Pasting behaviour suggests cryptic sociality in the striped hyaena, *Hyaena hyaena*

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ABSTRACT

Social evolution in the order Carnivora may be investigated through comparative studies of behaviourally diverse extant carnivores. The family Hyaenidae serves as a useful model in such interspecies comparisons, as its member species display various degrees of sociality. However, the behaviour of one of the hyaenids, the striped hyaena, *Hyaena hyaena,* is poorly understood. Further research into its social ecology will enhance the utility of the family Hyaenidae in elucidating the origins of sociality in carnivores. This research is also critical in conserving this rare and globally declining species. To better understand social behaviour in striped hyaenas, we examined chemical signaling in a population of striped hyaenas in southern Kenya. Although often overlooked in behavioural studies, chemical communication plays a central role in the sensory world of many carnivores, including hyaenids. We tested three non-mutually exclusive hypotheses about the function of "pasting," a scent-marking behaviour unique to hyaenids, in striped hyaenas. We found that pasting did not function to control food or den resources. We found no evidence that females pasted to demarcate territories. Females pasted at higher rates where their home ranges overlapped with multiple conspecific home ranges; that is, females

deposited paste where it was most likely to be detected by multiple conspecifics, suggesting that pasting plays a role in self advertisement. We have yet to find evidence of territoriality among females in this population, leading us to believe that this population may exhibit emergent social tolerance, highlighting its potential utility in studies of social evolution in the order Carnivora.

INTRODUCTION

The ecological conditions that gave rise to the evolution of sociality in members of the primitively solitary order Carnivora can be investigated through studies of social ecology in extant species. Social groups may form when the benefits of group living outweigh the costs, or when the costs are negligible. The resource dispersion hypothesis proposes that the cost of group living in carnivores decreases with increasing abundance, renewal rate, and spatial and temporal heterogeneity of resources (Waser, 1981; Macdonald, 1983; Johnson, Macdonald, Newman, & Morecroft, 2001; Johnson, Kays, Blackwell, & Macdonald, 2002; Wagner, Frank, & Creel, 2008). Should the costs be low enough, social groups may be formed and maintained even in the absence of direct benefits (Macdonald, 1983; Johnson et al., 2001; Johnson et al., 2002). When social tolerance permits the formation of social groups, benefits of group living, such as cooperation, may arise secondarily (Macdonald, 1983). However, investigation of these benefits in species that are currently gregarious may fail to reveal the origins of sociality in carnivores (Wagner et al., 2008). Instead, the selective pressures that drove the evolution of sociality in carnivores may be most effectively elucidated through studies of closely related species with diverse social behaviour, particularly of those exhibiting low or intermediate levels of sociality (Waser & Jones, 1983; Johnson et al., 2001; Johnson et al., 2002; Wagner et al., 2008).

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To date, studies of sociality in mammalian carnivores have focused largely on gregarious species, despite the fact that these comprise a very small proportion of extant carnivores (Smith, Lacey, & Hayes, in press). Less gregarious species, on the other hand, have been relatively understudied (Clark, Brown, Stechert, & Greene, 2012). Enhanced understanding of sociality in less gregarious species, especially if considered in comparative contexts, could shed considerable new light on social evolution in carnivores. Here we focus on the striped hyaena (*Hyaena hyaena*), a species in which social behaviour is very poorly understood.

The family Hyaenidae is characterized by the diverse diets and social behaviour of its four member species, making it an excellent model for studying ecological factors underlying the formation of social groups (Mills, 1989; Watts & Holekamp, 2007). The relationship between resource dispersion and social organization is exemplified by three of the four extant hyaenids: spotted hyaenas (*Crocuta crocuta*), aardwolves (*Proteles cristata*), and brown hyaenas (*Parahyaena brunnea*). The best-known hyaenid, the spotted hyaena, shows the most complex social structure of any terrestrial carnivore with hierarchically organized clans of up to 130 cooperating individuals (Holekamp, Dantzer, Stricker, Yoshida, & Benson-Amram, 2015). In the second hyaenid species, the aardwolf, social groups contain a single mated pair in which both members forages solitarily (Watts & Holekamp, 2007). The third hyaenid species, the brown hyaena, also scavenges solitarily but maintains small clans containing up to 11 individuals, and thus may be considered socially intermediate (Owens & Owens, 1979a).

The social ecology of the fourth and final member of Hyaenidae, the striped hyaena, remains very poorly understood (Wagner, 2006; Watts & Holekamp, 2007). Very few behavioural studies have been conducted on this species, perhaps because of its secretive and almost exclusively nocturnal behaviour, its low density, and the rugged terrain in which it often

lives (Kruuk, 1976; Wagner, 2006). Striped hyaenas have historically been described as strictly

solitary (Kruuk, 1976; Gorman & Mills, 1984), but recent studies in Kenya suggest that this may

not be correct (Wagner, 2006; Califf, Green, Wagner, & Holekamp, in review). Although striped

hyaenas forage solitarily, Wagner (2006) observed groups of up to four individuals resting

together in a population in Laikipia, Kenya. A fuller understanding of the behavioural ecology of

the striped hyaena may enhance the utility of the family Hyaenidae as a model for studies of

social evolution in carnivores. Furthermore, this information will likely have important

implications for the conservation of this near threatened and globally declining carnivore

(AbiSaid & Dloniak, 2015). Here we test predictions of hypotheses suggested as functions of

scent-marking behaviour in striped hyaenas.

Cryptic sociality may be revealed in many species formerly considered to be solitary by

examining chemical signals in addition to the more commonly investigated visual and acoustic

signals (Clark et al., 2012); this is particularly important in rare or secretive species (Campbell-

Palmer & Rosell, 2011). Although frequently overlooked in studies of animal behaviour

(Campbell-Palmer & Rosell, 2011; Clark et al., 2012), chemical communication plays a central

role in the sensory world of many carnivores, including hyaenids (Gorman & Trowbridge, 1989;

Hofer, East, Sämmang, & Dehnhard, 2001; Watts & Holekamp, 2007). All hyaenids perform a

specific scent-marking behaviour known as "pasting," in which an individual deposits a viscous

sebaceous glandular secretion, also known as "paste," onto an object, typically a stalk of grass, in

the animal's environment (Figure 1; Hofer et al., 2001; Woodmansee, Zabel, Glickman, Frank,

& Keppel, 1991; Mills & Gorman, 1987). Pasting on stalks of grass presumably increases the

likelihood of paste being detected by conspecifics (Gorman & Mills, 1984). These long-term

signals remain detectable for over a month in brown hyaenas (Mills, Gorman, & Mills, 1980) and for up to six months in aardwolves (Apps, Viljoen, Richardson, & Pretorius, 1989).

The function of pasting may vary among and within species (Theis, Heckla, Verge, & Holekamp, 2008; Johnson, 1973; Mills & Gorman, 1987). It is presumed to be involved in territorial defense in all hyaenids, though the spatial distribution of pasting behaviour within territories of hyaenas varies depending upon the size of the territory in relation to the size of the social group (Gorman & Mills, 1984; Mills & Gorman, 1987). Within a species, the function of pasting may vary both among populations (depending upon local ecological conditions) and within populations (depending upon age, sex, and social rank) (Theis et al., 2008; Johnson, 1973; Mills & Gorman, 1987; Woodmansee et al., 1991).

Here we examined the pasting behaviour of members of a small population of striped hyaenas near Shompole, Kenya, and inquired what role it might play in the social lives of these animals. Food resources near Shompole are relatively abundant, albeit patchy (Waser & Jones, 1983). A recent study by Califf et al. (in review) showed that females in this population have overlapping home ranges, suggesting social tolerance among females. In Laikipia, Kenya, on the other hand, food resources are significantly scarcer than they are near Shompole, and this ecological difference appears to drive differences in sociality. That is, compared to Shompole females, Laikipia females disperse farther, maintain more spatially separated home ranges, and exhibit reduced home range overlap with other females, suggesting territorial behavior among females (Wagner, 2006). Califf et al. (in review) proposed that relaxed resource competition in the Shompole population may have allowed for social tolerance to develop among females. This population may serve as a good model for studying the origins of social grouping in mammalian carnivores. Here we used data on pasting behaviour collected during focal follows of known

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individuals to test several non-mutually exclusive hypotheses regarding the function of pasting in this population, and inquired whether the Shompole population exhibits social tolerance. Hypotheses suggesting functions of pasting behaviour in striped hyaenas are shown below.

1. *Food or den resource control.* To investigate the role of pasting in maintaining control over food and den-site resources, we compared pasting rates among multiple behavioural contexts. If pasting functions to signal resource ownership, then the pasting rate while feeding or attending an active den (i.e. immediately exploiting a resource) should be higher than the pasting rate when hyaenas are travelling or resting. Alternatively, if pasting does not function to signal resource ownership, then the pasting rate while exploiting a resource should be lower than or equal to the pasting rate while travelling or resting.

2. *Self advertisement.* Self advertisement among conspecifics may be an important function of pasting among striped hyaenas. If pasting functions to advertise individual presence to conspecifics, then paste should be deposited where they are most likely to be detected, i.e. at home range junctions; that is, pasting rate should be positively correlated with the number of overlapping conspecific home ranges. Alternatively, if pasting does not function to advertise presence to conspecifics, then we would not expect to find a positive correlation between pasting rate and the extent of home range overlap among individuals.

3. *Territory demarcation.* If striped hyaenas paste to demarcate territories, then pasting events should be distributed with differential density between border and interior areas of the home range (Mills & Gorman, 1987). A recent study (Califf et al., in review) found that home ranges in the Shompole population show considerable overlap, suggesting that they may not be true territories, complete with advertisement and defense. Therefore, we expected social tolerance to be reflected in the spatial distribution of pasting events. If striped hyaenas do not

demarcate territories with paste, pasting density will not differ significantly between home range borders and interiors (interior henceforth referred to as "hinterland;" see Gorman & Mills, 1984; Mills & Gorman, 1987; Mills, 1989).

4. *Mate attraction.* Mate attraction represents a fourth possible function of pasting. This function may prove particularly interesting in this species, which may be polyandrous (Wagner, Creel, Frank, & Kalinowski, 2007a). This function of scent marking is often tested by comparing male and female scent marking rates over the course of an annual reproductive cycle (Kruuk, 1992; Lewis, 2006). However, reproduction in striped hyaenas in Kenya is not seasonal (Wagner, Frank, Creel, & Coscia, 2007b). Moreover, we were unable to compare male and female pasting rates here due to limited observations of male striped hyaenas at Shompole. Therefore, this hypothesis was not tested in this study, but may merit further research in the future.

MATERIALS AND METHODS

Field methods

Study area and subjects. We collected data for twenty-four consecutive months (February 2007-February 2009) from a population of 41 striped hyaenas on the Olkiramatian and Shompole Maasai Group Ranches, located in the southern Rift Valley of Kenya (Figure 2). The 41 individuals were identified based on their unique stripe pattern in photographs taken by a large grid of trail cameras (described in Schuette et al. 2103). The study area, of roughly 320 square km, abuts a conservation area, the Shompole Conservancy, on its southwest border, but the study area is seasonally home to Maasai pastoralists and their livestock. This entire area supports largely intact native herbivore and carnivore communities; a moderate to high density of

livestock (sheep, goats, and cattle); and a low density of semi-nomadic pastoralists (Schuette, 2012). This arid region has average low and high temperatures of 24.2 and 37.7° C, respectively, and an average annual rainfall of 317.5mm. The study area is flat, but bounded by escarpments, lava ridges, and valleys. The sandy terrain is covered by acacia woodlands and grasslands, alkaline grassland flats, riverine forests, swamps, and salt pans (Califf et al., in review).

Of the 41 striped hyaenas in the Shompole population, we captured 20 hyaenas in soft-catch foot-hold traps and anesthetized them by injecting a sedative (either 6.5 mg Telazol/kg body weight or a combination of 3.6 mg Ketamine HCl/kg body weight and 0.06 mg Medetomidine HCl/kg body weight) in a plastic dart delivered via a CO_2-powered rifle. Once anesthetized, we determined the sex of the striped hyaena and collected blood and tissue samples for genetic analysis. Of the 20 captured hyaenas, twelve adults were fitted with radio collars. Nine of these individuals (six females and three males) were fitted with VHF radio collars (Telonics, Inc., Mesa, AZ, U.S.A.; or SirTrack Ltd., Havelock North, NZ), which we used to locate them for behavioural sampling. The other three striped hyaenas (one female and two males) were fitted with global positioning system (GPS) collars (Savannah Tracking Ltd, Nairobi, Kenya). Geographic fixes were downloaded automatically from GPS collars every 20 minutes. Geographic fixes were collected for 26 days from the female and for 21 and 169 days for the two males, respectively. All sampling procedures were approved by the Institutional Animal Care and Use Committee at Michigan State University (AUF 07/08-099-00) and met guidelines approved by the American Society of Mammalogists (Sikes & Gannon, 2011).

Behaviour sampling. In addition to data collected via trail cameras and telemetry, we also obtained behavioural data from focal animal follows. We conducted 665 hours of focal follows across 16 subjects (f=7, m=8, u=1). To collect data during the nocturnal period of peak activity,

we conducted follows between 1830 and 0630 hours. We located individuals using their VHF radio collars and followed them for as long as the terrain or other conditions allowed. Subjects were followed at minimum distances of 100 meters for spotlight-habituated hyaenas and 200 meters for non-habituated hyaenas. During each follow, we recorded the subject's geographic coordinates every 10 minutes. We also recorded the behavioural context and all occurrences of critical incidents for the focal animal, including pasting. Observations were classified into three behavioural contexts: when *feeding,* the focal individual was in the presence of a food item; when *socializing*, the focal individual was with a another striped hyaena or at an active den; and when neither feeding nor socializing occurred, the behavioural context was classified as *"other,"* which usually involved travelling or resting away from a den. We also recorded whenever the focal individual was near a carnivore of another species, although this was rare during follows.

Spatial and statistical analyses of pasting behaviour

Testing the resource control hypothesis. We compared pasting rates among our three behavioural contexts: *socializing, feeding* and *other*. For each subject, we extracted the total number of pasting events observed and the total number of hours that individual was observed in each context. The shortest focal follow within which the subject pasted at least once was 0.51 hours. Therefore, we omitted entries for which a subject was observed for less than 0.50 hours, leaving 663 hours of follow data. Each subject observed within a context is represented by a single data point. The size of the dataset was not sufficient to allow for differentiation between males and females in this analysis.

To compare pasting rates among contexts, we used a generalized linear mixed model. We used a Poisson distribution to account for the small sample size and non-normal distribution of data. We used pasting event count as the dependent variable and included an offset for the time

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the subject was observed in the given context. Many subjects were observed in multiple contexts, violating the assumption of independence between samples; to correct for this violation, we included subject ID as a random effect in our model. This dataset also included excessive zeroes; that is, many subjects were observed in contexts in which they did not paste during follows, often due to very brief observations in a particular context during follows. We incorporated zero inflation to account for this but recognize that zero inflation may not be sufficient to adequately account for the excessive zeroes. Because multiple comparisons were made, we used the Bonferroni correction to derive a conservative alpha value of 0.0167 (=0.05/3 where three behavioural contexts were tested).

Testing the self advertisement hypothesis. Here we inquired whether pasting rates varied with the number of overlapping home ranges at a given location. We calculated a home range estimate for each individual for whom a minimum of 20 telemetry locations were recorded from radio collars. Out of the twelve hyaenas fitted with radio collars, ten (f=7, m=3) hyaenas met this requirement. These ten hyaenas remained in the population for the entire duration of the study. We then restricted our sample to hyaenas that were observed pasting 20 or more times during focal follows, leaving six females and one male. We omitted the single male, M103, limiting our spatial analyses to females only (f=6): F101, F102, F104, F105, F108, and F110.

To calculate each female's home range (f=6), we constructed a minimum convex polygon (MCP) enclosing all telemetry locations for that individual. We created MCPs using the "mcp" function in the adehabitatHR package in R. For these females, we represented each pasting event as a point location in ArcMap. We overlaid individual females' pasting locations on their home range polygons.

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We overlaid a fishnet with 500 by 500 meter cells on a map showing the pasting events and home range polygons (Figure 3). We tabulated the intersection between the fishnet and the merged home ranges to produce a table revealing which home ranges intersected each fishnet cell. We then tabulated the intersection between the fishnet and the pasting layer to produce a table revealing how many times each individual pasted within each fishnet cell. Finally, we created a relational join between the two output tables based on the fishnet cell ID number.

For each striped hyaena whose pasting events were included in this analysis, we extracted the following data for each fishnet cell intersecting its home range: the proportion of its home range area contained within the cell; the number of conspecific home ranges that intersected the cell, treating male and female home ranges equally; and the number of pasting events observed for that individual within the cell during focal follows.

We tested pasting rate as a function of conspecific home range overlap using a generalized linear mixed model. In this test, each datum represents a separate fishnet cell. If a cell intersected the home ranges of multiple subjects for whom pasting data were considered, multiple data points were drawn from it (one for each hyaena). To account for our small sample size and non-normal distribution of data, we used a negative binomial distribution, which we determined to be significantly more accurate than a Poisson distribution using a log-likelihood test. We used the pasting count as the dependent variable and included an offset for the total time for which the hyaena was observed during follows. We also included an offset for the proportion of the subject's home range contained within the fishnet cell. A separate datum was entered for each fishnet cell intersecting each subject's home range, yielding multiple data for each subject. To account for this violation of independence between samples, we included subject ID as a

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random effect. Zero-inflation was incorporated to account for frequent zero values. For this analysis, we used an alpha value of 0.05.

Testing the territory demarcation hypothesis. We tested the role of territory demarcation in female pasting using the same subjects (f=6) and methods for estimating home ranges that were described above in *testing the self advertisement hypothesis*. To test the predictions of the *territory demarcation hypothesis,* we compared female pasting density (pastings/km^2) between home range borders and hinterlands. For each subject, we constructed a 200 meter buffer around her home range boundary in ArcMap, and considered this to be the border of the territory. We extracted the pasting density within the buffer zone (border) and within the interior (hinterland) of the home range for each striped hyaena. To account for non-normality due to small sample size and for repeated measures, we compared these densities using a Wilcoxon rank sum test and an alpha value of 0.05. This analysis was then repeated with a 500 meter buffer. We performed spatial analyses using ArcMap version 10.1 with a Transverse Mercator projection (UTM zone 37S WGS 1984; WKID 32737, authority EPSG). We conducted all statistical analyses using R.

Mate attraction hypothesis. Due to excessive zero values, we had insufficient data to test for a sex difference in pasting rate. Instead, here we used descriptive statistics to represent female and male pasting rates in each of the three context categories. We calculated each pasting rate by dividing the sum of pasting events observed (across subjects) for the focal sex by the total number of hours observed during follows in that context for all subjects of the focal sex.

RESULTS

Spatial and statistical analyses of pasting behaviour

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Testing the resource control hypothesis. After omitting entries of less than 0.50 hours, 663 hours of focal follow data remained. No observations occurred in multiple behavioural contexts simultaneously. The rate of pasting differed significantly among the three contexts when compared using the sequential Bonferroni procedure ($\alpha = 0.0167$). Striped hyaenas pasted at a rate of 9.15 pasting events per hour while travelling or resting (*"other"*), which was significantly higher than the pasting rate while *feeding* (1.86 pasting events per hour; $p<0.001$) or *socializing* (0.60 pasting events per hour; $p<0.001$). The pasting rate while *feeding* was significantly higher than the pasting rate while *socializing* ($p=0.016$; Figure 4). These findings contradicted predictions of the *resource control hypothesis*, and suggested that striped hyaenas in this population did not paste to control food or den resources.

Socializing occurred both at and away from active dens. As many as three striped hyaenas, including three adults, were seen together during follows in encounters away from dens. In these encounters away from dens, the hyaenas were often travelling together. One female occasionally stopped to wait for another female striped hyaena, who followed her. Kin (e.g. mother and cubs) sometimes interrupted travelling to nurse, play, or allogroom. Adults sometimes took turns feeding from a carcass. Two antagonistic interactions were observed: once, an adult female chased an unrelated female, expelling her from the area; another time, a different adult female chased an unknown cub out of the immediate area.

Social encounters at dens consisted of as many as five striped hyaenas being present concurrently: the adult mother-daughter pair (F105 and F104, respectively) and their two litters of cubs. During one encounter, four adults rested together at a den site. These individuals were kin (F101 and M103 were the mother and father, respectively, of F108 and M109). Cubs from

two litters (mother F110) were observed concurrently at a single den, raising questions regarding the possibility of overlapping litters.

Not enough data were collected in the presence of other carnivore species to perform a statistical analysis; only two females were observed in the presence of another carnivore species for a total of at least thirty minutes during focal follows. Each was observed for a similar total period of time in the presence of another carnivore species both with and without food (1.17 hours and 0.88 hours, respectively, for female F104; 0.65 hours and 0.55 hours, respectively, for female F105). Each female pasted once when both food and another carnivore species were present (0.85 and 1.54 pastings per hour for F104 and F105, respectively) and zero times when another carnivore species was present but food was absent.

Testing the self advertisement hypothesis. Out of the twelve hyaenas fitted with radio collars, the minimum requirement of 20 telemetry locations was met by ten (f=7, m=3) hyaenas. These ten hyaenas remained in the population for the entire duration of the study. Of these ten hyaenas, only six female and one male striped hyaena were observed pasting twenty or more times during focal follows. Because only one male met this criterion, we eliminated him from our analysis and used the six females to investigate spatial correlates of pasting.

The strongest spatial correlate of female pasting proved to be home range overlap with conspecifics. For the six females included in this analysis, the number of overlapping conspecific home ranges varied from zero to six. The six females collectively appear to have deposited paste at higher densities at locations of high than low home range overlap (Figure 3), but this could occur even if individual females pasted randomly throughout their home ranges. Therefore, we tested whether individual females pasting rates were correlated with the number of overlapping conspecific home ranges at any given location.

The results of the generalized linear mixed model revealed that individual females pasted with exponentially increasing frequency based on the number of conspecific (both male and female) home ranges intersecting the females' home ranges at any given point (p<2e-16; Figure 5). Despite considerable variation across subjects (Figure 6), this supports the *self advertisement hypothesis*, suggesting that female striped hyaenas in this population pasted to advertise their presence to other striped hyaenas.

Testing the territory demarcation hypothesis. Territory demarcation by pasting was not evident among female striped hyaenas in the Shompole population. The pasting density of females in this population did not differ between home range borders and interiors. Analyses using a 200-meter buffer (Figure 7) and a 500-meter buffer both yielded non-significant results (W=16, p=0.818). These results are inconsistent with the predictions of the *territory demarcation hypothesis*.

Mate attraction hypothesis. The dataset did not allow for statistical analysis of sex differences in pasting rate. In each of the three contexts observed, a higher overall pasting rate was observed among male than female subjects (Figure 8). Note that the estimated pasting rate is lower than predicted in the previous analysis because no measures were used here to account for frequent zero values.

Spatial distribution of one male's pastings. The two minimum requirements for inclusion in spatial analysis, 20 telemetry locations and 20 pasting events observed during focal follows, were met by only one male striped hyaena, M103 (Figure 11). M103's home range overlapped with the home ranges of six of the seven known female home ranges and also with one of the two known male home ranges in our study area. It does not appear as though he pasted primarily near the border of his home range.

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Synthesis of spatial correlates of pasting. To visualize both spatial correlates of pasting (home range overlap and proximity to home range boundary), we view each female's pasting events in relation to her own home range as well as the home ranges of the other nine striped hyaenas (f=6, m=3) for which 20 or more telemetry locations were recorded (Figure 6). Viewing all female pasting events and known home range boundaries for this population (Figure 6), we found that females appear to skew their pasting behaviour towards regions of high home range overlap, regardless of proximity to their own home range boundaries; this is consistent with our statistical findings above.

Two small areas were marked by particularly high pasting density. Female F105 appeared to paste at the highest density in two locations (Figure 6). The westernmost, of these two areas was at the junction of five known female home ranges and two known male home ranges. The second, easternmost, area was at the junction of three known female home ranges, and was also contained with a male home range. The other five female subjects also appear to have engaged in a high density of pasting events at one or both of these home range junctions. Therefore, we explored the characteristics that distinguish these locations from others and thus may stimulate pasting behaviour.

These two areas were not only where multiple home ranges overlapped, but more specifically they occurred within at least one male home range. Because mate attraction might be a function of pasting, this merits closer investigation. The easternmost area encompassed the only location known to represent the intersection of two male home ranges; perhaps this explains the high female pasting density here. Furthermore, Female F108 was observed pasting intermittently while outside of her home range, but stopped and pasted many times upon encountering the boundary of a male home range (Figure 6). The easternmost location was also

contained within one known male home range, but this was insufficient to propose why females pasted primarily here rather than in the surrounding area, which was also contained within that male's home range. Therefore, we more closely inspected the easternmost location of high female pasting density.

The easternmost location was characterized by high home range overlap. This represents the junction of four home ranges (three female and one male). Interestingly, the intersection of these home ranges continued westward, yet pasting events only occurred on the eastern side of this intersection. This prompted us to wonder what other factors might be unique about this location, leading us to investigate the local land cover.

The easternmost area of particularly high pasting density was characterized primarily by grass and secondarily by wetlands; it was bordered by thick forest and bush on all but the northern side (Figure 9, Figure 10). It appears as though females pasted in the open area but not within the dense vegetation along its perimeter (Figure 6, Figure 9). This home range intersection was covered in forest and bush to the west, which might explain why the area of high pasting density was confined to the eastern side. This pattern may be interpreted in several ways. Perhaps this area was easier to traverse for signal senders (pasters) as well as receivers. Wind dispersal of scent may also be stronger in the open area. Otherwise, perhaps it is the presence of stalks of grass – the typical target of pasting hyaenids – in the open area that stimulated pasting. Whatever the cause, it appears as though home range overlap and land cover influence the spatial distribution of pasting in the Shompole female striped hyaenas.

DISCUSSION

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Our results suggest that pasting behaviour among Shompole striped hyaenas does not function to control food or den resources; advertisement of resource ownership failed to explain the observed rates of pasting among behavioural contexts. Striped hyaenas in the Shompole population pasted most frequently while travelling, at a rate of almost five times the rate of pasting while feeding or socializing. That is, striped hyaenas pasted at the lowest rates when in the presence of two key resources, food and den-sites. This suggests that pasting did not function to claim or announce control over these resources. Striped hyaenas may be most likely to transmit and receive signals to and from conspecifics successfully while they are travelling.

Consistent with these findings, rates of pasting by females increased exponentially with the number of conspecifics sharing overlapping home ranges at a given location, lending support to the *self advertisement hypothesis*. That is, female striped hyaenas placed their chemical signals where they were most likely to be detected by multiple conspecifics. Stimulation of pasting behaviour by signals from conspecifics has been documents in other hyaenid species; other hyaenids are known to paste upon discovering a conspecific's scent-mark, often directly on top of it (Kruuk 1972; Mills et al., 1980). We have yet to test the *self advertisement hypothesis* in male striped hyaenas or to distinguish the effects of home range overlap with same-sex versus opposite-sex conspecifics.

Self advertisement via pasting might be favoured for its role in signaling group membership or attracting mates. A close relative of striped hyaenas, the spotted hyaena, pastes at a high rate at communal dens, the clan's "social centre" (Hofer & East, 1993), where paste may signal clan membership, and perhaps prevent aggression due to mistaken identity. If this is correct, one would expect clan members to permit inspection of the anogenital region upon encountering one another, allowing for an individual to be matched with its scent (Hofer, 2001).

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Anogenital inspection behaviour has been documented in spotted hyaenas (East, Hofer, & Wickler, 1993; Smith, Powning, Dawes, Estrada, Hopper, Piotrowski, & Holekamp, 2011) as well as wild (Kruuk, 1976) and captive striped hyaenas (Fox, 1971). During focal animal follows of striped hyaenas, we observed at least seven different pairs of individuals that sniffed one another during social encounters. Sniffing behaviour was sometimes mutual and on at least one occasion, the individual being sniffed presented its anogenital region.

Our results were inconsistent with the *territory demarcation hypothesis*: we found no significant difference in female pasting density between home range borders and hinterlands. When pasting to demarcate territory, other hyaenid species deposit paste primarily in either the border areas or hinterlands of their home ranges, depending upon the length of the border in relation to the size of the social group (Mills, 1989). Border pasting provides the earliest sign of occupancy to intruders, but is only feasible when group size is sufficiently large to maintain border defense. When group size is small relative to the size of the territory, hyaenids primarily paste in the hinterland (Mills & Gorman, 1987). Because here we found no significant difference between border and hinterland pasting density in females, the *territory demarcation hypothesis* was not supported. However, our sample was small and we found considerable variability across subjects. Nonetheless, this finding is consistent with our prior knowledge for this population, that is, that home ranges exhibit considerable overlap and are therefore not exclusive or defended territories (Califf et al., in review).

Mate attraction could be considered a form of self advertisement. We could not address the *mate attraction hypothesis* in this study because we collected too few space use data from males. When comparing pasting rates across all subjects, the few males we observed collectively pasted more often than females in each of our three behavioural contexts. We could not

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investigate seasonal variation in pasting because breeding in striped hyaenas in Kenya in nonseasonal (Wagner et al., 2007b).

By addressing these non-mutually exclusive hypotheses about the function of pasting, we concluded that female striped hyaenas in the Shompole population paste to advertise their presence, which may help maintain social relationships or attract mates. We did not find evidence for a role of pasting in resource control or territory demarcation. In conjunction with the earlier findings of Califf et al. (in review), these results suggest that females do not defend true territories and are most likely to paste when and where these signals are most likely to be received conspecifics: when travelling and at home range junctions.

Due to limited observations of male striped hyaenas, we did not consider males when testing predictions of the above hypothesized spatial correlates of pasting rate: self advertisement and territory demarcation. We examined the spatial distribution of pasting events for the single male hyaena who met our requirements for the minimum number of telemetry locations and pasting events. This male did not appear to paste primarily in the border area of his home range. However, we cannot draw inferences from this one hyaena; an accurate understanding of the functions of male pasting in the Shompole can only be derived from a study of more male striped hyaenas.

In summary, pasting in this population apparently functions to advertise an individual's presence to conspecifics. We have yet to find evidence of territoriality in the Shompole population of striped hyaenas; this population may exhibit emergent social tolerance, making it an invaluable model population on which to study conditions that permit or promote the evolution of group living in a primitively solitary carnivore species.

This study is one of few behavioural studies ever conducted on striped hyaenas in Africa, and is the first to investigate *in situ* chemical communication in this species. Although their implications in conservation are often overlooked, studies of chemical communication hold great potential for informing conservation management, particularly in increasing the success of reintroductions and translocations (Campbell-Palmer & Rosell, 2011). We hope that this study will illustrate the importance of examining all senses that are central in shaping the *umwelt* of the striped hyaena. Research into the ecology of this rare and declining carnivore is critical to its conservation. Furthermore, further research into the social ecology of the striped hyaena may fill the lacunae in our knowledge of the social spectrum of the Hyaenidae, allowing for elucidation of the origins of sociality.

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