis and Pellis 2007, 2009). Drea et al. (1996) argue that the timing of social play in spotted hyena (*Crocuta crocuta*) ontogeny renders it a good candidate for developing social relationships within the communal den. Holmes (1995) reported similar findings for semi-captive golden-mantled ground squirrels (*Spermophilus lateralis*), concluding that play frequencies are higher between litter-mates to aid group social cohesion. However, Sharpe (2003, 2005a,b) found that social play in meerkats appeared to have no effect on social cohesion or bonding between group members, and it also failed to reduce aggression between play partners. Paquette (1994) speculates that rather than using traditional agonistic behavior to establish rank, chimpanzees (*Pan troglodytes*) use play because it allows them to demonstrate their strength and competitive ability without risk of injury. Certainly, social play offers many opportunities for complex social interactions, and it may be the perfect mechanism for both learning and exploiting physical and personality weaknesses among peers, while simultaneously avoiding serious injury. Such physical assessment may occur in adult-adult encounters, between potential mates or rivals, especially in nongregarious species (Pellis and Iwaniuk 1999a, 2000a). Although it is unlikely that specific juvenile playmates later become adult allies (e.g., Sharpe 2005c), it is possible that social play provides social experience that assists individuals to learn how to form coalitions and alliances. Among children, the most socially dominant individuals are highly social and co-operative with both their peers and educators, and are generally not perceived as aggressive; however, they are quite effective in using aggression to access resources (Pellegrini 2008). Additionally, because human playmates tend to avoid one another sexually in adulthood, play among littermates may reduce inbreeding (Charlesworth and Charlesworth 1987).

ADULT PLAY

Adult play has proven problematic for some researchers because it does not fit neatly with traditional views of play as preparatory behavior. Adults play in many species (Špinka et al. 2001), especially with infants and juveniles, but usually at far lower rates than do non-adults (Burghardt 2005). Adult-infant play is most common between kin, but playing with an unrelated infant may grant some level of status to an adult, while demonstrating a goodwill gesture to the infant's mother (Fagen 1981). Broadly, adult play may function as a form of assessment. Parents may invest in play to assist or assess offspring development (Chiszar 1985). Adult male polar bears (*Thalarctos maritimus*) appear to use play-fighting to assess strength in potential competitors (Latour 1981). Potential mates may use play as courtship or mate assessment or to reduce tension between unfamiliar partners (Pellis and Iwaniuk 1999a). Fertile bonobos (*Pan paniscus*) exhibit play faces more frequently during R&T, also as a form of social assessment (Palagi 2006). Sexual and nonsexual adult play can be independent and have different evolutionary origins, suggesting different functions and consequences (Pellis and Iwaniuk 1999a, 2000a).

COSTS AND BENEFITS

Most studies addressing the functions of play have assumed that play has immediate costs with delayed benefits, and that these long-term benefits should outweigh whatever costs are incurred (Fagen 1981; Chalmers 1984; Caro 1995). Various costs associated with playing include injury from falls or aggressive retaliation, reduced time spent in survival behaviors (e.g., foraging), expenditure of energy, and increased predation risk as a result of reduced vigilance and the conspicuousness of play to predators. The survivorship costs of play can be surprisingly high. In a field study of South American fur seals (*Arctocephalus australis*), it was noted that pups devote only 6% of their time to play. However, 85% of the 26 pups that became sea lion prey were playing

at the time they were captured (Harcourt 1991). Furthermore, play may be mediated by dopamine receptors in the basal ganglia and other areas of the brain and tap into mechanisms underlying addictive behavior (Pellis and Pellis 2009). Just as social drinking can move from benign to problematic, play, at least in humans, can also shift from fun to compulsive (e.g., gambling, running, and video gaming) (Burghardt 2005; Graham 2010).

Increasingly, play researchers are recognizing that play is likely to provide immediate benefits to young animals (e.g., Fagen and Fagen 2004). In fact, when juvenile mortality rates are high, delayed benefits should be of lower probability than immediate benefits (Burghardt 1984). Regardless of whether the benefits derived from play are immediate or long-term, play behavior cannot be considered adaptive unless it enhances an individual's inclusive fitness. Demonstrating that play improves individual survival or reproductive success is tremendously difficult. Current research, however, is finally making inroads into this critical area. Nunes (2004) found a positive relationship between rate of social play in females and subsequent reproductive success during their first breeding season in Belding's ground squirrels. Cameron et al. (2008) found that in feral horses (*Equus caballus*), foals that spent more time playing were more likely to survive their first year of life. Most importantly, Fagen and Fagen (2004) found a positive relationship between rate of play and survival in brown bear cubs (*Ursus arctos),* even after controlling for the potentially confounding variables of body condition, food availability, and maternal condition. While the causality of these relationships has yet to be confirmed experimentally, findings such as these finally quash the perception that play is functionless and frivolous and can be ignored with impunity by biologists.

Origins and Phylogeny of Play

There have been repeated calls for more comparative studies to further our understanding of the origins of play (Fagen 1981; Burghardt 1984). Promising play

candidate phenomena have recently been identified in species from many diverse phylogenetic groups, including lizards, turtles, frogs, fishes, cephalopods, crustaceans, and insects (e.g., Burghardt 2005; Dapporto et al. 2006; Mather 2008). Comparative studies have addressed evolutionary trends in the diversity of play (e.g., Byers 1999; Pellis and Iwaniuk 1999a,b, 2000a,b, 2002; Lewis and Barton 2004, 2006), but, historically, there has been little overlap between structural and functional approaches to play (Fagen 1978; Burghardt 1998). Neither approach alone fully informs us about play's origin, because there are problems distinguishing origin and phylogeny from function or current adaptiveness (Burghardt 1998; Pellis and Pellis 1998a,b). It is unlikely that different categories of play are homologous with identical evolutionary origins, causal mechanisms, or adaptive functions. In short, play probably arose repeatedly in different taxa (Burghardt 2005). Careful analysis of which species exhibit play, as well as of the general features of playfulness, can assist our understanding of both the plesiomorphic and derived aspects of play in different taxa.

WHICH ANIMALS PLAY?

Play is well-developed in primates, rodents, carnivorans, ungulates, elephants, and cetaceans. These playful orders contain numerous species that show great diversity in habitat, home range size, locomotor pattern, life history, body size, social organization, and diet. Interestingly, the complexity of play rarely correlates perfectly with phylogenetic relationships or even with patterns of sociality (Pellis and Iwaniuk 1999b; Burghardt 2005).

In order to understand the evolutionary origins of play, we especially need to consider the less playful orders of placental mammals, such as manids (pangolins), erinaceids (hedgehogs), soricids (shrews), talpids (moles), tubulidentates (aardvarks), and dermopterans (flying lemurs). Unfortunately, little is known of the behavior of these mammals, and accounts of their play are often derived from antiquated reports. Nonetheless, anecdotes, es-

pecially by reliable observers, can be useful (e.g., Bates and Byrne 2007). Some of these less-studied orders offer tantalizing insights into the evolution of play. For example, xenarthans (armadillos, sloths, and anteaters) have low metabolic rates, but they have longevity and parental care, thus suggesting a greater propensity towards play (Burghardt 2005). Although restricted to a few examples, chiropteran (bat) play is comparable with that of primates, rodents, and carnivorans, although many more species in the latter groups play, with the most variation occurring among rodents. There is good evidence of chasing and wrestling play in captive Old World fruit bats (*Pteropus rodricensis*, Carroll 1979), so perhaps bat play is common but difficult to observe (Fagen 1981). Although our knowledge is incomplete, play of some type is reported broadly across all major eutherian mammalian lineages.

Due to overlap in habitat types, diet, and behavioral specializations, metatherians offer a useful comparison with eutherian mammals (Fisher and Owens 2000). Marsupials provide interesting insights into functions of play due to their low metabolic rates and variability in brain size (Byers 1999). Indeed, the proportion of neocortex to brain size is surprisingly comparable across the two infraclasses (Burghardt 2005). With increasing understanding of marsupial behavior, we can now positively identify all three categories of play behavior across metatherian families (Croft 1982; Russell et al. 1989; Watson and Croft 1993; Burghardt 2005). Byers (1999) compared brain size and play across marsupial taxa. Measuring play on a three-point scale as absent, rudimentary, or common, he found that play frequency correlated with brain size at the family level, noting that numbats, potoroids, macropods, and wombats are the most playful marsupial families. Using phylogenetic comparative methods, Iwaniuk et al. (2001) extended Byers' analysis to include more species and confirmed some of his findings using an established phylogeny. Brain size is related to metabolic rate, and this varies less in marsupials relative to other mammals. Accounting for differ-

ences in body size, smaller-brained marsupials play less frequently and with less complexity relative to larger-brained marsupials—a trend noted across mammals, more generally (Iwaniuk et al. 2001; Špinka et al. 2001; Lewis 2003). Given their unusual development, marsupials are generally considered far more altricial than placental mammals. However, if we consider the time of actual emergence from the pouch, then marsupial "birth" is comparable to placental birth (Burghardt 2005). These factors are important considerations in the evolution of play behavior.

Evidence of play in monotremes, such as the platypus (*Ornithorhynchus anatinus*), is scarce and tends to focus on mother-infant interactions which may or may not include play (Fagen 1981; Burghardt 2005; Siviy, unpublished observation). The occurrence of play across such a range of extant mammals indicates its ancient roots, and reports of play in avian species further support this hypothesis. Since birds are not ancestral to mammals, play may have arisen independently in both birds and mammals from reptilian ancestors (Fagen 1981; Burghardt 1984). Many birds play, and all three play categories are represented. Herring gulls (*Larus argentatus*) play drop-catch games (Gamble and Cristol 2002), keas (*Nestor notabilis*) destroy inanimate objects and socially play with objects (Diamond and Bond 2004), raptors play with dead prey, ravens play "keep away," and parrots play bite (Fagen 1981; Burghardt 2005). Other birds chase and wrestle, playfully swoop and soar, and engage in jumping, hustling, and play-bathing (see Fagen 1981; Heinrich and Smolker 1998). Play signals such as bouncy walks and self-handicapping (Pellis 1981) suggest that some avian play compares with complex mammalian play. Of particular interest are the large-brained, social species that appear both cognitively accomplished and highly playful (Ortega and Bekoff 1987). Diamond and Bond (2003) found that the correlation between brain size and play behavior at the species level is weak, but that the length of the juvenile period correlates with play complexity. This finding is consistent with

those of Pellis and Iwaniuk (2000b) for both rodents and primates.

In recent years, play has been increasingly described in various captive, non-endothermic vertebrates. Studies have provided video documentation of turtles pushing basketballs and swimming through hoops (*Trionyx triunguis,* Burghardt 1998), monitor lizards (*Varanus* spp.) interacting with various objects and even playing tug-of-war with keepers (Burghardt et al. 2002), and alligators playfully snapping at water jets (Lazell and Spitzer 1977). The more well-documented examples clearly fulfill the five play criteria, offering exciting insights into the origins of play. For example, crocodilians share common behavioral traits, such as curiosity, parental care, and longevity, with other playful species. Parental care exists in dendrobatids (dart poison frogs) that wrestle, chase, and jump in ways that also meet the five play criteria (Burghardt 2005). Indeed, we are now in a position to test for play behavior in species that we might not have previously considered, such as fish. Many ichthyologists may be uncomfortable characterizing any fish behavior as play, but there are now a number of locomotor, object, and social play examples from a wide range of fishes, including cichlids, mormyrids, sharks, and rays (Burghardt 2005).

Some invertebrate behavior also seems to fulfill the five play criteria. Cephalopods, especially octopods, are known to be curious, and curiosity is frequently proposed as a precursor to playfulness (Burghardt 1984). Mather and Anderson's (1999) original octopus play findings and additional recent work by Kuba et al. (2006), Mather (2008), and Finn et al. (2009) continue to demonstrate the playful, curious, and cognitive aspects of octopuses. Play has also been documented in other invertebrates, including insects (e.g., wasps, Dapporto et al. 2006). Thus, using the five play criteria, there is now increasing experimental and comparative evidence for play in non-amniotic vertebrates and even in some invertebrate phyla. That play does not appear to fall neatly into phylogenetic categories (see Figure 1) provides a greater impetus to record and understand where it exists, the traits associated with its occurrence, and the play diversity found within and between orders and families.

THE ORIGINS OF PLAY

How does play originate and become, at least in some lineages, an important evolutionary factor? To characterize this generally, we can view play in a scenario of three processes that can occur in a sequence both ontogenetically and phylogenetically. *Primary process play* occurs sporadically as a result of factors such as low behavioral thresholds, behavioral maturation, boredom, and excess metabolic energy; such play has no necessary long-term effects (as suggested by SRT). S*econdary process play* helps maintain the condition of the animal physiologically, behaviorally, and perceptually. For example, physical exercise may be necessary for maintaining physiological systems, just as ambient light maintains visual functioning. Play may be a motivated and self-rewarding (autotelic) activity so as to accomplish this in animals where parental care eliminates the need for time-consuming survival behaviors in the young. *Tertiary process play* is helpful for reaching developmental milestones, as well as cognitive, physical, and social ones, and for behavioral innovations (Burghardt 2005). For example, the typical age at which human infants coordinate limb movements to open a box to retrieve a toy is 12 months. However, mere exposure to the box with the toy, allowing for playful manipulation of it, for 6 one-minute trials a week beginning at 6.5 months of age led to success at opening the box at an average of 8 to 9 months of age (Bojczyk and Corbetta 2004). Interestingly, as soon as babies mastered the task, parents spontaneously reported that their infants often became much more active and successful explorers at home, thus requiring cupboards to be baby-proofed.

The various theories of play reviewed above fall under one or more of these three processes. All three play processes can occur in the same species. This is es-

Figure 1. Frequency of Play Behavior among Vertebrate Taxa

Phylogenetic tree indicating whether confirmed play behavior is relatively common, infrequent, or unknown in major vertebrate taxonomic groups.

pecially notable in humans, where behaviors range from doodling when bored to risky adventure play.

While play is known to occur—and probably originated—in many taxa, it is most common in endothermic animals, and this can be explained through SRT. Endothermy is metabolically costly, but it often supports a more effective aerobic metabolism that allows sustained vigorous activity, such as the vigorous play of many mammals and birds, especially when food resources are abundant. Conversely, ectotherms, such as non-avian reptiles, rely on behavioral adaptations for thermoregulation and have low metabolic rates generally not conducive to sustained vigorous activity. The anaerobic metabolic processes on which they rely often require external heat (e.g., sunlight) to raise the body temperature to levels sufficient for vigorous activity. As such, ectotherms quickly tire (Burghardt 1984,

2005). Similarly, small endotherms with very high metabolic rates tend to play at low rates because they have high metabolic costs due to large surface-to-mass ratios. Consequently, some animals may simply have insufficient energy to devote to behaviors that are not directly related to current survival (Burghardt 1984). Indeed, having surplus time is an additional route to playfulness. For an animal whose time is purely devoted to survival behaviors, selection will work against diverting any excess time towards playing, in spite of its possible benefits in the future. This explains both the prevalence of play in juveniles and the importance of parental care in the most playful species, as parents give food and protection to their offspring. Another factor associated with playfulness is explained by animals with complex and diverse behavioral repertoires. Given that play behavior borrows elements from other behavior categories, play should be more varied in animals with a greater set of behavioral attributes, as these animals are capable of performing innovative—and possibly functionally adaptive—variable responses. Insofar as there are heritable aspects of this variation, selection can operate upon such variation and thus facilitate evolutionary behavioral change both directly and through a process such as the Baldwin Effect (Weber and Depew 2003; West-Eberhard 2003; Burghardt 2005).

Play usually occurs when animals are in good physical condition and under minimal chronic stress. Play probably originated, therefore, under conditions in which animals could regulate their body heat efficiently, had sufficient metabolic resources, and could accumulate more energy than required for growth and maintenance alone. Enriched captive conditions provide resources and safety, such as adequate nutrition, reduced need for extensive foraging time, and absence of predation risks, thus facilitating the expression of play. For these reasons, play is typically more frequent and intense in captivity than in the wild (e.g., Enomoto 1990; Pellis 1991; Sharpe and Cherry 2003; Palagi et al. 2004). Stone play in Japanese macaques

fits these predictions from SRT (Nahallage and Huffman 2007). Additionally, such captive animals probably had stable juvenile environments with high offspring survival rates. Energy involves motivational mechanisms, so play in young animals may rely on "innate precocial exploratory and arousal mechanisms" (Burghardt 1984). Data supportive of SRT are accumulating but will not be reviewed here (Pellegrini 2009; Pellis and Pellis 2009). The main point is that it helps to explain the origins of play in diverse taxa, and this is amenable to comparative testing. Additionally, the role of increased metabolic rates and the potential for sustained activity may allow for more innovative play responses and, consequently, more behavioral variability over less evolutionary time. Thus, increased behavioral activity in endotherms may positively increase the rate of behavioral and cognitive evolution, underlying the much faster macroevolutionary rates seen in many birds and mammals as compared to amphibians and reptiles.

Casual and Developmental Mechanisms in Play

Despite heavy focus on functional issues, attention has also been paid to proximate mechanisms, including analyses of brains, hormones, and physiological functions, as well as to the ontogenetic trajectory of play. Environmental stressors such as food deprivation, crowding, confinement, illness, and predators often act as play-reducing agents. Hungry Arabian babblers (*Turdoides squamiceps*), for example, do not play (Pozis-Francois et al. 2004), but playfulness rebounds to pre-hunger levels following a meal (see Baldwin and Baldwin 1976; Siviy and Panksepp 1985). That play is often more prevalent after feeding in some species (Burghardt and Burghardt 1972) suggests that the increase in energy and well-being after a meal can be diverted towards play. Conversely, playing immediately after feeding may be a product of eliminating a more pressing motivational system (i.e., hunger) rather than gaining metabolic energy from a meal. Following feeding, human infants initiate playful en-

counters with their mothers, rather than vice versa (Burghardt 2005), which may be a key time for brain stimulation, given the extra energy and close contact with the mother. Conversely, many species engage in play at high rates prior to feeding, such as meerkats (Sharpe and Cherry 2003) and otters (*Aonyx cinerea*) (Pellis 1991), as well as species that hunt cooperatively, such as African wild dogs (*Lycaon pictus*) and lions (*Panthera leo*). Hungry cats (*Felis cattus*) may play a good deal, especially when prey items are large, intimidating, or unfamiliar (Biben 1979). Captive chimpanzees play more before feeding (Palagi et al. 2004). In fact, chimpanzee and bonobo social play during pre-feeding periods may help to diffuse tension over food, especially between adults and juveniles, or among individuals of different rank (Enomoto 1990; Palagi et al. 2004). The relationship between play and hunger may be motivationally distinct and may differ between species (see Pellis 1991; Hall 1998). It is also possible that these findings are a product of captivity and obtaining food at a specific feeding time, rather than having to forage for it *ad libitum.*

Laboratory rats have been the focus of much of the available research on brain mechanisms in play (Pellis et al. 2010; Siviy 2010; Vanderschuren 2010). Panksepp (1998) argued that, along with a few other basic affective systems (e.g., fear, rage, bonding), play is a key component of the striatal-pallidal-limbic system organization of the mammalian brain. The effects of certain drugs on this part of the brain may mimic the affects of food shortages or confinement. Deak and Panksepp (2006) found that when the tropane alkaloid anticholinergic drug scopolamine was administered to one rat within a juvenile play dyad, play was reduced and could not be solicited by a non-drugged rat. However, normal play quickly resumed after the scopolamine treatment had ceased (see also Vanderschuren 2010).

Experiments in which animals are deprived of the opportunity to engage in social play have provided insights into the motivation, expression, and functions of play. Social isolation increases the motivation for social play in rats (Deak and Panksepp 2006; see also: Panksepp and Beatty 1980; Panksepp 1981; Beatty et al. 1982; Pellis and Pellis 1990; Vanderschuren 2010). Several studies have investigated the effect of predator stimuli on rat behavior. Aside from pied pipers, a rat's natural predator is the cat. Unsurprisingly, rats respond strongly to cues that suggest a cat's presence, such as its fur, scent, whiskers, or its actual presence, and will reduce their social play for extended periods accordingly. Presumably, it is the stress induced by a predator that causes this reduction (e.g., Panksepp 1998; Dielenberg and McGregor 1999, 2001; Siviy et al. 2006; Siviy 2010).

BRAINS AND LIFE HISTORY MEASURES

For many decades, play was viewed as a consequence of large brains and complex cognition, and any putative play in other species was largely dismissed (Fagen 1981). Although phylogenetic relatedness does not necessarily provide clear patterns of playfulness, broadly, playful species share some traits in common, such as a large relative brain size. Recent research shows that brain size is, at best, only an indirect measure of playfulness, and that the relative sizes of constituent parts of the brain are more reliable predictors (Iwaniuk et al. 2001). Certainly among primates, comparative studies suggest that the neocortex, cerebellum, amygdala, and hypothalamus are good predictors of social play frequency (Lewis 2000; Lewis and Barton 2004, 2006). In addition, relatively high metabolic rates tend to correlate with higher rates of play. Brain size and metabolic rate are closely correlated (Burghardt 1984), although this may have less to do with cognitive abilities and more to do with brains being metabolically expensive. There appears to be a trade-off between brains, metabolic rate, and play in small-bodied endotherms due to thermoregulatory heat loss. A further observation is that species living in large social groups tend to be more playful. Life in social groups may require more social processing power (Dunbar

1992), therefore engaging in social play may help facilitate social relationships in large groups (Lewis 2000). Burghardt (1982) questioned this generalization on the basis that both black bears (*Ursus americanus*) and orangutans (*Pongo pygmaeus*) play extensively as juveniles, but live largely solitary adult lives. This is also the case for many species of small, solitary carnivorans, such as polecats (*Mustela putorius*), and for dasyurids such as the chuditch (*Dasyurus geoffroii*), whose litters play socially at high rates (Poole 1966; Soderquist and Serena 2000). As primates are social animals, it is possible that the relative nongregariousness of wild orangutans is a relatively recent adaptation to changing environmental conditions (Galdikas 1995; Van Schaik et al. 2003).

SEX, HORMONES, AND PLAY

One prominent theme of play research concerns sex differences. Traditionally, it was speculated that males typically play more frequently than females, especially in terms of social and locomotor play. However, many apparent sex differences in play frequency are statistically non-significant (e.g., Caro 1980; Lee 1983; Soderquist and Serena 2000; Sharpe 2005c; Cameron et al. 2008). Males may play more roughly than females and initiate play bouts with partners more frequently (e.g., Cameron et al. 2008). Female rats, much like males, often become more aggressive in their play with increasing age, even when using the same tactics as younger animals (Foroud and Pellis 2003). Rather than finding the roughness of male play less appealing, female partner preferences are more intimately connected with the social functions of adult play, such as courtship and mate assessment (Pellis and Iwaniuk 1999a; Foroud and Pellis 2003). Play declines in frequency at puberty, and there are marked shifts in play tactics with increasing age, such as a tendency away from playful attack and toward playful defense (Foroud et al. 2004), or from affiliative to aggressive gestures that ultimately block reciprocal contact (Foroud and Pellis 2003). Socially isolated rats may still exhibit age-related changes in behavior; thus play experience is unlikely to activate these changes, as different neural control centers are likely involved. Social isolation during juvenility leads to long term cognitive deficits due to permanent changes in neural chemistry, such as reduced dopamine receptor density (Pellis and Pellis 2009). Rat studies show repeatedly and specifically that a lack of social play during development—rather than a simple lack of social contact—leads to cognitive and behavioral deficits later in life; playful experience, therefore, appears to be crucial (Pellis and Pellis 2009; Pellis et al. 2010; Siviy 2010; Vanderschuren 2010).

Puberty is a particularly critical developmental period, and it is of interest to play researchers in terms of the shift from juvenility—a life stage most associated with playfulness—to adulthood. The physiological and behavioral changes that occur during this time are largely due to the result of changes in gonadal hormonal actions—specifically, the secretion of androgens. These hormonal shifts are also likely to control changes in the relative roughness and vigor of play (e.g., Auyeung et al. 2009). Gonadectomy of newborn male rats leads to a predominantly female pattern of playfulness with increasing age (Pellis 2002). Testosterone generally contributes to increased play behavior (especially R&T) in males, but female spotted hyenas who receive high androgen levels in utero may also adopt male-like play patterns by being rough and vigorous (see Pellis 2002). In cooperatively breeding meerkats, females also have social and reproductive dominance; the most successful females have greater numbers of offspring than the most successful males. Interestingly, while male and female pups win the same percentage of heterosexual play fights, in both juvenile and subadult bouts, females won significantly more (Clutton-Brock et al. 2006). This situation parallels that of hyenas in that dominant females are both more aggressive and have high levels of circulating testosterone (Drea et al. 1996; Panksepp 1998).

As young mammals approach puberty, changing hormones trigger interest in sexual behavior, and youngsters might incor-

porate elements from a sexual behavioral repertoire into play behavior. Certainly, for adolescent males on the brink of adulthood who are unable to attract estrus females, (pseudo)-sexual play with other juveniles might be the next best thing (the label "pseudo-sexual" is appropriate because juvenile mounting does not result in a viable pregnancy). Cross-sex play in human adolescents may be used as a gambit for heterosexual interaction (Pellegrini 2003). Sexual selection has been posited as a factor in the development and maintenance of sex differences in human play, where males who engage in risky play or who are otherwise proficient in sports and public entertainment may be considered more attractive (Chick 2001).

The two brain regions that are specific targets for developmental androgens are the amygdala and hypothalamus. Both become sexually differentiated during development, giving rise to sex differences (Meaney and McEwen 1986; Collaer and Hines 1995; Lewis and Barton 2006) in sexual behavior, aggression, and play behavior. Given its association with emotion, the amygdala has long been associated with the development and exhibition of social behavior and sex-differentiated behaviors, and play researchers are increasingly finding links between the amygdala and play (Pellis and Iwaniuk 2002; Lewis and Barton 2006; Vanderschuren 2010). The amygdala helps enable the recognition of socially generated emotion and the content of emotionally charged expressions—for example, the facial expressions and associated cries of distressed infants. Thus, the socio-emotive aspects of play may be governed by the amygdala and perhaps by other limbic structures as well (Lewis and Barton 2006). Indeed, rats with damaged caudate-putamen areas significantly reduce or cease play behavior (Panksepp 1998). Pellis et al. (2006) additionally note that orbital frontal cortex (OFC) damage disrupts rats' ability to follow species-specific rules of play-fighting, yet it does not affect their ability to play; thus, the OFC is likely involved with the experience of social regulation and competence. This further provides a rationale for looking at specific brain regions in attempting to understand play behavior (see also Pellis et al. 2010). Perhaps playing helps young animals cope with the transition from juvenility to adulthood—behaviorally, hormonally, physically, cognitively, and socially. In rats, R&T is an enriching behavior regardless of whether a dominant or submissive role is adopted (Burgdorf et al. 2006), and it is a key element in the normal development of young animals, particularly with regard to social competence and social cognition (Lewis 2000; Pellis and Pellis 2007).

OTHER NEURAL MECHANISMS UNDERLYING PLAY: SMILES, LAUGHTER, AND SINGING

Humans associate play with laughter, especially in social situations. It is likely that human laughter evolved from mammalian social play (Fagen 1981; Kipper and Todt 2001; Burgdorf et al. 2007). Tickling or wrestling is the easiest way to elicit laughter, and this behavior has been observed in primates (e.g., chimpanzees [Spijkermann et al. 1997] and Barbary macaques, *Macaca sylvanus* [Kipper and Todt 2002; Vettin and Todt 2005]), but rats too give a play chirrup when tickled gently (Panksepp and Burgdorf 2000, 2003). Many fissiped carnivorans vocalize during play, possibly to demonstrate motivation to engage in play (Bekoff 1974, 1975; Rasa 1984; Peters and Wozencraft 1989). In rats, 50-kHz chirrups increase in frequency during R&T and during other behaviors associated with positive reward (Knutson et al. 1998; Burgdorf et al. 2006, 2007). In other words, humans and other animals laugh or chuckle when they experience pleasure (Burgdorf et al. 2006, 2007; Vanderschuren 2010). The lateral hypothalamus is one key brain region believed to be involved with the experience of pleasure (Von Borrell 2000; Burgdorf et al. 2007). Lewis and Barton (2006) demonstrated that evolutionary increases in hypothalamus size may be correlated with increases in the frequency of social—but not non-social—play behavior and suggested that the hypothalamus influences the proximal motivational aspects of play. Physical contact, critically important in

primate emotional development, may be a crucial variable in social play in many animals and may be more emotionally charged than either auditory or visual stimulation. Regardless, any long-term benefits will accrue as the result of playing for fun in the short-term (Pellis et al. 2010; Vanderschuren 2010). This is an example of the value of integrating the various conceptions of play, as well as the various levels of analysis.

The neurological association between positive and negative emotional states is of further interest. Although specific types of vocalizations are associated with specific emotional states, the difference between laughing and crying, neurologically, is miniscule (Panksepp and Burgdorf 2003). In humans, shared laughter or, conversely, shared grief can have important social meaning, and vocalizations associated with these emotional states may be linked. For example, hearing howls or cries without seeing the social context may lead to misinterpreting an individual's emotional state. Some animals play in silence (e.g., black bears), while others have specific vocalizations (Rasa 1984; Vettin and Todt 2005; Burgdorf et al. 2006, 2007). A playing animal is less vigilant, so playing quietly may reduce the risk of predation. Conversely, chimpanzees are rather noisy players, and their vocalizations may have more in common with human laughter, as both are tonal and are produced by expiration as well as inspiration. Loud play vocalizations may indicate to non-players that other conspecifics are playing (Vettin and Todt 2005). Some suggest that the undirected songs of male birds and the juvenile crowing of other birds (e.g., turkeys, chickens) may qualify as play (see Burghardt 2005). Juvenile ravens (*Corvus corax*) emit a variety of sounds in "long monologues" atypical of the adult vocal repertoire, even though some of the sounds are later produced by adults (Heinrich and Smolker 1998). Could this be vocal play? Human babies are hardwired to learn language, and their early babbling may encourage linguistic patterns. Similarly, songbird chicks appear to be predisposed to learn specific songs (Johnson et al. 2002). Both babies and chicks require socialization to develop their vocal skills, thus further supporting the tenet that vocal play is important for development (Lipkind et al. 2002).

Studies of the pons and its nuclei may also assist our understanding of play behavior. Situated above the medulla, the pons is functionally and strongly connected, at least in humans, to states of arousal and visual gaze. It also relays information between the cerebellum and the neocortex. Lewis (2003) found that in primates, social play was positively and significantly correlated with the relative size of the pons, medulla oblongata, neocortex (Lewis 2000), and cerebellum (Lewis and Barton 2004). It is possible, however, that evolutionary elaborations in the size of neural regions of interest is a byproduct of scaling and allometry (Lewis and Smith 2008). The trigeminal motor nucleus within the pons is vital to vocal control, forming a network between the amygdala and the spinal cord to control the sound, facial position, and respiratory movements required to emit controlled vocalizations (Jurgens 2002) as well as startle responses (Pissiota et al. 2002). The medulla oblongata may also be highly active during vocalizations. In domestic cats, for example, mews can be elicited by stimulation of the pons and medulla (Peters and Wozencraft 1989); this may also be the case for squirrel monkey vocalizations (Luthe et al. 2000). Vocalizations during play may certainly serve as an audible signal distinguishing play from other behaviors. Play vocalizations are very different in context from vocalizations that indicate distress. That we may observe play vocalizations and even equivalents of laughter across a variety of species is indicative of play's origins and its evolutionary significance (Panksepp and Burgdorf 2000, 2003; Burgdorf et al. 2006, 2007).

DEVELOPMENT OF PLAY

Play is a predominantly juvenile behavior. In mammals, play often shows a double spike in frequency: the first soon after play begins in infancy, and the second around weaning (Lewis 2005). Specific developmental timing of peaks and troughs in play

frequency may have evolved to ensure that the body and brain are honed through the exhibition of appropriate behaviors at sensitive developmental periods (Byers and Walker 1995; Lewis and Barton 2004).

A hypothesis derived from Groos (1898) is that play is more important to species with longer developmental periods (Pellis and Iwaniuk 2000b; Diamond and Bond 2003). All animals fall along a continuum of developmental maturity at birth or hatching from altricial (blind, helpless) to precocial (able to locomote, feed, and so on). Interestingly, in endotherms, altricial young often mature more quickly than precocial young (Promislow and Harvey 1990). Relatively precocial species, with protracted juvenile periods and slow life histories, are typically expected to be more playful (Lewis 2003). However, absolute statements about precociality and play require caution, as the more altricial species may play more within a given lineage (Fagen 1981; Burghardt 1984). For example, carnivorans are typically altricial and yet they are very playful, perhaps due to the highly social nature and relatively large brains of many species (Parker and McKinney 1999; Lewis 2003). Conversely, guinea pigs (*Cavia porcellus*) are extremely precocial at birth, but far less playful than more altricial rodents such as rats. What seems to be especially crucial is the length of the developmental period, and the amount and timing of parental care (Parker and McKinney 1999; Lewis 2003; Burghardt 2005). Thus, large-brained, social species with high metabolic rates and a long developmental period under parental care tend to play more frequently and with greater complexity. Reinhart et al. (2004) found that one strain of kindling-prone rat (FAST) that was more juvenilized (i.e., bred to retain juvenile traits) also played at higher frequencies at all ages than another less-juvenilized (SLOW) strain. Both strains had an adult-typical pattern of play, so it is likely that increased juvenility affects the frequency, but not the content, of play. A complication is that all life-history data need to be equated for both chronological time and developmental time. A short-lived species that

breeds three times in one year must have its developmental period calibrated against a species that may only reproduce once every two years.

GROWING UP AND PLAYING FAIR

The belief that play is significant in the development of young animals has a long history (Groos 1898; Piaget 1962; Vygotsky 1967; Fagen 1981), but ideas have outpaced data and hypothesis testing. Play may represent crucial experience in formulating novel behavior patterns that enable an animal to better adapt to its environment (Fagen 1981; Sutton-Smith 1997; Špinka et al. 2001; Burghardt 2005). Pellegrini et al. (2007) further suggest that in learning and practicing new behaviors within the safe confines of play, animals might influence their own adult phenotypes, in terms of increased cooperation, strength, and dominance status, and consequently, through selection, their genotypes (see also Burghardt 2005:175-177). In this way, Pellegrini et al. (2007) have reversed Haeckel's old adage, positing that through play, ontogeny may influence phylogeny.

Bateson (1981, 2005) revealed the enormous plasticity of cat play, which is dependent on both genetic and environmental factors, such as sex, parental age and disposition, and exposure to light. Play follows a general trajectory of high frequency during late infancy and early juvenility, which usually declines as the individual approaches adolescence and adulthood (although different play categories may fluctuate species-specifically) (Bateson 1981; Caro 1995; Spear 2000; Lewis 2005). Social play, involving both strong motor patterns and cognitive complexity, may reflect a variety of brain-behavior ontogenetic and evolutionary processes. Monkeys reared alone when very young play at far lower rates than those raised with peers (Harlow and Suomi 1970). The development of social skills is an important feature of early life for many mammals, and early mother-infant interactions likely help foster the development of behaviors that support social bonding, forming alliances, finding

mates, and securing other resources vital to the success of adult life. Additionally, mother-infant bonds seem to assist the development of emotional stability (Bastian et al. 2003; Kempes et al. 2008). Play likely contributes to the formation of socially appropriate behavioral responses upon which animals increasingly rely with age. Indeed, young monkeys that display elevated levels of aggression are at an increased risk of social ostracism (Bastian et al. 2003); therefore, learning how to read social situations appropriately is a key factor to social success (Pellis and Pellis 2009). However, Symons (1978) showed that because aggressive signals rarely occur in social play, young rhesus macaques (*Macaca mulatta*) do not use social play to learn appropriate responses to signals of aggression and submission.

Play may be important for the development of social flexibility. Young animals chase and lunge at one another in play, switching roles flexibly and self-handicapping (Pellegrini 1992). Playing animals seem to be aware of fairness and cooperation, and may even punish cheaters by avoiding playing with that partner in the future. Arguably, a 50:50 rule may exist, whereby a player in any dyad wins or loses in equal measure (Altman 1962), although play may be sustained without such reciprocity (Bauer and Smuts 2007). Pellis et al. (2006) note that if play-fighting is to remain within the realm of play, then players must overcome an urge to dominate one another fully, and conform to the species-specific rules of play-fighting (see Bekoff and Pearce 2009). It is likely that these rules become appropriately modified with increasing age. That animals play cooperatively may represent a suite of cooperative behaviors relevant to the evolution of sociality (Sussman et al. 2005) and behavioral codes of conduct (morality) (Bekoff 2001). Especially in animals with a high reliance on social rules, such as canids and primates, play may represent a developmentally safe time frame during which to learn the social rules associated with group living. The young can test the limits of others' tolerance in a relatively

risk-free environment—one that is not afforded to them as they pass out of juvenility and into adulthood. However, societies bound by strict hierarchy or stringent social rules may inhibit rather than encourage play (Iwaniuk and Pellis 2001; Palagi 2006). In either case, the observation that playful interactions are regulated by rule-like conventions in both humans and animals suggests that play may be important to the study of the evolution of morality (Bekoff 2001; Paglieri 2005). Play may help develop skills of response-appropriateness as well as the ability to treat play partners flexibly, and it may be indicative of varying levels of social complexity. Indeed, as social group living evolved and gave rise to brains of increasing complexity, it is probable that social and other play behaviors took on increasing importance in the development and socialization of young animals. For instance, the frequent claims that organized sports in childhood inculcate social values of rule following, cooperation, and fairness has a long history in discussions of human play (Burghardt 2005, 2010a).

Bastian et al. (2003) demonstrated how the rearing environment may be extremely important to acquiring later dominance status. Mother-raised monkeys are more likely to achieve higher status at all ages of life relative to monkeys raised in age-peer social groups, and peer-reared monkeys are more likely to require removal from a social group due to excessive aggression. Dominance may determine certain trends in play. Young avian Arabian babblers are fairly playful, but after the age of six months, lower-ranking babblers play more than higher-ranking ones. In play-wrestling, dominant young babblers engage in more pinning behavior than subordinate babblers, and lower-ranking individuals are more likely to attempt to leave the play bout (Pozis-Francois et al. 2004). Dominance rank may determine different trajectories of rules for players also, with subordinate males following different rules from dominant males in rat play-fighting (Pellis et al. 2006). Rear-

ing conditions alone are unlikely to be the sole factor responsible for later rank, but early social experiences evidently contribute towards the physical, cognitive, and emotional development of young animals.

Conclusions and Future Directions

Over a century of play research has brought us to a new understanding of animal play. Once considered to be useless, frivolous, or only for the direct practice of adult behavior patterns, today we recognize that play is a heterogeneous category of behavior with diverse causal mechanisms, evolutionary histories, developmental trajectories, and experiential components. These, in turn, are embedded in complex sequences and potential functions with adaptive consequences, the current form of which may differ from the original manifestations. Play, in spite of its phenotypic diversity, may be critical to our understanding of the facilitation, generation, and expression of cognitive and emotional aspects of social interactions and behaviors (Pellis and Pellis 2009). With advances in our knowledge of the neurobiology, development, and adaptive functions of play, along with advances in determining evolutionary relationships, we may be on the brink of a new phase in play research and a new appreciation of this enigmatic behavior. Advances in child developmental psychology, including dynamic systems theory, may prove useful in studying other species.

Play is also no longer considered exclusive to endotherms. Convincing data for play in many non-mammalian and non-avian orders are starting to emerge. For this reason, we advocate more empirical research on play in those species at which we might not have previously looked, such as in non-mammalian taxa. In particular, we suggest testing for play in species that show traits associated with playful behavior, such as parental care, metabolic flexibility, longevity, sociality, and neural complexity. It is likely that play is more prominent in species with more generalized feeding ecologies and complex behavioral repertoires; however, specific categories of play, such as object play, may be prevalent in species with specific dietary adaptations (e.g., carnivory). It is likely that play evolved repeatedly across taxa, and thus the form, function, and development of play probably has different causes and trajectories in different taxonomic orders. For this reason, we encourage researchers to be bold in testing for play in non-mammalian subjects, and to treat the study of play as a serious biological topic. Indeed, we feel that biologists, in particular, should become involved in play research across a broad and diverse range of species. In fact, play behavior may be reflected in mental rehearsal and may be tied in with mirror neurons and social imitation and learning in ways that we cannot yet fathom, but which may have played a critical role in evolution at many levels.

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Handling Editor: John J. Wiens