Patterns of scat deposition by brown hyaenas (*Hyaena brunnea*) in a mountain savannah region of South Africa

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Abstract

The brown hyaena (*Hyaena brunnea*) is a near threatened large carnivore inhabiting sub Saharan Africa. Like many other species of terrestrial carnivores, brown hyaenas often and repeatedly deposit scats at specific latrine sites as a means of olfactory communication. However, previous studies on brown hyaena latrine use have been constrained to the arid Kalahari region in southern Africa, an area of low resource abundance. To improve our understanding of geographic variation in the biology of this species, we monitored patterns of brown hyaena scat deposition in the Waterberg of northern South Africa, an area of higher net productivity than previous areas for published brown hyaena studies. Defecation rates at latrine sites were low in our study area (median less than 1 defecation in 30 days), but brown hyaenas visited sites significantly more often than they defecated at them (median 2.6 visits per 30 days). The temporal patterns of activity at defecation sites were significantly related to the overall temporal activity patterns of brown hyaenas on the roads within the reserve, and generally confirmed a nocturnal activity pattern in this species. Our result on brown hyaena scat deposition in the Waterberg region indicates a geographic variation in latrine use, and we suggest that such a variation could be linked to resource driven variation in social and spatial organisation.

Introduction

Many species of terrestrial carnivores use latrines, i.e. sites where faeces or scent marks are deposited, as a method of olfactory communication (Kleiman 1966, Brown & Macdonald 1985, Gorman & Trowbridge 1989). Such latrine use is observed in carnivore species from contrasting phylogenetic backgrounds, geographic distributions, and ecology (e.g., aardwolf *Proteles cristatus* Nel & Bothma 2002, coyote *Canis latrans* Ralls and Smith 2004, European badger *Meles meles* Roper et al. 1993, kit fox *Vulpes macrotis* Ralls and Smith 2004, small spotted genets *Geneta genetta* Espiro-Santo et al. 2007, striped hyaena *Hyaena hyaena* Macdonald 1980, spotted hyaenas *Crocuta crocuta* Gorman & Mills 1984, swift fox *Vulpes velox* Darden et al. 2008 and suricate *Suricata suricatta* Jordan et al. 2007). Latrine use has primarily been related to territorial marking and broadcasting of social rank or reproductive status, but the frequency with which specific latrines are visited differs both within and between carnivore species (Gorman 1990). Variation in latrine visitation rates has, among other things, been attributed to habitat (Trusso et al. 1998; Delehay 2007), proximity to territorial boundaries (Roper et al. 1993) and the presence of non-resident individuals (Jordan et al. 2007).

Like all hyaena species, brown hyaenas (*Hyaena brunnea*) often use latrines when defecating (Mills et al. 1980, Gorman and Mills 1984). Previous studies have indicated that brown hyaena latrines regularly are placed at conspicuous landmarks (e.g., Gorman and Mills 1984), and together with paste markings aid in informing conspecifics about individual movements and territory occupancy (Mills 1982a). Our knowledge of patterns of brown hyaena latrine use is however limited to studies in arid environments in the Kalahari Desert (Mills 1990, Owen & Owen 1996) and Namibia (Skinner et al. 1995). These are areas of low productivity and as a consequence carnivores have large home ranges in these regions (Eaton 1976). Since scent marking and latrine use are intimately connected to a species' social organisation (Gorman and Trowbridge 1989), a broader understanding of geographic variation in patterns of brown hyaena scat deposition could improve our understanding of how the social organisation of brown hyaenas varies over regions of contrasting resource abundance and distribution. Such an increased understanding of how brown hyaena ecology scale with local resource abundance and distribution could aid in area specific management and conservation strategies for the species (Wiesel et al. 2008). The aim of this study was therefore to examine patterns of brown hyaena scat deposition in a mountainous savannah region of South Africa, a more productive region than considered in previous studies, to improve our understanding of geographic variation in the biology of this little known large carnivore.

Materials and methods

We conducted the study in the Lapalala Wilderness, Limpopo Province, South Africa. The Lapalala Wilderness is a privately owned, fenced 35000 ha game reserve that constitutes approximately 35% of the core area of the UNESCO Waterberg Biosphere Reserve. The area consists of low rugged mountains intersected by valleys containing mainly Waterberg mountain bushveld vegetation (Mucina et al. 2006). It lies within a summer rainfall region with average annual rainfall ranging from 400 – 600 mm. The climate is mild with mean minimum and maximum monthly temperatures of 20°C and 20°C in July and 14°C and 30°C in January. The reserve currently hosts healthy populations of a variety of large herbivores, as well as resident populations of three other medium sized to large carnivores, African civet (*Civettictis civietta*), black-backed jackal (*Canis mesomelas*), and leopard (*Panthera pardus*).

During September 2008, we conducted an initial survey of Lapalala which identified 331 brown hyaena defecation sites by driving the majority of the roads within the reserve (Fig. 1). All roads in the study area are gravel roads, many with limited human activity since the reserve is currently not open for the public. Identified sites were typically situated along roadsides and occurred regularly at prominent features such as junctions, crossroads, and rivers, and often under a tree or a large bush. We identified brown hyaena scats by their size in combination with conspicuous white or grey coloration. From the total number of sites where we found scats during the initial survey, we selected 87 sites that we visited weekly during an observation period from January-March 2009 to monitor defecation rates. These sites were selected based on the number of deposited scats (>2) and signs of activity (mainly conspicuous signs of paste markings). Our rationale for selecting a subset of sites was partly due to logistical constraints, and partly to eliminate sites that had only been used once for adhoc defecation and consequently would not be likely as potential latrine sites. Although opportunistically selected, these 87 sites were evenly spread across the reserve and did not constitute a spatially biased sample (Fig. 1). In addition to the weekly visits, we set automatic camera traps at 22 of the 87 sites for more intensive monitoring (Claridge et al. 2004). These 22 sites were randomly selected but stratified to cover a large proportion of the study area. The cameras were passive motion triggered (Moultrie I40, Moultrie feeders, Alabaster, AL, USA) and set with a 1 minute delay between subsequent pictures. Each camera was left at a specific defecation site for a minimum of 10 nights, giving a total number of 257 monitoring nights across all sites. We checked cameras daily to make sure they functioned correctly. We used characteristic stripe patterns on the front and hind legs to individually identify brown hyaenas captured by the cameras. However, not all photographed animals could be identified because of poor picture quality, or because the legs or the required side of the animal was not visible in the picture. In addition to the activity patterns at brown hyaena latrine sites, we obtained diel patterns of brown hyaena activity from a camera survey carried out between November and December 2008, i.e. 2-3 months prior to the monitoring of defecation sites. In this survey, 39 camera sites were monitored for 7 days. The sites were spaced evenly throughout the reserve. Each site had two oppositely placed digital cameras of the same model and settings as used for the latrine monitoring. We followed O'Brien et al. (2003) and regarded hyaena pictures at the same site as independent visits if they had been taken more than 30 minutes apart, unless we could identify the animals as different individuals. We have presented number of scats per site, defecation rates and visitation rates as median and minimum and maximum ranges due to the heavily skewed distributions.

Results

In the initial survey in which 331 defecation sites were located, the number of scats per defecation site ranged from 1 to 34, with a median of 2 scats per site (Fig. 2A). However, in the subset consisting of 87 monitored sites we only found scats deposited at 12 sites (14%) during the three month observation period, with a maximum of three scats deposited at a single site. The median defecation rate (scats / site / 30 days) for all 87 monitored sites was close to zero, but with a maximum defecation rate of 1.67 (Fig. 2B). For the 12 sites where we found scats deposited during the observation period, median defecation rate was 0.65 scats per 30 days with a range from 0.19 to 1.67. We recorded brown hyaena activity during 25 of the 257 camera nights at 8 of the 22 sites monitored by digital cameras. Visitation rates (visits / site / 30 days) at the 22 monitored sites were significantly higher than the defecation rates for the same period (median visitation rates: 2.62, range 0 – 30; median defecation rate: 0, range 0 to 1.11; Wilcoxon paired signed rank test; $V = 36.0$, $n = 22$, $P = 0.01$, Fig. 2C). At the 22 sites, we only found 1 scat deposited during the time of camera monitoring. We recorded 33 independent brown hyaena pictures from which we could identify 4 individuals. One animal was identified at two different defecation sites. These sites were 230 meters apart and the different visits occurred with a time lag of over two weeks. One site was visited by >1 individual. These visits occurred 64 hours apart. There was a gradual increase in hyaena activity at defecation sites from 18:00 until 21:00, with a substantial decline in activity until 01:00, when a distinct peak in activity occurred (Fig. 3). The temporal patterns of activity at defecation sites were significantly related to the overall temporal activity patterns of brown hyaenas within the reserve, as indicated from a larger camera trap survey (Pearson $R = 0.62$, $t_{15} = 3.10$, $P < 0.01$). No activity at defecation sites was observed between 05:40 and 17:35. In addition to brown hyaenas, we also recorded one visit by a small spotted genet (*Geneta genetta*), two visits by leopards (*Panthera pardus*), and one visit by two honey badgers (*Mellivora capensis*) at the monitored defecation sites.

Discussion

In Lapalala Wilderness, defecation rates at the monitored brown hyaena defecation sites were generally low, mostly with less than one deposited scat per site per month, and often with no deposited scats over a period of 3 months. We suggest two, not necessarily exclusive, explanations for our result. Firstly, low defecation rates suggest that brown hyaenas do not reuse the same sites regularly for defecation in this area, and only rarely defecate at previously used defecation sites. Therefore, it is questionable if the sites monitored in this study can be referred to as latrines in a strict sense (sensu Gorman & Throwbridge 1989; i.e. locations where large accumulations of faeces occur due to repeated defecation, sometimes almost exclusively at these specific locations). Instead, they may represent sites that hyaenas frequently visit for scent marking using other means (e.g., pasting; Mills et al. 1980), and they only defecate at these sites ad hoc. A second explanation for our results could be that we underestimated defecation rates in our study due to methodological error. This could have happened in two different ways. We could either simply not have detected all deposited scats, or scats had degraded within the time between visits (mainly one week). Several lines of evidence contradict both of these explanations. We searched a total of 87 sites, either weekly or daily over a period of 3 months. It is therefore unlikely that we have missed enough scats to have caused such a strong bias in our results. The initial number of scats at many of the identified defecation sites was also low, which further suggest that they had not been used regularly. Moreover, it is not likely that scats had degraded within one week (the interval between latrine visits) since all detected scats were white and calcium rich, and previous work on spotted hyaenas suggest that such scats are not attractive to dung beetles (Cambefort 1984, Krell et al. 2003) and can remain visible for 14 months (Bearder et al. 1978).

Our results thus contrast data from more arid areas in the Kalahari which has suggested a more strict use of latrines for defecation in brown hyaenas (Mills 1982a), similar to for instance high-density badger populations (Delahay et al. 2007). In Southern Kalahari, up to 50 scats was found on a single site, and one site was recorded active for nearly a decade (Gorman and Mills 1984). Similar to our study, however, many sites were found at conspicuous land marks, and hyaena scent markings were observed in addition to defecations at latrines. Owen and Owen (1996) suggested a resource driven variation in social organisation of brown hyaenas between southern and central Kalahari. Although we do not have data on either social organisation or spatial patterns from our study area, we suggest that the observed geographic variation in scat deposition could be linked to such a resource driven variation in social organisation or density (e.g., Dalerum et al. 2006), which may relate to modes of olfactory communication (Kruuk 1978, Mills 1982b, Sillero-Zubiri & Macdonald 1998). We predict that our study area has higher densities and smaller brown hyaena home ranges compared to the Kalahari, caused by a higher net productivity and the presence of fences which prevents ungulate prey from large scale seasonal migrations. Thorn et al. (2009) for instance, estimated brown hyaena density in the Pilanesberg National park, an area more similar to Lapalala than the Kalahari, as 2.8 individuals per $100km^2$. This is almost three times as high as what has been estimated for the Kalahari (~1.1 individuals / $100km^2$, Mills and Hofer 1998). Interestingly, the limited use of latrines in our study compared to the Kalahari therefore seem contradict with what have been found in the Eurasian badger, where latrine use has been found to increase with increasing densities (Hutchins et al. 2002). Without specific knowledge of contrasts in sociality and density of brown hyaenas between areas of varying resource abundance it is difficult to hypothesize the cause for this difference. However, our results suggest that there is a need to explore the social organisation of brown hyaenas outside the arid Kalahari region to better understand how this species adapt ecologically and behaviourally to the local distribution of resources.

The monitored latrine sites were visited by brown hyaenas substantially more often than they were used for defecation. This supports our suggestion that the sites may not have been latrines in the strict sense but instead sites frequently visited for deposition of paste markings. Moreover, we found high variation in both defecation and visitation rates between individual sites. Such variation has been recorded in other species such as Eurasian badgers, where site specific scent marking rates has been related to proximity to territorial boundaries (Delahay et al. 2007). We also found that more than one hyaena visited a single site. This finding is consistent with data from aardwolves (Nel et al. 2002), and agrees with the suggested social structure of brown hyaenas, in which several members of a clan forage solitarily but share and possibly defend a common territory (Mills 1982b, Owens & Owens 1996). However, multiple individuals at a single site could also be explained by territorial intruders or by roaming individuals that have yet to establish a territory.

We recorded the majority of brown hyaena activity between sunset and sunrise. This result is consistent with previous studies from other areas (Mills et al. 1982a, Skinner et al. 1995) and lends support for brown hyaenas as an almost exclusively nocturnal species throughout its range. Moreover, we found that the temporal pattern of latrine activity was closely linked to the overall activity patterns of brown hyaenas on the reserve. This suggests that brown hyaenas visit defecation sites continuously throughout their active period, and that the visited sites are evenly spread throughout their territories (e.g., Mills et al. 1980).

In conclusion, brown hyaenas rarely defecated repeatedly at the same sites, but frequently visited previous defecation sites presumably for paste marking. Although our study took place over a relatively limited time period, our results contrast previous studies of brown hyaena latrine use. The hyaenas in Lapalala appeared to have used sites frequently visited for deposition of paste marks ad-hoc for defecation, and a more formal use of latrines as described for Namibia and the Kalahari seems to have been limited. We suggest that a geographic variation in patterns of brown hyaena scat deposition may be linked to resource driven variation in social and spatial organisation that relate to modes of olfactory communication, and that there is a need for evaluating the social ecology of this species in areas of contrasting productivity to better understand how it adapts to local resource abundance.

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References

Bearder, S.K. & Randall, R.M. 1978: The use of fecal marking sites by spotted hyenas and civets. - Carnivore 1: 32-48.

Brown, R.E. & Macdonald, D.W. 1985: Social odors in mammals. - Clarendon Press, Oxford, UK.

Cambefort, Y. 1984: Étude écologique des Coléoptères Scarabaeidae de Côte d'Ivoire. - Travaux des Chercheurs de la Station de Lamto 3: 1- 294. (In Frech)

Claridge, A.W., Mifsud, G., Dawson, J. & Saxon, M.J. 2004: Use of infrared digital cameras to investigate the behaviour of cryptic species. - Wildlife Research 31: 645 – 650.

Dalerum, F., Creel, S. & Hall, S. 2006: Behavioral and endocrine correlates of reproductive failure in captive wolverines. - Journal of Zoology 269: 527-537.

Delahay, R.J., Ward, A.I., Walker, N., Long, B. & Cheeseman, C.L. 2007: Distribution of badger latrines in a high-density population: habitat selection and implications for the transmission of bovine tuberculosis to cattle. - Journal of Zoology, London 272: 311-320.

Eaton, R.L. 1976. The brown hyaena: a review of biology, status and conservation. Mammalia 40:

377-399.
Gorman, M.L. 1990: Scent-marking strategies in mammals. - Revue Suisse de Zoologie 97: 3-29.
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: Gittleman, J.L. (Ed.); Carnivore behavior, ecology and evolution. Cornell University Press, Ithaca: 57–139.
Hutchins, M.R., Service, K.M., & Harris, S. 2002: Is population density correlated with faecal and urine scent markings in European badgers (Meles meles) in the UK? Mammalian Biology 67: 286-293.
Krell, F.T., Korb, J. & Walter P. 2003: The beetle fauna of hyaena latrines: coprocenoses consisting of necrophagous beetles (Coleoptera Trogidae Scarabaeidae) - Tropical Zoology 16: 145-152.
Kruuk, H. 1978: Spatial organisation and territorial behaviour of the European badger, *Meles meles*. - Journal of Zoology, London 184: 1–19.
Macdonald, D.W. 1980: Patterns of scent marking with urine and faeces amongst carnivore communities. - Symposia of the Zoological Society of London 45: 107–139.
Mills, M.G.L. 1982a: Hyaena brunnea. - Mammalian Species 194: 1-5.
Mills, M.G.L. 1982b: The mating system of the brown hyaena, *Hyaena brunnea* in the southern Kalahari. - Behavoral Ecology and Sociobiology 10: 131-136
Mills, M.G.L. 1990: Kalahari Hyenas: Comparative Behavioral Ecology of Two Species. Unwin Hyman, London.
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.
Mills, M.G.L. & Hofer, H. 1998. Hyaenas, status survey and conservation action plan. IUCN, Gland, Switzerland.
Mucina, L. & Rutherford, M.C. (eds.) 2006. The vegetation of South Africa, Lesotho and Swaziland. Sterlitzia 19. South African Biodiversity Institute, Pretoria, South Africa.
Nel, J.A.J. & Bothma, J.D.P. 2002: Scent marking and midden use by aardwolves (*Proteles cristatus*) in the Namib Desert. - Journal of Ecology 21: 25-39.
O'Brien, T.G., Wibisono, H.T. & Kinnaird, M.F. 2003: Crouching tigers, hidden prey: status of sumatran tigers in the Bukit Barisan Selatan National Park, Sumatra, Indonesia. - Animal Conservation 6: 131-139.
Owens, D. & Owens, M. 1996: Social dominance and reproductive patterns in brown hyaenas, *Hyaena brunnea*, of the central Kalahari desert. - Animal Behaviour 51: 535–551.
Roper, T.J., Conradt, L, Butler, J, Christian, S.E., Oostler, J. & Schmid, T.K. 1993: Territorial marking with faeces in badgers (*Meles meles*): a comparison of boundary and hinterland latrine use. - Behaviour 127: 289–307.
Sillero-Zubiri, C. & Gottelli, D. 1992: Feeding ecology of spotted hyaena (Mammalia: *Crocuta crocuta*) in a mountain forest habitat. - Journal of African Zoology 106: 169-176.
Sillero-Zubiri, C. & Macdonald, D.W. 1998: Scent-marking and territorial behaviour of Ethiopian wolves *Canis simensis*. - Journal of Zoology, London 245: 351-361.
Skinner, J.D., Van Aarde, R.J. & Gross, R.A. 1995: Space and resource use by brown hyaenas, *Hyaena brunnea,* in the Namib desert. - Journal of Zoology, London 237: 123-131.
Thorn, M., Scott, D.M., Green, M., Bateman, P.W. & Cameron, E.Z. 2009. Estimating brown hyaena occupancy using baited camera traps. South African Journal of Wildlife Research 39: 1-10.
Wiesel, I., Maude, G., Scott, D. & Mills, M.G.L. 2008: Hyaena brunnea. - In: 2008 IUCN Red List of Threatened Species. http://www.iucnredlist.org.

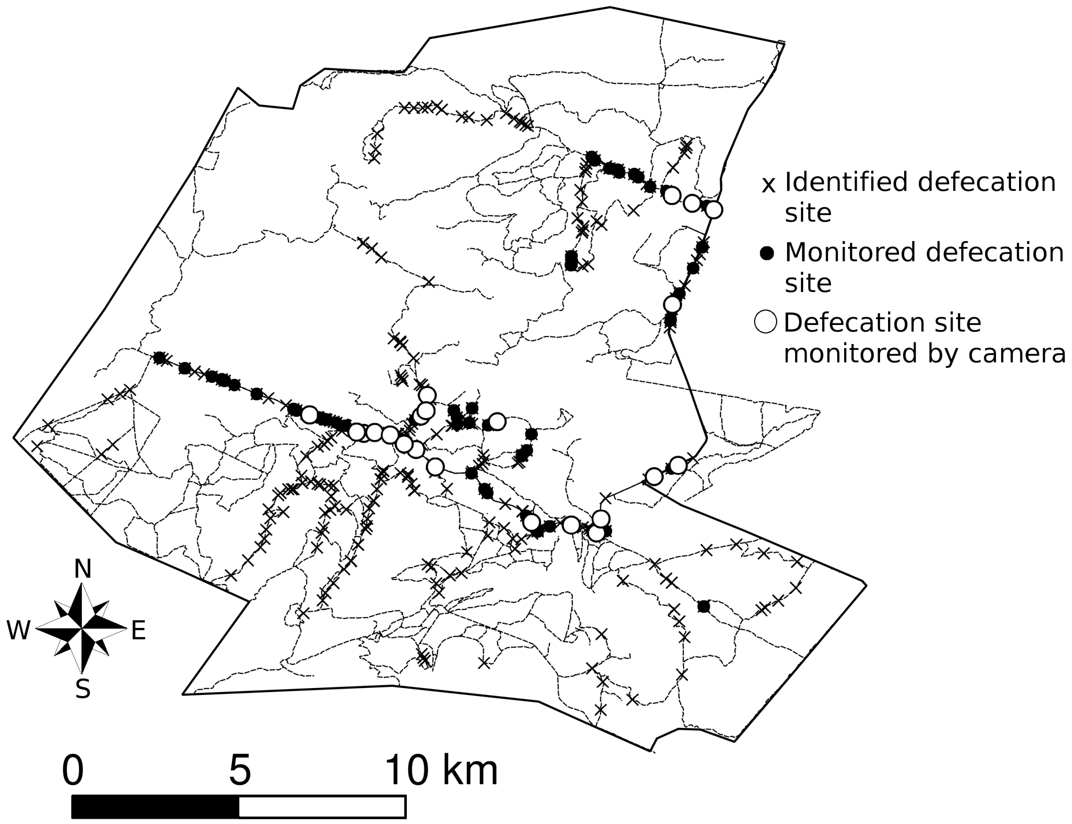

Fig. 1. Map of Lapalala Wilderness including 331 identified brown hyaena defecation sites, 87 defecation sites monitored during the study and 22 defecation sites monitored by automatic cameras.

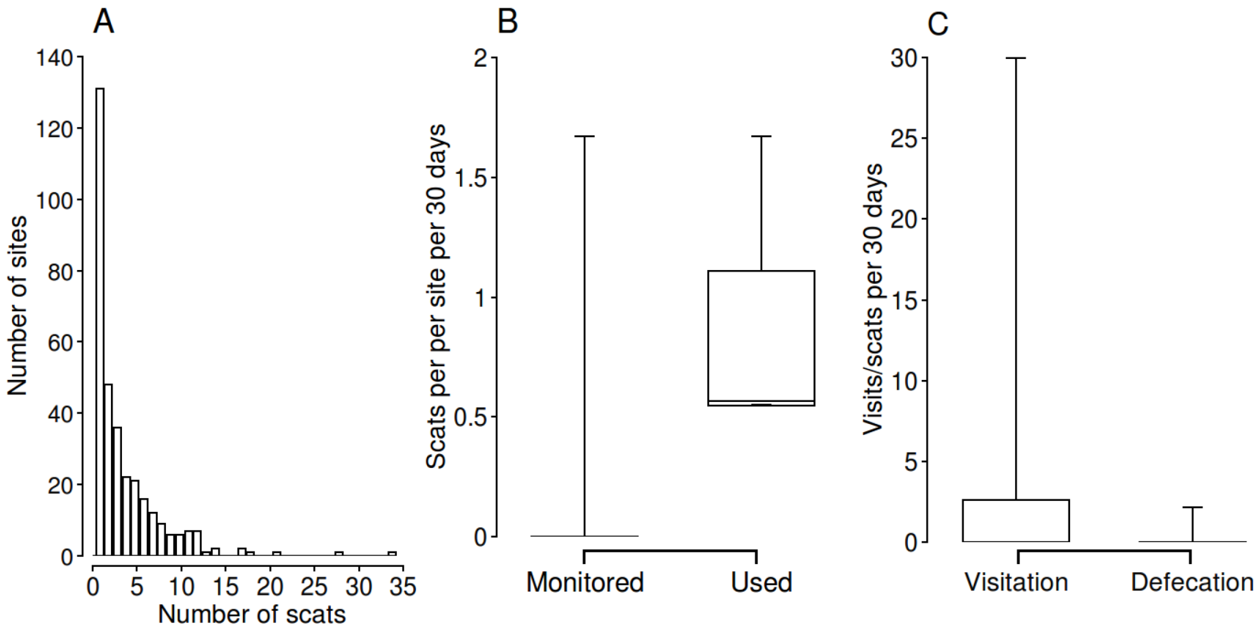

Fig. 2. Histogram of number of scats found at 331 brown hyaena defecation sites identified by an initial survey in September 2008 (A), defecation rates (median, 25 and 75% quartiles as well as maximum and minimum) at 87 of these brown hyaena defecation sites during the observation period January-March 2009 (B), and brown hyaena visitation and defecation rates at 22 defecation sites monitored by automatic cameras during January-March 2009 (C).

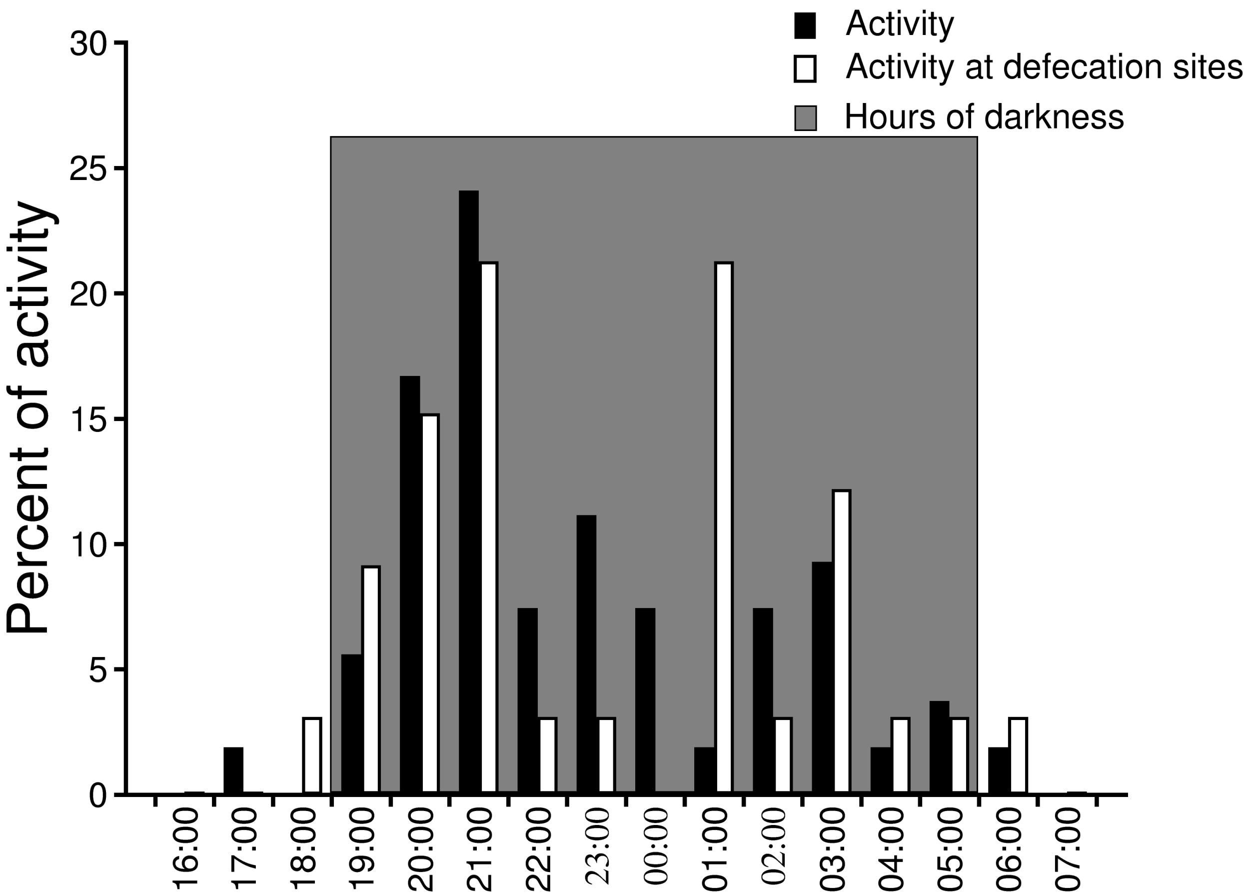

Fig. 3. Diel patterns of brown hyaena activity at camera sites during a larger camera trapping survey in the study area and at cameras placed at brown hyaena defecation sites. The area wide camera survey was conducted 2-3 month prior to the monitoring of defecation sites. The grey box represents the approximate period of darkness.