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Fine-scale movements and use of space by spotted hyaena (*Crocuta crocuta*) on Ongava Game Reserve, Namibia

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Abstract

We deployed Global Positioning System (GPS) collars on spotted hyaena, *Crocuta crocuta*, on Ongava Game Reserve in northern Namibia. We analysed the movement profiles recorded from three periods of fine temporal scale (15 min interval) GPS data – dry season data from a sub-adult female (36 days) and a lactating adult female (54 days), and wet season data from the same adult female (55 days). The hyaenas both had similar daily activity patterns – at rest between 12.00 and 18.00 hours, with a peak of activity in the 2-h period around sunrise. They exhibited one or two active periods each night, travelling up to 30 km and being active for up to 10 h. Daily rest sites were widely distributed across the reserve, typically located on elevated ground and never revisited on consecutive days. In the dry season, both hyaenas made extensive use of the reserve, plus adjacent areas in Etosha National Park (sub-adult home range 240 km^2, adult home range 366 km^2). The wet season data for the adult female showed a significant reduction of space used (home range 232 km^2). However, their utility distributions showed a nonuniform use of space, with multiple areas of high-density utilization located away from open terrain.

Key words: carnivore, *Crocuta crocuta*, global positioning system, home range, utility distribution

Résumé

Nous avons placé des colliers GPS sur des hyènes tachetées *Crocuta crocuta* dans la Réserve de Faune d'Ongava, dans le nord de la Namibie. Nous avons analysé le profil des déplacements enregistrés pendant trois périodes de données GPS à fine échelle temporelle (intervalles de 15 mins) – en saison sèche pour une femelle sub-adulte (pendant 36 jours) et une femelle adulte allaitante (54 jours), et en saison des pluies pour la même femelle adulte (55 jours). Les deux hyènes présentaient un schéma d'activité comparable – au repos entre 12.00 et 18.00 hours, avec un pic d'activité durant la période de deux heures qui entoure le lever du soleil. Elles présentaient une ou deux périodes actives chaque nuit, parcourant jusqu'à 30 km et restant actives jusqu'à ten heures d'affilée. Les sites de repos diurnes étaient dispersés largement dans toute la réserve et se situaient typiquement à des endroits surélevés, et ils n'étaient jamais revisités les jours suivants. En saison sèche, les deux hyènes ont intensément fréquenté la réserve en plus de zones voisines dans le Parc National d'Etosha (aire de dispersion de 240 km^2 pour la femelle sub-adulte et de 366 km^2 pour l'adulte). Les données de saison des pluies pour la femelle adulte ont révélé une réduction significative de l'espace fréquenté (aire de dispersion de 232 km^2). Cependant, les distributions utiles montraient une utilisation non uniforme de l'espace, avec de nombreuses zones de forte utilisation situées loin des espaces ouverts.

Introduction

The monitoring of carnivores in remote environments is difficult and often restricted to sightings at specific locations or opportunistic observations. This problem is exacerbated when the study species is both nocturnal and highly mobile. However, advances in animal-borne technology over the past 15 years, in particular Global Positioning System (GPS) devices, have allowed insights into previously cryptic movements and use of space (see review by Cagnacci *et al.*, 2010).

Spotted hyaenas, *Crocuta crocuta*, are large-bodied social carnivores that occupy well-defended home ranges (Boydston, Morelli & Holekamp, 2001). The fission-fusion nature of their society means that a single clan typically hunts and forages widely across its range in small groups,

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only coming together in specific circumstances such as defence of territories and shared resources, and protection from other large carnivores (Mills, 1990; Smith *et al.*, 2008). Ranging behaviour is typically, but not always, nocturnal, with individuals often moving long distances when active (Kruuk, 1972; Mills, 1990). Previous studies of the movements and use of space of spotted hyaenas have used direct observations, or behavioural follows supplemented by radio-tracking feedback, to analyse both daily patterns and utilization of territory (e.g. Kruuk, 1972; Frank, 1986; Mills, 1990; Kolowski *et al.*, 2007). Prior to this study, our knowledge of the way in which spotted hyaenas use Ongava Game Reserve was limited to observations made during fixed position nocturnal monitoring, or from responses to call-back experiments.

In GPS-based studies, there is always a trade-off between sampling interval and battery life – many researchers are interested in long-term patterns, and therefore record data at relatively slow rates. In order that we could reconstruct in detail the series of locations used by individual spotted hyaenas, we used short sampling intervals, typically 15 min when active. In this study, we analyse the movement profiles recorded from three periods of fine temporal scale GPS data – dry season data from both a sub-adult female and an adult female spotted hyaena, and wet season data from the same adult female.

Materials and methods

Study site

Ongava Game Reserve is located immediately to the south of Etosha National Park (ENP), covering an area of 300 km^2 (mean latitude S19.34, longitude, E15.80, see Fig. 1). Ongava is made up of flat calcrete sedimentary plains (about 35%) and dolomite hills (about 65%) with an altitude range of 1155–1287 m above sea level. There are few roads and tracks in the hilly areas, and to protect the fragile ecosystem, the reserve has a policy that bans all off-road driving. Ongava's northern boundary (common with ENP) is Namibia's veterinary 'red line' fence and is permeable to carnivores, but not to medium and large-sized herbivores. The other boundaries are electrified to prevent animals moving onto neighbouring farmland. The habitat is termed Karstveld, with vegetation primarily (up to 70%) *Colophospermum mopane* shrub and woodland. *Terminalia* and *Acacia* species on hill slopes provide differentiation of habitat (Berry & Loutit, 2002). There are natural water dams on the reserve, most of which only contain water during the rainy season. Water is therefore supplied via artificial waterholes. The weather zone for the reserve is typical for semi-arid northern Namibia, with an average annual rainfall of 380 mm. This rain usually falls in two

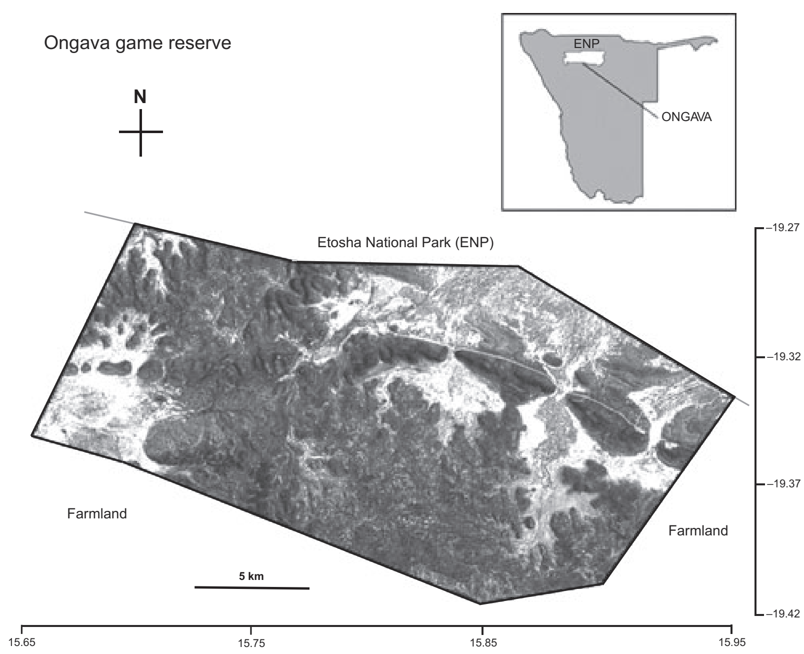

Fig 1 Ongava Game Reserve. Darker areas on image indicate higher elevations

Table 1 Candidate prey species for spotted hyaena on Ongava Game Reserve. Data from averaged aerial survey data for 5 years from 2006 to 2010. Other smaller antelope species (common duiker *Sylvicapra grimmia* and steenbok *Raphicerus campestris*) are also present

Common name	Scientific name	Relative % total prey	Density (per km^2)	Habitat
Oryx	*Oryx gazella*	30.7	3.20	All
Kudu	*Tragelaphus strepsiceros*	25.2	2.63	All
Springbok	*Antidorcas marsupialis*	8.5	0.88	Plains
Plains Zebra	*Equus burchellii*	7.1	0.74	Plains
Blue Wildebeest	*Connochaetes taurinus*	6.8	0.71	Plains
Black-faced Impala	*Aepyceros melampus petersi*	6.1	0.64	Predominantly Plains
Red Hartebeest	*Alcephalus buselaphus*	4.9	0.51	Plains
Waterbuck	*Kobus ellipsiprymnus*	3.7	0.39	Plains
Eland	*Taurotragus oryx*	3.7	0.38	Plains
Mountain Zebra	*Equus zebra hartmannae*	3.2	0.34	Slopes

periods – some in October and November, then the majority between December and March. We define the 'dry' season to run from April to the start of the primary rains, typically late December. We record the date at which water starts to collect in the pans each year, and define that as the transition to the 'wet' season. Ongava supports a range of mammalian herbivores that are candidate prey species for spotted hyaena (see Table 1). The overall herbivore density is *c.* 10.4 animals per km^2. In the dry season, herbivores congregate at waterholes, however, in the wet season, these species are distributed across the reserve.

Techniques

We used a Dan Inject CO_2 rifle system to dart free-ranging animals. With this system it is important to be able get close enough to the animal (<20 m) to get an accurate and safe shot. In 2008, to attract animals, we dragged a carcass past locations at which target animals had been observed. We called animals to the secured bait using prerecorded sounds (see Mills, Juritz & Zucchini, 2001; Trinkel, 2009 for protocols). In 2009, repeated attempts to attract hyaenas close to calling stations were unsuccessful. We therefore adopted a new strategy of waiting at lit waterholes that were known hyaena hot-spots. To assist with location of the animals after darting, we added radio-tracking devices to the darts (C. Dearden, University of Kwa-Zulu Natal).

In 2008, animals were sedated using Dormitor (reversed by Antisedan) and Zolitol and then moved at least 1 km from the darting site. Hyaenas recovering from this sedation regime became very agitated, so in 2009, we moved to Zoletil (Virbac)-based sedation and built a ventilated and padded recovery box. The hyaena allowed to recover in this box was significantly less stressed, allowed close approaches for monitoring and after a 6-h recovery period was able to move off showing no residual sedation effects.

We deployed GPS/Global System for Mobile Communications collars supplied by African Wildlife Tracking (Pretoria). We tracked collars via VHF beacons using both vehicle- and gyrocopter-based systems. GPS sampling schedules were set at fine-scale (15 min) for 17.00–08.00 hours Western Central African Time (WCAT), and otherwise at one hourly intervals (08.00–17.00 hours WCAT). GPS data were downloaded and imported to spreadsheets and our in-house Geographic Information System for further analysis. All descriptive statistics are reported as mean ± standard deviation, except where stated. Distances between successive GPS points were calculated using the great circle formula (http://en.wikipedia.org/wiki/Great-circle_distance). For each pair of successive GPS fixes, we calculated distance moved and normalized by interval duration to give 'movement rate'. This compensates for irregular sampling when GPS fixes fail (Hayward *et al.*, 2009).

To analyse periods of activity, we combined all contiguous 'active' intervals, where active was defined as moving faster than 0.2 km h^{-1} between successive GPS fixes. We called this sequence an 'active track'. Each active track has at least three points and may include single intervals in which the speed drops below 0.2 km h^{-1}. We defined a 'waterhole visit' to be one or more GPS locations recorded within 500 m of an open waterhole. We defined a 'daily rest site' to be the GPS location taken up by the hyaena for the longest interval in any day (00.00–23.59 hours).

Home ranges were calculated using minimum convex polygons (MCPs; Hayne, 1949), with more detailed assessments of use of space undertaken using utility distributions (UDs) calculated using a local convex hull methodology (*a*-LoCoH; Getz & Wilmers, 2004; Getz *et al.*, 2007). The *a*-LoCoH method performs better than other methods (MCP and parametric kernel construction methods) at estimating UDs for data that are nonuniform, contain unused areas and are constrained by hard boundaries (Getz *et al.*, 2007). In particular, the *a*-LoCoH method is not sensitive to outlying points.

To explore use of terrain, we implemented the methods proposed by Nathan *et al.* (2008) and Getz & Salz (2008) to overlay our movement data on landscape features. For this analysis, we considered simply a rectangular landscape raster matrix of 50 × 50 m cells, encoded with five parameters per cell: altitude, aspect (flat/sloping), slope parameter (direction/shape), water and general habitat type (barren, grassland, scrub, *Mopane-/*, *Cataphractus-/*, *Acacia*-dominated). We defined 'elevated' to be ground that is at least 50 m higher than the surrounding plains. We used an automated weather station (Davis WeatherPro) to measure rainfall during the study periods.

Results

GPS data

We deployed GPS collars on two hyaenas, SA148 (opportunistically) and AF250 (targeted as an adult female). We classified hyaena SA148 as a sub-adult female based on size, pelage pattern (high density of dark spots) and examination of genitalia. Female hyaena AF250 had clearly enlarged mammary glands, either at that time of nursing or recently having nursed cubs.

We recorded fine-scale GPS data for both hyaenas (SA148, 29/08/2008–02/10/2008, 36 days, 2086 points; AF250 30/10/2009–16/02/2010, dry season 54 days, 3282 points; wet season 55 days, 3172 points). For both individuals, GPS acquisition rates fell off significantly during daylight hours (SA148, 12.00–18.00 hours, 15%; AF250, 12.00–18.00 hours, 60%). The GPS acquisition rate during the daily 15-h fine-scale sampling period

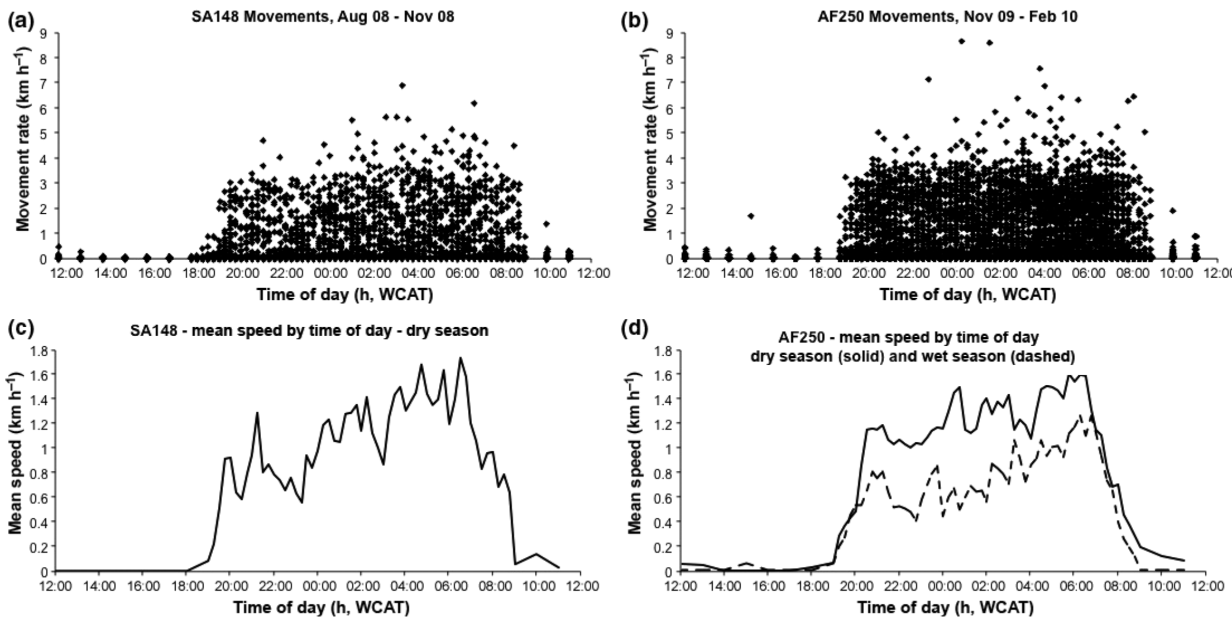

Fig 2 Daily Movement Patterns. (a) SA148, scatterplot of movement rate with time of day at the end of that interval, 36 days. (b) AF250, scatterplot of movement rate with time of day at the end of that interval, 109 days. (c, d) Mean movement rate at time of day for SA148 and AF250 (solid – wet season; dashed – dry season). Sunrise/sunset range in study periods 05.17–06.07/17.49–18.35 hours Western Central African Time, respectively

Table 2 Analysis of active tracks. Descriptive statistics for all contiguous intervals where a speed of more than 0.2 km h^{-1} was recorded between successive 15-min GPS samples (minimum two points). For each active track, duration refers to the total time active, distance is the total distance covered for that track, and track speed is the mean speed for the entire track. The number of points that occurred in plains habitat is expressed as a percentage of the total number of points. Data presented as Mean ± SD, (Min–Max)

	SA148 – Dry	AF250 – Dry	AF250 – Wet
Number of active tracks (n)	58	93	94
Duration (min)	220 ± 163 (27–600)	175 ± 164 (15–1050)	127 ± 106 (15–450)
Distance (km)	7.361 ± 6.249 (0.120–25.894)	6.964 ± 6.721 (0.084–29.682)	4.184 ± 4.317 (0.190–20.661)
Duration of longest track	10 h 00 m	8 h 45 m	7 h 00 m
Track speed (km h^{-1})	1.844 ± 0.651 (0.239–3.310)	2.153 ± 0.820 (0.290–4.220)	1.767 ± 0.624 (0.255–3.257)
% Track in plains habitat	17.1 ± 22.9 (0–70.6)	11.6 ± 20.8 (0–100)	19.7 ± 26.6 (0–100)

GPS, Global Positioning System.

(19.00–09.00) was 86.2% (SA148) and 96.5% (AF250). When seen by direct observation (four instances), SA148 was alone (twice) or with one other hyaena (twice), while AF250 was observed on five occasions, on each occasion with one or two mobile cubs (2nd phase of lactation, per Boydston *et al.*, 2003) and on three of those occasions as part of a group of 4–6 hyaenas.

Movement

For each animal, we examined the relationship between movement rate and time of day (Fig. 2). A clear pattern of activity, commencing at about 18.00 hours (just after sunset) and terminating after 09.00 hours (3 h after sunrise) is evident. Neither hyaena was active in the period 12.00–18.00 hours. The adult female showed a general reduction in movement patterns in the wet season. Both hyaenas showed a peak in daily activity around sunrise (close to 06.00 hours during all study periods; Fig. 2, Panels C and D). Overall daily activity rates were 52.6% for SA148, 50.3% for AF250 dry season and 38.1% for AF250 wet season.

Active tracks

A total of 58 and 187 active tracks were recorded for SA148 and AF250, respectively (see Table 2). Both hyaenas had similar daily active track frequencies (SA148: 1.61 tracks per 24 h, AF250: 1.63 tracks per 24 h). In general, active tracks avoided the existing road network, except for cleared paths next to the southern boundary fence (rarely used by vehicles).

There was no significant difference between active track durations and distances for the dry season movements of SA148 and AF250; however, AF250's wet season active tracks were of significantly shorter duration ($t_{157} = 2.368$, $P < 0.02$, comparing means, assuming unequal variances) and distance ($t_{157} = 3.361$, $P < 0.001$) than those for the dry season. Both hyaenas showed a strong correlation between active track duration and distance travelled (SA148-Dry: $R^2_{58} = 0.940$; AF250-Dry: $R^2_{93} = 0.892$; AF250-Wet: $R^2_{94} = 0.946$; All $P < 0.001$), and there were no significant differences between their active track speeds. We mapped each GPS point in each active track onto our landscape data and assessed the underlying features. On average, 80–88% of active track time was spent away from the plains areas of the reserve.

Waterholes

We analysed each active track to determine the frequency of visits to waterholes. For SA148 (dry season), 29 of 58 active tracks (50%) included a waterhole visit. For AF250, 34 of 93 (37%) dry season and 29 of 94 (31%) wet season active tracks included a waterhole visit. The time distribution of these visits was similar for both hyaenas, with nearly 80% of all visits occurring before midnight (17.00–21.00 hours: 43.5%; 21.00–00.00 hours: 35.9%; 00.00–03.00 hours: 17.4%; 03.00–09.00 hours: 3.2%).

To assess drinking dependence, we computed the time interval between active tracks that visited waterholes. The distributions of these intervals were highly skewed (SA148 median 17.6 h, three intervals>2 days, maximum 3 days; AF250 dry season median 22.6 h, four intervals>2 days, maximum 7 days; AF250 wet season median 19.4 h, five intervals>2 days, maximum 11 days). For SA148, no rain fell in the study period; however, for AF250, all large

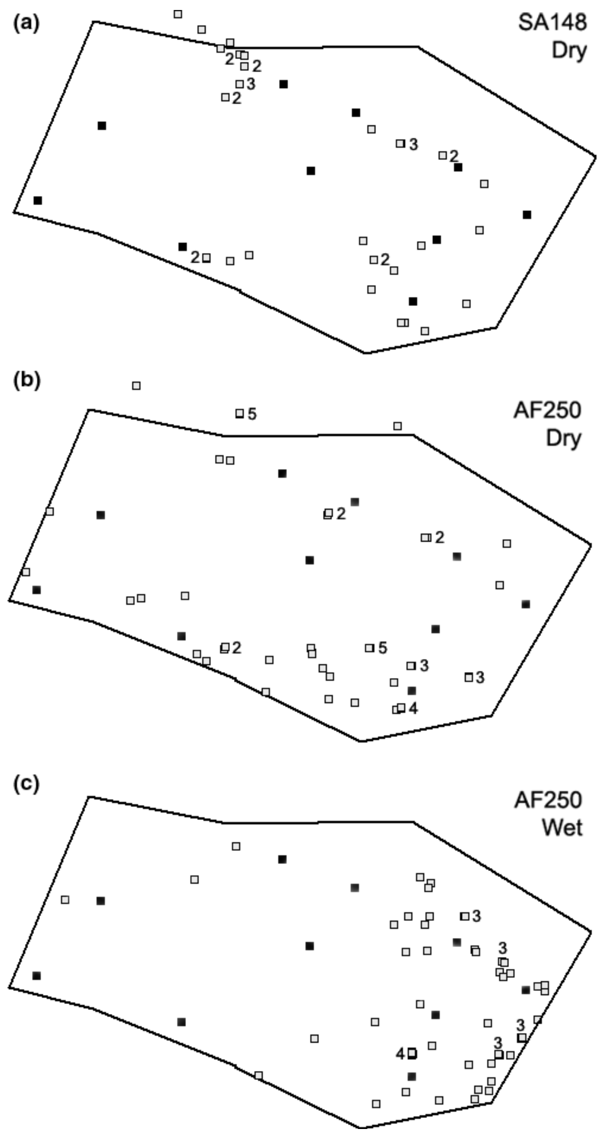

Fig 3 Daily Rest Sites. Distribution of daily rest sites (grey squares) for SA148 dry season 2008 (a) and SA250 dry season 2009 (b) and wet season 2009/2010 (c). Numbers indicate frequency of visits for sites with overlapping Global Positioning System locations. Dark squares are waterhole locations during all study periods

rainfall events (>10 mm in 1 day) were associated with increased drinking intervals.

As five of the ten waterholes open in these study periods have associated human activity (HA) and night lighting (lodges, dwellings), we assessed whether the hyaenas were biased in their selection of waterhole. SA148 showed no preference for either type of waterhole (17 HA, fourteen remote). SA250 preferred remote waterholes in the dry season (14 HA, 25 remote), but showed a significant preference for waterholes with HA in the wet season (28 HA, seven remote) ($P < 0.001$, Fisher's Exact Test, two-sided). In all study periods, the range covered by the hyaenas contained both types of waterholes.

Rest sites

Figure 3 shows the geographic distribution of daily rest sites for the study period. These sites were nonuniformly distributed on elevated ground across (and outside) the reserve. While some rest sites were revisited (up to five times), there was not a single occasion when a daily rest site was used by the same hyaena on consecutive days. All daily rest sites were located away from roads and tracks used by vehicles. Only three of the 36 daily rest sites used by SA148 in 2008 were used by AF250 the following year. In each instance, these were sites that were visited by AF250 more than once during the study period.

Use of space

Having a fine-scale record of GPS locations allows a detailed examination of use of space. Figure 4 (left-hand panels) shows all consecutive GPS locations linked by a solid line. Clusters of points indicate preferred locations. Both hyaenas moved outside Ongava during the dry periods, travelling up to 5 km into neighbouring ENP. Hyaena AF250 showed a contraction of range in the wet season. Conventional home range analysis using MCPs does enumerate these differences (SA148: 239.6 km^2; AF250 dry season: 365.9 km^2; AF250 wet season: 232.1 km^2), but it is clear from examination of the use of space that the movement profiles are nonuniform. We therefore used the a-LoCoH method to compute UDs for these spatial data. The right-hand panels in Fig. 4 show 20% UD intervals as grey-scale coded isopleths and show that areas of high use (darker zones) are small relative to the full UD, and that some areas contained within the UD boundary are not used at all (white zones). The full UD (100% isopleth) areas are smaller than the home ranges computed by MCP (SA148: 165.4 km^2; AF250 dry season: 314.6 km^2; AF250 wet season: 159.3 km^2), and in each case, the 50% isopleth areas are *c.* one-fifth of the full UD area.

We analysed how the UDs map on to the terrain features of Ongava (see also Fig. 1). The majority of daily rest sites were located within the area defined by the 50%

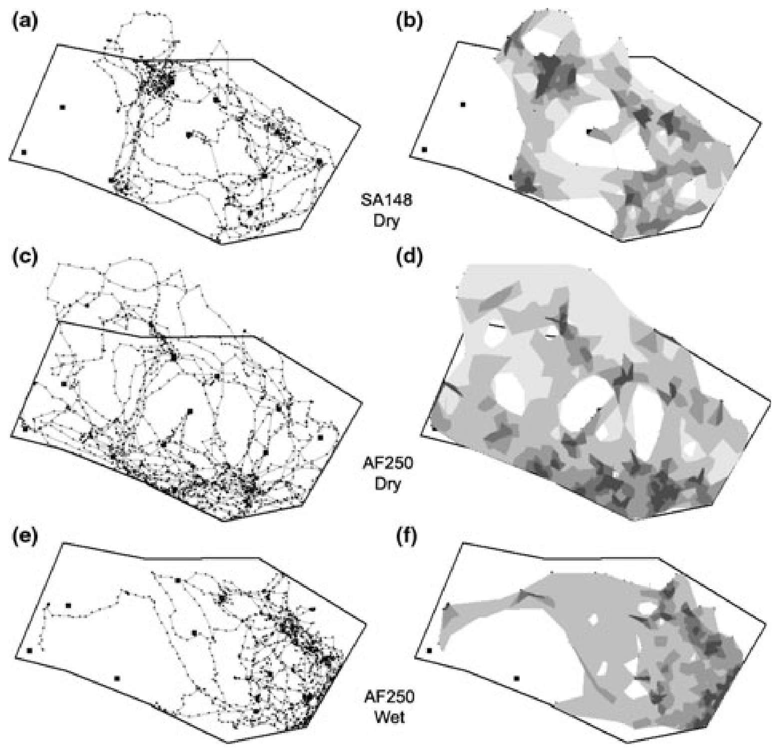

Fig 4 Use of Space. Left-hand panels: Full track plots for all consecutive Global Positioning System (GPS) locations for SA148 (a), AF250 dry season (c) and AF250 wet season (e). *a*-LoCoH Utility Distributions (b, d & f) for the same GPS data shown as five isopleth levels from 100% (dark) to 20% (light) reflecting relative use of space. Areas remaining in white were not used. Isopleth areas SA148: 100% 165.4 km^2, 80% 117.4 km^2, 60% 52.4 km^2, 40% 22.2 km^2, 20% 7.8 km^2; AF250 dry: 100% 314.6 km^2, 80% 211.2 km^2, 60% 79.7 km^2, 40% 36.5 km^2, 20% 12.6 km^2; AF250 wet: 100% 159.3 km^2, 80% 159.3 km^2, 60% 50.9 km^2, 40% 22.5 km^2, 20% 7.2 km^2; Waterholes active in the relevant study period are shown as closed squares

UD (SA148: 34 of 36, 95%; AF250 dry season: 51 of 54, 95%; AF250 wet season 48 of 55, 87%). About 70% of daily rest sites for AF250 were on sloping terrain (40 of 54 dry season; 27 of 55 wet season), while more than 85% of daily rest sites for SA148 were on sloping terrain (31 of 36). At least 50% of the sloping sites were south-facing. All daily rest sites for SA148 and more than 90% of AF250's daily rest sites (51 of 54 dry season; 50 of 55 wet season) were located in *Acacia*-dominated habitat.

Discussion

The data reported here for the detailed movements and use of space of two spotted hyaenas on Ongava Game Reserve show that they had predictable daily activity patterns – invariably at rest between 09.00 and 18.00 hours, with a peak of activity in the 2-h period around sunrise. Both hyaenas exhibited one or two active periods each night, presumably hunting and foraging for up to 10 h and travelling as far as 30 km. Waterholes were visited, predominantly before midnight, when no significant rainfall events had occurred. Daily rest sites were widely distributed across the reserve, typically located on elevated ground and never revisited on consecutive days.

In the dry season, both the sub-adult female and the adult female made extensive use of the reserve, plus adjacent areas in ENP via the permeable northern boundary; at no time did either animal cross the electrified boundaries. All exits to ENP were matched by a re-entry to Ongava, minimizing risk of conflict with neighbouring farmers (Woodroffe & Ginsberg, 1998). The UDs showed a non-uniform use of space, with both animals avoiding the plains. We saw no evidence of systematic use of particular locations (possible dens) by either animal during the study periods.

The drop-off in GPS fix success during daylight hours corresponds with the time that both animals occupied their rest sites, suggesting that the local features of the rest site obscured access to the GPS satellite network (also reported for leopard *Panthera pardus* – Swanepoel, Dalerum & Van Hoven, 2010). This is consistent with hyaenas using caves, dens and other hidden locations to rest. The drop in acquisition rate was greater for the sub-adult, suggesting that her rest sites were particularly well concealed. Most activity avoided the reserve road network, supporting the fact that spotted hyaenas are rarely seen by vehicle-based observers on Ongava.

The nocturnal/crepuscular activity times for these hyaenas are in agreement with those in other studies (Mills, 1990; Hayward & Hayward, 2006; Kolowski *et al.*, 2007), and also in temporal alignment with the activity patterns of lions on the reserve (see also Hayward & Hayward, 2006). We found that these hyaenas had higher overall activity levels (>50% dry season), compared with other locations: 31% (Kalahari Gemsbok Park); 27.5% (Kruger National Park); and 31.5% (Masai Mara National Park). Our activity levels suggest these hyaenas were active for about 12 h in each 24, again longer than the average of 7 h reported by Hayward & Slotow (2009). This may reflect the strict definition of 'active' that we were able to apply with fine-scale GPS data, but also may reflect availability of food or activity of other sympatric carnivores.

The movement rate of the Ongava hyaenas specific to active foraging was 2.0–2.3 km h^{-1}; however, the mean rate across nocturnal periods (*c.* 1 km h^{-1}) was similar to that found by Kolowski *et al.* (2007). The duration of our 'active tracks' (dry season mean *c.* 200 min) was longer than that reported for the Masai Mara ('active bouts' mean 62 min, Kolowski *et al.*, 2007). On average, these hyaenas travelled the same distances at night as the Mara hyaenas (*c.* 12 km), but significantly less than those in the Kalahari Gemsbok Park (*c.* 27 km; Mills, 1990). As noted in Kolowski *et al.* (2007), this is likely to reflect differences in home range sizes (Masai Mara: *c.* 60 km^2, Frank, 1986; Ongava: 230–360 km^2, this study; Kalahari Gemsbok Park: *c.* 1100 km^2, Mills, 1990) that are most likely a function of prey density (Tilson & Henschel, 1986) or food availability (Hayward *et al.*, 2009).

We found a significant change in use of space for the adult female between dry and wet seasons, with the wet season range being much smaller and focused on a different area of the reserve. She also made much shorter foraging trips. Spotted hyaena can change their use of space in response to seasonal variations in prey densities, such as migration and wet-season dispersal (Hofer & East, 1993; Trinkel, Fleischmann & Kastberger, 2006), but generally increase their home range size in the wet season. This hyaena preferred a different set of waterholes during the wet season, with a greater number of visits to those associated with HA. It may be that during the wet season, the vegetation offers additional cover (Kolowski & Holekamp, 2009) and that reduced guest activity during this season minimizes disturbance. Waterhole visit times were, however, similar for both hyaenas, typically in the early part of their active periods (43.5% before 21.00 hours).

The daily rest sites used by the hyaenas in this study were widely distributed and rarely re-used. Assessing their locations, we suggest that on foraging and hunting trips these hyaenas typically find safe, elevated, cool positions to use as temporary rest sites (see also Hayward & Slotow, 2009). These foraging and hunting trips occur predominantly (80–88%) on sloping terrain, and hence these hyaenas are more likely to encounter prey species that occupy these habitats. As spotted hyaenas are thought to not display any prey selectivity (Hayward, 2006), based on encounter rates, oryx and kudu, and to a lesser extent mountain zebra and other smaller browsing antelope, may be expected to be their primary prey on Ongava.

Spotted hyaenas can occupy many different habitats, and consequently home ranges can vary by a factor of 100, from as small as 13 km^2 to over 1000 km^2 (Trinkel, Fleischmann & Kastberger, 2006). The home range sizes of the Ongava spotted hyaenas (240–360 km^2 by MCP) corresponded closely with those recorded in similar terrain in ENP (160–320 km^2; Trinkel *et al.*, 2004). In terms of specific use of space as defined by the UD, the areas of the 50% UDs were all significantly less than the area of the 100% UD, typically about 20% (30–55 km^2). Both animals had multiple areas of high use distributed across the UD, as also reported for the Masai Mara (Boydston *et al.*, 2003). We do not know whether the 100% UD represents the defended home range of these hyaenas, implying a single clan (Boydston, Morelli & Holekamp, 2001), or whether excursions outside areas of high use cross into territory used by other clans.

We have shown that two female hyaenas of different ages display similarities in their detailed movement patterns and use of space. However, this small sample size may not represent the behaviour of the population in general, and additional studies will be required to assess this further. Nevertheless, given the constraints on data collection imposed by the terrain on Ongava, the GPS collar methodology has proved itself to be a valuable tool for field research in this species.

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