

Modeling play: distinguishing between origins and current functions

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Abstract

Why animals play has been a perennial question, but most of the thinking about this has been framed in terms of its fitness benefits. A review of our present knowledge about the comparative distribution of play suggests that such an approach that leads to claims that the “adaptive value of play is” are misplaced. Play is relatively rare in the Animal Kingdom, indicating that it arose multiple times and that different lineages that have evolved play have transformed it in both divergent and convergent ways. Moreover, some forms of play, especially in its earliest appearance, may have no functional value, with novel functions emerging later as play has been co-opted and transformed for utilitarian purposes. Thus, when it comes to modeling play, care must be taken to differentiate between attempts to explain the origins of play from its current functions, and when current functions are considered, then their variety and likely diverse distribution need be taken into account. Attention to these nuances in the empirical literature, and so developing more targeted models, will provide more focused theoretical developments that can, in turn, stimulate more precise empirical tests. Examples of such models are presented in this issue of the journal.

Keywords

Play behavior, development, evolution, mathematical models, origins, functions

The purpose of models is not to fit data but to sharpen questions.

(Samuel Karlin, at the 11th RA Fisher Memorial Lecture, April 20, 1983)

1 Introduction

The most common question that comes to mind when one thinks or talks about play is “Why do animals play?” The question was framed in this way from the first treatise published on the subject (Groos, 1898), and posed even earlier by writers such as Herbert Spencer (Burghardt, 2005). Implicit in this question are several assumptions that, more than a century after Groos’ seminal book, are known either not to be true or, at the least, untenable in the simplistic way they are usually expressed. First, although Groos framed this question concerning animals such as humans, dogs, cats and monkeys, species that undoubtedly play, we now know that the vast majority of animals do not play (Burghardt, 2005). Therefore, in some ways, asking the question as to “why do so few animals play?” may be more pertinent than asking “why do animals play?” Second, the “why” in the question of “why do animals

play?” is usually considered in terms of the adaptive benefits accrued to the players. This represents only one of the possible “why” questions that can be asked about a trait (Bolhuis & Verhulst, 2009; Burghardt, 2005). Moreover, if we assume that play improves fitness or some component of fitness, why do so few animals play? Third, Groos, and most modern writers, see play as a property of childhood, with the benefits accrued by playing at this period in life having an impact on the survival and reproductive success later in life (Fagen, 1981). This ignores the fact that in many

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species play persists into adulthood (Cohen, 2006; Cordoni, 2009; Palagi, 2006; Pellis & Iwaniuk, 1999, 2000), where, if benefits are present, are likely to be immediate (Palagi, 2011; Pellis, 2002).

Although the current view of play is now more nuanced than when Groos wrote, many empirical researchers and modelers still think like Groos when approaching the question of why animals play. In a series of workshops on the evolution of play held between 2011 and 2013, sponsored by the National Institute of Mathematical and Biological Synthesis (NIMBioS), it became clear that colleagues whose key interest is in using various mathematical approaches to answer this question continue to tackle the problem in a Groosian manner. After 3 years of debate, argument and exploration, it became evident to all that treating the “why” solely in terms of the function of play, treating animals that play as if they all played alike and posing the problem in terms of why young animals play, are simplifications that can no longer be justified by our current knowledge about the diversity of play in the Animal Kingdom.

We now know enough about the distribution of play to divide the question into more manageable sub-questions that more closely represent the diversity in nature that we need to explain. In this paper, we frame those sub-questions within the context of the deeper, comparative understanding we now have about play and provide some of the evidence that has led to that understanding. In turn, once so framed, the subsequent papers in this special issue will explore mathematical models and computer simulations models that tackle these more manageable questions. Even though simplifications are necessary for mathematical modeling, the iterative interactions between empirical researchers and modelers afforded by the NIMBioS workshops has meant that the simplifications are more realistic, yielding models that have higher fidelity to nature than would be otherwise and, in turn, the models generated point to more precise predictions that can direct the attention of researchers to new and specific empirical tests of what real animals actually do.

While definitions of play are many and varied (Fagen, 1981), Burghardt (2005) provides a definition in which the behavior under question has to pass five criteria to qualify as play. These are: (1) that the behavior is incompletely functional in the context expressed, (2) that it is voluntary or rewarding, (3) that it is, in some ways, modified developmentally or structurally compared with when it is used in its normal, functional context, (4) that it is performed repeatedly, but not necessarily in an invariant form, and (5) that it is initiated in healthy, relatively unstressed animals in a relaxed context. In applying these criteria, researchers have shown that not only does some behavior in mammals and birds such as dogs, monkeys, crows and parrots qualify as play (Burghardt, 2005), but that some

behavior in animals as diverse as turtles, crocodiles, fish, wasps, spiders and octopus also does so (e.g., Burghardt, Dinets & Murphy, 2015; Dapporto, Turillazzi & Palagi, 2006; Dinets, 2015; Kramer & Burghardt, 1998; Kuba, Byrne, Meisel & Mather, 2006; Pruitt, Burghardt & Reichert, 2012). While perhaps not foolproof, when all five criteria are fulfilled, we are alerted to the possibility that these myriad species are exhibiting comparable behavior that has emerged independently. In other words, play has emerged repeatedly in evolution, in both ancient and modern lineages.

2 Distinguishing origins from current functions

Nevertheless, only five of the 30 or so different phyla of animals contain species that play (Burghardt, 2005). Indeed, when we think of play, we think of mammals, such as kittens, young monkeys and children, but mammals are just one Class within one Phylum, and even within that Class, not all species play, nor do they all play in the same way. There are three major categories of play (Burghardt, 1998, 2005): play with a conspecific (social play), play with an inanimate object (object play) and play with one's own body movements in the absence of either social partners or objects (locomotor-rotational play) (Burghardt, 1998). There are complications with this simple schema, since these three types of play can be combined in various ways, such as object-social play (Shimada, 2012). Furthermore, in humans there may be forms of play that do not have any obvious analogies in non-human animals (Power, 2000). For example, children can engage in pretend play, in which they act out novel identities (Smith, 2010). However, these complications need not obscure the fundamental patterns. Some species engage in one of these three types of play to the exclusion of the others. For example, whereas hyrax engage only in social play, elephant shrews engage only in locomotor play and tree shrews engage in social and locomotor play, but not object play (Burghardt, 2005). This kind of distribution suggests that these are independent forms of play, with the mixing of these different types occurring only in species in which multiple types co-exist. Although humans may engage in some forms of play not seen in other animals, they definitely do engage in the forms that are present in other animals (Pellegrini, 2009), especially early in life; for comparative purposes, we can focus on the forms of play, such as rough-and-tumble play or play fighting, which is a form of play that can be simply envisioned as two animals wrestling one another, that humans share in common with other species.

The problem of species differences becomes more apparent when a single form of play is compared within a restricted taxonomic group. Play fighting in rodents provides an example (Pellis & Pellis, 1998a). Such play

usually involves one partner seeking some advantage over another, such as biting or otherwise contacting a particular body target (Aldis, 1975; Biben, 1998; Pellis, 1988). Unlike serious fighting, however, in which restraint in the fighting arises from the risk of injury due to possible retaliation by one's opponent (Blanchard & Blanchard, 1994; Geist, 1978; Pellis, 1997), in play fighting, partners often restrain themselves from taking advantage even when the opportunity arises, leading to frequent role reversals (Bekoff, 2004; Fagen, 1981). There is still much debate about how necessary such restraint is and how it is created during play fighting (Bauer & Smuts, 2007; Pellis & Pellis, 1998b; Thompson, 1998), but in part, much of this debate may be resolved by the finding that different lineages of animals may have evolved different mechanisms by which to solve the restraint problem (Pellis, Pellis & Reinhart, 2010b). Whatever the mechanisms involved may be, it is certain that while the risk of escalation from play to serious aggression is always present, such escalation is relatively rare (Aldis, 1975; Biben, 1998; Fagen, 1981; Pellis & Pellis, 1998b). Among an assortment of rodents studied, play fighting can be present or absent, and, when present, can be relatively simple or complex—with simple play fighting involving approach and withdrawal with little contact and complex play fighting involving protracted bouts of wrestling. Moreover, there are species that are intermediate between these extremes (Pellis & Pellis, 2009). Similarly, Palagi and Cordoni (2012) found that play fighting in bonobos escalated less frequently into overt aggression compared with juvenile chimpanzees, thus seeming better able to maintain a cooperative mood. Thus, even within a closely related lineage, social interactions that meet the criteria of being play, in this case play fighting that can occur with little likelihood of escalation to aggression, can vary markedly. Comparable points can be made about object play and locomotor play. The markers that distinguish play of any type from exploration can be debated, but exploration is universal, found even in amoeba and bacteria, whereas play is not (Pellis & Burghardt, in press).

The comparative data clearly show that play has emerged multiple times in the Animal Kingdom, but given the relative rarity of having done so, it suggests that the conditions fostering the development of play rarely occur (Burghardt, 2005). Two key conditions are: (1) excess resources in a slowly developing organism with a complex behavioral repertoire, and (2) some measure of protection from predation either because of parental vigilance or some fortuitous environmental context. Under these circumstances, play may arise as a feature of the organism's development (Burghardt, 1984, 1988). Such play would likely be rudimentary or *primary process play* (Figure 1)—play that only barely meets the criteria that would lead us to label it as play.

At this rudimentary stage of evolution, however, *primary process play* need not have any functions. That is, the play that emerges is a byproduct of a confluence of fortuitous conditions, and, as such, at this stage, there is no need to conceptualize real or imagined benefits for natural selection to facilitate the spread of this behavior across the population. Once present, however, play-like behavior may be further transformed, as it is co-opted to novel functions. For example, play may maintain and enhance physical ability and hone neural processing important for fluent movement (Byers & Walker, 1995), thus increasing fitness. But at this stage, while new functions emerge, little change in the play need occur and play may be only one of several means to provide such functions, though in a "safe" context. Such play constitutes Burghardt's *secondary process play* (Figure 1). Once a functional connection is established between play and the honing of neural processes, further transformations become possible. By modifying the content of the play to exaggerate those experiences that are most effective in facilitating neural refinement, the effect of play on fitness becomes stronger and the effects lead to a greater level of enhanced performance by those modified neural circuits (Pellis, Pellis & Bell, 2010a). This modified version of the play is conceptualized, in Burghardt's schema, as *tertiary level play* (Figure 1). Further co-option and transformation can yield play that has clear immediate functions in adults, not just the delayed benefits seen in juveniles (Palagi, 2011; Pellis & Pellis, 2009).

Bearing in mind this schema of levels of transformation, we would expect that the play we see in nature to be varied in prevalence, complexity and functions. As noted above, detailed comparison of play fighting across a range of rodent species supports this view (Pellis, Pellis, & Himmler, 2014). Play in the juvenile period of some rodents appears to have no impact on later adult behavior (Pellis, 1993). However, in some species, it does have an impact. Indeed, in some species, play as juveniles has an impact not only on later behavioral performance but also in a variety of higher-order cognitive skills. Furthermore, some species retain play fighting in adulthood and use it as a means of testing and managing social relationships. These latter functions in juveniles and adults are not present in all rodents that have complex play, but only some (for a review of the primary literature, see Pellis & Pellis, 2006, 2009). That is, the distribution of the structure and function of play fighting in rodents can be mapped onto the schema representing play as undergoing a series of transformations involving primary, secondary and tertiary processes as in Figure 1 (Pellis et al., 2014).

3 The functions of play

From the early formulation of the study of play by Groos (1898), the problem has persistently been seen in

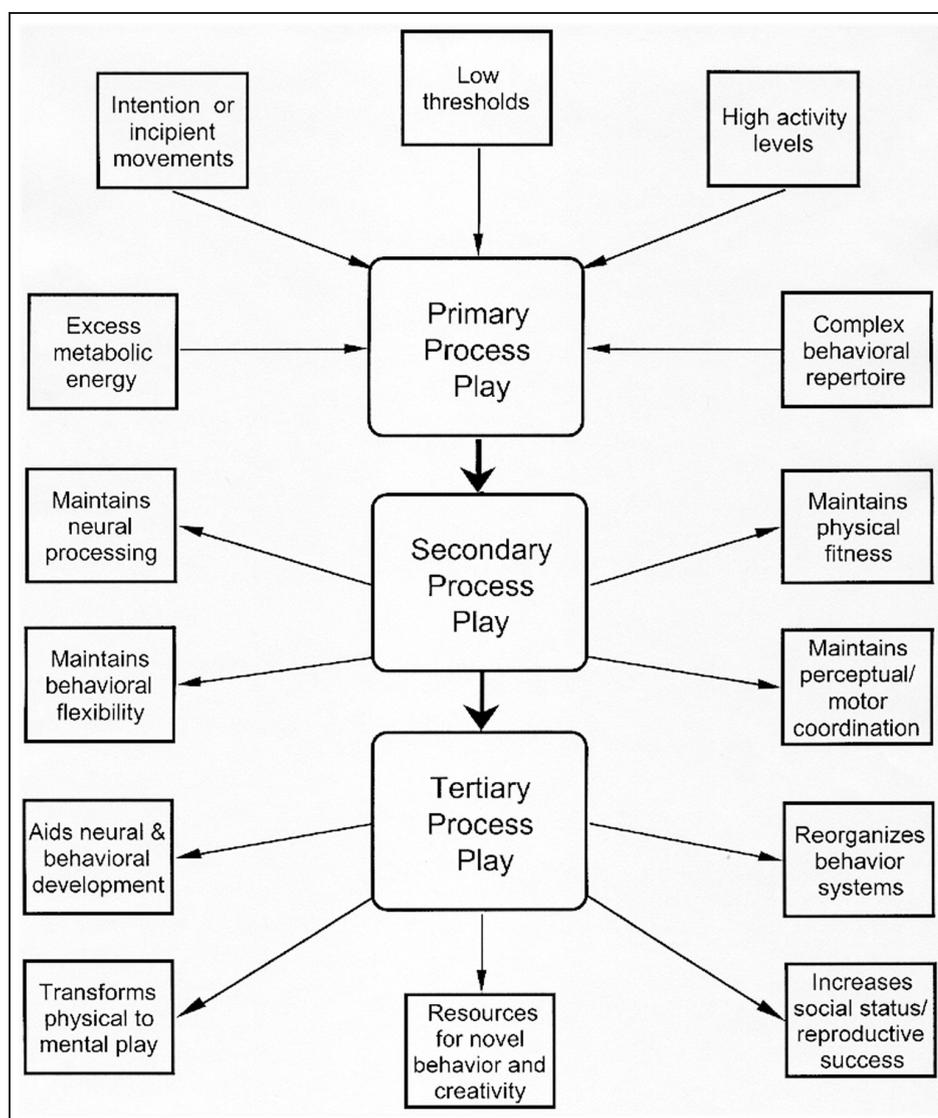


Figure 1. The diagram illustrates the sequential transformations that play can undergo over evolutionary time and the kinds of enabling factors that make such transformations possible. The first level represents the emergence or origin of play-like behavior and the subsequent levels represent the kinds of transformations possible once play is present. Reproduced with kind permission from MIT Press (Burghardt, 2005).

terms of the future benefits of playing in the juvenile period—the problem of delayed pay-off. A study on marmots provides convincing evidence in a free-living species for such a delayed pay-off—play in the juvenile period had an impact on dominance formation in adulthood (Blumstein et al., 2013). That is, the functional benefit of play is gained not when the play occurs, but at a later age. In contrast, another study on brown bears, showed that bear cubs that play more are more likely to survive their first year (Fagen & Fagen, 2004, 2009); thus by play making a more resilient juvenile, the pay-off is immediate. That is, the functional benefit of play is accrued at the same age as when the play is performed. The case for immediate benefits is even greater when play occurs in adults.

Play continues into adulthood in a variety of species of mammals, with the play most likely being retained in adulthood being social play, especially play fighting (Fagen, 1981). Cases in which adults seek out other adults with whom to play, rather than merely reacting to the playful solicitation of youngsters, are particularly interesting. Such adult-adult play occurs in around 50% of species of primates and is correlated with negotiating unpredictable social relationships (Pellis & Iwaniuk, 1999, 2000). Using play to assess and manipulate social relationships appears to be a major immediate function of play across a wide range of species, both in primates and non-primate mammals (Pellis, 2002). The precise ways of doing so vary across species. For example, in some species, subordinates use play

either to reaffirm their subordinate status or to test the possibility of gaining status (Pellis, Pellis, & McKenna, 1993; Smith, Fantella, & Pellis, 1999). In other species, play can be used by the dominant to reaffirm its own status (Jones, 1983). To reaffirm submission, the subordinate plays gently; to reaffirm dominance, the dominant plays roughly (Pellis, 2002). In some species, play provides a way for strangers to interact with a reduced risk of aggression (Antonacci, Norscia, & Palagi, 2010). Furthermore, in several species, play is used to regulate stress in anticipation of a stress-inducing context (Palagi, 2006) or to lower stress levels after a stress-inducing event has occurred (Darwish, Korányi, Nyakas, & Ferenz, 2001; Norscia & Palagi, 2011; van den Berg et al., 1999). Given the role of a relaxed field in defining play (Burghardt, 2005), it is important to note, that strong stressors, such as detecting a cue that a predator is nearby, suppress play (Siviy, Harrison, & McGregor, 1996). Indeed, having high physiological markers of stress, such as elevated cortisol levels, does not predict that an animal will play (Taylor, Mustoe, Hochfelder, & French, 2015). However, playing has been shown to reduce circulating levels of stress hormones (e.g., Darwish et al., 2001; Taylor et al., 2015), suggesting that for moderate levels of stress, play can be a useful avenue by which to attenuate stress.

While the ability of play to reduce stress following play is found in both adults and juveniles of several species (e.g., Darwish et al., 2001; Palagi, 2006; Mustoe, Taylor, Birnie, Huffman, & French, 2014), other immediate functions of play, such as navigating dominance relationships, are likely only to be the province of post-pubertal animals (for a review, see Pellis & Pellis, 2009). Given that the adult use of play as a tool for social assessment and manipulation waxes and wanes across the primate tree (Pellis & Iwaniuk, 2000), it is likely that the more sophisticated, socially manipulative functions represent tertiary process play, with the stress-regulation functions having appeared earlier, beginning with its role in the juvenile period. Higher-level transformations of the functional uses of play are also seen with regards to delayed functions.

The cognitive consequences of play deprivation in the juvenile period are seen in the rat, but not in other, commonly used laboratory rodents (Einon, Morgan, & Kibbler, 1978; Einon, Humphreys, Chivers, Field, & Naylor, 1981), including species that have patterns of play fighting that are nearly as complex as that of rats, such as Syrian hamsters (Pellis & Iwaniuk, 2004; Pellis & Pellis, 1998a). Play experience in rats during the juvenile period influences the development of the neurons of the medial prefrontal cortex (Bell, Pellis, & Kolb, 2010; Himmler, Pellis, & Kolb, 2013), and this is likely part of the play-induced changes that improve the executive functions of the brain that are regulated by the prefrontal cortex (Baarendse, Counotte, O'Donnell, &

Vanderschuren, 2013; Pellis et al., 2014; van den Berg et al., 1999). Thus, while secondary process play, common to both rats and mice, facilitates the development of the subcortical neural mechanisms that influence motor performance (Byers & Walker, 1995), in rats, play has undergone further modification, tertiary process play, the experience of which is able to affect some of the higher-order cognitive and emotional functions of the cortex (Pellis et al., 2010a).

4 Summary of the empirical findings

Species of primates that have to navigate more complex social systems, such as chimpanzees, spider monkeys and some species of macaques, in which social interactions require more nuanced responses, are also the ones that are more likely to use play in adulthood (Ciani, Dall'Olio, Stanyon & Palagi, 2012; Palagi, 2006; Pellis & Iwaniuk, 2000), and are, in the juvenile period, the species that have modified the content of play fights to exaggerate the experience of unpredictability and prolonged social contact (Palagi & Cordoni, 2012; Reinhart et al., 2010). That is, the play is transformed as it is in rats in a way that maximizes the experiences that promote the training of executive functions of the brain (Pellis et al., 2010a, 2014).

This similarity between some primates and some rodents highlights another important aspect of the evolutionary transformations in play. For many primates, play fighting is derived from simulating serious aggression—the same targets and tactics are involved (e.g., Aldis, 1975; Owens, 1975; Reinhart et al., 2010; Schaller, 1963; Symons, 1978). In contrast, play fighting in rats and their close relatives, is derived from simulating pre-copulatory behavior (Pellis, 1993). Yet rats and some primates have converged on modifying their play into a form that is suited to training the executive functions of the brain (Pellis & Pellis, 2009). Thus, looking at play through the lens of the hierarchical transformation model (Figure 1) not only indicates that the origins of play may involve different processes than those that have promoted its current functions, but also, that multiple layers of functions, with both divergences within lineages and convergences among lineages, are possible. Mathematical and computer models need to be sensitive to these various types of transformations if they are to point empirical research in novel directions.

5 Modeling play

Mathematical models can provide insights into the organization and functions of play. For example, the suggestion that for play fighting to remain playful, participants have to have an equal opportunity to win (i.e., the 50:50 rule; Altmann, 1962), has been supported by

a game theory model that showed that as the win–loss ratio deviates further from 50:50, the less likely that play is sustained (Dugatkin & Bekoff, 2003). Indeed, extreme deviation from 50:50 has been shown to lead to the breakdown of play fighting in real animals (e.g., Suomi, 2005; Wilmer, 1991). Yet, under some conditions play can be maintained even when winning is far from parity (e.g., Bauer & Smuts, 2007; Pellis, 2002). Clearly, while the Dugatkin and Bekoff (2003) model touches on a key feature of play fighting, it is incomplete. Nonetheless, this example illustrates the useful iterative interaction between mathematical models and empirical research. Similarly, formal mathematical models of the functions of play have attempted to formulate the cost-benefit ratios that can account for factors such as the age distribution of the frequency of play (e.g., Fagen, 1977, 1981). Such models have helped shape some empirical research (e.g., Byers & Walker, 1995; Palagi & Cordoni, 2012). However, the comparative variation in the occurrence and form of play suggests that models that posit blanket fitness benefits for all cases of play are unlikely to be widely applicable. Models that can help us distinguish between the conditions that give rise to play from the conditions that promote the co-option of playful behavior for fitness enhancing functions need to be formulated. Moreover, models can also allow us to consider the various kinds of functions that play can be co-opted to have. From the empirical data reviewed above, two conclusions are evident for modelers to consider.

First, detailed analyses of specific functions have, in most cases, failed to support many of the presumed functions of play (e.g., Sharpe, 2005a, b, c; Sharpe & Cherry, 2003). Such negative data have led to a pessimistic view about whether play has functions, and, if it does, how big an effect on fitness such functions may have (Martin & Caro, 1985). But support for some functions have clearly emerged (e.g., Blumstein et al., 2013; Fagen & Fagen, 2004, 2009; Nunes, 2014; Palagi, 2006; Pellis et al., 2010a). The levels of transformation model (Figure 1) suggest different species that play are likely to be located on different parts of the transformational hierarchy, so that even if a particular function is served by play, it is unlikely to be served in that manner in all species that play. This makes finding the right species to test a specific hypothesis challenging. Thus, the hit and miss in supporting particular hypotheses may be mainly due to the diverse species used in such testing. Second, the transformational model not only allows that the functions of play are likely multiple, but also cautions against assuming that they will all be of the form in which juveniles play to enhance some future fitness state. That is, play may also have some immediate functions.

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References

- Aldis, O. (1975). *Play fighting*. New York: Academic Press.
- Altmann, S. A. (1962). Social behavior of anthropoid primates: Analysis of recent concepts. In E. L. Bliss (Ed.) *Roots of behavior* (pp. 277–285). New York: Harper.
- Antonacci, D., Norscia, I., & Palagi, E. (2010). Stranger to familiar: Wild strepsirhines manage xenophobia by playing. *PLoS ONE* 5, <http://dx.doi.org/10.1371/journal.pone.0013218.e13218>
- Baarendse, P. J. J., Counotte, D. S., O'Donnell, P., & Vanderschuren, L. J. M. J. (2013). Early social experience is critical for the development of cognitive control and dopamine modulation of prefrontal cortex function. *Neuropsychopharmacology*, 38, 1485–1494.
- Bauer, E. B., & Smuts, B. B. (2007). Cooperation and competition during dyadic play in domestic dogs, *Canis familiaris*. *Animal Behaviour*, 73, 489–499.
- Bell, H. C., Pellis, S. M., & Kolb, B. (2010). Juvenile peer play experience and development of the orbitofrontal and medial prefrontal cortices. *Behavioural Brain Research*, 207, 7–13.
- Bekoff, M. (2004). Wild justice, cooperation, and fair play: Minding manners, being nice, and feeling good. In R. W. Sussman, & A. R. Chapman (Eds.), *The origins and nature of sociality* (pp. 53–80). New York: Aldine de Gruyter.
- Biben, M. (1998). Squirrel monkey play fighting: Making the case for a cognitive training function for play. In M. Bekoff, & J. A. Byers (Eds.), *Animal play: Evolutionary, comparative, and ecological perspectives* (pp. 161–182). Cambridge, UK: Cambridge University Press.
- Blanchard, R. J., & Blanchard, D. C. (1994). Environmental targets and sensorimotor systems in aggression and defense. In S. J. Cooper, & C. A. Hendrie (Eds.), *Ethology and psychopharmacology* (pp. 133–157). New York: John Wiley & Sons.
- Blumstein, D. T., Chung, L. K., & Smith, J. E. (2013). Early play may predict later dominance relationships in yellow-bellied marmots (*Marmota flaviventris*). *Proceedings of the Royal Society, B. Biological Sciences*, 280, article number: 20130485 (DOI: 10.1098/rspb.2013.0485)
- Bolhuis, J. J., & Verhulst, S. (2009). *Tinbergen's legacy*. New York: Cambridge University Press.
- Burghardt, G. M. (1984). On the origins of play. In P. K. Smith (Ed.), *Play in animals and man* (pp. 5–41). Oxford, UK: Blackwell.

- Burghardt, G. M. (1988). Precocity, play, and the ectotherm–endotherm transition: Profound reorganization or superficial adaptation? In E. M. Blass (Ed.), *Handbook of neurobiology*, Vol. 9, *Developmental psychobiology and behavioral ecology* (pp. 107–148). New York: Plenum Press.
- Burghardt, G. M. (1998). Play. In G. Greenberg, & M. Haraway (Eds.), *Comparative psychology: A handbook* (pp. 757–767). New York: Garland.
- Burghardt, G. M. (2005). *The genesis of animal play. Testing the limits*. Cambridge, MA: MIT Press.
- Burghardt, G. M., Dinets, V., & Murphy, J. B. (2015). Highly repetitive object play in a cichlid fish (*Tropheus duboisi*). *Ethology*, *121*, 38–44.
- Byers, J. A., & Walker, C. (1995). Refining the motor training hypothesis for the evolution of play. *American Naturalist*, *146*, 25–40.
- Ciani, F., Dall’Olio, S., Stanyon, R., & Palagi, E. (2012). Social tolerance and adult play in macaque societies: A comparison with human cultures. *Animal Behaviour*, *84*, 1313–1322.
- Cohen, D. (2006). *The development of play*. 3rd ed. New York: Routledge.
- Cordoni, G. (2009). Social play in captive wolves (*Canis lupus*): Not only an immature affair. *Behaviour*, *146*, 1363–1385.
- Dapporto, L., Turillazzi, S., & Palagi, E. (2006). Dominance interactions in young adult paper wasp (*Polistes dominulus*) foundresses: A playlike behavior? *Journal of Comparative Psychology*, *120*, 394–400.
- Darwish, M., Korányi, L., Nyakas, C., & Ferenz, A. (2001). Induced social interaction reduces corticosterone stress response to anxiety in adult and aging rats. *Klinikai és Kísérletes Laboratóriumi Medicina*, *28*, 108–111.
- Dinets, V. (2015). Play behavior in crocodylians. *Animal Behaviour and Cognition*, *2*, 49–55.
- Dugatkin, L. A., & Bekoff, M. (2003). Play and the evolution of fairness: A game theory model. *Behavioural Processes*, *60*, 209–214.
- Einon, D., Morgan, M. J., & Kibbler, C. C. (1978). Brief periods of socialization and later behavior in the rat. *Developmental Psychobiology*, *11*, 213–225.
- Einon, D., Humphreys, A. P., Chivers, S. M., Field, S., & Naylor, V. (1981). Isolation has permanent effects upon the behavior of the rat, but not the mouse, gerbil, or guinea pig. *Developmental Psychobiology*, *14*, 343–355.
- Fagen, R. A. (1977). Selection for optimal age-dependent schedules of play behavior. *American Naturalist*, *111*, 395–414.
- Fagen, R. A. (1981). *Animal play behavior*. New York: Oxford University Press.
- Fagen, R., & Fagen, J. (2004). Juvenile survival and benefits of play behaviour in brown bears, *Ursus arctos*. *Evolutionary Ecology Research*, *6*, 89–102.
- Fagen, R., & Fagen, J. (2009). Play behaviour and multi-year juvenile survival in free-ranging brown bears, *Ursus arctos*. *Evolutionary Ecology Research*, *11*, 1053–1067.
- Geist, V. (1978). On weapons, combat and ecology. In L. Krames, P. Pliner, & T. Alloway (Eds.), *Advances in the study of communication and affect*, Vol. 4, *Aggression, dominance and individual spacing* (pp. 1–30). New York: Plenum Press.
- Groos, K. (1898). *The play of animals*. New York: Appleton.
- Himmler, B. T., Pellis, S. M., & Kolb, B. (2013). Juvenile play experience primes neurons in the medial prefrontal cortex to be more responsive to later experiences. *Neuroscience Letters*, *556*, 42–45.
- Jones, C. B. (1983). Social organization of captive black howler monkeys (*Alouatta caraya*): Social competition and the use of non-damaging behavior. *Primates*, *24*, 25–39.
- Kramer, M., & Burghardt, G. M. (1998). Precocious courtship and play in emydid turtles. *Ethology*, *104*, 38–56.
- Kuba, M. J., Byrne, R. A., Meisel, D. V., & Mather, J. A. (2006). When do octopuses play? Effects of repeated testing, object type, age, and food deprivation on object play in *Octopus vulgaris*. *Journal of Comparative Psychology*, *120*, 184–190.
- Martin, P., & Caro, T. (1985). On the function of play and its role in behavioral development. *Advances in the Study of Animal Behavior*, *15*, 59–103.
- Mustoe, A. C., Taylor, J. H., Birnie, A. K., Huffman, M. C., & French, J. A. (2014). Gestational cortisol and social play shape development of marmosets’ HPA functioning and behavioral responses to stressors. *Developmental Psychobiology*, *56*, 1229–1243.
- Norscia, I., & Palagi, E. (2011). When play is family business: adult play, hierarchy, and possible stress reduction in common marmosets. *Primates*, *52*, 101–104.
- Nunes, S. (2014). Juvenile social play and yearling behavior and reproductive success in female Belding’s ground squirrels. *Journal of Ethology*, *32*, 145–153.
- Owens, N. W. (1975). A comparison of aggressive play and aggression in free-living baboons, *Papio anubis*. *Animal Behaviour*, *23*, 757–765.
- Palagi, E. (2006). Social play in bonobos (*Pan paniscus*) and chimpanzees (*Pan troglodytes*): Implications for natural social systems and interindividual relationships. *American Journal of Physical Anthropology*, *129*, 418–426.
- Palagi, E. (2011). Playing at every age: Modalities and potential functions in non-human primates. In A. D. Pellegrini (Ed.), *Oxford handbook of the development of play*. (pp. 70–82). Oxford, UK: Oxford University Press.
- Palagi, E., & Cordoni, G. (2012). The right time to happen: Play developmental divergence in the two *Pan* species. *PLoS ONE*, *7*(12), e52767. Doi:10.1371/journal.pone.0052767
- Pellegrini, A. D. (2009). *The role of play in human development*. New York: Oxford University Press.
- Pellis, S. M. (1988). Agonistic versus amicable targets of attack and defense: Consequences for the origin, function, and descriptive classification of play-fighting. *Aggressive Behavior*, *14*, 85–104.
- Pellis, S. M. (1993). Sex and the evolution of play fighting: A review and a model based on the behavior of murid rodents. *The Journal of Play Theory & Research*, *1*, 56–77.
- Pellis, S. M. (1997). Targets and tactics: The analysis of moment-to-moment decision making in animal combat. *Aggressive Behavior*, *23*, 107–129.

- Pellis, S. M. (2002). Keeping in touch: Play fighting and social knowledge. In M. Bekoff, C. Allen, & G. M. Burghardt (Eds.), *The cognitive animal: Empirical and theoretical perspectives on animal cognition* (pp. 421–427). Cambridge, MA: MIT Press.
- Pellis, S. M., & Burghardt, G. M. (in press). Play and exploration. In J. Call, (Ed.) G. M. Burghardt, I. Pepperberg, C. Snowdon, & T. Zentall (Assoc. Eds.), *APA handbook of comparative psychology, Vol. 1, concepts, history, and methods*. Washington, DC: American Psychological Association.
- Pellis, S. M., & Iwaniuk, A. N. (1999). The problem of adult play: A comparative analysis of play and courtship in primates. *Ethology*, *105*, 783–806.
- Pellis, S. M., & Iwaniuk, A. N. (2000). Adult–adult play in primates: Analyses of its origin, distribution and evolution. *Ethology*, *106*, 1083–1104.
- Pellis, S. M., & Iwaniuk, A. N. (2004). Evolving a playful brain: A levels of control approach. *International Journal of Comparative Psychology*, *17*, 90–116.
- Pellis, S. M., & Pellis, V. C. (1998a). Play fighting of rats in comparative perspective: A schema for neurobehavioral analyses. *Neuroscience & Biobehavioral Reviews*, *23*, 87–101.
- Pellis, S. M., & Pellis, V. C. (1998b). The structure–function interface in the analysis of play fighting. In M. Bekoff, & J. A. Byers (Eds.), *Animal play: Evolutionary, comparative, and ecological perspectives* (pp. 115–140). Cambridge, UK: Cambridge University Press.
- Pellis, S. M., & Pellis, V. C. (2006). Play and the development of social engagement: A comparative perspective. In: P. J. Marshall, & N. A. Fox (Eds.), *The development of social engagement: Neurobiological perspectives* (pp. 247–274). Oxford, UK: Oxford University Press.
- Pellis, S. M., & Pellis, V. C. (2009). *The playful brain. Venturing to the limits of neuroscience*. Oxford, UK: Oneworld Press.
- Pellis, S. M., Pellis, V. C., & Bell, H. C. (2010a). The function of play in the development of the social brain. *American Journal of Play*, *2*, 278–296.
- Pellis, S. M., Pellis, V. C., & Himmler, B. T. (2014). How play makes for a more adaptable brain: A comparative and neural perspective. *American Journal of Play*, *7*, 73–98.
- Pellis, S. M., Pellis, V. C., & Reinhart, C. J. (2010b). The evolution of social play. In: C. Worthman, P. Plotsky, D. Schechter, & C. Cummings (Eds.), *Formative experiences: The interaction of caregiving, culture, and developmental psychobiology* (pp. 404–431). Cambridge, UK: Cambridge University Press.
- Pellis, S. M., Pellis, V. C., & McKenna, M. M. (1993). Some subordinates are more equal than others: Play fighting amongst adult subordinate male rats. *Aggressive Behavior*, *19*, 385–393.
- Power, T. G. (2000). *Play and exploration in animals and children*. Mahwah, NJ: Lawrence Erlbaum Associates.
- Pruitt, J. N., Burghardt, G. M., & Riechert, S. E. (2012). Non-conceptive sexual behavior in spiders: A form of play associated with body condition, personality type, and male intersexual selection. *Ethology*, *118*, 33–40.
- Reinhart, C. J., Pellis, V. C., Thierry, B., & ... Pellis, S. M. (2010). Targets and tactics of play fighting: Competitive versus cooperative styles of play in Japanese and Tonkean macaques. *International Journal of Comparative Psychology*, *23*, 166–200.
- Schaller, G. B. (1963). *The mountain gorilla: Ecology and behavior*. Chicago, IL: The University of Chicago Press.
- Sharpe, L. L. (2005a). Play fighting does not affect subsequent fighting success in wild meerkats. *Animal Behaviour*, *69*, 1023–1029.
- Sharpe, L. L. (2005b). Play does not enhance social cohesion in a cooperative mammal. *Animal Behaviour*, *70*, 551–558.
- Sharpe, L. L. (2005c). Frequency of social play does not affect dispersal partnerships in wild meerkats. *Animal Behaviour*, *70*, 559–569.
- Sharpe, L. L., & Cherry, M. I. (2003). Social play does not reduce aggression in wild meerkats. *Animal Behaviour*, *66*, 989–997.
- Shimada, M. (2012). Social object play among juvenile Japanese macaques: Comparison between the provisioned Arashiyama–Kyoto troop and the non-provisioned Kinkazan troop. In J.-B. Leca, M. A. Huffman, & P. L. Vasey (Eds.), *The monkeys of Stormy Mountain: 60 years of primatological research on the Japanese macaques of Arashiyama* (pp. 258–283). Cambridge, UK: Cambridge University Press.
- Siviy, S. M., Harrison, K. A., & McGregor, I. S. (1996). Fear, risk of predation and playfulness in the juvenile rat. *Behavioral Neuroscience*, *120*, 49–59.
- Smith, L. K., Fantella, S.-L., & Pellis, S. M. (1999). Playful defensive responses in adult male rats depend upon the status of the unfamiliar opponent. *Aggressive Behavior*, *25*, 141–152.
- Smith, P. K. (2010). *Children and play*. Chichester, UK: Wiley-Blackwell.
- Suomi, S. J. (2005). Genetic and environmental factors influencing the expression of impulsive aggression and serotonergic functioning in rhesus monkeys. In R. E. Tremblay, W. W. Hartup, & J. Archer (Eds.), *Developmental origins of aggression* (pp. 63–82). New York: Guilford Press.
- Symons, D. (1978). *Play and aggression: A study of rhesus monkeys*. New York: Columbia University Press.
- Taylor, J. H., Mustoe, A. C., Hochfelder, B., & French, J. A. (2015). Reunion behavior after social separation is associated with enhanced HPA recovery in young marmoset monkeys. *Psychoneuroendocrinology*, *57*, 93–101.
- Thompson, K. V. (1998). Self assessment in juvenile play. In M. Bekoff, & J. A. Byers (Eds.), *Animal play: Evolutionary, comparative, and ecological perspectives* (pp. 183–204). Cambridge, UK: Cambridge University Press.
- van den Berg, C. L., Hol, T., van Ree, J. M., Spruijt, B. M., Everts, H., & Koolhaas, J. M. (1999). Play is indispensable for an adequate development of coping with social challenges in the rat. *Developmental Psychobiology*, *34*, 129–138.
- Wilmer, A. H. (1991). Behavioral deficiencies of aggressive 8–9 year-old boys: An observational study. *Aggressive Behavior*, *17*, 135–154.

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