The importance of farmland for the conservation of the brown hyaena *Parahyaena brunnea*

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Abstract The conservation of wide-ranging, territorial carnivores presents many challenges, not least the inadequacy of many protected areas in providing sufficient space to allow such species to maintain viable populations. As a result populations occurring outside protected areas may be of considerable importance for the conservation of some species, although the significance of these areas is poorly understood. Brown hyaenas *Parahyaena brunnea* are categorized as Near Threatened on the IUCN Red List and recent research suggests the species may be particularly vulnerable to habitat loss and the conversion of land to agriculture. Here we report on the population density and abundance of brown hyaenas in an area of commercial farmland in western Botswana. Mean brown hyaena density estimated from camera-trap surveys was 2.3 per 100 km^2 and from spoor surveys was 2.88 per 100 km^2, which are comparable to estimates reported for protected areas. Estimated densities were higher on farms used for livestock production than on those used for game farming, suggesting that the species can tolerate land use change where reliable alternative food resources exist. Our results indicate that populations of brown hyaenas in non-protected areas comprise a significant proportion of the global population and that such areas may be of critical importance for their conservation.

Keywords Botswana, brown hyaena, camera trap, carnivore, farmland, *Parahyaena brunnea*, spoor survey

Introduction

Historically, protected areas were considered the cornerstones of wildlife conservation. In recent years however, they have come to be seen as inadequate for the conservation of wide-ranging territorial carnivores that cannot be contained within the boundaries of patches of land, sometimes small and isolated, designated for the purpose. As a result the importance of landscape-scale conservation that encompasses non-protected areas is now acknowledged (Woodroffe & Ginsberg, 2000; Smith et al., 2011; Limiñana et al., 2012).

Loss of habitat is widely considered to be one of the major factors affecting the survival of mammalian predators. As human populations increase more land is appropriated for agriculture, resulting in conflict between landowners and wildlife (Nowell & Jackson, 1996; Sunquist & Sunquist, 2001). In sub-Saharan Africa life outside protected areas may be advantageous for species such as the cheetah *Acinonyx jubatus* and African wild dog *Lycaon pictus* that, inside protected areas, are subject to competition for resources from larger carnivores such as the lion *Panthera leo* and spotted hyaena *Crocuta crocuta* (Creel & Creel, 1996; Marker & Dickman, 2004). In some cases, populations in non-protected areas are considered to be essential to the conservation of the species as a whole (Woodroffe & Ginsberg, 1998, 2000) and it has been postulated that if such species can not be conserved in multi-use landscapes then they probably can not be conserved at all (Woodroffe et al., 2005).

The brown hyaena *Parahyaena brunnea* is endemic to southern Africa, inhabiting the South West Arid Zone, with Botswana believed to hold c. 50% of the estimated total population of c. 8,000 individuals (Mills & Hofer, 1998). However, despite the fact that it is categorized as Near Threatened on the IUCN Red List (IUCN, 2011), relatively little research has been undertaken on the brown hyaena and estimates of its global status are based on a small number of studies (mostly within protected areas). As a result, there is a need to determine the extent to which the brown hyaena persists outside such areas. A recent study in South Africa reported that density and occupancy of brown hyaenas in agricultural land is significantly lower than in protected areas (Thorn et al., 2011a), suggesting that the species may be particularly vulnerable to habitat loss and the conversion of land to agriculture. Nevertheless, the brown hyaena persists in areas of commercial farmland and its occurrence there has recently been shown to be more widespread than previously thought (Thorn et al., 2011b), reinforcing suggestions that such environments may be advantageous to the species (Skinner & van Aarde, 1987; Maude & Mills, 2005). Further information is therefore critical to determine the significance of non-protected areas for brown hyaenas.

Brown hyaenas generally live in clans that range from one female with cubs to up to 10 adults (Mills, 1990), with c. 8% of the subadult and adult population thought to be nomadic (Mills, 1982). Although research suggests they are primarily scavengers of mammal remains, they have also been found to eat insects, birds, eggs and fruit (Mills & Mills, 1978). Hunting comprises a relatively small proportion of their foraging behaviour (Mills, 1990) and, although they are not thought to be a major threat to livestock, certain individuals may sometimes take sheep, goats, calves or poultry (Skinner, 1976). Perceptions amongst farmers, however, often reveal a belief that brown hyaenas are problem animals (Wiesel et al., 2008; Kent, 2011) and in Botswana they are likely to be shot, poisoned or trapped, either deliberately or incidentally, despite being listed as a protected game animal (Mills & Hofer, 1998).

Estimates of brown hyaena density have previously been derived by extrapolating from group and territory size (Mills, 1990), spoor or track surveys (Funston et al., 2001), or from the use of camera traps using capture–recapture analysis (Thorn et al., 2009). Spoor density can be taken as an index of true density and Funston et al. (2010) provided a calibration equation for the conversion of large carnivore spoor density to an estimate of true density specifically applicable to sandy soils. However, double counting in spoor surveys can lead to overestimates of density, and it is preferable therefore to calibrate such estimates with other survey methodologies.

Camera-trap surveys have become increasingly important in the assessment of the status and conservation requirements of large carnivores, which tend to be elusive, nocturnal and difficult to study by other means (Nowell & Jackson, 1996; Sillero-Zubiri et al., 2004). A key requirement in the use of capture–recapture methods is the ability to identify individual animals for the purpose of gathering data on their movements

(Karanth & Nichols, 1998). Whereas the identification of individual brown hyaenas can be more difficult than for species with distinctive spots or stripes across their entire pelage, it is nevertheless possible using their unique leg stripe patterns, ear notches and other distinguishing features (Wiesel, 2006).

Recent advances have provided statistical tools appropriate for sampling medium and large carnivores that may have heterogeneous capture probabilities, occur at low densities and range widely. Spatially explicit capture–recapture models incorporate the spatial component of the camera array in their analyses, thereby eliminating the need for an ad hoc estimation of the sampling area. Two different approaches have been used in this regard, maximum likelihood (Efford et al., 2009) and Bayesian (Royle et al., 2009), with Bayesian considered to be of considerable importance for inference with small sample sizes (Gardner et al., 2010; Kéry et al., 2010). For both options user friendly software is available to facilitate analysis (Efford et al., 2004; Gopalaswamy et al., 2012).

In this study we utilized both camera traps and spoor surveys in an area of commercial farmland in western Botswana to obtain and calibrate density estimates for the brown hyaena. Our research objectives were to (1) assess the status and local abundance of brown hyaenas in an area of commercial farmland, (2) compare our density estimates with those available for protected areas and (3) assess whether areas of land given over to cattle farming were advantageous to the brown hyaena to a greater or lesser extent than those reserved for wildlife.

Study area

Ghanzi District is an area of semi-arid bush in west-central Botswana with a wet season from October to April and a mean annual rainfall of 400 mm. Temperatures range from -5°C(minus 5 degrees) in winter to 43°C in summer. The area comprises a multi-use landscape, with commercial farms that have both livestock (cattle, sheep and goats) and wildlife, communal farms, Wildlife Management Areas and protected areas. The District is bordered to the west by Namibia and to the east by the Central Kalahari Game Reserve. Ghanzi farm block is centred on the town of Ghanzi (×Fig. 1), the administrative centre of Ghanzi District. This c. 15,000 km^2 block consists of >200 farms. Most of these are commercial cattle operations but in recent years several farmers have converted, either in part or in full, to game farming for tourism and hunting. Many farmers also keep a few small stock and some farm small stock exclusively.

Methods

Three camera-trap surveys and two spoor surveys were undertaken in the Ghanzi farm block (×Fig. 2). Spoor survey protocols were based on methods developed by Stander (1998) and Funston et al. (2001). The first spoor survey was conducted during the wet season, on a mixed selection of farms that comprised a range of land uses: cattle, small-stock and game farming and one farm that had been unused for several years but was in the process of being prepared for cattle (Fig. 2). All are on the hardveld of the Ghanzi Limestone Ridge and were therefore characterized by a substrate of Kalahari sand interspersed with occasional outcrops of calcrete or rock. There were six transects (mean 10.74 ± SE 1.87 km; Fig. 2), surveyed between November 2008 and March 2009. The second spoor survey was conducted on a 20,000 ha cattle farm during the dry season. The farm is on the sandveld, with a substrate comprised entirely of soft loose Kalahari sand. This survey had five transects (mean 9.9 ± SE 2.91; Fig. 2), surveyed between May and September 2009. The routes used for the transects were all single track roads and spoor was counted only on the track itself. All transects were driven between sunrise and no later than 11.00 at a speed of 12–20 km^{-h} until a total of c. 1,000 km of transect had been surveyed (Table 1). Transects were not driven when rain had fallen in the previous 24 hours or when there was evidence of the track having been driven on by another vehicle in the previous 12 hours. A skilled Bushman tracker sat on the front of the vehicle and all fresh (≤ 24 hour old) spoor of medium- and large-sized predators were recorded. Bushmen are renowned for the accuracy and reliability of their tracking skills (Stander et al., 1997) and have been used in several spoor survey counts in southern Africa (cf. Stander, 1998; Funston et al., 2001). When spoor was encountered it was examined and monitored to determine the distance the animal had travelled along the road and in what direction the animal then went. To reduce the risk of double counting, fresh hyaena spoor encountered within 1 km of a previous sample was assumed to belong to the same animal and was not counted.

The three camera-trapping surveys were carried out using 26 Cuddeback Digital Expert cameras (Non Typical Inc., Wisconsin, USA). The first camera survey was conducted on the same cattle farm as the second spore survey, the second was primarily on two adjoining game farms in the centre of the group of farms surveyed in the first spore survey, and the third was on two cattle farms to the west of Ghanzi town (Fig. 2). Camera trapping protocols were based on methods developed for surveying tigers *Panthera tigris* (Karanth & Nichols, 2002), leopards (Henschel & Ray, 2003) and jaguars *Panthera onca* (Silver, 2004).

An array of 18–20 single camera stations was employed to maximize the number of stations and the area covered with the available cameras. These were supplemented with up to eight additional cameras distributed throughout the array to create paired stations to facilitate identification. The supplementary cameras were periodically moved during the surveys. The logic underlying this strategy is that it would only require one photographic capture of an animal with unique pelage markings at a paired station to provide images of both flanks. Subsequent captures of the same individual at a station with only a single camera would then make identification possible, regardless of which flank the photograph showed. However, there were animals for which photographs of only one flank was obtained and a choice was made as to whether to include the right or left-sided animals in the analysis based on which gave the maximum number of individuals. When it was possible to see genitalia in the photographs the sex of the animal was also recorded. Cameras were placed on farm tracks at 25–40 cm above the ground, which was optimal for capturing all predators. Camera spacing was 2–2.5 km in all surveys (surveys 1, 2 and 3: mean = 2.49, 2.2 and 2.5 km, respectively) and the size of the minimum convex polygons created by connecting the outer camera stations of the grid were 76.22, 59.19 and 61.73 km^2, respectively. Delay between consecutive exposures was set at 1 minute and sensitivity set to high. No bait or lure was used to attract predators. Cameras were checked weekly, when memory cards were changed and pictures downloaded and entered into *Camera Base v. 1.3* (Tobler, 2007). All surveys ran for a period of 62 days, cameras operated 24 hours per day and each 24-hour period constituted a sampling occasion. Sixty-two days was selected as a period that would ensure at least 1,000 camera-trap days (24-hour periods in which a camera station was operational) but that would not compromise population closure assumptions (Soisalo & Cavalcanti, 2006).

Spoor surveys were analysed using techniques developed by Stander (1998) and Funston et al. (2001). Following Funston et al. (2001, 2010), spoor frequency was defined as the number of km driven per set of tracks encountered, and spoor density as the number of individual tracks encountered for each 100 km driven. Sampling effort was determined by calculating the sum of the length of the transects expressed as a ratio of the size of the area surveyed. As the surveys were undertaken on farmland and utilized more than one farm unit, the calculation of total area surveyed had to be achieved using an ad hoc buffer technique. A 3 km buffer with dissolved boundaries was created around the transects, using *ArcGIS v. 9.3* (ESRI, Redlands, USA) and the area encompassed by the buffer assumed to be the area surveyed (Table 1). The precision of spoor estimates were assessed from the spoor frequency in each survey, and the distance between each set of tracks was measured and progressive means and standard errors calculated. Bootstrap analyses (Sokal & Rohlf, 1995), using *R v. 2.15* (R Development Core Team, 2012), were used to determine sampling intensity, following Stander (1998), where two samples were randomly selected and then progressively increased to 4, 6, 8,... *x*, with fresh means and confidence intervals calculated each time. These were then plotted against measures of sampling effort. The general large carnivore calibration equation for sandy soils (cf. Funston et al., 2010) was used to convert spoor density to true density (t_i=3.15x_i+0.40 where t_i is the observed spoor density and x_i is the observed carnivore density).

Camera survey data were analysed with Bayesian spatially explicit capture–recapture methods (Royle et al., 2009), using *SPACECAP v. 1.0.5* (Gopalaswamy et al., 2012) in *R*. Each survey was analysed separately. *SPACECAP* requires three input files: a capture history, the UTM coordinates of the camera array, including information on which trap locations were active on each sampling occasion, and a file of UTM coordinates of potential home range centres. Home ranges of brown hyaenas have been found to be significantly smaller (mean 192 km^2) in areas of livestock production than in protected areas (Maude, 2005), and the mean maximum distance moved by identified individuals here was 7.1 km. A buffer of 25 km was therefore considered to be of sufficient size to ensure that the probability of an individual animal being captured outside the buffered region was zero. The buffer was created around the trap array and this extended area was populated with equally spaced potential home range centres (Gopalaswamy et al., 2012) using *ArcGIS*. Here we utilized a home range centre spacing of 1 km (a 1 km^2 pixel). Potential home range centres that fell within areas considered unlikely to provide habitat for brown hyaenas (towns and villages) were classified as non-habitat. *SPACECAP* uses the half-normal detection function and the Bernoulli encounter process to analyse spatially explicit capture–recapture models. The trap response present option was used after a test run indicated a positive behavioural response was present. The number of Markov-Chain Monte Carlo iterations was set at 100,000 with a burn-in of 20,000 iterations for the first and third surveys and 21,000 for the second survey. Thinning was set at 1. The data augmentation value was set at 220 for the first survey and 200 for the second and third surveys. Convergence was checked by visual examination of the chains and, following Noss et al. (2012), by using the Geweke statistic in the *R* package *boa* (Smith, 2007).

Results

Spoor surveys

Brown hyaena spoor was recorded on 81 and 99 occasions in the first and second surveys, with spoor densities of 8.8 and 10.1 per 100 km, respectively. Bootstrapping analyses (combining all transects) reveal the points at which the variance of spoor frequency stabilized in each survey. In both surveys this occurred at c. 20 samples, at c. 170 and 120 km, respectively (Fig. 3). Sampling precision, as measured by the coefficient of variance (CV), increased rapidly in the first 10 samples in both surveys. In the first survey the asymptote was reached at c. 30 samples, after which the CV decreased by only 4.5% between 31 and 81 samples. Similarly in the second survey the asymptote was reached at c. 30 samples, with only a 1.5% increase in precision between 30 and 99 samples. The calibration equation for sandy soils gave density estimates of 2.67 and 3.08 hyaenas per 100 km^2 in the first and second surveys, respectively (mean 2.88 per 100 km^2).

Camera trapping

Camera trapping sampling effort totalled 3,187 camera-trap days from 56 camera stations on the three sites. Brown hyaenas were photographed at 46 stations. The number of independent photographic captures of brown hyaenas are provided in Table 2. Five brown hyaenas were individually identified in the first survey, with photographs of both flanks. A further four were identified from right-flank only images and three from left-flank only images (five females, two males and two of unidentified sex). The right-flank individuals were included in the analysis. In the second survey five hyaenas were identified from right- and left-flank photographs, two from right-flank photographs and one from a left-flank photograph (six females and one male). The animal photographed from the left flank only was omitted from the analysis. In the third survey eight hyaenas were identified from right- and left-flank photographs and one more each from right- and left-flank photographs only (five females, one male and three unidentified). The animal for which there was only a right-flank image had a wire snare around its neck and disappeared from the survey after 3 weeks. As this could contravene closure assumptions it was omitted from the analysis and the left-flank animal used (Table 3). The *SPACECAP* analysis resulted in density estimates of 2.81, 1.8 and 2.28 brown hyaenas per 100 km^2 in the first, second and third surveys, respectively (mean 2.3 per 100 km^2). Convergence was reached for the chains of all parameters in all three surveys. Details of the parameter values are provided in Table 4.

Discussion

This study utilized two methodologies to assess the status and density of brown hyaenas in an area of commercial farmland in Botswana. Density estimates from spoor surveys and camera trapping revealed a considerable population of the species existing in the Ghanzi farmlands, with higher density estimates on farms utilized for livestock farming than on those used exclusively for wild game species. These results suggest that commercial farmland may host significant brown hyaena populations in southern Africa and that non-protected areas may therefore be critical for their conservation.

The density estimates derived from spatially-explicit capture–recapture analysis of camera trapping data were equal to or higher than those reported in two separate studies in the southern Kalahari (1.8 hyaenas per 100 km^2; Mills, 1990; Funston et al., 2001) and comparable to that estimated for Pilanesberg National Park in South Africa (2.8 per 100 km^2), (Thorn et al., 2009), the latter using traditional capture-recapture analysis. Both of the density estimates derived from spoor surveys were higher than those derived from camera trapping in the same area, with one being higher than, and the other similar to, the estimate from Pilanesberg National Park. The lack of published density estimates in similar environments highlights the need for more research both within and outside protected areas.

In both the spoor and camera-trap surveys estimated density was lower in areas utilized for game farming than in those where livestock was farmed. In the camera surveys the density estimate obtained on the game farms was 21–36% lower than that found in either survey on the cattle farms, and the estimate from the spoor survey on the cattle-only farm was 11% higher than that recorded in the survey on the mixed selection of farms. This adds weight to the suggestion by Skinner & van Aarde (1987) and Maude & Mills (2005) that areas given over to the production of livestock may provide a beneficial environment for the brown hyaena. It is however in complete contrast to the findings of Thorn et al. (2011a) in the North West Province of South Africa where density extrapolated from occupancy was found to be considerably lower in farming areas than that in adjoining protected areas. Several factors may account for this difference. It is possible there is less antagonism towards brown hyaenas in the Ghanzi farmlands than in the South African study area (Kent, 2011), with other predators such as leopard, lion, cheetah and black-backed jackal *Canis mesomelas* provoking more hostility amongst livestock owners in Botswana (Maude, 2005; Kent, 2011). Livestock management practices may also have an effect; livestock on commercial farms are usually free-ranging, with a low level of human supervision, and cattle stocking densities are also generally lower than in South Africa because of the poor productivity of the Kalahari environment and the bush encroachment that has occurred in the area, which results in reduced and impoverished grazing (Ringrose et al., 2002). Added to this is the low density human population of 0.3 km^{-2} in Ghanzi District (Law, 2003) compared to c. 31 km^{-2} in North West Province (Statistics South Africa, 2011) and the lack of large-scale crop production. This combination of factors may serve to provide a less hostile environment for hyaenas, with considerably less human disturbance than the more densely populated agricultural areas of the North West Province.

The density estimate obtained in the first spore survey can be compared with a spoor survey carried out in 2007 on the same farms and with the same Bushman tracker, which reported brown hyaena density of 2.36 per 100 km^2 (Houser et al., 2007). Funston et al. (2010) found that in the Botswana section of the Kgalagadi Transfrontier Park only two surveys separated by a 1-year interval were required to detect a 10% increase or decrease in the population. The density estimated in 2007 is c. 12% lower than that obtained in our study in 2009, indicating that the brown hyaena population may have increased in the intervening period.

The use of more than one sampling technique to estimate density in this study provides valuable comparative estimates for the same population. The results derived from both the spoor and camera-trap survey methodologies indicate that brown hyaena density in the Ghanzi District is similar to that in protected areas and may therefore be an important part of the global population. In this respect the brown hyaena is similar to the cheetah, whose largest free-ranging population in southern Africa is thought to exist in the commercial farmlands of Namibia (Marker, 2002).

The two methodologies have different advantages. Spoor surveys are relatively cheap to undertake but are time consuming and prone to double counting, resulting in overestimation of density. Camera surveys are less time consuming, at least at the implementation stage, but require considerable financial outlay in the purchase of sufficient cameras. However, costs are coming down and the development of spatially-explicit capture–recapture analysis promises more accurate and reliable density estimates. These methods are now being recommended as the standard for camera-trap surveys (Royle et al., 2011; Noss et al., 2012) as they are more realistic than traditional capture–recapture methods, especially for wide-ranging species such as the brown hyaena that live at low density. With respect to the brown hyaena, however, there are potential problems with the assumptions of the spatially-explicit capture–recapture model. As most brown hyaenas live in clans it is probable that the activity centres are not independent, although the assumption of independent activity centres may not hold true for any territorial carnivore (Royle & Gardner, 2011; Foster & Harmsen, 2012). Simulation studies may be of use in determining the effectiveness of spatially-explicit capture–recapture methods for group- or clan-living species. An additional problem may be caused by nomadic individuals that pass through the area of a camera survey and inflate the density estimate, although again this is a problem that can affect surveys of any wide-ranging species.

Using *SPACECAP* it was impossible to achieve convergence of several parameters without employing the behavioural response option in the model, even when running 100,000 iterations. It it is unlikely, however, that the brown hyaenas were trap happy. No lure was used and there was no evidence of animals being attracted to particular camera stations. It is likely that, as suggested by Royle et al. (2009), the positive response was caused by a preferential use of certain trails by individuals within their territory.

Overall it is believed that the spatially-explicit capture–recapture model will provide a more accurate result than simple capture–recapture models (J.A. Royle, pers. comm.). For comparison, estimates obtained from our data with simple capture–recapture methods, using *CAPTURE* (Rexstad & Burnham, 1991), were 3.72, 3.13 and 4.63 brown hyaenas per 100 km^2, in the first, second and third surveys, respectively, using an estimated sampling area based on half the mean maximum distance moved by animals in the surveys, and 1.77, 1.43 and 2.15 per 100 km^2 using the full mean maximum distance moved (Kent, 2011). Such comparisons confirm recent recommendations to use the spatially-explicit capture–recapture models to avoid overestimation of population density and thus potentially inappropriate management actions (Noss et al., 2012).

Our study design, using a mix of single and paired camera stations, is unusual and was employed to maximize both area surveyed and animals identified with a limited number of cameras. With this method there is no restriction on the rotation of the paired stations during the study, providing the location of the stations themselves remain fixed. However, there remains a possibility that the use of this strategy may have resulted in a bias in the probability of identification for some individuals (simulation studies could be of use in determining this). It is preferable, when resources and funds allow, to use paired stations throughout the trap array, and the increasing affordability of remote-capture cameras will facilitate this.

An extrapolation of the mean density estimates derived from the spatially-explicit capture–recapture model and spoor density in this study to the whole of the Ghanzi farm block results in a population estimate of c. 345 and 430 brown hyaena, respectively. This would be 4–5% of the estimated global population of the species, emphasizing the importance of non-protected areas for its conservation. The area surveyed was relatively small in relation to the entire Ghanzi farm block, given the wide-ranging behaviour of the brown hyaena. This is, however, a problem encountered by many camera-trap studies in wilderness areas, and the use of three surveys in different locations attempted to address this. However, there is a need for further research in such areas to produce a more robust estimate of the status of the species. Our research suggests that it is possible that further camera-trap surveys would reveal higher densities of brown hyaena outside protected areas than previously thought, resulting in an increase in the global population estimate.

In conclusion, brown hyaenas in Botswana appear to be thriving in areas of commercial farmland given over to both domestic livestock and game species. It is likely that the availability of livestock carcasses provides a more reliable source of scavenged food for the species, and the lower level of competition from other predators allows the brown hyaena to feed undisturbed. Although they are undoubtedly the victims of persecution in the form of trapping and poisoning (Wiesel et al., 2008) much of this is incidental, being aimed at other species such as cheetah, leopard and black-backed jackal (Kent, 2011). The challenges faced by livestock farmers living alongside predators cannot be overemphasized but enhanced education, livestock and land management can facilitate coexistence at a range of levels (e.g. Mishra et al., 2003; Marker et al., 2010). It is thought likely therefore that a continued programme of education aimed at highlighting the beneficial effects of brown hyaenas as cleaners-up of the bush, with resultant prevention of disease, could allow areas of commercial farmland in Botswana and elsewhere to make an important contribution to the conservation of the species.

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Biographical sketches

Vivien Kent is a wildlife biologist specializing in carnivores and conflict and currently works on conservation of, and habitat restoration for, Eurasian otters in the United Kingdom.

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TABLE 1 Area size, number of transects and sampling effort of the two spoor surveys for brown hyaena *Parahyaena brunnea* undertaken in the Ghanzi farmlands (Fig. 1) in 2008–2009.

	Spoor survey 1	Spoor survey 2
Area size (km^2)	567	264
No. of transects	6	5
No. of times driven	16	20
Mean transect length (km)	10.74±1.87 SE	9.9±2.91 SE
Total length of transects (km)	64.43	49.5
Total distance sampled (km)	1,023[1]	990
Sampling effort[2]	8.08	5.33

[1]One 7.5 km section of one transect was only driven 15 times.

[2]Determined by calculating the sum of the length of the transects expressed as a ratio of the size of the area surveyed.

TABLE 2 Summary of camera trapping data from three 62-day surveys undertaken in the Ghanzi farmlands in 2009.

Survey	No. of stations	Camera days	Mean trapping days per station	No. of usable photos	Brown hyaena photos*/no. of stations at which captured
1	18	1,023	56.83	2,561	72/16
2	20	1,144	57.20	3,813	57/14
3	18	1,034	57.44	2,415	80/16
Total/ Mean	56	3,201	57.16	8,789	209/46

*Photographs of brown hyaena at the same station within a period of 30 minutes were not considered independent unless they were of identifiable individuals.

TABLE 3 Summary of capture frequencies for brown hyaenas in the three camera-trap surveys in the Ghanzi farmlands in 2009. Columns indicate number of captures, with number of individuals, and rows indicate the number of unique trap stations (e.g. in Survey 1 two individuals were captured twice at two different traps, and three individuals were captured four times at four different traps).

	No. of captures														
No. of traps	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
Survey 1															
1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2	0	2	2	0	0	0	0	0	0	0	0	0	0	0	0
3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
4	0	0	0	3	1	0	0	0	0	0	1	0	0	0	0
Survey 2															
1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
3	0	0	1	0	0	1	1	0	0	0	0	0	0	0	0
4	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
5	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0
6	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Survey 3															
1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
2	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0
3	0	0	1	2	0	1	0	0	0	0	0	0	0	0	0
4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
6	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
7	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
8	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1

TABLE 4 Posterior summary statistics from the spatial capture–recapture models fitted to the camera trapping data (Tables 2–3) from the three surveys. The state-space in all cases was a 25-km grid; *D* is density per 100 km^2; λ_0 is the expected encounter rate; $\sigma = \sqrt{(1/b2)}$ (where b2 is a regression coefficient on the effect of distance between individual activity centre and the location of the trap), and is a range parameter; *p*1 and *p*2 are measures of encounter probability because of behavioural response; *Ns* is *Nsuper* and is the population size for the state space.

Parameter	Mean	SD	95% HPD levels	
Survey 1				
D	2.8055	1.2258	0.7127	5.3592
λ_0	0.0182	0.0081	0.0056	0.0329
σ	3.9533	1.3135	2.3559	5.7207
*p*1	0.018	0.0079	0.0056	0.0323
*p*2	0.3055	0.2962	−0.3027	0.7676
Ns	98.4178	43	25	188
Survey 2				
D	1.7987	0.8441	0.1791	3.3768
λ_0	0.0163	0.005	0.0075	0.0265
σ	4.3278	1.3134	2.6985	6.5087
*p*1	0.0161	0.0049	0.0075	0.0262
*p*2	0.6306	0.1227	0.3889	0.8443
Ns	70.3124	32.9965	7	132
Survey 3				
D	2.2841	1.0822	0.2649	4.2979
λ_0	0.0158	0.0049	0.0065	0.0251
σ	4.8094	1.6871	2.6677	7.7616
*p*1	0.0157	0.0048	0.0065	0.0248
*p*2	0.7211	0.0936	0.5408	0.8877
Ns	77.5905	36.7629	9	146

FIG. 1 The Ghanzi farm block in Ghanzi District. The rectangle shaded area on the inset indicates the location of the main figure in western Botswana.

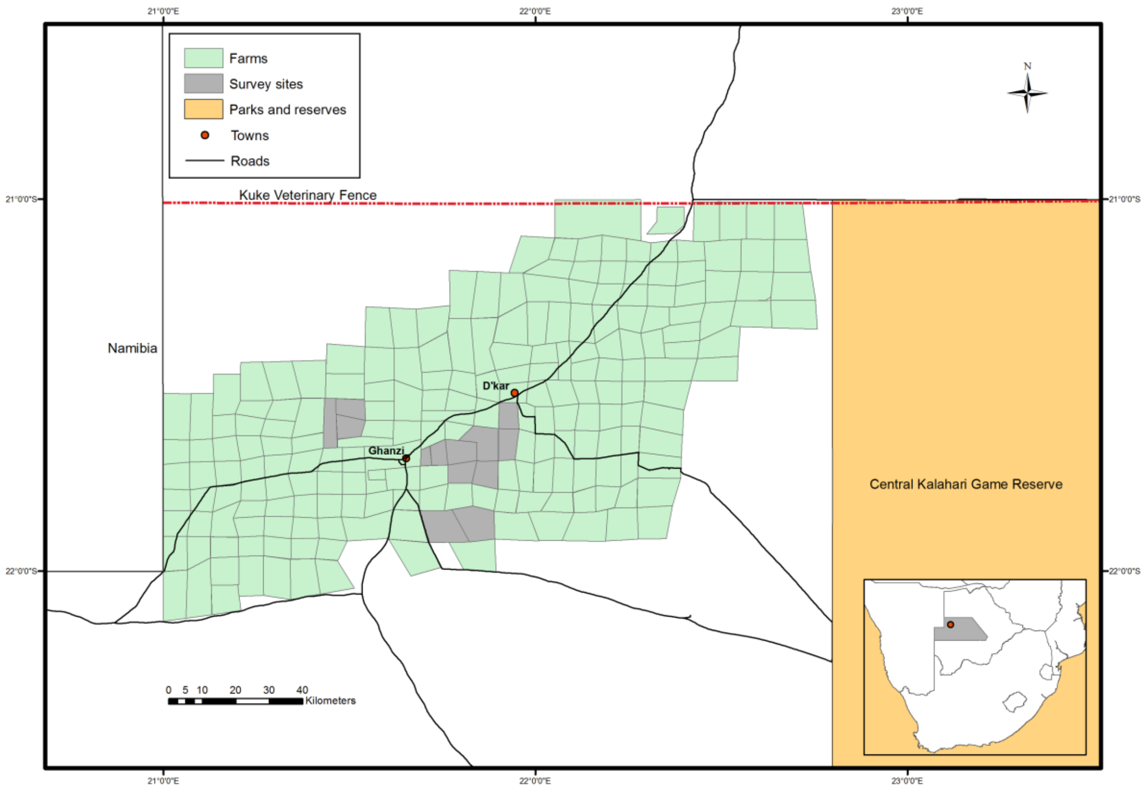

FIG. 2 The study area (see Fig.1 for location) showing locations of spoor (SS1, SS2) and camera-trap surveys (CS1, CS2 and CS3).

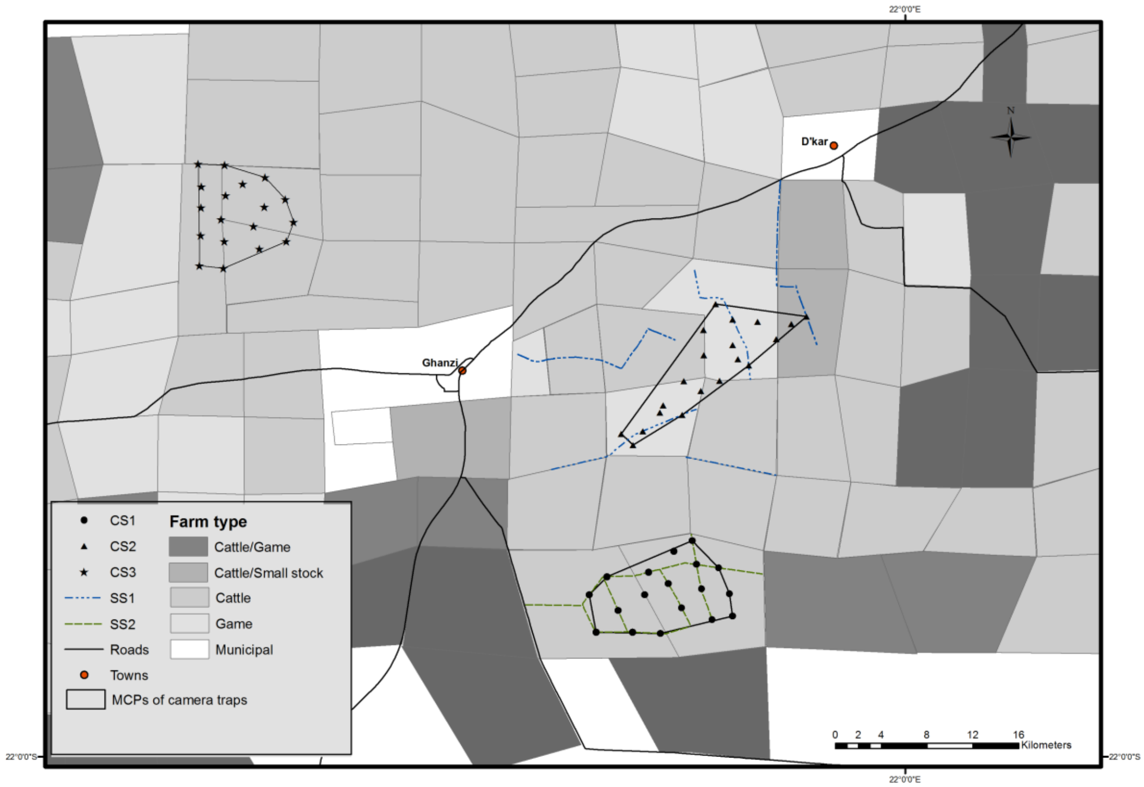

FIG. 3 The relationship between spoor frequency and increased sampling effort as measured by the number of detected spoor in the first (a) and second (b) surveys, with 95% confidence intervals.