

## **Evolving a Playful Brain: A Levels of Control Approach**

**Sergio M. Pellis**

*University of Lethbridge, Canada*

**and**

**Andrew N. Iwaniuk**

*Monash University, Australia*

Play is rare in the Animal Kingdom, but relatively common in the larger brained vertebrate taxa. Comparisons at the level of classes, orders, and, in some cases, families, suggest that larger brained taxa are more likely to contain playful species. However, at the species level, such relationships generally disappear. In some well documented mammalian taxa, such as Rodentia, it is clear that there are species which do not play at all, some where the play is quite complex and some showing all grades in between. Comparative methods are used here to supplement proximal analyses of the content of one particular form of play, play fighting, so as to identify the neurobehavioral mechanisms that are needed in rodents to evolve complex play from simpler antecedents. At least five independent neural mechanisms are shown to be necessary to produce the most complex example of play fighting in rodents. The identification of such levels of control provides a new method for systematizing the diversity of play present in mammals. Furthermore, this approach sets the stage for re-evaluating the relationship between brain size and play. That is, the issue can be reconceptualized in terms of whether species with larger brains are more likely to have a greater number of control mechanisms. It is not that larger brained species are more likely to play, but rather, that when they do play, the content of their play is more flexible. Suitable comparative data sets are needed to test these possibilities.

Casual inspection of the Animal Kingdom reveals that play behavior is a relatively rare phenomenon (Burghardt, 2004), and one that seems to arise most often in the larger brained lineages (Fagen, 1981). In fact, play is most common in mammals and birds, and in those groups, play is most prevalent in the lineages with the largest brains (Diamond & Bond, 2003; Iwaniuk, Nelson, & Pellis, 2001; Ortega & Bekoff, 1987). This seeming relationship between brain size and prevalence of play has led some to suggest that in large brained animals, play has the function of shaping the brain through the experiences generated (Allman, 1999). While some correlational data support such a claim (Byers & Walker, 1995; Fairbanks, 2000), it is unlikely that this functional relationship can account for the variation in prevalence and for the complexity of play present in closely related species (Pellis & Iwaniuk, 1999a). Indeed, among vertebrates, the relationship between brain size and play holds true only for comparisons using the larger taxonomic categories. The complexity and prevalence of play is positively correlated with increased brain size when classes are compared (Fagen, 1981), and when orders are compared within the classes Aves (Diamond & Bond, 2003; Ortega & Bekoff, 1987) and Mammalia (Iwaniuk et al., 2001). Comparisons of families within orders of mammals shows a weak relationship at best, and then only for some families (Byers, 1999; Iwaniuk et al., 2001).

We thank Donald Owings for providing us with the videos of California ground squirrels and Gordon Burghardt, Lori Marino, and Vivien Pellis for their valuable comments on earlier drafts of this paper. This work was supported by grants from the Natural Sciences and Engineering Research Council of Canada to the authors. Correspondence concerning this article should be addressed to Sergio M. Pellis, Department of Psychology & Neuroscience, University of Lethbridge, Lethbridge, T1K 3M4 Alberta, Canada (pellis@uleth.ca).

The relationship completely evaporates when comparisons are made at the species level within orders (Iwaniuk et al., 2001). There are two likely explanations for these findings. Firstly, there may not be a real causal link between these two biological traits. At a gross level, major increases in brain size may be spuriously correlated with a host of behavioral and cognitive traits, with play being a byproduct of one or more of those traits. The finding that even some invertebrates may engage in behavior with qualities comparable to mammalian and avian play (Burghardt, 2004; Mather & Anderson, 2000) supports this possibility. That is, it is not that a large brain is essential for play to occur, rather, it is simply that larger brained animals are more likely to have the traits necessary for play. Secondly, play is a heterogeneous category of behavior. Lumping all play together for large comparative surveys may produce a biologically meaningless category, so that when statistical comparisons are made, nonsensical results emerge. Further, using overall brain size as the basis for comparison may mask the fact that in different lineages, different brain areas may have differentially expanded, and that some forms of play may be functionally linked to some brain areas more than others. In fact, some preliminary studies of volumetric changes in specific brain regions with more circumscribed subsets of play have yielded significant and positive results (Lewis, 2000; Pellis & Iwaniuk, 2002).

In this paper, the approach taken to resolve these possibilities is to fractionate play into its biologically meaningful components and then attempt to link each of those components to particular aspects of brain function. This would identify a functional role for different brain systems in regulating the components of play. Variation across species for specific components of play may then suggest the kinds of changes in the relevant brain systems which may be needed to achieve that variation. In some cases, changes in the overall brain size or brain component size may be the appropriate avenue. In others, variation in behavior may be produced by changes in the wiring of cell assemblages or in the cellular organization of the cells of particular systems. Unless the behavioral system in question—play—is dissociated into its constituent elements, questions about evolved changes in neural mechanisms cannot be addressed without the risk of confounding categories and levels of analysis. This is particularly true given that some species within playful lineages do not play, and those that do may exhibit either simple or complex play (Pellis & Iwaniuk, 1999a). Therefore, the approach advocated here is that of identifying levels of control in regulating the frequency and content of play, and then using these postulated control systems to understand the evolution of play from its simplest expression to its most complex (see Moynihan, 1998, for a similar approach in the comparative analysis of competition and aggression). That is, what is required to make a non-playful brain into a playful one, and what needs to be added in order to increase the complexity of play?

The current state of knowledge about the neural bases for play suggests that many brain systems are involved (Burghardt, 2001). Unfortunately, there are two limitations to this knowledge. Firstly, except for some rare cases (Siviy, 1998), it is unclear whether the neural mechanisms concerned are related to general processes of behavioral regulation that affect play along with many other behaviors, or whether the neural systems are specific to the regulation of play. Even when seemingly linked to play rather than to behavior in general (Gordon et al., 2003), it is often unclear what features of play are regulated by a particular neural system.

Secondly, most of this work on the neurobiology of play has been of one species, the laboratory rat (*Rattus norvegicus*; see Panksepp, 1998; Pellis & Pellis, 1998b; Sivi, 1998; Vanderschuren, Niesnik, & Van Ree, 1997, for recent reviews). A limitation in using a single species is that it is unclear how representative its play is relative to that of other species (Pellis & Pellis, 1998b). Therefore, a comparative approach is adopted here so as to place the play of rats in an evolutionary context.

Before proceeding with the analysis, a suitable definition of play should be considered. While there have been long and unresolved debates about what constitutes an adequate definition of play (Fagen, 1981; Smith, 1978), some recent attempts may provide a much needed set of objective criteria that can be used to compare a wide range of species across many phyla (Burghardt, 2001, 2004). For present purposes, given the lack of necessary descriptive detail in much of the available literature, a commonly used, albeit deficient, definition will be used. That is, play can be recognized as behavior that is repeatedly performed and that does not appear to have an immediate function (Bekoff & Byers, 1981). Generally, such behavior is often associated with juveniles, although it need not be limited to juveniles (Pellis & Iwaniuk, 2000b). As will become apparent, seemingly similar looking play may involve different degrees of neural control in different species, and thus applying an overly rigorous definition at the beginning of the analysis may be unduly restrictive.

### **Play: One Motivational System or Many?**

For the sake of simplicity, this analysis will begin by breaking play into its three main subcategories: social play, object play and locomotor (or solo) play (Burghardt, 1998). A long standing debate has been whether these subcategories represent differing manifestations of a unitary play motivational system, or whether they reflect an underlying heterogeneity of play systems, where multiple and independent systems may exist (Power, 2000). The evidence supporting a single system view is that during play sessions, animals will shift rapidly across different categories of play, and that animals deprived of social partners will increase the time spent in nonsocial forms of play (Fagen, 1981). For example, Bekoff (1978) relates an observation where a juvenile coyote (*Canis latrans*) made several attempts to solicit social play with littermates. When no individual engaged the juvenile in social play, he began to chase his own tail. When the motivation to play is not satisfied in one way, it is satisfied in another. Other evidence comes from the finding that in dwarf mongooses (*Helogale undulata*), a play-specific vocalization is uttered continuously, irrespective of whether the play is social or solitary (Rasa, 1984).

The data in support of a multiple systems view are more widespread and less anecdotal. There is cross species variation in the prevalence of different types of play. For example, object play involves the use of many of the behavior patterns typical of predation and food handling. Not surprisingly, object play is most prevalent in groups such as carnivores and primates. Similarly, locomotor play typically involves many of the behavior patterns present in anti-predator avoidance. And again, not surprisingly, locomotor play is more common in species that are often prey, such as ungulates. In species where all three types of play are common, developmental dissociation can be seen. For example, in cats (*Felis catus*), locomotor

play emerges first. As it wanes, social play emerges. Finally, as social play wanes, object play becomes prevalent (Barrett & Bateson, 1978; Caro, 1981). When the developmental emergence of different forms of play are mapped, differential onsets and offsets of the types of play have been shown to be present across a range of species (e.g., Gomendio, 1988; Pellis, 1981; Pellis & Pellis, 1983; Schaller, 1972). Furthermore, in different breeds of dogs (*Canis familiaris*), neoteny seems to have led to developmental profiles exaggerating either social or predatory play to the diminution of the other (Coppinger et al., 1987). Thus, at a developmental level, these different types of play appear to represent different motivational systems. For species and at ages where more than one type of play is expressed, the pattern of use of the different types of play provides further support for a multiple systems view.

Australian magpies (*Gymnorhina tibicen*) live in open woodland and forage in patches of grassland (Rowley, 1974). Fledglings follow the parent's cycle of going to the ground in the morning, and foraging there until about midday. They then return to the trees for a couple of hours of rest before returning again to the ground to forage in the afternoon. Finally, they retire for the night in the trees (Pellis, 1981). While object play is correlated with the times that the birds are foraging, social play is correlated with the rest periods in between foraging bouts (Pellis, 1980). That is, object play is coupled with foraging, but social play is not. A possible confound with this example is that the opportunity to find objects suitable for play is more likely to occur when foraging. However, data from a different species support the possibility that this is a motivational difference and not one of opportunity.

In a captive troop of oriental small-clawed otters (*Anonyx cinerea*), cycles of diurnal activity occurred at about two hour intervals, with periods of rest in between. As is typical in many captive situations, the animals were fed at the same time each day. Three periods of activity were compared: the penultimate cycle before the afternoon feeding session, the cycle preceding feeding and the cycle following feeding. In the penultimate cycle, social play and object play waxed and waned simultaneously, with both reaching similar frequencies. In contrast, the cycle preceding feeding involved a differential increase in object play, whereas in the cycle following feeding, there was a differential increase in social play (Pellis, 1991). That is, object play, unlike social play, seems to be motivationally linked to the feeding system. Indeed, the pattern of object play, especially in the cycle preceding feeding, followed the full foraging sequence—at first, objects were found, held and transported, then, as the frequency of object play increased, the otters began to fragment any large objects they collected. Finally, as their play reached a crescendo, objects were held and chewed as if they were prey items, with the only difference being that the otters did not swallow the fragments they had chewed off (Pellis, 1983). Evidence that object play in carnivores is intimately tied to the foraging/feeding motivational system has received considerable supporting evidence (e.g., Adamec, 1975; Biben, 1979; Hall, 1998; Pellis et al., 1988; Wolgin, 1982). For our purposes, what these data show is that social play and object play are not regulated by the same motivational mechanisms. This seems true even when seemingly similar forms of play are involved.

Play fighting is the most commonly occurring form of social play (Pellis & Pellis, 1998b), involving competitive interactions where the partners each attempt

to gain some advantage over one another (Aldis, 1975; Fagen, 1981). The most common advantage sought is that of contacting some particular body target (Aldis, 1975). Such targets can be typical of those of conspecific aggression, sexual behavior or predation (Pellis, 1988; Pellis & Pellis, 1998a). That is, targets and tactics from several motivational systems may occur in play fighting. While casual observation suggests that animals fluidly mix behavioral elements from these different behavioral systems (Eibl-Eibesfeldt, 1982; Millar, 1981), detailed analyses of play fighting in species with more than one type of play fighting yield a different conclusion.

As is true for many other murid rodents (Pellis, 1993), grasshopper mice (*Onychomys leucogaster*) mostly engage in play fighting derived from precopulatory behavior. However, they also engage in play fighting involving predatory behavior (Pellis et al., 2000). Richardson's ground squirrels (*Spermophilus richardsonii*) mostly engage in sexual play, and, to a lesser extent, in aggressive play (Pasztor et al., 2001). In both cases, when the sequelae of play fights are analysed, two general organizational properties become evident. Once a playful attack involving a target from one system has begun, both partners will engage in patterns of attack and defense suitable for that target. If the defender counterattacks, it will do so by attacking the target type previously attacked by the partner. It is only when a sequence from one behavioral system is completed that one of the partners is likely to begin a new attack using a target from another behavioral system. That is, on a moment-to-moment basis, different behavioral systems are not mixed in play fighting; rather, behavioral systems seem to proceed in tandem, with switches only occurring once a sequence is completed.

Comparisons of different forms of play in different species further supports the multiple motivational systems hypothesis. If play represents a singular motivational system, then it would be predicted that for individuals, engagement in different types of play should be correlated. That is, an individual who plays a lot should play a lot in all kinds of ways. In contrast to this prediction, a study of three to five year old children found that the extent to which a child engages in solo play is not correlated with the extent to which that child engages in social play (Roper & Hinde, 1978). Similarly, it would be predicted that having the opportunity to play more in one way should reduce the likelihood of playing in a different way. In contrast to this prediction, it has been found that dogs living in multidog households play more with humans than dogs living in single dog households, suggesting that dog-human play is not just a substitute for dog-dog play (Rooney, Bradshaw & Robinson, 2000). Both these studies indicate that playing in one domain does not satisfy the motivation to play in another domain. Manipulation of neural systems in species with multiple types of play further support a multiple systems view of play. For example, pharmacological manipulation of opioid systems can modulate the occurrence of social play in common marmosets (*Callithrix jacchus*), yet have no effect on their object and locomotor play (Guard, Newman, & Roberts, 2002). Therefore, the balance of evidence from developmental, motivational and other analyses of the causal mechanisms underlying play strongly suggest that different types of play involve distinct motivational systems.

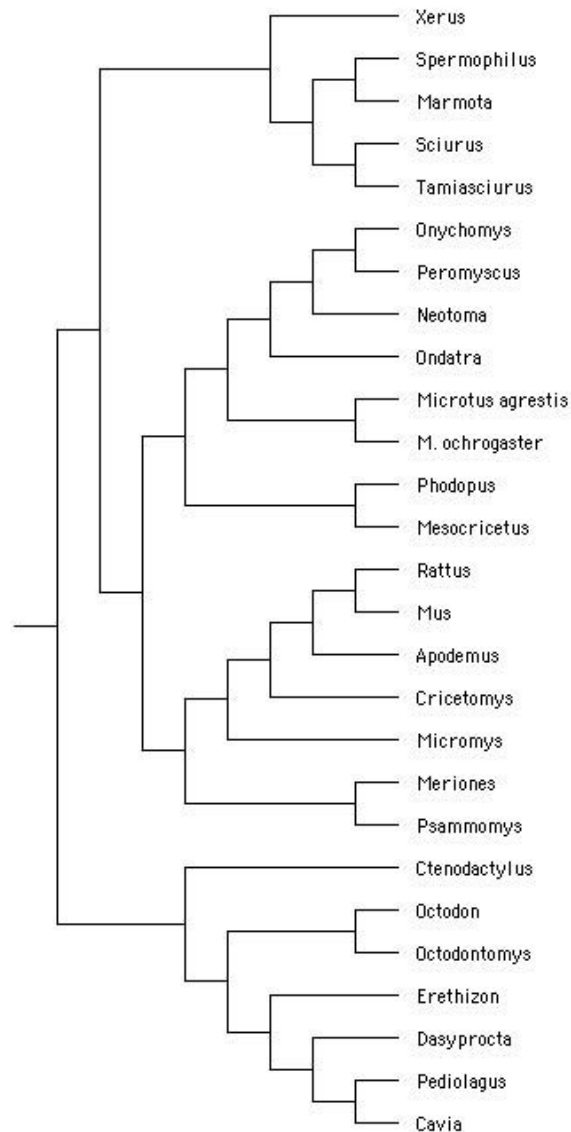
### **Do Different Types of Play Coevolve?**

Another avenue of evidence is from the evolutionary relationship between types of play. If all forms of play were an expression of a single system, then it would be predicted that for species with more than one type of play, all forms of play should covary. That is, species with highly complex and prevalent play should show complexity and prevalence in all the forms of play that they exhibit. Indeed, comparisons across orders of mammals indicate that having multiple types of play is just as likely a primitive state as is only having one type, and that the relationship between the number of play types and play complexity is equivocal (Burghardt, 2004). Rodents primarily engage in one of two types of play, social and locomotor (Hole & Einon, 1984); these can occur at varying degrees of complexity across the order (Fagen, 1981; Pellis & Iwaniuk, 1999a). If a single play system exists, then a species with complex social play should also have complex locomotor play, and species with simple social play should also have simple locomotor play.

For comparative purposes, a three-point rating scale, developed from one previously employed (Iwaniuk et al., 2001), was used for both play fighting—the most common form of social play—and locomotor play. At its most complex, play fighting involves wrestling; this is where the animals roll over one another, maintaining close body contact. In cases where wrestling is highly prevalent, species were given a score of 3. In cases where such wrestling is absent, species were given a score of 1. Finally, in cases where the animals engage in competitive body-body contact but not in prolonged wrestling, species were given a score of 2. Locomotor play was similarly scored. At its most complex, locomotor play involves runs with rapid turns and various head and body rotations. In cases where such complex playful locomotion is prevalent, species were given a score of 3. In cases where such locomotion is rare or absent, species were given a score of 1. Finally, in cases where at least some combination of locomotor activity was present in play, species were given a score of 2. Species from all three major lineages of rodents were included (Table 1). So as not to bias the analysis, more than one congener was used only if there was intrageneric variation for either trait. The relationship between play fighting and locomotor play was examined using both conventional statistics and comparative methods that incorporate phylogenetic information using the Kendall rank correlation coefficient with significance set at  $p < 0.05$ . The phylogenetic correction was included in the analysis since the evolution of play in some taxa appears to be constrained by ancestry (Pellis & Iwaniuk, 2000b; Thierry, Iwaniuk, & Pellis, 2000). That is, the clade within which a species belongs affects the likelihood that particular traits are present; therefore, comparative methods that incorporate phylogenetic information were employed to explore the correlated evolution of social and locomotor play.

In the phylogenetically corrected analysis, the species have to be placed on a known tree. The placement of each species on the hypothesized tree was based on phylogenies derived from morphological and molecular data (see references in Pellis & Iwaniuk, 1999a, as well as Blumstein & Armitage, 1998; DeBry & Sagel, 2001; Ebensperger & Cofré, 2001; Huchon & Douzery, 2001; Huchon et al., 2002; Martin et al., 2000; Michaux, Reyes, & Catzeflis, 2001; Montgelard et al., 2002; Rowe & Honeycutt, 2002; Verzi, 2001). Two trees were developed and used—one

fully resolved the relationship of all species (as shown in Figure 1), and the other, the clade including *Rattus*, *Mus*, *Apodemus*, *Cricetomys*, and *Micromys*, was left as an unresolved polytomy.



**Figure 1.** A cladogram shows the phylogenetic relationship of the rodent species used for the comparison of types of play. The clade on the top represents the sciurids, the one on the bottom, the hystricognath rodents. The large clade in the middle is that of the murids.

Two comparative methods were employed. In the first method, evolutionary changes for both play fighting and locomotor play were mapped on top of the two phylogenetic trees using MacClade (Maddison & Maddison 1992). Both traits were treated as ordered since the scores were ordinal rankings. It should be noted, however, that if the traits were treated as unordered, the results were qualitatively the same. Changes in the traits were then compared using nonparametric correlations. The second method employed was to use independent contrasts (Felsenstein, 1985). The program CAIC (Purvis & Rambaut, 1995) was used to calculate inde-

pendent contrasts; one for each of the two phylogenies. In both cases, unequal branch lengths were used since the phylogenies were composites from studies using a variety of phylogenetic methods and they provided adequately standardized contrasts (Garland et al., 1993).

Table 1  
*Relative Prevalence and Complexity of Social and Locomotor Play in Rodent Species Representing all Three Major Taxonomic Divisions.*

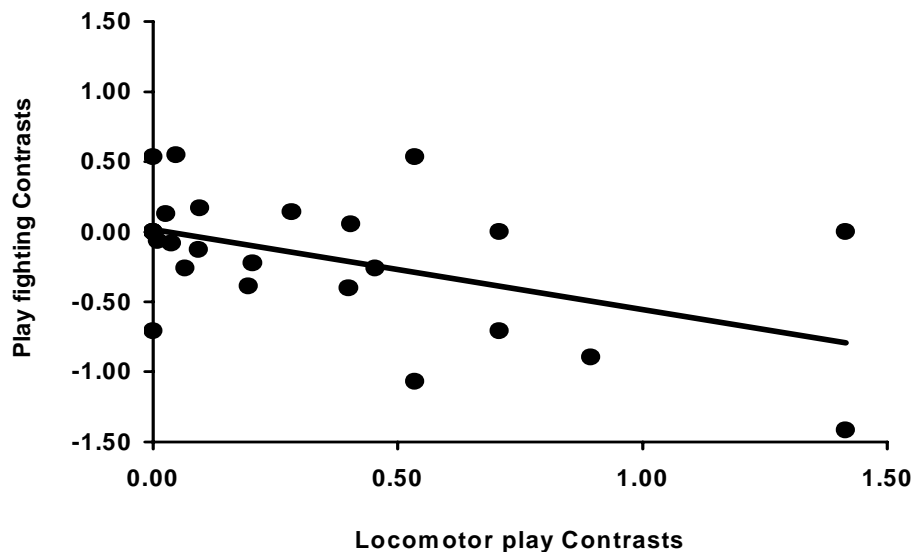
Species	Play fighting	Locomotor play
<i>Apodemus</i>	1	2
<i>Cavia</i>	1	3
<i>Cricetomys</i>	3	2
<i>Ctenodactylus</i>	1	2
<i>Dasyprocta</i>	1	2
<i>Erethizon</i>	2	2
<i>Marmota</i>	3	1
<i>Meriones</i>	2	2
<i>Mesocricetus</i>	3	1
<i>Micromys</i>	2	1
<i>Microtus agrestis</i>	1	3
<i>M. ochrogaster</i>	3	1
<i>Mus</i>	1	3
<i>Neotoma</i>	1	3
<i>Octodon</i>	3	2
<i>Octodontomys</i>	2	3
<i>Ondatra</i>	2	1
<i>Pediolagus</i>	1	3
<i>Peromyscus</i>	2	1
<i>Phodopus</i>	2	1
<i>Psammomys</i>	2	1
<i>Rattus</i>	3	3
<i>Sciurus</i>	1	3
<i>Spermophilus</i>	3	1
<i>Tamasciurus</i>	1	3
<i>Xerus</i>	1	3

**Note.** The ratings for murid rodents were obtained from Iwaniuk et al. (2001), and those for the other species were derived from the extant literature (Barash, 1973; Elliott, 1978; Ewer, 1966; Ferron, 1975, 1981; Gouat & Gouat, 1987; Harper, 1976; Horwich, 1972; Kunkel & Kunkel, 1966; Nowicki & Armitage, 1979; Pasztor et al., 2001; Roth-Kolar, 1957; Shaddle, 1943; Wilson & Kleiman, 1974). The ratings for the agouti (*Dasyprocta*) were based on 20 h of observations of a captive family held at the Auckland Zoological Gardens by S. Pellis in August, 2001.

A significant correlation was present between the play fighting and locomotor play scores using the raw species data,  $\tau(N = 27) = -0.543$ . This was corroborated by correlated evolutionary changes in the two types of play using the fully resolved,  $\tau(N = 23) = -0.441$  and partially unresolved,  $\tau(N = 24) = -0.351$

phylogenetic trees. Independent contrasts analysis yielded similar results. Using the fully resolved phylogeny, a significant negative correlation was present,  $\tau(N = 26) = -0.304$ ; this was also the case when using the partially resolved phylogeny,  $\tau(N = 23) = -0.409$ . Therefore, in general, as the rate and complexity of locomotor play increases, the rate and complexity of play fighting decreases (Figure 2).

These phylogenetic findings suggest that as a lineage increases the complexity of one type of play, it reduces the mechanisms available for the other. Not only do different types of play arise from different motivational systems, there may also be an antagonistic relationship among those systems. Again, these phylogenetic data add to those derived from other forms of analysis to support the hypothesis that there are multiple motivational systems for play. Given the support for this hypothesis, it is likely that meaningful comparisons between brain mechanisms and play can only be made for cases where the same type of play is being compared across species. Since play fighting is the most frequently reported type of play, and its structure varies among species, play fighting will be the focus of further analysis.



*Figure 2.* A scatter plot shows the independent contrast values for locomotor play and play fighting in rodents. Note that as the values for locomotor play increase, those for play fighting decrease.

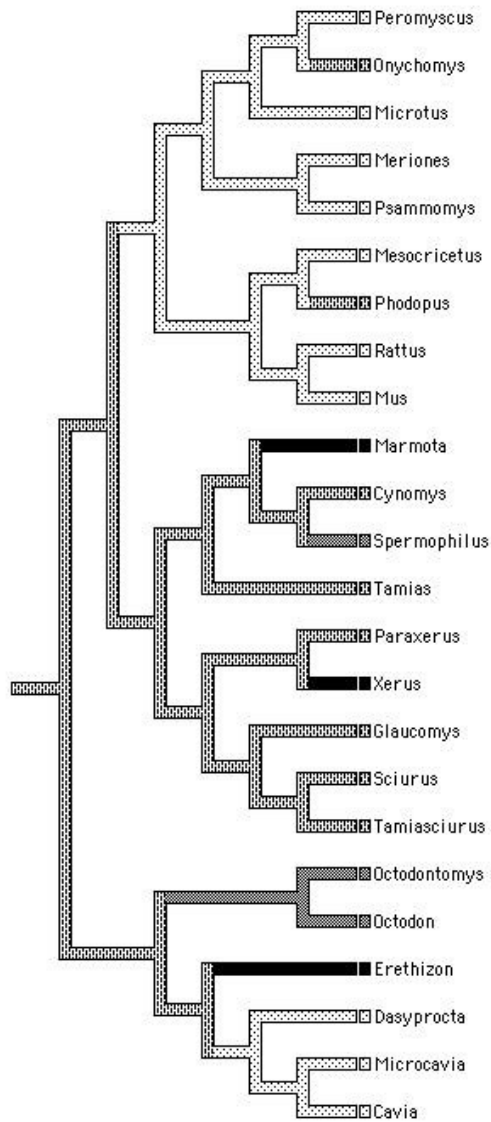
### Components of Play Fighting

As already noted, play fighting can arise from the competition for access to agonistic, sexual or predatory targets. It has also been demonstrated that play fights derived from different behavioral systems are not intermixed; this suggests that the presence or absence of play fighting provides insufficient information for cross species comparisons. Some of the most detailed comparative data available on the components of play fighting are for murid rodents (Pellis & Pellis, 1998b). However, this lineage of rodents is peculiar in that in most cases, the play fighting is limited to the use of the targets and tactics of precopulatory behavior (Pellis, 1988, 1993). Although the sexual form of play fighting has probably been underes-

timated in its prevalence (Mitchell, 1979; Pellis & Pellis, 1998b), it does appear that play fighting in most mammals is derived from agonistic behavior (Aldis, 1975; Fagen, 1981). Therefore, we need to determine whether murid rodents represent an aberrant lineage in which play fighting has been limited to sexual play, or if this taxa is derived from a more ancient lineage in which multiple forms of play fighting were present.

To test this, a range of rodents from all three major lineages were scored for the prevalence of sexual and agonistic play fighting. Species were scored on a four-point scale: species that engage in only sexual play were given a score of 1 (*Cavia*, *Cynomys*, *Dasyprocta*, *Mesocricetus*, *Meriones*, *Microcavia*, *Microtus*, *Mus*, *Onychomys*, *Peromyscus*, *Psammomys*, *Rattus*), species that engage in mostly sexual play were given a score of 2 (*Cynomys*, *Glaucomys*, *Onychomys*, *Paraxerus*, *Phodopus*, *Sciurus*, *Tamias*, *Tamiasciurus*), species that equally engage in sexual and agonistic play fighting were given a score of 3 (*Spermophilus*, *Octodon*, *Octodontomys*), and species that engage in mostly agonistic play were given a score of 4 (*Erethizon*, *Marmota*, *Xerus*). The rating for each species was based on the extant literature (in addition to the references listed on Table 1, see also Balph & Stokes, 1963; Barash, 1973, 1974, 1976; Eibl-Eibesfeldt, 1951; Ferron, 1985; Ferron & Ouellet, 1991; Fitzgerald & Lechleitner, 1974; Holmes, 1995; Kingdon, 1974; Nunes et al., 1999; Pizzimenti & McCleghan, 1974; Rood, 1972; Steiner, 1971; Viljoen, 1977). The play score was treated as an ordered character and mapped onto the previously used phylogeny (see above) using MacClade (Maddison & Maddison, 1992). For purposes of clarity and accuracy, only genera were compared. Some genera are well known and numerous (e.g., *Marmota*, *Spermophilus*), and so may bias the analysis compared to lesser known or species-poor genera (e.g., *Erethizon*, *Mus*). Also, attempting to include multiple species from single genera may introduce more inaccuracies, since fewer within genus phylogenetic relationships are fully resolved. Therefore, where congeners varied in the trait, an analysis was conducted using MacClade in order to determine the most likely ancestral state for that genus (see Pellis & Iwaniuk, 2000b).

Tracing the different character states for type of play revealed that the likely ancestral condition was to engage mostly in sexual play (Figure 3). Then, in the lineage leading to the murid rodents, only sexual play remains, except for a sporadic evolution of aggressive play and predatory play in two species (*Phodopus* and *Onychomys*, respectively). In other lineages, the occurrence of aggressive play is maintained or even increased (i.e., the sciurid clade encompassed by *Marmota* and *Tamiasciurus*). Among the hystricognath rodents, there is an initial increase in the amount of aggressive play fighting. This is then maintained (*Octodontomys*, *Octodon*), or even increased (*Erethizon*) in some lineages, while in others, there is a reversion to the performance of only sexual play (*Cavia*, *Dasyprocta*, *Microcavia*). Thus, although high rates of sexual play relative to aggressive play appear to be typical of rodents, many lineages have elevated the relative occurrence of aggressive play. Furthermore, aggressive play is present in the repertoire of the reconstructed rodent ancestor.



**Figure 3.** A cladogram comprising murids, scuriids and hystricognaths shows the changes in character state for the amount of play fighting based on sexual behavior versus aggressive behavior. Legend: dotted, sexual play only; dashed, mostly sexual play; grey, about equal amounts of sexual and aggressive play; black, mostly aggressive play.

The relative occurrence of play fighting based on sexual or aggressive behavior appears volatile, with lineages increasing and decreasing, one relative to the other. This is strikingly illustrated by the genus *Spermophilus*, where some species predominantly engage in sexual play (*spilosoma*, *beldingi*, *richardsonii*, *parryii*), while others predominantly engage in aggressive play (*mexicanus*, *tridecemlineatus*, *beecheyii*, *lateralis*, *armatus*, *columbianus*). Membership in a clade did not predict which type of play was predominant in a species. Furthermore, these differences between species can be quite extreme. For example, in Richardson's ground squirrels, 80% of all play fighting is sexual (Pasztor et al., 2001), whereas in the Californian ground squirrel (*Spermophilus beecheyii*), 80% of all play fight-

ing is agonistic (this percentage is based on an analysis of video tapes collected by Donald Owings of free-living animals). At present, we cannot account for why some lineages, or some species within lineages, mostly engage in one type of play rather than another. To our knowledge, at least two refinements are needed for a comprehensive analysis. Firstly, we need to know the quantitative differences in the relative frequency of the two forms of play across species—this enables more finely grained comparisons—and secondly, we need to resolve fully some of the phylogenies, especially for highly variable genera such as *Spermophilus*. However, for current purposes, it is evident that murid rodents are typical of a wider evolutionary pattern where different types of play fighting may be predominant in particular lineages. What makes the murid rodents seemingly aberrant is that they are such a speciose lineage, comprising around 1,336 species, and so are, by far, the most species-rich family of mammals (Nowak, 1999). Given that the relative predominance of different types of play fighting may show comparable lineage-specific trends in other mammalian taxa (Pellis & Pellis, 1998b), the murids can be used as a reasonable model for the analysis of the neurobehavioral evolution of play fighting in mammals. Furthermore, this family offers the advantage of being able to compare one type of play fighting (i.e., sexual play) across a variety of species while avoiding the possible confounds which may arise from the presence of other types of play fighting (e.g., aggressive play).

Play fighting, irrespective of the behavioral system from which the targets are derived, involves two components—attack and defense (Pellis & Pellis, 1998a). Developmental, causal and phylogenetic analyses all indicate that these two components are dissociable and so likely involve independent mechanisms. For example, in rats, as is typical of most of the species studied (Fagen, 1981), the frequency of play fighting waxes and wanes during development, reaching its peak during the juvenile phase (Thor & Holloway, 1984). All the developmental changes in the frequency of play fighting can be accounted for by changes in the frequency of playful attack (Pellis & Pellis, 1990, 1997). The probability that a rat will defend itself against a playful attack remains the same at all ages (Pellis & Pellis, 1987, 1990, 1991b, 1997). Furthermore, manipulations of testosterone exposure in the perinatal period—which form the basis for the higher rate of play fighting in males as compared to females (Meaney, 1988)—affect the frequency of playful attack (Pellis, Pellis, & McKenna, 1994; Thor & Holloway, 1985), but not the likelihood of defense or pattern of defense (Pellis, Pellis, & Kolb, 1992). Other manipulations of gonadal hormones can affect the pattern of defense used, but not the frequency of attack (Smith et al., 1996). This is also true for neonatal decortication (Pellis, Pellis, & Whishaw, 1992). Finally, rats that launch more playful attacks are not more likely to defend themselves (Pellis & Pellis, 1991b). Therefore, at the proximate level of analysis, the evidence supports the idea that playful attack and playful defense are regulated by different mechanisms (Pellis & McKenna, 1992). Furthermore, quantitative comparisons of several species of murid rodents indicate that the frequency of playful attack and the likelihood of playful defense can vary independently (Pellis, Pellis, & Dewsbury, 1989). Given the lack of a common mechanism regulating playful attack and defense, it would be predicted that these two components of play fighting are likely to have evolved independently.

Data on the relative frequency of playful attack and patterns of playful defense for twelve species of murid rodents from five families were available from a

previous study (Pellis & Pellis, 1998b). As described for the phylogenetic analysis above, both the raw scores and comparative methods that correct for degree of relatedness were used. A previously developed phylogenetic tree for these species was used (Pellis & Iwaniuk, 2000a). From the data available (Pellis & Pellis, 1998b), values from 1 to 8 were given for the frequency of playful attack. For playful defense, an index incorporating three features was developed so as to give an estimate of complexity. The first feature evaluated whether body contact promoting tactics, such as rotation to supine, which lead to wrestling, were used more or less frequently than evasive tactics, which minimize body contact. Three levels were scored: evasion was more common than supine defense (1), evasion and supine defense were equally frequent (2), and supine defense was more frequent than evasion (3). The second feature evaluated whether the pattern of defense was similar to that performed by the adults during precopulatory behavior, or whether playful defense was modified from that typical of sexual contexts (see below). Two levels were used: not modified (0) and modified (1). These two values were added together. The value was then multiplied by the third feature, which scored whether there was any defense at all. Two levels were scored: defense present (1) and defense absent (0). This final value corrected for species that did not defend themselves at all. The defense index could have any whole number between 0 and 7, with 7 representing the most complex defense present (Table 2).

Table 2

*Relative Frequency of Playful Attack and the Complexity of Playful Defense in Murid Rodents.*

Species	Playful attack (relative frequency)	Playful defense (complexity index)
Meriones	4	2
Mesocricetus	6	7
Microtus agrestis	4	0
M. montanus	6	4
M. ochrogaster	6	5
Mus	1	1
Notomys	4	0
Onychomys	6	3
Peromyscus	6	4
Phodopus	5	2
Psammomys	4	2
Rattus	8	7

*Note.* The ratings were derived from data presented in Pellis & Pellis (1998b).

Using species data, a significant positive correlation was present ( $\tau(N = 12) = 0.785$ ). However, this was not corroborated by any of the analyses using comparative methods. Thus, once phylogenetic information was incorporated, there does not appear to be a correlation between the relative rates of playful attack and the complexity of playful defense. That is, it is most likely that across species, the frequency of playful attack and the complexity of playful defense are independent. For both features of play fighting, an analysis using MacClade indicates that the ancestral condition was a moderate degree of both playful attack and complexity in playful defense. From this ancestral state, different lineages increased or decreased

the frequency and complexity of these two features of play. Given that these two features are not correlated, they likely were subjected to differing regimes of selection. At present, it is not clear what those differing selection pressures may have been (Pellis & Iwaniuk, 1999a). Irrespective of what caused the diversification of playful attack and playful defense, these comparative analyses support the proximate data in that they point to different neural regulatory mechanisms being involved for each.

The comparative data also indicate that there is a major difference in the pattern of defense exhibited by different species. In all species, the same tactics of defense that are used during play fighting are also those used during adult precopulatory behavior. Furthermore, in most species, the patterns of defense used during play fighting occur with the same frequency as they do in adult sexual encounters (Pellis, 1988, 1993; Pellis & Pellis, 1989; Pellis et al., 1989; Pierce et al., 1991). Variation among the frequency of defensive tactics can be accounted for by variation in the adult-typical use of those tactics. For example, the supine defense is used more often by prairie voles (*Microtus ochrogaster*) in both contexts, and standing on two legs and boxing is used more often by montane voles (*Microtus montanus*) in both contexts (Pellis & Pellis, 1998b). In contrast, supine defense is very common in the play fighting of rats and Syrian golden hamsters (*Mesocricetus auratus*), but rare in the sexual encounters of their adults (Pellis, 1988; Pellis & Pellis, 1987, 1988a, b, 1989). But how rare? And, when supine defense is used, is it used in the same contexts? To answer these questions, 12 male and female pairs of each species were observed across several estrous cycles, until most pairs copulated.

The subjects were all sexually naive adults, and were individually housed in standard wire mesh hanging cages (17 X 25 X 20 cm). Standard laboratory rodent chow and water were provided *ad libitum*. A specific male was always paired with the same female; these pairs were introduced daily into a neutral test enclosure. The rats' enclosure measured 46 X 46 X 50 cm, and a terrarium measuring 50 X 26 X 30 cm was used for the hamsters. The floors of both enclosures were covered by a 2.5 cm layer of processed corn cobs. Each encounter lasted for 30 min and was videotaped under red light. The rats were maintained on a 12:12 light-dark cycle with lights out at 1900 h, and the hamsters on a 13:11 cycle with lights out at 1500 h. The female estrous cycle was determined by vaginal lavage, using a 0.9% saline solution. The fluid washed from the vagina was then placed on a microscope slide inside a vaseline ring and allowed to dry overnight. The slides were then stained using the Shorr staining method. The presence of red-stained, cornified epithelial cells every fourth day for hamsters, and every fifth day for rats, indicated that estrous had occurred within the last 12 hours.

For both species, there were changes in the frequency and content of interactions over the females' estrous cycle. While the details of these changes will be reported elsewhere (in preparation), for current purposes, it is sufficient to note that interactions involving the targets typical of play fighting were contacted by the males in both species and that in these cases, the females' defensive responses could be ascertained. Such contact was relatively infrequent throughout the estrous cycle, averaging around 11% for hamsters and around 14% for rats in encounters which were initiated by the males. Therefore, in order to evaluate the relative rates

of the females' use of different defensive tactics in response to playful contact, all the cases of 'playful interactions' were combined for the entire estrous cycle.

In hamsters, play fighting involves competition for access to the cheeks, which are gently nibbled if contacted. In about 80% of all defensive responses, the recipient of the cheek contact rotates around its longitudinal axis to a fully supine position (Pellis & Pellis, 1988a). Cheek nibbling also occurs in adult precopulatory interactions, and in females that have been hormonally induced into being receptive; such contact typically promotes immobility. When the male contacts the female's anogenital area, this immobility leads to lordosis. If the female defends herself against contact on the cheeks, she does so by swerving laterally away from the male (Pellis & Pellis, 1988b). In the present study, in which the females were cycling naturally, cheek contact was more likely to induce a defensive response; this most often involved a lateral swerve away from the male. Indeed, rotating to supine in response to cheek contact occurred in only 9.7% of cases. This suggests that the pattern present in play fighting reverses the situation in sexual encounters. That is, in play fighting, defenders are more likely to rotate to supine than to dodge away, whereas in sexual encounters, defenders are more likely to dodge than to turn to supine.

In rats, play fighting involves competition for access to the nape area, which is gently nuzzled if contacted (Pellis & Pellis, 1987). In the juvenile period, about 60% of all defensive responses involve the recipient of the nape contact rotating around its longitudinal axis to a fully supine position (Pellis & Pellis, 1987, 1990; Pellis et al., 1989). Nape contact has also been reported in precopulatory encounters (Pellis, 1993). In the present study, females that were contacted by their partners placing their nose on their nape or adjacent areas, rolled to supine in 24.1% of cases. This number may mask the true likelihood of using the supine defense when contacted on the nape. In the majority of cases, the male actively grasped the female's flanks or climbed onto the female's back before she rotated to supine. Indeed, in many cases, the male was contacting the nape as the female continued to move away; then, when he began to climb onto her back, she rotated to supine. Therefore, we subtracted all cases where the male was making mounting-like movements; this left a female supine response rate of 6.9%. In the majority of cases, the females typically used some evasive tactic, such as dodging away laterally. In play fighting, such evasion occurs in only about 25% of cases, and mounting rarely occurs. When mounting does occur, the recipient is unlikely to rotate to supine (Pellis & Pellis, 1990). The findings for rats are consistent with those of the hamsters—the most prevalent form of defense in play fighting is the least prevalent in precopulatory encounters.

When the developmental pattern in defense during play fighting is mapped, the peculiarity of the pattern in rats is even more marked. As already noted, the frequency of supine defense in voles closely matches the species-specific frequency of this tactic during precopulatory interactions (Pellis et al., 1989; Pierce et al., 1991); with the onset of puberty, the similarity becomes greater (Pellis & Pellis, 1998b). For Syrian golden hamsters, supine defense during play fighting is always the most common tactic, from shortly after weaning into early adulthood (Pellis & Pellis, 1988a).

In rats, from the periweaning period through to the juvenile phase, puberty and young adulthood, evasion remains between 20-30% (Pellis & Pellis, 1990,

1997). The most common form of defense involves rotation around the longitudinal axis of the body; this can take one of two forms. In the form already discussed, the defender rotates to a fully supine position. In the second case, the defender rotates its forequarters towards the attacker, but maintains ground contact with one or both hindpaws. From the partially rotated position, the defender can push the partner with its forepaws or with its rump or rear into a boxing position (Pellis & Pellis, 1987). It is the relative frequency of these rotatory tactics that change over age (Pellis, 2002a). When play fighting emerges in the periweaning period, the first rotatory defensive tactic to appear is partial rotation. Then, in the following week, with the onset of the juvenile phase, the complete rotation tactic replaces the partial rotation tactic as the most frequent form of playful defense (Pellis & Pellis, 1997). Finally, with the onset of puberty, there is another reversal, one which differs between the sexes. While the complete rotation tactic remains the most frequent defensive maneuver for females, it declines in males as the partial tactic becomes most frequent (Pellis & Pellis, 1990). This final pattern persists into early adulthood, even though the frequency of play fighting diminishes (Pellis & Pellis, 1991b; Smith, Forgie & Pellis, 1998). Note that neither form of rotatory tactic was found to be frequent in adult precopulatory encounters.

In adulthood, rats also differ from other murid rodents in that they retain play fighting and use it in functional contexts other than precopulatory interactions (Pellis, 2002b). Voles, deer mice, grasshopper mice and Djungarian hamsters (Pellis & Pellis, 1989, 1992a; Pellis et al., 1989; Pellis et al., 2000; Pierce et al., 1991), as well as Syrian golden hamsters and rats (see above), all use play-like contact and defensive behavior in their precopulatory encounters. In addition to their use of such playful behaviour during courtship, adult male rats use play fighting for same sex social affiliation and social testing. Subordinate male rats initiate more playful contact with the resident dominant male than they do with other subordinate males or females (Pellis & Pellis, 1991a; Pellis, Pellis, & McKenna, 1993; Smith et al., 1998), and when the dominant male playfully attacks subordinate males, the subordinate males mostly use the complete rotation tactic (Pellis & Pellis, 1992b), as is typical of juveniles. When responding to playful attacks by other subordinate males (Pellis et al., 1993) or females (Pellis & Pellis, 1990), or in the absence of dominance relationships (Smith, Field, Forgie, & Pellis, 1996), subordinate males mostly use the partial rotation tactic, as is typical of adults (Pellis, 2002a). Resident subordinates may also challenge the resident dominant male in escalating the intensity of play fighting by using the partial tactic more often (Pellis & Pellis, 1992b; Pellis et al., 1993); this is also the case for either dominants or subordinates when they encounter an unfamiliar male in a neutral arena (Smith, Fantella & Pellis, 1999). Indeed, when encountering strangers, at least on neutral ground, male rats follow social investigation—which mostly involves anogenital sniffing—with playful fighting. It is only when the playful fighting fails to establish a dominance relationship that rats escalate to serious fighting (Smith et al., 1998, 1999). As is the case for murid rodents in general, serious fighting is characterized by bites directed to the rump and lower flanks (Pellis, 1997). The functional modulation in the use of play fighting present in adult rats is well contrasted with findings on Syrian golden hamsters.

Dominance relationships among male Syrian golden hamsters become well established with the onset of puberty, by which time they have dispersed and be-

come solitary (Goldman & Swanson, 1975). If maintained in groups (Pellis & Pellis, 1988a) or pairs (Pellis & Pellis, 1993), the effects of dominance on play fighting can be evaluated. Unlike rats, in Syrian golden hamsters, the dominant initiates most of the play, and when play fighting does occur, both dominant and subordinate are most likely to use the complete rotation tactic (Pellis & Pellis, 1988a, 1993). Thus, there is no evidence in these hamsters that play is modified for manipulating social relationships with familiar animals. Using the same experimental procedures described above for the analysis of precopulatory behavior in hamsters, twelve pairs of unfamiliar males were introduced into a neutral test enclosure. After initially exploring the enclosure, the males approached one another and engaged in social investigation—mostly anogenital sniffing. In eleven of the pairs, one or both hamsters attacked aggressively. The twelfth pair, after an initial social investigation, stayed apart for the remainder of the 30 min trial. Thus, in this experiment, there was no evidence of any playful contact preceding the serious fights. Therefore, even though Syrian golden hamsters have a modified pattern of defensive behavior in juvenile play fighting, as do rats, unlike rats, as adults, these hamsters do not have the ability to modify functionally the content of play fighting in non-sexual contexts.

As can be seen from the above survey of the content of play fighting, not only is play fighting comprised of several components, but further, there are differing degrees of modification of those components. The comparative data strongly suggest that these components of play fighting and the ability to modify them involves dissociable mechanisms that can be subjected to independent evolutionary change. If this is so, then a question arises: what are the neural mechanisms which regulate these different features of play fighting?

### **Neural Mechanisms Regulating Play Fighting**

A simple mechanism that could account for these species differences in the content of play fighting is differential rate of maturation. In a comparative analysis, it was found that rodents with more complex play fighting are born less mature at birth (Pellis & Iwaniuk, 2000a). That is, play fighting is more complex in species which have more of their physical maturation taking place after birth. This association was further supported by the finding that the adults of primate species that engaged in more play fighting also had a greater proportion of their brain developing after birth (Pellis & Iwaniuk, 2000a). Indeed, primates with larger brains have longer lasting juvenile phases (Sacher & Staffeld, 1974), and species with longer lasting juvenile periods have more social skills to acquire (Joffe & Dunbar, 1997). That overall postnatal brain growth influences the content of play fighting is further suggested by comparing house mice and rats. Although the former have a relatively larger brain than the latter (Iwaniuk et al., 2001), proportionately less of the rat's brain is mature at birth (Pellis & Iwaniuk, 2000a). Consistent with the above hypothesis is that play fighting in house mice is rudimentary when compared to that of rats (Pellis & Pasztor, 1999). It could be suggested that if more of the brain is developed after birth, more systems are open to be influenced by postnatal experiences, including play itself and the experiences derived from engaging in play. Two pieces of evidence are counter to such a developmental explanation for the content of play.

Firstly, house mice are simpler than rats in most facets of their behavioral repertoire; their ability to learn new tasks is slower and new skills reach a lower level of sophistication (Whishaw et al., 2001). However, even though play fighting is rudimentary in mice, locomotor play is complex (see Table 1). Secondly, in rats, play fighting undergoes highly programmed changes during development (see above), and these changes are not greatly influenced by previous experience (Foroud & Pellis, 2002, 2003; Foroud, Whishaw, & Pellis, 2004). Further, in rats, the manipulation of specific neural systems and hormonal events during development lead to highly specific changes in only particular aspects of play fighting (Pellis, 2002a; Pellis, Pellis & Whishaw, 1992). These findings suggest that delayed growth does not dictate the content of the play itself, although lower rates of postnatal neural development may still enable the experiences derived from play to have greater opportunities to influence the fine-tuning and functional range of expression of particular neural systems. Nonetheless, based on the conclusion that delayed brain growth does not affect the overall developmental pattern and content of play fighting, it is again evident that a single brain size or brain growth explanation is unlikely to account for species differences in the content of play. Rather, specific neural mechanisms regulating specific components and features of play need to be identified.

A clue that multiple mechanisms, arranged in an hierarchical organization, are involved in regulating play fighting is provided by studies of rats decorticated shortly after birth (Panksepp et al., 1994; Pellis et al., 1992). Decorticated rats engage in play fighting and show the age-typical waxing and waning of playful attack. As with intact rats, decorticates defend themselves against 80-90% of nape attacks and use the evasive defense in 20-30% of attacks. What is different about them as compared to intact rats is that they fail to show the age-related switches in the partial and complete rotation defensive tactics; at all ages decorticates use the partial tactic at the adult-typical frequency (Pellis et al., 1992). Thus, in decorticates, play fighting continues to show the deviation from adult precopulatory behavior in that it emphasizes rotatory defense rather than evasion, even though the changes in the type of rotatory defense no longer occur. Another feature of play fighting that remains unaltered in decorticates is the reciprocal alternation of attacker and defender. For play fighting to remain playful, both participants have to be able to gain nape contact around 50% of the time. If one partner gains the advantage and then consistently fails to relinquish that advantage in favor of its partner, the partner may escalate the encounter into a serious fight (Pellis & Pellis, 1998a). Therefore, given that the main components of play fighting, the ability to reciprocate, the modification of the precopulatory pattern of defense, and the age-related increase and decrease in initiating play fighting are left intact in decorticate rats, they must all be controlled subcortically.

The age-related modulation of the type of rotatory defense used is dependent on cortical control, as is the ability of subordinate males to modulate their play appropriately with the identity of the play partner (Pellis et al., 1992). These two forms of modulation appear to involve distinct parts of the cortex. Neonatal ablation of the frontal cortex disrupts the partner-related modulation, but not the age-related modulation (Kolb, Pellis, & Robinson, in press), suggesting that more posterior cortical systems are involved in regulating the latter form of modulation. These mechanisms must act on the subcortical systems to regulate their activity

and so modify the content of play. With regard to these subcortical systems, it seems likely that the regulation of the motivation to engage in play fighting, as measured by the frequency of launching playful attacks, appears to involve the ascending mesolimbic dopaminergic system (Panksepp, 1998; Siviy, 1998). Indeed, changes in this system with age may account for the developmental waxing and waning of the frequency of play fighting (Spear & Brake, 1983) which is dependent on the frequency of initiating play (i.e., playful attack; Pellis & Pellis, 1990). The other neural systems remain unspecified at present, but there are clues.

Rats reared without social experience during the juvenile period are hyper-defensive when confronted by other rats or by painful stimuli (Byrd & Briner, 1999; Einon & Potegal, 1991; Potegal & Einon, 1989). Toning down such strong responses to unfamiliar situations and animals involves inhibition by the amygdala (Emery et al., 2001). Interestingly, the use of play fighting in adult courtship is more prevalent in primate species where the partners are least familiar with one another (Pellis & Iwaniuk, 1999b), and these species have a larger amygdala (Pellis & Iwaniuk, 2002). Indeed, play fighting is brief and simple in young monkeys with amygdala lesions (Bachevalier, Malkova, & Mishkin, 2001; Beauregard, Malkova & Bachevalier, 1995). Further, autistic children, for whom amygdala dysfunction is a part of their pathology, cannot sustain social play because of their inability to reciprocate (Gray & Tonge, 2001; Wetherby, Prizant, & Hutchinson, 1998). Our own preliminary data on the play fighting of amygdalectomized rats also suggest that by regulating defensiveness, the amygdala may be crucial for reciprocity to occur during play fighting, especially in situations of uncertainty (work in progress). Therefore, the amygdala is a prime candidate for being part of a key circuit for the control of some aspects of play (Burghardt, 2001). Within the framework outlined in this paper, one likely role of the amygdala may be in regulating reciprocity, which it could do by correctly interpreting the threat posed by a partner's movements (e.g., Damasio, 1999).

The defensive behavior patterns themselves must be controlled by the circuitry involving hypothalamic and brainstem systems (Panksepp, 1998; Kruk et al., 1983; Siegel & Pott, 1988). However, while the engagement of defensive tactics must include this system, it remains unknown what rostral mechanisms are involved in modifying the thresholds for their expression during play fighting. Such modification is necessary in the transition from species which use defense tactics with the same frequency as in adult precopulatory behavior (such as prairie voles) and in species which do not (such as rats). Clearly, it is still too early a stage to describe the neural wiring diagram for play fighting, but at least some of the key behavioral components have been fractionated and some of the possible neural mechanisms have been identified. A tentative model based on the present framework is possible.

When reconsidering the series of murid rodents as organizational grades rather than as clades, it is apparent that in making the transition from a level with simple play to one with more complex play, novel control mechanisms have been added (Table 3). That the pyramid in the table represents stages of evolutionary addition is supported by the observation that rats appear from the base to the apex. The Syrian golden hamster drops out at the penultimate rung, and so on. Each species shares all the preceding control mechanisms plus the additional one which is not present lower down. Therefore, from the point of view of constructing complex

play fighting, new levels of control need to be added. This is not say that when viewed cladistically some lineages are likely to have reduced levels of control, and so have simplified their play (Pellis & Iwaniuk, 1999a). Nonetheless, more complex play fighting involves a greater number of control mechanisms distributed over more of the brain, including the cortex. The question is how these different levels of control interact with one another. Again, there are some clues.

Table 3  
*Levels of Control in the Regulation of Play Fighting in Murid Rodents are Used to Categorize Different Species.*

Levels of control	Species
Cortical modulation of play fighting	<i>Rattus</i>
Changed thresholds of use of defensive tactics relative to those used in adult sexual encounters	<i>Rattus Mesocricetus</i>
Tactics that enhance reciprocity	<i>Rattus, Mesocricetus, Microtus ochrogaster, M. montanus, Phodopus, Psammomys, Onychomys, Peromyscus</i>
Defense	<i>Rattus, Mesocricetus, Microtus ochrogaster, M. montanus, Phodopus, Psammomys, Onychomys, Peromyscus, Mus</i>
Attack	<i>Rattus, Mesocricetus, Microtus ochrogaster, M. montanus, M. agrestis, Phodopus, Psammomys, Onychomys, Peromyscus, Mus, Notomys</i>

*Note.* *Rattus* appears in all rows indicating that rats possess all five control mechanisms, whereas *Notomys* only appears in one row indicating the presence of only one control mechanism over play in hopping mice.

The prefrontal cortex has been shown to modulate the output of the mesolimbic and nigrostriatal systems (Whishaw et al., 1992). Rats with prefrontal ablation show the age-related waxing and waning of playful attack typical of intact rats, but the relative amount of play initiated as adults is greater than that of intact rats (Kolb et al., in press). These findings suggest that even though the regulation of the motivation to play is organized in some complex of systems involving the basal ganglia and/or limbic structures (Panksepp, 1998), there is also an inhibitory control exerted from the cortex. In addition, the cortex can also modulate the defensive responses used at different ages (nonprefrontal cortex) and with different partners (prefrontal cortex). At present, it is not known whether these two cortical mechanisms regulate the subcortical systems separately, or whether they act through some third common cortical mechanism. However it is they act, the conduit to modulating the defensive content of play in different functional contexts is

likely to involve a subcortical neural circuit which includes the amygdala. Finally, the signals from this system regulate the output of defensive acts organized in hypothalamic-brainstem circuits. The connection between these two systems is also likely to have been chronically modified in some species where the defensive content of play fighting is modified relative to that in the adult behavioral system being mimicked (e.g., rats, Syrian golden hamsters). This schema of levels of control over play fighting provides some novel insights for dealing with the problem of the relationship between brain size and play outlined in the Introduction.

### Conclusions

Species with larger brains may have greater potential for complex play because they have more neural tissue available to add new levels of control. This may explain the positive association between brain size and play when comparing across classes (Fagen, 1981) and orders (Diamond & Bond, 2003; Iwaniuk et al., 2001; Ortega & Bekoff, 1987). If so, one possible avenue for species level comparisons is to evaluate whether species with more levels of neural control over play have larger brains. In this regard, the schema developed here for murid rodents may only be a limited skeleton of what may be needed for some other taxa. For example, preliminary data on juvenile rats interacting with juvenile Syrian golden hamsters suggest that the rats are unable to modify their pattern of play to accommodate the needs of the hamsters (work in progress). Reports of rats playing with humans (Panksepp, 1998) show that it is the humans who modify their species-typical behavior to accommodate the rat. In contrast, dogs playing with humans modify their behavioral responses (Rooney et al., 2000). Similarly, preliminary data suggest that older rats do not modify their age-typical pattern of play fighting to accommodate younger play partners (work in progress), as some primates appear to do (Fagen, 1981). Therefore, there may be additional levels of control that need to be characterized for different mammalian taxa. Indeed, it should be stressed that most of what we know about brain mechanisms regulating play is limited to rodents, especially rats (Vandershuren et al., 1997).

Finally, while we have concentrated on control mechanisms that are specific to the production and regulation of play fighting, there may also be non-specific features of neural organization that may influence the content of play. For example, we have already noted that in comparison to rats, house mice may have a more limited capacity for behavioral flexibility in a variety of tasks (Whishaw et al., 2001). It is likely that this difference may affect the degree to which rats can modify play as compared to mice. Among primates, hominoids have more sophisticated levels of cognitive function than do monkeys and prosimians, and, furthermore, not surprisingly, hominoids, especially humans, are able to incorporate more pretense into their playful routines (Parker & McKinney, 1999; Russon, Vasey, & Gauthier, 2002). Therefore, it is likely that a complete understanding of the relationship between brain size and play will require a delineation of both those neural mechanisms that are specific to play and of those that reflect more general changes in behavioral capacity.

### References

- Adamec, R. (1975). The behavioral basis of prolonged suppression of predatory attack in cats. *Aggressive Behavior*, **1**, 297-314.

- Aldis, O. (1975). *Play fighting*. New York: Academic Press.
- Allman, J. (2000). *Evolving brains*. New York: Scientific American Library.
- Balph, D. F., & Stokes, A. W. (1963). On the ethology of Uinta squirrels. *American Midland Naturalist*, **69**, 106-126.
- Barash, D. P. (1973). The social biology of the Olympic marmot. *Animal Behaviour Monographs*, **6**, 171-245.
- Barash, D. P. (1974). The social behaviour of the hoary marmot (*Marmota caligata*). *Animal Behaviour*, **22**, 256-261.
- Barash, D. P. (1976). Social behaviour and individual difference in free-living Alpine marmots (*Marmota marmota*). *Animal Behaviour*, **24**, 27-35.
- Barrett, P., & Bateson, P. P. G. (1978). The development of play in cats. *Behaviour*, **66**, 110-120.
- Bachevalier, J., Malkova, L., & Mishkin, M. (2001). Effects of selective neonatal temporal lobe lesions on socioemotional behavior in infant rhesus monkeys (*Macaca mulatta*). *Behavioral Neuroscience*, **115**, 545-559.
- Beauregard, M., Malkova, L., & Bachevalier, J. (1995). Stereotypies and loss of social affiliation after early hippocamectomy in primates. *Neuroreport*, **6**, 2521-2526.
- Bekoff, M. (1978). Mammalian dispersal and the ontogeny of individual phenotypes. *American Naturalist*, **111**, 715-732.
- Bekoff, M. & Byers, J. A. (1981). A critical re-analysis of the ontogeny and phylogeny of mammalian social and locomotor play: An ethological hornet's nest. In K. Immelman, G. W. Barlow, L. Petrinovich, & M. Main (Eds.), *Behavioral development: The Bielefeld interdisciplinary project* (pp. 269-337). Cambridge, UK: Cambridge University Press.
- Biben, M. (1979). Predation and predatory play behavior of domestic cats. *Animal Behaviour*, **27**, 81-94.
- Blumstein, D. T., & Armitage, K. B. (1998). Life history consequences of social complexity: A comparative study of ground-dwelling sciurids. *Behavioral Ecology*, **9**, 8-19.
- Burghardt, G. M. (1998). Play. In G. Greenberg & M. M. Haraway (Eds.). *Comparative psychology. A handbook* (pp. 725-735). New York: Garland.
- Burghardt, G. M. (2001). Play: Attributes and neural substrates. In E. M. Blass (Ed.), *Handbook of behavioral neurobiology, Vol. 13, Developmental psychobiology* (pp. 317-356). New York, NY: Kluwer Academic/Plenum Publishers.
- Burghardt, G. M. (2004). *The genesis of play: Testing the limits*. Cambridge, MA: MIT Press.
- Byers, J. A. (1999). The distribution of play behavior among Australian marsupials. *Journal of Zoology, London*, **247**, 349-356.
- Byers, J. A., & Walker, C. (1995). Refining the motor training hypothesis for the evolution of play. *American Naturalist*, **146**, 25-40.
- Byrd, K. R., & Briner, W. E. (1999). Fighting, nonagonistic social behavior, and exploration in isolation-reared rats. *Aggressive Behavior*, **25**, 211-223.
- Caro, T. M. (1981). Predatory behaviour and social play in kittens. *Behaviour*, **76**, 1-24.
- Coppinger, R., Glendinning, J., Torop, E., Mathay, C., Sutherland, M. & Smith, C. (1987). Degree of behavioral neoteny differentiates canid polymorphs. *Ethology*, **75**, 89-108.
- Damasio, A. R. (1999). *The feeling of what happens*. New York: Harcourt Brace.
- DeBry, R. W., & Sagel, R. M. (2001). Phylogeny of rodentia (mammalia) inferred from the nuclear-encoded gene IRBP. *Molecular Phylogenetics and Evolution*, **19**, 290-301.
- Diamond, J., & Bond, A. B. (2003). A comparative analysis of social play in birds. *Behaviour*, **140**, 1091-1115.
- Eibl-Eibesfeldt, I. (1951). Beobachtungen zur Fortpflanzungsbiologie und Jungendentwicklung des Eichornchens (*Sciurus vulgaris* L.). *Zeitschrift für Tierpsychologie*, **8**, 370-400.
- Eibl-Eibesfeldt, I. (1982). The flexibility and affective autonomy of play. *The Behavioral and Brain Sciences*, **5**, 160-162.
- Einon, D. F., & Potegal, M. (1991). Enhanced defense in adult rats deprived of playfighting experience as juveniles. *Aggressive Behavior*, **17**, 27-40.
- Emery, N., Capitano, J. P., Mason, W. A., Machado, C. J., Mendoza, S. P., & Amaral, D. G. (2001). The effects of bilateral lesions of the amygdala on dyadic social interactions in rhesus monkeys (*Macaca mulatta*). *Behavioural Neuroscience*, **115**, 515-544.
- Ebensperger, L. A., & Cofré, H. (2001). On the evolution of group-living in the New World cursorial hystricognath rodents. *Behavioral Ecology*, **12**, 227-236.

- Elliott, L. (1978). Social behavior and foraging ecology of the eastern chipmunk (*Tamias striatus*) in the Adirondack mountains. *Smithsonian Contributions to Zoology*, **265**, 1-107.
- Ewer, R. F. (1966). Juvenile behaviour in the African ground squirrel, *Xerus erythropus* (E. Geoff.). *Zeitschrift für Tierpsychologie*, **23**, 190-216.
- Fagen, R. F. (1981). *Animal play behavior*. New York: Oxford University Press.
- Fairbanks, L. A. (2000). The developmental timing of primate play. A neural selection model. In Parker, S. T., Langer, J., & McKinney, M. L. (Eds.), *Biology, brains, and behavior. The evolution of human development*. Santa Fe, NM: School of American Research Press.
- Felsenstein, J. (1985). Phylogenies and the comparative method. *American Naturalist*, **125**, 1-15.
- Ferron, J. (1975). Solitary play in the red squirrel (*Tamiasciurus hudsonicus*). *California Journal of Zoology*, **53**, 1495-1499.
- Ferron, J. (1981). Comparative ontogeny of behaviour in four species of squirrels (Sciuridae). *Zeitschrift für Tierpsychologie*, **55**, 193-216.
- Ferron, J. (1985). Social behaviour of the golden-mantled ground squirrel (*Spermophilus lateralis*). *Canadian Journal of Zoology*, **63**, 2529-2533.
- Ferron, J., & Ouellet, J.-P. (1991). Physical and behavioural postnatal development of woodchucks (*Marmota monax*). *Canadian Journal of Zoology*, **69**, 1040-1047.
- Fitzgerald, J. P., & Lechleitner, R. R. (1974). Observations on the biology of Gunnison's prairie dog in central Colorado. *American Midland Naturalist*, **92**, 145-163.
- Foroud, A., & Pellis, S. M. (2003). The development of "roughness" in the play fighting of rats: A Laban movement analysis perspective. *Developmental Psychobiology*, **42**, 35-43.
- Foroud, A., & Pellis, S. M. (2002). The development of 'anchoring' in the play fighting of rats: Evidence for an adaptive age-reversal in the juvenile phase. *International Journal of Comparative Psychology*, **15**, 11-20.
- Foroud, A., Whishaw, I. Q., & Pellis, S. M. (2004). Experience and cortical control over the pubertal transition to rougher play fighting in rats. *Behavioural Brain Research*, **149**, 69-76.
- Garland, T. Jr., Dickerman, A. W., Janis, C. M., & Jones, J. A. (1993). Phylogenetic analysis of covariance by computer simulation. *Systematic Biology*, **42**, 265-292.
- Goldman, L., & Swanson, H. H. (1975). Developmental changes in pre-adult behavior in confined colonies of golden hamster. *Developmental Psychobiology*, **8**, 137-150.
- Gomendio, M. (1988). The development of different types of play in gazelles: Implications for the nature and function of play. *Animal Behaviour*, **36**, 825-836.
- Gordon, N. S., Burke, S., Akil, H., Watson, S. J., & Panksepp, J. (2003). Socially-induced brain 'fertilization': Play promotes brain derived neurotrophic factor transcription in the amygdala and dorsolateral frontal cortex in juvenile rats. *Neuroscience Letters*, **341**, 17-20.
- Gouat, J., & Gouat, P. (1987). Le répertoire comportemental du goundi *Ctenodactylus gundi* (Rongeurs, Ctenodactylidae) II. Ontogénèse. *Mammalia*, **51**, 173-193.
- Gray, K. M., & Tonge, B. J. (2001). Are there early features of autism in infants and pre-school children? *Journal of Paediatrics and Child Health*, **37**, 221-226.
- Guard, H. J., Newman, J. D., & Roberts, R. L. (2002). Morphine administration selectively facilitates social play in common marmosets. *Developmental Psychobiology*, **41**, 37-49.
- Hall, S. L. (1998). Object play by adult animals. In M. Bekoff & J. A. Byers (Eds.), *Animal play: Evolutionary, comparative, and ecological perspectives* (pp. 45-60). Cambridge, UK: Cambridge University Press.
- Harper, L. V. (1976). Behavior. In J. E. Wagner & P. J. Manning (Eds.), *The biology of the guinea pig* (pp. 31-51). New York: Academic Press.
- Hole, G., & Einon, D. F. (1984). Play in rodents. In P. K. Smith (Ed.), *Play in animals and man* (pp. 95-117). Oxford, UK: Basil Blackwell.
- Holmes, W. G. (1995). The ontogeny of littermate preferences in juvenile golden-mantled ground squirrels: Effects of rearing and relatedness. *Animal Behaviour*, **50**, 309-322.
- Horwich, R. H. (1972). The ontogeny of social behavior in the gray squirrel (*Sciurus carolinensis*). *Zeitschrift für Tierpsychologie*, Supplement No. 8, 1-103.
- Huchon, D., & Douzery, E. J. P. (2001). From the Old World to the New World: A molecular chronicle of the phylogeny and biogeography of hystricognath rodents. *Molecular Phylogenetics and Evolution*, **20**, 238-251.
- Huchon, D., Madsen, O., Sibbald, M. J. J. B., Ament, K., Stanhope, M. J., Catzeflis, F., de Jong, W. W., & Douzery, E. J. P. (2002). Rodent phylogeny and a timescale for the evolution of

glires: Evidence from an extensive taxon sampling using three nuclear genes. *Molecular Biology and Evolution*, **19**, 1053-1065.

Iwaniuk, A. N., Nelson, J. E., & Pellis, S. M. (2001). Do big-brained animals play more? Comparative analyses of play and relative brain size in mammals. *Journal of Comparative Psychology*, **115**, 29-41.

Joffe, T. H., & Dunbar, R. I. M. (1997). Visual and socio-cognitive information processing in primate brain evolution. *Proceedings of the Royal Society of London: Biological*, **264**, 1303-1307.

Kingdon, J. (1974). *East African mammals: An atlas of evolution in Africa*. Vol. II. Part B (*hares & rodents*). London, UK: Academic Press.

Kolb, B., Pellis, S. M., & Robinson, T. E. (in press). Plasticity and functions of the orbital frontal cortex. *Brain and Cognition*.

Kruk, M. R., Van der Poel, A. M., Meelis, W., Hermans, J., Mostert, P. G., Mos, J., & Lohman, A. H. (1983). Discriminant analysis of the localization of aggression-inducing electrode placements in the hypothalamus of male rats. *Brain Research*, **260**, 61-79.

Kunkel, P., & Kunkel, I. (1964). Beitrage zur Ethologie des Hausmeerschweinchens *Cavia aperea f. porcellus* (L.). *Zeitschrift für Tierpsychologie*, **21**, 602-641.

Lewis, K. P. (2000). A comparative study of primate play behaviour: Implications for the study of cognition. *Folia Primatologica*, **71**, 417-420.

Maddison, W. P., & Maddison, D. R. (1992). *MacClade: Analysis of phylogeny and character evolution*. Version 3.05. Sunderland, MA: Sinauer.

Martin, Y., Gerlach, G., Schllötterer, C., & Meyer, A. (2000). Molecular phylogeny of European murid rodents based on complete cytochrome *b* sequences. *Molecular Phylogenetics and Evolution*, **16**, 37-47.

Mather, J. A., & Anderson, R. C. (1999). Exploration, play and habituation in octopus (*Octopus dofleini*). *Journal of Comparative Psychology*, **113**, 333-338.

Meaney, M. J. (1988). The sexual differentiation of social play. *Trends in Neuroscience*, **11**, 54-58.

Michaux, J., Reyes, A., & Catzeflis, F. (2001). Evolutionary history of the most speciose mammals: Molecular phylogeny of murid rodents. *Molecular Biology and Evolution*, **18**, 2017-2031.

Millar, S. (1981). Play. In D. McFarland (Ed.), *The Oxford companion to animal behaviour* (pp. 457-460). Oxford, UK: Oxford University Press.

Mitchell, G. (1979). *Behavioral sex differences in nonhuman primates*. New York: Van Nostrand Reinhold.

Montgelard, C., Bentz, S., Tirard, C., Verneau, O., & Catzeflis, F. M. (2002). Molecular systematics of sciurognathi (Rodentia): The mitochondrial cytochrome *b* and 12S rRNA genes support the anomaluroidea (Pedetidae and Anomaluridae). *Molecular Phylogenetics and Evolution*, **22**, 220-233.

Moynihan, M. H. (1998). *The social regulation of competition and aggression in animals*. Washington, DC: Smithsonian Institution Press.

Nowak, R. M. (1999). *Walker's mammals of the world*, 2nd edition. Baltimore, MA: The Johns Hopkins University Press.

Nowicki, S., & Armitage, K. B. (1979). Behavior of juvenile yellow-bellied marmots: Play and social integration. *Zeitschrift für Tierpsychologie*, **51**, 85-105.

Nunes, S., Muecke, E.-M., Anthony, J. A., & Batterbee, A. S. (1999). Endocrine and energetic mediation of play behavior in free-living Belding's ground squirrels. *Hormones and Behavior*, **36**, 153-165.

Ortega, J. C., & Bekoff, M. (1987). Avian play: Comparative evolutionary and developmental trends. *Auk*, **104**, 338-341.

Panksepp, J. (1998). *Affective neuroscience*, New York: Oxford University Press.

Panksepp, J., Normansell, L., Cox, J. F., & Siviy, S. M. (1994). Effects of neonatal decortication on the social play of juvenile rats. *Physiology and Behavior*, **56**, 429-443.

Parker, S. T., & McKinney, M. L. (1999). *Origins of intelligence: The evolution of cognitive development in monkeys, apes, and humans*. Baltimore, MA: The Johns Hopkins University Press.

Pasztor, T. J., Smith, L. K., McDonald, N. K., Michener, G. R., & Pellis, S. M. (2001). Sexual and aggressive play fighting of sibling Richardson's ground squirrels. *Aggressive Behavior*, **27**, 323-337.

- Pellis, S. M. (1980). *A developmental and comparative study in the understanding of play behaviour*. Unpublished Ph.D thesis, Monash University, Australia.
- Pellis, S. M. (1981). Exploration and play in the behavioural development of the Australian magpie *Gymnorhina tibicen*. *Bird Behaviour*, **3**, 37-49.
- Pellis, S. M. (1983). The frequency and pattern of play behaviour. *Bird Behaviour*, **4**, 57-62.
- 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. (1991). How motivationally distinct is play? A preliminary case study. *Animal Behaviour*, **42**, 851-853.
- Pellis, S. M. (1993). Sex and the evolution of play fighting: A review and a model based on the behavior of muroid rodents. *Journal of Play Theory and Research*, **1**, 56-77.
- Pellis, S. M. (1997). Targets and tactics: The analysis of moment-to-moment decision making in combat. *Aggressive Behavior*, **23**, 107-129.
- Pellis, S. M. (2002a). Sex differences in play fighting revisited: Traditional and non-traditional mechanisms for sexual differentiation in rats. *Archives of Sexual Behavior*, **31**, 11-20.
- Pellis, S. M. (2002b). 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., & Iwaniuk, A. N. (1999a). The roles of phylogeny and sociality in the evolution of social play in muroid rodents. *Animal Behaviour*, **58**, 361-373.
- Pellis, S. M., & Iwaniuk, A. N. (1999b). The problem of adult play: A comparative analysis of play and courtship in primates. *Ethology*, **105**, 783-806.
- Pellis, S. M., & Iwaniuk, A. N. (2000a). An analysis of the role of postnatal development in the expression of play fighting in primates and muroid rodents. *Developmental Psychobiology*, **36**, 136-147.
- Pellis, S. M. & Iwaniuk, A. N. (2000b). Adult-adult play in primates: Comparative analyses of its origin, distribution and evolution. *Ethology*, **106**, 1083-1104.
- Pellis, S. M., & Iwaniuk, A. N. (2002). Brain system size and adult-adult play in primates: A comparative analysis of the roles of the non-visual cortex and the amygdala. *Behavioural Brain Research*, **134**, 31-39.
- Pellis, S. M., & McKenna, M. M. (1992). Intrinsic and extrinsic influences on play fighting in rats: Effects of dominance, partner's playfulness, temperament and neonatal exposure to testosterone propionate. *Behavioural Brain Research*, **50**, 135-145.
- Pellis, S. M., & Pasztor, T. J. (1999). The developmental onset of a rudimentary form of play fighting in mice, *Mus musculus*. *Developmental Psychobiology*, **34**, 175-182.
- Pellis, S. M., & Pellis, V. C. (1983). Locomotor-rotational movements in the ontogeny and play of the laboratory rat *Rattus norvegicus*. *Developmental Psychobiology*, **16**, 269-286.
- Pellis, S. M., & Pellis, V. C. (1987). Play fighting differs from serious fighting in both target of attack and tactics of fighting in the laboratory rat *Rattus norvegicus*. *Aggressive Behavior*, **13**, 227-242.
- Pellis, S. M., & Pellis, V. C. (1988a). Play fighting in the Syrian golden hamster *Mesocricetus auratus* Waterhouse, and its relationship to serious fighting during post-weaning development. *Developmental Psychobiology*, **21**, 323-337.
- Pellis, S. M., & Pellis, V. C. (1988b). Identification of the possible origin of the body target which differentiates play-fighting from serious fighting in Syrian golden hamsters *Mesocricetus auratus*. *Aggressive Behavior*, **14**, 437-449.
- Pellis, S. M., & Pellis, V. C. (1989). Targets of attack and defense in the play fighting by the Djungarian hamster *Phodopus campbelli*: Links to fighting and sex. *Aggressive Behavior*, **15**, 217-234.
- Pellis, S. M., & Pellis, V. C. (1990). Differential rates of attack, defense and counterattack during the developmental decrease in play fighting by male and female rats. *Developmental Psychobiology*, **23**, 215-231.
- Pellis, S. M., & Pellis, V. C. (1991a). Role reversal changes during the ontogeny of play fighting in male rats: Attack versus defense. *Aggressive Behavior*, **17**, 179-189.
- Pellis, S. M., & Pellis, V. C. (1991b). Attack and defense during play fighting appear to be motivationally independent behaviors in muroid rodents. *Psychological Record*, **41**, 175-184.

- Pellis, S. M., & Pellis, V. C. (1992). An analysis of the targets and tactics of conspecific attack and predatory attack in northern grasshopper mice *Onychomys leucogaster*. *Aggressive Behavior*, **18**, 301-316.
- Pellis, S. M., & Pellis, V. C. (1992b). Juvenilized play fighting in subordinate male rats. *Aggressive Behavior*, **18**, 449-457.
- Pellis, S. M., & Pellis, V. C. (1993). The influence of dominance on the development of play fighting in pairs of male Syrian golden hamsters (*Mesocricetus auratus*). *Aggressive Behavior*, **19**, 293-302.
- Pellis, S. M., & Pellis, V. C. (1997). The pre-juvenile onset of play fighting in rats (*Rattus norvegicus*). *Developmental Psychobiology*, **31**, 193-205.
- Pellis, S. M., & Pellis, V. C. (1998a). The structure-function interface in the analysis of play fighting. In M. Bekoff & J. A., Byers (Eds.), *Play behavior: Comparative, evolutionary, and ecological aspects* (pp. 115-140). Cambridge, UK: Cambridge University Press.
- Pellis, S. M., & Pellis, V. C. (1998b). The play fighting of rats in comparative perspective: A schema for neurobiological analyses. *Neuroscience and Biobehavioural Reviews*, **23**, 87-101.
- Pellis, S. M., Pellis, V. C., & Dewsbury, D. A. (1989). Different levels of complexity in the play fighting by murid rodents appear to result from different levels of attack and defense. *Aggressive Behavior*, **15**, 297-310.
- Pellis, S. M., Pellis, V. C., & Kolb, B. (1992). Neonatal testosterone augmentation increases juvenile play fighting but does not influence adult dominance relationships in male rats. *Aggressive Behavior*, **18**, 437-447.
- 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.
- Pellis, S. M., Pellis, V. C., & McKenna, M. M. (1994). A feminine dimension in the play fighting of rats (*Rattus norvegicus*) and its defeminization neonatally by androgens. *Journal of Comparative Psychology*, **108**, 68-73.
- Pellis, S. M., Pellis, V. C., & Whishaw, I. Q. (1992). The role of the cortex in play fighting by rats: Developmental and evolutionary implications. *Brain, Behavior and Evolution*, **39**, 270-284.
- Pellis, S. M., Pasztor, T. J., Pellis, V. C., & Dewsbury, D. A. (2000). The organization of play fighting in the grasshopper mouse (*Onychomys leucogaster*): Mixing predatory and sociosexual targets and tactics. *Aggressive Behavior*, **26**, 319-334.
- Pellis, S. M., O'Brien, D. P., Pellis, V. C., Teitelbaum, P., Wolgin, D. L., & Kennedy, S. (1988). Escalation of feline predation along a gradient from avoidance through "play" to killing. *Behavioral Neuroscience*, **102**, 760-777.
- Pierce, J. D. Jr., Pellis, S. M., Dewsbury, D. A., & Pellis, V. C. (1991). Targets and tactics of agonistic and precopulatory behavior in montane and prairie voles: Their relationship to juvenile play fighting. *Aggressive Behavior*, **17**, 337-349.
- Pizzimenti, J. J., & McClenghan, L. R. Jr., (1974). Reproduction, growth and development, and behavior in the Mexican prairie dog, *Cynomys mexicanus* (Merriam). *American Midland Naturalist*, **92**, 130-145.
- Potegal, M., & Einon, D. F. (1989). Aggressive behaviors in adult rats deprived of play-fighting experience as juveniles. *Developmental Psychobiology*, **22**, 159-172.
- Power, T. G. (2000). *Play and exploration in children and animals*. Mahwah, NJ: Erlbaum.
- Purvis, A., & Rambaut, A. (1995). Comparative analysis by independent contrasts (CAIC): An Apple Macintosh application for analysing comparative data. *Computer Applications in the Biosciences*, **11**, 247-251.
- Rasa, O. A. E. (1984). A motivational analysis of object play in juvenile dwarf mongooses (*Helogale undulata rufula*). *Animal Behaviour*, **32**, 579-589.
- Rood, J. P. (1972). Ecological and behavioural comparisons of three genera of Argentine cavies. *Animal Behaviour Monographs*, **5**, 1-83.
- Rooney, N. J., Bradshaw, J. W. S., & Robinson, I. H. (2000). A comparison of dog-dog and dog-human play behaviour. *Applied Animal Behaviour Science*, **66**, 235-248.
- Roper, R., & Hinde, R. A. (1978). Social play behaviour in a play group: Consistency and complexity. *Child Development*, **49**, 570-579.
- Roth-Kolar, H. (1957). Beitrage zu einem Aktionssystem des Aguti (*Dasyprocta aguti aguti* L.). *Zeitschrift für Tierpsychologie*, **14**, 362-375.
- Rowe, D. L., & Honeycutt, R. L. (2002). Phylogenetic relationships, ecological correlates, and molecular evolution within cavioida (mammalia, rodentia). *Molecular Biology and Evolution*, **19**, 263-277.

- Rowley, I. (1974). *Bird life*. Sydney, Australia: Collins.
- Russon, A. E., Vasey, P. L., & Gauthier, C. (2002). Seeing in the mind's eye: Eye-covering play in orangutans and Japanese macaques. In R. W. Mitchell (Ed.), *Pretending and imagination in animals and children* (pp. 241-254). Cambridge, UK: Cambridge University Press.
- Sacher, G. A., & Staffeldt, E. F. (1974). Relation of gestation time and brain weight of placental mammals: Implications for the theory of vertebrate growth. *American Naturalist*, **108**, 593-615.
- Schaller, G. B. (1972). *The Serengeti lion*. Chicago, IL: University of Chicago Press.
- Shadde, A. R. (1943). The play of the American porcupines (*Ethrithizon d. dorsatum* and *E. epixanthum*). *Journal of Comparative Psychology*, **37**, 145-150.
- Siegel, A. & Pott, C. B. (1988). Neural substrate of aggression and flight in the cat. *Progress in Neurobiology*, **31**, 261-283.
- Siviy, S. M. (1998). Neurobiological substrates of play behavior: Glimpses into the structure and function of mammalian playfulness. In M. Bekoff & J. A., Byers (Eds.), *Play behavior: Comparative, evolutionary, and ecological aspects* (pp. 221-242). Cambridge, UK: Cambridge University Press.
- Smith, E. O. (1978). A historic view on the study of play statement of the problem. In E. O. Smith (Ed.), *Social play in primates* (pp. 1-32). New York: Academic Press.
- Smith, L. K., Fantella, S.-F., & 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, L. K., Forgie, M. L., & Pellis, S. M. (1998). Mechanisms underlying the absence of the pubertal shift in the playful defense of female rats. *Developmental Psychobiology*, **33**, 147-156.
- Smith, L. K., Field, E. F., Forgie, M. L., & Pellis, S. M. (1996). Dominance and age-related changes in the play fighting of intact and post-weaning castrated males (*Rattus norvegicus*). *Aggressive Behavior*, **22**, 215-226.
- Spear, L. P., & Brake, S. C. (1983). Periadolescence: Age-dependent behavior and psychopharmacological responsivity in rats. *Developmental Psychobiology*, **16**, 83-109.
- Steiner, A. L. (1971). Play activity of Columbian ground squirrels. *Zeitschrift für Tierpsychologie*, **28**, 247-261.
- Thierry, B., Iwaniuk, A. N. & Pellis, S. M. (2000). The influence of phylogeny on the social behaviour of macaques (Primates: Cercopithecidae, genus *Macaca*). *Ethology*, **106**, 713-728.
- Thor, D. H., & Holloway, W. R., Jr. (1984). Developmental analysis of social play behavior in juvenile rats. *Bulletin of the Psychonomic Society*, **22**, 587-590.
- Thor, D. H., & Holloway, W. R., Jr. (1985). Play soliciting behavior in prepubertal and postpubertal male rats. *Animal Learning and Behavior*, **13**, 327-330.
- Vanderschuren, L. J. M. J., Niesnik, R. J. M., & Van Ree, J. M. (1997). The neurobiology of social play behavior in rats. *Neuroscience and Biobehavioral Reviews*, **21**, 309-326.
- Verzi, D. H. (2001). Phylogenetic position of abalasia and the evolution of the extant octodontine (rodentia, caviomorpha, octodontinae). *Acta Theriologica*, **46**, 243-268.
- Viljoen, S. (1977). Behaviour of the bush squirrel, *Paraxerus cepapi cepapi* (A. Smith, 1836). *Mammalia*, **41**, 119-166.
- Wetherby, A. M., Prizant, B. M., & Hutchinson, T. A. (1998). Communicative, social/affective, and symbolic profiles of young children with autism and pervasive developmental disorders. *American Journal of Speech-Language Pathology*, **7**, 79-91.
- Whishaw, I. Q., Metz, G. A. S., Kolb, B., & Pellis, S. M. (2001). Accelerated nervous system development contributes to behavioral efficiency in the laboratory mouse: A behavioral review and theoretical proposal. *Developmental Psychobiology*, **39**, 151-170.
- Whishaw, I. Q., Fiorino, D., Mittleman, G., & Castaneda, E. (1992). Do forebrain structures compete for behavior expression? Evidence from amphetamine-induced behavior, microdialysis, and caudate-accumbens lesions in medial frontal cortex damaged rats. *Brain Research*, **576**, 1-11.
- Wilson, S. C., & Kleiman, D. G. (1974). Eliciting play: a comparative study. *American Zoologist*, **14**, 341-370.
- Wolgin, D. L. (1982) Motivation, activation, and behavioral integration. In R. L. Isaacson & N. E. Spear (Eds.), *The expression of knowledge* (pp. 243-290). New York: Plenum Press.

Received June 1, 2003.

Revision received August 18, 2003.

Accepted October 13, 2003.