

Responses to Olfactory Stimuli in Spotted Hyenas (*Crocuta crocuta*): I. Investigation of Environmental Odors and the Function of Rolling

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Olfaction is crucial to spotted hyenas (*Crocuta crocuta*), yet there are no controlled studies of their reactions to odors. In Experiment 1, the authors examined responses of captive hyenas to various environmental (prey, nonprey animal, and plant) odors. Subjects approached and sniffed all odors equally but preferentially licked prey odors, scent marked next to odors, and rolled in animal-based odors. In Experiment 2, the authors examined the function of rolling by applying odors to the pelts of captive hyenas. When hyenas wore carrion, they gained positive social attention (increased investigation and allogrooming) from pen mates, but when they wore camphor, the normal social greeting ceremony was curtailed. Thus, olfactory stimuli elicit specific responses, influence where behavior is directed, and can be used to affect social interaction.

As crepuscular hunters and scavengers that compete against other predators, spotted hyenas rely on their olfactory sense to locate prey and to warn of danger (Kruuk, 1972; Mills, 1990). As highly territorial carnivores that defend core space against hostile intruders, spotted hyenas also depend on odor cues for intraspecific communication—to advertise ownership (Henschel & Skinner, 1991; Kruuk, 1972; Mills & Gorman, 1987). Finally, as gregarious animals that live in stable clans and maintain enduring social relationships (Frank, 1986a, 1986b), spotted hyenas use olfaction to synchronize or facilitate group behavior (Glickman et al., 1997; Kruuk, 1972; Woodmansee, Zabel, Glickman, Frank, & Keppel, 1991). Although the “hyena’s sense of smell is almost proverbial” (Kruuk, 1972, p. 216), no studies have systematically examined

their behavioral responses to odors. Therefore, in a series of experiments (presented here and in our companion article: Drea, Vignieri, Kim, Weldele, & Glickman, 2002), we studied the spotted hyena’s basic pattern of olfactory investigation, focusing on two prominent responses: scent marking and rolling.

Scent marking is widespread in mammals (Brown & Macdonald, 1985; Eisenberg & Kleiman, 1972; Gorman, 1990) and, among terrestrial carnivores (Ewer, 1973), often occurs in connection with rolling, also called *scent rubbing* (Rieger, 1979) or *self-scenting* (Zimen, 1981). Whereas scent marking transfers the animal’s scent to its surroundings, rolling presumably transfers odoriferous substances from the environment to the animal’s body (Rieger, 1979). Rolling in strong odors such as carrion, feces, or vomit is particularly manifest in spotted hyenas, both in the wild (Goodall & van Lawick, 1970) and in captivity (Drea et al., 2002; Glickman et al., 1997; Rieger, 1979). We distinguish this behavior from rubbing that may serve to deposit odor (Kleiman, 1966), to scratch oneself, to remove parasites, or to display exuberance.

Spotted hyenas also have an elaborate scent-marking repertoire (Kruuk, 1972; Mills, 1990) that includes urinating and defecating in conspicuous latrines located throughout their territory (Bearder & Randall, 1978). They possess two sets of specialized scent glands: interdigital glands and supra-anal sacs (Kruuk, 1972). Interdigital glands leave scent in furrows produced when an animal scratches the ground—behavior that frequently accompanies excretion (Bearder & Randall, 1978). By combining visual and olfactory components, degradation-resistant scat and scratching constitute long-lasting, composite signals (Bekoff, 1979). Likewise, supra-anal sacs produce a thick, durable, glandular secretion or *paste* (Buglass, Darling, & Waterhouse, 1990) that is extruded by squatting and everting the anal pouch over the item being marked (Kruuk, 1972; Mills, 1990). Similar to many mammals that display competitive scent marking (Johnson, 1973), also termed *countermarking* or *overmarking*, hyenas often deposit paste on or near the mark of a conspecific (Kruuk, 1972; Tilson & Henschel, 1986; Woodmansee et al., 1991).

For animals possessing a keen olfactory sense, odor cues can reveal a wealth of information. Accordingly, different classes of

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odors should elicit different responses. For instance, prey-related odors might initiate approach (Mills, 1990) or gustatory responses, whereas carnivore odors might trigger competitive scent marking or avoidance behavior (Kruuk, 1972). Similarly, novel odors or certain classes of odors reportedly stimulate rolling (Ryon, Fentress, Harrington, & Bragdon, 1986). Experiment 1 characterizes the spotted hyena's response sequence and specificity to odors representing three classes of environmentally relevant stimuli: prey animals, nonprey animals, and plants. Following examination of various hypotheses advanced to explain rolling, Experiment 2 provides evidence to support a social function of rolling in spotted hyenas.

Experiment 1

Following presentation of odors derived from prey animals, nonprey animals, or plants, we asked whether hyenas would approach some odors and avoid others, limit their gustatory responses to prey odors, or show stronger responses to animal than to plant odors. We also examined whether any of their responses differed by sex. Moreover, as olfactory investigation is a primary antecedent to scent marking (Kruuk, 1972) and rolling (Rieger, 1979), we focused on the elicitation and site specificity of these responses.

With respect to scent marking, a growing body of literature examines the topographical relation between conspecific marks. Such research shows that animals preferentially value the top scent in overmarks, thereby revealing specialized perceptual mechanisms by which mammals evaluate and discriminate scent (Ferkin, Dunsavage, & Johnston, 1999; Johnston & Bhorade, 1998; Wilcox & Johnston, 1995). By contrast, we found no reports detailing the site of scent deposition in response to other classes of odors. Therefore, we also tested the generality of overmarking in response to odors by examining patterns of spatial overlap between

odor presentation and scent marking. For heuristic purposes, we borrow and modify the term *overmarking* to describe paste deposition *on any odor* and the term *adjacent marking* to refer to pasting *next to any odor*. Likewise, with respect to rolling, we examined site and odor specificity to support our premise that rolling facilitates the acquisition of particular odors.

Method

Subjects and housing. Eight captive, reproductively intact spotted hyenas (*Crocuta crocuta*; 4 males and 4 females) served as subjects. Three hyenas had been collected in Kenya as infants (at 1 week to 2 months of age); the other 5 were captive born. At the time of testing, 6 were adults (4–9 years old) and 2 were juveniles (1-year-old mixed-sex twins). The hyenas were housed socially at the Field Station for Behavioral Research, University of California, Berkeley. Six were housed in yards (6.9 m × 18.6 m) with daily access to covered enclosures (4.5 m × 8.7 m), and 2 were in covered enclosures continuously. All pens had open-air fencing. The hyenas were fed carnivore zoo diet (Nebraska Brand Feline Food; Central Nebraska Packing, Inc., North Platte, NE) and pork bones each morning, and fresh straw for bedding was routinely provided.

Odors. We based selection of seven test odors on prior odor classifications (Amoore, 1969; Harper, Bate Smith, & Land, 1968). Odors, qualified as *novel* or *rare*, were derived from animal or plant sources (see Table 1). The chemical composition was known only for commercially available odors. All odors were strong smelling, easily differentiated by humans, and presented in liquid form.

Procedure. We presented each odor to each subject once in 10-min trials (for 56 trials total) conducted in the covered enclosures on windless afternoons. We placed two straw piles (each 0.16 m³ or approximately one sixth of a flake) about 3 m apart along the wall farthest from the hyena's entryway and distributed the odor (3 ml) atop one pile, leaving the other pile unscented. Odor placement varied randomly between left and right piles. We presented odors in random order within and across subjects. Trials began once the hyena entered the enclosure from an adjoining pen. We removed straw piles and cleaned the room after each test.

Table 1
Classification of Seven Odors Presented to Captive Spotted Hyenas

Odor	Source and derivation	Novelty classification and explanation
Carrion	Prey animal: Liquid, presumably containing mercaptans or thiols, produced by placing ground beef in an unrefrigerated container, allowing it to rot for a minimum of 3 weeks, and finally forcing it through a syringe.	Rare: More potent than any rancid meat odor previously encountered by the hyenas; nevertheless, beef constituted part of the normal diet and therefore may not have been purely novel.
Bacon	Prey animal: Burnt grease, presumably containing nitrogenous compounds, obtained by frying bacon.	Novel: Cooked, salted, and processed pork was not part of the hyenas' normal diet.
Sweat	Animal: Isovaleric acid derived from sweat or anal glands, ^a found in the anal secretions of carnivores but also present in mammalian blood and sweat; therefore, potentially both prey and nonprey.	Novel: The hyenas had not previously encountered this odor in its purified form.
Skunk	Nonprey animal: Skunk-It and Skunk-Essence solutions derived from the anal scent glands of striped skunks. ^b	Rare: Skunks are not indigenous to Africa (Verts, 1967) and would be novel in the wild, but the hyenas have encountered the diffuse odor of skunks, although not in this form.
Musk	Nonprey animal: ω -pentadecalactone derived from angelica root but classified as an animal odor by the manufacturer. ^a	Novel: The hyenas had never been exposed to musk.
Camphor	Plant: 1,8-cineole, terpene isolated from eucalyptus. ^a	Rare: Eucalyptus trees are present at the Berkeley Field Station, but to the human nose this extract smells different from the landscape.
Mint	Plant: <i>l</i> -carvone, terpene derived from spearmint. ^a	Novel: The hyenas had never been exposed to mint.

^a Obtained commercially from Olfacto-Labs (El Cerrito, CA) and presented in dilution with mineral oil calibrated to a mean threshold level of 0 decismels.

^b Obtained commercially from M & M Fur Co. (Bridgewater, SD).

Data collection. Two observers, situated in covered hallways about 2 m from the fencing of the test enclosure, scored behavioral responses (see Table 2) in real time using a laptop computer and recorded several trials using a handheld video camera. We calculated inter- and intra-observer reliability at the beginning and end of testing as the percentage of agreement between a data set scored in real time and a data set scored from a video recording of the same trial, by either the same or different observers. Reliability scores exceeded 89% agreement.

Data analyses. To address age differences between subjects, we first examined individual responses (e.g., see Table 3). As we found the behavior of juveniles to be consistent with that of adults, we collapsed age categories for all analyses. We tested for sex effects in two series of two-factor analyses of variance (ANOVAs). The first series assessed male and female responses across odors; the second combined odors and assessed male and female response allocations between straw piles. The variances for behavioral measures in these and all subsequent analyses were homogeneous (according to an *F*-maximum test for homogeneity of variances). As these analyses revealed only one significant sex effect, we collapsed sexes in further analyses.

Next, we tested for differences in responsiveness and site specificity between odors using two-factor ANOVAs. We resolved significant main effects of odor type using Newman–Keuls ranked pairwise comparisons, and we resolved interactions between odor and straw pile using *F* tests for simple effects (Bruning & Kintz, 1977). Finally, to test for differences in response latencies across odors, we used one-way ANOVAs, calculating latencies as the elapsed time from the start of a test to the first occurrence of the behavior, with a maximum latency of 10 min when a behavior never occurred.

We present data primarily on behavior occurring within 1 m of the straw piles. Exceptions include state behavior (e.g., vocalization and erection)

that continued outside the vicinity of straw piles and scent marking that often occurred throughout the enclosure. We analyzed the data using UNIX/STAT compact analysis programs (Perlman, 1986), and we report all values as mean frequencies or durations (\pm *SEs*), with significance set at $\alpha \leq .05$.

Results

The hyenas' responses to environmental odors generally followed a chronological pattern that included approaching, sniffing, licking, rolling, and scent marking. (The one exception involved skunk odor, which was rolled in prior to being licked.) We therefore present the data by behavioral categories, organized according to the typical temporal sequence of response.

Approach and initial investigation (sniffing). Each hyena approached every odor, thus no odor was avoided (see Table 3). On average, there were no differences across odors in hyena approach frequency, $F(6, 42) = 0.94, p = .48$ (data not shown in table), or latency, $F(6, 42) = 0.85, p = .54$ (see Table 4). Similarly, the hyenas spent about one third of the trial period in proximity to straw piles, regardless of the odor presented, $F(6, 42) = 1.24, p = .31$. Although, for each odor, they approached both straw piles with equal frequency, $F(1, 7) = 0.37, p = .56$ (data not shown in table), overall they spent over twice as much time near scented (2.48 ± 0.29 min) as unscented (1.13 ± 0.15 min) straw, $F(1, 7) = 11.46, p < .02$. This preference for scented straw was equally evident across odors, $F(6, 42) = 0.41, p = .87$ (see Table 4). Once in proximity, the hyenas sniffed all odors with equal frequency,

Table 2
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). Frequency scored in bouts, 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.
Erectile display	Partial or full penile or clitoral erection (Frank, Glickman, & Powch, 1990). State behavior scored as frequencies, from onset of tumescence to detumescence.
Vocalize	Low groaning sounds.
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.
Rest	Reclining in substrate or settling down anywhere in enclosure, terminated by animal rising to its feet.

Note. This table contains only the subset of recorded behavior that is reported on in the text. In Experiment 1, the targets were straw piles, and the distinction between whether the straw was scented or unscented was noted. In Experiment 2, the target was another hyena, and the body parts investigated (mouth, cheek, head, neck, back, flank, genitals, and anal region) were noted.

Table 3
Total Frequency of Approaches to Straw Piles per Spotted Hyena Following Presentation of Environmental Odors

Odor	Males				Females			
	Adult	Adult	Adult	Juvenile	Adult	Adult	Adult	Juvenile
Carrion	3	14	12	12	23	18	16	12
Bacon	34	4	17	17	24	8	13	14
Sweat	1	3	9	10	14	21	10	20
Skunk	7	7	18	15	9	13	4	21
Musk	18	8	10	10	3	13	5	28
Camphor	5	3	20	26	11	16	4	14
Mint	6	11	4	3	10	16	5	16

Note. Response distributions had a slight positive skew of 0.27 on average.

$F(6, 42) = 0.51, p = .80$, and equal latency, $F(6, 42) = 0.75, p = .61$, but sniffed scented straw more often than unscented straw, $F(1, 7) = 28.80, p < .001$ (see Table 4). Thus, the hyenas' initial responses, including the frequency, latency, and duration of approaches as well as the frequency, latency, and site specificity of sniffing, was similar across odors.

Licking. After sniffing, the hyenas proceeded to lick all odors, licking scented straw more often than unscented straw, $F(1, 7) = 21.37, p < .002$ (see Figure 1A). Nevertheless, the frequency of licking varied across odors, $F(6, 42) = 5.85, p < .001$, with carrion eliciting more licking than other odors ($p < .01$). Moreover, the distribution of licking between the two straw piles varied across odors, $F(6, 42) = 7.25, p < .001$. Paired comparisons showed that enhanced licking of scented straw was significant for all but the nonprey animal odors (musk and skunk; see Figure 1B). The same patterns (or preferences) emerged in latency measures, in that hyenas licked carrion within 1 min and bacon within 2 min, but 5 min elapsed before they licked other odors (with skunk in last place). Thus, prey odors were tasted more often and faster than nonprey odors ($p < .05$).

Rolling. Generally, the hyenas rolled more in scented than unscented straw, $F(1, 7) = 10.45, p < .05$ (see Figure 2A), but paired comparisons revealed that this main effect was primarily attributable to nonprey skunk and musk odors (see Figure 2B). Thus, certain odors elicited far more rolling than others, $F(6, 42) = 8.09, p < .001$. The most rolling occurred in skunk ($p < .01$),

with musk and carrion eliciting moderate responses. Similar patterns were evident in response latencies, $F(6, 42) = 7.90, p < .001$, which were shortest for skunk (2.68 ± 1.60 min), carrion (4.21 ± 1.72 min), and musk (4.44 ± 1.70 min, $p < .05$). Although these latencies were exaggerated by nonresponders, the general order was consistent. In a final comparison of novel versus rare odors, we found that the hyenas rolled more frequently, on average, in straw scented with rare odors (2.60 ± 0.98) than in straw scented with novel odors (0.50 ± 0.18), $F(1, 7) = 7.17, p < .05$.

Other behavior. The hyenas also displayed erections in the presence of odors, indicating general arousal (see Table 5). Although skunk odor failed to elicit erections, there was no significant difference in display frequency across odors, $F(6, 36) = 1.38, p = .25$. Similarly, there was no sex effect in that males (0.68 ± 0.11) displayed erections as often as did females (0.82 ± 0.45), $F(1, 6) = 0.10, p = .77$. In addition, the hyenas sometimes vocalized during trials, with females (3.75 ± 1.48) groaning more frequently than males (0.36 ± 0.20), $F(1, 6) = 7.04, p < .05$. Although the hyenas never vocalized in the presence of camphor, there were no significant differences in vocalization frequencies across odors, $F(6, 36) = 0.98, p = .45$ (see Table 5).

Scent marking. Urination and scratching occurred infrequently and away from the straw piles. Moreover, the combined frequencies of urination and scratching were equivalent across odors, $F(6, 36) = 1.55, p = .19$ (see Table 5). The main form of scent marking

Table 4
Latency of Investigative Behavior and Response Allocations to Scented Versus Unscented Straw by Spotted Hyenas Following Presentation of Environmental Odors

Odor	Proximity ($M \pm SE$)			Sniff ($M \pm SE$)		
	Latency (min) scented	Duration (min)		Latency (min) scented	Frequency	
		Scented	Unscented		Scented	Unscented
Carrion	0.18 \pm 0.05	2.47 \pm 0.36	0.93 \pm 0.33	0.46 \pm 0.18	9.75 \pm 2.33	2.87 \pm 0.74
Bacon	0.54 \pm 0.33	1.93 \pm 0.54	1.06 \pm 0.28	0.59 \pm 0.33	6.00 \pm 1.00	2.75 \pm 0.45
Sweat	0.64 \pm 0.40	2.09 \pm 0.70	1.21 \pm 0.35	1.51 \pm 1.22	6.50 \pm 1.41	4.62 \pm 1.32
Skunk	0.15 \pm 0.05	3.73 \pm 0.80	1.46 \pm 0.51	0.22 \pm 0.05	6.12 \pm 2.55	1.62 \pm 0.91
Musk	0.19 \pm 0.06	2.74 \pm 1.02	1.28 \pm 0.60	0.25 \pm 0.07	9.00 \pm 3.81	2.50 \pm 1.12
Camphor	0.33 \pm 0.10	1.71 \pm 0.65	1.00 \pm 0.27	0.58 \pm 0.19	6.25 \pm 1.72	2.75 \pm 0.90
Mint	0.44 \pm 0.19	2.65 \pm 1.08	0.96 \pm 0.43	0.48 \pm 0.19	5.62 \pm 1.28	3.37 \pm 1.41

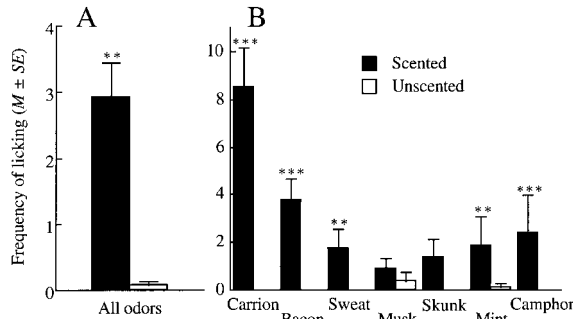


Figure 1. Mean (\pm SE) frequency and spatial distribution of licking by captive spotted hyenas across all odors (A) and by individual odors (B). The interaction effect in B was resolved as follows: Hyenas licked scented straw more often than unscented straw for all but musk and skunk odors. ** $p < .025$. *** $p < .001$.

expressed during trials was pasting. This response was unique in that it occurred more frequently in the unscented (0.48 ± 0.15) than in the scented (0.13 ± 0.08) straw, $F(1, 7) = 7.29, p < .05$. This pattern of adjacent marking was underrepresented, however, because pasting (similar to urination and scratching) also occurred elsewhere in the enclosure. Therefore, we combined frequencies of pasting in unscented straw with pasting in the enclosure and compared those values with pasting in scented straw. Analyses of these adjusted values showed that males (0.32 ± 0.12) and females (0.91 ± 0.24) pasted equally, $F(1, 6) = 1.26, p = .30$, with both sexes avoiding scented straw, $F(1, 7) = 8.92, p < .025$ (see Figure 3A). They also deposited paste more frequently around certain odors, $F(6, 42) = 2.86, p < .025$, specifically camphor, but they never deposited paste around musk ($p < .05$; see Figure 3B). Moreover, pasting occurred sooner around certain odors, $F(6, 42) = 4.49, p < .001$, with more rapid pasting in the presence of camphor (4.51 ± 1.26 min) and both prey odors, bacon (4.62 ± 1.48 min) and carrion (5.09 ± 1.27 min), than in the presence of other odors ($p < .05$).

Discussion

Spotted hyenas responded differently and with varying intensity to animal- versus plant-based odors, suggesting that olfaction

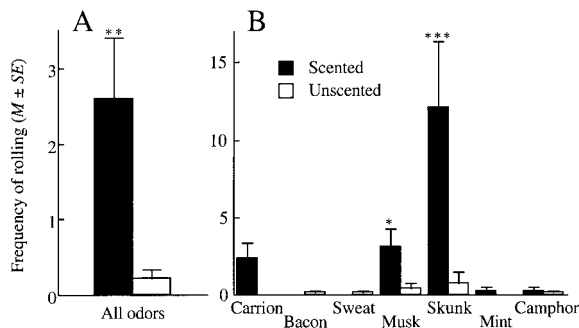


Figure 2. Mean (\pm SE) frequency and spatial distribution of rolling by captive spotted hyenas across all odors (A) and by individual odors (B). The interaction effect in B, $F(6, 42) = 5.50, p < .001$, was resolved as follows: Hyenas rolled more often in scented than unscented straw only for skunk and musk odors. * $p < .05$. ** $p < .025$. *** $p < .001$.

Table 5
Frequency of Behavior Occurring Anywhere in the Test Enclosure by Spotted Hyenas Following Presentation of Environmental Odors

Odor	Frequency of behavior ($M \pm SE$)		
	Erection	Vocalization	Urination and scratching
Carrion	0.75 \pm 0.49	2.75 \pm 1.50	1.88 \pm 0.88
Bacon	1.25 \pm 0.62	0.88 \pm 0.58	0.13 \pm 0.13
Sweat	1.00 \pm 0.53	3.88 \pm 3.31	1.00 \pm 0.63
Skunk	0	1.00 \pm 0.76	4.88 \pm 2.31
Musk	0.25 \pm 0.16	5.38 \pm 3.90	3.13 \pm 2.84
Camphor	1.25 \pm 0.49	0	0.50 \pm 0.27
Mint	0.75 \pm 0.49	0.50 \pm 0.33	0.88 \pm 0.30

serves a discriminatory function in assessing the environment. Their initial response invariably involved investigative behavior (approach and sniffing), displayed equally toward all odors. Subsequently, various odors elicited differences in the type, magnitude, latency, and site of responding. For instance, prey odors were licked soonest and most frequently, presumably serving a preconsummatory function. Nevertheless, the hyenas licked all odors, suggesting that a gustatory response may be part of a generalized sequence of chemosensory investigation, in which the communicative agent may be transmitted via taste or the vomeronasal organ (Eisenberg & Kleiman, 1972). Odor identification by licking is consistent with descriptions of spotted hyena responses to conspecific odor (Drea et al., 2002; East, Hofer, & Wickler, 1993; Kruuk, 1972; Mills, 1990).

Following licking, the hyenas displayed site- and/or odor-specific responses, including scent marking and rolling. Scent marking was a common response to encountering odors. Although the frequencies varied, pasting, scratching, and urinating occurred in the presence of both rare and novel odors, showing that many odors (including the smell of plain straw) may elicit scent marking. This apparent lack of source specificity agrees with observations of wild hyenas pasting in various contexts, such as near a kill or carcass, in the presence of lions, around a den, at marking posts, and at latrines throughout the interior or along the periphery of

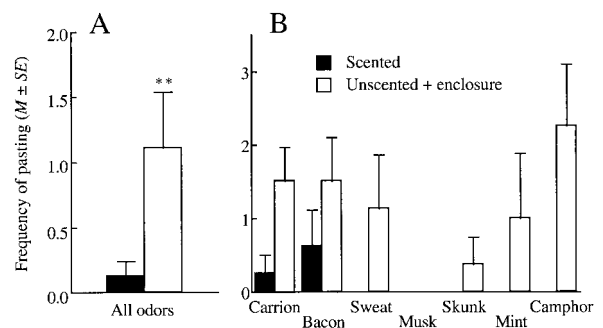


Figure 3. Mean (\pm SE) frequency and spatial distribution of pasting by captive spotted hyenas across all odors (A) and by individual odors (B). The spatial distribution compares the scented straw pile with anywhere else in the enclosure (including the unscented straw pile). The interaction effect in B was not significant, $F(6, 42) = 1.31, p = .27$. ** $p < .025$.

territories (Henschel & Skinner, 1991; Kruuk, 1972; Mills, 1990; Mills & Gorman, 1987; Tilson & Henschel, 1986).

To the extent that pasting occurred adjacent to the odor source, one can describe scent marking as *site specific*. The subjects effectively avoided covering the existing odor by depositing paste in the unscented straw pile or elsewhere in the enclosure, potentially to keep the odor source or their own scent pure. Thus, the topographical specificity of overmarking in spotted hyenas may be peculiar to conspecific odor (e.g., Woodmansee et al., 1991), whereas adjacent marking may occur in response to both conspecific and environmental odors. These findings suggest that scent marking may be influenced by various odor cues as well as by tactile or visual stimuli and possibly serves multiple functions. To further investigate scent marking and to clarify the function of such ubiquitous behavior, in our companion study we explored the potential information conveyed in paste (Drea et al., 2002).

In contrast to scent marking, rolling was both an odor- and a site-specific response, occurring *in* rather than *next to* select odors only. The site specificity of rolling confirms that this behavior facilitates odor acquisition (Rieger, 1979) in spotted hyenas. Despite the prevalence of rolling among mammals, the functional significance of wearing an odor remains unclear. The camouflage hypothesis proposes that rolling serves to mask a hunter's own odor so that it can better sneak up on its prey (Zimen, 1981). This hypothesis predicts that hyenas should select plant odors over the scent of other carnivores, as the latter would defeat the purpose of disguise. Nevertheless, we found that hyenas rarely rolled in plant odors but rather, rolled in strong animal-based odors, concordant with observations of wild and captive hyenas rolling in carrion and regurgitated masses (Goodall & van Lawick, 1970; Rieger, 1979). Perhaps more to the point is that spotted hyenas do not hunt by stealth (Kruuk, 1972). Therefore, the camouflage hypothesis is unlikely to explain rolling in this species.

According to the advertisement hypothesis, rolling in carrion by wolves may call other pack members' attention to an available food source (Zimen, 1981). Spotted hyenas, however, are intensely competitive feeders (Frank, 1986b; Kruuk, 1972; Mills, 1990) and do not cooperatively provision their young (Holekamp & Smale, 1990; Kruuk, 1972; Mills, 1985), thereby diminishing the benefits of food advertisement. Moreover, they roll in putrescent substances that have little or no nutritive value. The odor rolled in soonest (i.e., skunk) was the last tasted, consistent with a negative correlation in wolves between substances rolled in and substances tasted (Ryon et al., 1986). Rolling is therefore unlikely to serve this type of communicative function in spotted hyenas.

Alternatively, because some carnivores tend to roll in novel odors or on new objects (Glickman & Sroges, 1966; Kleiman, 1966; Ryon et al., 1986), the habituation hypothesis suggests that rolling may reduce novelty through familiarization (Fox, 1971) or by serving as a mnemonic device (Ryon et al., 1986). According to this hypothesis, all novel odors should equally elicit rolling, more so than would rare or familiar odors. Our findings showed the reverse to be true; namely, spotted hyenas rolled more in rare than in novel odors. Similarly, the familiar, fetid odor of regurgitated hair masses never fails to produce enthusiastic rolling (Glickman et al., 1997; Goodall & van Lawick, 1970). Because the type of odor rather than its novelty predicts the extent of rolling, hyenas do not appear to roll in previously unknown substances as a means of increasing odor familiarity.

Finally, the attractant hypothesis, based on the observation that social canids roll more than solitary canids, proposes that wearing scent increases individual attractiveness to conspecifics, thereby increasing social investigation (Fox, 1971). This last function seems a likely candidate for explaining rolling in spotted hyenas, as this species is highly social (Frank, 1986a, 1986b; Kruuk, 1972) and displays a complex array of behavioral and olfactory mechanisms to maintain social cohesion (Drea & Frank, in press; East et al., 1993; Holekamp, Boydston, & Smale, 2000; Kruuk, 1972; Mills, 1990). Our following experiment specifically tested this hypothesis.

Experiment 2

The prominent olfactory component of spotted hyena social behavior is illustrated, for example, by the greeting ceremony. As clans have a fission–fusion organization, members repeatedly transition between solitary and social lifestyles, with reassembly involving elaborate, ritualized ceremonies (Kruuk, 1972). During a greet, participants first sniff each other's mouth, head, and back, and then, while displaying erections, stand head to tail to mutually inspect each other's genitals, flanks, and bulging anal pouch (Krusko, Weldele, & Glickman, 1988). This unique behavior serves to reaffirm social bonds (East et al., 1993).

In nature, a hyena that rolls in an odoriferous substance ultimately brings that odor back to the clan. If rolling serves a social function, its consequences are likely to be evident when hyenas reunite. We therefore tested the attractant hypothesis by examining behavioral interactions following reunion of a scent-anointed hyena (the odor wearer) with its companion (the odor perceiver). We predicted that captive hyenas would receive more social investigation and affiliative behavior from companions when carrying an odor than when unscented. In particular, the companion should prefer to investigate the wearer when the latter is scented with an odor that normally elicits rolling (a roll-inducing odor) than when scented with an odor that typically fails to elicit rolling (a control odor).

Method

Subjects and housing. The subjects were 18 reproductively intact, adult hyenas (*Crocuta crocuta*; 9 males and 9 females), aged 6–14 years. Two females and 3 males had served as subjects in Experiment 1, but testing occurred 5 years later. Of the 13 new subjects, 3 males had been collected in Kenya as infants (at 1 week to 2 months of age); the other 10 were captive born. The hyenas were housed in three male–male, three female–female, and three male–female pairs, without other pen mates. Pairs occupied yards with access to covered enclosures and were fed as before.

We knew the dominance relations for all pairs of hyenas. Status differences between unrelated pairs had been assessed through dyadic bone tests that simulate the competitive feeding situation in the wild and reveal priority of access to food (Jenks, Weldele, Frank, & Glickman, 1995). Rank relations in 4 sibling pairs had been assessed by counting the frequency of displacements during ontogenetic studies of the first month of life (Drea, Hawk, & Glickman, 1996) and had remained consistent in later bone tests (Weldele, 1998).

Odors. Although skunk odor had produced the most rolling in Experiment 1, we selected carrion as the roll-inducing odor because it also elicits rolling in the field (Kruuk, 1972) and is thus more ecologically valid. It was prepared as before and additionally diluted in mineral oil. We chose

camphor as the control odor because it had previously produced minimal rolling. It was extracted from *Eucalyptus globulus* and also diluted in mineral oil.

Procedure. Each hyena pair was tested in 8 trials of 10 min each (for 72 trials total). Pairs received a single trial every 2–3 days, with testing occurring in the yards during the afternoon. Testing followed an ABAB paradigm, in which A involved a baseline condition of no odor and B involved an odor condition of either carrion or camphor. Prior to testing, we assigned the initial role of wearer to 1 hyena per pair and that of perceiver to its companion, randomizing assignments with respect to social status (dominant vs. subordinate). The roles were repeatedly switched as we used a within-subjects design, such that each member of a pair was a wearer and a perceiver once for each condition. Thus, each A or B condition involved two trials. The order of odor presentation was counter-balanced (as best possible for 9 pairs).

On test days, we isolated the wearer indoors for 10 min. During this time, one experimenter (Christine M. Drea) scratched the subject on the neck for the baseline condition or both scratched the subject on the neck and squirted 3 ml of odor (carrion or camphor) from a syringe onto the subject, targeting the backside of the head (hereafter, *head*), neck, and shoulder region. These are the areas that typically come in contact with an odor when a hyena rolls. Because wearing odors in different places may serve different functions (Rieger, 1979), we applied odors in the same manner and to the same body parts throughout the study. We then released the odor wearer to the yard and scored the behavioral interactions with its companion. On the next trial, we reversed the wearer and perceiver roles of the hyenas.

Data collection and analyses. We collected data and measured general odor-related responses as before. In addition, we scored social interactions between the wearer and perceiver (see Table 6). We analyzed the data in two stages, keeping the two baseline conditions separate. *Odor condition* therefore refers to Baseline 1, Baseline 2, carrion, or camphor. We first tested for sex and/or rank effects in a series of two-factor ANOVAs (Odor Condition \times either Sex or Rank). Because these analyses revealed only one main effect each of sex and rank (see *Results*), we collapsed these variables in subsequent analyses. We then tested for effects of odor condition and hyena condition (wearer vs. perceiver) in a second set of two-factor ANOVAs. We confirmed homogeneity of variances and resolved signifi-

cant effects as in Experiment 1. Likewise, we report values as mean frequencies or durations (\pm SEs), with significance set at $\alpha \leq .05$.

Results

Sex and rank effects. The only significant sex difference in behavior during trials was in scent marking (the combined frequencies of pasting, pawing, urinating, and defecating). Males (1.11 ± 0.25) scent marked more often than did females (0.18 ± 0.09), $F(1, 16) = 4.62$, $p < .05$, regardless of odor condition, $F(3, 48) = 0.97$, $p = .42$.

The only significant effect of rank was on aggression. Aggression occurred infrequently; nevertheless, dominant hyenas (0.54 ± 0.17) displayed more aggression (threats and bites combined) than did subordinates (0.01 ± 0.01), $F(1, 16) = 4.67$, $p < .05$. Likewise, subordinates (1.40 ± 0.39) displayed more submissive behavior (appeasement, withdrawals, and giggles combined) than did dominant hyenas (0.04 ± 0.04), $F(1, 16) = 6.75$, $p < .025$. There were no significant interaction effects between odor condition and aggressive behavior, but there was one significant interaction between rank and odor condition. This effect involved the frequency of approaches, $F(3, 48) = 3.25$, $p < .05$, in which dominant hyenas approached subordinates more often during carrion trials ($p < .01$).

Approach and proximity. Odor applied to the wearer significantly influenced social contact between hyenas, $F(3, 51) = 3.19$, $p < .05$, with more approaches occurring in the presence of carrion than no odor ($p < .05$; see Table 7). Similarly, the type of odor affected the time hyenas spent near one another, $F(3, 51) = 9.62$, $p < .001$, with carrion doubling time in proximity compared with camphor or no odor ($p < .01$; see Table 7). Finally, hyenas assumed responsibility for social contact in a different manner across odors: Proximity was initiated significantly more often by the perceiver, $F(1, 17) = 6.09$, $p < .025$, but it was terminated

Table 6
Behavioral Definitions for Social Interactions Between Odor-Wearing and Odor-Perceiving Spotted Hyenas

Behavior	Definition
Threat	Behavior, such as lunging or attempted biting, performed with any combination of aggressive body postures (i.e., ears forward, tail up, or mane erect).
Bite	Grabbing with teeth, ranging from quick, forceful nips to prolonged or intense contact with shaking of head, directed toward any part of recipient's body.
Appease	Behavior performed with any combination of submissive body postures (i.e., ears flattened, tail tucked under, crouching, open-mouthed grimace, or head wagging).
Withdraw	Moving away in apparent avoidance of another animal.
Giggle	Distress vocalization often emitted by an animal that is the target of aggression.
Greet	Ritualized ceremony involving animals standing head to tail, lifting their legs, and presenting their genitals (usually erect) for inspection. Initiation, reciprocation, and termination were noted for each participant.
Allogroom	Extended licking, sometimes with nibbling, of another animal's body (location on body noted). Differentiated from more discrete bouts of licking by fuller tongue protrusion and involvement of exaggerated head movement in an upward direction. Recipient often closes eyes, stretches, and presents body to be groomed.
Yawn	Full opening of mouth with baring of teeth. Seemingly friendly behavior that often occurs when an animal is being groomed by another hyena. In these instances, the groomer often investigates the open mouth of the groomee.
Anal bulge	Extruding anal pouch without engaging in pasting activity.

Note. This table contains only the subset of recorded behavior that is reported on in the text.

Table 7
Frequency and Duration of Social Contact and Behavioral Interaction Between Odor-Wearing and Odor-Perceiving Spotted Hyenas

Odor condition	Time (min) in proximity ($M \pm SE$)	Frequency ($M \pm SE$)		
		Approach	Sniffing ^a	Licking ^b
Baseline 1	2.42 \pm 0.58	2.33 \pm 0.41	0.64 \pm 0.24	0.11 \pm 0.07
Baseline 2	2.36 \pm 0.44	2.97 \pm 0.38	0.89 \pm 0.22	0.36 \pm 0.13
Carrion	4.76 \pm 0.42	4.42 \pm 0.64	8.44 \pm 1.42	0.75 \pm 0.23
Camphor	2.61 \pm 0.49	3.22 \pm 0.46	2.78 \pm 0.93	0.14 \pm 0.09

^a Directed at head, neck, and back. ^b Directed at mouth, cheek, flank, and genitals.

more often by the wearer, $F(1, 17) = 18.78, p < .001$, only when hyenas wore carrion odor (see Figure 4).

Investigation. Hyenas investigated their odor-wearing companions more frequently when the latter were perfumed with carrion than when they either were perfumed with camphor or were not anointed (see Figure 5). Their pattern of investigation also differed across different portions of the body. Odor condition influenced sniffing, $F(3, 51) = 28.64, p < .001$ (see Table 7), and licking, $F(3, 51) = 32.75, p < .001$ (see Figure 5A), of the head, neck, and back, with carrion initiating the most intense investigation ($p < .01$). These body parts were sniffed, $F(1, 17) = 27.63, p < .001$, and licked, $F(1, 17) = 24.75, p < .001$ (see Figure 5A), more often by the perceiver than by the wearer. Sniffing, $F(3, 51) = 11.58, p < .001$ (see

Figure 5B), and licking, $F(3, 51) = 4.27, p < .01$ (see Table 7), of the mouth, cheek, flank, and genitals also varied by odor condition, again with carrion producing the most investigation ($p < .05$). Investigation of these body parts, however, was reciprocal between the wearer and perceiver, $F(1, 17) < 2.70, ns$ (see Figure 5B). Thus, carrion-scented body parts were investigated unilaterally by the perceiver, whereas nonscented body parts were mutually investigated.

Social interaction. Odor condition significantly influenced allogrooming, $F(3, 51) = 25.59, p < .001$, with more grooming of the wearer by the perceiver (1.57 ± 0.39) than of the perceiver by the wearer (0.32 ± 0.17), $F(1, 17) = 19.32, p < .001$, and more grooming in the presence of carrion than in the presence of either camphor or no odor ($p < .01$; see Figure 6A).

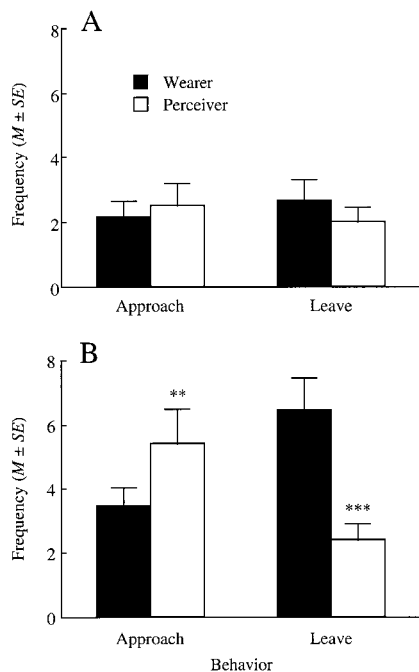


Figure 4. Mean ($\pm SE$) frequency of approaching and leaving a companion by captive spotted hyenas that were either wearing or perceiving no odor (A) or carrion odor (B). Both hyenas initiated behavior equally in A; however, in B, the odor perceiver initiated contact more frequently, but the odor wearer terminated contact more frequently. ** $p < .025$. *** $p < .001$.

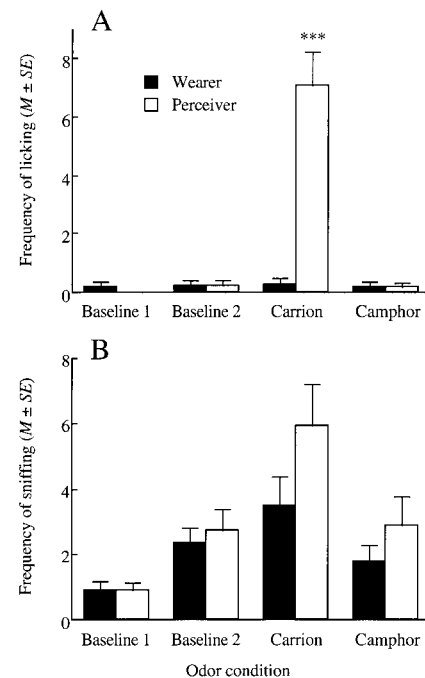


Figure 5. Mean ($\pm SE$) frequency of licking the back, head, and neck (A) and sniffing the mouth, cheeks, flanks, and genitals (B) by captive odor-wearing and odor-perceiving spotted hyenas. No odors were used in the baseline conditions. Resolution of the significant interaction in A, $F(3, 51) = 12.92, p < .001$, revealed enhanced licking by the odor perceiver compared with the odor wearer in the carrion condition. *** $p < .001$.

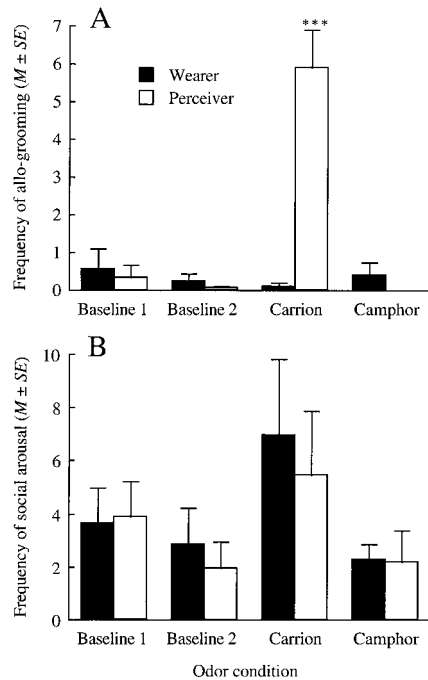


Figure 6. Mean (\pm SE) frequency of allogrooming (A) and social arousal, including anal bulging, groaning, and yawning (B), by captive odor-wearing and odor-perceiving spotted hyenas. No odors were used in the baseline conditions. Resolution of the significant interaction in A, $F(3, 51) = 20.83$, $p < .001$, revealed increased grooming of the odor wearer by the odor perceiver in the carrion condition. *** $p < .001$.

Anal bulging, groaning, and yawning, which occur when hyenas are aroused or involved in social interaction, individually showed higher frequencies during carrion trials. Grouping these categories revealed a significant influence of odor condition, $F(3, 51) = 5.15$, $p < .005$, with carrion (6.19 ± 1.84) enhancing the occurrence of these activities over the other odor conditions (Baseline 1, 3.78 ± 0.92 ; Baseline 2, 2.39 ± 0.83 ; camphor, 2.22 ± 0.65 ; $p < .05$). Whereas the perceiver predominantly displayed allogrooming, both hyenas displayed anal bulging, groaning, and yawning equally, $F(1, 17) = 0.47$, *ns* (see Figure 6B).

Three other behavior categories associated with the greeting ceremony (erection, greet initiation, and greet reciprocation) individually showed higher frequencies during baseline trials. Grouping these categories revealed an influence of odor condition, $F(3, 51) = 7.51$, $p < .001$, with less greet-associated behavior during camphor trials (0.42 ± 0.11) than baseline trials (1.03 ± 0.18 ; $p < .05$).

Solitary behavior. As a corollary to the increase in social behavior during carrion trials, there was a reduction in solitary activities. Thus, the hyenas showed different resting patterns across odor trials, $F(3, 51) = 3.43$, $p < .025$, resting less in the presence of carrion (0.64 ± 0.11) than in the absence of odor (1.14 ± 0.13 ; $p < .05$).

Discussion

As predicted by the attraction hypothesis (Fox, 1971), wearing certain potent odors appears to confer a social benefit to spotted

hyenas. When 1 member of a pair wore carrion odor, pen mates spent more time in proximity to each other, with the perceiver typically initiating social contact. The wearer, regardless of its dominance status, eventually terminated contact, typically by peacefully walking away. By comparison, greeting ceremonies are frequently terminated by the subordinate member of the greeting pair and may involve aggression (East et al., 1993). In our study, physical proximity appeared friendly, involving increased social sniffing and licking, neither of which was limited to the body parts where the carrion odor had been applied. Again, these findings suggest that licking was not solely a gustatory response.

The most apparent immediate benefit to the hyena wearing carrion odor was an increase in the amount of grooming it received. Although spotted hyenas regularly groom themselves (Kruuk, 1972), our impression is that allogrooming occurs infrequently and, outside of the mother–infant relationship, is usually directed from a subordinate to a higher-ranking hyena. If so, the present increase in allogrooming regardless of the recipient's social status suggests that a subordinate may receive inordinate attention when it dons an attractive odor. Moreover, although the wearer received the most attention, carrion increased mutual investigation, suggesting that rolling in certain odors may promote reciprocal interest between two hyenas. Enhanced social interaction in the presence of carrion was additionally reflected in increased frequencies of anal bulging, groaning, and yawning, and in a decrease in restful behavior.

Rolling in desirable odors, therefore, may serve the proximate goal of increasing attractiveness and social attention, especially for subordinates. If so, field studies might test the prediction that rolling should be observed most frequently by hyenas that are most likely to benefit from enhanced investigation (e.g., juveniles, subordinates, and immigrant males). As olfactory cues and social sniffing are frequently used to unify the clan or to rally hyenas into group activity (Drea & Frank, in press; East et al., 1993; Holekamp et al., 2000; Kruuk, 1972), rolling may ultimately promote social cohesion. Rolling in undesirable odors, on the other hand, may be socially neutral or even costly. For instance, companions separated for even brief periods will engage in a greeting ritual on reunion (Krusko et al., 1988), and although our results replicated these findings, the greeting ceremonies in our study were curtailed by camphor. If greeting strengthens or reaffirms social bonds (Kruuk, 1972), then interference with this ceremony might be considered a penalty.

A caveat to these interpretations is that our procedure mimicked the odoriferous consequences of rolling without necessarily affecting the behavior of the odor wearer. Hyenas clearly noticed the odors on their bodies, investigating the syringe prior to application and turning to smell their backs after application, but they may not have behaved like hyenas that roll voluntarily. It is our impression, however, that behavior toward their companion was, if anything, subtler than that of a hyena that actually rolls in an odor. In later presentations of commercial scent lures (obtained through the M & M Fur Co., Bridgewater, SD), hyenas that voluntarily engaged in rolling subsequently sought out companions, rubbed against them, caused a frenzy of investigation, and ultimately enjoyed lavish social attention (Simpson, Frank, & Drea, 1999). The effects we report under the present experimental conditions were similar, if somewhat muted. Thus, our procedure may not

have replicated the motivation of rolling, but the social consequences were consistent.

General Discussion

By describing responsiveness to various novel and rare odors, Experiment 1 showed that spotted hyenas use chemosensory cues to assess their surroundings. As some of their responses involved the deposition of scent, spotted hyenas also use odor cues to modify their environment. Moreover, Experiment 2 showed that spotted hyenas influence social interaction with conspecifics through the use of olfactory stimuli present in their environment. In particular, rolling appears to be a means by which spotted hyenas promote affiliative social interaction and potentially maintain group cohesion. By demonstrating individual scent discrimination, our companion article (Drea et al., 2002) addresses the importance of olfaction in intraspecific communication, both for claiming ownership and for advertising reproductive status. Together, these studies highlight the significance of olfaction as a means of communication in the spotted hyena.

Two additional observations in our studies merit mention. First, the sex difference reported in Experiment 2, in which males scent marked more than females, is consistent with some field reports (Mills & Gorman, 1987) but not with others (Henschel & Skinner, 1991). Experiment 1 also failed to find a sex difference in scent marking. This variability suggests that scent marking may serve different functions and that its elicitation may be context dependent (Drea et al., 2002). Second, during several of the greeting ceremonies in Experiment 2, we noticed hyenas rubbing their cheeks against the extruded anal pouch of their companion, suggesting that they were attempting to anoint themselves with the scent of their pen mate. Such observations echo the findings of other captive studies (Drea et al., 2002; Rieger, 1979) in which hyenas rolled in the paste of conspecifics, a behavior rarely described in nature (e.g., see Goodall & van Lawick, 1970). Nevertheless, other mammals (Gosling, 1982, 1990), including many carnivore species (Frame, Malcolm, Frame, & van Lawick, 1979; Rieger, 1979; Roeder, 1983), commonly anoint themselves with the substance used for scent marking by their conspecifics. The consequences of wearing conspecific odor might therefore prove to be a profitable area for future investigation.

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