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Socioecology of a high-density brown hyaena population within an enclosed reserve

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Abstract
Understanding the spatial ecology of wildlife is an essential prerequisite for making informed management decisions and is of particular importance for those species residing in enclosed reserves where space use may be influenced by restricted dispersal and high population densities. As the brown hyaena *Parahyaena brunnea* is a species likely to increasingly rely on enclosed protected areas for its long-term persistence, due to the intense persecution experienced outside of protected areas, we examined the spatial ecology of 10 brown hyaenas from a high-density population, within a small (200 km^2) enclosed reserve in north-central Namibia. Spatial data, in combination with camera trap data from communal den sites, suggested six clans and at least one nomadic individual in the reserve. A mean home range size of 37 km^2 (± 21 km^2, range 16–97 km^2) was recorded, with 92% of the reserve utilized as brown hyaena home range. Whilst these home range sizes are some of the lowest recorded for brown hyaena, the degree of overlap between neighbouring clans was similar to that recorded for open systems. Given that the majority of the reserve is utilized as brown hyaena home range, options for dispersing subadults may be limited and these individuals may represent ideal candidates for translocation into other enclosed reserves as part of metapopulation management schemes.

Keywords Brown hyaena · Enclosed reserve · Home range · Permissible home range estimation · Spatial ecology · Wildlife management

Introduction

Home range behaviour is the product of decision-making processes shaped by natural selection to increase the contributions of spatially distributed resources to individual fitness (Mitchell and Powell 2004). A home range can be thought of as a cognitive map that represents an interplay between the environment and an individual's understanding of that environment (Borger et al. 2008). Home ranges therefore arise as a result of the particular tactics employed to maximize fitness in response to intrinsic and extrinsic factors (Erlinge and Sandell 1986). For example, the home range size of carnivores can be related to a number of factors including metabolic requirements based on body mass (Harestad and Bunnel 1979; Gittleman and Harvey 1982), habitat quality and reproductive attributes (Machado et al. 2017). In certain species, home range size may be influenced by sex, social dominance or spatial tactics employed by individuals. For example, male cheetah *Acinonyx jubatus* are known to employ two distinct spatial tactics, territory holder or non-territorial (floater), which, in central-Namibia have resulted in mean home range sizes of 379 km^2 (± 161 km^2) and 1595 km^2 (± 1151 km^2), respectively (Melzheimer et al. 2018). Space use by an individual can arise from a number of behavioural activities linked to fitness, such as finding food, shelter and mates (Krebs and Davies 1997). Furthermore, knowledge of spatial ecology is an important requirement for species management (Rachlow et al. 1999; Ofstad et al. 2016), especially when the species in question is of conservation concern (Owen 2013).

Whilst home range sizes and the factors determining them have received extensive attention in open systems, the home range sizes of carnivores residing in enclosed areas, and the

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impacts of fencing on the spatial ecology of such populations, has only recently received attention (Hayward et al. 2009). Such a limited understanding of the spatial ecology of wildlife in enclosed populations is concerning given the increasing frequency with which fencing is being used as a wildlife management and conservation strategy throughout Africa, where protected, fenced areas are argued to be the main strategy for species conservation (Saout et al. 2013). Within South Africa alone, there has been a rapid increase in the number of small (< 1000 km^2), enclosed reserves established during recent years, the majority of which have been developed with the twin aims of ecotourism and conservation (Trinkel et al. 2008). As large carnivores top the lists of species that visitors want to see at such reserves (Lindsay et al. 2007), these reserves often stock large carnivores at artificially high levels (Tambling and du Toit 2005).

The limited dispersal of wildlife in enclosed areas can lead to increased population densities (e.g. Graf et al. 2009; Edwards et al. 2019), which may, in turn, influence space use by individuals (Owen-Smith 1982; Rachlow et al. 1999). Not only are the home ranges of large carnivores in enclosed areas substantially smaller than those in open systems but also fenced carnivores often use less space than the space available to them (e.g. Lehmann et al. 2008; Darnell et al. 2014). These uncharacteristically small carnivore home ranges are attributed to the high density of prey in enclosed areas, whose populations are inflated due to restricted dispersal in fenced areas (Hayward et al. 2009). However, Owen (2013), found a prey-rich environment did not translate to small home ranges for leopard (*Panthera pardus*); rather, home range size was determined by foraging strategies, matching the resources of their preferred prey and riparian areas. Additionally, the use of space within enclosed areas may be influenced by the presence and space use of dominant competitors. For example, within Hluhuwe-iMfolozi Park, South Africa, Darnell et al. (2014) found African wild dog (*Lycaon pictus*) avoided lions (*Panthera leo*) but not spotted hyaena (*Crocuta crocuta*). Although carnivores are known to be highly adaptable in their use of space, management interventions may be required if adaptations within enclosed areas become maladaptive, e.g. home ranges become too small to afford reproductive opportunities or individuals experience unsustainable levels of intra- or interspecific competition.

Brown hyaena (*Parahyaena brunnea*) is the rarest member of the Hyaena family, with an estimated population of just 10,000 mature adults and is listed as Near Threatened by the International Union for Conservation of Nature (IUCN) (Wiesel 2015). Experiencing intense persecution outside of protected areas across its range, following real or perceived involvement in human-wildlife conflict (Wiesel 2015), brown hyaena is one species likely to benefit from the existence of enclosed protected areas for its long-term persistence. However, given that the species harbours an extremely low genetic diversity at both the mitochondrial and nuclear level (Westbury et al. 2018), brown hyaena populations within enclosed areas will require intensive metapopulation management to ensure genetic integrity and long-term persistence. Whilst brown hyaena home range size has been known to vary by an order of magnitude in open systems (Richmond-Coggan 2014), their spatial ecology within enclosed systems is limited to a number of studies from reserves in South Africa into which the species was introduced (Welch et al. 2016; Richmond-Coggan 2014). Brown hyaena are a social species, forming groups known as clans, which consist of related females and their offspring and non-natal males. Individuals within a clan essentially share the same home range, and all clan members are involved in raising cubs at communal den sites (Mills 1990). In addition to clan-living individuals, approximately 8% of the population consists of nomadic individuals, described as those moving through several clan territories with no obvious regard for territory boundaries, and having no lasting relationships with conspecifics (Mills 1990). Given the complex social structure and large variation in home range size across its range, coupled with its conservation status, the brown hyaena presents an interesting and important candidate for examining spatial ecology within an enclosed system.

Here, we examined the socioecology of a high-density brown hyaena population living within a fully enclosed reserve in north central Namibia, using GPS collars fitted to 10 brown hyaenas. Using permissible home range estimation (Tarjan and Tinker 2016) to define home ranges, we examined how many brown hyaena clans were present at the study site, the home range sizes of individual hyaenas and the degree of home range overlap both between and within clans. Given the high density of hyaenas within the study area, we predicted that multiple clans would be present. Mills (1982) previously described brown hyaena home range size to be related to the distribution of food resources within an area. Given the relatively high year-round abundance of herbivores and high density of leopards within the reserve, from which brown hyaena are known to kleptoparasitise and scavenge kills (Edwards et al. 2019), it was predicted that brown hyaena home ranges would be small in comparison to open systems, and a large percentage of the study site would be utilized as brown hyaena home range. Furthermore, as brown hyaena are a highly territorial species (Mills 1990), it was predicted that neighbouring clans would experience small degrees of home range overlap. Previously, studies have shown animals may spend longer amounts of time in areas of their home range adjacent to impenetrable barriers and spend time travelling along such barriers (Ruby et al. 1994; Peaden et al. 2017) Therefore, we also examined if brown hyaenas use the areas directly adjacent to the fence lines more often than expected, which might be expected if fences represented a barrier to movement.

Methods

Study site

The study was conducted on Okonjima Nature Reserve (ONR), a privately owned reserve, located approximately 50 km south of Otjiwarongo, north-central Namibia. The ONR perimeter fence traces a central plateau, at an average altitude of 1600 m, surrounded by the Omboroko Mountains. The 200 km^2 reserve receives an average annual rainfall of 450 mm, which falls during the hot-wet season from October to March. Perennial water is provided from a total of 18 artificial waterholes across the reserve. The vegetation is predominantly tree and scrub savannah, interspersed with silver terminalia *Terminalia sericea* and several acacia species. The ONR is fully enclosed by an electrified perimeter fence, of 2.40 m in height, with the first 1.80 m having a mesh wire, with 10 strands of electrified wire of 7000–10,000 V, which was erected in 2010. Two tourism lodges, staff housing and offices are situated in the south-east section of the reserve, and the 20 km^2 surrounding these buildings is also enclosed with an electric wildlife proof fence, resulting in a total of approximately 180 km^2 of the ONR over which a variety of wildlife occur.

The ONR perimeter fence was erected around a naturally occurring brown hyaena population, which was recently estimated to occur at a density of 24.01 brown hyaena/100 km^2 (Edwards et al. 2019). No species management has taken place since the erection of the fence. Leopard *Panthera pardus* density within the reserve is relatively high, having been estimated at 14.51 adult/100 km^2 during a 2015–2016 density survey (Noack et al. 2019), in comparison to an estimated density of 3.60 leopard/100 km^2 from the commercial farmlands bordering the Waterberg Plateau Park (Stein et al. 2011), approximately 100 km straight line distance from the study site. Herbivore densities within the ONR are also high, for example 244 kudu *Tragelaphus strepsiceros*/100 km^2, 290 impala *Aepyceros melampus*/100 km^2 and 420 gemsbok *Oryx gazelle*/100 km^2 were recorded during the 2018 aerial game survey.

GPS collars

Between January 2018 and November 2018, 10 adult brown hyaenas, constituting four males and six females, were immobilized and monitored with GPS collars, across ONR, for spatial data collection. Brown hyaenas were either free darted ($n = 6$) or captured within a large (approx. 2 m × 3 m) wire box trap internally lined with industrial grade conveyor belt rubber, fitted with a live-feed camera and remotely triggered door ($n = 4$). The internal rubber lining ensured hyaenas could not damage their teeth or foot pads by biting or digging at the wire. The live-feed camera and a remotely triggered door system ensured the capture team was able to dart the hyaena in less than 45 min after closing the door, minimizing stress on the animal. Brown hyaenas were darted using a Pneudart projector, using an average weight of 50 kg per animal for dose calculation. A combination of Ketamine (Intersana, Windhoek, Namibia) 125 mg, Medetomidine 2.5 mg (Kyron Laboratories, Johannesburg, RSA); Butorphanol 12.5 mg (Kyron Laboratories, Johannesburg, RSA) was used. If sedation was not deep enough, Ketamine at a dose of 0.5 mg/kg (approx. 20–25 mg) was intravenously injected via the saphenous vein. A minimum time lapse of 45 min was used before the antidote 'Antisedan' (Zoetis, Santon, South Africa) was given, at dose of 2.5 mg intravenously and 5 mg intramuscularly, and 'Trexonil' at 12.5 mg intravenously and 25 mg intramuscularly (Wildlife Pharmaceuticals, White River, South Africa). Hyaenas were collared with Wireless Wildlife (Potchefstroom, RSA) GPS collars, from which data were remotely transferred via ultra-high frequency (UHF) base stations and repeaters. As brown hyaena are mainly nocturnal (Mills 1990), GPS collars were scheduled to take one fix every 30 min at night (19:00 to 07:00 local time) and one fix every 2 h during the day.

Communal den camera traps

To confirm clan membership of GPS monitored individuals, camera traps were used to monitor communal den sites (i.e. sites used by clans to raise cubs, once cubs reach the age of 3 months, before this the cubs live at a natal den which only their mother attends, with adult clan members of both sexes bringing food back for the cubs (Mills 1990)). The repeated presence of an individual at a den site was assumed to be an indication of an individuals' membership within a clan. Dens were located by plotting brown hyaena GPS data in QGIS 2.8.4 Wien (Quantum GIS Development Team 2015), and connecting consecutive GPS points by lines, using the 'points to path' function. When points and lines are plotted in this way, dens reliably show up at clusters of points, with movement lines from all directions centring on the den site (Wiesel et al. 2019). Each den site was monitored using a single Cuddeback X-Change 11,339 infra-red camera trap (Non Typical Inc., Wisconsin, USA), housed within a protective Cuddesafe metal box, mounted on a metal pole. Camera traps were focused on the main den burrow entrance, set to medium sensitivity, three photos per trigger and 1 min between triggers, at a photo quality of 20 M-pixel. Individuals were identified by the lead author using the individually unique front leg stripe patterns (Mills 1990).

Data analysis

Permissible home range estimation

Brown hyaena space use was directly restricted by ONR's fences, and hyaenas frequented the areas adjacent to the fenced reserve boundary. To accommodate these complex

boundaries in home range estimates, home ranges were defined using Permissible Home Range Estimation (PHRE) (Tarjan and Tinker 2016). Kernel density estimation was initially performed in three dimensions, comprising x and y Cartesian coordinates and distance to the inner and outer fence lines. We employed the default smoothing parameter in the 'ks' package (Duong et al. 2019) in R (R Core Development Team 2014). Using PHRE, these estimates were then converted to probability densities at Cartesian coordinates, and the 95% probability kernel was used to define home range boundaries, whilst the 50% probability kernel was used to define core-use areas.

Brown hyaena spatial data were likely to be autocorrelated (the violation of the assumption of independence between successive points (Legendre 1993)), due to their feeding ecology; individuals were observed localizing on parts of the home range when large carcasses were available. For example, a camera trap set at a giraffe *Giraffa giraffa* carcass showed individual brown hyaenas utilizing the carcass several times daily for up to 4 days, and individual brown hyaenas have been observed around leopard kills for up to 2 days (S. Edwards, pers. obs.). Whilst location observations may be autocorrelated on the scale of days, the duration of tracking any individual hyaena (range 93–500 collar days) vastly surpasses this period of autocorrelation and location data were used exclusively to describe space use during the course of the study. Furthermore, the issue of autocorrelation has become a long-debated topic within the literature regarding its impact on home range estimates (Legendre 1993). The removal of autocorrelated data prior to analysis can result in the loss of biological information and fine-scale details of movement (Kie et al. 2010). Furthermore, it has been argued that the original work describing the negatively biased estimates caused by autocorrelation is based on a flawed approach (Otis and White 1999). De Solla et al. (1999) found subsampling of spatial data did not reduce autocorrelation, and that home range size was better represented by autocorrelated data, and recommended that a maximum number of observations, with constant time intervals are used to increase both accuracy and precision of home range estimates. Therefore, GPS positions were sub-setted to every 2 h, producing consistent gaps between positions during day and night for use in home range estimation.

Compositional analysis

Compositional analysis (Aebischer et al. 1993) was used to assess if brown hyaena preferentially use areas adjacent to fences. Compositional analysis uses the individual animal as a sampling unit and is robust to autocorrelation of spatial data points (Aebischer et al. 1993); therefore complete spatial datasets were used. To perform the compositional analysis, a buffer area of 50 m inside of the fence was created (*c.f.* Welch et al. 2016) within QGIS 2.8.4 Wien (Quantum GIS Development Team 2015), and the proportion of each individual brown hyaena's home range occupied by the buffer was used as a representation of site availability. The number of GPS positions within the buffer area for each individual was used as a representation of site use. Compositional analysis was performed using the package in statistical programme R (R Core Development Team 2014), using the package 'adehabitatHS' (Calenge 2006). Within the analysis, chi-square (χ^2) with an alpha value of 0.05 was used for significance testing, and, as all brown hyaena home ranges included areas adjacent to the fence, all individuals were included.

Results

Due to the period over which the individuals were monitored, variations in battery life and collar failures, the number of GPS positions and collar days acquired varied between individuals (Table 1); the number of GPS positions collected per individual ranged from 2791 to 15,099, and the number of collar days achieved ranged from 93 to 500 per individual. No GPS positions from any individual fell outside of the ONR boundary fence, and thus for brown hyaena, the fence is considered impermeable.

During the study period, spatial data indicated five communal den sites (two belonging to the same clan who moved dens during the study period) across ONR (Fig. 1). Brown hyaenas are known to only use communal dens whilst raising cubs; therefore, the absence of cubs recorded for the two of the collared individuals during the study period explains why dens were not detected for all individuals. Camera trap data indicated one to two collared individuals visiting each den site (Table 2). Both camera trap and spatial data indicated individual hyaenas did not visit more than one den site, with the exception of OHB02's clan members visiting both den sites the clan used during the study period. Individual hyaenas OHB05, OHB04, OHB06 and OHB09 were not recorded at any communal den site during the study period.

Brown hyaena home ranges, as expressed by 95% KD contours, varied between individuals and ranged from 16 km^2 to 97 km^2, with a mean home range of 37 km^2 (± 21 km^2) (Table 1, Figure 2). Brown hyaena core areas ranged in size from 2 km^2 to 12 km^2, with a mean size of 6 km^2 (± 3 km^2). Eight of the collared brown hyaenas used only specific sections of the ONR, suggesting multiple social groups, each with defended territories. Individuals OHB05 and OHB09 ranged across the home ranges of five and four clans respectively, suggesting them to be potentially nomadic individuals. When removing nomadic individual home ranges, mean home range size was reduced to 28 km^2 (± 8 km^2) and core area to 5 km^2 (± 2 km^2).

Table 1 Summary of brown hyaenas collared, total spatial GPS data collected on ONR and home range sizes, as expressed by 95% KD contours, and core area sizes, as expressed by 50% KD contours. Dashed horizontal lines used to group clan members and shaded grey used for potentially nomadic individuals

ID	Sex	Monitoring start date	# of GPS positions	# monitoring days	Age and breeding status*	95 KD (km^2)	50 KD (km^2)
OHB01	M	25/01/2018	7017	228	Adult	29	6
OHB03	M	29/01/2018	4299	152	Adult	23	4
OHB02	F	8/2/2018	13,935	353	Adult – confirmed breeder	32	6
OHB04	F	2/12/2018	12,231	500	Adult – confirmed breeder	25	4
OHB06	F	6/4/2018	9072	345	Adult – confirmed breeder	16	2
OHB07	M	5/6/2018	2791	93	Adult	27	4
OHB08	F	18/06/2018	11,766	386	Adult – confirmed breeder	44	9
OHB10	F	14/11/2018	6037	227	Adult – confirmed breeder	33	6
OHB05	M	15/03/2018	15,099	476	Adult	97	12
OHB09	F	12/10/2018	2280	136	Adult – presumed breeder	41	5

*Breeding status of females; confirmed if cubs were recorded during monitoring, presumed status given if teats, upon inspection during sedation for collaring, looked long, i.e. cubs had previously suckled from them

Home range overlap was calculated as the degree of overlap between two 95% KD home ranges, taken as the percentage of the largest home range within the pair. Due to the movement of potentially nomadic individuals across multiple clan home ranges, OHB05 and OHB09 were excluded from overlap analysis. Inter-clan individual home range overlap ranged from 0% to 22%, with a mean of 10% (± 7%) (Table 3). Intra-clan individual home range overlap was calculated for four individuals, comprising two clans—OHB01 and OHB03 from the clan within the southeast section of ONR and OHB07 and OHB08 from the northwest. Home range overlap within the southeast clan was 72%, whilst within the northeast clan, it was 57%. Whilst inter-clan overlap was high based on the 95% KD home ranges, there was no core overlap based on the 50% KD

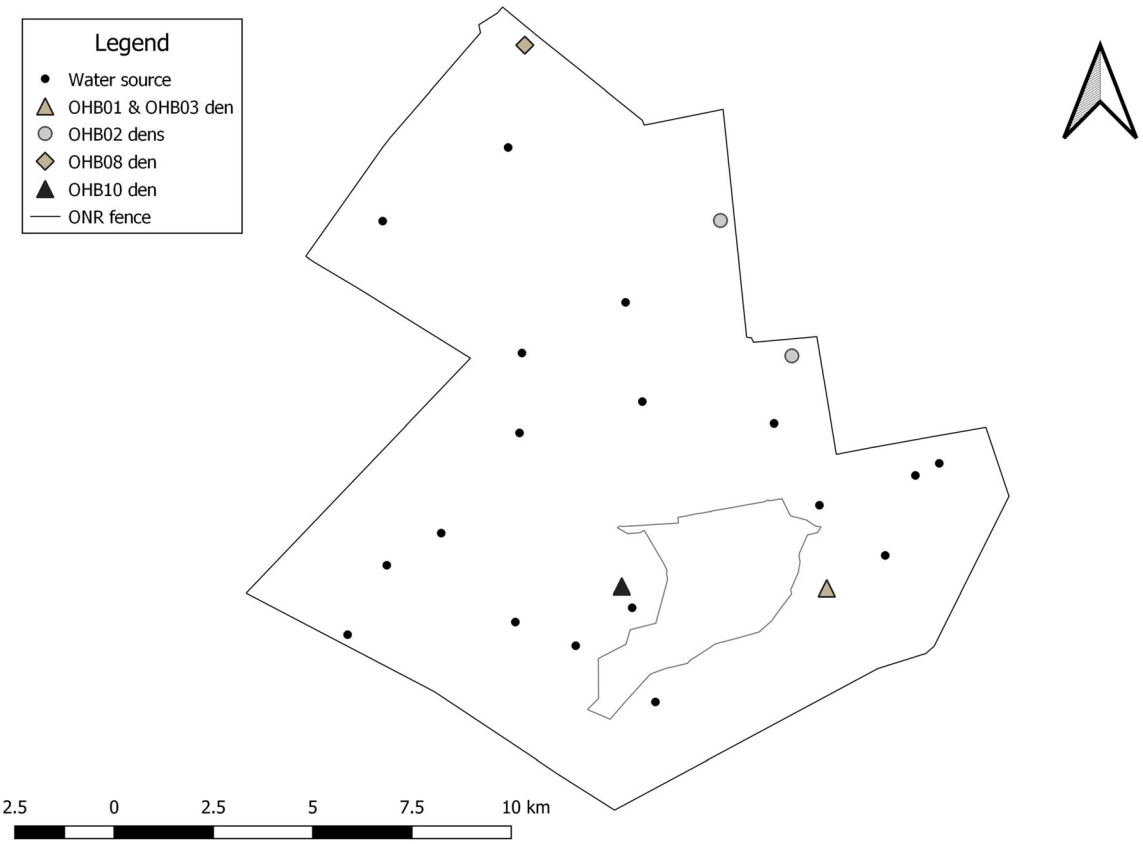

Fig. 1 Map of monitored brown hyaena communal den sites and water sources on ONR

Table 2 Summary of brown hyaena communal den sites monitored on ONR

ID	Monitoring start	Monitoring end	Total camera trap days	Minimum number of adults recorded	Minimum number of cubs and subadults recorded
OHB01 & OH-B03	11/1/2019	Ongoing at time of writing	> 200	8	6
OHB02 *	13/2/2019	Ongoing at time of writing	> 120	5	2
OHB07 & OH-B08	21/11/2018	11/6/2019	202	4	3
OHB10	17/12/2018	Ongoing at time of writing	> 200	3	3

*Two den sites were detected for OHB02, with den sites being changed during the study period

home ranges; however, intra-clan core area overlap was calculated at 40% of the southeast clan members and 17% for the northwest clan members (Table 3).

The use of camera traps at den sites confirmed that when two individuals had large percentages of home range overlap (> 50%); they were part of the same social group, i.e. both collared individuals showed frequent visits to the communal den sites. Communal den camera trap data and home range analysis suggested there to be six clans present within ONR. Two individuals, OHB05 and OHB09, covered large sections of the reserve without visiting known communal den sites and are thus classed as nomadic individuals. Combining all 95% KD home ranges from collared individuals, a polygon of 171 km^2 was produced, equating to a total of 92% of the ONR being occupied by brown hyaena home range (Fig. 2). Compositional analysis indicated brown hyaenas did not show selection for areas directly adjacent to the fences ($\chi^2 = 0.67$, $p = 0.06$).

Discussion

Understanding the spatial ecology of wildlife residing in enclosed reserves is an important prerequisite for producing informed management guidelines and sustainable wildlife populations, and thus ensuring such areas are beneficial for conservation (Lehmann et al. 2008). Using high-resolution

Fig. 2 Home range estimates for individual brown hyaena on ONR and all home ranges areas merged to show the extent of ONR occupied by brown hyaena home ranges in the final map; 95% KD home ranges represented by grey polygons, and 50% KD core areas represented by black polygons

Table 3 Summary of inter- and intra-clan overlap of brown hyaena within ONR

Overlap type	ID pair	Overlap (km^2)	% overlap
Inter-clan	OHB01-OHB02	2	5
Inter-clan	OHB02-OHB03	1	3
Inter-clan	OHB02-OHB04	3	11
Inter-clan	OHB02-OHB08	7	17
Inter-clan	OHB02-OHB07	1	2
Inter-clan	OHB04-OHB08	4	9
Inter-clan	OHB04-OHB07	0	0
Inter-clan	OHB04-OHB10	2	6
Inter-clan	OHB06-OHB10	7	22
Inter-clan	OHB06-OHB01	5	16
Inter-clan	OHB06-OHB03	4	18
Intra-clan	OHB01-OHB03	21	72
Intra-clan	OHB07-OHB08	25	57

GPS data, we were able to estimate brown hyaena home range and core area sizes in a small, enclosed reserve in Namibia, and found the home range estimates produced were some of the smallest recorded for the species. Within an area of approximately 180 km^2, a total of six clans and two nomadic individuals were recorded, with the majority (92%) of the reserve currently utilized as brown hyaena home range. Despite the presence of the impermeable fence and previous research suggesting that animals preferentially use fence lines (Rhodes and Rhodes 2004), brown hyaena were not found to significantly select for areas adjacent to the fence. This could imply that hyaena have learned that fences are an impenetrable barrier. They would therefore not be expected to revisit the fence line unless they experience social pressure or dire shortages of resources.

Brown hyaena home ranges, as estimated by comparable kernel density estimates, are known to vary widely across their range; from 32 km^2 in the coastal Namib desert (Skinner et al. 1995) to 2670 km^2 from the inland section of the Sperrgebiet National Park, western Namibia (Wiesel 2006). The home range estimate of 2670 km^2 from Wiesel (2006) is over 14 times the size of the section of the ONR on which brown hyaena occur, illustrating the behavioural plasticity of the brown hyaenas when residing in enclosed reserves. Brown hyaena home range estimates from enclosed reserves have previously been restricted to a small number of sites in South Africa, in which Welch et al. (2016) estimated 95% kernel density home ranges of 34–63 km^2 for Shamari Private Game Reserve, 43–80 km^2 in Kwandwe Private Game Reserve and 172–205 km^2 in the Mountain Zebra National Park. Richmond-Coggan (2014) estimated brown hyaena home range size in the Madikwe Game Reserve at 121 km^2 and a mean home range size of 100 km^2 (± 53 km^2) in Pilanesberg National Park. The mean home range size of brown hyaena within ONR is therefore amongst the lowest recorded for the species from both open and enclosed systems, and notably, lower than those recorded by Welch et al. (2016) for enclosed reserves of similar size to ONR.

Mills (1982) found in the southern Kalahari that brown hyaena territory size was influenced primarily by the way food resources were distributed throughout the environment, and, more specifically, territory size was correlated with the mean distances travelled by individual brown hyaenas between successive mammalian food items. The high density of brown hyaena on ONR has been attributed to a range of factors, including the year-round high abundance of herbivores providing food resources in the form of non-violent mortalities, as well as the high density of leopard within the reserve providing additional carcass availability to the brown hyaena via scavenging and kleptoparasitism (Edwards et al. 2019). Therefore, the high abundance of food resources available to brown hyaena throughout the ONR may not only result in a high density of individuals but also, relatively small territory sizes.

When discussing the potential reasons for small home range sizes of brown hyaenas in enclosed reserves, Welch et al. (2016) suggested that the high densities of individuals in such areas may constrain individual space use. Furthermore, Welch et al. (2016) suggested that being highly territorial, the small home ranges of brown hyaenas may have resulted from territory packing to reduce overlap between neighbouring clans. Mills (1982) found within the southern Kalahari, overlap between neighbouring clans never surpassed 20%, whilst Welch et al. (2016) reported 15%–34% inter-clan overlap and 98% intra-clan overlap in Kwandwe Private Game Reserve. Within ONR, smaller levels of inter-clan overlap were found, ranging from 0% to 22%, with a mean of 10% overlap between neighbouring clans. Intra-clan overlap was also less than Kwandwe; 72% and 57% for the two clans with two clan members collared. The reasons for the smaller amount of overlap seen between ONR brown hyaenas are unclear but may reflect the differences in home range sizes and the potential for encounter rates between inter-clan individuals. The population density on ONR was higher, 24/100 km^2, compared to 15/100 km^2 on Kwandwe, and the home range sizes on ONR are smaller, equating to higher encounter probabilities which might be mitigated by a smaller degree of overlap, as a mechanism for avoiding aggressive encounters between inter-clan individuals. Alternatively, differences may result from differences in the history of the brown hyaenas in each area; the Kwandwe population was introduced 10 years prior to the study, as a founder population of six individuals, in contrast, the ONR population was naturally occurring and an unknown number of individuals were enclosed on the reserve when the predator-proof fence was erected in 2010. Recording spatial and social organization dynamics of expanding brown hyaena populations in

enclosed areas might therefore help to better understand the differences in home range overlap, and long-term monitoring of brown hyaena populations is recommended.

Nomadic individuals are estimated to make up 8% of subadult and adult brown hyaena population in the Kalahari, and 33% of the adult male segment of the population (Mills 1990). The spatial data of OHB05, coupled with his absence at any monitored communal den site on ONR suggests he is a nomadic individual; the first described for an enclosed population. When examining all movement tracks from OHB05, the data show extensive use of all parts of the reserve, with the exception of the territory of the clan of OHB01 and OHB03, which was strictly avoided (Supplementary Material 1). Such a pattern might suggest OHB05 to have previously been a breeding male within that clan, and, being an older male, his tenure has now ended and is no longer tolerated by clan members. Camera trap data, sightings and examination during collaring revealed extensive scar tissue on the neck as well as frequent fresh wounds and abscesses on the neck, indicating OHB05 to be regularly involved in fights.

The data of OHB09 shows movement across the home ranges of OHB04, OHB10 and OHB07/8. However, unlike OHB05, she does not move across the entire reserve. This female was determined to be an older individual, based on her dental wear, and the appearance of the nipples suggests she had bred previously, and like OHB05, has substantial scarring on the neck. Although limited spatial data is available for OHB09, we postulate she was previously a breeding female within a clan who has since been pushed out by a younger female. However, more spatial data would be required to confirm her status as nomadic. Given that the majority of ONR is used as brown hyaena home range, there are limited options for any nomadic individuals to avoid the territories of clans, and thus frequent fights may occur when nomadic individuals are encountered by same-sex clan individuals. Such results may suggest negative individual welfare implications for nomadic individuals in enclosed reserves and would further strengthen the argument for translocating subadults in high-density populations as part of metapopulation management schemes (Edwards et al. 2019).

Whilst the total number of nomadic individual brown hyaena on ONR is currently unknown, previous research has suggested the proportion of non-territorial individuals in enclosed populations may be higher than in open systems. For example, Rachlow et al. (1999) found that whilst the spatial patterns of white rhinoceros *Ceratotherium simum* were similar, a higher proportion of the male population were non-territorial in enclosed areas, in comparison to open systems. Rachlow et al. (1999) hypothesized this result was due to the fence restricting the dispersal of young males, which would normally move out of high-density areas to establish territories on the edges. Long-term monitoring of the entire ONR brown hyaena population using camera traps at both latrines and communal den sites should allow a better understanding of the proportion of nomadic individuals within the population in comparison to open populations.

When merging all individual brown hyaena 95% KD home ranges, a total of 92% of ONR was found to be utilized as brown hyaena home range, equating to an area of 14 km^2 currently unutilized. The area not used by brown hyaenas exists as pockets of space where no monitored hyaenas were recorded within a home range. These unused areas could be used by monitored hyaenas outside the study period or constitute the home range of an individual not collared during the study period. However, based on current home range estimates from ONR, the unused area is substantially smaller than the home ranges of individuals on ONR, and therefore, it is unlikely that ONR could support the formation of a new clan without reductions in the current home ranges of existing clans. As brown hyaena home ranges fluctuate with seasonal changes in food abundance (Maude 2005), it is possible clans on ONR may expand their home ranges during times of low food abundance, for example following the sale and removal of herbivores, and as such the 'free-space' may be utilized on a temporary basis. The long-term monitoring of hyaena spatial ecology would be of interest to see how the 'free-space' is utilized over time.

With no space available for the formation of another clan without reductions in the home range sizes of existing clans, limited options exist for dispersing brown hyaena on ONR. Within the Kalahari, Mills (1990) recorded both males and females emigrating from their natal clans, with 67% of emigrating individuals leaving their natal clans as subadults. However, only males were recorded immigrating into non-natal clans, and the ultimate fate of emigrating female brown hyaenas within the Kalahari was unknown. Whilst emigrating males on ONR may be able to successfully emigrate into non-natal clans and become breeding adults, the high density of brown hyaenas within the reserve might suggest high levels of competition for such positions, and with only six clans within the reserve, a limited number of potential positions. Males may become nomadic, either permanently, or before immigrating into a non-natal clan, as seen within the Kalahari for two out of five emigrating males (Mills 1990). The spatial data of individuals OHB05 and OHB09 suggests that both male and female nomads are potentially present on ONR.

Further research into the spatial ecology and social tactics employed by both male and female dispersing brown hyaenas on ONR and in other enclosed systems will be highly useful for producing management guidelines. Metapopulation management schemes frequently involve human-mediated movement of individuals between fragmented populations to maintain the genetic integrity of such populations (Akcakaya et al. 2007). The successful integration of a young female brown hyaena, translocated due to human-wildlife conflict, into an existing clan within the vicinity of the release site was

hypothesized to be due to the young age of the individual (Weise et al. 2015). Therefore, subadults may represent good candidates for translocations between enclosed reserves (Edwards et al. 2019). Releasing animals outside of the park is an unlikely solution to limited dispersal options; the surrounding area is farmland and the hyaenas in the reserve are habituated to humans; thus this strategy would likely lead to sizable human-wildlife conflict and potential hyaena mortality through lethal removal by farmers. If dispersing subadult brown hyaena on ONR are ultimately becoming nomadic individuals, which typically experience low reproductive success (Mills 1990) and lower individual welfare, these individuals could be used to increase the genetic diversity of other enclosed populations, provided they are able to successfully integrate into existing clans at the release sites, or form new clans where suitable habitat and space allow.

If the fences of enclosed reserves are barriers to movement, Welch et al. (2016) hypothesized brown hyaenas might spend a disproportionate amount of time near boundary fences. However, no evidence for brown hyaena space use being related to reserve boundaries was found across the three study sites in South Africa (Welch et al. 2016), leading to the suggestion that the observed small home ranges sizes were not an artefact of small reserve size. Our results also support the findings of Welch et al. (2016); the compositional analysis showed brown hyaena did not show significant selection for areas directly adjacent to fence lines. The potentially nomadic female OHB09 did spend a considerable amount of time at the fence line; the area adjacent to the fence constituted 17% of her home range, yet 65% of the GPS positions were located in that area. However, such a result might rather reflect the use of the roads along the fence lines serving as territorial boundaries, as previously recorded for brown hyaena (Mills et al. 1980). Alternatively, as the ONR brown hyaena population has been enclosed within the area since the erection of the fence in 2010, individuals may simply have become habituated to its presence.

The estimated brown hyaena home ranges within the ONR are some of the smallest recorded to date, and our results add to the growing body of literature showing home ranges of carnivores residing in enclosed reserves are often substantially smaller than those individuals in open systems (e.g. Lehmann et al. 2008; Owen 2013; Welch et al. 2016). However, such results are not necessarily due to the presence of the boundary fence, for example Lehmann et al. (2008) and Hayward et al. (2009) found home range sizes of lion and spotted hyaena respectively, in enclosed reserves were smaller than the space available to them. Hayward et al. (2009) suggest such results show that the use of impermeable fences for wildlife management does not affect the behaviour of large carnivores and that the home ranges are determined by the abundance of prey in such areas. However, testing this hypothesis for brown hyaena will be difficult given that they scavenge the vast majority of their food resources in inland systems and are known to supplement their diet with wild fruits and insects during times of low food abundance (Mills 1990), making resource availability calculations difficult.

With enclosed reserves becoming increasingly common for the management and conservation of wildlife across southern Africa, understanding the spatial ecology of species residing in such areas is now essential for ensuring sound management guidelines are produced for such areas (Rachlow et al. 1999; Miller et al. 2015). By monitoring a relatively large number of individual brown hyaena, in comparison to previous studies, we were able to gain an in-depth understanding of the spatial ecology of a high-density population within an enclosed reserve. Our results showed home ranges of all individual brown hyaena were smaller than the total space available to them and that despite home ranges being substantially smaller than those recorded for brown hyaenas elsewhere, inter-clan overlap was similar to that recorded for open systems. Furthermore, the results suggest that limited options might be available for dispersing subadults, and from observations of a nomadic male, the welfare status of such individuals may be compromised given the limited spatial refuges that exist in which to partition from territorial animals. However, subadult individuals could represent good candidates for human-mediated translocations as part of structured metapopulation management schemes, and further research regarding the spatial tactics employed by dispersing individuals in high-density populations are suggested as next steps to producing management guidelines for brown hyaenas within enclosed reserves.

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