JDP FORUM

Why Does Carnivore Play Matter?

Camille Ward
Department of Psychology
University of Michigan
rameses@umich.edu

Barbara B. Smuts
Department of Psychology
University of Michigan
bsmuts@umich.edu

The Tanner, Smale, and Holekamp study is the first to document the ontogeny of play behavior in wild spotted hyenas (*Crocuta crocuta*). In this Forum, we will discuss why such studies are important as well as why play needs to be studied at different levels of detail.

Studies like this one are surprisingly rare. Although play has been documented in all of the carnivore families, few systematic data on play exist for most of the more than 270 carnivore species, and information on play in the wild is even rarer. For example, we know that adult wolves and domestic dogs engage in social play, but we know very little about how common adult play in is in other social carnivores. We do not know if male carnivores engage in more rough and tumble play than females, as is the case in a number of other mammals (e.g., rats, horses, rhesus monkeys, humans). We also know little about when carnivore play begins, or whether players develop specific partner preferences, as they do in sable antelope, wild bison, rhesus monkeys, and domestic dogs. Lions have abundant opportunities to play when young because litters from different mothers are reared communally. Yet, despite many years of intensive study of wild lions, no systematic data on play are available.

These lacunae reflect a long-standing bias among researchers as a whole (with notable exceptions) to consider play less important than more "serious" behaviors like hunting, mating or fighting. Perhaps this reflects a Western tendency to sharply differentiate work and play. Work is what we must do to make a living and survive; play is just something fun we do when we don't have to work. Yet the very fact that play is so much fun should clue us in to its biological significance. Good play is as rewarding to many people as a fantastic meal or lustful sex. We love food and sex because they are necessary to survival and reproduction. Could the same be true for play?

Perhaps, but scientists have not reached agreement about the functions of play. The most commonly proposed benefits have to do with practicing some skills needed later

(e.g., components of mating or fighting) or developing affiliative bonds useful now, later, or both. It's easy to imagine how play might be beneficial, but it's much harder to actually test these hypotheses.

For example, suppose we are interested in the hypothesis that, among humans, juvenile social play is critical to successful social development. Experimental methods are of limited value in testing this hypothesis: We can't intentionally deprive humans of opportunities to play, and even if we ignore the ethical problems with conducting such experiments among nonhumans, it is difficult and perhaps impossible to prevent young animals from playing without depriving them of social interactions in general. But if not through experiments, then how?

We turn to the comparative method, a fundamental investigative approach in evolutionary biology. To use this method, we need information on various traits (like brain size or foraging behavior) from a wide variety of animals. When we compare the distribution of measures of these traits across a sample, an informative pattern may emerge. In fact, there exists a relationship between brain size and foraging behavior. Monkeys who feed on dispersed, hard-to-find resources have larger brains (in relation to body size) than monkeys who eat leaves and other foods that are abundant and easy to find. Similar results have been obtained for bats and carnivores. These results suggest that brain size is driven, at least in part, by the cognitive challenges of foraging.

The comparative method is very powerful, but for it to work, we need relevant data for a sufficiently large number and variety of species. This is one reason why the Tanner et al. study is so important—and why, if we are to understand play, we need many more studies of play in carnivores and other species.

Studying play (and other behaviors) in carnivores is important for a second, more specific, reason. Most attempts to model human social evolution are based on comparisons with nonhuman primates, because they are our closest relatives. However, several social carnivores (e.g., wolves, African wild dogs, lions, dholes) share a set of traits with human hunter-gatherers that do not occur in combination in any nonhuman primate species. These traits include cooperative hunting, cooperative protection of offspring, food-sharing with young by non-parents as well as parents, and cooperative territorial defense. For understanding certain human behaviors, comparisons with social carnivores may therefore prove as useful—or even more useful—than comparisons with other primates.

Suppose we are interested in whether aspects of social play in boys reflect the importance to our ancestors of cooperative hunting by men. Specifically, consider the hypothesis that social play helps boys develop skills to enable them to coordinate their actions with those of other group members during a hunt. If we were thinking only about our own order, Primates, we could test this hypothesis by comparing the frequency of specific maneuvers during juvenile social play in nonhuman primates that hunt cooperatively with those which do not. We would not get very far, however, because simultaneous hunting by several individuals does not occur in most primates, and even where it has been observed (as in chimpanzees), debate exists as to whether the hunting is truly cooperative.

Among carnivores, in contrast, many show cooperative hunting, whereas others hunt alone or show some combination of cooperative and solitary hunting. Interest-

ingly, closely related species can show very different behaviors. Lions in the African savanna, for example, are quintessential cooperative hunters, but as far as we know their closest relative, Asian tigers, hunt alone. A comparison of play behavior in tiger versus lion cubs might help identify play behaviors specific to cooperative hunters.

Continuing with this example, among the 36 species in the dog family (canids), some species are obligate cooperative hunters (African wild dogs) or obligate solitary hunters (fennec foxes); others mainly hunt in packs (gray wolves, dholes); some hunt mostly alone (South American grey foxes, Ethiopian wolves, red foxes); and still others, such as coyotes, hunt both in packs and alone, depending on habitat and prey (this is also true in lions). If juvenile play behavior is important to adult hunting skills, certain aspects of play (for example, how often juveniles coordinate joint ambushes on a third party during play) should be more similar in wild dogs and wolves than they are, for example, in wolves and their close relatives, jackals, who usually hunt alone. Along similar lines, it would be interesting to know whether boys show coordinated maneuvers during play that more closely resemble play behaviors among cooperatively-hunting carnivores than among nonhuman primates.

In short, these examples demonstrate that if we want to pursue an evolutionary perspective on human behavior, it is essential to include data from a wide variety of species, such as carnivores and primates, which have independently evolved particular patterns of social behavior and organization. A comparative approach can shed light on how similar selection pressures work on different taxa in broadly similar ways.

Two Ways of Studying Social Play

The study of social interactions, including play, can occur on two levels: the macro and micro levels. The macro level deals with overall group or population patterns, whereas the micro level deals with individual or dyadic variations and with the processes by which individuals or relationships change over time. Analyses aimed at examining the intricacies of play at both levels are essential to understanding the evolutionary processes responsible for shaping play behavior.

In their very thorough analysis, Tanner et al. employ a macro level approach to examine the ontogeny of play in wild spotted hyenas. They found that rates of play by immature animals did not vary by sex or intra-litter rank of the cubs. However, cubs of high-ranking mothers played more than those of low- or mid-ranking mothers. This is an interesting result that is difficult to interpret using the comparative method, since rank-related differences in play among young animals have rarely been studied. Additionally, cubs played more when prey availability was low, in contrast to meerkat pups, who played more when their nutritional status was good. To the best of our knowledge, the current work on spotted hyenas and recent research on the development of play in meerkats (*Suricata suricatta*,) are the only studies that describe and quantify the development of play in wild social carnivores.

We studied the ontogeny of play in another social carnivore—the domestic dog (*Canis lupus familiaris*)—using both macro and micro level analyses. In what follows, we first compare some of our findings for domestic dogs with the data on wild hyena

cubs (macro level). Then we describe deviations from population patterns in some dyads of dogs (micro level).

We collected data on four litters of dogs (three different purebred litters and one mixed-breed). In all cases, the dams of each litter were house dogs. Although the hyenas in the Tanner et al. study were from a wild population and dogs are a domesticated species, some researchers suggest that studying dogs living with humans is akin to studying them in their natural habitat. Data from hyenas were presented for cubs from 8–12 weeks of age, and our data from the dogs were based on puppies between 3–40 weeks old.

There were both similarities and differences between hyena and dog social play. In wild hyenas, males engaged in more play mounting than females, but we found no such sex differences in mounting within litters of dogs. Interestingly, play mounting in hyenas vanished at approximately 12 months of age in females and 16 months of age in males, but some male and female dogs continue to mount well into adulthood. It would be especially interesting to have data on sex differences and the development of play mounting in other social carnivores in which it occurs to be able to make cross-species comparisons.

In hyenas, males and females engaged in social play at roughly equal rates, and this was also true for dogs up until about 6 months of age. At 6 months, male dogs initiated play more often with other males than with females. However, these data on rates of play between the two species are only roughly comparable because Tanner et al. measured social play for hyenas based on rates of male and female play regardless of who initiated, and we measured play based on individual rates of initiation by sex and dyadic composition (i.e., female-female, male-male, female-male).

The findings described above were consistent in different puppy litters, but some dyads diverged from typical patterns. One example concerns the extent to which play is "fair." Some researchers have proposed that for a dyad to maintain play over time, winning and losing roles must be more or less equal (e.g., puppies take turns being in the "top dog" position); this is called the "50:50" rule. Other researchers have argued that during play-fighting, both animals usually "play to win," implying that significant asymmetry in roles reflects individual differences in ability or motivation to win. In the puppies overall, winning and losing roles within dyads deviated from 50:50, which is more consistent with the play-to-win hypothesis (we found the same among dyads of unrelated adult dogs). Some clear exceptions, occurred, however. Between 3–23 weeks of age, in one dyad of mixed puppies, both individuals won exactly 50% of play bouts, and a second dyad of Labrador retrievers adopted nearly equal roles (54 vs. 46% of wins.). The question then becomes why, during play, do some dyads end up with roughly equal wins and losses, whereas in the majority of dyads, one pup wins much of the time? Given the intensity of female-female competition within hyenas and the unusual pattern of female dominance over males, it would be very interesting to test the 50:50 rule for hyena playmates.

The overall tendency for puppies to behave as if playing to win went one step further for puppies between 27–40 weeks of age. During this time, littermates initiated play more often with individuals that they could dominate in the play context. However, in one dyad that consisted of two females, both initiated play with each other

more often than they initiated with any of their other littermates (i.e., they were each others' preferred play partners), even though their play was completely asymmetrical: Blue Puppy won 100% of play encounters with her sister, Pink Puppy. (Among adult dogs, we also observed dyads characterized by frequent play initiations by a dog who always lost to that partner.) Why did Pink Puppy choose to initiate play with a littermate who dominated her in 100% of all play encounters?

In standard statistical analyses documenting behavioral patterns by category (e.g., as a function of age, sex, or perhaps experimental treatment), variation is treated as noise, which is appropriate to what we call the macro level approach. However, new and interesting questions emerge when we also examine tendencies specific to certain individuals or relationships. This micro level approach opens the door to some exciting new possibilities for understanding both non-human and human-animal relationships.

Studying behavior at the level of relationships is not new but it remains a minority approach, no doubt in part because it is typically more time-consuming. However, the relative scarcity of relationship-centered research also reflects the fact that methods and concepts in the behavioral sciences have largely been developed to address macro level questions. More recently, the study of social relationships has been enriched by new theories and methods developed by systems researchers—that is, scientists who study phenomena in terms of whole systems, rather than focusing mainly on the parts. (In the examples we've discussed above, the system is the dyadic relationship, although it is also essential to examine systems at higher levels, such as triads and groups). This approach, often termed *dynamic systems theory*, views social relationships as complex systems that change over time. From this perspective, behavioral interactions are often best understood not as linear alternating action-reactions chains, but rather in terms of bidirectional causation, feedback loops, and emergent patterns at the relationship level (e.g., such as degree of symmetry/asymmetry in play roles). Dynamic systems theory has been used primarily to study human relationships, but its value in studying relationships in other animals is becoming increasingly realized.

Case studies are at the heart of the dynamic systems approach to understanding social relationships. We will illustrate the value of a case-study approach by examining the play relationship between two dogs who live with the first author. Acorn was a 6 year-old, 60 lb. female Doberman pincher when Sage, a male German shepherd, joined the household at 7 weeks, 12 lbs. They played from the start. Sage is now 3 years old and weighs 90 lbs. The two play every day, and Acorn is clearly in control of their play relationship. During play, she often self-handicaps by throwing herself on her back in front of Sage to entice him to move towards her. Sometimes he rushes in and takes advantage of her down position by biting at her neck or body. When he does this, she often leaps up and snarls while showing her teeth, snaps at him, and walks into him, forcing him to move backwards. They often repeat this process a number of times within a play bout.

An observer meeting these two dogs for the first time would immediately be struck by the way Acorn, 30 lbs. lighter and past her prime, totally dominates Sage during play (as well as in other contexts). However, their behaviors become understandable

given their history. From the day Sage arrived, Acorn ruled, both in and out of the play context, by showing her teeth at Sage, standing over him, taking objects from him, etc. She never harmed him, but she was relentless in making sure he knew who was boss. In other words, Acorn trained Sage to defer to her in many different situations, and she trained him well.

When Acorn and Sage play, we see lots of growling, body slamming, and other forceful behaviors. To the untrained eye, their play might look like fighting but, following Gregory Bateson, we think of their play as a kind of metacommunication. Metacommunication is communication about other communication; it often occurs right before or after an action that could be interpreted in different ways. Examples include humans smiling and changing tone of voice when teasing someone in order to show that they are joking or the dramatic play signals (e.g., the canine play bow) shown in many species that indicate that whatever follows is "just play."

We propose that entire play bouts or sequences of play bouts over time can function as metacommunication about the playing animals' relationships. In the case of Acorn and Sage, Acorn appears to be reminding Sage over and over that she is top dog, and Sage, by always deferring, seems to acknowledge this asymmetry (both inside and outside of play). It appears as if the rules of their relationship outside of play were established and continue to be maintained through play fighting. By using play and other special contexts (such as greetings, courtship, or ritualized fighting) to communicate about relationships, animals can convey intentions and emotions and negotiate and re-negotiate the terms of a relationship while minimizing the risk of injury or misunderstanding.

Through such interactions the partners co-create a sort of virtual reality that is definitely meaningful but not quite real in the same way that, say, fighting or mating is. Sometimes behaviors acceptable during play would never be tolerated outside of play. For example, during play, Sage can force Acorn to the ground or do a "chin over" (i.e., he puts the underside of his chin over the top of Acorn's neck). He has never directed either of these dominance-related behaviors to Acorn outside of the play context, but during play, the rules of their relationship are more relaxed and flexible. Such virtual reality for playing dogs may create an experience that is similar to the experience teenagers get hooked on when they hunt down the villain in video games or to children's experiences when they ask their parents to "be the monster" or go visit scary haunted houses around Halloween. In all of these scenarios, individuals can feel intense emotions, practice various strategies, and communicate about their relationships in a safe context. Of course, play fighting in dogs could always escalate into a real fight, but in our research experience, this very rarely happens between well-socialized dogs who are familiar with each other and get along in a non-play context. Perhaps experiences like play, where things happen that do not often occur during ordinary times, are the original virtual realities—ancient creations that may convey adaptive advantages in both humans and other animals.

In some cases, behaviors shown during play also occur outside of play, but the meaning of the behavior changes in different contexts. For example, when playing with Sage, Acorn will sometimes growl or snap at him, but she may follow that up with a play bow or by turning her back to him and shaking her head from side-to-side

(a somewhat idiosyncratic play signal not shown by all dogs). Play typically continues despite the growls and snarls. However, Acorn also growls at Sage outside of play. In one incident, she was on the bed resting. Sage entered the room, and Acorn growled at him. This growl, unlike her play growl, was deep and menacing. Her body was stiff, and her stare was hard and directly focused at Sage. Sage took one look at Acorn and knew this was not play. He scurried out of the room with his body low to the ground and his ears pinned completely back against his head. Both his body and ear positions indicated slight fear and submission.

Although Acorn and Sage have a specific play relationship that could change through time, Sage has a different play relationship with other dogs. For example, Sage plays with another male dog (Sam) frequently, and he tends to be much more forceful and domineering in his play style—pinning the other dog to the ground over and over again. Sage plays one way with Acorn and a completely different way with Sam. Given this, the nature of Sage's play can only be truly defined at the relationship or dyadic level.

We are not suggesting that an analysis of play or any other social behavior at the micro level should replace data collected at the macro level. However, we do think that micro level analyses should be used alongside macro level, population-based studies to enrich our understanding of socio-biological behavioral processes and take into account interesting variation at the relationship level. Additionally, micro-level cross-species comparisons of social play could increase our understanding of the interplay between cognitive and emotional skills during development.

Cross-species comparisons of rough-and-tumble play may prove especially interesting, since in this context actions are the primary medium of communication in humans and nonhumans alike. Such comparisons could help us to understand why evolution has maintained in children the desire for such intimate, physical engagement, and what children might lose if opportunities for this kind of play continue to diminish. We hope to see more studies that focus on the development of social play in young animals in their natural habitats, including those who populate the playground and schoolyard.

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