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Evidence of a high-density brown hyena population within an enclosed reserve: the role of fenced systems in conservation

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Abstract

Small, enclosed reserves are now common across Africa, and their conservation importance as wildlife refuges is increasingly acknowledged. Whilst such reserves represent areas safe from human persecution, they can also become threats themselves when the natural processes of emigration and immigration are prohibited. As a result, wildlife populations residing in enclosed reserves require careful management to safeguard their long-term persistence. As successful conservation management relies on precise population estimates, we estimated brown hyena density within a 180-km^2 enclosed reserve in north-central Namibia. Using camera trapping methods in combination with spatially explicit capture-recapture (SECR) models, brown hyena density was estimated at 24.01 brown hyenas/100 km^2 (± 3.47, 95% CI's 18.12–31.81), the highest recorded to date for the species. The high density is attributed to the relatively high density of leopard within the reserve, which may facilitate brown hyenas by providing access to the large herbivore biomass through kleptoparasitism, coupled with protection from human persecution. Results highlight the potential for enclosed reserves to host high-density populations of a persecuted large carnivore and show that, despite their often small size, such systems can aid conservation efforts. However, such results suggest reserve managers will be increasingly faced with the dilemma of dealing with surplus individuals when populations exceed carrying capacity. Therefore, the development of methods estimating carrying capacity for scavenging species, along with creating meta-population management schemes for all large carnivore species are essential next steps for conservation in Africa.

Keywords Brown hyena · Conservation · Density · Enclosed reserve · *Parahyaena brunnea* · Species management

Introduction

Within Africa, there is an urgent need to secure a lasting place for biodiversity, due to the complex tug-of-war between resource use and conservation (Massey et al. 2014). The establishment of protected areas across the continent is argued to be the main driver for the long-term conservation of its diverse wildlife (Saout et al. 2013). However, the isolation and/or small size of many such protected areas in combination with edge effects caused by human activities at their margins contribute to the continued decrease and extinction of wildlife populations (Estes et al. 2006). A popular strategy to mitigate such edge effects has been the use of fences to effectively separate protected areas from surrounding human communities (Massey et al. 2014). The importance of such reserves as refuges for wildlife, especially for species of conservation concern, is becoming increasingly acknowledged (Hayward et al. 2007b). For example, in a meta-analysis of lion (*Panthera leo*) in fenced and unfenced lands across 11 African countries, Packer et al. (2013) found fencing to be critical to conserving the species, with 50% of lion populations within unfenced areas facing extinction within the next 20–40 years.

Fenced reserves can also represent threats when the natural processes of emigration, immigration and expansions of species ranges are stopped (Caughley 1994). Such effects may consequently result in inbreeding depression and, at an extreme level, extinction of a species within a protected area. Additionally, with no options for dispersal, populations may exceed the carrying capacity of an area, which may quickly result in dramatic declines in prey species or vegetation degradation (Tambling and du Toit 2005). As a consequence, wildlife populations within fenced reserves are classified as fragmented and require

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careful management to ensure demographic and genetic viability (Marnewick 2015). For these reasons, the use of fencing has become a contentious issue amongst conservation practitioners (Creel et al. 2013), and the topic of wildlife management within fenced reserves is gaining increasing attention. Despite such interest, few published studies have focused on the effects of fencing on protected animal populations, necessitating the need for rigorous quantitative research on the subject (Hayward and Kerley 2009).

Wildlife populations often increase rapidly in the absence of threatening processes (Smith 2006), and within enclosed reserves large carnivores are often stocked at densities beyond natural levels (Tambling and du Toit 2005) as they, along with mega-herbivores, top the preference list of visitors to protected areas (Lindsey et al. 2007). As such, enclosed reserves may increasingly represent important strongholds for carnivores, especially for species which suffer from human persecution outside of protected areas. One such species likely to benefit from enclosed reserves is brown hyena (*Parahyaena brunnea*). Listed as Near Threatened by the International Union for Conservation of Nature (IUCN), it is the rarest member of the hyena family, with less than 10,000 individuals remaining worldwide (Wiesel 2015). Across its range, it is often considered a problem animal by farmers and consequentially suffers from deliberate and incidental persecution in the form of shooting, poisoning and trapping (Wiesel 2015). Welch and Parker (2016) demonstrated the potential for brown hyenas to reach high population density and show rapid population growth in a small reserve; they reported a 367% population increase, equating to a density of 15.3 brown hyenas/100 km^2 on Kwandwe Private Game Reserve, South Africa, following the reintroduction of six individuals 10 years prior. In comparison, previously recorded brown hyena densities outside protected areas have ranged between 0.15/100 km^2 across the North West Province, South Africa (Thorn et al. 2011) and 2.30–2.80/100 km^2 on commercial farmlands in western Botswana (Kent and Hill 2013).

The challenges associated with managing fragmented populations, combined with the previously documented potential for brown hyenas to reach relatively high densities in enclosed reserves, suggest the species to be an important and interesting candidate for further assessing densities in enclosed reserves. Here, we estimate the density of a naturally occurring brown hyena population within a small, enclosed reserve in north-central Namibia. Mills (1984) demonstrated that brown hyena abundance is positively linked to resource abundance, with areas harbouring more food resources, supporting a higher number of individuals. Therefore, given the relatively high density of herbivores within the reserve, and protection from human persecution, we hypothesised the density of brown hyenas within the reserve would be high in comparison with non-protected, open areas.

The study was conducted on Okonjima Nature Reserve (ONR), a privately-owned reserve which lies 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 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 180 km^2 of the ONR over which a variety of wildlife occur. During 2018, 10 adult brown hyenas were fitted with Wireless Wildlife (Potchefstroom, RSA) global positioning system (GPS) collars, scheduled to take one position every 30 min between 19:00 and 07:00 local time, and one position every 2 h during the rest of the day. No GPS positions were recorded outside of the perimeter fence, or within the central lodge area, suggesting the fences are impenetrable to brown hyena movements (Edwards et al. in prep). Additionally, fence patrols are conducted every second day on ONR and any holes found immediately fixed. However, the presence of an electrified wire close to the ground on both sides of the fence should mean larger species such as brown hyena trying to move through such holes would receive a large electric shock sufficient to stop such movements.

The ONR perimeter fence was erected around a naturally occurring brown hyena population, of unknown size, with no species management having 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. in prep), in comparison with an estimation 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. Additionally, two introduced spotted hyenas (*Crocuta crocuta*) and six rehabilitated, introduced cheetah (*Acinonyx jubatus*) were present within the ONR during the survey period. The reserve receives an average annual rainfall of 450 mm, which falls during the hot wet season from October to March. The vegetation is predominantly tree and scrub savannah, interspersed with silver *Terminalia* (*Terminalia sericea*) and several *Acacia* species. Perennial water is provided from a total of 18 artificial waterholes across the reserve. Herbivore densities within the ONR are 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.

Brown hyena density survey

To estimate brown hyena density, a total 40 camera trap stations were deployed throughout the 180-km^2 section of the reserve in which brown hyenas occur, for an 80-day survey period (20 June 2018 to 7 September 2018), which should meet the demographic closure assumption (Karanth and Nichols 1998). Stations were positioned at a mean nearest neighbour distance of 1.65 km (SD = 0.55), based on the maximum distance between camera traps (2.89 km) used by Welch and Parker (2016) to calculate brown hyena density on a closed reserve, as the radius of the smallest brown hyena home range recorded on the study site. To maximise capture probability and the probability of capturing non-blurry photos of both front leg stripe patterns, camera stations were primarily set up at latrines ($n = 34$), which represent predictable areas of brown hyena activity (Mills 1990). In areas in which latrines could not be found, camera traps were deployed at crossroads ($n = 6$), as brown hyenas are known to use roads when travelling (Mills 1990; Welch et al. 2015) (Fig. 1). Each camera trap station consisted of a single Cuddeback X-change 11339 infra-red camera trap (Non Typical Inc., Wisconsin, USA) housed within a protective CuddeSafe metal box, mounted on a metal pole at a height of ~50 cm from the ground. Camera stations were positioned ~2 m from a latrine in a way which did not block nearby roads or game trails, and when placed at crossroads were positioned ~1 m from the edge of the road, facing towards the centre of the crossroads. Camera trap stations were programmed to take three photos per trigger, with no delay between triggers, and photo quality of 20 MP. Cameras were checked every 10–14 days to replace batteries and SD cards.

Brown hyena photos were identified to individual level using unique front leg stripe patterns, by the first author using camera trap records obtained during the survey and an identification catalogue made from camera records from previous camera trapping activities on ONR. Juveniles and sub-adults were excluded from analysis. Individual detection histories were constructed using a 24-h sampling occasion, which started at 12:00 midday and ended at 11:59 am the following day. Such an approach was used to avoid the so-called 'midnight problem' in which a nocturnal animal visiting a camera trap site either side of midnight is recorded on two consecutive sampling occasions when using a standard day starting at midnight (Jordan et al. 2011).

Density estimation

Spatially explicit capture-recapture (SECR) models are increasingly used class of models for estimating population density (Kidney et al. 2016), which allow for individual

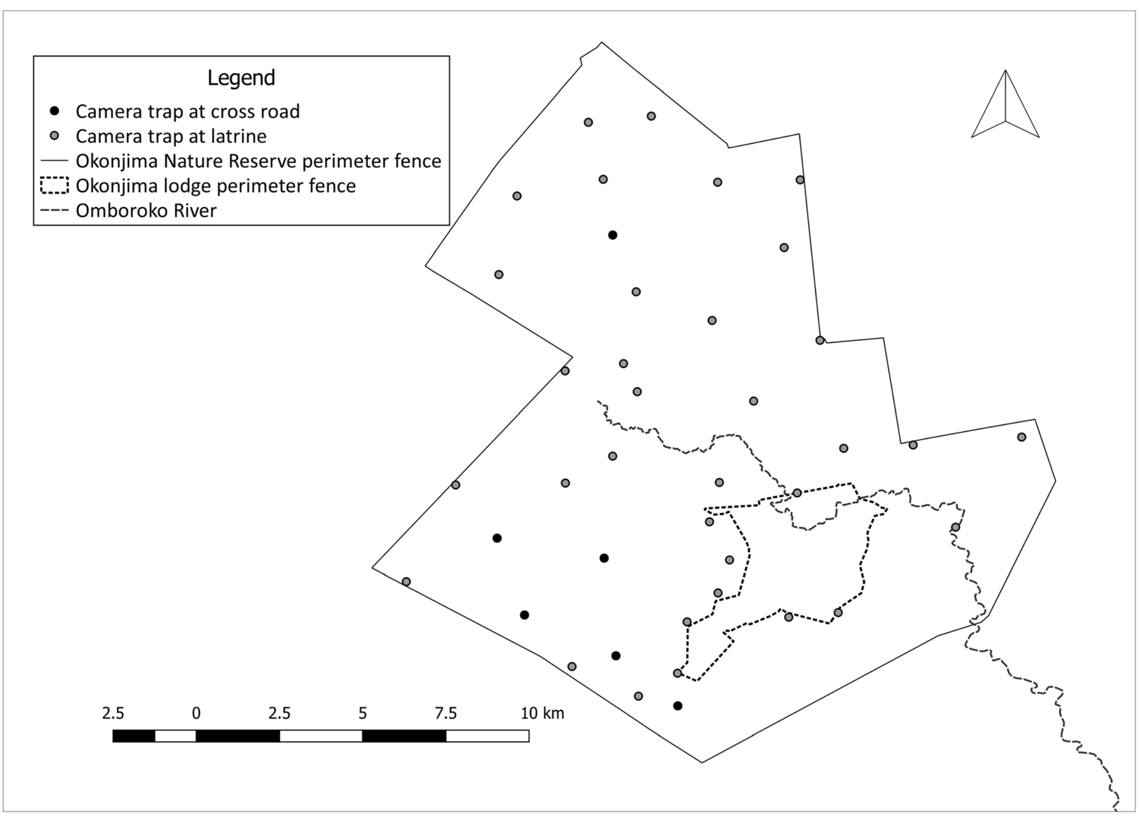

Fig. 1 Camera trap stations deployed on Okonjima Nature Reserve to estimate brown hyena density

movement outside of the survey grid, thus overcoming the challenges associated with defining the survey area in traditional, non-spatial capture-recapture models (Royle et al. 2014). SECR models assume every individual within the survey population, *i*, has a permanent, yet unobserved activity centre, *si*, and that the probability of detecting that individual is a monotonically decreasing function of the distance from the activity centre to the detector *j* (e.g. camera trap), *yji* (Sollmann et al. 2011). The models combine a state model, which represents the geographical distribution of potential individual home ranges, treated as homogenous Poisson point process model, with an observation model, which estimates the probability of encountering an individual at a given detector, as a function of the detector's distance from the individual home range centre (Borchers and Efford 2008).

The R (R Development Core Team 2014) package 'secr' (Efford 2012) was used to estimate density using a maximum likelihood framework. The package requires three input files; the first, the 'capture history' file, contains the individual detection histories of brown hyenas, constructed using 24-h sampling occasions. The second input file, the 'trap deployment' file, details the UTM GPS locations of camera traps, along with a binary string to represent when a particular detector was active ('1'), or inactive ('0') during a sampling occasion, and in this case a column detailing a trap level covariate 'traptype', corresponding to the camera trap being placed at a latrine or crossroad. The third input file, the habitat mask, represents the habitat in the vicinity of the detectors potentially occupied by the species of interest and can delineate habitat and non-habitat sites within the outer limit (Efford 2012). As brown hyenas are known not to move beyond the outer perimeter fence of the ONR, or within the inner lodge area, the ONR shapefile of the area over which brown hyenas occur was used as the state space. Along with density, SECR models produce an estimate of g0 (λ_0), the capture probability at the centre of an individual's activity centre and sigma (σ), a function of the scale of animal movement. Models within 'secr' can be run in which λ_0 and σ are influenced by various factors. Two models were ran: (1) a null model in which both g0 and sigma were constant ($\lambda_0 \sim 1$, $\sigma \sim 1$) and (2) a trap covariate model ($\lambda_0 \sim$ traptype, $\sigma \sim 1$) in which the capture probability was influenced by the trap of camera placement, either latrine or crossroad. Behavioural response to a camera trap was not expected, as camera traps as passive detectors placed at naturally occurring latrines, therefore, models in which λ_0 or σ where influenced by reaction to a camera trap were not considered. As sex could not be determined for all individuals recorded on camera trap, sex-specific models were not run. All models were ranked using AIC_c values (Akaike 1973). Population closure was tested by performing the closure test (Otis et al. 1978) within the 'secr' package.

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During the 80-day survey period, a total of 3125 camera trap nights were achieved during which 1002 independent brown hyena visits were recorded, of which 79 were blurry and could not be identified to the individual level. A further nine independent events showed sub-adults and thus excluded from analysis. Due to the placement of the majority of camera trap stations at latrines, both left and right hand flank photographs were largely obtained during one visit as individuals often turned around when performing sniffing and marking behaviours. Therefore, it was not necessary to split the dataset into left and right hand flank sub-sections for analysis (c.f. Welch and Parker 2016). The total of 932 independent visits used for analysis comprised 48 individuals, of which sex could not be determined for all individuals. Mean individual capture frequency across camera stations was 18.42 (SD = 18.62) and ranged from two to 68 independent events Fig. 2), whilst the mean number of spatial recaptures was 4.89 (SD = 4.07, range = 1–13 spatial recaptures). The closure test showed no evidence for violation of the closure assumption ($z = -3.05$, $p = 0.03$).

The trap covariate model was determined as best fitting, with the null model not considered a competing model due to having an $\Delta AICc > 2$ (Table 1). The trap covariate model estimated density at 24.01 (± 3.47, 95% CI 18.12–31.81), with a λ_0 value at latrines of 0.09 (± 0.004, 95% CI 0.08–0.10), and a λ_0 value at crossroads of 0.02 (± 0.004, 0.02–0.03). Sigma was estimated at 3044.45 m (± 84.58, 95% CI 2883.14–3214.79).

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Thorough knowledge of large carnivore densities is of vital importance for managing small enclosed reserves (Hayward et al. 2007b), as these systems have been shown to have the potential to host high species densities (e.g. Welch and Parker 2016). Here, we present the first brown hyena density estimates for an enclosed reserve in Namibia. The density estimate reported is currently the highest published estimate for this species. Whilst this result further highlights the potential for enclosed reserves areas to provide a safe refuge for relatively large numbers of individuals, the negative implications of having such high numbers within enclosed systems must be considered, and appropriate management actions are taken to ensure the long-term persistence of such populations.

Brown hyena density estimates have been shown to vary widely across their range: 0.15/100 km^2 within the North West Province of South Africa (Thorn et al. 2011), 1.8/100 km^2 in the southern Kalahari (Mills and Mills 1982), < 2.00/100 km^2 within the Makgadikgadi region, Botswana (Maude 2005), 2.30–2.80/100 km^2 on commercial farmland, western

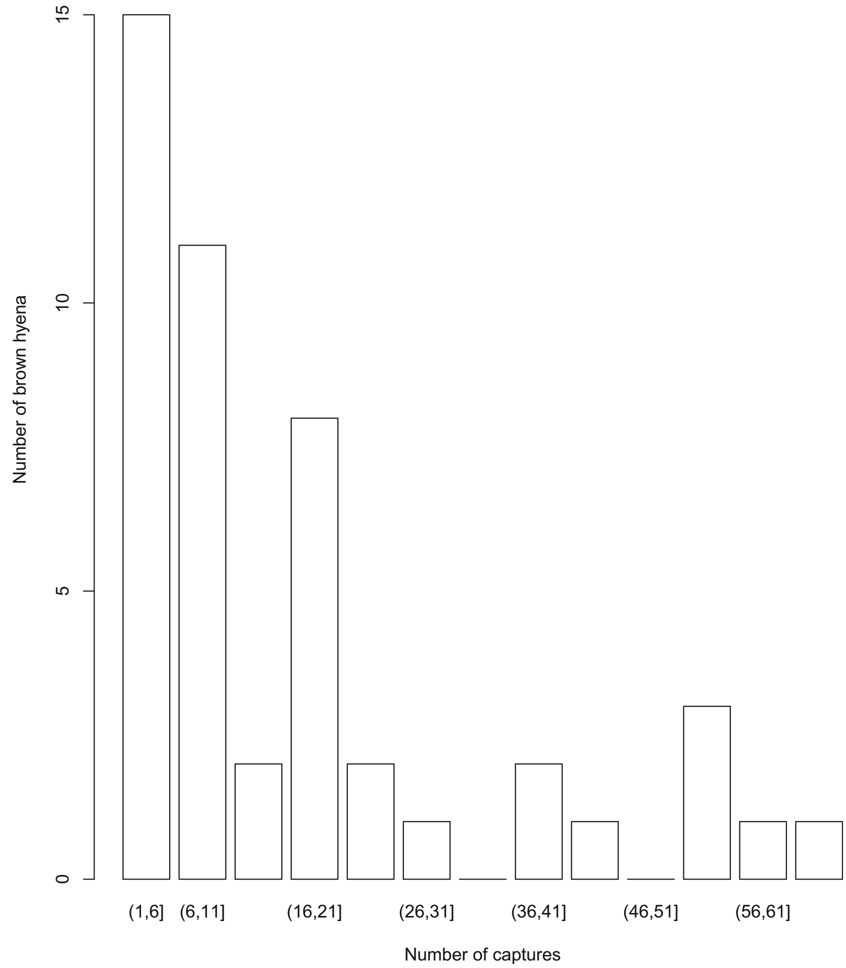

Fig. 2 Barplot displaying the number of captures per individual brown hyena attained during the density survey

Botswana (Kent and Hill 2013), 2.8/100 km^2 in Pilanesberg National Park, South Africa (Thorn et al. 2009), 2.16–3.71/100 km^2 in the southern stratum of the Central Kalahari Game Reserve, Botswana (Winterbach et al. 2017) and 15.3/100 km^2 on Kwandwe Private Game Reserve, South Africa (Welch and Parker 2016). Our brown hyena density of 24.01/100 km^2 is therefore the highest reported in the published literature to date, being nearly twice as much as that recorded by Welch and Parker (2016), for an enclosed reserve.

Many studies have shown carnivore density to be positively related to prey abundance/biomass (Fuller and Sievert 2001; Hayward et al. 2007b), and this factor could provide one possible explanation the high brown hyenas estimated on ONR, as accessed via non-violent mortalities. High prey abundance may positively influence carnivore density by leading to increases in the proportion of productive females in a population, increased litter size and offspring survival (Fuller and Sievert 2001). For example, Watts and Holekamp (2009) reported per capita prey availability to have a positive influence on spotted hyena reproduction, and Balme et al. (2012) suggested newly independent leopard cub survival increased with prey abundance. Whilst limited data exists for the influence of food resources on the population dynamics of scavenging species, James (2014) found black-backed jackal (*Canis mesomelas*) abundance to be significantly higher on farms with predator feeding programmes, in comparison with jackal abundance on comparative predator neutral game farms in South Africa. Furthermore, James (2014) found high food availability reduced dispersal in black-backed jackals. The high densities of herbivores within the ONR may therefore contribute to the high density of brown hyena, through increased reproductive success.

Table 1 Model comparison table for SECR models ran for estimating brown hyena density

Model	Notation	AICc	ΔAICc	AICc wt	Log-likelihood
Trap covariate	($\lambda_0 \sim$ traptype, $\sigma \sim 1$)	7859.52	0	0.99	− 3926.44
Null	($\lambda_0 \sim 1$, $\sigma \sim 1$)	7952.28	92.76	0.01	− 3962.64

Brown hyenas are known to scavenge the majority of their food resources; Mills (1990) estimated just 5.60% of the diet of brown hyenas in the Kalahari to be from kills made themselves. Whilst a high abundance of live herbivores should equate to availability of food resources through non-violent mortalities, it has been hypothesised that brown hyenas may additionally benefit from the presence of larger carnivore species through increased scavenging opportunities (Mills 1982; Yarnell et al. 2013). For example, in the southern Kalahari, lions (*Panthera leo*) provided 42.6% of carcasses of known provenance utilised by brown hyenas (Mills 1990). Within the ONR, the most numerous large carnivore species for brown hyenas is a leopard, which is known to hoist approximately 50% of kills into trees (J. Noack, pers. obs.). During daily tracking of leopard, brown hyenas are frequently recorded as present at leopard kills, often stealing kills or utilising those left on the ground after the leopard left the area (J. Noack, pers. obs.). Such observations suggest brown hyenas access the large herbivore biomass of ONR via both kleptoparasitism and non-violent mortalities and thus the presence of leopard on ONR facilitates brown hyena. This is further evidenced by brown hyenas being detected on camera trap carrying warthog remains, which is the most frequently taken prey item of leopard on the ONR (J. Noack, pers. obs.), and warthog remains (i.e. tusks, skin, skulls) being the most numerous species remains found at all brown hyena den sites on the ONR (S. Edwards, pers. obs.). No interactions between cheetah and spotted hyena with brown hyena are recorded at kill sites, and thus the influence of these species on brown hyenas on ONR is therefore considered negligible.

The density of brown hyenas on ONR is almost twice as much as that estimated by Welch and Parker (2016) of 15.3/100 km^2 on the Kwandwe Private Game Reserve, South Africa. A fundamental difference in the history of the brown hyena populations within the two fenced systems exists which may explain the large density difference. The brown hyena population on Kwandwe was introduced with a founder population of just six individuals, 10 years prior to the study, with results suggesting a 367% population growth rate since introduction. In contrast, the ONR brown hyena population is naturally occurring, being present when the perimeter fence was erected in 2010; however, no population estimates are available for that time period. The brown hyena population enclosed with the erection of the ONR fence may have been larger than the six individuals introduced to Kwandwe, thus potentially explaining the density difference seen between the two studies. Furthermore, the relatively high density of lion on Kwandwe (5/100 km^2) may negatively impact the brown hyena population, via intraguild predation (Mills 1990).

The high-density estimate reported for brown hyenas on the ONR could be due to the state space of SECR models used restricted to the ONR borders to reflect the lack of movement across the fence by the 10 GPS collared brown hyenas. Welch and Parker (2016) also used the Kwandwe outer perimeter fence as the state space when running SECR models for brown hyena; however, no information was given regarding movement of brown hyenas across the fence at the study site. Although no evidence exists to imply ONR brown hyenas move out of the reserve, any such movements would have to be incorporated into SECR models by extending the state space beyond the ONR borders which would potentially result in a lower density estimate.

Our results add to the body of literature showing that small enclosed reserves are able to provide secure environments for high densities of brown hyenas, aiding conservation efforts for the species. However, when the natural processes of immigration and emigration are halted by fences, small reserves present risks to the species within, in the form of the genetic factors of inbreeding depression and loss of genetic diversity due to the potential for closely related individuals breeding (Caro 2000; Trinkel et al. 2010). This may be of particular concern for brown hyenas, which have recently been shown to have very low levels of both mitochondrial and nuclear genetic diversity, lower even than cheetah (Westbury et al. 2018), and as such assessing the genetic diversity of the ONR population should be set as research priority to further understand its management needs and goals. Davies-Mostert et al. (2009) propose that, in situations where species exist in small, fragmented populations, meta-population management schemes are needed, whereby individuals are moved between reserves to replicate the natural dispersal and maintain the genetic diversity of these populations. There is, however, a lack of published studies regarding the success of translocations into enclosed reserves already inhabited by the focal species, with the majority of studies focusing on species reintroductions (e.g. Hayward et al. 2007a; Yiu et al. 2017).

Within open and unprotected areas, large carnivore translocations are largely unsuccessful (Fonturbel and Simonetti 2011), given the reduced survivorship of translocated individuals (Bradley et al. 2005; Chipman et al. 2008) and lack of release site fidelity (Stander et al. 1997). Potential disease risks to both introduced and resident individuals are also posed (Kock et al. 2010). Furthermore, for social species such as brown hyena, translocation may be further complicated, when individuals are moved, rather than entire clans (Mills and Hofer 1998). However, Weise et al. (2015) reported a single case study of a successful brown hyena conflict-related translocation of a sub-adult female, which showed successful clan assimilation within the vicinity of the release site. Such success of clan integration was attributed to the premature age of the individual (Weise et al. 2015), suggesting when moving brown hyenas between reserves for meta-population management, sub-adult individuals could represent the most ideal candidates.

When dealing with high-density populations within enclosed systems, managers are likely faced with the dilemma of managing the population, without knowing the carrying capacity of their reserves (Hayward et al. 2007b). Hayward et al. (2007b) demonstrated carrying capacity can be predicted for carnivores which prey on large, readily surveyed wildlife; however, estimating carrying capacity for a predominantly scavenging species is likely to be more complicated given the variety of ways food resources that may be obtained. Additionally, brown hyenas are known to supplement their diet with wild fruit and insects during times of low food abundance (Mills 1990). Given that the two highest recorded densities for brown hyenas have come from enclosed reserves, the development of carrying capacity estimation methods for scavenging species is needed, which can then be utilised by reserve managers to aid species management. Even when carrying capacity can be estimated, choosing appropriate management methods may be difficult, given the complex logistical and moral issues associated with dealing with surplus individuals, or just maintaining population density within a certain level. Whilst translocation to mimic open systems, i.e. the presence of nomadic and immigrant males in brown hyenas, has been suggested as the most ethical way to manage population growth (Ferreira and Hofmeyr 2014), the option will only work when suitable protected release sites are available, with established brown hyena clans already present. Other options include contraception (Bertschinger et al. 2008), or performing a unilateral hysterectomy to reduce litter sizes (Miller et al. 2013). Alternatively, culling of individuals may be considered; however, regardless of the moral issues surrounding the practice, culling may agitate the problem when populations respond with high growth rates (Slotow et al. 2008).

As enclosed small reserves become increasingly common throughout southern Africa, the status of wildlife populations residing within them, now, more than ever, requires careful monitoring and management to ensure their long-term persistence. Here, we further demonstrate the potential for brown hyena, a persecuted large carnivore, to reach its highest density within an enclosed reserve, highlighting the possible role such areas can play in boosting species conservation efforts, despite their often, small size. Whilst enclosed reserves can aid species conservation, reserve managers will likely be increasingly faced with the dilemma of what to do with surplus individuals whilst simultaneously securing the genetic integrity of their populations. As a result, the development of methods for estimating carrying capacity for scavenging species, along with the establishment meta-population management schemes for all large carnivores residing in enclosed reserves are likely to require increasing attention and should be viewed as essential next steps for conservation within Africa.

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