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The Cognitive Animal

Empirical and Theoretical Perspectives on Animal Cognition

Edited by: Marc Bekoff, Colin Allen, Gordon M. Burghardt

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Play is usually thought of as a phenomenon of childhood (Burghardt 1998; Power 2000). In some species, however, playful modes of behavior are retained into adulthood (Pellis and Iwaniuk 1999b). Most often, adult–adult play involves play fighting (Aldis 1975; Fagen 1981). Unlike play fighting in juveniles, where the evidence for its functions has been difficult to discern, play among postpubertal individuals is more clearly associated with fitness-enhancing consequences. The literature shows that when it occurs in subadults and adults, play fighting is used in two general contexts—social bonding and social testing (Pellis and Pellis 1996; Pellis and Iwaniuk 2000). That is, play fighting is a tool that can be used to assess and manipulate conspecifics (Breuggeman 1978). A comparison of species with and without this tool offers some insight into the value of such play.

While an adult male mouse or rat will attack a male intruder (R. J. Blanchard and Blanchard 1994), there is a striking species difference when they encounter one another in a neutral arena. Mice follow one of two options: They aggressively attack the opponent or ignore him (Brain 1981; R. J. Blanchard et al. 1979). Rats have a third option: They engage in playful fighting akin to that of juveniles (Smith et al. 1999).¹ Such play fighting may lead to the establishment of a dominance relationship as in colonies (Pellis and Pellis 1992; Pellis et al. 1993). If such play fails to resolve the relationship, the encounter may escalate into a serious fight (Smith et al. 1998, 1999). In rats, unlike mice, such play fighting leads to a social world with more shades of gray, and so a greater demand for more sophisticated information processing (Whishaw et al. 2001). Therefore, play fighting among adults can be used as a window into social cognition.

Two questions arise from the finding that adults use play fighting to assess and manipulate others (Breuggeman 1978; Pellis and Iwaniuk

2000). What kind of information about the other animal can be acquired via play, and what are the structural properties of play fighting that make it a suitable means of assessment and social manipulation? Studies in my laboratory of play fighting among adult rats (*Rattus norvegicus*) illustrate some of the possibilities.

Play and Social Information

Within a colony, adult male rats form a dominance hierarchy (D. C. Blanchard and Blanchard 1990; Calhoun 1963; Flannery and Lore 1977). When two unfamiliar male rats confront one another in a neutral arena, the home status of the unfamiliar opponents affects the pattern of play and aggression that ensues (Smith et al. 1999). All males initiate play with a subordinate less often than with a dominant, and are more likely to evade the playful contact of a subordinate. However, they are more likely to engage a dominant in more prolonged physical contact. That is, during these encounters, the unfamiliar animals appear to recognize each other's respective home-colony status. What is not known is whether the unfamiliar pairmates actually need to engage in play fighting to make that determination, or whether nonplayful cues can provide such information. Rats are known to recognize dominant males by olfactory cues (Brown 1985). Indeed, before play fighting begins, rats engage in mutual anogenital investigation. It is also possible that visual cues may be involved (Calhoun 1963), such as a “macho” swagger (Dittman 1992) or hypermasculine body proportions (Karen Dean, personal communication). Recent studies in my laboratory have shown that whatever these cues are, rats can make these judgments at a distance.

Under laboratory conditions, rats are typically maintained on a nutritious but boring diet of

processed rodent chow. Therefore, when they are offered a fat-rich and delectable treat such as a sunflower seed, they take it readily. However, they must first husk the seed, a task that takes them several days of practice before they achieve a high level of proficiency. When it is done properly, a rat can split the husk neatly into two halves (Whishaw et al. 1998). My postdoctoral research associate, Karen Dean, used seed husking to develop a sensitive test of social knowledge. Once this task is fully learned, both dominant and subordinate male rats maintain a high level of proficiency regardless of whether a dominant or a subordinate is present on the other side of a wire mesh partition in the test enclosure. However, when they are placed as an intruder in someone else's home cage, dominants and subordinates differ markedly in how they husk the seeds.

The dominant rat will continue to split his seeds neatly whether the dominant or subordinate resident is sitting on the opposite side of the partition. In contrast, the subordinate will perform normally if he is sitting next to the subordinate resident, but will shred the seed to pieces when the dominant resident is sitting next to him. That is, the subordinate's performance severely deteriorates in the presence of an unfamiliar dominant. It is important to note that in this test paradigm, the rats do not press against the wire partition and investigate one another; rather, they sit facing the experimenter, at least a body length away from each other. Therefore direct contact is not needed for a rat to recognize the relative status of the animal sitting next to it. Given that the resident's home cage is not washed before testing, the general odor of both residents, dominant and subordinate, must pervade the whole enclosure; this suggests that the intruders are using a combination of olfactory and visual cues to evaluate the neighboring animal (see Pellis et al. 1996). Whatever means they are using, they are doing so without having to interact physically. This suggests that when strangers meet, play is not necessary to assess the

status of the opponent. Rather, play may be used to assess other features of the opponent. The play that occurs between colony members offers a clue as to what that assessment may involve.

In their home colony, the subordinates initiate more playful encounters with the dominant than they do with each other (Pellis et al. 1993). Furthermore, when they are playfully contacted by a dominant, they are more likely to roll over onto their backs, as they did as juveniles (Pellis and Pellis 1987). When contacted by another subordinate, they are more likely to remain standing and to push against the attacker with their flank (Pellis et al. 1993), as is typical of a dominant male (Pellis and Pellis 1991, 1992). In the absence of dominance relationships, all postpubertal males are more likely to stand and push than to roll over to a supine position (Pellis and Pellis 1990; Smith et al. 1996, 1998, 1999). Subordinates' frequent soliciting of playful contact with dominants, and their juvenilelike response to those dominants, suggests that the play fighting is used as a means of maintaining "friendly" relations with the dominant (Pellis et al. 1993). However, not all subordinates are equally obsequious.

The greater the dominance asymmetry between pairmates, the more juvenilelike the playful responses by the subordinate (Pellis and Pellis 1992). Furthermore, it is those pairmates that are least asymmetrical in their play relations that are the most likely to escalate the playful encounter into a serious fight (Pellis and Pellis 1991). Similarly, when male rats that are unfamiliar with each other are placed in a neutral arena, the dominant-dominant combinations are the ones most likely to escalate into serious fights (Smith et al. 1999). Close inspection of those escalations suggests that the play fighting preceding the serious fight is rougher. These observations suggest that when animals are testing their opponent's ability to maintain or gain a position of superior dominance, the play can escalate into a quasi-aggressive intensity. Therefore there are two extremes in the style of play available to an individual: a gentler form, seen when a subordinate is

“sucking up” to a dominant, and a rougher form, seen when one rat is probing another for weaknesses. These differences in play intensity can be explicitly converted into formal rules of engagement, and so provide a basis for judging how such play can be used to assess and manipulate a partner.

The Rules Underlying Play Fighting

For play fighting to remain playful, it needs to follow the 50:50 rule (Aldis 1975; Altmann 1962). That is, both pairmates have to win close to 50 percent of the playful encounters. To achieve this, the rules of attack and defense differ from those in serious fighting (Pellis and Pellis 1998a). When an attack is launched during a serious fight, the attacking animal has to guard against retaliation from the opponent. To do so, the attacker typically incorporates some defensive tactic into its attack; this limits the defender’s opportunity to counterattack (Pellis 1997). Similarly, when defending itself against a serious attack, the defender uses an intensity of defense that reduces the likelihood of a successful penetration by the attacker (Pellis 1997). In contrast, during play fighting, the attacker does not typically incorporate defensive maneuvers into its attack; this facilitates successful counterattacks by the defender (Pellis and Pellis 1998a). Also, when defending itself against a playful attack, the defender uses an intensity of defense that is lower than that in serious fights; this increases the likelihood of a successful contact by the attacker (Pellis and Pellis 1998a). Therefore, in play fighting, the tactics of attack and defense are decoupled to ensure that both animals get to contact their partner successfully. Following such a rule structure in serious fighting would be suicidal, since an opponent could seize upon an unguarded moment with great severity (Geist 1971).

An examination of the instances where play fights escalate into serious fights reveals that one

of the partners, either when attacking or when defending, shifts the rule structure from the playful to the serious mode. This typically leads to the other animal switching from playful attacks to serious attacks (Pellis and Pellis 1998a). Nonetheless, bending the 50:50 rule provides a means of using play fighting for assessment and manipulation. For example, when a subordinate rat uses play fighting for social bonding with the dominant male in the colony, he bends the 50:50 rule in the dominant’s favor. However, when a subordinate uses play fighting to probe the dominant for weakness, he bends the rule in his own favor. In the second case, the subordinate can assess how much of a deviation from equality the dominant will tolerate before retaliating aggressively. In such a scenario, the subordinate may follow a simple rule of thumb—if the dominant tolerates this deviation away from the 50:50 rule, then escalate further until the status is reversed; but if the dominant starts to respond forcefully, then back down before the encounter escalates into a serious fight.²

Species Comparisons

As noted earlier, play fighting is used by adults in two functional contexts: social bonding and social testing. These can be further subdivided, with social bonding including courtship and sexual and nonsexual pair bonding. Similarly, social testing can include some form of jostling for social status within an established group or evaluating the social potential of a stranger. In species that play as adults, there is considerable variation as to whether play fighting is used in all or only some of these contexts (Pellis and Iwaniuk 1999b, 2000). Some comparisons of related species illustrate this diversity.

Both male rats and hamsters can engage in playful fights as a precursor to copulation (personal observation). However, rats, but not hamsters, also use play fighting for bonding with dominants in their home colony, and for testing

dominance relationships with both colony mates and strangers (Pellis et al. 1993; Pellis and Pellis 1993; Smith et al. 1999). Whereas both the slow loris (Erhlich and Musicant 1975) and the greater galago (Erhlich 1977) use play fighting within their colonies for social affiliation, only the galago uses play fighting in encounters with unfamiliar animals in a neutral arena (Newell 1971). Similarly, while subadult spotted hyenas appear to use play fighting for affiliation and hence integration into the clan (Drea et al. 1996), subadult brown hyenas preferentially engage the adults in play fights, indicating that they are probing for a position in the clan's dominance hierarchy (Mills 1990). What are needed are comparative studies that can explicitly evaluate the possible causal mechanisms that have generated this diversity (Pellis and Iwaniuk 1999b, 2000). Unfortunately, given the lack of information on most species, this is difficult to do at present.

An insight into why some species have chosen play as a solution for particular kinds of social problems would greatly enhance our ability to characterize the cognitive mechanisms involved. For example, comparative analyses of adult–adult play in primates indicate that both the sexual and nonsexual use of play is more likely in species with social systems that lead to lower levels of contact and familiarity among social partners (Pellis and Iwaniuk 1999b, 2000). Furthermore, it seems to be most common in species with relatively impoverished repertoires of signals useful for communication at a distance (Pellis and Iwaniuk 2000). Touch, which is necessary for play fighting to occur, may be a crucial means of evaluating a social fellow you cannot be sure about. Indeed, such information may also be valuable for individuals that know each other well. For example, following an argument, a “no” from your significant other in response to the question “Are you still mad at me?” may or may not reflect their true feelings. A touch on the shoulder when the question is asked obtains more honest information. Subtle perturbations in

rehearsed play routines between well-acquainted individuals may provide a means of evaluating changes in the relationship (Wolf 1984).

Conclusions

Several researchers have begun to analyze play in juveniles from a cognitive perspective (e.g., Allen and Bekoff 1997; Biben 1998; Thompson 1998). Two difficulties with this have emerged. First, there are not only superficial species differences in the content of the behavioral repertoire used in play, but there are also deep organizational differences (Pellis 1993; Pellis and Iwaniuk 1999a). Because of this, it is difficult to generalize from in-depth studies of single species. Therefore, broader comparative studies are needed even though these are more difficult to conduct (e.g., Lewis 2000; Parker and McKinney 1999). Second, as noted earlier, the fitness-enhancing outcomes of play by juveniles have been elusive. It is thus difficult to evaluate the variability present in play. The variability may reflect an inability to follow a plan or it may reflect adaptive adjustments that ensure a particular outcome is obtained. Clear end points would aid greatly in distinguishing between these possibilities. Shifting the focus to play between adults would help with both problems. The distribution of play in adulthood is more restricted and its content is less diverse than is the case for juveniles. Also, the play fighting present in postpubertal animals has more clearly discernible fitness-enhancing outcomes than is the case for play in juveniles. The use of an adult's perspective on play may also afford us an unexpected benefit—that of re-examining childhood play.

If the cognitive skills required for adults to engage in manipulative play fighting are taken as a developmental end point, then the play occurring in childhood can be reexamined for evidence that it is structured to enhance the development of those skills. Two lines of converging evidence support such a possibility. Even though social

deprivation studies are limited by difficulties in ensuring that only certain experiences are restricted (Bekoff 1976), species comparisons reveal some intriguing differences. Deprivation of social play in the juvenile phase produces severe cognitive deficits in rats, whereas comparable experiments on other laboratory rodents do not (Einon et al. 1978, 1981). Such comparisons suggest that while rats need juvenile play to develop cognitive skills, other species, even though they engage in play as juveniles, do not.

Evidence from my laboratory has shown that play fighting in muroid rodents resembles species-typical patterns of adult precopulatory behavior (Pellis 1993). The resemblance is in both the body targets attacked and in the defensive maneuvers used to block attacks. During post-weaning development, playful interactions involve the use of behavior patterns at frequencies typical of adult sexual encounters (Pellis and Pellis 1998b). This is not the case for rats. In adult sexual encounters, most of the female's defensive maneuvers involve evasion, whereas in play, most involve turning to face the attacker. Whereas the former limits body contact, the latter enhances it. Indeed, changes in tactics occurring at the onset of the juvenile phase and at puberty (Pellis and Pellis 1990, 1997a) ensure that the body contact in play is further enhanced and exaggerated. That is, the species of rodent that has a pattern of juvenile play most different from the adult behavior being mimicked uses play fighting as an adult social strategy and is the one most adversely affected if deprived of play as a juvenile. This offers the opportunity to link specific childhood experiences to particular sociocognitive skills in adulthood (Pellis et al. 1999).

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Notes

1. Whereas playful attacks in rats involve nosing the nape of the partner, agonistic attacks involve bites directed at the lower dorsum or the face (R. J. Blanchard et al. 1977; Pellis and Pellis 1987; Siviý and Panksepp 1987).
2. Some species have affiliative signals that demonstrate playful intention. When available, such signals may be able to increase the flexibility of the playful-serious gradient because they can be used to diffuse unwanted escalations (see Bekoff 1995; Pellis and Pellis 1996, 1997b).

References

- Aldis, O. (1975). *Play Fighting*. New York: Academic Press.
- Allen, C. and Bekoff, M. (1997). *Species of Mind*. Cambridge, Mass.: MIT Press.
- Altmann, S. A. (1962). Social behavior of anthropoid primates: Analysis of recent concepts. In *Roots of Behavior*, E. L. Bliss, ed., pp. 277–285. New York: Harper and Brothers.
- Bekoff, M. (1976). The social deprivation paradigm: Who's being deprived of what? *Developmental Psychobiology* 9: 499–500.
- Bekoff, M. (1995). Play signals as punctuation: The structure of social play in canids. *Behaviour* 132: 419–429.
- Biben, M. (1998). Squirrel monkey playfighting: Making the case for a cognitive training function for play. In *Animal Play. Evolutionary, Comparative, and Ecological Perspectives*, M. Bekoff and J. A. Byers, eds., pp. 161–182. Cambridge: Cambridge University Press.
- Blanchard, D. C. and Blanchard, R. J. (1990). The colony model of aggression and defense. In *Contemporary Issues in Comparative Psychology*, D. A. Dewsbury, ed., pp. 410–430. Sunderland, Mass.: Sinauer Associates.
- Blanchard, R. J. and Blanchard, D. C. (1994). Environmental targets and modeling of animal aggression. In *Ethology and Psychopharmacology*, S. J. Cooper and C. A. Hendrie, eds., pp. 133–157. New York: Wiley.
- Blanchard, R. J., Blanchard, D. C., Takahashi, T., and Kelly, M. J. (1977). Attack and defense behaviour in the albino rat. *Animal Behaviour* 25: 6222–6634.

- Blanchard, R. J., O'Connell, V., and Blanchard, D. C. (1979). Attack and defense behaviors in the albino mouse. *Aggressive Behavior* 5: 341–352.
- Brain, P. F. (1981). Differentiating types of attack and defense in rodents. In *Multidisciplinary Approaches to Aggression Research*, P. F. Brain and D. Benton, eds., pp. 53–77. Amsterdam: Elsevier/North-Holland Biomedical Press.
- Breuggeman, J. A. (1978). The function of adult play in free-ranging *Macaca mulatta*. In *Social Play in Primates*, E. O. Smith, ed., pp. 169–192. New York: Academic Press.
- Brown, R. E. (1985). The rodents II: Suborder Myomorpha. In *Social Odours in Mammals*. Vol. 1, R. E. Brown and D. W. MacDonald, eds., pp. 345–457. Oxford: Clarendon Press.
- Burghardt, G. M. (1998). Play. In *Comparative Psychology: A Handbook*, G. Greenberg and M. Harraway, eds., pp. 757–767. New York: Garland.
- Calhoun, J. B. (1963). *The Ecology and Sociology of the Norway Rat*. Washington, D.C.: U.S. Department of Health, Education, and Welfare, Public Health Service.
- Dittman, R. W. (1992). Body positions and movement patterns in female patients with congenital adrenal hyperplasia. *Hormones and Behavior* 26: 441–456.
- Drea, C. M., Hawk, J. E., and Glickman, S. E. (1996). Aggression decreases as play emerges in infant spotted hyaenas: Preparation for joining the clan. *Animal Behaviour* 51: 1323–1336.
- Einon, D., Morgan, M. J., and Kibbler, C. C. (1978). Brief periods of socialization and later behavior in the rat. *Developmental Psychobiology* 11: 213–225.
- Einon, D., Humphreys, A. P., Chivers, S. M., Field, S., and Naylor, V. (1981). Isolation has permanent effects upon the behavior of the rat, but not mouse, gerbil, or guinea pig. *Developmental Psychobiology* 14: 343–355.
- Erhlich, A. (1977). Social and individual behaviors in captive greater galagos. *Behaviour* 63: 192–214.
- Erhlich, J. F. and Musicant, A. (1975). Social and individual behaviors in captive slow lorises. *Behaviour* 60: 195–220.
- Fagen, R. (1981). *Animal Play Behavior*. New York: Oxford University Press.
- Flannelly, K. and Lore, R. (1977). Observations of the subterranean activity of domesticated and wild rats (*Rattus norvegicus*): A descriptive study. *Psychological Record* 2: 315–329.
- Geist, V. (1971). *Mountain Sheep*. Chicago: University of Chicago Press.
- Lewis, K. P. (2000). A comparative study of primate play behaviour: Implications for the study of cognition. *Folia Primatologica* 71: 417–421.
- Mills, M. G. L. (1990). *Kalahari Hyenas. Comparative Behavioural Biology of Two Species*. London: Unwin Hyman.
- Newell, T. G. (1971). Social encounters in two prosimian species: *Galago crassicaudatus* and *Nycticebus coucang*. *Psychonomic Society* 2: 128–130.
- Parker, S. T. and McKinney, M. L. (1999). *Origins of Intelligence*. Baltimore, Md: Johns Hopkins University Press.
- Pellis, S. M. (1993). Sex and the evolution of play fighting: A review and model based on the behavior of muroid rodents. *Play Theory and Research* 1: 55–75.
- Pellis, S. M. (1997). Targets and tactics: The analysis of moment-to-moment decision making in animal combat. *Aggressive Behavior* 23: 107–129.
- Pellis, S. M. and 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. and Iwaniuk, A. N. (1999b). The problem of adult play fighting: A comparative analysis of play and courtship in primates. *Ethology* 105: 783–806.
- Pellis, S. M. and Iwaniuk, A. N. (2000). Adult-adult play in primates: Comparative analyses of its origin, distribution and evolution. *Ethology* 106: 1083–1104.
- Pellis, S. M. and 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. and 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. and Pellis, V. C. (1991). Role reversal changes during the ontogeny of play fighting in male rats: Attack versus defense. *Aggressive Behavior* 17: 179–189.
- Pellis, S. M. and Pellis, V. C. (1992). Juvenilized play fighting in subordinate male rats. *Aggressive Behavior* 18: 449–457.

- Pellis, S. M. and Pellis, V. C. (1993). 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. and Pellis, V. C. (1996). On knowing it's only play: The role of play signals in play fighting. *Aggression and Violent Behavior* 1: 249–268.
- Pellis, S. M. and Pellis, V. C. (1997a). The prejuvenile onset of play fighting in laboratory rats (*Rattus norvegicus*). *Developmental Psychobiology* 31: 193–205.
- Pellis, S. M. and Pellis, V. C. (1997b). Targets, tactics, and the open mouth face during play fighting in three species of primates. *Aggressive Behavior* 23: 41–57.
- Pellis, S. M. and Pellis, V. C. (1998a). The structure–function interface in the analysis of play fighting. In *Animal Play. Evolutionary, Comparative, and Ecological Perspectives*, M. Bekoff and J. A. Byers, eds., pp. 115–140. Cambridge: Cambridge University Press.
- Pellis, S. M. and Pellis, V. C. (1998b). Play fighting of rats in comparative perspective: A schema for neuro-behavioral analyses. *Neuroscience and Biobehavioral Reviews* 23: 87–101.
- Pellis, S. M., Pellis, V. C., and 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., McKenna, M. M., Field, E. F., Pellis, V. C., Prusky, G. T., and Whishaw, I. Q. (1996). Uses of vision by rats in play fighting and other close-quarter social interactions. *Physiology and Behavior* 59: 905–913.
- Pellis, S. M., Field, E. F., and Whishaw, I. Q. (1999). The development of a sex-differentiated defensive motor pattern in rats: A possible role for juvenile experience. *Developmental Psychobiology* 35: 156–164.
- Power, T. G. (2000). *Play and Exploration in Children and Animals*. Mahwah, N.J.: Lawrence Erlbaum Associates.
- Siviy, S. M. and Panksepp, J. (1987). Sensory modulation of juvenile play in rats. *Developmental Psychobiology* 20: 39–55.
- Smith, L. K., Field, E. F., Forgie, M. L., and Pellis, S. M. (1996). Dominance and age-related changes in the play fighting of intact and post-weaning castrated male rats (*Rattus norvegicus*). *Aggressive Behavior* 22: 215–226.
- Smith, L. K., Forgie, M. L., and 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., Fantella, S.-L. N., and Pellis, S. M. (1999). Playful defensive responses in adult male rats depend on the status of the unfamiliar opponent. *Aggressive Behaviour* 25: 141–152.
- Thompson, K. V. (1998). Self-assessment in juvenile play. In *Animal Play. Evolutionary, Comparative, and Ecological Perspectives*, M. Bekoff and J. A. Byers, eds., pp. 183–204. Cambridge: Cambridge University Press.
- Whishaw, I. Q., Sarna, J. R., and Pellis, S. M. (1998). Evidence for rodent-common and species-typical limb and digit use in eating, derived from a comparative analysis of ten rodents. *Behavioural Brain Research* 96: 79–91.
- Whishaw, I. Q., Metz, G. A. S., Kolb, B., and 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.
- Wolf, D. P. (1984). Repertoire, style and format: Notions worth borrowing from children's play. In *Play in Animals and Humans*, P. K. Smith, ed., pp. 175–193. Oxford: Basil Blackwell.

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