

Aggression decreases as play emerges in infant spotted hyaenas: preparation for joining the clan

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Abstract. The early social development of spotted hyaenas, *Crocuta crocuta*, is marked by a dramatic transition at 2–3 weeks of age, when infants are taken from the isolation of their natal den, where they are intensely aggressive, to the communal den, where they meet most clan members for the first time. This study examined behaviour patterns in eight sets of captive twins during the first month of life to document the changes that prepare young hyaenas for social integration at the communal den. Bite shakes, the most extreme aggressive behaviour, declined markedly within the first week of life, but other forms of aggression remained constant. During week 1, low-intensity prosocial behaviour occurred primarily between mother and cub. By week 2, higher-intensity social play emerged, occurring mainly between siblings. In weeks 3 and 4, cub interactive play was most frequent, lasted longer and was more vigorous. Locomotor and object play did not emerge until weeks 3 and 4, respectively. Dominance relations between siblings were operationally defined by submissive withdrawals. Accordingly, aggression was unidirectional, with dominants initiating most interactions. By contrast, play was reciprocal and equally initiated by dominant and subordinate cubs. Maternal interruption of cub behaviour mainly occurred during extreme aggressive interactions, but rarely during vigorous play. Results showed that prosocial behaviour emerged in captive hyaena cubs following a decline in severe aggression and before the time wild cubs are taken from the natal to the communal den. It is suggested that play may modulate aggression, following the establishment of a dominance relationship, and may serve an immediate prosocial function to prepare aggressive infant hyaenas for integration into the clan.

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The apparent delay in benefits of play behaviour, despite potentially immediate costs to the players, has long perplexed researchers (Fagen 1981; Smith 1982). Theories on the possible utility of play fall into four broad categories, including play as a modulator of physical training and motor development, a mediator of cognitive learning, a facilitator of socialization and a means of energy regulation (Bekoff & Byers 1981). Despite the widely accepted view that benefits are accrued in adulthood, some recognize that play may be more immediately advantageous (Bekoff & Byers 1981; Martin & Caro 1985; Gomendio 1988; Caro 1995). Moreover, discontinuities in the development of play suggest that play is not a unitary category and that its various components may

have different functions at different times (Barrett & Bateson 1978).

Studies of play have focused on carnivores, with felids and canids featuring prominently. In this study, we documented early behavioural development in the spotted hyaena, *Crocuta crocuta*, a social carnivore known for its aggressive rather than playful behaviour. We argue that, in this species, the relation between play and other aspects of infant social development is best explained if play is considered to have immediate socialization benefits. Inferences about the immediacy of benefits are drawn from a sequential behavioural development that correlates with a changing schedule of social pressures.

Spotted hyaenas hunt communally, live in relatively stable clans (Kruuk 1972) and have a female-dominated, matrilineal social system (Frank 1986b). They are unusual among mammals in that they display absence or reversal of

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sexual dimorphism (Matthews 1939; Glickman et al. 1993). In common with some social carnivores (African wild dogs, *Lycaon pictus*: Frame et al. 1979; social mongooses, *Helogale parvula* and *Mungos mungo*: Rood 1986), spotted hyaenas rear their young in communal dens (Kruuk 1972). As with some other social carnivores (lions, *Panthera leo*: Rudnai 1973; brown hyaenas, *Hyaena brunnea*: Owens & Owens 1979), however, they give birth in private and initially keep their young isolated (Goodall & van Lawick 1970; Kruuk 1972).

The natal den, usually an abandoned aardvark, *Orycteropus afer*, burrow, has a narrow entrance that prevents access by large predators and other adult hyaenas (East et al. 1989; Henschel & Skinner 1990). Consequently, the den also constrains maternal contact, with cubs emerging primarily to nurse (Kruuk 1972). While sequestered at the natal den, the twins that typically constitute a litter are intensely aggressive (Frank et al. 1991). Moreover, cubs are precocial, born with their eyes open and incisor and canine teeth fully erupted (Matthews 1939; Pournelle 1965). Studies of captive animals reveal that the first interactions between siblings, occurring within minutes of birth, involve vying for position until one cub latches onto its sibling's upper shoulder region with its teeth, shaking vigorously and often remaining attached despite the sibling's efforts to dislodge its attacker (Frank et al. 1991). Uninterrupted stereotypic 'bite-shake' attacks can produce severe flesh wounds that, in the wild, may ultimately contribute to the death of one sibling (Frank et al. 1991).

This early aggression is in marked contrast to the early behaviour of most carnivores. For instance, in many canids (wolves, *Canis lupus*, beagles, *C. familiaris*: Bekoff 1974; maned wolves, *Chrysocyon brachyurus*, crab-eating foxes, *Cerdocyon thous*, and bush dogs, *Speothos venaticus*: Biben 1983) and felids (domestic cats, *Felis domesticus*: Barrett & Bateson 1978; cheetahs, *Acinonyx jubatus*: Caro 1995) the earliest interactions between siblings occur days or even weeks later in development and are usually prosocial or playful. Intra-litter aggression, when it occurs, emerges later than in spotted hyaenas and is less severe (coyotes, *C. latrans*: Bekoff 1974, 1978). Similarly, other hyaena species show no evidence of early aggression and engage in play behaviour, such as muzzle wrestling, at a later age (about 4

weeks in striped hyaenas, *H. hyaena*: Rieger 1981; about 6 weeks in brown hyaenas: Owens & Owens 1978; Mills 1990).

Once spotted hyaena cubs are 2–3 weeks old, mothers transfer them to the communal den, where they are introduced to peers and other clan members (Kruuk 1972; East et al. 1989; Henschel & Skinner 1990). The communal den includes several underground cavities and a network of tunnels that, like the natal den, provides shelter but is inaccessible to adults (Kruuk 1972; Mills 1990). The transition is critical because cubs still require their mother's protection, yet maternal attendance is constrained by the structure of the den and by her hunting obligations (East et al. 1989). Furthermore, young cubs continue to be agonistic, not only towards siblings but towards peers and older juveniles (Holekamp & Smale 1993). Although the presence of mothers during their offspring's aggressive interactions strongly influences the outcome (Holekamp & Smale 1993), cub behaviour is often not monitored.

The unusual aggressiveness of infant spotted hyaenas raises a number of interesting questions (Glickman et al. 1993; Frank, in press), one of which is, how do young cubs survive the early transition from the natal to the communal den? If their behaviour were limited to aggression, their introduction to older, larger animals would be particularly difficult and maladaptive. We propose that to successfully integrate within the clan, infants must arrive at the communal den with a behavioural repertoire that permits the development of affiliative as well as competitive social relationships.

To date, there has been no study of infant spotted hyaena social behaviour, largely because interactions are not readily observable under natural conditions (e.g. Henschel & Skinner 1990). The present study focused on the time course of aggressive and prosocial interactions, including play, in captive animals, during the first month of life, in an artificial denning situation. As we show, the early emergence of aggression and play, as simultaneous elements of the spotted hyaena behavioural repertoire, provides an opportunity to examine the structural relation between the two. We would expect their developmental patterns to be correlated if both are part of a single system, but not if they are separable.

We sought to determine whether a decline in aggression and concurrent development of

prosocial behaviour occurred on a schedule that would prepare the infant for meeting clan members at the communal den. If it were advantageous for the cub to be as aggressive as possible, we would not expect to see play behaviour any earlier than in related species. If, on the other hand, the development of an affiliative system were required for successful integration, we would expect to see prosocial or play behaviour emerge as early as at two weeks of age. Other forms of affiliative behaviour, such as greeting ceremonies, are important in the formation and maintenance of social bonds (Kruuk 1972; Mills 1990; East et al. 1993), but have only been documented in older cubs once they are already at the communal den.

Given the extreme masculinization of female spotted hyaenas, who are both more aggressive and more playful than males in adolescence (Pedersen et al. 1990) and adulthood (Glickman et al. 1993), we also examined whether this reversal of the typical sex bias in aggression and play was present in younger animals. We propose that the early emergence of prosocial and play behaviour in infant spotted hyaenas might promote immediate social integration and ultimately maintain social cohesion, and that an early female bias in play might be a first step towards establishing social relations and alliances in this female-bonded society.

METHODS

Subjects, Husbandry and Housing

The subjects were five adult female spotted hyaenas and their eight litters of twins (five female–female, two female–male and one male–male pairs). Four of the mothers were captured as infants in the Narok District of Kenya, in 1985 or 1986, and reared at the Field Station for Behavioral Research in Berkeley, California. The remaining mother and all cubs were born and reared at the Field Station. Animals were provided daily with bones and a commercially prepared diet for feline carnivores. Water was freely available.

Following mating, adult females were anaesthetized and monitored by ultrasound (Berger et al. 1992). Pregnancies can be detected at two weeks of gestation and ultrasonic measurements provide reliable indices of fetal age. We removed pregnant females from their social group approximately one

week before parturition and housed them separately in temperature-controlled, indoor whelping pens (2 × 2 m) containing straw bedding.

Siblings were born, on average, two hours apart. We removed neonates (1–5 days of age) from their mothers for 1–2 h for routine physical examination, sexing and dye marking (Lady Clairol). As in nature, mothers and their cubs were isolated from other animals; unlike the natural situation, however, mothers had continuous access to their cubs, potentially allowing increased mother–infant interactions. Animals were released into larger outdoor enclosures after one month and then were gradually introduced to the mother's original social group (Berger et al. 1992).

Data Collection and Behavioural Definitions

We monitored whelping pens by a wide-angle video camera for 12–16 h each day and selected tapes from the video record to represent the beginning, middle and end of each week of the cubs' first month of life. On average, we obtained 15 h of observation per week for each litter. For most litters, observations began on day 1, with the day of birth considered day 0. We viewed tapes in their entirety and scored them in real time for all occurrences of aggression, submission, prosocial behaviour, social play, solitary play, exploration and maternal behaviour (Table I).

Controversy over an acceptable definition of play has been an enduring problem (Beach 1945), although play behaviour can be studied empirically (Bekoff 1976; Fagen 1981; Martin & Caro 1985). We characterized social play according to a structuralist approach (Fagen 1981) by reference to the altered motor actions usually observed in dominance displays or aggressive contexts (Pedersen et al. 1990; Table I). Behavioural context was important in differentiating play from non-play, because play was indicated when otherwise aggressive acts did not elicit flight, agonism or vocalizations. In addition, social play is often initiated and maintained by species-typical signals (Bekoff 1974). In spotted hyaenas, these distinguishing characteristics include postures, gaits, facial expressions, and tail and ear position, all of which are absent from agonistic encounters. Because the potential for ambiguity remained, we coded borderline events that neither fully met the criteria for aggression nor play, and could not be

Table I. Definitions for the categories of aggressive, questionable, submissive, prosocial, social play, solitary play, exploratory and maternal behaviour

Behaviour	Definition
Aggression	Behaviour performed with any combination of aggressive body postures (i.e. ears forward*, tail up, mane erect) and frequently accompanied by distress vocalizations of recipient.
Bite shake	Grasping with teeth and forceful, rapid sideways motion of head, typically directed towards shoulder region of recipient.
Bite	Grabbing with teeth, ranging from quick forceful nips to prolonged or intense contact, directed towards any part of recipient's body.
Bite attempt	Opening of mouth with snapping of teeth, without physical contact.
Displace from nipple	Shoving a nursing cub away from the mother's nipple.
Push	Full body contact that displaces another animal.
Shadow	Pursuit, ranging from walking close behind to chasing.
Threat	Lunging.
Questionable	Behaviour performed with a combination of aggressive and non-aggressive body postures or in which the posturing of the actor is not matched in kind by that of the recipient.
Aggressive play	Vigorous interaction, with physical contact, that is not clearly aggressive nor playful.
Submission	Behaviour performed with any combination of submissive body postures (i.e. ears flattened*, tail tucked under, arched back).
Withdrawal	Moving away in apparent avoidance of another animal.
Prosocial	Behaviour performed with any combination of non-aggressive body postures, that appears 'friendly' but is almost lethargic, lacking the characteristic vigour of play.
Prone interactions	Low intensity pawing/batting or mouthing, while in a prone position, without changing or jostling for position.
Social play	Behaviour performed with any combination of non-aggressive body postures (i.e. ears lowered*, tail down, relaxed body posture, smooth hair), in the absence of vocalizations.
Play bite	Short nips that are not forceful.
Play shake	Non-harmful open-mouth contact with slow side-to-side motion of head.
Play chase	Pursuit with a bouncy gait.
Play wrestle	Vigorous mutual rolling around or pushing, including play biting.
Play invite	Jerky body movement directed at another animal, including tilting or rocking of head, with open mouth and lowered ears, and repeated approach/withdrawal sequences.
Unreciprocated play	Playful body contact and invitation that is unsuccessful.
Solitary play	Either locomotor activity that appears pleasurable but has no recipient or behaviour directed at an object.
Jump	Upward leap while walking or running.
Object play	Biting, chewing, carrying, pulling or batting an object.
Roll	Sideways motion with feet up, while in a prone position.
Romp run	Rapid, exaggerated forward locomotion, including trotting and jumping with a rocky or bouncy gait.
Run	Rapid forward locomotion.
Exploration	Solitary behaviour that does not appear playful but rather purposive.
Climb	Upward crawling motion, usually on top of the mother and frequently accompanied by head bobbing.
Dig	Repetitive pawing at any substrate, often associated with unrest.
Maternal	Behaviour directed from mother to one or both cubs.
Interrupt aggression	Any behaviour that results in the termination of cub aggression.
Interrupt play	Any behaviour that results in the termination of cub play.
Lick	Extended groom-licking.
Restrain	Holding cub with mouth or paw.
Retrieve	Fetching and carrying cub in mouth.

*Ear position cannot be used to distinguish play from non-play in very young animals, because their ears are flat against their head for about the first week.

resolved from contextual cues, as 'aggressive play' (Table I). This separate 'questionable' category probably reflected behaviour patterns that originated as play but rapidly escalated into aggression. Ambiguous behaviour ultimately accounted for only a small percentage of total observations (see Results). Finally, because vigour is a frequently cited characteristic of play (Fagen 1976), we defined low-intensity behaviour that was either interactive or clearly directed from one individual to another, as prosocial behaviour (Table I).

Despite definition difficulties, hyaena play is readily recognized, as in other species, with high inter-observer reliability (Pedersen et al. 1990). At the start of the study, observers viewed training tapes with representative examples of all behaviour categories to standardize data collection. For reliability estimates, observers scored a given tape twice, once at the beginning and once at the end of data collection. We calculated reliability scores as the percentage agreement between two data sets. We considered differences in the chronology or labelling of events and differences in duration that exceeded 5 s as disagreements. Intra- and inter-observer reliability scores exceeded 80% agreement for aggression, submission, prosocial behaviour, social play and maternal behaviour and exceeded 75% agreement for solitary play and exploration.

Analyses

All data validation, extraction and analyses used UNIX/STAT compact data analysis programs (Perlman 1986), with statistics reported as means \pm SEs and significance set at $\alpha=0.05$. We analysed developmental changes in sibling interactions and maternal behaviour by comparing mean weekly frequency and duration for each action pattern. We assessed differences using one-way analyses of variance (ANOVAs) and resolved significant effects using Newman-Keuls' multiple-range tests (Bruning & Kintz 1977). Whenever variances were non-homogeneous, we analysed log transformations of the data. For comparisons between behaviour types (i.e. aggressive bite versus play bite) or between partners (i.e. cub behaviour directed towards sibling versus towards mother), we used two-way ANOVAs and *F*-tests for simple effects. We assessed dominance effects on the initiation of behaviour using two-tailed *t*-tests; however, we excluded early trials, before

cubs were dye-marked, from these analyses. We studied sex effects on frequency and duration measures using two-factor ANOVAs. For these analyses, we combined the female-male and male-male litters into a single category. We compared this category of twins, in which at least one sibling was male, to an all-female category. Sex differences have been detected using this approach (Caro 1981). We quantified maternal interruption of cub behaviour (frequencies per h) and standardized values by dividing them by rates of relevant cub behaviour.

RESULTS

Cub Aggressive and Submissive Behaviour

Both the frequency and duration of bite shakes, the most intensely aggressive behaviour between cubs, changed over time ($F_{3,21}>8.5$, $P_s<0.001$), with a marked decline following week 1 (Fig. 1a, b). The variance within the first week reflects a rapid and steady daily decline (Frank et al. 1991). All other categories of aggression (including bites, bite attempts, displacements at the nipple, pushes, shadows and threats) occurred at equal rates across weeks, whether these measures were assessed independently ($F_{3,21}<1.8$, NS) or were combined ($F_{3,21}<0.8$, NS; Fig. 1a, b). The frequency and duration for the questionable category of 'aggressive play' also showed no change over time ($F_{3,21}<2.3$, NS). Weekly consistency, compared with changing patterns of play behaviour (see below) suggests that this behaviour is more properly classified as aggression. As such, it only accounted for small percentages (<6.8%) of total aggressive interactions.

Rates of submissive withdrawals by cubs mirrored the constant rates of aggression by showing consistency across weeks ($F_{3,21}<1.0$, NS). We assigned dominance labels within litters by examining the pattern of total monthly withdrawals. We referred to the cub with the highest frequency of withdrawal behaviour (17–250 per litter) as subordinate and to the one with the lowest frequency (0–7 per litter) as dominant. Withdrawal frequencies showed strongly unidirectional patterns, with subordinates accounting for 92–100% of all occurrences. Within the first week, subordinates accounted for 86–100% of withdrawals, which predicted the pattern of submission in

later weeks. These consistent differences showed that dominance relationships were established early and underwent no subsequent reversals.

Cubs directed some aggression (i.e. bites, bite attempts and bite shakes) towards their mother,

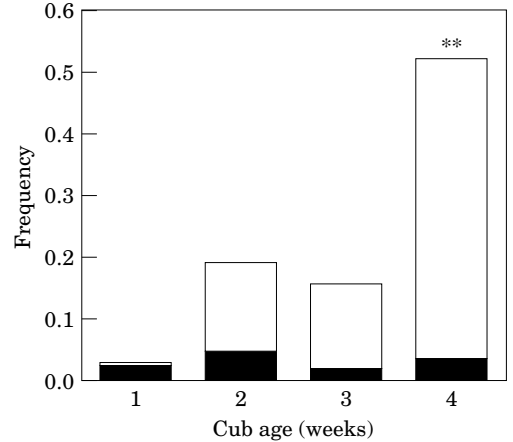
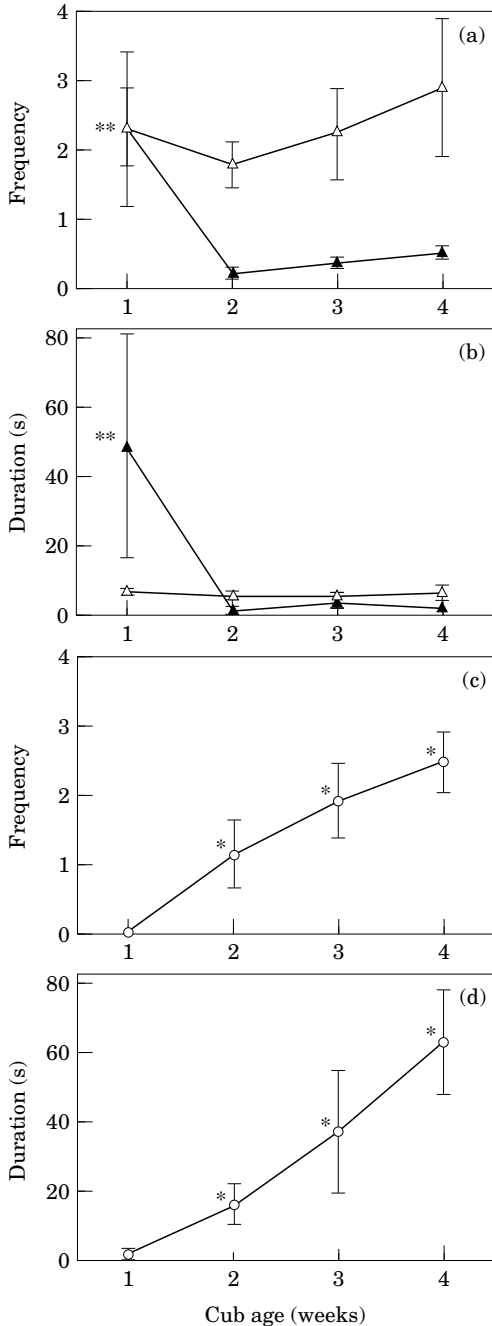


Figure 2. Mean hourly rates of hyaena cub engagement in prosocial activity with sibling (□) versus with mother (■) during the first month of life. Cub-cub frequencies during week 4 exceeded those during weeks 1, 2 and 3 (** $P_s < 0.01$ Newman-Keuls'), but cub-mother frequencies showed no weekly change ($F_{3,21} < 0.3$, NS).

but at a lower frequency than they did toward each other ($F_{3,21} > 6.7$, $P_s < 0.05$). Cubs showed a non-significant tendency to bite-shake their mother more frequently during week 1 ($\bar{X} \pm SE = 0.16 \pm 0.08$) than in later weeks ($< 0.04 \pm 0.02$; $F_{3,21} = 2.6$, $P = 0.075$).

Cub Prosocial Behaviour

Cubs engaged in low-intensity prosocial behaviour within the first week. This activity increased in frequency and duration across weeks ($F_{3,21} > 8.2$, $P_s < 0.001$), peaking in week 4 (Fig. 2). They engaged in prosocial behaviour with their mother less than with each other ($F_{3,21} > 6.9$, $P_s < 0.05$) and at equal rates across weeks (Fig. 2). Cubs also showed a change in partner preference across weeks ($F_{3,21} > 4.9$, $P_s \leq 0.01$), tending

Figure 1. Mean \pm SE hourly rates for the (a) frequency of aggression, (b) duration of aggression, (c) frequency of social play and (d) duration of social play between spotted hyaena siblings during their first month of life. Levels of aggressive bite shakes (▲) were higher during week 1 than weeks 2, 3 or 4 (** $P_s < 0.01$); total other aggression (△), excluding bite shakes, showed no weekly differences; for total social play (○), each week showed higher levels than the previous week (* $P_s < 0.05$; Newman-Keuls').

Table II. Mean \pm SE weekly frequencies of total mutual social play between spotted hyaena cubs and percentages of the different types of play behaviour

Week	Mutual social play	Composition by play type (%)			
		Wrestle	Bite	Shake	Chase
1	0.05 \pm 0.03	37	63	0	0
2	0.84 \pm 0.37	46	38	10	6
3	1.42 \pm 0.40	50	39	7	4
4	1.66 \pm 0.25	57	34	4	5

to engage in more prosocial activity with their mother during week 1, but showing increasing preference for their sibling that reached significance by week 4 ($P_s < 0.001$).

Cub Social Play Behaviour

The most frequent type of social play between cubs, averaged across their first month of life, was play wrestling, followed by play biting. These two types of play steadily increased in frequency and duration over the four-week period ($F_{S_{3,21}} > 6.2$, $P_s < 0.005$). Play chases and play shakes, which occurred less frequently, did not significantly increase across weeks ($F_{S_{3,21}} < 1.6$). Play solicitations often preceded bouts of playful activity; in some instances, however, play invitations were ignored and resulted in short bouts of unreciprocated play. Play solicitations between siblings increased across weeks ($F_{S_{3,21}} > 6.7$, $P_s < 0.005$), but unreciprocated play did not ($F_{S_{3,21}} < 1.6$, NS), suggesting that solicitations were becoming more successful in initiating play. When we combined all categories of social play, each week showed a significant increase in total frequency and duration over the preceding week (Fig. 1c, d).

To investigate changing patterns of social play behaviour, we combined all categories of mutual social play (excluding solicitations and unreciprocated play) and compared weekly percentages of the different types (Table II). This analysis revealed that play bites, the least vigorous of social play categories, dominated week 1. Moreover, play chases and play shakes were absent during this time. By week 2, the variety of mutual social play increased, as did the percentage of more rough-and-tumble play wrestling. Therefore, not only did overall frequency and duration of play increase over the first month (Fig. 1c, d), but the type of play became more vigorous (Table II).

Cubs engaged in a limited social play repertoire (including play bites and play shakes) with their mothers; nevertheless, they showed similar rates of these activities with their mothers as they did with each other ($F_{S_{1,7}} < 3.4$, NS). Cubs solicited less play from their mothers than they did from each other ($F_{S_{1,7}} > 14.6$, $P_s < 0.01$), and their preference for soliciting their sibling became more pronounced in later weeks ($F_{S_{3,21}} > 6.8$, $P_s \leq 0.005$). A cub's unreciprocated attempts at initiating play were equally directed towards mothers and siblings ($F_{S_{1,7}} < 2.4$, NS).

Cub Solitary Play and Exploratory Behaviour

Cubs showed different weekly levels of independent object play ($F_{S_{3,21}} > 3.3$, $P_s < 0.05$) which, compared to social play, emerged later (Fig. 3). Solitary locomotor play showed inconsistent patterns across different play types: although cubs engaged in gradually increasing levels of romp running across weeks ($F_{S_{3,21}} > 6.2$, $P < 0.005$), they maintained consistently low levels of jumping, rolling and running ($F_{S_{3,21}} < 1.5$, NS; Fig. 3). Thus, some forms of solitary play increased and others did not. Similarly, exploratory digging showed a gradual increase ($F_{S_{3,21}} > 11.1$, $P_s < 0.001$), with higher values in weeks 3 and 4 than in weeks 1 and 2 ($P_s < 0.05$), but climbing showed no change in frequency or duration over time ($F_{S_{3,21}} < 2.8$, NS).

Comparison of Cub Aggression to Cub Play

One of the distinguishing characteristics of play is that its actions tend to be exaggerated (Loizos 1966; Fagen 1981), potentially reflected in the prolonged duration of bouts (Hill & Bekoff 1977). For sibling interactions, we compared the average weekly bout duration (total daily duration divided by total daily frequency) of aggressive bites to that

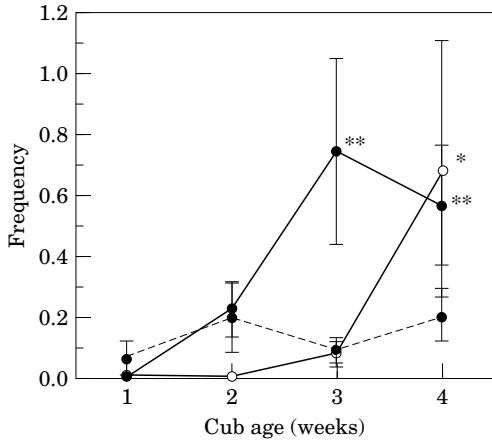


Figure 3. Mean \pm SE hourly frequency of solitary object play (\circ) and locomotor play (\bullet), including romp running (solid line) and rolling (dashed line), by infant spotted hyaenas across the first four weeks of life. Cubs engaged in more object play during week 4 than in previous weeks ($*P < 0.05$), and in more romp running during weeks 3 and 4 than in week 1 ($**P < 0.01$; Newman-Keuls'). Rolling, like jumping and running (data not shown), showed no weekly change ($F_{3,21} = 1.0$, NS).

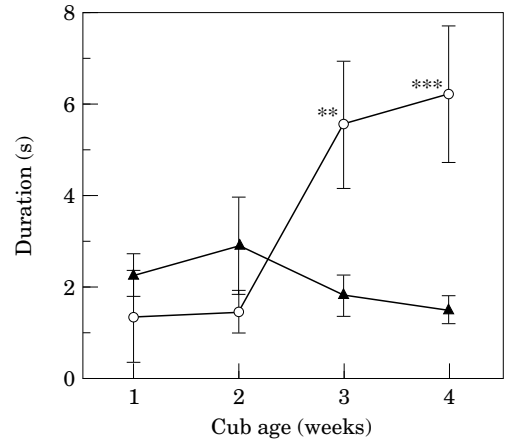


Figure 4. Mean \pm SE bout duration (s/h) of aggressive bites (\blacktriangle) compared to play bites (\circ) between spotted hyaena siblings across the first four weeks of life. Bouts of play biting and bouts of aggressive biting were of equal duration in weeks 1 and 2 ($F_{3,21} < 1.2$, NS), but bouts of play biting were longer than bouts of aggressive biting in weeks 3 and 4 ($F_{3,21} > 7.5$, $**P < 0.005$, $***P < 0.001$; F -tests for simple effects).

of play bites (Fig. 4). A significant interaction ($F_{3,21} = 5.3$, $P < 0.01$) revealed that initially bouts were equal in length, but bouts of play biting eventually grew longer (Fig. 4).

Another characteristic of social play is that rank relations apparent during aggression appear to be ignored or temporarily reversed (Bekoff 1974). Using dominance labels established by cub withdrawal patterns (see above), we analysed the direction of sibling aggressive and playful interactions. Although the dominant cub initiated more aggressive interactions than its subordinate sibling, both cubs initiated social play equally (Fig. 5). Thus, the initiation of aggression was unidirectional, but the initiation of play was reciprocal. There were no significant differences between dominant and subordinate cub behaviour directed towards mothers ($F_{3,7} < 2.4$, NS); however, patterns were consistent in that dominant cubs tended to be more aggressive than, but equally playful as, subordinate cubs in interactions involving mothers.

Sex Differences

Because of the small number of male cubs, investigations of sex differences were limited to

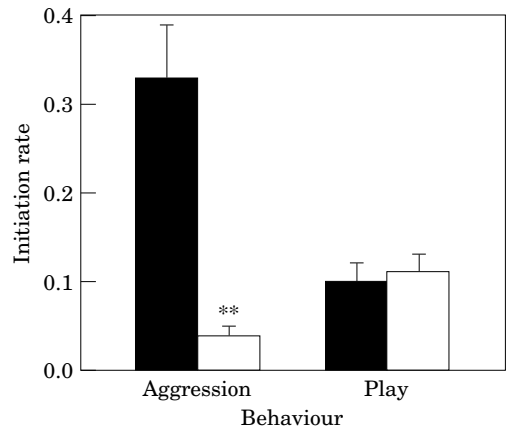


Figure 5. Mean \pm SE hourly initiation rate of aggression and play by the dominant (\blacksquare) and subordinate (\square) cub within twins of spotted hyaenas. Dominant cubs initiated more aggression than subordinate cubs ($t = 4.57$, $df = 7$, $**P < 0.005$), but both initiated play equally ($t = 0.27$, $df = 7$, NS; two-tailed t -test).

assessing differences between the five sets of twins in which both siblings were female and the three sets in which at least one sibling was male (Table III). There were no main effects of sex on aggression (e.g. bite shake) or play (e.g. play wrestle)

Table III. Mean \pm SE hourly rates of aggression and play, between siblings or between one cub and its mother, by all-female twins of spotted hyaenas and by twins in which at least one sibling is male

Behaviour	Hourly rate of behaviour		
	All female twins	Twins with male(s)	$F_{1,6}$
Cub-cub aggression			
Bite shake (freq)	0.98 \pm 0.49	0.61 \pm 0.15	0.31
Bite shake (dur)	18.99 \pm 13.56	5.24 \pm 2.13	0.66
Cub-cub play			
Play wrestle (freq)	0.63 \pm 0.18	0.32 \pm 0.10	1.95
Play wrestle (dur)	31.22 \pm 9.98	14.80 \pm 5.06	1.17
Cub-adult aggression			
Bite shake (freq)	0.02 \pm 0.01	0.13 \pm 0.06	13.90**
Bite shake (dur)	0.38 \pm 0.26	0.35 \pm 0.15	0.01
Other aggression (freq)	0.02 \pm 0.01	0.49 \pm 0.25	9.35*
Other aggression (dur)	0.08 \pm 0.05	2.08 \pm 0.97	8.46*
Cub-adult play			
Play bite (freq)	0.19 \pm 0.08	0.46 \pm 0.23	2.90
Play bite (dur)	2.51 \pm 0.92	8.42 \pm 4.43	5.85†

Frequency (freq) is reported as rate per hour; duration (dur) is reported as seconds per hour.

** $P < 0.01$, * $P < 0.05$, † $P = 0.052$.

($F_{s_{1,6}} < 3.2$; $F_{s_{1,6}} < 2.7$, respectively; Table III). Reliable sex differences appeared only in the behaviour that cubs directed towards their mother, in that twins with at least one male were more aggressive to their mother, especially in the first week, and tended to play-bite their mother more than all-female twins (Table III).

Maternal Interruption of Cub Behaviour

Mothers attended to their fighting offspring by watching, moving towards and physically interrupting aggression, either by restraining or retrieving a cub. Mothers interrupted aggressive bouts ($N=46$) at different rates across weeks, with 77% of all maternal intervention occurring in week 1 (Fig. 6). Even when we standardized frequencies to account for potentially different weekly rates of cub aggression, mothers still interrupted aggression at different rates, more frequently in week 1 than week 4 ($F_{3,21} = 3.5$, $P < 0.05$). A linear regression between frequencies of maternal intervention (Fig. 6) and cub bite shakes (the only category of cub aggression to show a similar decline, Fig. 1a) showed a positive correlation that accounted for over 95% of the variance, suggesting a relationship between these two events. A sequence analysis revealed that 85% of maternal interruption was

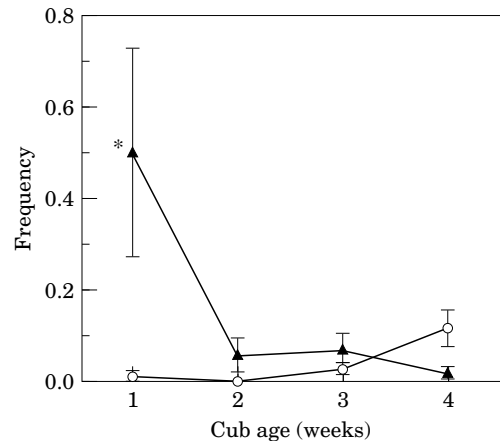


Figure 6. Mean \pm SE hourly frequency of maternal interruption of cub aggression (▲) compared to maternal interruption of cub play (○) across the first four weeks of life. Maternal interruption of aggression changed across weeks ($P < 0.05$), with an initial decline that matched the decline in cub bite shakes, but maternal interruption of play did not change, remaining low across weeks.

immediately preceded (within less than 1 min) by bouts of bite shaking between siblings. The remainder followed bouts of biting, bite attempts, shadowing and submissive behaviour, in similar

proportions. Thus, given the potential for access to their cubs, mothers intervened only during the most severe instances of infant aggression.

Mothers rarely interrupted the prosocial or play behaviour of their cubs ($N=18$), as shown by weekly frequencies (Fig. 6), and standardized rates of maternal play interruption showed no weekly change ($F_{3,21}=1.1$, ns). A sequence analysis revealed that play interruption occurred under a broader range of cub behaviour; i.e. following unreciprocated play (5.5%), prosocial behaviour (16.7%), play bites (16.7%), object play (22.2%) and play wrestles (38.9%). Moreover, play interruption appeared less deliberate, most often arising from the mother's approach or behaviour (such as digging) that distracted cubs from their play (38.9%). In some cases, mothers joined in their cubs' play or appropriated the objects with which they were playing (33.3%); in other cases, mothers interrupted play by groom-licking their cubs (11.1%). Only once (5.6%) did a mother restrain her playing cub and in two cases (11.1%) mothers muzzled between cubs during vigorous play that ultimately escalated into aggression. Thus, mothers interrupted their cubs more often when they were engaged in aggressive interactions than during play.

DISCUSSION

A dramatic behavioural reorganization occurred in infant spotted hyaenas at about two weeks of age, including a rapid reduction in aggression, the emergence of a peer preference during prosocial interactions and the development of vigorous social play. These behaviour patterns appear on a developmental schedule that is ideally synchronized for introduction of young cubs to their peers and other clan members at the communal den. The absence of a temporal correlation between aggression and play suggests that the two reflect differing underlying systems in the behavioural repertoire of the spotted hyaena. We argue that aggression helps to establish dominance and hone competitive abilities, and play helps to establish affiliative relations and promote social cohesion.

Initial interactions between siblings were intensely aggressive, as previously reported (Frank et al. 1991). In nature, this early aggression has been linked to the death of one sibling in same-sex litters (Frank et al. 1991). The present

data show for the first time, however, that mothers will intervene when possible to curtail infant aggression. Although aggression within the burrow system is unchecked by the mother, she can interrupt behaviour once cubs emerge. If maternal intervention occurs in nature, female hyaenas could influence the survival of their offspring, biasing the sex ratio of individual litters (Frank, in press). The rapid decline in severe aggression may reflect the early establishment of a dominance relationship between siblings. This interpretation is supported by the appearance, within the first week, of a stable, unidirectional pattern of submission, consistent with previous reports (Smale et al. 1995). The early establishment of dominance has immediate effects (influencing access to the nipple) as well as more enduring effects (influencing feeding order at communal kills; Holekamp & Smale 1993).

Low-intensity prosocial behaviour appeared in the first week of life, followed by the emergence of higher-intensity social play in the second week. Thus, play developed earlier than has been reported in other species (Bekoff 1974, 1978; Barrett & Bateson 1978; Biben 1983; Loeven 1994), perhaps owing to differences in precocity. As in other species (Caro 1995), spotted hyaena locomotor and object play appeared after social play. The progression from low-intensity prosocial behaviour to more vigorous interactive play may correspond to developmental changes in motor and sensory abilities, yet because different categories of play showed different developmental trajectories, intensity changes within any given category may not merely reflect physical development.

Along with enhanced physical ability, the transformation of play probably involved maturing social skills. For instance, play is often identified by species-specific signals that serve to initiate or maintain social play (Bekoff 1974). These signals must be learned and recognized to communicate intent effectively. Several lines of evidence from our study suggest that communication of playful intent was becoming more effective. Notably, play solicitations were increasingly followed by play bouts rather than ignored. Moreover, although bouts of play biting were initially equal in length to bouts of aggressive biting, play bouts eventually lasted longer. This changing pattern may reflect effective communication, the pleasurable nature of play (Bekoff 1976) or one aspect of the

exaggerated quality of play (Loizos 1966; Fagen 1981). Finally, cubs increasingly solicited their sibling, the preferred play partner, rather than their mother. This peer preference is consistent with the fact that, in nature, cubs spend most of their time in the company of siblings. Play cues were recognized not only by the participants but also by observers, specifically mothers, who selectively intervened during extreme aggression but not during vigorous play.

Aggressive interactions were initiated and won by the dominant cub, in marked contrast to playful interactions, where the subordinate and dominant cub initiated and engaged in play at equal rates. Dominance relations were established early and showed no reversals, but were ignored, absent or temporarily reversed during play. This 'breakdown' of dominance relations is consistent with reports of role reversal and self-handicapping during play in other species (Bekoff 1974). Unlike most species in which play appears before fighting (Bekoff 1974) and may serve to establish dominance (Panksepp 1981), however, spotted hyaena play involves reciprocity in a dominance relationship previously established through aggression. This latter pattern is similar to that reported for coyotes (Bekoff 1978) and suggests that play is not necessary for the establishment of dominance in these species, and may instead contribute to the termination of serious aggression.

Theories on the functional significance of play have focused on the delayed accrual of benefits through the early rehearsal of behaviour (Fagen 1981; Smith 1982). We argue, as have others (Barrett & Bateson 1987; Gomendio 1988; Caro 1995), that play in spotted hyaenas potentially serves different functions at different ages. Although juvenile and adolescent play may develop strength and endurance through exercise (Fagen 1976) and may serve a preparatory role for social hunting, the early play of infants is less likely to have similar functions. We propose instead that the early emergence and development of interactive play in infant spotted hyaenas may have an immediate benefit, notably providing a mechanism through which social bonds are formed, strengthened and maintained, as has been suggested for other species (Bekoff & Byers 1981; Panksepp 1981; Lee 1983).

Because play and aggression share similar behavioural components, many have argued that play provides a safe substitute for the practice and

fine-tuning of intraspecific aggressive skills (Smith 1982); however, this 'training' hypothesis does not appear to explain early spotted hyaena play. Notably, a stereotypical, adult-like pattern of intraspecific aggression (i.e. the bite shake) is present shortly after birth, before the emergence of play, and is already severe, effective and sometimes lethal (Frank et al. 1991). Although further training may be necessary, the indirect contribution from play seems negligible compared to the direct experience obtained from engagement in aggressive behaviour throughout development (Holekamp & Smale 1993). Moreover, if play were a substitute for aggression, one would expect the components of play to reflect necessary aggressive skills, but play shakes (the play 'equivalent' of bite shakes) accounted for only a small percentage of overall play activity. Rather than rehearsing aggression, play appeared to borrow actions from the established aggression repertoire, becoming increasingly modified, elaborated and marked by unique, identifiable cues. Together, the unusual sequence of behavioural development and the features of play suggest that social play is more likely to serve to modulate aggression than to practice the motor skills of aggression.

Similarly, the early play behaviour of spotted hyaenas does not appear to serve an immediate 'training' function for interspecific aggressive skills. Young cubs must quickly learn to strike a balance between their competitive behaviour and their affiliative or cooperative behaviour (Smale et al. 1995), making social integration a pressing environmental demand for young spotted hyaenas. By contrast, the need to learn hunting skills is comparatively delayed. Spotted hyaena cubs remain dependent on maternal milk for the first 12–15 months, longer than in other large carnivores, and do not accompany their mothers on hunting forays until they are about 8–12 months old (Mills 1990; Holekamp & Smale 1993). If play serves to practice predatory skills in other carnivores, it is inconsistent for play to emerge earlier in a species that shows delayed weaning and hunting. Nevertheless, cumulative effects on later behaviour may stem from early play, and as play develops, its relative composition and function may change (Barrett & Bateson 1978). In our study, chasing was not a prominent component of infant play, and object play appeared only in the fourth week; however, both are major features of juvenile and adolescent play (Goodall & van

Lawick 1970; Kruuk 1972; Pedersen et al. 1990). The gradually changing topography of play, possibly meeting environmental demands, suggests that later features of spotted hyaena play may be increasingly related to the practice of hunting abilities, as has been suggested in other species (Caro 1995).

We suggest that the 'socialization' hypothesis is consistent with the early development of social play in spotted hyaenas, because the timing of its emergence is ideally suited to enable integration at the communal den. Specifically, the change from elevated aggression without play to reduced aggression with the onset of play occurred at a crucial time, before mothers normally transfer their cubs from the natal to the communal den. Having an established play repertoire could have immediate benefits to a young animal being introduced to clan members for the first time. Although social play between siblings may help cubs to acquire necessary skills that prepare them for tempered interactions with unfamiliar peers, early play with mothers may facilitate interactions with older animals. Whether mother-cub interactions are more prominent in singleton litters, in which a peer playmate is unavailable, is unknown.

Early play could also have cumulative socialization benefits. In brown hyaenas, one of the proposed advantages of communal denning is that it provides opportunities to play, thereby preparing young animals for adult encounters (Owens & Owens 1979). In spotted hyaenas, early interactive play may assist in the development and maintenance of social relationships, having both immediate and cumulative consequences, accrued in adulthood, and possibly affecting fitness. For instance, a female sex bias in play, although socially modulated, is evident in adolescent spotted hyaenas (Pedersen et al. 1990). This bias is consistent with the suite of sex-reversed traits, including increased aggression in females (Matthews 1939; Kruuk 1972), and suggests androgenic organization of play (Pedersen et al. 1990).

Although we could not adequately address sex differences in the present study because of sample size limitations, the reversal of sex biases may appear at an earlier age than previously reported (Pedersen et al. 1990). For instance, female-female twins tended to fight more intensely and engage in more rough-and-tumble play, but twins

in which at least one sibling was male, directed more aggression and play to their mothers. Sex differences in play are either absent in other young carnivores (Bekoff 1974, Biben 1983) or appear at a later age (Barrett & Bateson 1978; Caro 1981). If sex differences in hyaena play exist, then animals may be differentially 'prepared' by early experiences for later social integration, with the bias placing females at an advantage over males. Young males remain in the clan only until puberty, when they disperse and join other clans, but females spend their entire lives within their natal clan (Frank 1986a; Henschel & Skinner 1987; Mills 1990). The early establishment of social relations and alliances between females has obvious evolutionary implications for female-bonded societies and requires further investigation.

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REFERENCES

- Barrett, P. & Bateson, P. 1978. The development of play in cats. *Behaviour*, **66**, 106-120.
- Beach, F. A. 1945. Current concepts of play in animals. *Am. Nat.*, **79**, 523-541.
- Bekoff, M. 1974. Social play and play-soliciting by infant canids. *Am. Zool.*, **14**, 323-340.
- Bekoff, M. 1976. Animal play: problems and perspectives. In: *Perspectives in Ethology*, Vol. 2 (Ed. by P. P. G. Bateson & P. H. Klopfer), pp. 165-188. New York: Plenum Press.
- Bekoff, M. 1978. Behavioral development in coyotes and Eastern coyotes. In: *Coyotes: Biology, Behavior, and Management* (Ed. by M. Bekoff), pp. 97-126. New York: Academic Press.
- Bekoff, M. & Byers, J. A. 1981. A critical reanalysis of the ontogeny and phylogeny of mammalian social and

- locomotor play: an ecological hornet's nest. In: *Behavioral Development: The Bielefeld Interdisciplinary Project* (Ed. by K. Immelmann, G. W. Barlow, L. Petrinoich & M. Main), pp. 296–337. Cambridge: Cambridge University Press.
- Berger, D. M. P., Frank, L. G. & Glickman, S. E. 1992. Unraveling ancient mysteries: biology, behavior, and captive management of the spotted hyena, *Crocuta crocuta*. *Proc. Am. Assoc. Zoo Vet., Am. Assoc. Wildlife Vet.*, pp. 139–148.
- Biben, M. 1983. Comparative ontogeny of social behaviour in three South American canids, the maned wolf, crab-eating fox and bush dog: implications for sociality. *Anim. Behav.*, **31**, 814–826.
- Bruning, J. L. & Kintz, B. L. 1977. *Computational Handbook of Statistics*. 2nd edn. Glenview: Scott, Foresman.
- Caro, T. M. 1981. Sex differences in the termination of social play in cats. *Anim. Behav.*, **29**, 271–279.
- Caro, T. M. 1995. Short-term costs and correlates of play in cheetahs. *Anim. Behav.*, **49**, 333–345.
- East, M., Hofer, H. & Turk, A. 1989. Functions of birth dens in spotted hyaenas (*Crocuta crocuta*). *J. Zool., Lond.*, **219**, 690–697.
- East, M. L., Hofer, H. & Wickler, W. 1993. The erect 'penis' is a flag of submission in a female-dominated society: greetings in Serengeti spotted hyenas. *Behav. Ecol. Sociobiol.*, **33**, 355–370.
- Fagen, R. M. 1976. Exercise, play, and physical training in animals. In: *Perspectives in Ethology*, Vol. 2 (Ed. by P. P. G. Bateson & P. H. Klopfer), pp. 189–219. New York: Plenum Press.
- Fagen, R. M. 1981. *Animal Play Behavior*. Oxford: Oxford University Press.
- Frame, L. H., Malcolm, J. R., Frame, G. W. & van Lawick, H. 1979. Social organization of African wild dogs (*Lycaon pictus*) on the Serengeti Plains, Tanzania 1967–1978. *Z. Tierpsychol.*, **50**, 225–249.
- Frank, L. G. 1986a. Social organization of the spotted hyaena (*Crocuta crocuta*). I. Demography. *Anim. Behav.*, **34**, 1500–1509.
- Frank, L. G. 1986b. Social organization of the spotted hyaena *Crocuta crocuta*. II. Dominance and reproduction. *Anim. Behav.*, **34**, 1510–1527.
- Frank, L. In press. Female masculinization in the spotted hyena: endocrinology, behavioral ecology, and evolution. In: *Carnivore Behavior, Ecology and Evolution* (Ed. by J. L. Gittleman). Ithaca, New York: Cornell University Press.
- Frank, L. G., Glickman, S. E. & Licht, P. 1991. Fatal sibling aggression, precocial development, and androgens in neonatal spotted hyenas. *Science*, **252**, 702–704.
- Glickman, S. E., Frank, L. G., Holekamp, K. E., Smale, L. & Licht, P. 1993. Costs and benefits of 'androgenization' in the female spotted hyena: the natural selection of physiological mechanisms. In: *Perspectives in Ethology*, Vol. 10 (Ed. by P. P. G. Bateson, P. H. Klopfer & N. S. Thompson), pp. 87–117. New York: Plenum Press.
- Gomendio, M. 1988. The development of different types of play in gazelles: implications for the nature and functions of play. *Anim. Behav.*, **36**, 825–836.
- Goodall, J. & van Lawick, H. 1970. *Innocent Killers*. London: Collins.
- Henschel, J. R. & Skinner, J. D. 1987. Social relationships and dispersal patterns in a clan of spotted hyaenas *Crocuta crocuta* in the Kruger National Park. *S. Afr. J. Zool.*, **22**, 18–24.
- Henschel, J. R. & Skinner, J. D. 1990. Parturition and early maternal care of spotted hyaenas *Crocuta crocuta*: a case report. *J. Zool., Lond.*, **222**, 702–704.
- Hill, H. L. & Bekoff, M. 1977. The variability of some motor components of social play and agonistic behaviour in infant eastern coyotes, *Canis latrans* var. *Anim. Behav.*, **25**, 907–909.
- Holekamp, K. E. & Smale, L. 1993. Ontogeny of dominance in free-living spotted hyaenas: juvenile rank relations with other immature individuals. *Anim. Behav.*, **46**, 451–466.
- Kruuk, H. 1972. *The Spotted Hyena: a Study of Predation and Social Behavior*. Chicago: University of Chicago Press.
- Lee, P. C. 1983. Play as a means for developing relationships. In: *Primate Social Relationships* (Ed. by R. A. Hinde), pp. 82–89. Oxford: Blackwell Scientific Publications.
- Loeven, J. C. 1994. The ontogeny of social play in timber wolves, *Canis lupus*. M.S. thesis, Dalhousie University.
- Loizos, C. 1966. Play in mammals. *Symp. zool. Soc. Lond.*, **18**, 1–9.
- Martin, P. & Caro, T. M. 1985. On the functions of play and its role in behavioral development. *Adv. Study Behav.*, **15**, 59–103.
- Matthews, L. H. 1939. Reproduction in the spotted hyaena, *Crocuta crocuta* (Erleben). *Phil. Trans. R. Soc. Ser. B*, **230**, 1–78.
- Mills, M. G. L. 1990. *Kalahari Hyaenas: Comparative Behavioural Ecology of Two Species*. London: Unwin-Hyman.
- Owens, D. D. & Owens, M. J. 1979. Communal denning and clan associations in brown hyenas (*Hyaena brunnea*, Thunberg) of the central Kalahari Desert. *Afr. J. Ecol.*, **17**, 35–44.
- Owens, M. J. & Owens, D. D. 1978. Feeding ecology and its influence on social organization in brown hyenas (*Hyaena brunnea*, Thunberg) of the central Kalahari Desert. *E. Afr. Wildl. J.*, **16**, 113–135.
- Panksepp, J. 1981. The ontogeny of play in rats. *Dev. Psychobiol.*, **14**, 327–332.
- Pedersen, J. M., Glickman, S. E., Frank, L. G. & Beach, F. A. 1990. Sex differences in the play behavior of immature spotted hyenas, *Crocuta crocuta*. *Horm. Behav.*, **24**, 403–420.
- Perlman, G. 1986. *UNIX/STAT Manuals: Data Analysis Programs on UNIX and MSDOS*. Tyngsboro, Massachusetts: Wang Institute.
- Pournelle, G. H. 1965. Observations on birth and early development of the spotted hyena. *J. Mammal.*, **46**, 503.
- Rieger, I. 1981. *Hyaena hyaena*. *Mamm. Sp.*, **150**, 1–5.
- Rood, J. P. 1986. Ecology and social evolution in the mongooses. In: *Ecological Aspects of Social Evolution* (Ed. by D. I. Rubenstein & R. W. Wrangham), pp. 131–152. Princeton: Princeton University Press.

- Rudnai, J. 1973. Reproductive biology of lions (*Panthera leo massaica* Neumann) in Nairobi National Park. *E. Afr. Wildl. J.*, **11**, 241–253.
- Smale, L., Holekamp, K. E., Weldele, M., Frank, L. G. & Glickman, S. E. 1995. Competition and cooperation between litter-mates in the spotted hyaena (*Crocuta crocuta*). *Anim. Behav.*, **50**, 671–682.
- Smith, P. K. 1982. Does play matter? Functional and evolutionary aspects of animal and human play. *Behav. Brain Sci.*, **5**, 139–184.