

Responses to Olfactory Stimuli in Spotted Hyenas (*Crocuta crocuta*): II. Discrimination of Conspecific Scent

Christine M. Drea, Sacha N. Vignieri, H. Sharon Kim, Mary L. Weldele, and Stephen E. Glickman
University of California, Berkeley

Scent marking in spotted hyenas (*Crocuta crocuta*) includes the deposition of anal sac secretions, or “paste,” and presumably advertises territorial ownership. To test whether captive hyenas classify and discriminate individuals using odor cues in paste, the authors conducted behavioral discrimination bioassays and recorded hyena investigation of paste extracted from various conspecific donors. In Experiment 1, subjects directed most investigative behavior toward scents from unfamiliar hyenas and members of the opposite sex. In Experiment 2, male hyenas discriminated between concurrent presentations of paste from various unfamiliar females in similar reproductive states. Thus, pasted scent marks convey information about the sex, familiarity, and even identity of conspecifics. Aside from territory maintenance, scent marking may also communicate information about individual sexual status.

Individual recognition, essential for regulating intergroup and intragroup relations, is particularly germane for territorial species that live in complex social groups (Gorman & Trowbridge, 1989). Moreover, in terrestrial mammals occupying large home ranges or organized in fission–fusion societies, nonvisual modalities of identification can be especially advantageous. One means of signaling identity is through unique odor cues, or “signatures,” deposited as scent marks (Halpin, 1986). Many animals produce social odors that provide enduring spatial records of individual activity (Brown, 1979) and serve a variety of functions (Eisenberg & Kleiman, 1972; Ralls, 1971). This article examines intraspecific olfactory communication in the highly territorial and gregarious spotted hyena (Drea & Frank, in press; Frank, 1986a, 1986b; Henschel &

Skinner, 1991; Hofer & East, 1993a, 1993b; Kruuk, 1972) and asks whether scent signatures are discriminated in this species, possibly to advertise one’s presence and communicate reproductive status.

Members of both sexes in all four extant species of Hyaenidae share several means of scent marking, the most prominent of which is *pasting*, the deposition of secretions from supra-anal sacs (spotted hyenas: Kruuk, 1972; brown hyenas: Mills, Gorman, & Mills, 1980; striped hyenas: Kruuk, 1976; aardwolves: Kruuk & Sands, 1972). Pasting is long lasting signals, remaining potent for at least 30 days in brown hyenas (Mills et al., 1980) and up to 6 months in aardwolves (Apps, Viljoen, Richardson, & Pretorius, 1989). The quantities and proportions of the different chemical compounds in paste vary between individuals (Apps et al., 1989; Mills et al., 1980), suggesting that, as with anal secretions in other carnivores, conspecific and individual recognition is at least possible on the basis of chemical fingerprints (Gorman, 1976; Rasa, 1973).

Despite similarities in pasting behavior across hyenids, species differences in the chemical composition of paste (Buglass, Darling, & Waterhouse, 1990) as well as in social organization and behavioral ecology (Mills, 1990) suggest that pastings may serve different functions between species (Johnson, 1973). Likewise, the ubiquity of pasting (Drea, Vignieri, Cunningham, & Glickman, 2002; Kruuk, 1972) suggests that it might serve various functions within species (Johnson, 1973). The brown hyena illustrates both points, as it is the only family member to produce two kinds of paste—a white, sebaceous secretion and a black, epocrine secretion (Mills et al., 1980). Whereas the longer lasting white mark might broadcast more permanent territorial boundaries to neighbors, the ephemeral black mark may inform clan members about temporary events, such as recent foraging activity (Gorman & Mills, 1984; Mills et al., 1980).

As in many other mammals (Gosling, 1982), hyena scent marking advertises territorial ownership by establishing an asymmetry of odor cues between residents and intruders (Gorman & Mills, 1984; Kruuk, 1972; Mills & Gorman, 1987; Mills et al., 1980; Tilson & Henschel, 1986). Hyena pasting behavior often occurs

Christine M. Drea and Mary L. Weldele, Department of Psychology, University of California, Berkeley; Sacha N. Vignieri and H. Sharon Kim, Department of Integrative Biology, University of California, Berkeley; Stephen E. Glickman, Departments of Psychology and Integrative Biology, University of California, Berkeley.

Support was provided by National Institute of Child Health and Human Development National Research Service Award HD07684 to Christine M. Drea and by National Institute of Mental Health Grant MH39917 to Stephen E. Glickman. As part of the Office of Laboratory Animal Care of the University of California, Berkeley, the Field Station for Behavioral Research is fully accredited by the American Association for the Accreditation of Laboratory Animal Care.

We thank the Office of the President, the Department of Wildlife Conservation and Management, and the Narok County Council, Republic of Kenya, for permission to export infant hyenas to the Berkeley facility. We also thank Paul Licht for performing the radioimmunoassays, Jason Hawk and Micah Lubensky for help with data collection, and the staff of the Office of Laboratory Animal Care for animal management. Finally, we express our gratitude to Laurence Frank and Jim Patton for their helpful suggestions.

Correspondence concerning this article should be addressed to Christine M. Drea, who is now at the Department of Biological Anthropology and Anatomy, Duke University, 08 Biological Sciences Building, Science Drive, Box 90383, Durham, North Carolina 27708-0383. E-mail: cdrea@duke.edu

spontaneously to delineate and maintain territories, but it is also elicited by the pasting activity of companions (Woodmansee, Zabel, Glickman, Frank, & Keppel, 1991) or by the presence of hostile trespassers (Kruuk, 1972). Moreover, residents respond to encountered paste by depositing their own scent, frequently overmarking the original odor source. The social facilitation of pasting suggests a role in coordinating group behavior, possibly to maximize collective output or rally residents into group defense. As a corollary, animals typically refrain from pasting during extraterritory excursions (Richardson, 1990) and react aversively to pastings encountered at the periphery of their range (Kruuk, 1976).

Although not all scent marking is territorial (Ralls, 1971), less research emphasis has been placed on a possible reproductive function of hyena pasting. Nonetheless, pastings are potentially used by both sexes to attract mates or to synchronize mating (Sliwa & Richardson, 1998). Moreover, intruder males may paste to intimidate resident males and to obtain extrapair mating opportunities (Richardson, 1987). Brown hyenas have been observed overmarking paste encountered along the territorial border (and presumably deposited by a foreigner) but marking adjacent to a companion's paste encountered inside the territory (Mills et al., 1980). Each tactic may serve a different purpose, from staking claim by competitive masking to conveying social information by keeping signals pure. The latter could be particularly advantageous if information on female reproductive cycles or male sexual prowess were conveyed in paste.

For scent marks to function in warning or repelling intruders or in tracking potential mates, information contained in paste should vary at least by broad categorizations of the demarcating animals, if not by individual animals (Gosling, 1982). Indeed, a stranger's paste produces increased sniffing and flehmen in the aardwolf (Sliwa & Richardson, 1998), and brown hyenas distinguish between pastings deployed by group members and those deposited by strangers (Mills et al., 1980). Similarly, aardwolves differentiate paste by sex and reproductive status (Sliwa & Richardson, 1998). As no comparable information exists for spotted hyenas, our first goal was to test whether this species discriminates between paste derived from males versus females and familiar versus unfamiliar animals. We further suspect that scent signatures exist in spotted hyenas, therefore our second goal was to determine whether, beyond differentiating sex and familiarity, spotted hyenas distinguish between paste derived from different individuals.

Experiment 1

To test the hypothesis that spotted hyenas discern information about sex or degree of familiarity in the pasted scent marks of conspecifics, we examined the responses of captive male and female hyenas (recipients) to paste extracted from familiar and unfamiliar animals of both sexes (donors). We expected investigation of paste to vary by donor sex, recipient sex, and degree of familiarity between donor and recipient. Because of differences in site specificity of pasting, that is, overmarking versus adjacent marking (as defined in Drea et al., 2002), we specifically examined site specificity of response.

Method

Subjects and housing. Eight captive, reproductively intact, adult spotted hyenas (*Crocuta crocuta*; 4 males and 4 females) served as subjects.

Two hyenas had been collected in Kenya as infants (1 week to 2 months of age); the other 6 were captive born. All but 1 were the same as those used in Experiment 1 of our companion study (Drea et al., 2002), conducted 2 years prior. The hyenas were housed socially in yards (6.9 m × 18.6 m), with open-air fencing and daily access to covered enclosures (4.5 m × 8.7 m), at the Field Station for Behavioral Research, University of California, Berkeley. Each morning, the hyenas were fed carnivore zoo diet (Nebraska Brand Feline Food; Central Nebraska Packing, Inc., North Platte, NE) and pork bones and were provided fresh straw for bedding.

Paste. We collected samples of paste from the anal pouches of reproductively intact colony members (male and nonpregnant female donors) during routine physical examinations for which the animals were anesthetized with intramuscular injections of ketamine (4–6 mg kg⁻¹) and xylazine (1 mg kg⁻¹), according to published procedures (Berger, Frank, & Glickman, 1992). We stored paste samples at –40 °C. We verified each recipient's familiarity with the paste donors through housing records, defining a familiar donor as having previously cohabited with the recipient (i.e., shared the same enclosure or occupied an adjacent enclosure with a direct fence boundary) and an unfamiliar donor as never having had any contact with the recipient. (Familiarity typically involved sharing space over a period of at least several weeks within a year of testing.) Accordingly, the four donor categories per recipient included familiar male or female and unfamiliar male or female.

Procedure. The recipients individually received 10 trials (8 paste trials and 2 baseline trials) of 10 min each, with no more than one trial per day (see Figure 1), conducted in the covered enclosures on windless afternoons. All 80 trials involved the presentation of two straw piles (each 0.16 m³ or approximately one sixth of a flake) placed about 3 m apart along the wall farthest from the hyena's entryway. During paste trials we scented one straw pile with a sample of donor paste, but during baseline trials we left both straw piles unscented.

The testing sequence followed an ABBA design, where each A involved 4 consecutive paste trials (total: 8 subjects × 4 paste samples = 32 trials) and each B involved a single baseline trial (totaling 8 trials). (This paradigm is modified from that typically used because we lost an earlier set of baseline data.) In the first A series, we presented each hyena with paste from an unfamiliar male, unfamiliar female, familiar male, and familiar female, in that order, and after a break in testing (3–5 days) between the two B phases, we reversed this order using different donors in the second A series (see Figure 1).

We thawed the paste samples a minimum of 1 hr before testing. Using a clean scalpel, we smeared paste (approximately 0.3 ml) on a piece of straw and placed it in the middle of one of the two straw piles. Odor placement varied randomly between left and right straw piles. Trials began once the hyena entered the enclosure from an adjoining pen. We removed straw piles and cleaned the room after each test.

Data collection and analyses. Two observers, situated in covered hallways about 2 m from the fencing of the test enclosure, scored behavioral responses (see Table 1) in real time using a laptop computer. In the second A set of 32 trials, all but three paste samples came from donors that differed from those used in the previous set. As 61 of the 64 recipient–donor combinations were unique, we treated the two exposures to each paste category as replicates and averaged the hyenas' responses for the duplicate paste and baseline trials, respectively.

To confirm behavioral differences between baseline and paste trials, we lumped all other variables (subjects, donor sex, donor familiarity, and straw piles) in an initial series of *t* tests. To assess differences in behavioral allocations to straw piles during paste trials only, we lumped subjects and donor variables in a second series of *t* tests. The next analyses evaluated overall paste responses regardless of allocation to the straw piles, using three-factor analyses of variance (ANOVAs; Recipient Sex × Donor Sex × Donor Familiarity). The final analyses ran three-factor ANOVAs (Donor Sex × Donor Familiarity × Straw Pile) independently for male and female recipients. We resolved significant interaction effects using

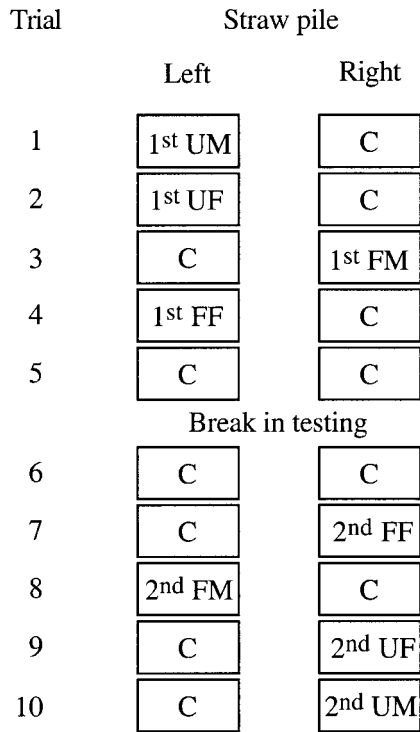


Figure 1. Example of the procedural design for Experiment 1. Straw piles were either scented with paste from a spotted hyena donor (UM, UF, FM, or FF) or were unscented (C). Placement of paste varied randomly from left to right. The second set of five trials replicated, in reverse and counter-balanced order, the first set of five trials, using different conspecific paste donors. For example, 10 consecutive trials presented Female Subject 16 with paste from UM 52, UF 7, FM 9, and FF 32, then with plain straw twice, then with paste from FF 31, FM 17, UF 1, and finally UM 45. UM = unfamiliar male; UF = unfamiliar female; FM = familiar male; FF = familiar female; C = control.

Newman-Keuls multiple range tests, and we used *F* tests for simple effects in planned comparisons for each variable. We report all values as mean frequency or duration ($\pm SE$), with significance set at $\alpha \leq .05$.

Results

Baseline versus paste trials. The hyenas investigated (sniffed and licked) straw more intensely during paste trials (in the presence of conspecific odor) than during baseline trials (in the presence of fresh straw only, see Table 2). They rolled only during paste trials but showed no significant differences across trials in pasting (see Table 2). The other forms of scent marking (urinating, defecating, and scratching) occurred rarely (data not shown). Remaining analyses address paste trials.

Unscented versus scented pile. The subjects responded more to straw scented with paste than to unscented straw (see Table 3). They spent more time in proximity to conspecific odor, sniffing scented straw more frequently and for longer than unscented straw. In addition, they licked and rolled only in scented straw, thereby tasting and wearing the donor's paste. The scent marking of recipients had no spatial precision, however, and was equally distributed between both piles.

Donor familiarity. The hyenas generally investigated the paste of unfamiliar donors more than that of familiar donors. Collectively, recipients sniffed scented straw longer if the paste came from unfamiliar (1.21 ± 0.17 min) than familiar (0.93 ± 0.09 min) donors, $F(1, 7) = 6.11, p < .05$. Likewise, they licked scented straw more often if the paste was from unfamiliar (2.56 ± 0.80) than familiar (0.31 ± 0.10) donors, $F(1, 7) = 6.44, p < .05$ (see Figure 2A). Although the hyenas urinated infrequently (0.20 ± 0.03 times during paste trials), virtually all occurrences were when unfamiliar male paste was present. Conversely, the recipients pasted more often in the presence of paste from familiar (1.31 ± 0.24) than unfamiliar (0.95 ± 0.19) donors, $F(1, 7) = 6.18, p < .05$.

Table 1
Behavioral Definitions for Spotted Hyenas Responding to Odors

Behavior	Definition
Approach	Number of times animal comes within 1 m of target.
Proximity	Time animal spends within 1 m of target.
Sniff	Flaring of nostrils with audible sound of nasal air expulsion directed at target (i.e., nose within 10 cm of target). Scored in bouts (frequency and duration), terminated by animal lifting or turning its head away.
Lick	Tongue in contact with target. Scored as bout frequencies, composed of several repeated licks.
Roll	Cheek, neck, shoulder, then back in contact with a substrate. Sometimes followed by sideways motion with feet up while in a prone position. Scored in bouts terminated by the animal getting up or settling down.
Paste	Scent marking by depositing paste from extruded anal glands.
Scratch	Vigorously pawing at ground, floor, or straw with front feet, presumably for depositing interdigital scent. Usually involves repeated scraping by first one paw and then the other and is distinguished from more gentle stroking to uncover an item. Scored in bouts, terminated if activity was interrupted for 3 s.
Urinate	Squatting and evacuating urine on feet. Frequently associated with other forms of scent marking, such as scratching.
Defecate	Evacuating bowels, usually in a latrine. As latrines are typically located in outdoor enclosures, this behavior was primarily observed in Experiment 2.

Note. This table contains only the subset of recorded behavior that is reported on in the text. The targets were straw piles, and the distinction between whether the straw was scented or unscented was noted.

Table 2
Behavioral Responses During Baseline and Paste Trials by Spotted Hyenas

Behavior	Responses to straw piles ($M \pm SE$)		Statistics	
	Baseline	Paste	$t(7)$	p
Approach frequency	24.37 \pm 5.50	19.12 \pm 1.05	0.95	<i>ns</i>
Time in proximity (min)	2.61 \pm 0.37	3.42 \pm 0.39	1.92	.097
Sniff frequency	11.62 \pm 1.37	12.78 \pm 1.12	1.10	<i>ns</i>
Sniff duration (min)	0.68 \pm 0.10	1.53 \pm 0.23	4.56	< .005
Lick frequency	0	1.44 \pm 0.53	2.72	< .05
Roll frequency	0	0.83 \pm 0.36	2.32	.05
Paste frequency	2.37 \pm 0.88	2.27 \pm 0.69	0.83	<i>ns</i>

Recipient and donor interactions. Specific response patterns differed slightly by recipient sex, with subjects often responding more strongly to donors of the opposite sex. Female recipients budgeted their time differently when approaching donor paste, $F(1, 3) = 21.99, p < .02$, spending more time in proximity to paste from unfamiliar or male donors (range: 1.94 ± 0.31 – 2.08 ± 0.57 min) than familiar females (1.40 ± 0.26 min; $p < .05$). Moreover, female recipients sniffed male paste (7.00 ± 1.32) more often than female paste (5.37 ± 0.58), $F(1, 3) = 19.50, p < .025$, and sniffed male paste (0.97 ± 0.11 min) longer than female paste (0.68 ± 0.12 min), $F(1, 3) = 114.21, p < .005$. The frequencies with which male recipients sniffed donor paste also differed, $F(1, 3) = 10.47, p < .05$, but were greater for familiar females (7.19 ± 1.13) than other donors (range: 6.06 ± 1.44 – 6.75 ± 0.90).

Finally, the distribution of rolling differed according to donor sex and familiarity, $F(1, 7) = 5.64, p < .05$, as straw scented with paste from familiar females (0.53 ± 0.26) and unfamiliar males (0.53 ± 0.29) elicited almost twice as much rolling as the other two donor categories. Because of low frequencies, male and female patterns were not further resolved, but females appeared to roll most in unfamiliar male paste, whereas males appeared to roll most in paste from familiar females (see Figure 2B).

Experiment 2

Spotted hyenas responded differently to paste obtained from various classes of individuals in Experiment 1, showing that they

Table 3
Behavioral Response Allocations to Unscented Versus Scented Straw by Spotted Hyenas During Presentation of Conspecific Odors

Behavior	Response allocation to straw piles ($M \pm SE$)		Statistics	
	Unscented	Scented	$t(7)$	p
Approach frequency	9.73 \pm 1.05	9.39 \pm 1.12	0.74	<i>ns</i>
Time in proximity (min)	1.45 \pm 0.20	1.97 \pm 0.22	4.21	< .005
Sniff frequency	5.56 \pm 0.48	7.20 \pm 0.67	4.69	< .002
Sniff duration (min)	0.46 \pm 0.07	1.07 \pm 0.16	6.02	< .001
Lick frequency	0	1.44 \pm 0.53	2.72	< .05
Roll frequency	0	0.83 \pm 0.36	2.32	.05
Paste frequency	1.25 \pm 0.45	1.02 \pm 0.28	0.83	<i>ns</i>

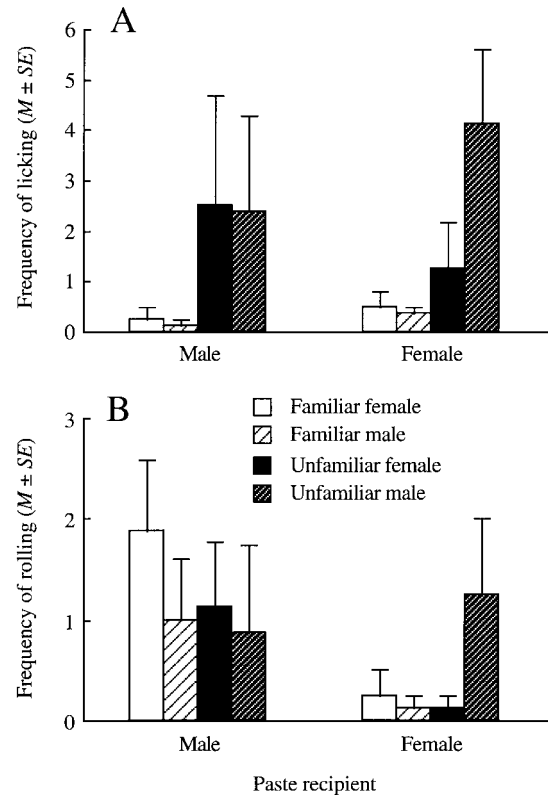


Figure 2. Mean ($\pm SE$) frequency of licking (A) and rolling (B) by captive male and female spotted hyenas in response to the presentation of paste from various donors: familiar females, familiar males, unfamiliar females, and unfamiliar males.

at least discriminate conspecific odors by sex and familiarity of the originator. In Experiment 2, we tested the hypothesis that spotted hyena males can rely on paste from unfamiliar females to discriminate between individuals in similar reproductive states. We used a modification of the habituation–discrimination paradigm, the premise being that an animal will spend more time investigating a novel scent than one previously encountered (Halpin, 1986).

Method

Subjects and housing. Four reproductively intact and sexually experienced adult male spotted hyenas (*Crocuta crocuta*; 5–9 years of age) served as subjects. Three had been collected in Kenya as infants (1 week to 2 months of age); the other was captive born. These subjects differed from those used in Experiment 1 (1 was the replaced male from our first companion article and the other 3 were new to odor testing). They were housed and fed as previously described.

Female paste and reproductive state. To control for previous social interaction as a variable in this study, we tested each male recipient with paste from unfamiliar female donors, according to the familiarity criterion described previously. Following the procedures of Experiment 1, we collected and stored five samples of paste at different times over a 2-year period from 10 anesthetized, reproductively intact colony females. In addition, we collected concurrent blood samples from the females' jugular veins using a sterile 22-gauge needle and sterile evacuated tubes containing a clotting agent and an inert serum separation medium (Vacutainer, Becton-Dickinson, Rutherford, NJ). We allowed blood to clot at ambient

temperature, centrifuged the samples at 1,000 *g* for 5 min, drew off the supernatant plasma in aliquots, and stored the aliquots at -80°C . We assayed the plasma samples for estradiol and progesterone concentrations by radioimmunoassay, following published methods (Licht, Zucker, Hubbard, & Boshes, 1982). The details, as revealed by chromatographic separation prior to assay, were also previously provided (Glickman, Frank, Pavgi, & Licht, 1992). Because the antibody used to measure estradiol cross-reacted significantly with other estrogens in hyena plasma, we have followed the conservative procedure of designating these steroid concentrations as *estrogen* (Glickman et al., 1992).

As little is known about female spotted hyena reproductive cycles (Glickman et al., 1992), we divided the paste samples into two categories, low and high, according to plasma concentrations of progesterone, with the upper limit for the low group being 20 ng ml^{-1} . Higher concentrations indicate possible pregnancy (Licht et al., 1992). Individuals classified as having low versus high concentrations of plasma progesterone ($M \pm SE$: 2.82 ± 0.60 vs. 91.73 ± 26.23 ng ml^{-1} , respectively), $t(9) = 3.36$, $p < .01$, had correspondingly low versus high concentrations of plasma estrogen ($M \pm SE$: 52.62 ± 6.66 vs. 331.01 ± 120.58 pg ml^{-1} , respectively), $t(9) = 2.33$, $p < .05$, consistent with previous findings of a significant positive correlation between these two steroids in female spotted hyenas (Licht et al., 1992). To avoid complications of varying female hormonal state, we selected 16 paste samples from females in the low category. The concurrent, mean plasma estrogen concentration for these donors was 53.49 pg ml^{-1} .

Procedure. The subjects received four trials each (see Figure 3). The elapsed time between the end of Trial 1 and the beginning of Trial 2 was about 25 min (the same was true for Trials 3 and 4), but there was a week-long break in testing between Trials 2 and 3. All 16 trials involved the presentation of three straw piles placed equidistantly along the far wall of the enclosure (a slight modification of prior procedures). We placed paste (0.03 ml, measured by filling a tuberculin syringe) from an unfamiliar female (UF) on each of the two outer piles, but left the center control pile unscented throughout testing (see Figure 3). We used a smaller quantity of paste than in Experiment 1 to allow several presentations from the same day's sample. In Trial 1 (exposure trial), both outer piles contained paste obtained on the same day from the same UF (first UF). In Trial 2 (discrimination trial), we smeared another sample of that same paste on only one outer pile, presenting paste from a different UF (second UF) on the other outer pile. We randomly assigned location of the novel paste (second UF) to the left or right. Trials 3 and 4 replicated this procedure

using paste samples from two different UFs (third and fourth UFs). The only difference was that to control for possible place preference, we reversed the left and right locations of the novel paste in Trial 4 (fourth UF) compared with Trial 2.

Data collection and analyses. On the basis of the results of Experiment 1, we scored only the duration of sniffing. We averaged the hyenas' responses to the replicate paste presentations across the initial exposure trials (1 and 3) and across the subsequent discrimination trials (2 and 4), respectively. We used two-tailed paired *t* tests throughout and report all values as mean frequency or duration ($\pm SE$), with significance set at $\alpha \leq .05$. When *p* values ranged between .05 and .10, we refer to the effects as *tendencies* requiring further investigation.

Results

During exposure trials (1 and 3), male hyenas tended to spend more time sniffing straw scented with UF paste than plain straw, $t(3) = 2.77$, $p = .07$ (see Figure 4). During discrimination trials (2 and 4), males spent more time sniffing straw scented with novel paste compared with straw scented with paste they had encountered only once before, $t(3) = 4.55$, $p = .02$ (see Figure 4). They also tended to sniff novel paste more than unscented straw, $t(3) = 2.45$, $p = .09$. There was no difference, however, between the amount of sniffing directed to the previously encountered paste and unscented straw, $t(3) = 0.61$, $p > .50$.

Moreover, there was no difference, $t(3) = 1.03$, $p > .30$, in total amount of sniffing directed toward both piles of scented straw during exposure trials (56 ± 17 s) compared with the total amount of sniffing directed toward both piles of scented straw during discrimination trials (41 ± 11 s). Likewise, there was no difference in the amount of sniffing directed to unscented straw between exposure and discrimination trials, $t(3) = 1.25$, $p > .20$. Therefore, the males' decreased attention to unfamiliar, but previously encountered, female paste during discrimination trials can be accounted for only by their increased attention directed toward novel unfamiliar paste.

General Discussion

Field studies have demonstrated individual differences in and recognition of vocalizations in spotted hyenas (East & Hofer, 1991a, 1991b; Holekamp et al., 1999). These auditory signals provide rapid identification but are time limited. By contrast, olfactory signals can persist for some temporal period after being deposited. Thus, the potential to rely on both nonvisual modalities of communication for individual recognition likely serves different, but complementary, functions. Gosling (1982) argued that odors demarcating a territory should be unique to the producer. For paste to fulfill a territorial function in the group-living spotted hyena, animals should at least detect conspecific odors and distinguish strangers from known clan members.

Experiment 1 showed that captive spotted hyenas differentiate conspecific paste on the basis of not only familiarity but also sex of the odor producer. Paste from unfamiliar hyenas elicited stronger responses (including approach, sniffing, and licking) than did paste from familiar animals, and females rolled most often in paste from unfamiliar males. In addition, hyenas sniffed and rolled in paste from members of the opposite sex more frequently than from same-sex animals. These results show that spotted hyenas can use olfactory cues to discriminate between classes of conspecifics and

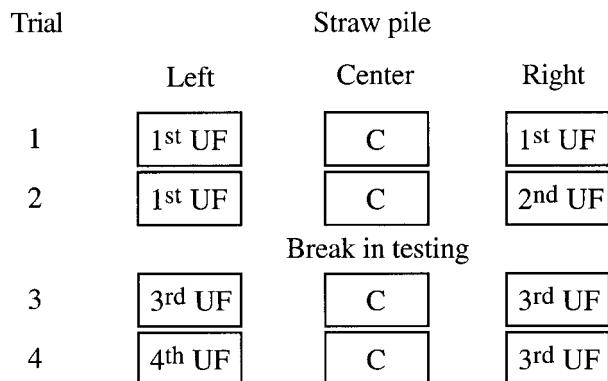


Figure 3. Example of the procedural design for Experiment 2. Straw piles were either scented with paste from a spotted hyena donor (UF) or were unscented (C). The second set of two trials replicated the first set of two trials, but with new conspecific paste. Placement of paste from a novel donor in Trial 2 varied randomly from outer left to outer right and was counterbalanced in Trial 4. UF = unfamiliar female; C = control.

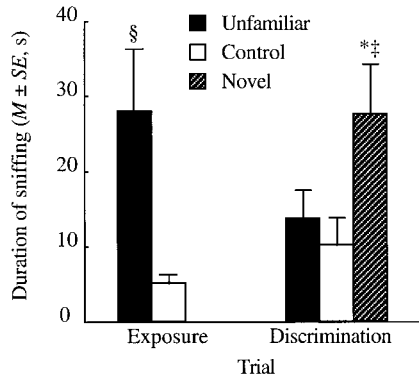


Figure 4. Mean duration (\pm SE; in seconds) of sniffing directed by male spotted hyenas toward straw scented with paste from various unfamiliar females compared with unscented straw (Control). In the exposure trials, both concurrently presented samples of paste were derived from the same female (Unfamiliar), whereas during subsequent discrimination trials, one of the two paste samples was derived from a different female (Novel). In exposure trials, males tended to sniff paste more than plain straw (§ $p = .07$). In discrimination trials, novel paste received more male attention than formerly encountered paste (* $p = .02$). The same trend appeared in a comparison between novel paste and plain straw (‡ $p = .09$, *ns*, paired t tests).

provide circumstantial evidence that this species has distinct chemical signatures.

That males reliably discriminated between paste derived from different, unknown females (in similar reproductive state) in Experiment 2 supports this interpretation and is consistent with the possibility of individual scent recognition (Halpin, 1986). Comparable findings of individual discrimination on the basis of glandular secretions have been documented in other carnivores (e.g., Kruuk, Gorman, & Leitch, 1984; Rasa, 1973; Roeder, 1983). It also seems probable that hyenas, like wolves (Ryon & Brown, 1990), can distinguish female reproductive state through olfactory investigation, but a detailed analysis of this ability awaits a better understanding of the estrous cycle of the spotted hyena. Together, our findings are consistent with a territorial function for paste (Kruuk, 1972) but also suggest a possible function in communicating reproductive status.

Scent Investigation

Spotted hyenas initially responded to conspecific paste (especially from unfamiliar hyenas) in much the same manner as they did to novel environmental odors (Drea et al., 2002), approaching, sniffing, and licking the odor source. Consistent with prior observations of wild hyenas (East, Hofer, & Wickler, 1993; Kruuk, 1972; Mills, 1990), licking appears to be involved in conspecific odor identification, implicating vomeronasal organ involvement in individual odor discrimination (Johnston & Peng, 2000). Prolonged investigation of a stranger's scent may reflect greater interest in a novel scent or greater effort necessary to process new information. Our findings are concordant with Gosling's (1982) theory of scent matching, which proposes that an animal should acquaint itself with the odor of a resource holder (i.e., the hyena that deposited the paste). By learning the odors of unfamiliar

resource holders, an animal can recognize those individuals as worthy competitors and avoid serious conflict in the event of an encounter (for further discussion of hyena scent matching, see Richardson, 1991).

Scent Marking

Although paste presentations influenced a variety of responses, they did not affect the baseline frequencies with which hyenas scent marked (including pasting, scratching, urinating, or defecating) or the site specificity of marking, with hyenas displaying both adjacent marking and overmarking. As pasting behavior is socially facilitated (Kruuk, 1972; Woodmansee et al., 1991), the observed frequencies may have been partially attributable to the solitary testing conditions. In addition, conspecific paste may not always be the most potent elicitor of scent marking, as numerous environmental odors also elicit pasting (Drea et al., 2002).

Variation in scent marking activity may also reflect adaptive responses to local conditions (Mills et al., 1980). For instance, spatial distribution, frequency, and concentration of pastings vary according to group number or territory size (Gorman & Mills, 1984; Tilson & Henschel, 1986). When territories are rich and therefore small enough to be effectively monitored, hyenas concentrate their scent along the exterior—the first line of defense—with residents regularly visiting and replenishing scent marks during border patrols (Henschel & Skinner, 1991; Kruuk, 1972; Kruuk & Sands, 1972; Richardson, 1990). By contrast, small clans that occupy large depauperate territories deploy paste at “hotspots” of activity throughout the interior (Gorman & Mills, 1984; Mills & Gorman, 1987; Mills et al., 1980). Thus, an unmarked but behaviorally active site within the territory (i.e., plain straw) may elicit pasting as effectively as does a site previously claimed by a clan member (i.e., straw scented with familiar paste). Indeed, although pasting occurred in and around plain straw, the pasting that occurred in the presence of conspecific scent was more often in response to the odor of familiar than unfamiliar animals. Such subtleties in the contextual variables regulating paste deposition point to the need for continued field studies of scent marking.

Rolling

In a survey of carnivores, Rieger (1979) cited the “scent markings of conspecifics or the scent rubbing animals themselves” (p. 17) as elicitors of rolling. Rieger (1979, 1981) primarily observed captive striped hyenas in zoological settings and noticed anal gland secretions on their neck fur, at the site where rubbing occurs. Likewise, Goodall and van Lawick (1970) described an instance of a male rolling in a freshly pasted scent mark of a female. Otherwise, similar behavior has not been described by most hyena field researchers or in a previous laboratory study (Woodmansee et al., 1991). Nevertheless, we found that captive spotted hyenas rolled only when paste was present and only in scented straw, suggesting that rolling serves to transfer the paste of another hyena onto the recipient's coat. Similarly, we have seen hyenas rubbing their cheek against the everted anal pouch of another animal, either while the latter was pasting or while both were engaged in a greeting ceremony (Drea et al., 2002). Variation across captive studies raises the possibility of contextual differences (e.g., solitary vs. social testing), tactile differences (e.g., rolling in a pile of straw

vs. on a blade of grass), or age differences (e.g., adult vs. juvenile behavior). More work is necessary to fully appreciate the frequency and conditions of appearance of paste-related rolling.

If rolling in conspecific odor by spotted hyenas proves more common in nature than previously observed, one might argue for a possible function in social or reproductive behavior. Notably, we see natural parallels for the females' preference for unfamiliar male paste and the corresponding males' preference for familiar female paste. In spotted hyena society, males are the dispersing sex, leaving their natal clan at puberty, either to become transient males or to join a new clan (Frank, 1986a). Transient or immigrant males scent mark most frequently, possibly to advertise their presence to resident females (Mills & Gorman, 1987). Thus, female attention to foreign males in captivity might reflect similar reproductive interests of wild females. By contrast, resident males that gain increased mating opportunities through length of tenure (Frank, 1986b) might preferentially seek potential mates among known females. Rolling in paste may therefore reflect partner choices and function to encourage social contact (Drea et al., 2002). A similar situation has been described in African wild dogs, in which emigrating females scent rubbed on urine of the males they were attempting to join (Frame, Malcolm, Frame, & van Lawick, 1979).

We have found that spotted hyenas have acute olfactory abilities, relying on odor cues not only to assess or modify the environment (Drea et al., 2002; Kruuk, 1972) and influence social interaction (Drea et al., 2002) but also to obtain information about conspecifics (Gorman & Trowbridge, 1989). Olfactory cues are therefore important in the context of both intergroup and intragroup relations. Definitive functional explanations require knowing precisely what information is communicated via paste.

References

- Apps, P. J., Viljoen, H. W., Richardson, P. R. K., & Pretorius, V. (1989). Volatile components of anal gland secretion of aardwolf (*Proteles cristatus*). *Journal of Chemical Ecology*, *15*, 1681–1688.
- 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*. *Proceedings of the American Association of Zoo Veterinarians, American Association of Wildlife Veterinarians*, 139–148.
- Brown, R. E. (1979). Mammalian social odours: A critical review. *Advances in the Study of Behaviour*, *10*, 103–162.
- Buglass, A. J., Darling, F. M. C., & Waterhouse, J. S. (1990). Analysis of the anal sac secretion of the Hyaenidae. In D. W. Macdonald, D. Müller-Schwarze, & S. E. Natynczuk (Eds.), *Chemical signals in vertebrates 5* (pp. 65–69). New York: Oxford University Press.
- Drea, C. M., & Frank, L. G. (in press). The social savvy of spotted hyenas. In F. B. M. de Waal & P. L. Tyack (Eds.), *Animal social complexity: Intelligence, culture, and individualized societies*. Cambridge, MA: Harvard University Press.
- Drea, C. M., Vignieri, S. N., Cunningham, S. B., & Glickman, S. E. (2002). Responses to olfactory stimuli in spotted hyenas (*Crocuta crocuta*): I. Investigation of environmental odors and the function of rolling. *Journal of Comparative Psychology*, *116*, 331–341.
- East, M. L., & Hofer, H. (1991a). Loud calling in a female-dominated mammalian society: I. Structure and composition of whooping bouts of spotted hyenas, *Crocuta crocuta*. *Animal Behaviour*, *42*, 637–649.
- East, M. L., & Hofer, H. (1991b). Loud calling in a female-dominated mammalian society: II. Behavioural contexts and functions of whooping of spotted hyenas, *Crocuta crocuta*. *Animal Behaviour*, *42*, 651–669.
- 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. *Behavioral Ecology and Sociobiology*, *33*, 355–370.
- Eisenberg, J. F., & Kleiman, D. G. (1972). Olfactory communication in mammals. *Annual Review of Ecology and Systematics*, *3*, 1–32.
- Frame, L. H., Malcolm, J. R., Frame, G. W., & van Lawick, H. (1979). Social organization of African wild dogs (*Lycyaon pictus*) on the Serengeti plains, Tanzania 1967–1978. *Zeitschrift für Tierpsychologie*, *50*, 225–249.
- Frank, L. G. (1986a). Social organization of the spotted hyena (*Crocuta crocuta*): I. Demography. *Animal Behaviour*, *34*, 1500–1509.
- Frank, L. G. (1986b). Social organization of the spotted hyena *Crocuta crocuta*: II. Dominance and reproduction. *Animal Behaviour*, *34*, 1510–1527.
- Glickman, S. E., Frank, L. G., Pavgi, S., & Licht, P. (1992). Hormonal correlates of “masculinization” in female spotted hyenas (*Crocuta crocuta*): I. Infancy to sexual maturity. *Journal of Reproduction and Fertility*, *95*, 451–462.
- Goodall, J., & van Lawick, H. (1970). *Innocent killers*. London: Collins.
- Gorman, M. L. (1976). A mechanism for individual recognition by odour in *Herpestes auropunctatus* (Carnivora: Viverridae). *Animal Behaviour*, *24*, 141–145.
- Gorman, M. L., & Mills, M. G. L. (1984). Scent marking strategies in hyenas (Mammalia). *Journal of Zoology, London*, *202*, 535–547.
- Gorman, M. L., & Trowbridge, B. J. (1989). The role of odor in the social lives of carnivores. In J. L. Gittleman (Ed.), *Carnivore behavior, ecology, and evolution* (pp. 57–88). Ithaca, NY: Comstock Publishing Associates.
- Gosling, L. M. (1982). A reassessment of the function of scent marking in territories. *Zeitschrift für Tierpsychologie*, *60*, 89–118.
- Halpin, Z. T. (1986). Individual odors among mammals: Origins and functions. *Advances in the Study of Behavior*, *16*, 39–70.
- Henschel, J. R., & Skinner, J. D. (1991). Territorial behaviour by a clan of spotted hyenas *Crocuta crocuta*. *Ethology*, *88*, 223–235.
- Hofer, H., & East, M. L. (1993a). The commuting system of Serengeti spotted hyenas: How a predator copes with migratory prey. I. Social organization. *Animal Behaviour*, *46*, 547–557.
- Hofer, H., & East, M. L. (1993b). The commuting system of Serengeti spotted hyenas: How a predator copes with migratory prey. II. Intrusion pressure and commuters' space use. *Animal Behaviour*, *46*, 559–574.
- Holekamp, K. E., Boydston, E. E., Szykman, M., Graham, I., Nutt, K. J., Birch, S., et al. (1999). Vocal recognition in the spotted hyena and its possible implications regarding the evolution of intelligence. *Animal Behaviour*, *58*, 383–395.
- Johnson, R. P. (1973). Scent marking in mammals. *Animal Behaviour*, *21*, 521–535.
- Johnston, R. E., & Peng, M. (2000). The vomeronasal organ is involved in discrimination of individual odors by males but not by females in golden hamsters. *Physiology and Behavior*, *79*, 537–549.
- Kruuk, H. (1972). *The spotted hyena: A study of predation and social behavior*. Chicago: University of Chicago Press.
- Kruuk, H. (1976). Feeding and social behaviour of the striped hyena (*Hyaena vulgaris* Desmarest). *East African Wildlife Journal*, *14*, 91–111.
- Kruuk, H., Gorman, M., & Leitch, A. (1984). Scent-marking with the subcaudal gland by the European badger, *Meles meles* L. *Animal Behaviour*, *32*, 899–907.
- Kruuk, H., & Sands, W. A. (1972). The aardwolf (*Proteles cristatus* Sparrman) 1783 as predator of termites. *East African Wildlife Journal*, *10*, 211–227.
- Licht, P., Frank, L. G., Pavgi, S., Yalcinkaya, T. M., Siiteri, P. K., & Glickman, S. E. (1992). Hormonal correlates of “masculinization” in female spotted hyenas (*Crocuta crocuta*). 2. Maternal and fetal steroids. *Journal of Reproduction and Fertility*, *95*, 463–474.

- Licht, P., Zucker, I., Hubbard, G., & Boshes, M. (1982). Circannual rhythms of plasma testosterone and luteinizing hormone levels in golden-mantled ground squirrels (*Spermophilus lateralis*). *Biology of Reproduction*, 27, 411-418.
- Mills, M. G. L. (1990). *Kalahari hyenas: Comparative behavioural ecology of two species*. London: Unwin Hyman.
- Mills, M. G. L., & Gorman, M. L. (1987). The scent-marking behaviour of the spotted hyaena *Crocuta crocuta* in the southern Kalahari. *Journal of Zoology*, London, 212, 483-497.
- Mills, M. G. L., Gorman, M. L., & Mills, M. E. J. (1980). The scent marking behaviour of the brown hyaena *Hyaena brunnea*. *South African Journal of Zoology*, 15, 240-248.
- Ralls, K. (1971, February 5). Mammalian scent marking. *Science*, 171, 443-449.
- Rasa, A. E. (1973). Marking behaviour and its social significance in the African dwarf mongoose *Helogale undulata rufula*. *Zeitschrift für Tierpsychologie*, 32, 293-318.
- Richardson, P. R. K. (1987). Aardwolf mating system: Overt cuckoldry in an apparently monogamous mammal. *South African Journal of Science*, 83, 405-410.
- Richardson, P. R. K. (1990). Scent marking and territoriality in the aardwolf. In D. W. Macdonald, D. Müller-Schwarze, & S. E. Natynczuk (Eds.), *Chemical signals in vertebrates 5* (pp. 378-387). New York: Oxford University Press.
- Richardson, P. R. K. (1991). Territorial significance of scent marking during the non-mating season in the aardwolf *Proteles cristatus* (Carnivora: Proteleidae). *Ethology*, 87, 9-27.
- Rieger, I. (1979). Scent rubbing in carnivores. *Carnivore*, 2, 17-25.
- Rieger, I. (1981). Hyaena hyaena. *Mammalian Species*, 150, 1-5.
- Roeder, J.-J. (1983). Memorisation des marques olfactives chez la Genette (*Genetta genetta* L.): Durée de reconnaissance par les femelles de marques olfactives de males. [Memorization of scent marks in genets (*Genetta genetta* L.): Duration of female memory of male scent marks]. *Zeitschrift für Tierpsychologie*, 61, 311-314.
- Ryon, J., & Brown, R. E. (1990). Urine marking in female wolves (*Canis lupus*): An indicator of dominance status and reproductive state. In D. W. Macdonald, D. Müller-Schwarze, & S. E. Natynczuk (Eds.), *Chemical signals in vertebrates 5* (pp. 346-351). New York: Oxford University Press.
- Sliwa, A., & Richardson, P. R. K. (1998). Responses of aardwolves, *Proteles cristatus*, Sparrman 1783, to translocated scent marks. *Animal Behaviour*, 56, 137-146.
- Tilson, R. L., & Henschel, J. R. (1986). Spatial arrangement of spotted hyaena groups in a desert environment, Namibia. *African Journal of Ecology*, 24, 173-180.
- Woodmansee, K. B., Zabel, C. J., Glickman, S. E., Frank, L. G., & Keppel, G. (1991). Scent marking (pasting) in a colony of immature spotted hyenas (*Crocuta crocuta*): A developmental study. *Journal of Comparative Psychology*, 105, 10-14.

Received September 5, 2001

Revision received January 25, 2002

Accepted February 2, 2002 ■

ORDER FORM

Start my 2003 subscription to the *Journal of Comparative Psychology*! ISSN: 0735-7036

\$33.00, APA MEMBER/AFFILIATE _____
 \$66.00, INDIVIDUAL NONMEMBER _____
 \$166.00, INSTITUTION _____
In DC add 5.75% / In MD add 5% sales tax
TOTAL AMOUNT ENCLOSED \$ _____

Subscription orders must be prepaid. (Subscriptions are on a calendar year basis only.) Allow 4-6 weeks for delivery of the first issue. Call for international subscription rates.



AMERICAN
PSYCHOLOGICAL
ASSOCIATION

SEND THIS ORDER FORM TO:
American Psychological Association
Subscriptions
750 First Street, NE
Washington, DC 20002-4242

Or call (800) 374-2721, fax (202) 336-5568.
TDD/TTY (202) 336-6123.
For subscription information, e-mail:
subscriptions@apa.org

Send me a FREE Sample Issue

Check enclosed (make payable to APA)

Charge my: VISA MasterCard American Express

Cardholder Name _____

Card No. _____ Exp. Date _____

Signature (Required for Charge)

BILLING ADDRESS: _____

City _____ State _____ Zip _____

Daytime Phone _____

SHIP TO:

Name _____

Address _____

City _____ State _____ Zip _____

APA Member # _____ COMA13