

What is play fighting and what is it good for?

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Abstract Play fighting is a common form of play reported among species of mammals, birds, and some other taxa. The competition present in play fighting revolves around gaining some advantage, such as biting a partner without being bitten. The behavior simulated during play fighting need not be restricted to that present in adult serious fighting, but can involve competitive interactions derived from amicable behavior, such as sex and social grooming, or from nonsocial competition, such as predation. What unifies play fighting, irrespective of the functional behavior being simulated, is that it involves some degree of reciprocity, or turn taking, that requires that the competition be attenuated by cooperation. However, there are several different ways in which cooperation can be inserted into playful interactions, and these vary in use across different species. The moderation of competition with cooperation forces animals to monitor their own actions and those of their partners, and this common feature appears to be one vehicle through which the experience of play fighting in the juvenile period can train animals for greater psychological resilience. The monitoring and contextual adjustment of actions influences the development of executive functions of the brain, which, in turn, leads to the development of more adaptable adults.

Keywords Reciprocity · Targets · Tactics

Play fighting, or rough-and-tumble play, is a commonly reported form of play (Pellis & Pellis, 1998a) that occurs in a

wide range of species (Aldis, 1975; Burghardt, 2005; Fagen, 1981). As the term suggests, it is seen as a form of nonserious fighting, an image that has been reinforced by reports that in many species, the same body areas that are bitten or struck during serious fighting are also the ones that are competed over during play fighting (e.g., Aldis, 1975; Fox, 1969; Havkin & Fentress, 1985; Owens, 1975a, 1975b; Pellis, 1981; Symons, 1978). Such a view, however, does not adequately take into account the diversity of interactions that have been labeled as “play fighting.”

In Fig. 1, a sequence of play fighting is shown for a pair of domesticated juvenile rats (*Rattus norvegicus*). The rat on the left approaches another rat (a), and then, from the rear, reaches toward the nape of its neck with its snout (b). However, before contact can be made, the defender rotates around its longitudinal axis (c) to face its attacker (d). By moving forward, the attacker pushes the defender onto its side (e). The defender then rolls over onto its back as the attacker continues to reach for its nape (f–h). Once in the supine position, the defender launches an attack on its partner’s nape (i), but this fails due to its partner’s use of its hind foot (j, k). Eventually, the rat on top (l) is pushed off by the supine animal (m), which then regains its footing (n) and lunges towards its partner’s nape (o). The whole sequence involves repeated attack and defense of the nape of the neck, which if contacted is nuzzled with the snout (Pellis, 1988; Pellis & Pellis, 1987; Siviý & Panksepp, 1987).

In marked contrast to this playful fighting, rats engaged in serious fighting compete to bite their opponent’s lower flanks and rump (Blanchard, Blanchard, Takahashi, & Kelley, 1977; Pellis & Pellis, 1987). Moreover, playful fights that escalate into serious fighting not only involve a shift from targeting the nape to targeting the rump, but also the emission of various signals, such as piloerection, tail rattling, lateral display, and vocalizations that are associated with aggression (Grant, 1963; Kisko, Euston, & Pellis, 2015; L. K. Smith, Fantella, & Pellis,

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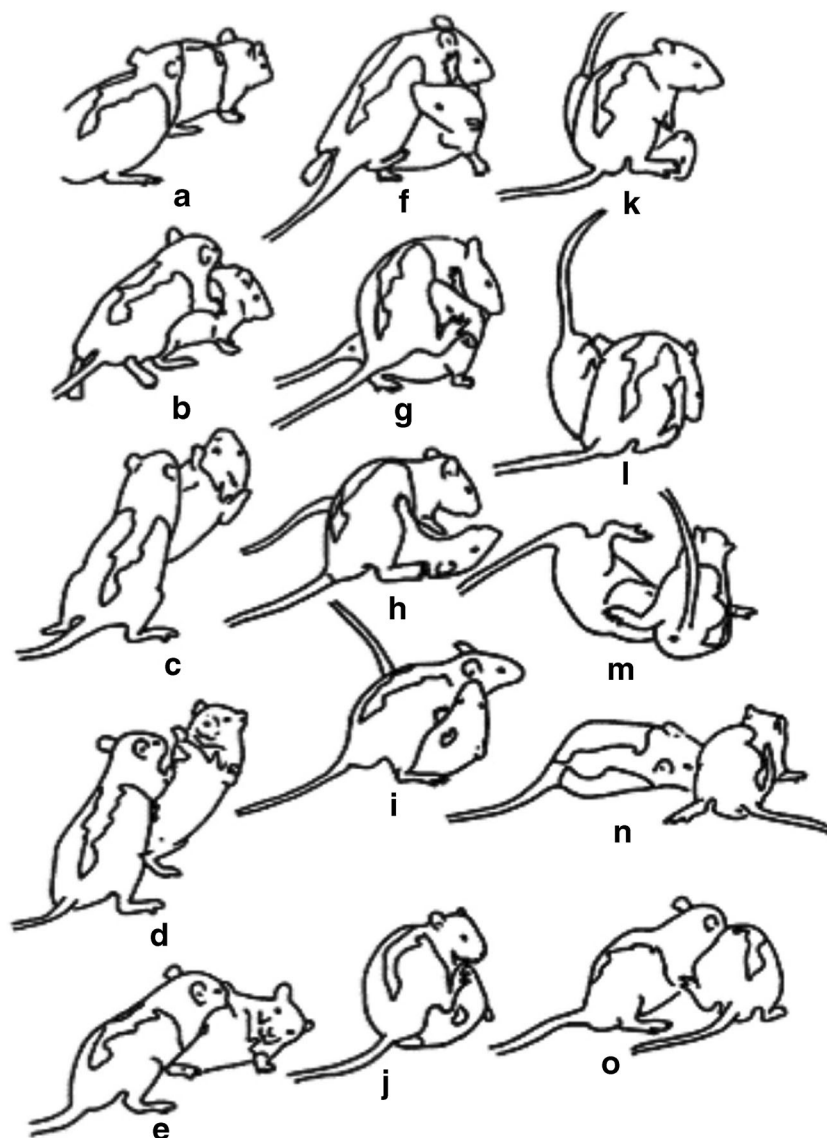


Fig. 1 Drawings taken from a filmed sequence of play fighting of two juvenile male rats show their repeated attack and defense of the nape of the neck. See the text for details. From “Play-Fighting Differs From Serious Fighting in Both Target of Attack and Tactics of Fighting in the

Laboratory Rat *Rattus norvegicus*,” by S. M. Pellis and V. C. Pellis, 1987, *Aggressive Behavior*, 13, p. 235. Copyright 1987 by John Wiley & Sons, Inc. Reprinted with permission

1999; Takahashi, 1986). Thus, even though the playful competition evident in the social play of rats has led authors to label it “play fighting” or “immature aggression” (e.g., Hurst, Barnard, Hare, Wheeldon, & West, 1996; Silverman, 1978; G. T. Taylor, 1980), it is not a simulation of adult aggression. The difference in targets distinguishes the two and also influences the types of tactics used and how they are executed (Pellis & Pellis, 1987). The insight that play fighting involves competition for some advantage, and that that advantage in many species involves contacting a particular body target on the partner (Aldis, 1975), has been critical in focusing attention on the targets competed over during play fighting (Pellis & Bell, 2011; Pellis & Pellis, 2015). However, such a focus has also revealed that, in many species, the targets of competition

during play fighting are not the same as those in serious fighting (Pellis, 1988). In rats, for instance, the target competed over during play fighting simulates precopulatory behavior, as the male attempts to contact the female’s nape with its snout and then uses this contact as an anchor to orient to her dorsum and mount (Pellis & Iwaniuk, 2004).

Comparison of the play fighting and serious aggression in other murid rodents (i.e., those in the same family as rats) supports this conclusion (Pellis, 1993). In all species examined, whereas serious fighting involves biting attacks to the lower flanks and dorsum (Pellis, 1997), play fighting involves competing for different targets. For example, in Djungarian hamsters (*Phodopus campbelli*), the competition is for access to the partner’s mouth, which is licked if contacted (Pellis &

Pellis, 1989); in Syrian golden hamsters (*Mesocricetus auratus*), it is the cheeks that are nibbled (Pellis & Pellis, 1988a); in montane voles (*Microtus montanus*) and prairie voles (*M. ochrogaster*), the nape of the neck is nuzzled (Pellis, Pellis, & Dewsbury, 1989); and in Northern grasshopper mice (*Onychomys leucogaster*), the lateral edge of the shoulder and side of the neck is licked and nuzzled (Pellis, Pasztor, Pellis, & Dewsbury, 2000). Although the play targets differ across these species, what they have in common is that these are the same targets that are contacted during adult pre-copulatory behavior (Pellis, 1993).

Similarly, nonagonistic targets are the focus of playful competition in a variety of other species from several mammalian lineages. For example, pottos (*Perodicticus potto*) and giant mouse lemurs (*Mirza coquerelli*) playfully grapple as they compete to groom one another (Epps, 1974; Pagés, 1978); marmots (*Marmota* spp) playfully grapple as they compete to make mouth-to-mouth contact, a body target associated with greeting behavior (Armitage, 1962; Barash, 1973); and finally, squirrels (*Sciurus carolinensis*, *Uroditellus* [formerly *Spermophilus*] spp), slender loris (*Loris tardigradus*), and fat-tailed lemurs (*Cheirogaleus medius*) playfully compete to mount one another (Goonan, 1993; Hoffman & Foerg, 1983; Horwich, 1972; Nunes, Muecke, Anthony, & Batterbee, 1999; Pasztor, Smith, MacDonald, Michener, & Pellis, 2001). The conclusion to be drawn from these species comparisons is that what has been labeled as “play fighting” may in fact involve partners competing for some advantage, but that advantage may not be limited to simulating serious fighting. Pairs of animals engaged in play fighting may be competing to gain the advantage typical of sex and other amicable social behaviors, predation, or conspecific aggression (Pellis, 1988). It could be argued that only play fighting simulating serious fighting should be labeled “play fighting,” but this creates several problems.

First, all five criteria developed by P. K. Smith (1997) to distinguish playful from serious fighting—(1) a resource, such as a piece of food, is not gained or protected; (2) the contact is restrained, or at least there are no combat-induced injuries; (3) there are frequent role reversals between a pair, with partners alternating as to which is the attacker and which is the defender; (4) even if chasing ensues following contact, further affiliation is likely; and (5) the presence of play signals—apply to all species that engage in play fighting, irrespective of the target of competition. Second, in some species play fighting with peers may involve competition for targets derived from more than one functional context (e.g., Goonan, 1993; Hoffman & Foerg, 1983; Pagés, 1978). For example, in Djungarian hamsters, about 70% of play fights involve competition for licking the mouth, and the remainder for biting the lower flanks and rump (Pellis & Pellis, 1989). Similarly, in species of ground squirrels (*Uroditellus*) play fighting can involve competition to mount one another, simulating sex,

or biting the partner’s shoulders, simulating conspecific fighting (Nunes et al., 1999; Pasztor et al., 2001), but in some of these species sex play encompasses 80% of all play fighting, whereas in others, 80% is aggressive play (Pellis & Iwaniuk, 2004). Those interactions that involve competing for nonagonistic targets are no less competitive than those involving agonistic ones, so it would seem arbitrary to label only some of these interactions as “play fighting.” Third, in most cases in the literature, the targets or other advantage being competed over are not specified, so it is not possible to know whether the play fighting being reported is a simulation of conspecific fighting or of something else.

What unifies all cases of play fighting is the appearance of animals competing in a way that does not look serious and does not lead to the outcomes that are typically associated with the behavior being simulated—delivering injurious bites or strikes (i.e., as conspecific aggression), lethal bites (i.e., as in predation), or copulation (i.e., as in sex). The distinction is in how the tactics of attack and defense are deployed in playful as compared to serious contexts (Pellis & Pellis, 1998b).

It is not what you compete for, but how you compete that matters

As is shown in Fig. 1, the original defender can launch counterattacks (i) and eventually become the attacker (o). Thus, the play fight involves a role reversal. Moreover, in play fighting, unlike in serious aggression or in sexual encounters in which the female is unreceptive to the male, rats and other animals engage in actions that facilitate such role reversals. In serious fighting, animals do their best to avoid being bitten or struck (Blanchard et al., 1977; Geist, 1978), but in play fighting, the animal in the advantageous position may relax its guard, giving its partner an opportunity to successfully reverse roles. For example, in rats, a common defensive configuration to adopt in play fighting is for the defender to roll over onto its back, thus protecting its nape, with its partner standing over it (Fig. 1h). From the on-top position, the attacker can use its forepaws to restrain and block the movements of its supine partner (Fig. 2a), thus maintaining an advantageous position. Indeed, in serious combat, this position is similarly used to block the supine animal’s ability either to escape or launch retaliatory attacks (Blanchard et al., 1977). However, sometimes during play fighting, the on-top rat does something never seen during serious fighting—it stands on top of its supine partner with all four of its paws (Fig. 2b). When standing on top with its hind paws anchored on the ground, the likelihood that an attack launched by the supine rat (see Figs. 1h–k) will be successful is about 30%, but when the on-top rat stands on its partner with all four of its paws, the success rate increases to over 70% (Pellis, Pellis, & Foroud, 2005).

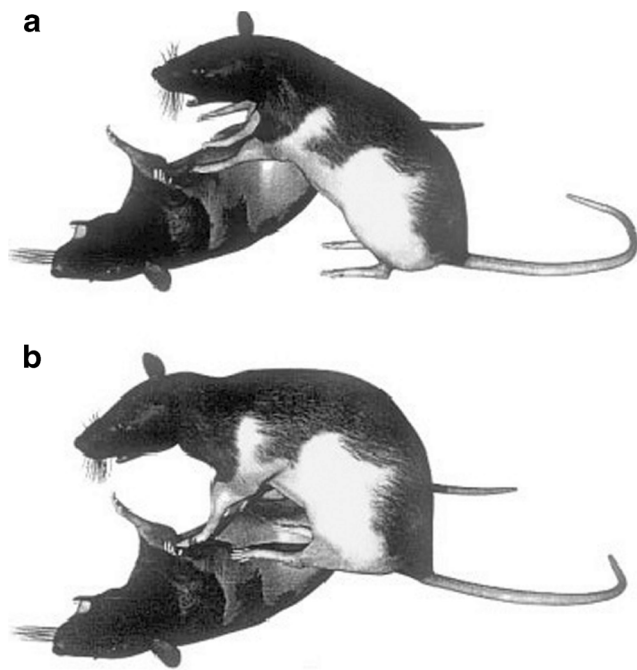


Fig. 2 Drawings taken from still frames of filmed sequences of play fighting in rats show two possible postures for the rat standing over its supine partner. In the first, (a) the partner on top stands with its forepaws holding its partner and with its hind paws anchored on the ground. In the second, (b) the animal on top stands on its supine partner with all four of its paws. From “The Development of ‘Roughness’ in the Play Fighting of Rats: A Laban Movement Analysis Perspective,” by A. Foroud and S. M. Pellis, 2003, *Developmental Psychobiology*, 42, p. 41. Copyright 2003 by John Wiley & Sons, Inc. Reprinted with permission

Irrespective of species differences in the targets or other advantages competed over and the species-typical tactics used (Aldis, 1975; Meaney, Stewart, & Beatty, 1985; Pellis, 1988), play fighting is characterized by competition that is curtailed by cooperation that enables role reversals. A first attempt to characterize turn taking in play fighting was the 50:50 rule (Altmann, 1962), which implies that, for play fighting to remain playful, the animals have to have equal chances of gaining the advantage (Dugatkin & Bekoff, 2003). Subsequent empirical studies have shown that play fighting can be substantially asymmetrical and still remain playful (Bauer & Smuts, 2007; Cordoni, Nicotra, & Palagi, 2016; Pellis, Pellis, & McKenna, 1993), although not if one partner completely dominates the interactions (Suomi, 2005; Wilmer, 1991). Thus, although the degree of reciprocity, or turn taking, can vary markedly with the species, age, sex, and dominance status of the participants (e.g., Bauer & Smuts, 2007; Biben, 1998; Cordoni & Palagi, 2011; Pellis et al., 1993), at least some degree of reciprocity is needed to sustain play (Bekoff, 2014; Palagi, Cordoni, Demuru, & Bekoff, 2016), and this is true whether the play fighting is derived from sex or aggression (Pellis & Pellis, 1988a, 1988b; Reinhart et al., 2010).

The many routes to restraint during play fighting

As is noted by P. K. Smith’s (1997) criteria for distinguishing play fighting from serious fighting, play signals are an integral part of what helps partners convey their playful intentions. Such signals include the open-mouth play face seen in primates and the play bow of canids. Many species can use these signals to avoid escalation from playful to serious fighting, or to de-escalate encounters if an action by one partner is misinterpreted. Such signaling has been extensively studied over several decades (for a recent review, see Palagi, Burghardt, et al., 2016). Less well studied has been how the rules of combat are followed during play fighting to ensure that a degree of reciprocity is maintained in these encounters (Pellis & Pellis, 2009), and this is the central focus of the present article. The rules followed to restrain competition with some level of cooperation, and so make play fighting reciprocal, can vary markedly across species; to our knowledge, three types of strategies have been characterized for keeping play fighting playful (Pellis & Pellis, 1998b, 2016a; Pellis, Pellis, & Reinhart, 2010).

(1) Self-handicap oneself while executing combat tactics

When launching an attack during serious fighting, an attacker often incorporates a defensive maneuver to reduce the risk of retaliation by its opponent (Geist, 1978). For example, in rats an attacker will maneuver to deliver a bite to its partner’s lower flanks. To defend itself, the defender raises itself on its hind feet, pointing its forepaws and teeth at its attacker’s head. As the attacker maneuvers to gain access to one of its opponent’s flanks, the defender pivots, continuing to orient its teeth at its attacker’s head, so that when the attacker lunges to bite, the defender can also then lunge, delivering a retaliatory bite, or strike with its forepaws, to the side of its opponent’s face (Blanchard et al., 1977). When confronting an upright defender, an attacker approaches in a broadside orientation (Blanchard et al., 1977). In this position, the attacker presses its flank against its opponent’s ventrum while keeping its own head out of reach, so that if the defender is successfully knocked over, the attacker can then swing around laterally and bite its opponent’s exposed flank (Pellis & Pellis, 1987). That is, the lateral attack combines a defensive element that protects the head from a retaliatory bite while simultaneously pressing the attack (Pellis & Bell, 2011; Pellis & Pellis, 2015).

During play fighting, rats are less likely to integrate such defensive actions into their attacks, which increases the likelihood of a successful counterattack by the partner (Pellis & Pellis, 1987). Indeed, as is illustrated in Fig. 2b, the animal in the more advantageous position can engage in a maneuver that reduces that advantage, thus increasing the likelihood of a successful counterattack by its partner, and so a role reversal (Pellis et al., 2005). Detailed studies of some primate species, such as spider monkeys (*Ateles geoffroyi*) and macaques

(*Macaca* spp), have similarly shown that, during play fighting, attack and defense are not integrated as effectively as they are in serious fighting, leading to attacks that expose the attacker to counterattack (Pellis & Pellis, 1997; Reinhart et al., 2010).

It is possible that the poor integration of attack and defense is due to a lack of motor competency in juveniles, rather than it being a characteristic of their play. That this is unlikely is suggested by the finding that adult rats follow the same rules as juveniles when play fighting but can also follow the rules involving close integration of attack with defense when they are engaged in serious fighting (Pellis & Pellis, 1987, 1998b). Indeed, the same individuals can switch from one to the other over the course of an interaction if it escalates from playful to serious fighting (Pellis et al., 1993; L. K. Smith et al., 1999). Although less systematic, our prolonged observations of play in spider monkeys (Pellis & Pellis, 1997, 2011) and in macaques (Pellis, Pellis, Reinhart, & Thierry, 2011; Reinhart et al., 2010) have revealed that, when playful encounters escalate to serious fighting, there is more integration of the tactics of attack and defense. Although much more empirical study is needed, it would seem to be the case that, at least in part, the different ways in which defense is used in combination with attack during play, as compared to serious fighting in these species is an attribute of play, not of age or experience. Cooperation in the play fighting of these species, then, involves restraining the effectiveness of at least some combat tactics.

(2) Execute combat actions without restraint, but refrain from taking advantage of a successful maneuver In the play fighting of the punaré (*Trichomys apereoides*), a South American rodent, the interactions are so vigorous that Thompson (1998) drew the conclusion that these animals “play to win”—the implication being that they do not restrain their combat actions. A comparison of the play fighting and serious fighting of another South American rodent, the degu (*Octodon degu*), illustrates an alternative way in which reciprocity can be incorporated into play fighting that yields interactions that involve less restraint on the actions performed (Pellis, Pellis, & Reinhart, 2010). During both playful and serious fighting, the attacking degu directs bites at its opponent’s shoulders. To protect against an opponent maneuvering to gain access to a shoulder, the animals grapple each other with their forepaws, rear on their hind feet, and maintain a face-to-face configuration. From this position a degu can maneuver, kicking its opponent in its ventrum with its hind feet, which, if successful, can knock an opponent onto its side or back. The actions are indistinguishable between the two types of fighting; what differs is the action taken by the winner of that combat maneuver.

In about 97% of the cases of serious fighting in degus, if an opponent is knocked over, the winner, on regaining its composure, immediately lunges to bite its opponent’s shoulder,

and only fails to do so if its opponent manages to regain its footing and blocks the attack. In contrast, in only 13% of cases is an attack pursued by the winning degu during play fighting. Rather, in the majority of cases, the encounter ceases, and in 30% of cases, the winner stops, stands on all four of its paws and remains inert, allowing the loser to regain its footing and launch an attack (Pellis, Pellis, & Reinhart, 2010). Cooperation in species like degus does not involve restraining the execution of combat tactics, but restraint in taking advantage of a successfully executed maneuver.

(3) Execute combat actions without restraint, do not refrain from taking advantage of a successful maneuver, but cease and desist if the loser signals submission The play fighting of various species of pigs can be so vigorous and so much like serious fighting that some authors use scare quotes—“play fighting”—implying that the interactions may be more agonistic than playful (Estes, 1993). Indeed, the same targets and tactics involved in serious fighting are also used in play fighting, with the reduced likelihood of combat injuries arising from the immaturity of their weapon systems, not from the lack of vigor in their actions (e.g., Newberry, Wood-Gush, & Hall, 1988; Rushen & Pajor, 1987; Šilerová, Špinka, Šárová, & Algers, 2010). An analysis of combat maneuvers in interactions that met P. K. Smith’s criteria of qualifying as play fighting was conducted on juvenile Visayan warty pigs (*Sus cebifrons*) to evaluate whether restraint was present (Pellis & Pellis, 2016a).

In members of the genus *Sus*, the snout is elongated and slender, with adult males having protruding canines—these are used to slash the side of the opponent’s shoulder and face. To gain access to the side of an opponent’s face or the side of its shoulders, an attacker attempts to maneuver so as to face its opponent in a frontal oblique or perpendicular orientation. The opponent can prevent this by turning to face its attacker. As both pigs jockey for an advantageous position from which to strike, they sustain a face-to-face configuration. From this configuration, they can “fence” with their snouts and attempt to slash one another on their faces and upper flanks (Barrette, 1986; Frädrieh, 1974). In such cases, especially in serious fighting, damage to the side of the face, including shredded ears, can arise (Rushen, 1989; Rushen & Pajor, 1987). To overcome each others’ defensive maneuvering, they can also push forward head-to-head, so that if one loses its footing, the winner can immediately lunge and strike at its opponent’s exposed flank. We analyzed this head-to-head pushing in Visayan warty pigs.

Unlike what is seen in the play fighting of rats, in this context, one piglet does not successfully overpower its opponent because the loser has slackened its defense (Pellis & Pellis, 1998b), but because one partner has managed to push harder. Once it has successfully overpowered its opponent, unlike degus (Pellis, Pellis, & Reinhart, 2010), the winner

does not refrain from prosecuting its attack. An attack is not prosecuted only if the pig that is overpowered flees or adopts a submissive posture (Pellis & Pellis, 2016a). That is, play fighting in warty pigs resembles serious fighting, in that a winner does not refrain from taking advantage of the opponent's weakened defenses (Geist, 1978), unless the loser signals submission (Bradbury & Vehrencamp, 2011). Given the close similarity, it could be argued that such interactions are indeed aggressive and not playful. Although this interpretation is possible, the interactions fit four of the criteria used by P. K. Smith (1997) that we could use to distinguish playful from serious fights: No resource was gained or protected, no combat-induced injuries occurred, subsequent affiliation was likely, and most critically, there were role reversals between attacker and defender. That is, unlike in serious fighting, and consistent with the reciprocity typical of play fighting, in 30% of cases the pig adopting the submissive posture launches a playful attack against its partner once it has ceased its attack (Pellis & Pellis, 2016a). Of course, the case in warty pigs may be specific to the peculiar combat tactics of the genus *Sus*, and may not apply to other species of the pig family that have differing combat styles (Cumming, 1984). We tested this possibility by applying the same methods used to study the Visayan warty pigs to the play fights in two other species of pigs from two different genera.

Red river hogs (*Potamochoerus porcus*) have long snouts like *Sus*, but they also have boney bumps on their foreheads, so that their fighting involves a combination of snout fencing and clashing foreheads, which can include mutual pushing. Even more divergent is the fighting of warthogs (*Phacochoerus africanus*). In this species, the snout is broad and flat, with boney lumps, and the adult males, especially, have large, laterally upcurving tusks. These facial structures facilitate face-to-face grappling and wrestling, which, with twisting and pushing, can force an opponent to fall off balance, allowing a strike to be delivered to an exposed flank (Cumming, 1984; Estes, 1993; Frädriich, 1974; Geist, 1966).

Two litters of red river hogs (San Diego Zoo, 2007: two males, one female; Calgary Zoo, 2009: two males, three females) and two of warthogs (Calgary Zoo, 2000: two males; Calgary Zoo, 2002: two males, two females) were observed and videotaped when still of suckling age (up to about three months). To compare with the case of the Visayan warty pigs, equal numbers of play-fighting sequences were analyzed in the head-to-head configuration for the different litters. In a head-to-head configuration, all three pig species can place the upper tip of their snout beneath the lower tip of their partner's jaw, and, with an upward and oblique movement, the head of the partner can be flung to one side, momentarily giving the attacking pig an opportunity to lunge at its partner's exposed shoulder. The warthogs also have another maneuver, not apparent in the other two species: One can press its forehead down on its partner's forehead and rapidly rotate its head,

with the focus of the rotation being on the forehead. The direction of this rotation is opposite to that involving the upward flick of the snout, and, if successful, has the effect of overbalancing the recipient, again providing a window of opportunity for the attacking warthog to lunge and strike at its partner's exposed shoulder. In a variation of head-to-head pushing, the red river hogs, having stockier bodies than either of the other two species, rely more on pushing forward, rather than maneuvering to swing around to the sides. Thus, there are similarities and differences in the combat styles of the three species.

Despite the differences in combat styles, as with the Visayan warty pigs, in the red river hogs and warthogs, in the vast majority of cases, when one piglet was overpowered, it was not because it had relaxed its forward pushing so that it lost its footing, but rather because the winner exerted sufficient force to overcome the forward push of the partner (red river hogs, 96.7% of 30 encounters; warthogs, 93.3% of 30 encounters). Similarly, in the majority of cases, once one piglet was overbalanced, the winner did not refrain from attacking its disadvantaged partner (red river hogs, 100% of 30 encounters; warthogs, 96.7% of 30 encounters). Therefore, all three species do not exhibit restraint in executing combat tactics, nor in taking advantage of a successfully executed maneuver. There are, however, species differences in the use of signals by which a loser can mitigate further attack.

In Visayan warty pigs, about half of the terminations involved one of the partners fleeing, and the remainder involved the pig either submissively crouching or abruptly turning away (Pellis & Pellis, 2016a). Analysis of play fights in which the terminating actions by both partners were unobstructed from view showed that, for both the red river hogs and the warthogs, crouching was rare or absent. However, they differed in the alternatives they used most frequently—warthogs fled in the majority of cases, and red river hogs mostly turned away (Table 1). Moreover, whereas in Visayan warty pigs and warthogs a rapid turning away rarely leads to the winner prosecuting the attack, in red river hogs the winning pig often lunges at and nibbles and rubs at its partner's exposed shoulder. In such cases, the pig that turns simply stands motionless until its partner ends the contact. It should be noted that the

Table 1 Comparison of termination events for play fights in three species of pigs, expressed as percentages of the total play fights observed

Species	Behavior		
	Crouch	Turn Away	Flee
Warty pigs*	30	20	50
Red river hogs** (<i>n</i> = 40)	0	75	25
Warthogs** (<i>n</i> = 40)	2.5	32.5	65

* From Pellis and Pellis (2016a), averaging the results from two samples.

** Samples based on equal numbers from the two contributing litters

contact on the shoulder is much more gentle following this turning away action than when the shoulder is attacked following the partner being knocked off balance. Although these species differences in signaling submission need to be assessed thoroughly and empirically, what is evident is that, in all three of these pig species, the withdrawal or signaling of submission is what leads to the immediate or eventual cessation of an attack. That is, cooperation arises neither from restraint in executing tactics, as in rats, nor from withholding taking advantage of a successfully executed tactic, as in degus, but from the winner of the combat exchange honoring the signals of submission of the loser.

As is shown above, different lineages of species incorporate cooperation in their play fighting in different ways, leading to species-typical levels of reciprocation. Also, as we have already noted, within a species variation in reciprocation is likely present, based on age, sex, and dominance relationships. For example, animals not familiar with one another may have different rates of reciprocation than those that are familiar with one another (e.g., Bauer & Smuts, 2007; Norman, Pellis, Barrett, & Henzi, 2015). Nonetheless, it should be noted that the examples cited above for spider monkeys, macaques, rats, degus, and the various species of pigs all involved animals that were familiar with one another. Moreover, juvenile rats have similar frequencies of role reversals whether they are playing with a littermate or an unfamiliar peer (Himmler, Himmler, Pellis, & Pellis, 2016). Therefore, it is reasonable to conclude that these are species-level differences in how reciprocation during play fighting is achieved.

Restrained competition is still competition

During play fighting in juvenile rats, counterattacks—in which the defending partner launches a nape attack (see panel i in Fig. 1)—occur in about 45% of encounters (Pellis & Pellis, 1990; Pellis et al., 1989), but the rate of role reversals is about 25%–30% (S. M. Himmler et al., 2016), suggesting that the recipient of a counterattack can successfully resist some of the counterattacks (see panel j in Fig. 1). That is, while rats engage in cooperative actions during play fighting to facilitate role reversals, they also actively compete to block their partner. Play fighting is thus a blend of competition and cooperation (Pellis & Pellis, 1998b; Pellis, Pellis, & Reinhart, 2010). Indeed, although play fighting in rats is associated with the activation of the brain's reward mechanisms (Siviy & Panksepp, 2011; Trezza, Baarendse, & Vanderschuren, 2010; Vanderschuren, 2010), simply gaining access to the partner's nape is only partially rewarding (Pellis & McKenna, 1995), suggesting that for play fighting to be fully rewarding, successful contact with the partner's play target has to be in the context of actively competing for that access (Vanderschuren, Acterberg, & Trezza, 2016).

In rats, virtually all play fights begin with one partner lunging at its partner's nape, with such attacks being defended against in 90% or more of cases (B. T. Himmler, Stryjek, et al., 2013; S. M. Himmler, Modlińska, et al., 2014). Therefore, directing an attack to a partner's nape almost invariably leads to the experience of having to compete to gain access to the nape. For other species, the probability of defensive response to a playful attack can be substantially less (Pellis & Pellis, 1998a; Pellis et al., 1989), which would make the experience of competition less likely for any given attack, or there may be cross-species variance in both the relative rewarding properties of gaining access to the play target and the competitive actions taken to gain such contact. In analyzing the play fights of pigs (see above), we noticed that, even though the shoulders were the targets, many encounters started with the attacker contacting its partner's face. We formally evaluated the pattern of play initiation in the warthogs, which exhibit the most extreme version of head-to-head wrestling.

Initiation of play fighting was scored as starting with head contact on either a partner's shoulder or the front of its face, but with the attacker approaching from the rear or side prior to contact. Attacks in which the recipient turned to face its attacker immediately prior to contact being made were not scored—only those interactions in which the attacker could freely choose between contacting the shoulder or head of the partner were included in the analysis. The first 20 such initiations occurring in the videotaped material were scored per litter (see above). Of the 40 attacks scored, 82.5% involved the attacker contacting the recipient head-to-head ($\chi^2 = 16.90$, $df = 1$, $p < .01$). The preference for initiating head contact is markedly illustrated when the initiator attacked a squatting pig from the side. In such cases, the attacker swerved around to orient to its partner's face, thus bypassing the exposed and vulnerable shoulder. When contacting its partner's head, the attacker then made wrestling movements (i.e., snout or forehead rotations), which led to the partner that had been squatting standing up and engaging in a head-to-head clash, with repeated attempts to gain access to each others' shoulders. That is, the initiating pig solicited a playful wrestle and then competed for access to the play target. The warthog example reinforces the view that playful competition to gain an advantage is as an important part of what makes play fighting rewarding (Pellis & McKenna, 1995; Vanderschuren et al., 2016).

The functions of play fighting

The kinds of experiences created by play fighting would likely influence the kinds of benefits that can be derived. A commonly held view is that because play fighting simulates the actions performed during serious fighting, the former provides

practice for the latter (e.g., Fagen, 1981; Groos, 1898; Pellis, 1981; P. K. Smith, 1982; Symons, 1978). The discussion above of what constitutes play fighting undermines this functional relationship. First, species in which partners compete for access to body targets derived from sex, grooming, or predation have limited opportunities to practice the tactics appropriate for accessing the targets of conspecific fighting. Second, even play fighting that simulates conspecific fighting could be more or less suitable as a means of practicing the tactics of combat, depending on whether the rules of reciprocity were followed. That is, following rules of reciprocity typical of rats, in which the combat tactics are executed with restraint, would provide poor practice, whereas following the rules used by pigs would provide strong opportunities for practicing the execution of combat tactics. Such variation may underlie the conflicting results as to whether juvenile play experience enhances adult combat skills (e.g., Blumstein, Chung, & Smith, 2013; Sharpe, 2005).

Irrespective of the origins of play fighting and the rules followed to sustain playfulness, a commonality of experience in all species that engage in play fighting points to a potential core function. Play fighting involves restrained competition, which requires participants to monitor their own actions and those of their partner continuously. Even though escalation is rare, the risk of play fighting escalating to serious fighting is present (Fagen, 1981) and primarily occurs when one partner uses excessive force or fails to follow the rules that allow for some reciprocity (Palagi, Burghardt, et al., 2016; Pellis & Pellis, 1998b). Moreover, during play fighting, again irrespective of the origins of the behavior being simulated, animals may even exaggerate the experience of a loss of control and dealing with unpredictable situations (e.g., Foroud & Pellis, 2003; Petrů, Špinka, Lhota, & Šípek, 2008). Thus, the experience of play fighting may train performers to keep calm when confronting unexpected, potentially dangerous situations, and so develop appropriate solutions (Pellis, Pellis, & Bell, 2010; Špinka, Newberry, & Bekoff, 2001). This may be achieved by play influencing the development of executive functions, such as attention, short-term memory, impulse control, and emotional regulation (Pellis, Pellis, & Himmler, 2014; Vanderschuren & Trezza, 2014).

Rats reared in isolation over the juvenile period—that is, from around weaning to sexual maturity (approximately between 24 and 50 days of age)—exhibit higher levels of stress and anxiety when confronted with threatening social and non-social situations (e.g., Arakawa, 2002; Lopes da Silva, Ferreira, de Padua Carobrez, & Morato, 1996; von Frijtag, Schot, van den Bos, & Spruijt, 2002); are hyperdefensive when confronting conspecifics, and so more likely to attract attacks (Byrd & Briner, 1999; Einon & Potegal, 1991; Potegal & Einon, 1989; van den Berg et al., 1999); and have reduced impulse control, responding to stimuli more rapidly than is appropriate (Baarendse et al., 2013). Moreover, rats reared in

isolation have altered development of brain areas, such as the prefrontal cortex, that are involved in regulating executive functions (Baarendse, Counotte, O'Donnell, & Vanderschuren, 2013; Hall, 1998; van Kerkhof, Damsteegt, Trezza, Voorn, & Vanderschuren, 2013). Of course, social isolation deprives animals of more than just the opportunity to engage in play fighting (Bekoff, 1976), so it is not possible to attribute the deprivation-induced changes solely to the lack of play experience. However, rearing juveniles with partners that either are not playful or provide a much reduced opportunity to play likewise leads to abnormal development of the prefrontal cortex and other neural systems, as well as altered pain thresholds and reduced cognitive abilities, including ones that are associated with dealing with social situations (Bell, Pellis, & Kolb, 2010; Einon, Morgan, & Kibbler, 1978; B. T. Himmler, Pellis, & Kolb, 2013; Schneider, Bindila, et al., 2016; Schneider et al., 2014; Schneider, Pätz, Spanagel, & Schneider, 2016), indicating that at least some of the deficits emerging from rearing in isolation arise from the lack of play fighting (Pellis & Pellis, 2006).

One possibility is that social isolation increases the animals' emotional reactivity, which can affect performance in a variety of social and nonsocial tasks, whereas the lack of play fighting experience may more specifically influence particular cognitive skills. For example, rearing a more playful strain of rats with a less playful strain of rats leads to the members of the more playful strain having deficiencies in social-cognitive tasks without any increases in anxiety and fear (Schneider, Bindila, et al., 2016). Rats reared in isolation have deficiencies in coordinating social actions in a food protection task (Pellis, Field, & Whishaw, 1999). Indeed, these rats react to the approach of the robber rat at a greater distance (Bell, 2014), indicating that these rats are hyperdefensive. Given that being reared with a nonplayful partner leads to atypical development of the medial prefrontal cortex (mPFC; Bell et al., 2010; B. T. Himmler, Pellis, & Kolb, 2013), some of the changes in behavioral and cognitive deficits in play-deprived rats may arise from altered development of this brain region. As expected, rearing rats socially but with damage to the mPFC produces animals that have difficulty coordinating their social actions during both play fighting (Bell, McCaffrey, Forgie, Kolb, & Pellis, 2009) and a food protection task (B. T. Himmler, Bell, et al., 2014). Most critically, the reduced social coordination in the food protection task among rats with damage to the mPFC is not as extreme as that present in the rats reared in isolation (Pellis et al., 1999), nor is their distance from their partner when they begin their food defensive action any different than among controls. Therefore, the mPFC damage reduces the rat's ability to coordinate actions effectively with those of its partner, but the damage seems to do so without making a rat hyperdefensive. That is, socio-cognitive skills are affected by damage to the mPFC, whereas being reared in social isolation affects both cognitive

skills and emotional regulation. Nonetheless, there is some evidence that play fighting experience does improve emotional reactivity (e.g., Mustoe, Taylor, Birnie, Huffman, & French, 2014; J. H. Taylor, Mustoe, Hochfelder, & French, 2015), suggesting that there may be species and context differences as to whether and to what degree play influences social and cognitive skills by attenuating the control over emotional reactivity (Pellis & Pellis, 2016b).

Whether or not the change occurs via improved emotional regulation, play fighting improves executive function (Pellis et al., 2014; Vanderschuren & Trezza, 2014). Moreover, whether in some species play fighting provides opportunities to practice the motor acts typical of the behavior system being simulated (e.g., play experience improves sexual performance in rats; Moore, 1985), the actions performed during play fighting challenge an animal's ability to control its performance (Foroud & Pellis, 2003; Petrú et al., 2008), and so provides opportunities to experience how to cope with unpredictable situations (Pellis, Pellis, & Bell, 2010; Špinka et al., 2001). Different lineages of species may have capitalized on such opportunities to varying degrees (Pellis et al., 2014). Indeed, species in which the predominant form of play involves locomotion and rotational movements of the head and body, rather than playful competition involving wrestling, such as in the house mouse (Pellis & Pasztor, 1999), if anything show a reverse relationship between the amount of play experience and emotional regulation (Richter, Kastner, Kriwet, Kaiser, & Sachser, 2016). In contrast, in the Syrian golden hamster, in which social play involves play fighting with extensive wrestling (Pellis & Pellis, 1988a), the prevention of such play in the juvenile period alters the development of the mPFC and reduces social skills (Burlinson et al., 2016). Therefore, for species in which a predominant form of play involves play fighting, it is certainly possible that one avenue through which play fighting could convey a selective advantage may be to enhance some of the benefits accrued from improved executive functions, and so improve resilience in the face of unpredictable disturbances.

Conclusion

The case of warthogs supports the overall evidence that the attack and defense associated with play fighting is a central part of the reward gained from these interactions (Pellis & McKenna, 1995; Vanderschuren et al., 2016). As the present review has made clear, for play fighting to remain playful, some degree of cooperation is necessary, to ensure some level of reciprocity. However, the rewards accrued from actually engaging in play fighting suggest that competition is also essential. During play fighting, animals perform actions that ensure cooperation and other actions that ensure the perpetuation of competition (Pellis & Pellis, 2016a; Pellis, Pellis, &

Reinhart, 2010). Obviously, one avenue for future research will be to unravel the reward mechanisms that fine-tune this balance (Vanderschuren et al., 2016).

In addition, from a functional perspective, it would be important to understand why species from different lineages have emphasized targets from different functional systems in their play, and also why the relative balance between competition and cooperation differs across species. Modern statistical comparative methods could be used to evaluate several hypotheses (O'Meara, Graham, Pellis, & Burghardt, 2015). For example, it appears that ground squirrel species that predominantly engage in playful competition by mounting tend to live in social systems that have little male–female contact, whereas species that predominantly engage in playful competition for biting agonistic targets tend to live in more socially coherent groups (Pellis & Iwaniuk, 2004). It could be hypothesized that the main target of competition during play fighting depends on a species' social system. The data on ground squirrels are limited, but a more intensively studied taxon, such as primates, could be used to test whether the predicted associations with social system were present. Similarly, comparison of play fighting in two species of macaques suggests that the species that retain play fighting as a tool for social assessment and manipulation in adulthood are also the ones that in their juvenile play incorporate more cooperative actions that are consistent with training the executive functions and that impinge on social skills (Ciani, Dall'Olio, Stanyon, & Palagi, 2012; Reinhart et al., 2010). Again, comparative techniques could be used to test whether the presence of adult–adult play in the species of a taxon, such as primates, predicts the presence of more cooperation in the play in the juveniles.

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