

Scent Marking (Pasting) in a Colony of Immature Spotted Hyenas (*Crocuta crocuta*): A Developmental Study

Katya B. Woodmansee, Cynthia J. Zabel, Stephen E. Glickman,
Laurence G. Frank, and Geoffrey Keppel
University of California, Berkeley

Pasting, a stereotypic form of anal gland scent marking, was studied in 2 cohorts ($N=20$) of captive spotted hyenas (*Crocuta crocuta*). A significant increment in the frequency of pasting occurred in both cohorts as the animals approached sexual maturity; however, gonadectomy during the early juvenile age period had no significant effects on subsequent pasting frequency. Dominant hyenas in both cohorts tended to scent-mark more frequently than subordinates during the late subadult period. Pasting was facilitated by the immediately preceding pasting activities of other hyenas, as has been reported to occur in nature, and olfactory investigation was the most common behavior preceding pasting.

Spotted hyenas (*Crocuta crocuta*) are nocturnal social hunters, living in relatively stable groups (*clans*) that consist of resident females, their cubs, and immigrant males (Frank, 1986a; Henschel & Skinner, 1987; Kruuk, 1972). Hyenas scent-mark within their home range defecating at latrines, scratching the ground (which deposits scent from the interdigital glands), and *pasting* (Bearder & Randall, 1978; Kruuk, 1972; Mills & Gorman, 1987). Pasting behavior involves depositing anal gland secretions, which have a strong soapy odor, on objects in the environment, typically stalks of grass. It is performed by using a stereotyped pattern of forward movement with tail elevated, anal pouch bulging above the anus (Matthews, 1939), and the hindquarters lowered in a semisquatting position. Both sexes scent-mark and use the same posture while pasting.

Observations contained in this report were gathered during the course of a developmental study of hormones and social behavior of spotted hyenas. This species has been chosen for study because it exhibits absence or reversal of many sexual dimorphisms typical for mammals. Female spotted hyenas have no normal external genitalia; rather, the clitoris is hypertrophied so that it is very similar to the male penis and is traversed by a central urogenital canal (Kruuk, 1972; Matthews, 1939). It is fully erectile, and the female mates and gives birth through it. Females also are heavier than males and are more aggressive (Frank, 1986a; Frank, Glickman, & Zabel, 1989). Within a clan, adult females dominate adult males during feeding at kills and in most other social situations (Frank, 1986b; Kruuk, 1972).

Contemporary understanding of sexual differentiation (e.g., Goy & McEwen, 1980) suggests that the preceding character-

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Correspondence concerning this article should be addressed to Stephen E. Glickman, Department of Psychology, University of California, Berkeley, Berkeley, California 94720.

istics may be produced by the presence of androgens in female spotted hyenas during their fetal or neonatal development. In addition, prepubertal female hyenas display elevated plasma levels of androgen, relative to those of males (Glickman, Frank, Davidson, Smith, & Siiteri, 1987; Lindeque, Skinner, & Millar, 1986). The primary androgen found in female plasma during this time is androstenedione, and it is of gonadal origin. Gonadal androgens have commonly been identified as organizing or activating agents of mammalian scent marking (Yahr, 1983), especially in those cases for which scent marking is sexually dimorphic. Our study was concerned with the following developmental-hormonal questions: (a) Does the frequency of pasting increase as the animals approach puberty?, (b) is the frequency of pasting sexually dimorphic?, and (c) is pasting dependent on gonadal secretions during prepubertal period?

In nature, males typically disperse at puberty (approximately 2 years of age; Frank, 1986a). Females remain in their native clan and acquire the social rank of their mothers. The clans, therefore, comprise groups of matriline with relative ranking that remains stable over generations. Dominance rank of cubs, juveniles, and subadults is also very highly correlated with maternal rank, irrespective of the sex of the cubs (Frank, 1986b; Frank et al., 1989). Since the operation of this powerful maternal influence would have obscured our attempts to examine the emergence of sex differences per se, hyenas were collected as infants and reared in peer groups, without a maternal presence. Although this is a highly unnatural situation, many fundamental aspects of hyena social behavior emerged in our peer-reared cohorts before puberty, including species-typical patterns of play (Pedersen, Glickman, Frank, & Beach, 1990), meeting ceremonies (Krusko, Weldele, & Glickman, 1988), and dominance relationships (Frank et al., 1989).

In addition to the developmental-hormonal questions mentioned above, we were interested in three social questions: (a) Is pasting correlated with dominance status in hyenas as in a number of other mammalian species (e.g., Ralls, 1971)?, (b) does pasting by one hyena stimulate pasting by another hyena, as was observed in nature by Kruuk (1972)?, and (c) in what behavioral contexts does pasting occur?

Method

Subjects

The subjects of this study were two cohorts of hyenas collected in Narok District, Kenya, in December-January, 1984-1985, and November-December, 1985. The animals ranged from 1 week to 2 months of age at the time of collection. The first cohort consisted of 7 females and 3 males, and the second cohort, of 5 females and 5 males. Two females from the first cohort and 2 females and 2 males from the second cohort were gonadectomized at 4-6 months of age in order to permit a preliminary assessment of the effects of gonadal hormones on their behavior.

Behavioral data were available for the hyenas when average estimated ages of the two cohorts were between 12-22 and 7-22 months of age, respectively. The observations were terminated when the cohorts had to be divided into smaller groups because of increased levels of aggression associated with the approach of puberty. In order to assess developmental trends, we divided this subadult age into two periods, early subadult (between 12 and 18 months) and late subadult (between 19 and 22 months). This division was based on nipple development in intact (but not gonadectomized) females and rising gonadal steroid levels in both sexes during the last 3 months of data collection (Frank, 1990; Licht, 1990). In addition, the second cohort was observed at an earlier juvenile age between 7 and 10 months.

Housing and Maintenance

Animals were housed in peer groups from the time of collection. They were fed a diet of enriched milk until 2 months of age and then gradually transferred to a commercial carnivore diet and lamb bones.

The hyenas were housed in 12 x 30 m indoor-outdoor enclosures illuminated by halogen security lights for nocturnal observation. Such lighting had no detectable effects on the behavior of the subjects. Identification of individual hyenas was facilitated by dyeing patterns on the fur of the back with commercial hair dye.

Procedure

Data were collected between 1800 and 2200 hr with a critical-incident sampling procedure. The first cohort was observed for 61.7 hr during the early subadult and 18.7 hr during the late subadult age period. The second cohort was observed for 25.1, 64.9, and 48.4 hr during the juvenile, early subadult, and late subadult age periods, respectively.

Observers recorded behaviors with a voice-activated tape recorder. An electronic timer was used to indicate 30-s intervals. Every incident of pasting behavior was recorded, and absolute pasting rates were used for calculations. In addition, a set of aggressive and submissive

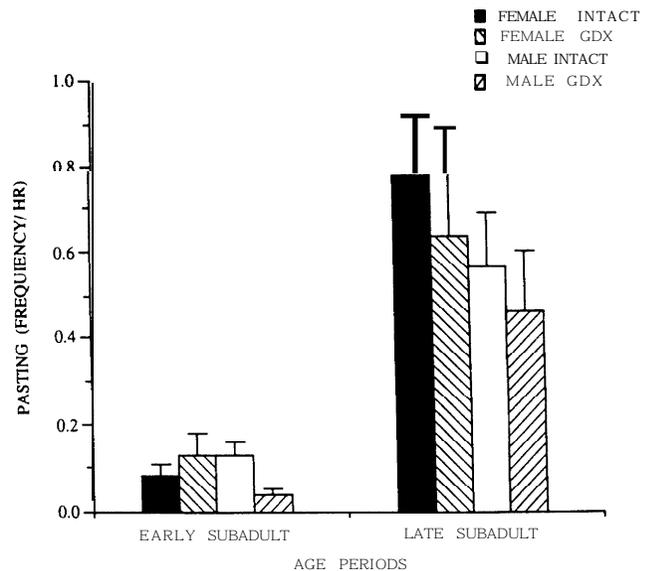


Figure 1. Average rates of pasting as a function of age, sex, and gonadal status in prepubertal spotted hyenas ($M \pm SE$). (GDX = gonadectomized.)

behaviors was recorded, as well as instances of play, meeting ceremonies, and olfactory investigation. Aggressive behaviors included threats (forward movement accompanied by erect ear position and mane), bites, attempted bites, and attacks (forward movement accompanied by biting). Submissive behaviors included avoidance of a threatening hyena and a varied set of species-characteristic postures (open mouth grin with ears flattened against the head, or rapid, repetitive movements of the head up and down or side to side) emitted by hyenas under threat or attack. Although playful activities were recorded as object, locomotor, or social play, they are grouped in this article for purposes of contextual analysis. A complete description of hyena play can be found in Pedersen et al. (1990). Meeting ceremonies (Krusko et al., 1988; Kruuk, 1972) are highly stereotyped patterns of olfactory investigation, in which the subordinate hyena typically approaches a more dominant animal, raises an inside rear leg, and offers its anogenital region for examination by the dominant. Finally, olfactory investigation was subdivided according to the nature of the target, that is, other hyenas, paste deposited by a hyena, or objects (including a latrine and the ground) in the test enclosure.

Dominance ranks were assessed by testing each cohort in a highly competitive feeding situation, simulating what is typical of wild hyenas (for description, see Frank et al., 1989). Rankings were based on submission matrices, with the dominant animal in each cohort ranked as number one (Lehner, 1979). In both cohorts, rankings were relatively stable, particularly at the top and middle of the hierarchy (Frank et al., 1989).

Table 1
Effects of Age on the Frequency of Pasting per Hour in Prepubertal Spotted Hyenas

Cohort	n	Age period		
		Juvenile	Early subadult	Late subadult
		$M \pm SD$	$M \pm SD$	$M \pm SD$
1	10		0.080 \pm 0.055	0.767 \pm 0.459
2	10	0.052 \pm 0.050	0.121 \pm 0.080	0.531 \pm 0.262

Note. There are no data available for cohort 1 during the juvenile age period.

Results

Nineteen of the 20 hyenas increased the frequency of pasting from the early subadult to the late subadult age period that marked the beginning of puberty (Table 1). Both cohorts demonstrated significant increases in pasting with age, $t_s(9) = 4.85$ and 6.11 , $p < .001$, for the first and second cohorts, respectively. A 2×2 analysis of variance (ANOVA) with cohort membership and age as grouping variables revealed

Table 2
Spearman Rank Correlation Coefficients (*Rho*) Between Dominance Rank and Pasting Rates in Prepubertal Spotted Hyenas

Cohort	<i>n</i>	Age period		
		Juvenile	Early subadult ^a	Late subadult ^b
1	10		.499	.468
2	10	.082	.494	.590

Note. There are no data available for cohort 1 during the juvenile age period.

^a $p < .10$ for correlation coefficients from both cohorts combined.

^b $p < .05$ for correlation coefficients from both cohorts combined.

that there was a significant effect of age, $F(1, 18) = 49.00$, $p < .001$, but not of cohort membership, $F(1, 18) = 1.15$, $p > .10$. The interaction was of only borderline significance, $F(1, 18) = 3.12$, $p < .10$, which suggests only slight differences between the two cohorts. The second cohort provided information on the rates of pasting during the juvenile age period. Although absolute rates were low for this period, pasting also increased significantly, $t(9) = 2.34$, $p < .05$, between the juvenile and early subadult age (Table 1).

Data from both cohorts for the two subadult age periods were combined for analyses of the effects of sex and gonadectomy (Figure 1). A three-way ANOVA was performed with age, sex, and gonadal status as independent variables and pasting frequency as the dependent measure. There was a significant effect of age, $F(1, 16) = 27.91$, $p < .001$, but no significant effects of sex, $F(1, 16) = 0.21$, $p > .10$, or gonadal status, $F(1, 16) = 0.40$, $p > .10$. The three-way interaction of age, sex, and gonadal status was not significant, $F(1, 16) = 0.22$, $p > .10$.

Rank order correlation coefficients for dominance rank and pasting rate are presented in Table 2. During the two subadult age periods, rho values for both cohorts were between 0.5 and 0.6. When correlation coefficients from the two cohorts were combined within age periods for purposes of statistical evaluation (McNemar, 1969, p. 158), the correlation between dominance ranks and pasting rates was significant during the late subadult age period, $t(14) = 2.23$, $p < .05$, but only of borderline significance during the early subadult period, $t(14) = 1.91$, $p < .10$.

Field observations suggest that pasting may be a socially facilitated behavior (Kruuk, 1972). We therefore examined the potential influence of pasting by one hyena on subsequent pasting by other group members. If pasting was socially facilitated, we expected an increment in the frequency of pasting by a second hyena during the interval immediately after the initial act. Such an increment would then be followed by a decline to the base rate of pasting during succeeding intervals. Our analysis was restricted to the late subadult age period when pasting rates were sufficiently high to reveal social facilitation effects. After each instance of pasting, the data set was searched in four consecutive 30-s intervals for pasting by a second hyena, with consecutive pastings by the same animal omitted.

Individual rates of socially facilitated pasting were computed for each hyena. A 2×2 ANOVA revealed a highly

significant effect of time interval after pasting by an initial actor, $F(3, 18) = 10.29$, $p < .0001$, which indicates a substantial social facilitation effect (Figure 2). There was also a marginally significant effect of cohort membership: Hyenas in the first cohort exhibited more socially facilitated pasting than did those in the second cohort, $F(1, 18) = 4.14$, $p < .06$. The interaction was not statistically significant, $F(3, 18) = 0.99$, $p > .10$.

In order to compare pasting rates obtained during the peak intervals of socially facilitated pasting with the overall "base" rates presented in Table 1 and Figure 1, it is necessary to express both values in the same units. Because the greatest social facilitation effect occurred during the first two 30-s intervals (Figure 2), we combined these rates to obtain the values of socially facilitated pasting per minute of observation. These values were 0.36 and 0.20 pastings per minute for the first and second cohorts, respectively. The overall base rate values (Table 1 and Figure 1) were divided by 60 to obtain frequencies per minute. Calculated in this manner, base rate values (which include all instances of socially facilitated pasting) indicate the frequency of pasting per minute that is expected by random sampling. These values were approximately 0.013 for the first cohort and 0.009 for the second cohort during the late subadult age period. Rates of socially facilitated pasting, therefore, exceeded base rates by greater than 20 times.

Consistent with the preceding observation, the proportion of pastings that occurred in bouts was higher than the proportion of solo pastings. (A *pasting bout* was defined as an initial pasting by one animal followed by subsequent pastings by other animals within 2 min of each other.) During the late subadult age period, 89% of pastings in the first cohort ($N = 143$) and 74% of pastings in the second cohort ($N = 255$) were instances of pasting that occurred in bouts.

To determine the context of scent marking, we conducted a retrospective search of the data set, using the combined information from early and late subadult periods. We examined behaviors of hyenas during each 1-min interval imme-

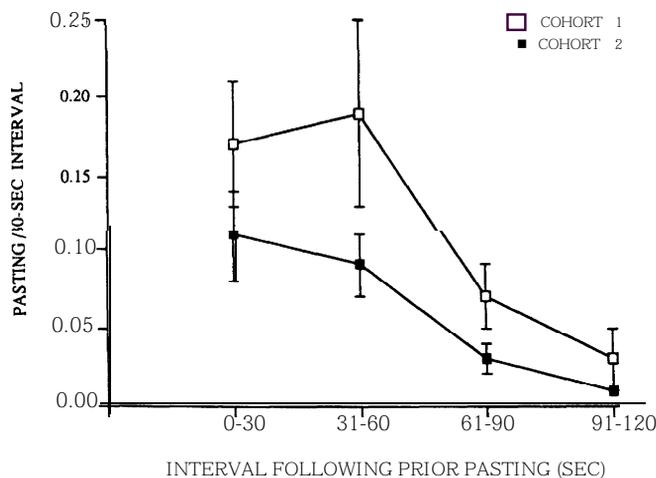


Figure 2. Social facilitation of pasting in two cohorts of subadult spotted hyenas ($M \pm SE$).

diately preceding pasting and found that olfactory investigation of other animals and of fresh paste marks was the most common behavior. Preceding behaviors could not be identified in 14.0% and 23.1% of all instances of pasting in the first ($N = 193$) and second ($N = 333$) cohorts, respectively. For the remaining cases, behaviors were divided into the seven most common categories. These seven categories accounted for 87.4% of known preceding behaviors in the first cohort and 90.6% in the second cohort. The seven categories comprised: (a) sniffing or being sniffed by other animals, (b) sniffing one's own or another animal's paste marks, (c) sniffing the ground, the latrine area, or other objects, (d) pasting, (e) involvement in aggressive or submissive interaction, (f) participation in object, locomotor, or social play, and (g) participation in a meeting ceremony (Kruuk, 1972, p. 226). Olfactory interactions with other animals, sniffing paste marks, and the act of pasting represented 71.5 % of preceding behaviors in the first cohort and 72.5% in the second cohort (Table 3). For each of these behaviors, the frequency with which they preceded pasting significantly exceeded the expected (i.e., base) frequency during 1-min intervals during which the animals were identified as active in the data set (Table 3). Although playful and aggressive behaviors were relatively common activities of hyenas during this age period, these behaviors were less likely to precede pasting than was expected by chance, as was sniffing directed at areas or objects not marked with fresh paste (Table 3). The results were very similar in both cohorts. Participation in meeting ceremonies before pasting occurred at a frequency which was not significantly different from chance.

Discussion

Our results show a significant increase in rates of pasting behavior with age as the hyenas approached puberty but no sex difference in the frequency of pasting. The absence of a sex difference in the frequency of scent marking during the prepubertal period is in accord with Mills and Gorman's (1987) observations in nature.

Increased scent marking associated with the onset of puberty is a common pattern in mammals (Yahr, 1983) and has

generally been linked to an increase in gonadal activity. For example, in Mongolian gerbils (*Meriones unguiculatus*), ventral gland scent marking by males increases as they approach sexual maturity, and gonadectomy markedly reduces the rates of marking (Thiessen & Yahr, 1977). At the conclusion of our observations, there was evidence of increased gonadal activity in both male and female hyenas. Males were approaching sexual maturity, and even though females were more than one year from true reproductive maturity, they showed indications of sustained ovarian activity associated with puberty. For example, nipple diameter nearly doubled in intact females between the early and late subadult age periods, whereas ovariectomized females exhibited minimal nipple development (Frank, 1990). However, the gonadectomized hyenas scent-marked as frequently as intact subjects. Our results suggest that the increment in scent marking observed in prepubertal hyenas is not due to activational effects of gonadal hormones, although the very small number of experimental subjects provides a very weak test of any modulatory influence of androgens.

Larger sample sizes may have revealed more subtle effects of gonadectomy. In addition, effects of gonadectomy may be expressed only in certain social situations. For example, in the saddle back tamarin (*Saguinus fuscicollis*), prepubertal castration reduced marking activity in adults, but the reduction was specific to social encounters with intruders and was absent during tests with novel objects (Epple, 1981). Detailed tests of pasting in different social situations may uncover similar, more complex influences of gonadal steroids in hyenas.

Finally, hormonal manipulations on the captive hyenas occurred after the time when organizational effects of androgens on scent marking are commonly anticipated (Yahr, 1983). It is possible that pasting behavior is influenced by pre- or perinatal androgenic secretions in both female and male hyenas (Glickman et al., 1987) but detecting such effects will require intervention at the appropriate sensitive period.

Pasting behavior in captive peer-reared hyenas was similar to that observed in nature in that there was powerful social facilitation of pasting. In addition, olfactory investigation of and by other hyenas and olfactory investigation of paste marks

Table 3
Behavioral Context of Pasting

Behavior	Cohort I		Cohort 2		Z score for combined cohorts
	Base rate	Rate before pasting	Base rate	Rate before pasting	
	$M \pm SD$	$M \pm SD$	$M \pm SD$	$M \pm SD$	
Social sniff	31.22 ± 2.64	43.10 ± 13.69	27.07 ± 2.59	41.14 ± 19.23	2.875*
Sniff object	20.47 ± 2.71	10.38 ± 7.74	16.11 ± 2.06	6.45 ± 7.59	3.621**
Sniff paste	0.78 ± 0.33	22.21 ± 15.28	0.52 ± 0.20	18.91 ± 9.79	3.823**
Paste	0.70 ± 0.40	6.17 ± 5.58	1.02 ± 0.37	12.49 ± 11.84	2.876*
Aggression or submission	28.13 ± 3.19	9.29 ± 9.87	17.73 ± 2.94	10.77 ± 10.33	3.323**
Play	11.85 ± 1.98	2.72 ± 3.89	44.84 ± 8.60	7.30 ± 6.56	3.920**
Meeting ceremony	3.27 ± 0.77	6.18 ± 10.26	5.13 ± 0.73	3.32 ± 2.77	0.709

Note. *Base rate* is the mean value of the number of 1-min intervals in which a subject emitted the behavior divided by the number of intervals in which the subject was active. *Rate before pasting* is the mean value of the number of 1-min intervals in which a subject emitted the behavior before pasting divided by the number of instances of pasting by the subject in which a preceding behavior was identified.

* $p < .05$, Wilcoxon's matched-pairs signed-ranks test. ** $p < .01$, Wilcoxon's matched-pairs signed-ranks test.

were the most common precursors of pasting. Kruuk (1972) noted that pasting in hyenas was "very much stimulated by the presence of secretion from other hyenas; as soon as a hyena smells the paste on a grass stalk, he will walk up to it, sniff it elaborately, and then paste his own on top" (p. 222). Mills and Gorman (1987, p. 494, Figure 10) also described bouts of intense, socially facilitated pasting at territorial borders. As captive hyenas approached puberty, they were significantly more likely to paste in bouts (several animals' pasting after each other) than individually.

Scent marking in wolves (*Canis lupus*) has been associated with aggressive behavior (Peters & Mech, 1975). However, there was no evidence of an association between immediately preceding aggression and pasting in hyenas, despite the relatively high frequencies of aggressive and submissive behaviors in our sample. Various types of olfactory investigation were the primary antecedents of pasting among the hyenas. This is in accord with many reports on wolves (Asa, Seal, Plotka, Letellier, & Mech, 1986; Peters & Mech, 1975; Rothman & Mech, 1979). Although our observations of socially facilitated pasting in neutral or prosocial contexts are compatible with field reports of territorial marking, any inferences are severely limited by the relatively small size of our enclosures and the absence of data on the locus of marking within those enclosures.

We have found a modest positive correlation between dominance rank and frequency of scent marking in both cohorts. This finding is consistent with similar reports in wolves (Lockwood, 1976; Peters & Mech, 1975) European badgers (*Meles meles*; Gorman, Kruuk, & Leitch, 1984), and a variety of other mammals (Ralls, 1971). In Mills and Gorman's (1987) field study of spotted hyenas, they concluded that there was no correlation between marking and dominance in adults. However, their conclusion was based on a general comparison between adult males and females, which ignores rankings within the intrasexual hierarchies characteristic of hyenas in nature. It is conceivable that the positive correlation between dominance rank and frequency of pasting observed in our study will disappear when our animals reach sexual maturity. Alternately, it is possible that a positive correlation between dominance rank and pasting will be found in nature, if frequency of pasting is correlated with the ordinal ranks of hyenas within the female and male hierarchies.

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