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# Ontogenetic Variation in the Play Behavior of Spotted Hyenas

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**Abstract:** *Despite the fact that play behavior is common during the early post-natal development of many mammals, it remains a process about which we know remarkably little. In a population of free-living spotted hyenas* (Crocuta crocuta) *1–30 months old, we documented ontogenetic patterns in rates of five types of play: social play, romping, object play, play-mounting and non-nutritive chewing. Because spotted hyenas exhibit several sexually dimorphic traits that are "sex-role reversed" relative to those found in other mammals, we also inquired about sexual dimorphism in rates of play. In addition, we tested hypotheses about the environmental factors that influence rates of play in hyena cubs 2–4 months old, the period during which play occurs most frequently. Social play occurred at higher rates, and continued for a longer period during ontogeny, than did any other type of play. Whereas social play is more frequent in males than females of many other mammalian species, this was not the case in spotted hyenas; this may be related to female dominance later in life in these animals. However, as is typical of other mammals, male hyena cubs engaged in play-mounting at much higher rates than did females. At 2–4 months of age, cubs of high-ranking mothers exhibited higher rates of social play than did cubs of low-ranking mothers. These varying ontogenetic patterns suggest that some benefits derived from play may be immediate, whereas other benefits may be deferred until later stages of development. They also suggest that the genetic and neuroendocrine mechanisms mediating expression of this heterogeneous behavior most likely vary among different forms of play. These suggestions may apply to play in humans as well as in hyenas. Thus, although the ontogenetic patterns and forms of play differ between hyenas and humans, the underlying mechanisms and the long-term benefits of play behavior may, in fact, be remarkably similar.*

## Introduction

Play is one of the most ubiquitous developmental processes known to occur in mammals, yet it also remains one of the most poorly understood. Because little is currently known about its functions, we adopt the structural definition of play suggested by Bekoff and Byers (1981, pp. 300–301), as "any post-natal motor activity that appears to be purposeless, in which motor patterns from other contexts may often be used in modified forms and temporal sequencing." Although this definition implies that play may serve no purpose, the frequency with which play occurs among juveniles, its wide taxonomic distribution (Fagen, 1981), and its costs with respect to energy expenditure and predation risk (Harcourt, 1991) suggest that play probably has important fitness consequences in the lives of mammals. Bekoff (1984) and Byers (1998) have argued that careful documentation of the occurrence of play during ontogenetic development in a wide array of species is a necessary prerequisite for evaluating alternative hypotheses that suggest specific functions of play. Among mammals, rates of play are frequently highest, and the forms of play most diverse, in primates and carnivores (Fagen, 1981). Thus, the study of play in members of these orders may provide useful insights into the adaptive significance of these behaviors. Here we report on play behavior in a highly gregarious carnivore, the spotted hyena (*Crocuta crocuta*).

Spotted hyenas live in complex social groups, called clans, which may contain up to 90 individuals (Kruuk, 1972). Every clan is structured by a strict linear dominance hierarchy, and an individual's position in the hierarchy determines its priority of access to food (Engh et al., 2002; Kruuk, 1972). Juvenile hyenas "inherit" the social ranks of their mothers (Holekamp & Smale, 1993; Smale, Frank, & Holekamp, 1993) via the same mechanisms as those operating in cercopithecine primates (Engh, Esch, Smale, & Holekamp, 2000).

Female *Crocuta* give birth in an isolated natal den to litters of one, two, or rarely three cubs. Cubs remain at the natal den for the first 2–5 weeks of life (East, Hofer, & Turk, 1989; Kruuk, 1972). They are then brought to the clan's communal den where the cubs of multiple females are sheltered together in an underground burrow system. Cubs live in a communal den until 8–12 months of age, after which they cease using the den for shelter, and begin traveling around the clan's territory with their mother. The communal den serves as the social center of the clan and is periodically visited by all clan members. When older hyenas are present at the den, cubs emerge to nurse, rest, and play.

As in other mammals, the play behavior exhibited by hyenas and other carnivores takes a variety of forms. These include play-fighting, sexual play, object play, and solitary locomotor play. Although it is widely recognized that each form of play behavior might have its own function, and thus offer unique benefits to the individual, it is not always clear whether such benefits are immediate for the developing animal or deferred until adulthood (Pellegrini & Smith, 1998). One of the goals of this study was to assess the various forms of play behavior exhibited by spotted hyenas in their natural habitat, and to document the relative frequency at which each form of play occurs throughout ontogeny. Like Byers (1998), we view this as a critical first step toward understanding the functional significance of each type of play.

Another goal of our study was to evaluate sexual dimorphism in play behavior. In many mammals (Bekoff, 1974), including humans (Hines, 2003), some forms of play appear strongly sexually dimorphic whereas others do not. In those species for which the physiological substrates of play have been examined, sexually dimorphic forms of play are mediated by pre- or early post-natal exposure to androgenic hormones or their metabolites (monkeys, Goy, 1996; Goy, Bercovitch, & McBrair, 1988; Goy & Wallen, 1979; humans, Hines, 2003; ground squirrels, Nunes, Muecke, Anthony, & Batterbee, 1999).

The spotted hyena is a particularly interesting species in which to examine sexual dimorphism in play behavior because many aspects of the behavior and morphology of female hyenas are heavily masculinized. For example, females are more aggressive than males (Szykman et al., 2003), and as adults, females are also socially dominant to males (Kruuk, 1972). In these respects, spotted hyenas are thus "sex-role reversed" relative to mammalian norms. Furthermore, the external genitalia of female hyenas are strongly virilized; the hypertrophied clitoris forms a large and fully erectile pseudopenis, and the fused vaginal labia form a structure resembling the scrotal sac of the male. Recent experimental work with captive hyenas has shown that, although androgens later modify the fine structure of the phallus, these odd genitalia develop before androgens are present and therefore formation of the genitalia must be largely androgen-independent (Drea et al., 2002; Drea et al., 1998; Glickman, Cunha, Drea, Conley, & Place, 2006; Glickman, Short, & Renfree, 2005). However, the maternal ovary produces high concentrations of a weak androgen called androstenedione, which is transformed by placental enzymes into testosterone that reaches developing fetuses via the umbilical vein (Licht et al., 1998; Yalcinkaya et al., 1993). Fetal hyenas of both sexes are thus apparently bathed in androgens late in gestation.

Work with primates and rodents has shown that perinatal androgen exposure masculinizes social and sexual play behavior in juveniles, even in the absence of any circulating hormone during the period of ontogeny when play occurs (Goy, Bercovitch, & McBrair, 1988; Goy & Wallen, 1979; Nunes, Muecke, Anthony, & Batterbee, 1999; Pellis, 2002). Furthermore, the masculinizing effect of androgen on juvenile play behavior is separated in time from its masculinizing effect on genital differentiation (Wallen & Baum, 2002). In rhesus monkeys, for example, androgen exposure early in fetal development masculinizes the genitalia of the female but has no effect on juvenile play behavior; by contrast, androgen exposure late in gestation produces no genital masculinization, but strongly affects juvenile rough-and-tumble play and play-mounting (Goy, Bercovitch, & McBrair, 1988). Similarly, in humans, girls affected with congenital adrenal hyperplasia (CAH), and consequently exposed to heightened levels of testosterone prenatally, exhibit more male-typical toy preferences and more masculine play behaviors than unaffected girls (Hines, 2003).

Interestingly, in both humans (Hines, 2003) and spotted hyenas (Dloniak, French, & Holekamp, 2006), naturally-occurring variations in concentrations of maternal androgens during pregnancy are associated with variations in the sexually dimorphic play behavior of the offspring resulting from those pregnancies. That is, in both species, higher androgen concentrations in pregnant females are later associated with higher rates of some forms of male-typical play in female offspring. However, it is not currently known how many different forms of play are sexually dimorphic among young spotted hyenas, nor which forms of play might be influenced by prenatal androgen exposure. If androgens influence play in spotted hyenas as they do in primates and other mammals, then patterns of both social play and play-mounting in female hyenas should be similar to those of males. Pedersen et al. (1990) found that, among captive hyenas in same-sex groups, females engaged in more social play than did males. In the current study, we evaluated this possibility in wild spotted hyenas.

Our final goal was to test two hypotheses about particular classes of environmental variables known to influence rates of play in other mammals: energy availability and social context. Numerous studies on juvenile animals ranging from birds to primates have shown that rates of play decrease when energy supplies decline (Baldwin & Baldwin, 1976; Barrett, Dunbar, & Dunbar, 1992; Bateson, Mendl, & Feaver, 1990; Nunes, Muecke, Anthony, & Batterbee, 1999; Nunes et al., 2004; Pozis-Francois, Zahavi, & Zahavi, 2004; Rajpurohit, Sommer, & Mohnot, 1995; Sharpe, Clutton-Brock, Brotherton, Cameron, & Cherry, 2002). However, in some species the opposite relationship has been shown. For instance, a reduction in energy availability, inducing an early onset of weaning, increases rates of social and locomotor play in domestic cats (Martin & Bateson, 1985). Similarly, underfed rats play more than well-fed individuals (Loranca, Torrero, & Salas, 1999), and captive chimpanzees and bonobos engage in more social play before than after feeding; in these species play might function to reduce the intensity of aggression and competition around food (Palagi, Cordoni, & Borgognini Tarli, 2004; Palagi, Paoli, & Borgognini Tarli, 2006).

Here we tested several predictions of a hypothesis suggesting that low levels of available energy are associated with relatively low rates of play in hyena cubs. Because intra-litter rank has a significant effect on cub growth rates (Hofer & East, 1996; Wahaj & Holekamp, 2006), we inquired whether rates of play behavior also varied here with intralitter rank. If so, we expected dominant cubs within twin litters to play at higher rates than their subordinate siblings, as they enjoy superior access to the mother's milk. Social dominance determines priority of access to food resources in this species, with high-ranking individuals enjoying better food access than low-ranking ones (Kruuk, 1972). Therefore, if the hypothesis is correct that energy affects hyena play, we expected that rates of play would be elevated in cubs with high-ranking mothers relative to those with lower-ranking mothers. Furthermore, after controlling for numbers of potential play partners, we expected singleton cubs, which have sole access to their mother's milk and therefore grow faster than twins (Hofer & East, 1996), to exhibit more play than cubs from twin litters. Additionally, if food availability affects rates of play, then play rates should be lower in all cubs during periods when food is scarce than during periods of prey abundance.

Finally, one important feature of the immediate social context that might influence rates of play is the number of potential play partners available to an animal (Poirier & Smith, 1974). The number of available partners can be quite variable for spotted hyena cubs, which live for several months at a communal den where offspring of two to several adult females may reside. If availability of play partners affects rates of play, we expected that individuals from large cohorts of cubs would play at higher rates than individuals from small cohorts. We emphasize that hypotheses suggesting energetic and social variables as determinants of play rates are not mutually exclusive, and that multiple variables might be operating concurrently to affect rates of play.

## Materials and Methods

### Study Animals

We collected data from members of one large clan of spotted hyenas inhabiting the Talek region of the Masai Mara National Reserve in southwestern Kenya (Boydston, 2001; Frank, 1986). Adult and sub-adult hyenas were identified individually by their unique spot patterns. Young cubs, which have a solid black lanugo, were identified on the basis of distinctive scars, nicks on the ears and patterns of molt. Relationships between mothers and offspring were determined based on nursing associations, and birth dates were estimated (± 7 days) based on the appearance of cubs when they were first observed (Holekamp, Smale, & Szykman, 1996). Cub sex was determined from the dimorphic shape of the glans of the erect phallus (Frank, Glickman, & Powch, 1990).

### Data Collection

Repeated focal animal samples (Altmann, 1974), lasting on average 27 ± 2.11 minutes, were conducted on individual hyenas ranging in age from less than 1 month to adulthood. All occurrences of play were recorded during focal sampling. Ontogenetic data were collected between June 15, 1988 and August 14, 1998 from 24 males and 20 females, including 13 singletons and 31 animals from twin litters. Most cubs were sampled biweekly between birth and 30 months of age, with an average of 2.05 ± 0.21 hours of focal animal sampling for each individual during every two-month age interval. A total of 691 focal sampling hours were included in this component of the study. Den-dwelling cubs spend much of the day underground, typically entering the den 2–3 hours after sunrise and emerging again in the late afternoon, approximately 2–3 hours before sunset. Behavioral data were therefore collected mainly during daylight hours between 0600 h and 0900 h, and again between 1600 h and 1930 h.

The same two observers (K.E.H. and L.S.) collected all data included in the 2–4 month and play-mounting analyses. However, the larger ontogenetic study, which spanned a decade, included observations made by sixteen observers who usually worked in pairs. All observers were blind with respect to the hypotheses tested here, and all were trained individually by K.E.H. for several months. Observers were allowed to collect data independently only once they could consistently and accurately identify all of the study animals as well as all play behaviors described below.

Play was consistently recognized by observers based on exaggerated movements, apparent purposelessness, specific initiation postures, and the absence of either aggressive posturing or vocalizations indicative of pain inflicted when bitten by another individual. We observed five types of play behavior: social play, romping, object play, play-mounting and non-nutritive chewing. *Social play* involved multiple individuals engaged together in chasing, wrestling, jumping or chewing on one another. *Romping* was identified as exaggerated running and jumping behavior exhibited by solitary individuals. *Object play* occurred when we observed an animal running with or tugging on sticks, bones, feathers or old scraps of skin. *Play-mounting* involved one cub approaching another from behind and placing its forepaws on the back of another cub to assume a posture like that exhibited by adult males during copulation; the phallus was often erect during play-mounting, but was not a necessary condition for us to record the occurrence of this form of play. If the animal being mounted did not pull away immediately, then the mounting animal typically also exhibited thrusting behavior, but no intromission. Lastly, one additional type of object play recorded here, seen mainly in carnivores, is *non-nutritive chewing*. This is defined as biting or gnawing on objects from which little or no energy or nutrients could be derived, including plants, sticks, or old dried pieces of bone (Fagen, 1981; Power, 2000). To determine whether non-nutritive chewing might simply reflect a process similar to the teething behavior seen in human infants, we examined non-nutritive chewing here in relation to patterns of tooth eruption and replacement in hyenas.

All types of play behavior occurred in bouts lasting from a few seconds to several minutes. In order to compare rates of play and examine effects of energetic and social variables on play rates, we recorded all play behaviors as states rather than discrete events. That is, if any play of a particular type occurred within a given minute of observation, then that 60-second interval was counted as a minute of play of that type. If a particular type of play occurred in multiple shorter bouts within a single minute, this was nevertheless counted as having occurred only once. Hourly rates of play behavior of each type were calculated for every individual in each two-month age interval from birth to 30 months of age. Rates were calculated by dividing the number of minutes in which each type of play occurred by the number of minutes in which that animal was observed as a focal animal during each age interval.

Although rates of play-mounting were recorded as states for purposes of comparison with other types of play, for more detailed analyses of play-mounting we also recorded each mount by a particular individual as a discrete event, such that it could be recorded as occurring multiple times within a given minute of observation. Each occurrence of play-mounting was recorded as a critical incident (Altmann, 1974) from 21 male cubs and 15 female cubs monitored throughout the first 8 months of life during all observation sessions at dens. An observation session began when we arrived at the den, and ended when observers left the den. Observation sessions at dens ranged in duration from 5 minutes to several hours. Cubs included in this analysis of play mounts as critical incidents were each observed at dens for an average of 117 ± 4 hours. These data were collected during 4212 hours of observation of all cubs individually.

In order to examine potential effects on play rates of social (cohort size) and energetic variables (prey density, litter size, intralitter rank and maternal social rank) we focused exclusively on the 2–4 month age interval because this proved to be the period during which the highest rates of play were observed. Of the original 44 cubs observed in the overall ontogenetic analysis, 40 (23 males and 17 females) were included in analyses focused exclusively on the 2–4 month age interval. We used a mean of 7.00 ± 0.48 focal animal samples per individual in this analysis (3.58 ± 0.23 focal samples per individual per month), such that each individual was observed for an average of 3.36 ± 0.22 hours during the 2–4 month age interval. The total observation time used for focal animal sampling in this component of the study was 134 hours.

We evaluated dominance relationships among mothers on the basis of the direction of submissive behaviors (Holekamp & Smale, 1993); by convention, the highest ranking female was assigned a rank of one. Cubs were assigned the same social ranks as their mothers. The hierarchy was then divided into equal thirds and individuals were assigned to one of three categories; high-, mid- and low-ranking. Throughout the study period bi-weekly prey censuses were conducted by counting all ungulates within 100m of each of two 4 km transects to monitor local prey availability in the Talek area. Prey availability was categorized as either high or low at each census based on whether the count was above or below the mean prey density for the entire study period. For each individual, its cohort size was calculated as the number of cubs born within six months of its birth date. Rank relations within litters were determined both by outcomes of dyadic aggressive interactions between littermates and by nursing positions. The dominant cub within a litter usually assumes a preferred nursing position against the mother's belly whereas the subordinate cub typically nurses while lying between the mother's hind legs (Wahaj & Holekamp, 2006).

## *Statistical Analyses*

For the overall ontogenetic analysis we used non-parametric statistics to evaluate effects of age and sex on play rates because these data were not normally distributed. Within each age interval we compared rates for males and females, using the Mann-Whitney-U test statistic, and we examined changes across all age intervals with a Kruskal-Wallis ANOVA, followed by multiple comparisons among specific intervals using Bonferroni corrections. We used a Friedman test statistic to analyze variation in play rates throughout ontogeny for individuals for which we had data from all age intervals. For each sex we examined variation in the number of play mounts exhibited during the first 8 months of life using the Friedman test statistic, followed by comparisons among specific intervals using Wilcoxon Signed Ranks tests. A Spearman's correlation coefficient was calculated to examine relationships between maternal social rank and rates of play-mounting. These statistical analyses were performed in STATISTICA 6.1 (Statsoft, 2002).

To test hypotheses about the effects of social and energetic factors on rates of play during the 2–4 month age interval, we used a generalized linear model (GLIM) with binomial error distributions and a logit link function to analyze each play type. A quasi-binomial distribution was used in order to correct for over dispersion in the model, and the significance of each term was evaluated using an F test (Crawley, 1993). The number of minutes during which a cub was observed engaging in a particular type of play throughout the 2–4 month age interval, and the number of minutes observed in which that type of play did not occur, comprised the binomial response variable in each model. This approach analyzes the proportion of minutes in which a specific type of play was observed, but weights the analysis based on the number of minutes observed (Venables & Ripley, 1999). The same predictor variables were initially used in each model, with cohort size as a continuous predictor and sex, litter size (singleton or twin), social rank (high, mid, low) and prey availability (high, low) as categorical predictors. Each model was then simplified by eliminating any variables that did not contribute to its explanatory power. Only individuals observed for at least 30 minutes during the 2–4 month age interval were included in this analysis. The GLIM analysis was conducted using R software version 2.1.1 (R Core Development Team, 2005).

Finally, to evaluate the effect of intra-litter dominance on rates of play during the 2–4 month age interval we performed Wilcoxon matched pairs analyses between dominant and subordinate littermates. Differences between groups were considered significant when $\alpha < 0.05$ after Bonferroni correction, and mean values are presented as ± SE throughout.

## Results

### *Ontogenetic Variation in Rates of Play*

Social play was the type of play behavior most frequently observed, occurring on average during more than 12 minutes in each hour observed during the 2–4 month age interval (Figure 1a). The overall mean rate of social play between birth and 30 months of age was 4.50 ± 0.38 min/hr, but rates peaked during the second 2-month age interval, and then declined (Figure 1a, Kruskal-Wallis H (18,268), $F = 121.6$, $p < 0.00001$). As we did not manage to sample every cub in every age interval, we performed a repeated-measures ANOVA on only the subset of cubs ($n = 13$) sampled in every interval from 0–20 months, and we observed a pattern of results identical to that in our original analysis (Friedman test statistic = 41.46, Kendall coefficient of concordance = 0.39, $df = 8$, $p < 0.00001$). We found no sex difference in rates of social play (Mann-Whitney $U = 204$, $p = 0.40$). Interestingly, social play continued into adulthood at hourly rates much higher than those observed for any other form of play (Figure 1).

Romping occurred, on average, during 1.61 ± 0.20 min/hr between birth and 30 months of age. The highest rates of romping occurred during the first two months of life ($\bar{x} = 7.83 \pm 1.97$ min/hr), and dropped to near-zero values after 6 months of age (Figure 1b, Kruskal-Wallis H (18,268), $F = 155.04$, $p < 0.00001$). Analysis of the subset of cubs sampled in every age interval produced the same pattern (Friedman test statistic = 46.98, Kendall coefficient of concordance = 0.45, $df = 8$, $p < 0.00001$). We found no sex difference in rates of romping (Mann-Whitney $U = 190.5$, $p = 0.24$).

Play-mounting was the only type of play for which we found a significant sex difference (Figure 1c, Mann-Whitney $U = 94$, $p = 0.0005$), with males engaging in this activity at much higher rates than females. Play-mounting occurred at lower rates throughout development than did either social play or romping (males: $\bar{x} = 0.30 \pm 0.07$ min/hr; females: $= 0.05 \pm 0.02$), but there was significant variation among age classes (Figure 1c, Kruskal-Wallis H (18, 268), $F = 66.78$, $p < 0.00001$). For males, a peak in mounting rates occurred during the second age interval, at 2–4 months of age (Figure

FIGURE 1A.

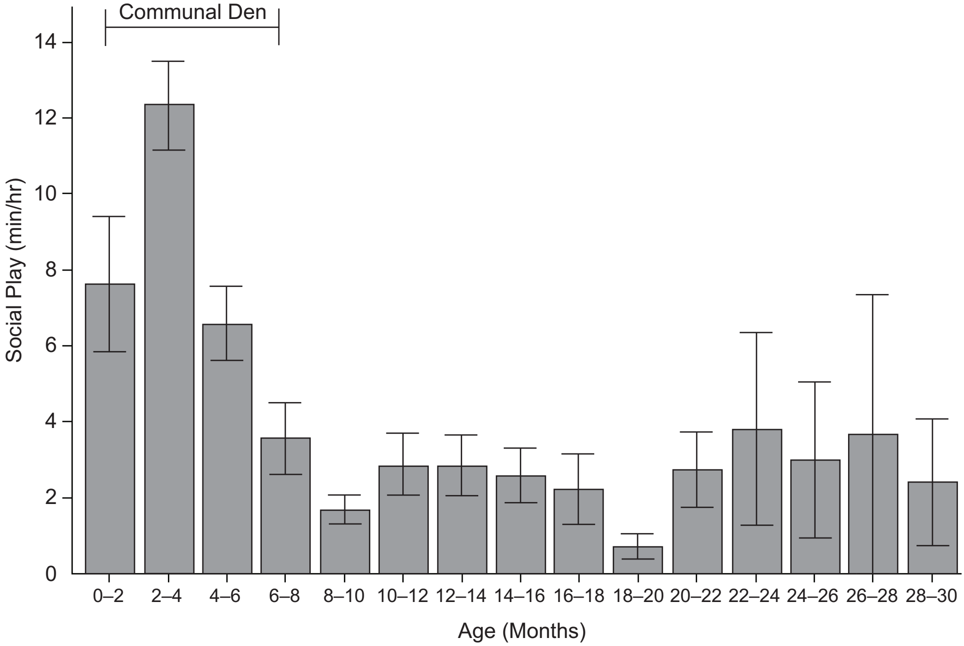


FIGURE 1B.

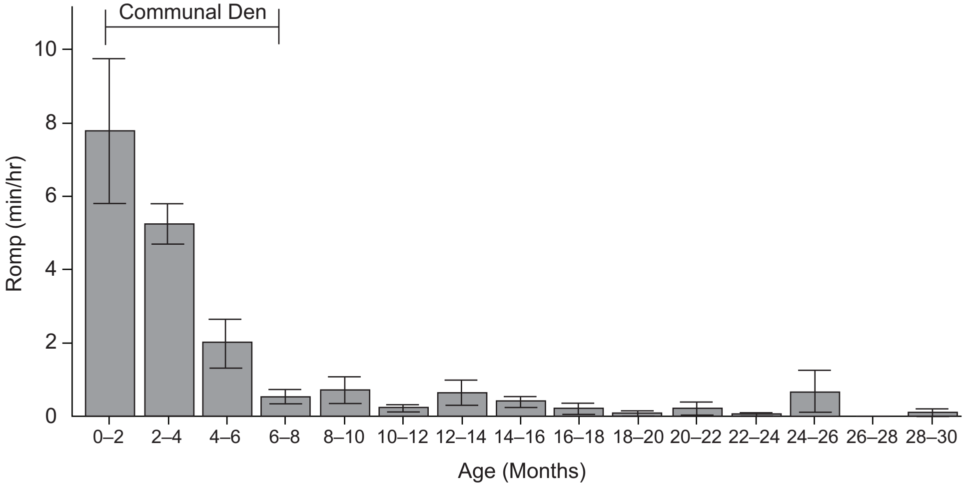


FIGURE 1. Ontogenetic variation in rates of (a) social play, (b) romping, (c) play-mounting, (d) object play and (e) non-nutritive chewing in spotted hyenas. Age classes represent two month intervals (e.g., 0–2 month interval includes individuals from 0.1 months to 2 months of age). Because no significant sex differences were found in other forms of play, separate rates for males and females are shown only in "c." Horizontal bars indicate the period during which cubs live at the clan's communal den on all graphs and on (e) periods of tooth eruption. Note that y-axis scales vary considerably.

FIGURE 1C.

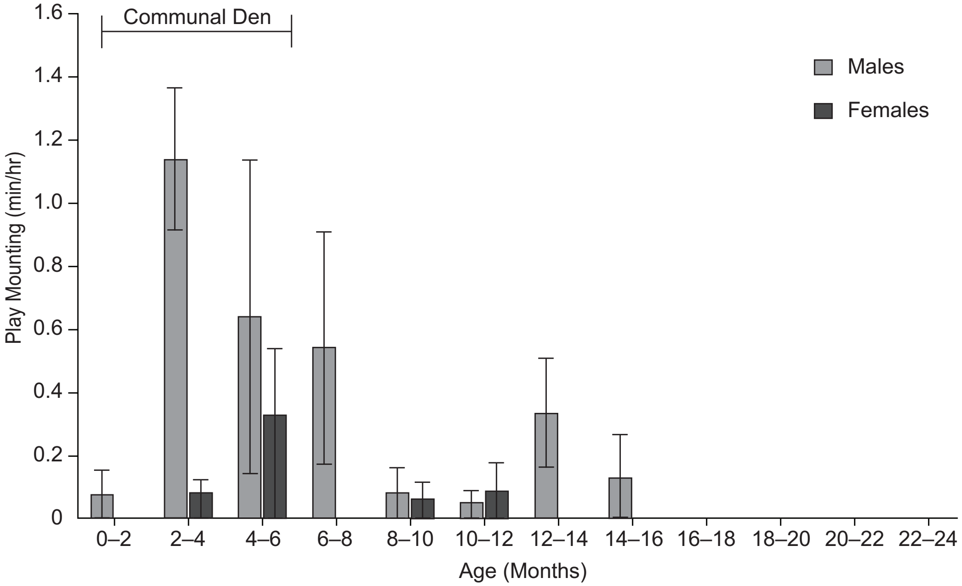
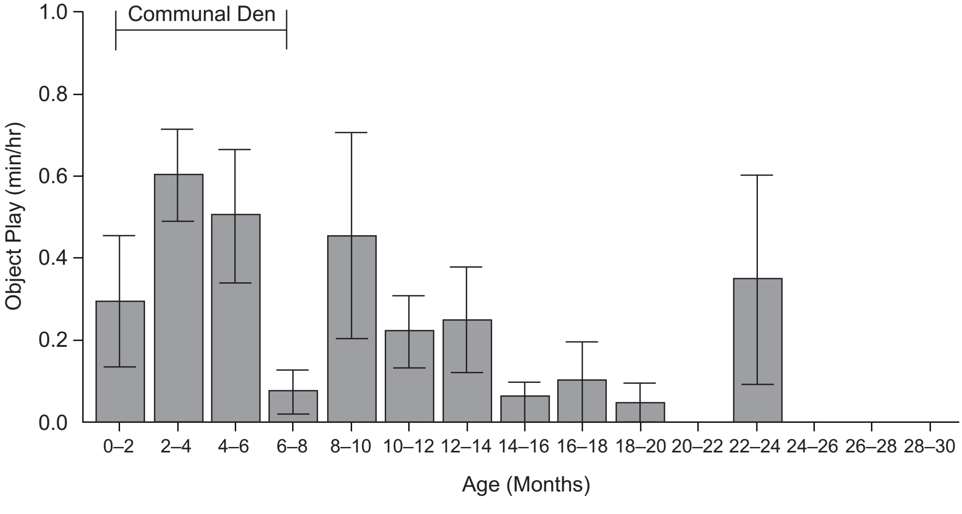


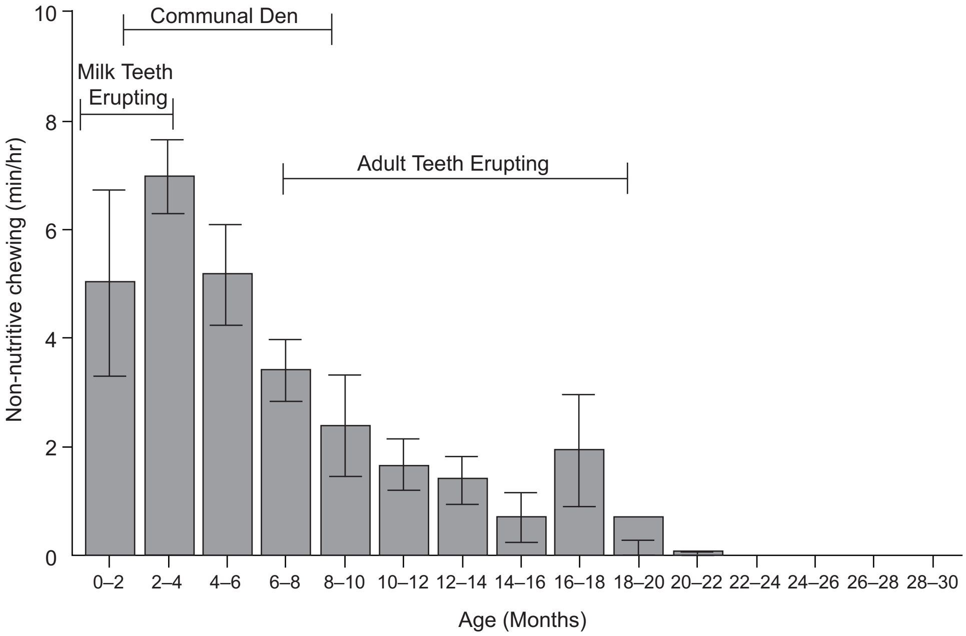
FIGURE 1D.



1c). Mounting behavior vanished from the play repertoire much earlier than did other forms of play; it was never observed after 12 months of age among females, nor after 16 months of age among males. Male spotted hyenas pass through puberty at around 24 months of age (Holekamp & Smale, 1998).

Object play occurred at the lowest rates of any play type observed ($\overline{x} = 0.25 \pm 0.03$ min/hr). Although we observed significant variation among age classes in rates of object play for all individuals, and also for those individuals sampled in every age inter-

FIGURE 1E.



val (Figure 1d, Kruskal-Wallis H (18, 268), F= 148.34, $p < 0.00001$; Friedman test statistic = 25.96, Kendall coefficient of concordance = 0.25, df = 8, $p < 0.0011$), the ontogenetic pattern in object play was less clear than for other forms of play. Rates of object play appeared to be largely determined by availability of suitable objects in the immediate environment of each focal cub at the time it was sampled. We found no significant difference between males and females in rates of object play (Mann-Whitney U = 204, p = 0.39).

After social play, the mean rate of non-nutritive chewing was the highest of the various types of play observed between birth and adulthood ($\overline{x}$ = 2.61 ± 0.24 min/hr), with cubs 2–4 months old spending a mean of 7 minutes of every hour observed engaged in this activity. We documented significant ontogenetic variation in rates of non-nutritive chewing (Figure 1e, Kruskal-Wallis H (18, 268), F = 148.34, $p <0.00001$; Friedman test statistic = 39.53, Kendall coefficient of concordance = 0.38, df = 8, $p < 0.00001$). Chewing rates were highest between two and four months of age ($\overline{x}$ = 6.98 ± 0.68 min/hr), and then declined to nil by 24 months of age.

To inquire whether higher rates of non-nutritive chewing reflected teething, we examined rates of this form of play in temporal relation to eruption of both deciduous (milk) teeth and adult dentition. Although *Crocuta* cubs are born with fully erupted deciduous incisors and canines (Frank, Glickman, & Licht, 1991), the deciduous cheek teeth erupt during the first several weeks after birth, and this process is complete by 2 months of age (Figure 2). There is then a 4-month hiatus before the adult teeth start to erupt at 6–7 months of age, followed by a period during which both milk and adult teeth are present concurrently. The adult teeth are fully erupted by 18 months of age

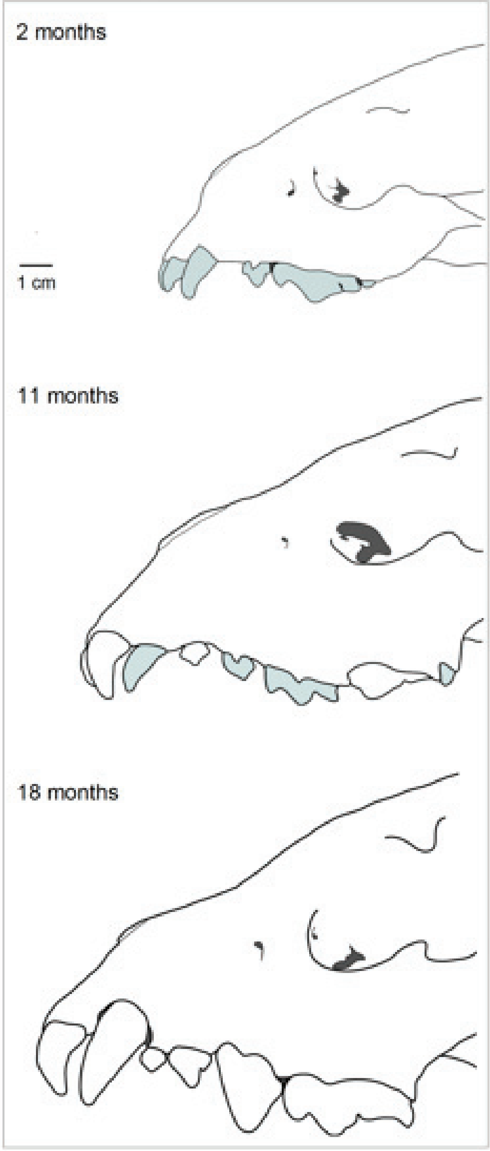


FIGURE 2. The eruption of the deciduous dentition (shaded) is complete by 2 months of age. Adult teeth (white) begin to erupt around 6 months but are not fully erupted until 18 months of age.

(Van Horn, McElhinny, & Holekamp, 2003).

The highest rates of non-nutritive chewing occurred during the period (2–4 months of age) between eruptions of deciduous and adult teeth; rates declined significantly before initial eruption of the adult teeth (Figure 1e, multiple comparisons with corrected p-values: 2–4 months vs. 1–2 months, $p < 0.000001$; 2–4 months vs. 4–6 months, $p < 0.00001$; 2–4 months vs. 6–8 months $p < 0.0001$). This pattern was largely inconsistent with the hypothesis that this behavior represents teething. Furthermore, non-nutritive chewing was observed, albeit at low rates, at 18–22 months of age, after all adult teeth have fully erupted (Figure 1e).

### *Analysis of Play Mounts as Events*

Mean rates of play-mounting were significantly higher among males than females during all but the youngest age interval (Figure 3a), during which 14 of 15 females exhibited no mounting at all but one female engaged in this behavior at an extremely high rate. Interestingly, as an adult, this female (RV) never reproduced and appeared to be infertile, so she may have been exposed *in utero* to an unusually high concentration of androgens relative to other females. Yalcinkaya et al. (1993) suggested that early exposure of female spotted hyenas to androgens appears to severely modify ovarian histology, and it may be that this occurred in RV and impaired such physiological processes essential for female reproduction as oogenesis or ovulation. Among females, rates of play-mounting were generally low, and did not vary significantly with age (Friedman test statistic = 4.220, Kendall coefficient of concordance = 0.094, df = 3, $p > 0.05$; Figure 3a).

FIGURE 3A.

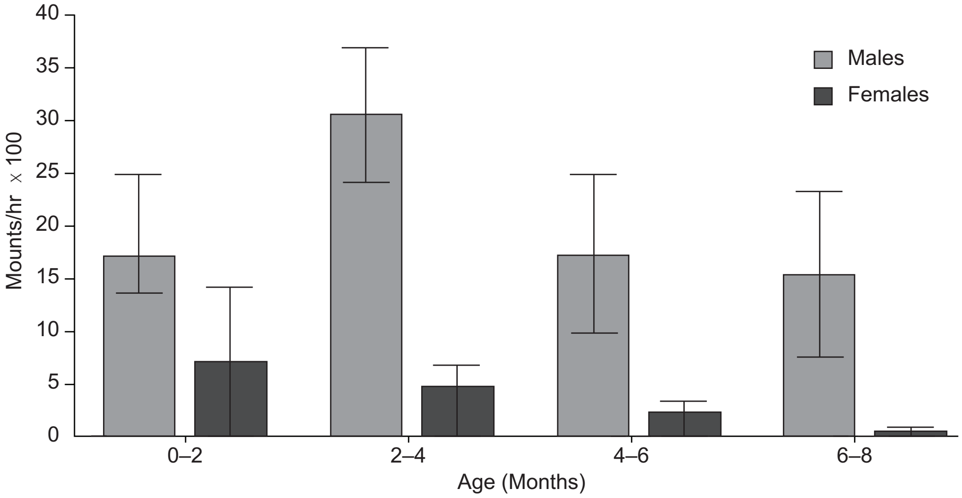


FIGURE 3B.

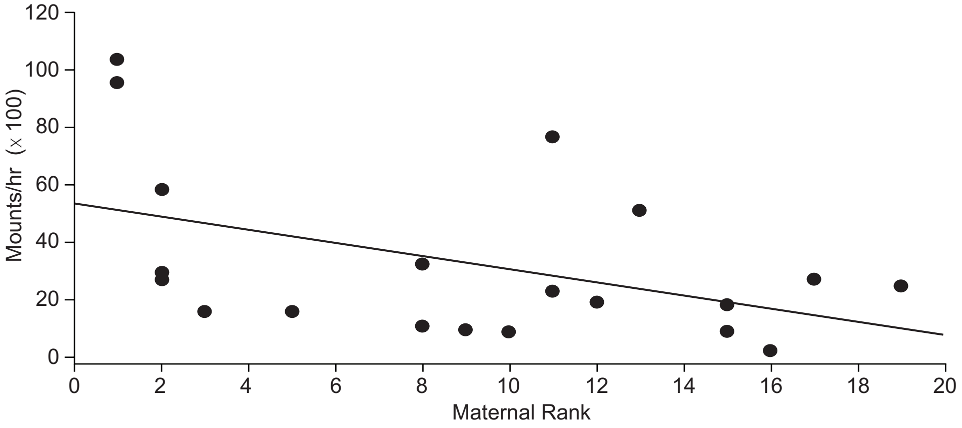


FIGURE 3. Rates of play-mounting when individual mounts were recorded as events a) among males and females throughout the first 8 months of life, b) among males between 2–4 months of age, as a function of their mothers' social ranks.

Among males, rates of play-mounting varied significantly with age (Friedman test statistic = 15.857, Kendall coefficient of concordance = 0.252, $p < 0.001$; Figure 3a). Specifically, play-mounting rates were relatively low from 0–2 months, peaked during the 2–4 month age interval, decreased between 4–6 months, and subsequently remained relatively low between 6 and 8 months of age. Finally, mounting rates among males 2–4 months of age were positively correlated with maternal rank such that sons of high-ranking females engaged in this behavior at significantly higher rates than did sons of low-ranking females (Figure 3b; Spearman's R= 0.389, F= 4.306, $p < 0.05$).

### *Modulating Influences on Play at 2–4 Months of Age*

Table 1 presents mean rates of play of each type during the 2–4 month age interval, and shows how mean values for each play type were affected by each categorical predictor variable. Table 2 summarizes results from analyses using generalized linear models, indicating which independent variables had significant or near-significant effects on rates of play of each type. Because play-mounting was strongly sexually dimorphic, we included only males in the 2–4 month GLIM of this type of play. There was a trend for more romping to occur among males than females, but sex was not a significant predictor of romping rates (Table 2, GLIM, $F_{1,38} = 5.29$, $p = 0.09$), nor was any other independent variable included in the final model for this form of play.

Singleton cubs engaged in object play at higher hourly rates than did cubs from twin litters (Tables 1 & 2, GLIM, $F_{1,\,38} = 4.71$, $p = 0.04$), but litter size did not appear to affect rates of any other play type. None of the independent variables examined here had any appreciable influence on rates of non-nutritive chewing during the 2–4 month age interval. Similarly, intralitter rank appeared not to affect rates of any form of play, as we found no significant effects of this variable (Wilcoxon Matched Pairs, *social play*: n = 15, T = 55, p = 0.78; *romp*: n = 15, T = 53, p = 0.69; *object play*: n = 15, T = 19, p = 0.12; *non-nutritive chewing*: n = 15, T = 47, p = 0.73). Maternal dominance status had a significant effect on rates of social play, with high-ranking cubs engaging in more play than either mid- or low-ranking animals (Figure 4; Table 2, GLIM, $F_{2,\,36} = 3.27$, $p = 0.049$). Unexpectedly, social play occurred more frequently during periods of low prey availability than during periods when prey were abundant (Tables 1 & 2, GLIM, $F_{1,32} = 4.79$, $p = 0.04$). Similarly, rates of play-mounting among males 2-4 months of age were higher during low than high prey periods (Table 2, GLIM, $F_{1,18} = 5.29$, $p = 0.03$). We observed a trend towards higher rates of social play in cohorts of large size (Table 2, GLIM, $F_{1,\,38} = 3.23$, $p = 0.08$).

## Discussion

Play appears to be a significant component of the behavioral repertoire of wild spotted hyenas, particularly during early development. Drea et al. (1996) examined the emergence of play behavior in captive *Crocuta* cubs from twin litters in the first four weeks of life, a period during which wild cubs are seldom seen above ground, and found that rates of social play increased over these first few weeks. These authors hypothesized that early social play promotes the development of a repertoire of social behavior that prepares young cubs to become integrated into the clan when they are moved to the communal den (Drea, Hawk, & Glickman, 1997). When these results from captivity are combined with the data presented here from free-living *Crocuta*, we have, for the first time, a comprehensive description of the ontogenetic patterns of play in this gregarious carnivore.

### *Factors Modulating Rates of Play*

Our results were mixed with respect to the potential effects of availability of energy and social partners on rates of play by hyena cubs. We documented a trend toward

**Table 1.**

Mean rates (min/hr) and SE by categorical predictor of each play type for *Crocuta* cubs 2–4 months of age. Significant ($p < 0.05$) predictors from generalized linear models are highlighted in **bold** font.

| | | **Sex** | | **Litter Size** | | **Social Rank** | | | **Prey** | |
|---|---|---|---|---|---|---|---|---|---|---|
| **Play Type** | **$\bar{x}$** | **Male** | **Female** | **Singleton** | **Twin** | **High** | **Mid** | **Low** | **High** | **Low** |
| Social | 12.47±1.09 | 13.35±1.68 | 11.27±1.19 | 13.40±1.50 | 12.15±1.37 | **15.81±2.32** | 9.76±1.38 | 11.46±1.41 | 8.77±2.02 | **13.54±1.23** |
| Chew | 6.86±0.70 | 7.26±0.99 | 6.33±0.99 | 8.83±1.62 | 6.21±0.75 | 7.45±1.30 | 6.08±1.15 | 6.95±1.24 | 6.58±2.00 | 7.85±0.71 |
| Romp | 5.46±0.56 | 6.46±0.87 | 4.10±0.47 | 6.63±1.15 | 5.06±0.64 | 6.96±1.19 | 4.45±0.92 | 4.82±0.65 | 4.82±1.03 | 5.64±0.67 |
| Mount | 0.98±0.22 | **0.98±0.22** | 0.08±0.04 | 1.16±0.45 | 0.92±0.26 | 1.27±0.35 | 0.95±0.59 | 0.59±0.21 | 0.27±0.16 | **1.23±0.27** |
| Object | 0.61±0.12 | 0.63±0.18 | 0.59±0.16 | **1.04±0.34** | 0.47±0.11 | 0.58±0.25 | 0.54±0.18 | 0.72±0.19 | 0.56±0.57 | 0.81±0.14 |

**Table 2.**

Factors associated with rates of play in 2–4 month old spotted hyena cubs (n = 40), identified in generalized linear models. Only significant terms (*), and terms that indicate trends, are presented.

| Play Type | Effect | Model Term | *F* | df | *p* |
|---|---|---|---|---|---|
| Social | Low > high | Prey category | 4.79 | 1,32 | 0.04* |
| | High > mid & low | Rank category | 3.27 | 2,36 | 0.05* |
| | Larger > smaller | Cohort size | 3.23 | 1,38 | 0.08 |
| Romp | M > F | Sex | 5.29 | 1,38 | 0.09 |
| Play mount (males only) | High > low | Prey category | 5.29 | 1,18 | 0.03* |
| Object | Singleton > twin | Litter size | 4.71 | 1,38 | 0.04* |
| Non-nutritive chewing | | All N/S | | | |

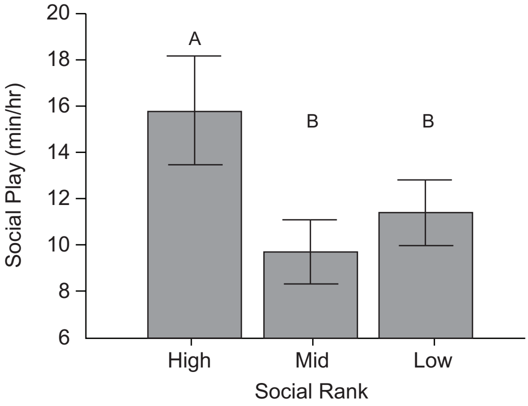


FIGURE 4. Rates of social play among cubs 2–4 months old in relation to maternal social rank category. Letters indicate significant difference among maternal rank categories.

higher rates of social play among cubs that grew up with the largest cohorts of peers. This suggests, but cannot confirm, that partner availability influences patterns of play in spotted hyenas. Similarly, although the influence of available energy on play rates was suggested by our finding that rates of all five play types were higher in singletons than in twins, none of these differences were statistically significant. Cubs of the highest-ranking females engaged in social play at significantly higher rates than did their lower-ranking peers (Figure 4). This result is consistent with the notion that energy availability affects play rates, but an alternative explanation is that it reflects a preference among clan members for high-ranking play partners. Indeed, although partner preferences have not yet been examined in young hyenas, adult females prefer to associate with high-ranking females (Holekamp et al., 1997). More detailed analysis of play initiation is needed to evaluate kin and rank-related partner preferences during play among free-living *Crocuta*.

We found that prey density was actually inversely related to rates of play among hyenas. Although this was surprising, there are at least two possible explanations. First, prey availability is relatively high throughout the year in the Masai Mara National Reserve (Ogutu & Dublin, 2002), where our Talek study site was situated. It is therefore possible that, even during periods of low prey abundance, energy resources are sufficient to support high rates of play among Talek cubs. Indeed, fluctuations in prey abundance do not appear to affect cub survival in this study population (Watts, 2007). Alternatively, our time frame for looking at energy availability may have been too broad, and may therefore have obscured relationships between food intake and play. A finer-grained analysis of play in temporal relation to nursing bouts for individual cubs might reveal a different pattern from that observed here. Nevertheless, neither of these explanations could account for our observation of significantly higher rates of play during low than high prey periods.

Some studies of other species have reported higher rates of play during periods of low than high food availability (Loranca, Torrero, & Salas, 1999; Martin & Bateson, 1985; Palagi, Cordoni, & Borgognini Tarli, 2004; Palagi, Paoli, & Borgognini Tarli, 2006). It has been suggested that play under these conditions may function to reduce stress associated with competition for limited food resources which might conceivably be the case among Talek hyenas. However, this seems unlikely among hyenas because, when we observe den-dwelling cubs that are energetically stressed after their mothers die, play is one of the first activities to disappear from their behavioral repertoire. Lastly, it is possible that female *Crocuta* spend more time in search of food during periods of prey scarcity, and less time at the den, than when prey are abundant. Therefore, increased rates of social play during the former periods might reflect more "free" time available to cubs lacking opportunities to nurse. This pattern appears to occur in juvenile vervet monkeys (*Cercopithecus aethiops*) in which play rates are elevated when mothers are absent (Govindarajulu, Hunte, Vermeer, & Horrocks, 1993). We are currently examining the relationship between prey availability, den attendance, and other aspects of maternal care.

## *Possible Functions of Play in Spotted Hyenas*

Although our goal was not to test specific hypotheses about the functions of each type of play, the ontogenetic patterns we observed here suggest some ways in which play might enhance fitness in spotted hyenas. In the wild, social play occurred more frequently and continued until much later in life than did any other form of play (Figure 1). The highest rates of social play occurred when cubs were 2–4 months old, during which time individuals engaged in vigorous social play for roughly 20% of each hour observed. This pattern suggests that the benefits derived from this form of play must be considerable in order to outweigh the energetic costs associated with it. These high rates of social play were observed shortly after cubs were brought to the clan's communal den, when *Crocuta* cubs must learn not only the identities of their group members, but also their own places in the social hierarchy (Holekamp & Smale, 1993).

The ontogenetic pattern observed here suggests that social play facilitates the acquisition of social knowledge and integration into the clan (Gomendio, 1988). It seems unlikely that adults would continue to engage in this activity if no benefits were accruing from it. Indeed, the persistence of social play behavior from the natal den into adulthood suggests that the benefits from this form of play probably continue to accrue long after cubs become independent of the den. Although adults were observed playing away from the den, their play rates may largely reflect interactions with den-dwelling cubs when older focal individuals returned to the den to visit. It may be that the older individuals are gaining information about new members of the clan by playing with them, or that they are honing their own parental skills during their extensive playful interactions with young cubs.

Rates of romping were highest during the first two months of life, but subsequently decreased. The first months of life are critical for developing locomotor skills, and it is likely that romping enhances the development of coordination and movement in very young cubs, as predicted by the motor training hypothesis (Spinka, Newberry, & Bekoff, 2001). The gradual decrease in romping after two months of age may also reflect a transition from individual play to social play that accompanies transfer from the natal den to the communal den between 2–5 weeks of age. That is, to the extent that play facilitates development of coordination and other motor skills, these benefits may be attained mainly from vigorous social play, rather than solitary romping, after the first few weeks of life.

Social play, play-mounting and non-nutritive chewing all reached their peaks during the 2–4 month age interval, shortly after cubs were moved to the clan's communal den. However, these rates of play were not merely a response to living at the communal den, as they dropped to adult levels before cubs became independent of the den. Furthermore, captive cubs play at high rates during the first few weeks of life, even in the absence of a communal den (Drea, Hawk, & Glickman, 1996). If these forms of play facilitate acquisition by cubs of new information about their social and physical environments, the fact that play rates drop even before wild cubs leave the den suggests that the ability to capture new information via playful interactions is declining. We found that solitary object play occurred quite infrequently throughout ontogeny, but the rarity of this play type may merely reflect a shortage of suitable objects ("toys") at the den, or the abundance of playmates there.

Non-nutritive chewing is not likely to be primarily associated with tooth eruption or alveolar development in spotted hyenas, as the highest rates of this form of play were observed during an age interval when no tooth eruption is occurring (Figure 1e). Additionally, the skull and jaw muscles of a spotted hyena continue to develop even after 32 months of age (Tanner, 2007), whereas rates of non-nutritive chewing drop dramatically after 18 months, and this behavior is no longer observed after 22 months of age. Although we are unable to rule out the possibility that non-nutritive chewing might stimulate musculo-skeletal development early in life, its occurrence certainly does not correspond well with the period of most pronounced change in the morphology of the feeding apparatus. Another possible function of non-nutritive chewing is that it allows individuals to explore their immediate environment. Spotted hyenas, like other cursorial carnivores, are limited in their abilities to manipulate objects with their forelimbs when compared with primates or even with more dexterous carnivores such as bears or raccoons (Glickman & Sroges, 1966). Hyenas may therefore rely heavily on their mouths for gaining information about objects encountered in their environments. Thus it is not surprising that the rates of this activity are highest after individuals have moved to a new environment when they are transferred to the clan's communal den.

## *Sex Differences in Play and Their Implications*

The variation observed here among the different types of play suggests that the mechanisms underlying their development might also vary. Although we found that rates of play-mounting were higher in male than female hyena cubs, rates of social play did not differ between the sexes. By contrast, in many other mammalian species including humans, males typically engage in higher rates of both of these forms of play than do females (Table 3). In a study of captive spotted hyenas, Pedersen et al. (1990) found that females engaged in more social play than males when they were monitored in same-sex groups, but these investigators observed no sex differences when youngsters were in mixed-sex groups (Pedersen, Glickman, Frank, & Beach, 1990). The results from the mixed-sex groups in captivity are most easily comparable to those from the current study, as both male and female cubs were present at communal dens in the wild. In a study on another female-dominated species, the ring-tailed lemur (*Lemur catta*), Gould (1990) similarly found no sex differences in social play, but did observe dimorphic sex play (Table 3).

The lack of sexual dimorphism in social play is intriguing given the sex-role reversal seen in both lemurs and spotted hyenas with regard to social dominance. A popular hypothesis for the function of social play in general, and rough-and-tumble play in particular, is that it serves as practice for aggressive encounters in adulthood (Maestripieri & Ross, 2004; Smith, 1982; Spinka, Newberry, & Bekoff, 2001). Therefore, the higher rates of rough-and-tumble play observed among the males of many other mammalian species have been attributed to the male's greater need to practice for male-male combat in adulthood (Pellis, Field, Smith, & Pellis, 1997; Smith, 1982).

Although overall rates of aggressive behavior are higher among adult female than male *Crocuta* (Szykman et al., 2003), both sexes engage in considerable aggression, particularly in the context of intrasexual interactions during feeding competition, and when members of neighboring clans encounter each other. Therefore, the absence of a sex difference in social play within female-dominated species such as spotted hyenas and ring-tailed lemurs is consistent with the hypothesis that social play provides practice for agonistic encounters in adulthood. However, sexual monorphism in social play has also been found in some other carnivore species studied in captivity, including cats, ferrets and various canids, all of which hunt terrestrial vertebrate prey (Table 3). Therefore, rough-and-tumble play among young carnivores may provide practice for skills necessary in pursuing and capturing prey as well as for adult combat; presumably, development of these skills would be just as important for females as for males in predatory species (Fagen, 1981).

Copulation represents an unusually difficult challenge for the adult male spotted hyena (Drea et al., 2002). First, he must be tolerated by the large, socially dominant and highly aggressive adult female. Then he must insert his erect phallus into her flaccid one, which is positioned far more anteriorly than is the vaginal opening in other carnivore species. To achieve successful mating in adulthood, the male hyena may thus need practice earlier in life, and the communal den may offer the male his only opportunity for such practice. We found that male hyena cubs engaged in play-mounting at rates considerably higher than those exhibited by females (Figure 3a).

**Table 3.**

Sex differences in play behavior in various mammal species. Female-dominated species are indicated in **bold** font.

| Species | Social / Rough-and-Tumble Play | Sex Play | Source |
|---|---|---|---|
| Carnivores | | | |
| **Spotted hyena (wild)** | M = F | M > F | Present study |
| **Spotted hyena (captive)** | M < F (in same sex groups)<br>M = F (in mixed sex groups) | —— | (Pedersen, J., et al., 1990) |
| Domestic cat (*Felis cattus*) | M = F | —— | (Barrett, P. & Bateson, P., 1978) |
| Coyotes, wolves and beagles (*Canis spp.* ) | M = F | M > F | (Bekoff, M., 1974) |
| Ferret (*Mustela furo*) | M = F | M > F | (Biben, M., 1982; Stockman et al., 1986) |
| Galapagos fur seal (*Arctocephalus galapagoensis*) | M > F | —— | (Arnold, W. & Trillmich, F., 1985) |
| Rodents | | | |
| Belding's ground squirrel (*Spermophilus beldingi*) | M = F | M > F | (Nunes, S., et al., 1999; 2004) |
| Richardson's ground squirrel (*Spermophilus richardsonii*) | M = F | M > F | (Pasztor, T. J., et al., 2001) |
| Golden hamsters (*Mesocricetus auratus*) | M > F | —— | (Vieira, M. L., et al., 2005) |
| Rats (*Rattus norvegicus*) | M > F | —— | (Pellis, S. M., 2002) |
| Ungulates | | | |
| Cuvier's gazelle (*Gazella cuvieri*) | M > F | M > F | (Gomendio, M., 1988) |
| Lambs (*Ovis aries*) | M > F | M > F | (Orgeur, P., 1995) |
| Primates | | | |
| Japanese monkey (*Macaca fuscata*) | M > F | —— | (Koyama, N., 1985) |
| Rhesus macaque (*Macaca mulatta*) | M > F | M > F | (Goy, R. W., et al. 1988; Wallen, K., 1996) |
| **Ring-tailed lemur (Lemur catta)** | M = F | M > F | (Gould, L., 1990) |
| Humans (*Homo sapiens*) | M > F | —— | (Pellegrini A. D. & Smith, P. K., 1998; Scott & Panksepp, 2003) |

Dimorphic sex play is seen among juveniles of a variety of mammalian species (Table 3), and these sex differences are promoted by differential exposure to testosterone earlier in development (Goy, 1996).

Both male and female *Crocuta* cubs are exposed to androgens late in gestation (Licht et al., 1998; Yalcinkaya et al., 1993). Although prenatal treatment with antiandrogens can de-masculinize certain aspects of the genitalia and nervous system of the spotted hyena (Drea et al., 2002; Drea et al., 1998; Fenstemaker, Zup, Frank, Glickman, & Forger, 1999; Forger, Frank, Breedlove, & Glickman, 1996), it is not currently known whether, or to what extent, such treatment also affects the sexually dimorphic patterns of play observed here among young hyenas. Three mechanistic hypotheses might account for the patterns observed here. First, sex differences in play may be androgen-independent in this species, although this seems unlikely because it would make spotted hyenas unique among mammals in this regard. Second, it may be that the critical period for sensitivity of key neural substrates to testosterone does not occur during prenatal development in this species, but instead occurs during the first month after birth, when testosterone concentrations are higher in male than female cubs (Frank, Glickman, & Licht, 1991). Finally, there may be a sex difference in prenatal testosterone exposure or receptor density in this species that has not yet been detected.

The rates of play-mounting observed here were affected by maternal rank as well as by offspring sex. Specifically, at 2–4 months of age, sons of high-ranking mothers mounted other cubs at higher rates than did sons of lower-ranking mothers. Interestingly, this pattern was apparent before the ages at which maternal rank begins to influence dominance relations among cubs (Holekamp & Smale, 1993). Mounting rates among young male *Crocuta* are correlated with maternal androgen concentrations late in gestation, and these, in turn, vary with maternal rank such that sons of high-ranking females are exposed to higher androgen concentrations in utero than are sons of low-ranking females (Dloniak, French, & Holekamp, 2006).

## Conclusions

The patterns of development described here are consistent with the notion that some forms of play confer immediate benefits whereas other forms confer benefits later in life. Here it appeared that most benefits conferred to hyenas by romping and non-nutritive chewing were probably largely immediate, whereas those conferred by play-mounting were most likely delayed until later in life; furthermore, it appeared that social play might confer both immediate and delayed benefits. The five types of play we documented in hyenas pale in comparison to the broad array of human behaviors that fit the definition of play adopted here (from Bekoff & Byers 1981). Nevertheless, as appears to be true of hyena play, some forms of human play may help children cope with specific challenges encountered during one or more early stages of development, whereas others may have long-lasting consequences for individual welfare in adulthood. Just as social play may help young *Crocuta* cubs become integrated into the clan, there also appears to be a relationship between rough-and-tumble play in male children and measures of social competence (Pellegrini, 1995). Although it is not known to what extent play reorganizes the individual's behavioral phenotype, anecdotal evidence from humans indicates that early play deprivation is often closely associated with pathological behavior in adulthood (Brown, 1998). This suggests that play importantly affects structural or functional aspects of brain development that enhance the individual's ability to cope effectively with environmental complexity in general, and with specific stressors in particular (Siviy, 1998).

Finally, the patterns observed here highlight the fact that mammalian play must be heterogeneous in its regulatory mechanisms as well as in its form and function. We observed a great deal of variability among the different forms of hyena play in regard to their patterns of occurrence during development. This suggests that the genetic and neural substrates regulating expression of one form of play are not necessarily the same as those regulating expression of other forms. For example, we found that patterns of temporal variation differed strikingly between non-sexual social play and play mounting. Furthermore, we found that one of these two forms of social play, both of which are sexually dimorphic in many other mammals, is "masculinized" in female spotted hyenas (non-sexual social play), but the other (play mounting) is not. These data suggest that genetic mechanisms and neural circuits regulating developmental patterns differ between these two forms of social play. Although the specific motor patterns involved and the exact patterns of sex differences in hyena and human play are distinctly different, overall it appears that the general principles concerning the functions of play, as well as the heterogeneous nature of the mechanisms regulating its development and its expression, may be surprisingly similar in these two distantly related species.

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