

The use of GPS telemetry data to study parturition, den location and occupancy in the brown hyaena

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Inferences about space use, activity and reproduction require an understanding of the behavioural processes that influence animal movements. Large volumes of movement data derived from GPS telemetry devices offer the opportunity to analyse animal behaviour on a very fine scale. GPS and satellite collars were fitted to female brown hyaenas (*Parahyaena brunnea*) as part of a long-term monitoring study in southwestern Namibia. The date of parturition was determined by comparing changes in movement data and successful GPS positioning attempts. Distances moved on the day of parturition dropped to zero and frequent, unsuccessful GPS positioning attempts on the same day indicated locations in underground dens. Daily distances moved pre-partum, during parturition and post-partum differed significantly and reflected behavioural changes that can be monitored and used to draw inferences about the reproductive state of female brown hyaenas. The main predictors for den occupancy were the age of cubs, distance to closest food source and individual den. Mean occupancy over the entire denning period was 23 days, indicating that brown hyaenas readily move between dens, but individual breeding females showed den site fidelity. Therefore, GPS telemetry is a useful tool to accurately determine parturition in brown hyaenas to draw inferences about den occupancy.

Keywords: animal movement, GPS telemetry, brown hyaena, *Parahyaena brunnea*, parturition, den site fidelity.

INTRODUCTION

Free-ranging animal movement data, derived from GPS and satellite trackers, have become useful research and conservation tools in recent years (Schick *et al.*, 2008; De Mars, Auger-Méthé, Schlägel & Boutin, 2013). Inferences about space use, resource use, breeding success, migration and dispersal may be drawn using such techniques (Mauritzen, Derocher & Wiig, 2001; Matthiopoulos, 2003) and may enable land and wildlife managers to make timely and informed mitigation decisions, especially in areas that are threatened by land use and development through humans increasingly encroaching into pristine habitats for recreational purposes.

Protected areas that can support herbivore and large carnivore populations may become especially popular ecotourism destinations. However, large carnivores often show ecological stress

before other species are affected, due to their large area requirements, low reproductive rates and low densities (Gittlemann, 2001). This can be expressed by changes in activity patterns, displacement, spatial avoidance, changes in foraging behaviour or denning activity (Bromley, 1985; Linnell, Swenson, Andersen & Barnes, 2000), and may ultimately influence a species' fitness on the individual and population level. Core areas, including active dens, may temporarily be protected by land and resource managers through placing land-use restrictions; *e.g.* wolf (*Canis lupus*) dens: (Thiel, Merrill & Mech, 1998).

However, pregnancy and the location and time of parturition is often difficult to detect in wild carnivores, particularly in species that show no visual signs of a change in reproductive state, such as genital swelling (Van Meter *et al.*, 2008), or in non-seasonal breeders that give birth underground. Existing methods to detect pregnancy or parturition are mostly invasive and include blood serum analysis, ultrasonography, and analysis of faecal and urinary hormone metabolites (Kahn, 1992;

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Kumar *et al.*, 2013). Using these methods on wild mammals is challenging (Friebe, Zedrosser & Swenson, 2013), especially when individuals cannot be followed and sampled over extended periods. Knowledge about a female's reproductive state, however, is useful for understanding her behaviour and requirements, and the species' population ecology in order to protect it and mitigate impacts during denning when females may be especially vulnerable (Maestripietri, 1999; Schneider, Blum, Wade, 2000; Altmann, Lynch, Nguyen, Alberts & Gesquiere, 2004).

Brown hyaenas (*Parahyaena brunnea*) are non-seasonal breeders with inter-birth intervals of up to 41 months (Mills, 1982a). They give birth in natal dens to litters of between one and four cubs before moving their cubs to larger communal dens (Owens & Owens, 1979; Mills 1983). These dens are visited by all clan members once the cubs are approximately four months old to socialize and to provide solid food until they are weaned at approximately 15 months (Mills, 1983). Within a clan's territory, several natal dens exist and several different communal dens are used during a single denning season, with movement caused mainly by accumulations of parasites, caving in of dens and disturbance (Mills, 1982a; Mills, 1983).

GPS telemetry can be a helpful tool to obtain exact activity data indicating parturition in brown hyaenas. Because natal dens are either located underneath dense vegetation or in caves in rocky areas, higher numbers of unsuccessful GPS positioning attempts are expected and daily activity of female brown hyaenas should decrease to zero during parturition. Thus, GPS data can be screened for such events to pin-point the birthing period. This paper presents a robust analysis of GPS movement data that can be used to monitor brown hyaena reproduction, subsequent den use and den site location.

MATERIALS AND METHODS

Study area

Data were collected in the Tsau//Khaeb National Park in southwestern Namibia (S–26.85, E15.20) as part of a long-term study on brown hyaenas that commenced in 1997. The area receives an average of 16.7 mm of rain each year (Muller, Reason & Fauchereau, 2008) and vegetation is dominated by dwarf shrubs that are sparsely scattered on rocky ridges and plains (Burke, 2006). Herbivore abundance is low with gemsbok (*Oryx gazella*)

and springbok (*Antidorcas marsupialis*) being the predominant species. Two large mainland and two offshore Cape fur seal (*Arctocephalus pusillus pusillus*) breeding colonies form the basis of a year-round reliable food source for carnivores, such as black-backed jackals (*Canis mesomelas*) and brown hyaenas.

Animal capture

Five breeding females were fitted with GPS telemetry collars (Followit Sweden AB, Lindesberg, Sweden) between 2006 and 2017 (Table 1). Data download options varied from USB cable data transfer after drop-off, remotely *via* a VHF or UHF data link to a hand-held receiver and laptop or web-based *via* Iridium satellite link. All collars were equipped with drop-off devices that could be triggered remotely *via* UHF radio transfer once battery voltage was low, indicated by a recovery VHF signal. Most collar schedules were standardized and each collar was programmed to obtain a GPS location on each full hour. Two Iridium collars, however, were programmed to obtain only 18 GPS positions per day to maximize battery life. The GPS receiver tried a maximum of 90 seconds to successfully obtain locational data, if this was not achieved, 'time out' information was recorded.

Three females were re-collared immediately after their previous collar ceased functioning, allowing for long-duration data collection and repeat monitoring of parturition in these three females over two and a half, six and seven years, respectively (Table 1).

Brown hyaenas were captured by attracting them to a fixed bait where they were darted with a Pseudart rifle at 20 metres distance. Immobilization was achieved by using a combination of medetomidine (Domitor[®], Pfizer Animal Health, Exton, U.S.A.; 0.035–0.045 mg/kg) and ketamine (Ketaset[®], Zoetis, Parsippany, U.S.A.; 3–4 mg/kg) ($n = 12$) or tiletamine hydrochloride/zolazepam hydrochloride ($n = 1$; Zoletil[®], Virbac, Centurion, South Africa; 5 mg/kg). Animals were transferred into a recovery cage and released once fully recovered ($n = 1$) or reversed with atipamezole ($n = 12$; Antisedan[®], Pfizer Animal Health, Exton, U.S.A.; 5 times the milligram dose of medetomidine induction intramuscularly) a minimum of 60 minutes after darting. Capture and handling procedures were approved and permitted through annually reviewed research permits issued to the lead author by the Namibian Ministry of Environment and Tourism (Windhoek, Namibia). All captures

Table 1. GPS telemetry collar information for five breeding females, period of data collection and GPS location schedule.

Hyaena ID	Collar type – data transfer mode	Data collection period		Hourly GPS schedule
		From	To	
Alaika	GPS-VHF	04 May 2009	22 July 2009	0:00–23:00
Alaika	GPS-UHF	22 May 2011	10 March 2013	0:00–23:00
Alaika	GPS-UHF	23 March 2013	04 August 2013	0:00–23:00
Alaika	GPS-UHF	27 March 2014	11 June 2015	0:00–23:00, *(2:00, 8:00, 14:00, 20:00)
KC Sowande	GPS-Iridium	18 March 2013	14 December 2013	0:00–23:00
KC Sowande	GPS-UHF	31 March 2014	2 February 2015	0:00–23:00
KC Sowande	GPS-Iridium	11 June 2015	29 September 2015	17:00–9:00, 12:00
Minerva	GPS drop-off	16 June 2007	25 December 2007	0:00–23:00
Obelixa	GPS-VHF	11 May 2009	13 May 2011	0:00–23:00
Obelixa	GPS-VHF	13 May 2011	01 April 2012	0:00–23:00
Obelixa	GPS-VHF	01 April 2012	10 November 2013	0:00–23:00
Obelixa	GPS-VHF	25 March 2014	13 November 2014	0:00–23:00
Obelixa	GPS-Iridium	03 June 2015	04 July 2016	17:00–9:00, 12:00
Tosca	GPS-VHF	07 May 2009	05 October 2010	0:00–23:00

*Collar schedule change due to malfunction from 17 June 2014.

were done under veterinary supervision and annual reports were submitted to the relevant authorities.

Parturition date determination

Brown hyaena activity was determined by calculating the direct distances (km) between successive GPS positions. As brown hyaenas are predominately nocturnal, 24-hour distances obtained between 12:00 and 11:00 the following day were summed to obtain the minimum daily distance for each activity period. Subsequently, mean daily (12:00–11:00), daytime (7:00–18:00) and night-time (19:00–6:00) distances two weeks prior to parturition, on the day of parturition and the four subsequent days, and two weeks after parturition were calculated. These were compared for differences with a univariate ANOVA and *post hoc* Tukey test using the Type III model to test for main effects of female ID as a fixed factor in the statistical software package SPSS 20. Furthermore, the number of ‘time out’ records per activity period was determined.

At the time of capture, the age class and breeding status of the animals was determined, age by tooth wear and eruption (Mills, 1982b) and breeding status by external examination and assessment of the nipples (Mech, Meier & Seal, 1993). Subadults (age class 2) and adult females of age class 3 with small nipples were classified as

non-breeders. Two females were monitored from birth and breeding status was known, whereas a third female’s status was assessed from age and nipple appearance. All three gave birth to their first litter after being fitted with a telemetry collar and all had subsequent litters. The other two females included in the analysis were known to have bred previously. Distances moved after parturition of primiparous and multiparous females were compared using a Mann Whitney *U*-test. Finally, descriptive statistics were calculated for the inter-birth intervals of individual primiparous and multiparous females.

Den site location and occupancy at dens

GPS location data of all females were imported into ArcGIS 10.5 (ESRI, Redlands, California) and the movement patterns were plotted by creating a polyline connecting successive positions using the Points-to-Line tool. GPS positions of point locations were determined when clusters of lines pointed to that location from multiple directions (Fig. 1), indicating the location of a den site. Previously unknown den site locations (12 of a total of 28 identified dens) were confirmed during field visits. Dens were classified as natal if the female gave birth there and if the den was not used more than once during the same denning period. Otherwise they were classified as communal. Size classes were assigned to each den. Small dens

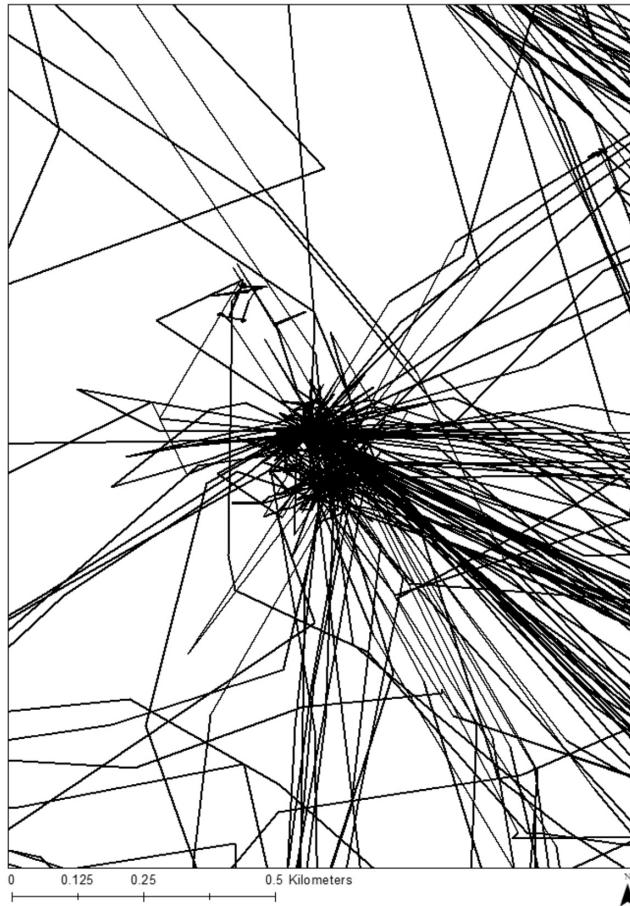


Fig. 1. Example of a multidirectional movement towards an active den site.

were inconspicuous without any prey remains scattered in front of the entrance or nearby area. When prey remains (accumulations of bones and/or carcasses) were found in an area of up to 300 m² and larger than 300 m² adjacent to the den entrances, they were classified as medium and large, respectively.

For den occupancy analysis, all datasets were screened for unsuccessful GPS position attempts. In cases of 'time out' occurrences, the distance (km) between the previously successfully recorded position and the next available successfully recorded position was calculated. If the distance was equal to or less than 100 m, which was the maximum positional error determined during stationary collar tests (I. Wiesel, unpubl. data), it was assumed that the animal had not moved between positions. In such cases, the GPS position before the 'time out' record replaced the gaps. This modification was necessary as breeding

females spend up to 82% of the day inactive inside and around the den, both at night and during the day (Goss, 1986). True occupancy could be overlooked when not accounting for 'time out' positions creating a bias towards GPS positions taken when active (*e.g.* foraging). The GPS locations of each female and all den sites were plotted in ArcGIS 10.5. Dens were spatially joined to the GPS locations of each female by finding the closest point from a den to a GPS location. These distances were stored in an attribute table and imported into MS Excel 2016. Finally, conservatively accounting for positional error as above, all GPS positions, including 'time out' positions of the breeding female, within a 100 m buffer around each den location were recorded to obtain occupancy data.

Starting from the parturition date, the number of GPS positions at each den was recorded. In most cases the active den could easily be determined as GPS positions were recorded on more than two

consecutive days. GPS positions were usually not recorded at other den sites at the same time with the exception of single day visits to other dens that were regarded as resting site visits, or times of overlapping den use of not more than two days when cubs were moved between dens. A denning period ended with the birth of the next litter.

A Generalized Linear Model was performed in SPSS 20. We tested whether occupancy could be predicted using the individual den that was used, the type of den (natal, communal), its size (small, medium, large), the breeding females' identity as factors and each den's distance to the main food source (seal colony, Elizabeth-Bay beach, rubbish dump) and the calculated age of the cubs based on GPS data as covariates. The Type III model tested for main effects of all factors and covariates. Wald chi-square statistics were used to test for model effects using a 95% confidence interval level.

The sizes of the individual denning areas used for each litter were calculated in ArcGIS 10.5 by using the Minimum Convex Polygon method. The frequency of moves between dens and distances (km) between successive dens were calculated, as was den site fidelity by determining individual den site use for females with multiple litters.

RESULTS

Parturition, post-partum behaviour and reproduction

A total of 16 births were determined by screening the GPS data of all breeding females (Table 2). Continuous GPS data were available for 15 of these birthing events. Activity, expressed as the mean daily distance moved, dropped to zero at the date of parturition (Fig. 2). There were significant differences in the distances moved (mean \pm S.D.) prior to parturition, during parturition and post-partum ($F_{2,494} = 63.73$, $P < 0.001$). Mean daily distances moved prior to parturition were significantly higher (15.8 ± 8.1 km) than the distances moved during parturition (2.6 ± 5.7 km, $P < 0.001$) and post-partum (11.9 ± 11.3 km, $P < 0.001$), as were the mean daily distances during the post-partum period compared to parturition ($P < 0.001$). Female ID influenced overall results ($F_{4,494} = 20.17$, $P < 0.001$). KC Sowande's mean daily distances moved prior, during and post-parturition of 20.5 ± 12.1 km, 7.7 ± 16.0 km and 35.4 ± 18.8 km, respectively, were significantly different to the distances moved by all other females ($P < 0.001$).

Table 2. Date of birth and inter-birth interval derived from GPS telemetry data calculations.

Hyaena ID	Date of birth	Inter-birth interval (months)
Alaika ¹	31 March 2012	
Alaika	14 July 2013	15.70
Alaika	22 September 2014	14.50
KC Sowande ¹	23 September 2014	
KC Sowande	29 September 2015	12.40
Obelixa ¹	21 June 2009	
Obelixa	05 March 2010	8.60
Obelixa	07 July 2011	16.30
Obelixa	09 July 2012	12.30
Obelixa	29 January 2013	6.80
Obelixa	18 August 2013	*6.70
Obelixa	19 September 2014	13.10
Obelixa	26 July 2015	10.40
Obelixa	06 January 2016	*5.50
Minerva	08 August 2007	
Tosca	02 January 2010	

*Litter lost.

¹Primiparous.

However, when excluding KC Sowande from the analysis, female ID had no significant influence on distances moved ($F_{3,461} = 2.18$, $P = 0.090$), but distances moved prior, during and post-parturition were still significantly different ($F_{2,461} = 81.08$, $P < 0.001$). Therefore, data of all females were analysed together for all subsequent analyses.

The mean proportion of missed daily fixes also differed ($F_{2,30} = 150.71$, $P < 0.001$) and was highest during parturition compared to before ($P < 0.001$) and after ($P < 0.001$) parturition. There were significantly less fixes missed before parturition than after ($P < 0.001$) (Fig. 2).

Night-time and daytime distances differed significantly, also between reproductive states ($F_{5,60} = 59.90$, $P < 0.0001$). Night-time distances were significantly higher prior to parturition than daytime distances (Fig. 3; $P < 0.001$) and post-partum night-time distances ($P < 0.001$). However, there was no significant difference between post-partum night-time and daytime distances, with daytime distances increasing significantly from the pre-partum and parturition phase ($P < 0.05$).

Obelixa's age at first parturition was estimated from tooth wear at five years. Alaika was born to Tosca in 2006 and KC Sowande was Obelixa's offspring from 2010, hence they were six (Alaika) and 4.5 (KC Sowande) years old at first parturition. The mean (\pm S.D.) daily distances that females moved

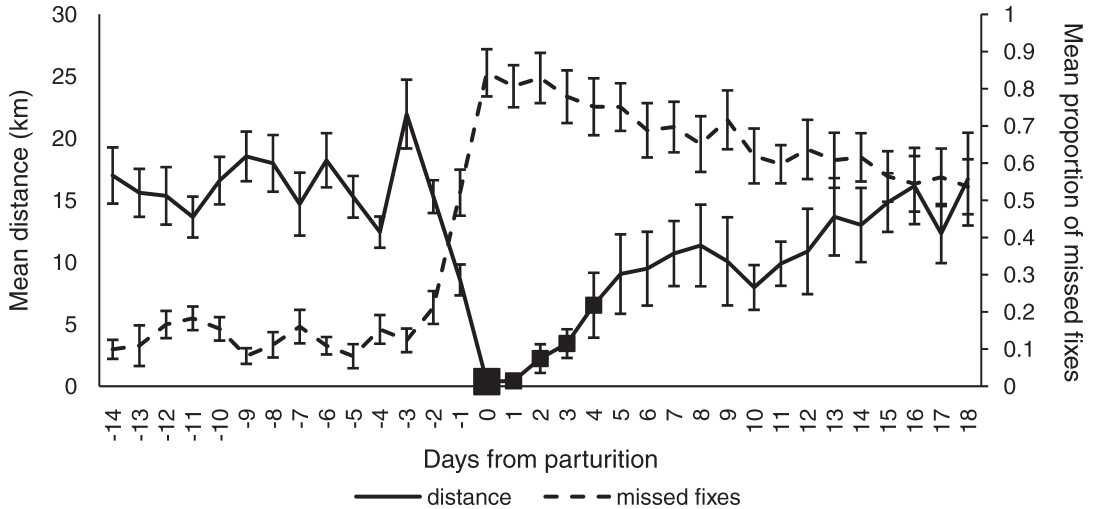


Fig. 2. Mean distance moved per activity period and proportion of missing GPS positions (\pm S.E.) prior to parturition, during parturition (square markers) and post-partum ($n = 15$).

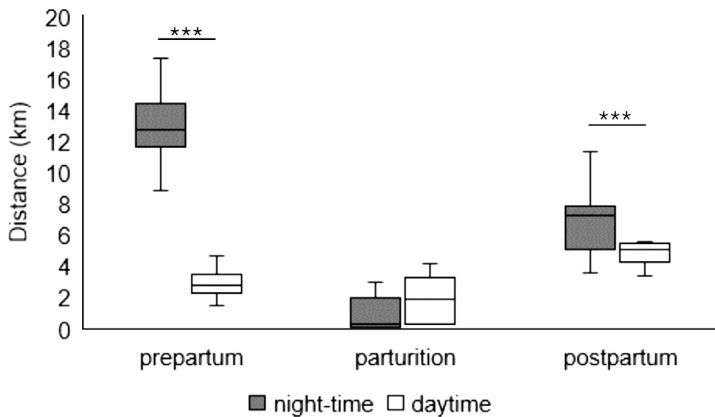


Fig. 3. Distances moved at night-time and daytime by breeding females before, during and after parturition (median, quartiles, minimum and maximum).

per day after parturition when primiparous were significantly higher than the distances moved when multiparous (25.2 ± 15.0 km vs 8.5 ± 7.0 km: $U = 1151$, $P < 0.0001$). Post-partum mean daily distances of Alaika and Obelixa did not differ from their respective pre-partum mean daily distances (Alaika: $t = 0.89$, $P = 0.38$; Obelixa: $t = 0.86$, $P = 0.40$), but KC Sowande moved greater distances per day after parturition than before ($U = 48.00$, $P = 0.02$).

The mean (\pm S.D.) inter-birth interval of multiparous females was 10.7 ± 4.0 months ($n = 6$) and 12.2 ± 3.3 months ($n = 4$) for successfully raised litters. Primiparous females inter-birth interval was 12.2 ± 3.6 months ($n = 3$). Alaika had the longest inter-birth interval of 15.1 ± 0.9 months

($n = 2$), followed by KC Sowande of 12.4 ($n = 1$) and Obelixa with 10.0 ± 3.7 months ($n = 8$) and 11.3 ± 3.4 months ($n = 6$) when only accounting for successfully raised litters.

Occupancy at dens

Multi-directional movement was recorded to 28 different den sites of which Obelixa, KC Sowande, Alaika, Tosca and Minerva used 15, four, five, four and three, respectively. Median (\pm S.D.) occupancy was 13.0 ± 29.9 days ranging from 1 to 170 days. The individual den, distance to closest food source and the age of cubs had an influence on occupancy (den d.f. = 1, $P = 0.02$, distance d.f. = 1, $P = 0.04$, age d.f. = 1, $P = 0.045$).

Only Obelixa was tracked continuously for four

entire denning periods from 2009 to 2016. Out of the 15 dens that she used, she alternated between two natal dens and the same communal dens ($n = 7$) were used up to four times (mean (\pm S.D.): 2.6 ± 1.2), indicating site fidelity. Natal and communal dens used by breeding females for individual litters on average covered an area of 6.7 ± 3.9 km² (range: 1.1–12.3 km²), with median (\pm S.D.) distances between successive dens of 1.8 ± 2.1 km (range: 0.3–14.6 km).

DISCUSSION

Brown hyaena reproductive behaviour has only been observed during two long-term studies in the Kalahari (Mills, 1982a; Mills, 1983; Owens & Owens, 1979; Owens & Owens, 1996) and in studies of captive animals in zoos (Lang, 1958; Eaton, 1981; Ensely, Wing, Gosink, Lasley & Durrant, 1982; Volf, 1998; Brandl, Capova & Kucera, 2001). However, some recent studies have used GPS tracking technologies to observe brown hyaena movements, assess space use, habitat preferences and human–carnivore conflict (Weise, Wiesel, Lemeris & van Vuuren, 2015; Welch *et al.*, 2015), but none have made inferences about reproductive behaviour.

Parturition and post-partum behaviour

Our study accurately determined parturition date from GPS location and movement data. On the day of parturition, daily distance moved and the number of successfully taken GPS positions decreased to almost zero, indicating that the female had given birth underground (see Nonaka, 2011). Such changes in movement and activity have also been recorded for wolves, brown bears (*Ursus arctos*) and woodland caribous (*Rangifer tarandus caribou*), in which sudden decreases in movement rates and activity or spatial clustering were indicative of parturition (Nonaka, 2011; De Mars *et al.*, 2013; Friebe *et al.*, 2013).

Brown hyaena mothers showed little activity for the first five days after giving birth. Average daily distances moved were 2.6 km as opposed to 15.8 km before parturition. Volf's (1998) report of a captive brown hyaena that started to feed three days after parturition and that could only be separated from its cubs on the fifth day after parturition conforms with our results. Daily movement distances are also reduced in gray wolves when pups are small and require care and attendance (Jędrzejewski, Schmidt, Theuerkauf, Jędrzejewska & Okarma, 2001; Alfredéon, 2006).

Maned wolves (*Chrysocyon brachyurus*) reduce their daily range and home range size on the days after parturition (Bandeira de Melo, Sábato, Vaz Magni, Young & Coelho, 2006). Nagy (2011) describes three movement states for caribou at approximately 10 days around parturition, starting with high daily movements with a subsequent sudden, steep decline to near zero on the day of parturition and a gradual increase in daily movement rates afterwards. The same applies to the brown hyaenas in our study. The females' mean daily distances showed a peak three days before parturition, followed by a steep decline to zero and then a steady increase up to day eight post-partum, when overall daily movements started to fluctuate, reaching pre-partum levels around day 15.

Prior to parturition, brown hyaenas were almost completely nocturnal. After parturition, however, brown hyaenas seemed to compensate for the time they spent nursing and looking after the cubs at night with increased daytime activity. Pre-partum distances were not reached though, indicating a tendency to save metabolic expenditures during reproduction by reducing overall activity levels (Gittlemann & Thompson, 1988). In the central Kalahari, for instance, female brown hyaenas invested a lot of time with infant cubs, visiting them two to three times per night for periods of up to five hours (Owens & Owens, 1979). Similarly, female wolves move the shortest daily distances when their pups are small and require nearly constant care and attendance (Jędrzejewski *et al.*, 2001). In contrast, primiparous brown hyaenas almost instantly reached pre-partum mean daily distances after parturition. One of the females even moved significantly longer distances. The reason was that her natal den was situated 15 km away from her mother's active den, which she continued to visit regularly before moving her own cubs there. High post-partum activity levels of primiparous females may be related to inexperience, as post-partum behaviour conformed with other multiparous females from the second litter onwards. General behavioural differences between primiparous and multiparous females are well documented in other species, such as in primiparous rhesus monkey (*Macaca mulatta*) mothers, who show higher anxiety levels when dealing with stress by expressing threatening behaviours more frequently (Mitchell & Stevens, 1968), and sheep (*Ovis* spp.), which show differences in recognition of their lambs (Keverne, Levy, Guevara-Guzman &

Kendrick, 1993; Keller *et al.*, 2003). Cub mortality can also be related to maternal experience and is higher in captive zoo-kept primiparous striped hyaena (*Hyaena hyaena*) (Rieger, 1979).

Brown hyaenas in our study gave birth to their first litters when they were more than four years old, which differs to records from captive-born brown hyaenas that were 33 and 34 months old at first parturition (Shoemaker, 1978).

Reproduction

The inter-birth intervals between successfully raised litters of 10.7 and 12.2 months in our study are shorter than the ones recorded in the southern Kalahari that average 20.7 months (range: 12–41) (Mills, 1990), but longer than records from zoos, where inter-birth intervals of 4–7 months were recorded when litters were not removed (Lang, 1958; Shoemaker, 1978; Eaton, 1981). The shortest intervals recorded in our study were 5.5 and 6.7 months after the female had lost her litters at 0.9 and two months, respectively. Mills (1983) describes the brown hyaena as polyoestrous (\varnothing 47.6 days determined by mating observations: Eaton, 1981), with a lactational anoestrous. The loss of the litters in our study may have induced ovulation as described from captive brown hyaenas, whose litters were removed shortly after giving birth (Rieger, 1979). However, the short intervals of 6.8 and 8.6 months between births without loss may be an indication of other underlying factors that influenced reproduction. Lactational anoestrous may for instance be related to the weight of cubs or influenced by suckling frequency (Steward, 1988; Lee, Majluf & Gordon, 1991). Mills (1983) observed that brown hyaena mothers start visiting the den less frequently once cubs are four months old, at which time the milk diet is increasingly supplemented by food carried back to the den. Between 10 and 15 months of age, brown hyaena cubs predominately survive on solid food. Therefore, if a low suckling frequency is required to end the lactational anoestrous, the cub weaning process in our study should have started at three and four months of age, but during this time they are still highly dependent on milk, despite other clan members starting to supplement their diet with solid food (Owens & Owens, 1979; Mills, 1983). A complete lactational anoestrous seems therefore unlikely, considering an average gestation period of 95.8 days (Eaton, 1981) and prolonged courtship periods (Mills, 1983).

The short inter-birth intervals in a wild population recorded in this study may be influenced by the unique environmental factors along the southern Namib Desert coast. Food is available in abundance due to the existence of two large mainland and two offshore seal breeding colonies in the study area. Alaika had the longest inter-birth interval of 15.1 months and her home range included the two mainland seal colonies, where food is localized and predictably available year-round (Wiesel, 2010), which may render seasonality redundant. On the other hand, KC Sowande and Obelixa predominately foraged along beaches, where most seal pup mortalities are only seasonally available from December through to the end of January each year (De Villiers & Roux, 1992). Sixty-three per cent of the litters in the study were born two to five months before the onset of the seal pupping season in November (David, 1987) and the mean inter-birth interval between successfully raised litters was approximately one year, indicating that births may be synchronized with the seal pupping season. The onset of the seal pupping season would then coincide with the time that clan members would start supplementing solid food, and when breeding females invest much energy in nursing, as milk forms an important part of the cubs' diet until they are approximately 10 months old (Mills, 1983). Eaton (1981) also suggested some seasonality in relation to rainy seasons and the abundance of food resources, despite erratic inter-birth intervals, from a review of reproductive data originating from zoo registries and from Lang (1958). Brown hyaenas in our study seemed to increase their reproductive success by producing litters more frequently than elsewhere in their range, showing annual seasonality in relation to the reproductive cycle of their main prey species. Cub mortality, however, was similar to that recorded in other wild populations (11%: Mills, 1990) with 12.5% of litters lost, but considerably lower than that recorded for striped hyaenas in captivity (40%: Rieger, 1979).

Occupancy

The importance of the localized food source was also reflected by its influence on den occupancy. The three dens in inland areas, located far from the coastal food source, were occupied for shorter periods than coastal dens. However, age of the cubs was the driving factor determining the length of den occupancy. Median den occupancy of 13 days recorded in the southern Namib Desert was

shorter than the average occupancy of 3.6 months in the southern Kalahari (Mills, 1990), but it ranged widely and could be as long as 5.6 months when cubs were older. Cubs were moved frequently and it has been documented that brown hyaenas move cubs from minor, natal dens to larger, often communal dens, at approximately three months of age (Owens & Owens, 1979; Mills, 1983). In the southern Kalahari, clans used up to 14 dens in total during the course of the development of the cubs (Mills, 1983), covering areas of 1.5–5 km². On the southern Namib desert coast, four to 12 dens within areas of up to 12 km² were used for individual litters, indicating that dens were further apart and that the median distance of 1.8 km per move was higher than in the Kalahari.

Brown hyaenas in our study used the same dens over several denning seasons. Some of these dens showed signs of long-term use and locations were known from various sources (I. Wiesel, unpubl. data; K. Wolhuter, pers. comm.), suggesting long-term den site fidelity, particularly for large, communal dens that may have proven to offer adequate protection for the cubs. Coastal black-backed jackals in northern Namibia have also been observed using the same dens between years despite shifts of territory boundaries (Jenner, Groombridge & Funk, 2011). Other species, such as paired crested porcupines (*Hystrix cristata*) select previously used dens over several seasons, as do female raccoons (*Procyon lotor*), when suitable dens are limited (Endres & Smith, 1993; Monetti, Massolo, Sforzi & Lovari, 2005).

CONCLUSIONS

GPS telemetry may be a suitable method for demographic studies, delivering reliable results about pregnancy, parturition and also offspring survival (*cf.* De Mars *et al.*, 2013; Friebe *et al.*, 2013). Our study showed that parturition in brown hyaenas can be accurately determined from GPS data and that inferences about den occupancy and reproductive rate can be drawn. However, additional non-invasive monitoring of dens using, for instance, camera traps may provide additional information about litter size, attendance patterns and activity (Ballard, Ayres, Garnder & Foster, 1991; Theuerkauf *et al.*, 2003; Merrill & Mech, 2003; Mech & Cluff, 2009). Clan size and membership may also be monitored because of the social importance of these sites.

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