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Conservation implications of brown hyaena (*Parahyaena brunnea*) population densities and distribution across landscapes in Botswana

Authors:
Christiaan W. Winterbach[1,2]
Glyn Maude[3]
Gosiame Neo-Mahupeleng[4]
Rebecca Klein[5]
Lorraine Boast[5]
Lindsey N. Rich[6]
Michael J. Somers[2,7]

Affiliations:
[1]Tau Consultants (Pty) Ltd, Maun, Botswana

[2]Centre for Wildlife Management, University of Pretoria, South Africa

[3]Kalahari Research and Conservation, Maun, Botswana

[4]Botswana University of Agriculture & Natural Resources, Gaborone, Botswana

[5]Cheetah Conservation Botswana, Gaborone, Botswana

[6]Department of Fish and Wildlife Conservation, Virginia Tech, United States

[7]Centre for Invasion Biology, University of Pretoria, South Africa

Corresponding author:
Christiaan Winterbach,
tauconsultants@gmail.com

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The brown hyaena (*Parahyaena brunnea*) is endemic to southern Africa. The largest population of this near-threatened species occurs in Botswana, but limited data were available to assess distribution and density. Our objectives were to use a stratified approach to collate available data and to collect more data to assess brown hyaena distribution and density across land uses in Botswana. We conducted surveys using track counts, camera traps and questionnaires and collated our results and available data to estimate the brown hyaena population based on the stratification of Botswana for large carnivores. Brown hyaenas occur over 533 050 km² (92%) of Botswana. Our density estimates ranged from 0 brown hyaenas/100 km² in strata of northern Botswana to 2.94 (2.16–3.71) brown hyaenas/100 km² in the southern stratum of the Central Kalahari Game Reserve. We made assumptions regarding densities in strata that lacked data, using the best references available. We estimated the brown hyaena population in Botswana as 4642 (3133–5993) animals, with 6.8% of the population in the Northern Conservation Zone, 73.1% in the Southern Conservation Zone, 2.0% in the smaller conservation zones and 18.1% in the agricultural zones. The similar densities of brown hyaenas in the Central Kalahari Game Reserve and the Ghanzi farms highlight the potential of agricultural areas in Botswana to conserve this species. The conservation of brown hyaenas in the agricultural landscape of Botswana is critical for the long-term conservation of the species; these areas provide important links between populations in South Africa, Namibia and Zimbabwe.

Conservation implications: Botswana contains the core of the brown hyaena population in southern Africa, and conflict mitigation on agricultural land is crucial to maintaining connectivity among the range countries.

Introduction

The brown hyaena (*Parahyaena brunnea*) has an estimated population size of < 10 000 mature individuals and is therefore listed as near threatened on the International Union for Conservation of Nature (IUCN) Red List (Wiesel 2015). The species is endemic to southern Africa with range countries including Botswana, Namibia, South Africa, Angola and Zimbabwe (Mills & Hofer 1998; Wiesel 2015). The largest population of brown hyaena is found in Botswana (Wiesel 2015), a country that hosts one of the most diverse carnivore assemblages in Africa. The large carnivore guild includes lion (*Panthera leo*) (IUCN/SSC 2006), cheetah (*Acinonyx jubatus*) and wild dog (*Lycaon pictus*) (IUCN/SSC 2007) and significant populations of spotted hyaena (*Crocuta crocuta*) and leopard (*Panthera pardus*) (Jacobson et al. 2016).

The brown hyaena occurs over most of Botswana, except the Okavango Delta and sections in the north (Wiesel 2015). The range includes a diversity of human land uses such as conservation areas (Keeping 2014; Maude & Mills 2005), commercial farms (Boast & Houser 2012; Kent & Hill 2013) and communal land used for subsistence livestock farming (Muir 2009; Schiess-Meier et al. 2007).

The large carnivore guild in Botswana comprises a strong, interspecific dominance hierarchy including subordinate competitors (cheetahs, African wild dogs and brown hyaenas), dominant competitors (lions and spotted hyaenas) and leopards (i.e. the large carnivore least affected by interspecific competition) (Marker & Dickman 2005; Mills 2015). The interactions among carnivore guild members as well as their interactions with prey species are important

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components of biodiversity (Dalerum et al. 2008; Mills 2005). Conservation of the intact carnivore guild has a higher priority than the conservation of individual species (Woodroffe & Ginsberg 2005).

To conserve the intact guild, a mosaic of high and low densities of the dominant competitors is required to provide refuge areas for the subordinate competitors (Winterbach et al. 2013). Botswana has two large conservation zones with the potential to conserve the intact carnivore guild (Winterbach, Winterbach & Somers 2014). The Southern Conservation Zone is characterised by a mosaic of low and medium densities of wild prey for lions and spotted hyaenas (Winterbach et al. 2014), and both carnivores occur at low to medium densities (Funston et al. 2001; Maude & Selebatso 2012; Mills 2015; Mudongo & Dipotso 2010). The Northern Conservation Zone has a mosaic of high, medium and low prey densities for large carnivores, with the highest prey densities in and around the Okavango Delta and along the Kwando/Linyanti/Chobe river system (Winterbach et al. 2014). High densities of lions and spotted hyaenas have been recorded in the Okavango Delta and low densities in the dry parts of the Northern Conservation Zone (Cozzi et al. 2013; Winterbach & Maude 2015; Winterbach & Winterbach 2003).

In addition to these conservation zones, the long-term conservation of brown hyaenas depends on the agricultural areas in Botswana (Boast & Houser 2012; Kent & Hill 2013). These areas do not have the potential to conserve the intact carnivore guild (Winterbach et al. 2014). They do, however, provide an opportunity to conserve the less dominant species including brown hyaenas, cheetahs, leopards and wild dogs (Boast & Houser 2012; IUCN/SSC 2007; Kent & Hill 2013; Klein 2007; Maude & Mills 2005; Winterbach et al. 2015).

Conservation of carnivores in the agricultural areas requires mitigation measures (Winterbach et al. 2013). Although brown hyaenas are mainly scavengers (Maude & Mills 2005; Mills 1990, 2015) and a low level of conflict is expected with livestock owners, human persecution is a significant threat to the species in the range countries (Mills & Hofer 1998; Wiesel 2015). In the North West province of South Africa, 40% of livestock owners regard the brown hyaena as a problem animal (Thorn 2008), and in Namibia, 72% of livestock owners believe that brown hyaenas were responsible for livestock depredations (Lindsey et al. 2013). Weise et al. (2015) confirmed conflict with brown hyaenas in Namibia, and according to farmers, conflict happens especially during peak calving or lambing seasons. Although faecal analysis and inspection of food remains at den sites showed cattle were a significant food source in the farming areas of the Gauteng and Limpopo, discussions with farmers indicated that the killing of cattle by brown hyaena was probably rare and that removing the individual responsible solved the problem (Skinner 1976). Although translocation can solve the conflict, one should consider brown hyaena sociality as part of the decision process to translocate individuals (Weise et al. 2015). Some cattle farmers in Botswana believe that brown hyaenas kill new born calves when the calves are left hidden while the mothers go foraging (M. Bing, pers. comm., n.d.). Maude and Mills (2005) reported that only 25% of cattle post owners around Makgadikgadi Pans National Park, Botswana, believed that brown hyaenas might cause livestock losses. They also found no loss of livestock because of brown hyaena predation around Makgadikgadi Pans National Park in a 5-year period, but did show that carcasses of livestock were an important food source to sustain brown hyaena populations in agricultural areas. Furthermore, brown hyaenas were a minority of the problem animal incidents reported in the Kweneng district, a livestock area south of the Central Kalahari Game Reserve in Botswana (Schiess-Meier et al. 2007). Boast (2014) recorded low levels of conflict with brown hyaenas and that they are the most tolerated large carnivore in Botswana.

The wide distribution of brown hyaenas on both conservation and agricultural land requires density estimates for all ecosystems and land uses in Botswana. Data to assess the large carnivore populations in Botswana are available in peer-reviewed articles and internal and unpublished reports. We reviewed articles and reports to identify some of the areas that were data deficient and conducted large carnivore surveys at multiple sites in Botswana. Here we present our data on brown hyaenas, collated with other published studies and unpublished or internal reports from the research community in Botswana to provide a countrywide population estimate of brown hyaenas in Botswana. We discuss the implications of the results for carnivore conservation.

Research method and design

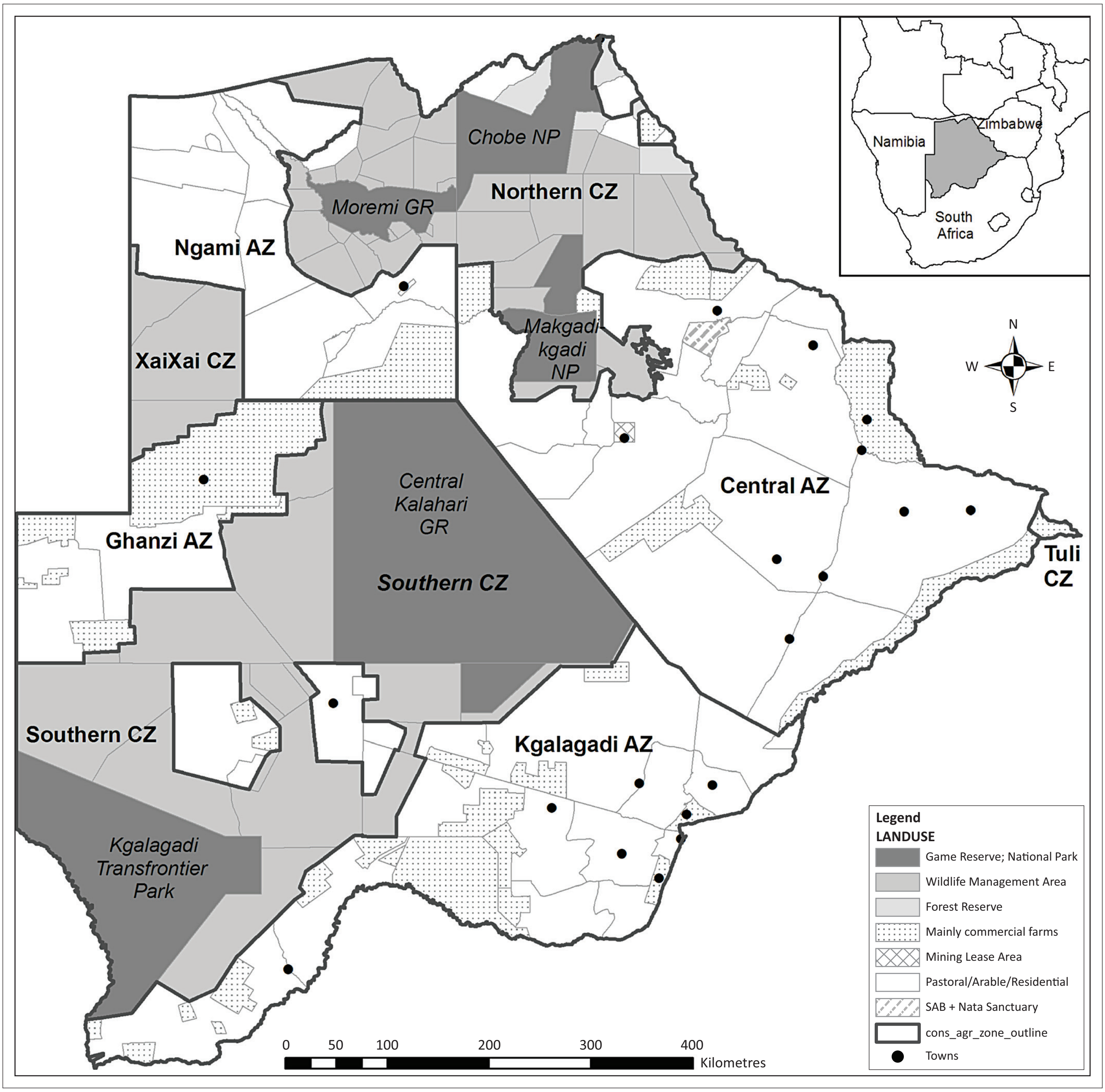
Study area

The Republic of Botswana is a landlocked country of 582 000 km^2, sharing international boundaries with Namibia, South Africa, Zimbabwe and Zambia. Altitude ranges from 515 m a.s.l. to 1491 m a.s.l. Most of Botswana is arid to semi-arid, with the Kalahari ecosystem occupying approximately 82% of the country. Rainfall is erratic and the mean rainfall ranges from 250 mm per year in the south-west to over 650 mm in the north-east (Department of Surveys and Mapping 2001). Over 90% of rainfall occurs in the summer months between November and April. Apart from the Okavango Delta and the perennial Kwando/Linyanti/Chobe river system, the only other surface water occurs in rivers and pans during the rainy season (Department of Surveys and Mapping 2001). The mean minimum temperatures range from 5 °C in July to 19 °C in January with the mean maximum daily temperatures ranging from 22 °C in July to 33 °C in January (Department of Surveys and Mapping 2001).

Vegetation over most of the country is shrub and tree savannah, which is classified as Sandveld (Department of Surveys and Mapping 2001). The Hardveld vegetation types are associated with hills and rocky outcrops in the eastern part of Botswana. The Northern Conservation Zone comprises the wetland of the Okavango Delta, Sandveld, mopane *Colophospermum mopane* dominated vegetation types and limited Miombo woodland in the north-east. The Okavango Delta consists of a mosaic of islands, waterways and seasonal floodplains (Department of Surveys and Mapping 2001).

Seventeen percent of Botswana is fully protected as designated national parks and game reserves, and a further 21% is partially protected as designated Wildlife Management Areas (WMAs). Only 5% of the country is designated as urban. The balance of 57% comprises uncultivated rangeland consisting of approximately 5% freehold land, 25% state land and 70% tribal/communal grazing land (Department of Surveys and Mapping 2001). Commercial livestock production occurs on freehold, state and tribal lands.

Winterbach et al. (2014) identified four conservation zones and four agricultural zones in Botswana based on primary land use. The conservation zones consist of the large Northern Conservation Zone and Southern Conservation Zone, and the two smaller conservation zones of XaiXai and Tuli. The Northern Conservation Zone includes Chobe National Park, Moremi Game Reserve, Nxai Pan National Park, Makgadikgadi Pans National Park and the associated WMAs. The Central Kalahari Game Reserve, Kgalagadi Transfrontier Park and associated WMAs form the Southern Conservation Zone (Figure 1). The agricultural zones are Ngami, Central, Ghanzi and Kgalagadi (Figure 1).



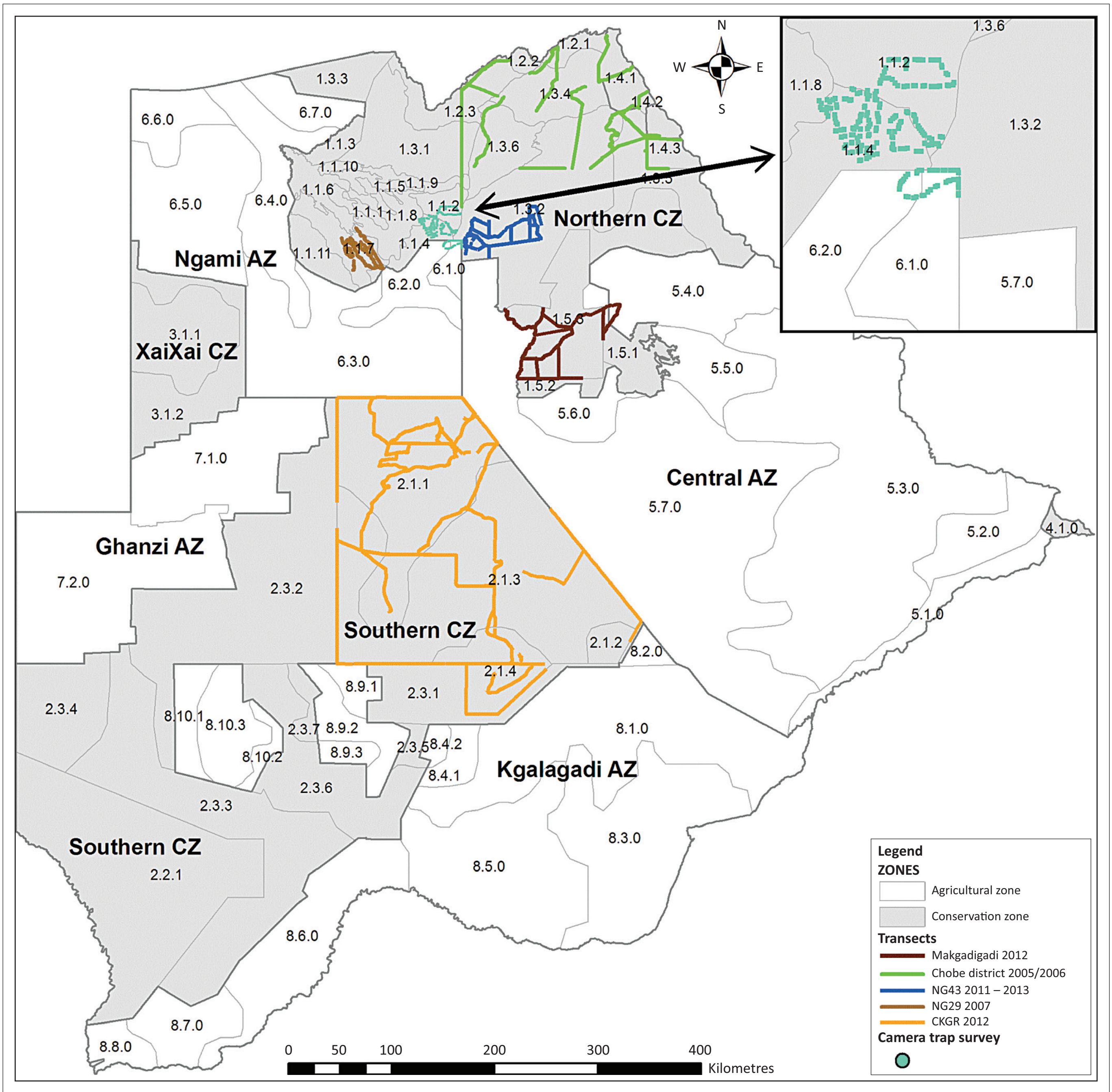
Source: Department of Surveys and Mapping (2001) and Winterbach et al. (2015)

FIGURE 1: Primary land use in Botswana, including the conservation zones (national parks, game reserves and Wildlife Management Areas) and agricultural zones (commercial farms and communal land with cattle posts). Insert shows Botswana in relation to southern Africa.

Livestock (mainly cattle) rearing forms 70% – 80% of the contribution of the agricultural sector to the gross domestic product (Botswana Ministry of Agriculture 2011). The national herd was 2.6 million cattle, 1.8 million goats and 300 000 sheep in 2012. Traditional cattle posts on communal grazing land are the most common livestock production system (Botswana Ministry of Agriculture 2011). There were 109 ranches producing game or cattle and game in 2013; these cover approximately 11 500 km^2 (Boast 2014). Approximately half of the population of 2 million people live in rural villages and small settlements and are thus partially or fully dependent on livestock for their livelihoods (Central Statistics Office 2014).

Procedure

We conducted track counts following the methodology of Stander (1998) and Funston et al. (2010). Existing roads and 4 × 4 trails were used for transects, covering parts of the Northern Conservation Zone and the Central Kalahari Game Reserve in the Southern Conservation Zone (Figure 2). Two trackers identified the tracks from a vehicle driven at slow speeds not exceeding 15 km/h. All fresh tracks (< 24 h old) of large carnivores were identified and recorded with the date, GPS location, species and number of individual animals. Data recording excluded roads disturbed by vehicles or rain in the previous 24 h. Each individual should only be recorded



Stratification of Botswana is following Winterbach et al. (2015). Stratum identification numbers are shown on the map for reference.

FIGURE 2: Stratification of Botswana and locations of track surveys and camera trap survey (detail on inset) conducted between 2005 and 2015 to estimate brown hyaena (*Parahyaena brunnea*) densities.

once per day on the survey (Stander 1998). Multiple track incidences (observations of tracks) from the same species on the same transect were reviewed with the trackers to determine whether the tracks belonged to the same or new individuals.

We deployed Panthera v4 incandescent-flash and Bushnell TrophyCam infra-red camera traps at 221 locations across a 550 km^2 study area in the Northern Conservation Zone and Ngami Agricultural Zone between February and July 2015. We used 5 km^2 grid cells to guide the placement of cameras and ensure systematic coverage of the entire study area. We deployed two camera stations within each grid cell, one on the road closest to the predetermined centre point of each grid cell and the second on the road closest to a predetermined random point within each grid cell. We placed all cameras on sand roads to increase our probability of photographing carnivores given that large predators and carrion feeders often use lightly travelled roads as movement corridors (Forman & Alexander 1998). If cameras had been placed randomly or on the extensive network of game trails, we believe our detection rates would have been prohibitively low. Each camera station included two opposing cameras mounted on trees, offset by 0.5 m – 1 m. If there were no trees available, we mounted cameras on metal fence posts hammered into the ground. We secured cameras at knee height and positioned cameras to photograph flanks of passing animals. We programmed cameras to take three photos at each trigger event in the daytime with a delay of 30 s between trigger events. At night-time, the infra-red cameras took three photos when triggered but the incandescent-flash cameras could only take one photo every 15 s because of the flash having to recharge. For each station, we combined information from the two opposing cameras using the time or date stamps on the photographs.

We used a rotational system for camera deployment. We divided our study area into five sub-areas of approximately 110 km^2 each and sequentially sampled each area for 30 nights. We deployed an average of 44 camera stations (i.e. 88 cameras) within each sub-area. We checked cameras every 5–10 days to download photos, replace batteries and ensure cameras were still operational.

Distribution records of brown hyaenas consisted of track observations we recorded during our surveys, supplemented with brown hyaena observation records from publications, reports and verifiable observations between January 2005 and April 2016. Brown hyaena status, collected as part of a larger questionnaire survey conducted during 2012 and 2013, was recorded as present (visual sightings or tracks seen at least quarterly), transient (visual sightings or tracks seen less frequently than quarterly) or absent (never seen brown hyaena or its tracks). Klein (2013) surveyed cattle posts and commercial farms in the Kalahari region of Botswana, and Boast (2014) targeted primarily game ranchers and commercial livestock farmers in the game ranching regions of the Central, Ghanzi, Ngamiland and North East regional districts.

Data analysis

Transects were pooled per stratum for analysis, following the landscape stratification of Botswana for large carnivores (Figure 2) from Winterbach et al. (2015). The ratio of stratum size and transect length was used to calculate penetration (km²/km of transect) as an index of sampling effort (Funston et al. 2010). We calculated track density (number of individual tracks/100 km sampled) per transect, treating each repetition an individual record. Following Funston et al. (2010), we calculated the mean and standard deviation of the distance (km) between track incidences for each stratum sampled. Funston et al. (2010) recommended that the coefficient of variance (CV) of distance between track incidences (standard deviation × 100/mean km per track incidence) should be less than 20% to ensure appropriate precision of the density estimate. This generally occurs after 19–30 track incidences (Funston et al. 2010). We provide penetration, distance between track incidences with the CV and number of track incidences as indicators of the quality of density estimates in each stratum. We estimated brown hyaena densities from track densities using the extended carnivore model for sandy substrates formula 'animal density = track density/3.26' from Winterbach et al. (2016).

We included density data from other studies for the national population estimate (Table 1-A1). We sourced articles and reports from the research community in Botswana. We recalculated the density estimates from other track surveys using the extended carnivore model for sandy substrates (Winterbach et al. 2016) for consistency of density calculation methods across studies. The population estimates were calculated per stratum from the density estimates, size of the stratum and the proportion of that stratum included in the brown hyaena range (stratum population = density × stratum size/100 km^2).

No density estimates were available for some strata. Where we deemed strata to be similar (general habitat and general land use) to areas with reference data, we assumed similar population densities. In all other cases for strata lacking suitable reference data, we followed the same approach as the Namibia Large Carnivore Atlas (Hanssen & Stander 2004; Stein et al. 2012) using standardised density categories of low, medium or high:

- Assumed low density: 0.085 brown hyaenas/100 km² (range 0.07–0.10).
- Assumed medium density: 0.125 brown hyaenas/100 km² (range 0.10–0.15).
- Assumed high density: 0.575 brown hyaenas/100 km² (range 0.15–1.0).

Because of the limited number of brown hyaenas recorded during the camera trap survey we could not calculate density. The camera trap records were used to indicate the presence and absence as part of mapping distribution. Locations from our surveys and questionnaires were plotted with other reliable location records collected from publications, reports and personal communications.

We used a chi-square test with Bonferroni simultaneous confidence intervals (Byers, Steinhorst & Krausman 1984) to compare frequencies that respondents reported brown hyaenas as present or transient or absent on commercial livestock farms and cattle posts compared to game farms, whose frequencies were defined as the expected values.

Results

Density estimates

We present data from track surveys we conducted between 2005 and 2007 (Chobe district and Okavango Delta) and between 2011 and 2013 (NG43, Makgadikgadi Pans National Park and the Central Kalahari Game Reserve) (Table 1). The lack of roads and 4 × 4 trails limited access to large parts of the study area and resulted in a low sampling effort in some strata as measured by the penetration index (Table 1). Penetrations ranged from 8.5 km²/km to 118.5 km²/km of transect. The surveys conducted during 2005 and 2006 totalled 3000 km of north-eastern Botswana (Figure 2). We completed 844 km in NG43 (WMAs near the Okavango Delta) during 2011, partially covering Stratum 1.3.2 (Figure 2). As part of long-term monitoring, we repeated surveys in NG43 during 2012 and 2013 (Table 1). During 2012, we completed the following transects: a total of 482 km in Makgadikgadi Pans National Park (Stratum 1.5.3), 1120 km in the northern Central Kalahari Game Reserve (Stratum 2.1.1), 1022 km in southern and eastern Central Kalahari Game Reserve (Strata 2.1.2 and 2.1.3) and 397 km in Khutse Game Reserve (Stratum 2.1.4).

The track incidences recorded in Makgadikgadi Pans National Park and the Central Kalahari Game Reserve ranged from 17 to 87 per stratum with mean distance between track incidences of 11.76 km – 22.47 km (Table 2). The CV was

TABLE 1: Summary of track surveys completed between 2005 and 2013 to estimate brown hyaena (*Parahyaena brunnea*) densities in study areas across Botswana.

Survey year	Description	Stratum ID	Total distance of roads (km)	Study site (km²)	Penetration (km²/ km transect)	Total distance sampled (km)	Mean transect length (km) ± SE	Number of transects (*n*)
2005–2006	Dry Woodland	S 1.1.2	19.5	1261	64.9	19.5	19.5 ± 0.0	1
2005–2006	Seasonal Floodplain North East	S 1.1.9	9.5	930	98.2	18.9	9.5 ± 0.0	2
2005–2006	Chobe	S 1.2.1	65.8	1070	16.3	285.0	21.9 ± 0.2	13
2005–2006	Kwando Linyanti	S 1.2.3	126.4	3576	28.3	732.8	18.3 ± 0.9	40
2005–2006	Kwando Delta link	S 1.3.1	58.7	6957	118.5	176.1	19.6 ± 0.1	9
2005–2006	Masame	S 1.3.2	191.5	19 933	104.1	273.9	24.9 ± 3.0	11
2005–2006	Nogatsaa and Nunga	S 1.3.4 and S1.3.5	286.8	11 374	39.7	894.4	18.6 ± 2.1	48
2005–2006	Savuti Mababe	S 1.3.6	80.7	3684	45.7	261.4	20.1 ± 0.3	13
2005–2006	Pandamatenga	S 1.4	127.6	4202	32.9	338.6	17.8 ± 2.2	19
2007	NG29 and NG30 (partial S1.1.7)	S 1.1.7	158.6	1506	9.5	582.7	20.1 ± 5.3	29
2011	NG43 (partial S 1.3.2)	S 1.3.2	355.3	3454	9.7	843.7	18.3± 5.0	46
2012	NG43 (partial S 1.3.2)	S 1.3.2	220.9	3454	15.6	550.4	17.8 ± 4.7	31
2013	NG43 (partial S 1.3.2)	S 1.3.2	406.1	3454	8.5	573.0	19.8 ± 7.1	29
2012	Makgadikgadi Pans National Park	S 1.5.3	482.4	7549	15.6	482.4	25.4 ± 5.0	19
2012	Central Kalahari Game Reserve North	S 2.1.1	1119.5	18 850	16.8	1119.5	22.8 ± 5.2	49
2012	Central Kalahari Game Reserve South	S 2.1.3 and S 2.1.2	1021.6	31 088	30.4	1021.6	22.2 ± 4.4	46
2012	Khutse	S 2.1.4	396.9	4902	12.4	396.9	23.3 ± 4.6	17

TABLE 2: Results of track surveys completed between 2005 and 2013 to estimate brown hyaena (*Parahyaena brunnea*) densities in study areas across Botswana.

Survey year	Description	Stratum ID	Track incidences: *n*	Mean distance between track incidences: number km/set of tracks ± SE (CV)	Tracks/100 km: mean ± SE	Tracks/100 km: (95% CI)	Animals/100 km²: (95% CI)
2005–2006	Dry Woodland	S 1.1.2	0	-	0	-	0
2005–2006	Seasonal Floodplain North East	S 1.1.9	0	-	0	-	0
2005–2006	Chobe	S 1.2.1	0	-	0	-	0
2005–2006	Kwando Linyanti	S 1.2.3	0	-	0	-	0
2005–2006	Kwando Delta link	S 1.3.1	0	-	0	-	0
2005–2006	Masame	S 1.3.2	0	-	0	-	0
2005–2006	Nogatsaa and Nunga	S 1.3.4 and S 1.3.5	1	-	0.13 ± 0.88	-0.12–0.37	0.04 (-0.04–0.11)
2005–2006	Savuti Mababe	S 1.3.6	0	-	0	-	0
2005–2006	Pandamatenga	S 1.4	0	-	0	-	0
2007	NG29 and NG30 (partial S1.1.7)	S 1.1.7	0	-	0	-	0
2011	NG43 (partial S 1.3.2)	S 1.3.2	3	-	0.42 ± 1.63	-0.06–0.89	0.14 (-0.02–0.27)
2012	NG43 (partial S 1.3.2)	S 1.3.2	0	-	0	-	0
2013	NG43 (partial S 1.3.2)	S 1.3.2	1	-	0.15 ± 0.83	-0.15–0.46	0.09 (-0.05–0.14)
2012	MP NP	S 1.5.3	37	12.81 ± 18.37 (143%)	8.30 ± 6.70	5.29–11.32	2.55 (1.62–3.47)
2012	Central Kalahari Game Reserve North	S 2.1.1	53	20.72 ± 21.06 (102%)	5.69 ± 7.55	3.58–7.81	1.75 (1.10–2.39)
2012	Central Kalahari Game Reserve South and South East	S 2.1.3 and S 2.1.2	87	11.76 ± 13.41 (114%)	9.57 ± 8.71	7.05–12.09	2.94 (2.16–3.71)
2012	Khutse	S 2.1.4	17	22.47 ± 26.16 (116%)	4.50 ± 4.24	2.48–6.51	1.38 (0.76–2.00)

CV, coefficient of variance.

between 102% and 143%, exceeding the 20% guideline (Funston et al. 2010). Although we completed 5550 km of track surveys north of Makgadikgadi Pans National Park, we only recorded tracks of brown hyaenas on five occasions. We could not calculate CV for the track frequency in this area because of the small sample size. The density estimates were between 0.00 animals/100 km² and 0.14 animals/100 km². The southern Central Kalahari Game Reserve had the highest density of brown hyaenas (2.94 animals/100 km²), followed by 2.55 animals/100 km² in Makgadikgadi Pans National Park (Table 2).

The camera trap survey yielded only five records of brown hyaenas from 11 618 trap nights. These data were not sufficient to estimate density, but provided confirmation of the edge of the brown hyaena range in part of northern Botswana.

Distribution

Brown hyaenas occur over 533 050 km² (92%) of Botswana (Figure 3). Previous studies recorded the presence of brown hyaenas in the Kgalagadi Transfrontier Park and surrounding WMAs (Funston et al. 2001; Keeping 2014; Mills 1990, Mudongo & Dipotso 2010) and Ghanzi (Boast & Houser 2012; Kent 2011; Kent & Hill 2013). These studies and the location data from our track surveys, camera trap survey, questionnaire survey and additional observation records are shown in

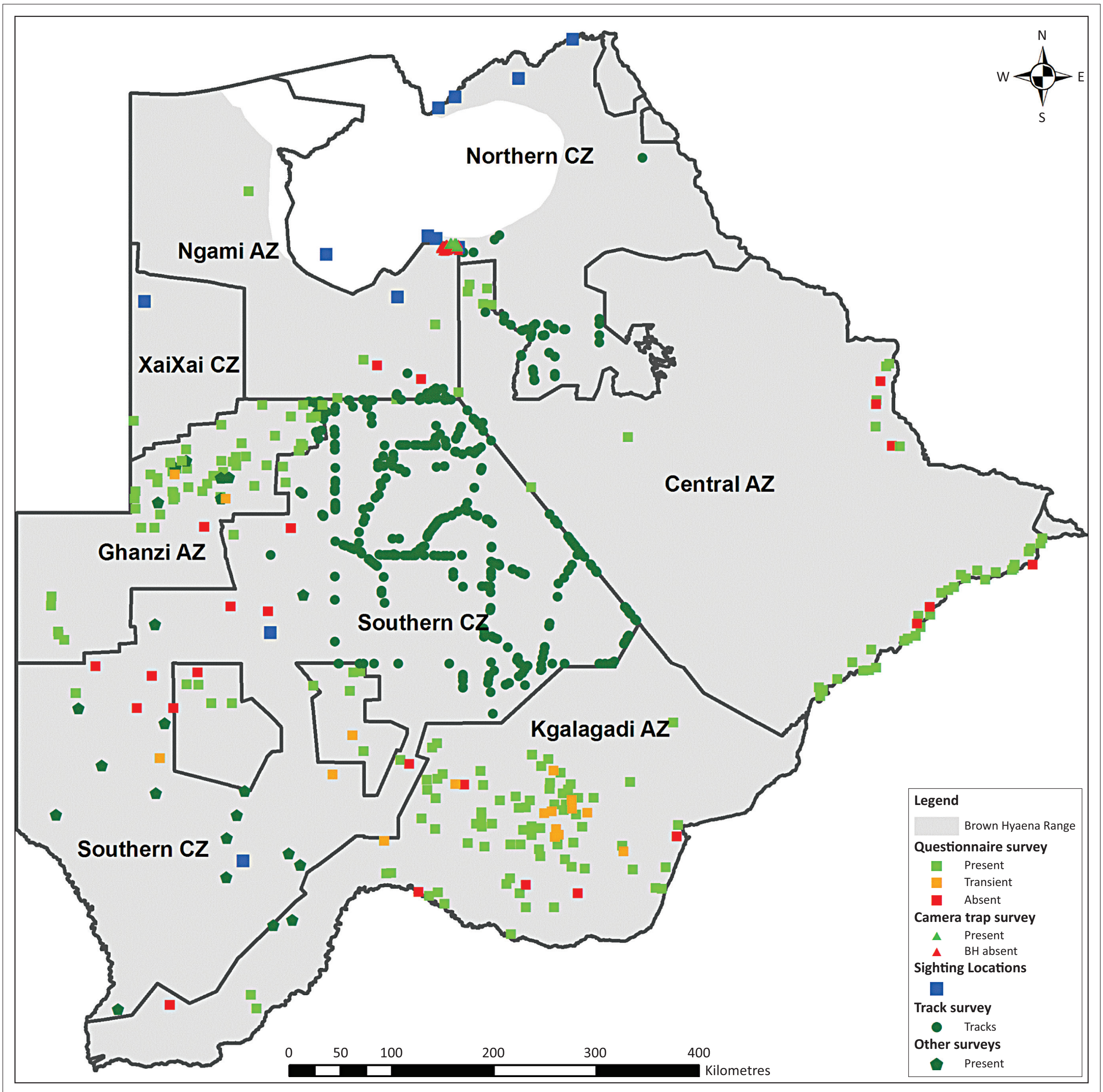


FIGURE 3: Brown hyaena (*Parahyaena brunnea*) distribution range in Botswana based on occurrences recorded between 2005 and 2016.

Figure 3. Only a few records of brown hyaenas were recorded north of Makgadikgadi Pans National Park despite 5550 km of track surveys completed. The concessionaire reported that they only saw brown hyaena tracks in the southern half of NG43 during 15 years of operation (1999–2013) (J. van Rensburg, Kgori Safaris, pers. comm., n.d.). The results of the camera trap survey support that this was the northern edge of the brown hyaena range as brown hyaena were only recorded at the southern stations of the camera survey.

Eighty-two of 418 respondents did not record brown hyaenas as present, transient or absent and were excluded from further analysis. The questionnaire survey provided presence records of brown hyaenas in all four agricultural zones (Figure 3). Respondents recorded brown hyaenas as present (91.6%) and absent (8.4%) on game ranches (n = 107). Presence of brown hyaena was 85.5% on commercial farms (n = 55) and 53.4% on cattle posts (n = 174). The observed frequency of presence and absence or transience differed (χ^2 = 331.25, df = 3, p < 0.001). Brown hyaenas were reported absent or transient more frequently and present less frequently on cattle posts than on game ranches (p = 0.001). It did not differ significantly between commercial livestock farms and game ranches (Table 3).

Population estimates

Our data and data from other sources that we used for the population estimates are summarised in Table 1-A1. Large parts of the Northern Conservation Zone are outside brown hyaena range or are part of the northern limit of their range. We calculated three density estimates north of Makgadikgadi Pans National Park, all between 0.04 animals/100 km² and 0.14 animals/100 km². The five track records obtained along the 5550 km track survey were too low for robust density estimates and may indicate a patchy distribution towards the northern limit of the brown hyaena range. We therefore assumed (Table 1-A1) that brown hyaenas occur at extremely low densities north of Makgadikgadi Pans National Park (range 0.0 animals/100 km² – 0.1 animals/100 km² and mean 0.05 animals/100 km²). Recorded densities (Table 1-A1) varied between 1.13 animals/100 km² and 3.90 animals/100 km² in the Southern Conservation Zone (Funston et al. 2001; Keeping 2014, Maude & Selebatso 2012, Mills 1990; Mudongo & Dipotso 2010). Brown hyaena densities were estimated between 1.89 animals/100 km² and 3.10 animals/100 km² in the Ghanzi farms (Boast & Houser 2012; Kent 2011; Kent & Hill 2013).

No density data were available for the Central Agricultural Zone (north-east Botswana) and Kgalagadi Agricultural Zone (south-east Botswana). These two zones border on the North West province in South Africa where Thorn et al. (2011) estimated overall density of brown hyaenas in agricultural land as 0.15/100 km² ± SE 0.08. Based on this, we assumed a medium density with 0.125 brown hyaenas/100 km², ranging from 0.1 animals/100 km² to 0.15 animals/100 km² in these two agricultural zones (Table 1-A1).

For substrata 6.5.0 (Ngamiland) and 7.2.0 (Ghanzi), we assumed high density (0.575 brown hyaenas/100 km² [range 0.15–1.00]) based on the high densities recorded in neighbouring areas (Table 1-A1). The low-density assumption (0.085 brown hyaenas/100 km² [range 0.07–0.10]) was applied to the substrata of Ngami Agricultural Zone, as this is part of the northern edge of brown hyaena distribution (Table 4).

We estimated the brown hyaena population of Botswana as 4642 animals (3133–5993) (Table 4). Seventy-three percent of the brown hyaena population (approximately 3393 animals) occurred within the Southern Conservation Zone (Table 4) and 18.1% in the agricultural zones (843 brown hyaenas). The remaining 6.8% occurred in the Northern Conservation Zone and 2% in conservation zones of XaiXai and Tuli. The estimated and assumed densities are shown in Figure 4.

Discussion

Our study combined information from track surveys, camera trap surveys, questionnaires and previous studies to estimate local densities and distribution of brown hyaenas across Botswana. Information on brown hyaena populations is vital to making informed conservation decisions and to mitigating population declines, particularly as the species is listed as near threatened (Wiesel 2015). Because of the large scale of this study, however, our data had several limitations.

The data collection span over a decade of research, and there is a risk that carnivore densities may have changed because of ecological factors or changes in land use as demonstrated in Zimbabwe (Williams et al. 2016). No large-scale changes in land use occurred in Botswana during the past 15 years. The brown hyaena density estimates in Kgalagadi Transfrontier Park area of Mills (1990), Funston et al. (2001) and Keeping (2014) were very similar despite

TABLE 3: Bonferroni simultaneous confidence intervals for the presence and absence ortransience of brown hyaena (*Parahyaena brunnea*) based on questionnaires (2008–2009 and 2011–2012) completed by farmers on game ranches (n = 107), commercial livestock farms (n = 55) and traditional cattle posts (n = 174) in the agricultural zones of Botswana.

Land use and status	Expected	Observed	Chi-square	Expected proportion *Pio*	Bonferroni intervals for observed proportion *Pi*	Use index *Pi/Pio*	Significant (α = 0.001)
Absent + transient cattle post	14.64	81	300.93	0.0639	0.2380 ≤ Pi ≤ 0.4694	5.53	+
Present cattle post	159.36	93	27.64	0.6959	0.2873 ≤ Pi ≤ 0.5250	0.58	-
Absent + transient commercial livestock	4.63	8	2.46	0.0202	-0.0095 ≤ Pi ≤ 0.0794	1.73	0
Present commercial livestock	50.37	47	0.23	0.2200	0.1075 ≤ Pi ≤ 0.3030	0.93	0
Total	**229.00**	**229**	**331.25**	**1.0000**	**-**	**-**	**-**

The proportions of present (91.6%) and absent or transient (8.4%) recorded on game farms were used as the reference to calculate the expected proportions for commercial livestock farms and cattle posts (k = 4, α = 0.001, Z = 3.6623).

TABLE 4: Population estimates per stratum of brown hyaenas (*Parahyaena brunnea*) in Botswana based on surveys conducted between 2005 and 2015.

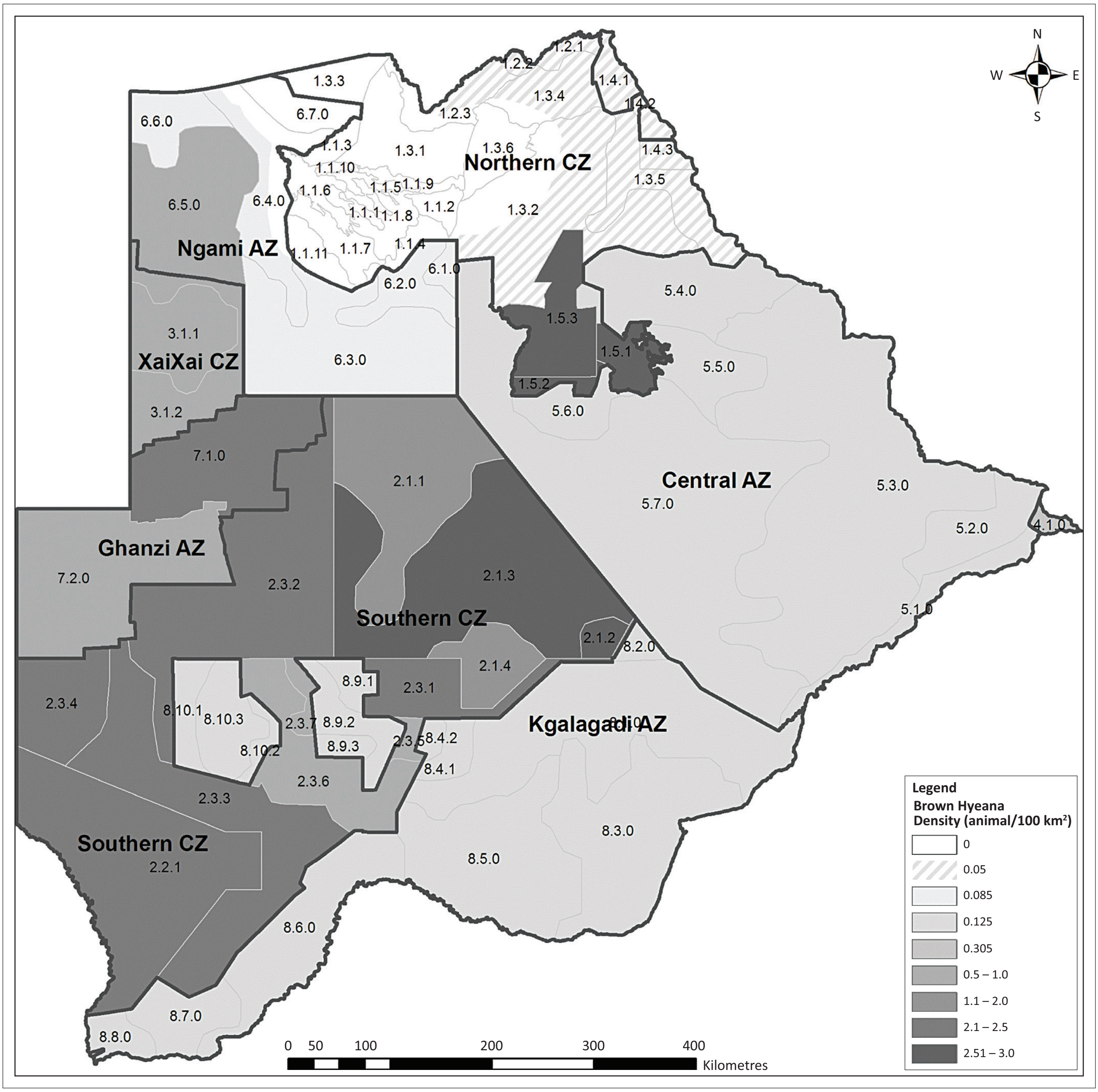
Zone	Stratum	Size (km²)	Population estimate	Range minimum	Range maximum
Northern CZ	1.1 Okavango Delta	16 045	0	0	0
Northern CZ	1.2 Kwando/Chobe	5103	1	0	2
Northern CZ	1.3 Dry North	44 899	13	0	27
Northern CZ	1.4 Pandamatenga	4202	2	0	4
Northern CZ	1.5 Pans	11 684	298	190	406
Southern CZ	2.1 Central Kalahari GR & Khutse	54 841	1309	917	1702
Southern CZ	2.2 KTP	26 210	603	419	734
Southern CZ	2.3 KTP WMA	73 697	1481	999	1840
Xaixai CZ	3.1 Xaixai	15 597	90	23	156
Tuli CZ	4.1 Tuli GR	686	2	0	4
Central Agric	5.1 Central Tuli farms	4345	5	4	7
Central Agric	5.2 Central Agric Molalatau	5978	7	6	9
Central Agric	5.3 Central Agric East	50 837	64	51	76
Central Agric	5.4 Central Agric North	12 161	15	12	18
Central Agric	5.5 Central Agric Pans	5593	7	6	8
Central Agric	5.6 Central Agric Mopipi	4013	5	4	6
Central Agric	5.7 Central Agric West	53 688	67	54	81
Ngami Agric	6.1 Ngami East	1060	1	1	1
Ngami Agric	6.2 Ngami Thamalakane Boteti	3908	2	2	3
Ngami Agric	6.3 Ngami South	18 886	16	13	19
Ngami Agric	6.4 Ngami Panhandle	8696	4	3	4
Ngami Agric	6.5 Ngami Tsodilo	14 169	81	21	142
Ngami Agric	6.6 Ngami North West	4164	4	3	4
Ngami Agric	6.7 Ngami North East	3303	0	0	0
Ghanzi Agric	7.2 Ghanzi Agric	34 894	439	305	591
Kgalagadi Agric	8.1 Kgalagadi Kweneng	26 059	33	26	39
Kgalagadi Agric	8.2 Kgalagadi Dithopo	1057	1	1	2
Kgalagadi Agric	8.3 Kgalagadi Gaborone	18 545	23	19	28
Kgalagadi Agric	8.4 Kgalagadi Kane	2763	3	3	4
Kgalagadi Agric	8.5 Kgalagadi Molopo	17 550	22	18	26
Kgalagadi Agric	8.6 Kgalagadi Tsabong	11 970	15	12	18
Kgalagadi Agric	8.7 Kgalagadi Middelpits	4888	6	5	7
Kgalagadi Agric	8.8 Kgalagadi Bokpits	2159	3	2	3
Kgalagadi Agric	8.9 Kgalagadi Kang	6580	8	7	10
Kgalagadi Agric	8.10 Kgalagadi Hukuntsi	8915	11	9	13
Grand Total	**-**	**57 9144**	**4642**	**3133**	**5993**

CZ, Conservation Zone; GR, Game Reserve.

covering more than 20 years. The long-term study of Maude (2010) found no population declines in the Makgadikgadi region. Despite this long timespan, our data sets are the best indication of the national population of brown hyaena in Botswana.

The recommended sampling effort of 19–30 recorded track incidences per sampling unit should result in a CV below 20% for mean distance between track incidences (Funston et al. 2010; Kent 2011). Despite us recording track incidences of 37, 53 and 87 in three strata of the Central Kalahari Game Reserve, the CVs of these strata still exceeded 100%. This contradicts the results from localised surveys in the Ghanzi farms area (Boast & Houser 2012; Kent 2011) that achieved CVs of less than 20%. These studies recorded densities varying between 1.89 brown hyaenas/100 km² and 3.10 brown hyaenas/100 km² on small units within the Stratum 7.1.0 Ghanzi farms. Similarly, brown hyaena densities varied among habitats within Stratum 2.2.1, the Kgalagadi Transfrontier Park (1.13 brown hyaenas/100 km² – 2.17 brown hyaenas/100 km²) (Funston et al. 2001) and among locations in the surrounding WMAs (2.36 brown hyaenas/100 km² – 3.90 brown hyaenas/100 km²) (Mudongo & Dipotso 2010). The above mentioned studies show heterogeneity in brown hyaena densities across landscapes in conservation and agricultural zones of Botswana on a finer resolution than the stratification we used. Therefore, we should expect heterogeneity in brown hyaena densities in the large survey strata that result in high CVs.

Although our current estimate of 4642 (3133–5993) brown hyaenas is higher than the previous estimates of 3900 (3500–4500) (Mills & Hofer 1998) and 2636 (1990–3282) (Winterbach & Winterbach 2003), it probably does not reflect a population increase. Rather, it indicates that the population was previously underestimated because of a lack of comprehensive data. Although there is evidence that brown hyaenas are persecuted in Botswana (Maude & Mills 2005), we found no indication of a population decline. This is supported by a long-term study on brown hyaenas in the Makgadikgadi region of Botswana by Maude (2010). He concluded that brown hyaenas are sufficiently adaptable to live alongside people in agricultural areas and are thus not



Stratum identification numbers are shown on the map for reference.

FIGURE 4: Estimated and assumed densities per stratum of brown hyaenas (*Parahyaena brunnea*) in Botswana based on surveys conducted between 2005 and 2015.

vulnerable to significant population declines under current land uses (Maude 2010).

The similar brown hyaena densities recorded in Ghanzi and the Southern Conservation Zone (Table 1-A1) highlight the importance of agricultural zones in Botswana for brown hyaena conservation (Boast & Houser 2012; Kent & Hill 2013). Furthermore, Maude and Mills (2005) showed that brown hyaenas occurred at higher densities in the communal land in the agricultural zone around Makgadikgadi Nxai Pan National Park, where home range sizes are smaller and clan numbers are higher than inside the national park. In contrast to these findings, Thorn et al. (2011) estimated a much lower density of brown hyaenas in agricultural land (0.15/100 km^2 ± SE 0.08) than in Pilanesberg National Park, North West province of South Africa. Less antagonism, lower human density, a lack of large-scale crop production and differences in livestock management practices may contribute to a more hospitable environment for brown hyaenas in Ghanzi than the North West province (Kent & Hill 2013).

The findings of Maude and Mills (2005), Schiess-Meier et al. (2007) and Kent and Hill (2013) indicated that we can potentially have relatively high brown hyaena densities in the Ngami, Central and Kgalagadi agricultural zones. We lacked density data in these areas that include large parts of communal land with cattle posts. Brown hyaena densities in Botswana, apart from the north, varied between 1.2 animals/100 km² and 3.9 animals/100 km² (Table 1-A1). However, our questionnaire surveys showed that brown hyaenas were more likely to be reported as transient or absent on the communal land with cattle posts than on commercial and game farms. This can be the result of observer bias, with the respondents either over- or under-reporting the presence of brown hyaena. The alternative is that brown hyaena did occur less on communal land. Our current data are not suitable to clarify this. The brown hyaena densities recorded elsewhere in Botswana might not be representative of these agricultural zones, and therefore, we opted for the conservative density assumption of 0.15 animals/100 km² based on the results of Thorn et al. (2011).

The communal farmlands with cattle posts in these three agricultural zones represent a major gap in our knowledge of brown hyaenas in Botswana. Brown hyaenas can thrive in agricultural areas of Botswana (Boast & Houser 2012; Kent & Hill 2013; Maude & Mills 2005). Therefore, we recommend that future brown hyaena surveys focus particularly on the Ngami, Central and Kgalagadi agricultural zones, which may be strongholds for the species.

A significant proportion (18.1%) of the brown hyaena population in Botswana occurred in agricultural areas of Botswana. For example, our estimates showed more brown hyaenas in the Ghanzi farms (Stratum 7.1.0) than all of the Northern Conservation Zone. The agricultural zones are not only key areas for the conservation of brown hyaenas in Botswana but also essential to maintain links with populations in Namibia and South Africa.

The stronghold for brown hyaenas in the Northern Conservation Zone is the Makgadikgadi Pans. This area and the strata in the Northern Conservation Zone without perennial water have low prey densities and should be refuge areas for subordinate carnivores (Winterbach et al. 2014). However, we recorded brown hyaena infrequently in the strata north of Makgadikgadi, despite low densities of lion and spotted hyaena (unpublished data from our surveys). Annual rainfall increases from 400 mm in Makgadikgadi to 700 mm in the north-east of the Northern Conservation Zone (Department of Surveys and Mapping 2001). This may be a factor that limits brown hyaena in the Northern Conservation Zone directly or indirectly, because brown hyaena occurs in areas with rainfall up to approximately 700 mm (Wiesel 2015). Also, the species does not occur in the Okavango Delta, the area around Moremi Game Reserve, an area that supports high densities of lions and spotted hyaenas (Cozzi et al. 2013; Winterbach & Winterbach 2003). Mills and Mills (1982) and Mills (2015) found that spotted hyaenas out-compete brown hyaenas and this interspecific competition may explain why the Okavango Delta is not part of the brown hyaena's range (Mills & Hofer 1998; Wiesel 2015). Although it is not clear from our distribution and density data whether brown hyaenas are resident in localised areas or merely transient through the northern part of their range in Botswana, the Northern Conservation Zone provides the link between the Botswana and Zimbabwe populations.

Botswana supports the highest number of brown hyaenas of all the range countries (Wiesel 2015), and a significant proportion of this national population occurs on agricultural land. The focus of carnivore conservation in Botswana should be on maintaining the intact large carnivore guild in the conservation zones, complimented by a species conservation approach in the agricultural zones. We recommend that future surveys in Botswana specifically include density estimates for brown hyaenas on communal farmland in the Ngami, Central and Kgalagadi agricultural zones.

Less livestock owners in Botswana regard brown hyaenas as a risk to livestock than their counterparts in South Africa and Namibia (Lindsey et al. 2013; Maude & Mills 2005; Thorn 2008), which may be related to farming practices, that can increase the risk of brown hyaenas killing new born and weak calves (M. Bing, pers. comm., n.d.). Regional and individual differences in behaviour of brown hyaenas may contribute to the lower perceived threat in parts of Botswana. Although brown hyaenas may on rare occasions cause livestock losses (Skinner 1976; Weise et al. 2015), they are not a significant problem animal species.

Persecution of brown hyaenas in the livestock areas of Botswana may impact negatively on the long-term conservation of the species across its distribution range in southern Africa. The resident brown hyaena population in the livestock areas of Botswana is not only a significantly large population, but is also critical to maintain links among the conservation zones in Botswana and the neighbouring range countries Namibia, South Africa and Zimbabwe. The information provided here should be incorporated into conservation strategies for large carnivores in Botswana.

Conclusion

We found no indication that the estimated population of 4642 (3133–5993) brown hyaenas in Botswana declined. Brown hyaena densities were heterogeneous across landscapes in conservation and agricultural zones on a finer resolution than the stratification we used. We lack data to assess the population in large parts of the agricultural areas and recommend that future brown hyaena surveys focus particularly on the Ngami, Central and Kgalagadi agricultural zones, which may be strongholds for the species. The agricultural areas in Botswana are important to maintain population links between Namibia, South Africa and Zimbabwe.

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Competing interests

The authors declare that they have no financial or personal relationships that may have inappropriately influenced them in writing this article.

Authors' contributions

C.W.W. was the project leader. C.W.W., G.N-M. and G.M. designed and conducted the track surveys. L.N.R. designed and conducted the camera trap survey. R.K. and L.B. provided the brown hyaena results from their questionnaire surveys. C.W.W. performed the data analysis. M.J.S. made conceptual contributions. All authors contributed to the writing and editing of the manuscript.

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Appendix starts on the next page →

Appendix 1

TABLE 1-A1: Summary of reference data to estimate density of brown hyaenas (*Parahyaena brunnea*) in Botswana.

Zone	Sub-stratum	Range (% of unit)	Location	Reference	Method and year	Mean track dens	Density
Northern CZ	1.1.1 Chiefs Island	0	-	-	-	-	0.00
Northern CZ	1.1.2 Dry Woodland	0	-	-	-	-	0.00
Northern CZ	1.1.3 Eretsa community	0	-	-	-	-	0.00
Northern CZ	1.1.4 Lower Delta	0	-	-	-	-	0.00
Northern CZ	1.1.5 Permanent Swamp East	0	-	-	-	-	0.00
Northern CZ	1.1.6 Permanent Swamp Central	0	-	-	-	-	0.00
Northern CZ	1.1.7 Seasonal Floodplain West	0	-	C.W. Winterbach	Track survey 2007: 83 km, no tracks.	0.0	0.00
Northern CZ	1.1.8 Seasonal Floodplain Central	0	-	-	-	-	0.00
Northern CZ	1.1.9 Seasonal Floodplain North East	0	-	-	-	-	0.00
Northern CZ	1.1.10 Seasonal Floodplain North West	0	-	-	-	-	0.00
Northern CZ	1.1.11 Western Delta and Sandveld Tongue	0	-	-	-	-	0.00
Northern CZ	1.2.1 Chobe	100	-	G. Neo Mapuleng	Track survey 2005/2006: 285 km, no tracks.	0.0	0.00
Northern CZ	1.2.1 Chobe	100	-	-	Assume extremely low density.	-	0.05 (0.00–0.10)
Northern CZ	1.2.2 Enclave community	100	-	-	Assume extremely low density.	-	0.05 (0.00–0.10)
Northern CZ	1.2.3 Kwando Linyanti	19	-	G. Neo Mapuleng	Track survey 2005/2006: 733 km, no tracks.	0.0	0.00
Northern CZ	1.2.3 Kwando Linyanti	19	-	-	Assume extremely low density.	-	0.05 (0.00–0.10)
Northern CZ	1.3.1 Kwando Delta link	0	-	G. Neo Mapuleng	Track survey 2005/2006: 176 km, no tracks.	0.0	0.00
Northern CZ	1.3.2 Masame	76	-	G. Neo Mapuleng	Track survey 2005/2006: 274 km, no tracks.	0.00	0.00
Northern CZ	*1.3.2 Masame*	*76*	*NG43*	*C.W. Winterbach*	*Track survey 2011: 844 km, 3 individuals, Track Frequency 0.42.*	*0.42*	0.13 (-0.02–0.27)
Northern CZ	*1.3.2 Masame*	*76*	*NG43*	*C.W. Winterbach*	*Track survey 2012: 550 km, 0 individuals*	*0.00*	0.00
Northern CZ	*1.3.2 Masame*	*76*	*NG43*	*C.W. Winterbach*	*Track survey 2013: 573 km, 1 individuals, Track Frequency 0.15.*	*0.15*	0.05 (-0.05–0.14)
Northern CZ	1.3.2 Masame	76	NG43		Assume extremely low density.	-	0.05 (0.00–0.10)
Northern CZ	1.3.3 Ngami North	0	-	-	-	-	0.00
Northern CZ	1.3.4 Nogatsaa	100	-	-	Assume extremely low density.	-	0.05 (0.00–0.10)
Northern CZ	*1.3.4 & 1.3.5*	*100*	-	*G. Neo Mapuleng*	*Track survey 2005/2006: 894 km, 1 individual, track frequency 0.13.*	*0.126*	0.04 (-0.04–0.11)
Northern CZ	1.3.5 Nunga	100	-	-	Assume extremely low density.	-	0.05 (0.00–0.10)
Northern CZ	1.3.6 Savuti Mababe	0	-	G. Neo Mapuleng	Track survey 2005/2006: 261 km, no tracks.	0	0.00
Northern CZ	*1.4*	*100*	*1.4.1, 1.4.2 and 1.4.3 combined*	*G. Neo Mapuleng*	*Track survey 2005/2006: 339 km, no tracks.*	*0*	0.00
Northern CZ	1.4.1 Kazangula	100	-	-	Assume extremely low density.	-	0.05 (0.00–0.10)
Northern CZ	1.4.2 Panda farms	100	-	-	Assume extremely low density.	-	0.05 (0.00–0.10)
Northern CZ	1.4.3 Pandamatenga	100	-	-	Assume extremely low density.	-	0.05 (0.00–0.10)
Northern CZ	1.5.1 Pans Community	100	-	Maude (2008)	Assume = Pans NP 2012 survey.	-	2.55 (1.62–3.47)
Northern CZ	1.5.2 Pans Community Area	100	-	Maude (2008)	Assume = Pans NP 2012 survey.	-	2.55 (1.62–3.47)
Northern CZ	*1.5.3 Pans NP*	*100*	*Pans*	*Maude (2008)*	*Collars*	-	1.20 (0.90–1.50)
Northern CZ	1.5.3 Pans NP	100	Pans	G. Maude	Track survey 2012: 482.2 km, 40 individuals, Track Frequency 8.3.	8.30	2.55 (1.62–3.47)
Southern CZ	-	*100*	*Central Kalahari Game Reserve North and south combined, including Khutse*	*G. Maude*	*Track survey 2012: 2538 km, 172 individuals, track freq 7.1.*	*7.10*	2.18 (1.73–2.63)
Southern CZ	-	100	*Central Kalahari Game Reserve*	*Senior Wildlife Biologist (2000)*	*Track survey 2000: Small sample.*		2.60 (2.00–3.20)

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CZ, Conservation Zone; GR, Game Reserve; CV, coefficient of variance; NP, National Park; SE, South East.

Table 1-A1 continued on the next page →

TABLE 1-A1:(Continues...) Summary of reference data to estimate density of brown hyaenas (*Parahyaena brunnea*) in Botswana.

Zone	Sub-stratum	Range (% of unit)	Location	Reference	Method and year	Mean track dens	Density
Southern CZ	2.1.1 Central Kalahari Game Reserve North	100	Central Kalahari Game Reserve Central Kalahari Game Reserve North (2.1.1) and northern boundaries	G. Maude	Track survey 2012: 1119.5 km, 60 individuals, Track Frequency 5.69.	5.69	1.75 (1.10–2.39)
Southern CZ	2.1.2 Central Kalahari Game Reserve SE	100	Central Kalahari Game Reserve South (2.1.3) and south east (2.1.2) combined with boundary	G. Maude	Track survey 2012: 1021.6 km, 95 individuals, Track Frequency 9.57.	9.57	2.94 (2.16–3.71)
Southern CZ	2.1.3 Central Kalahari Game Reserve South	100	Central Kalahari Game Reserve South (2.1.3) and south east (2.1.2) combined with boundary	G. Maude	Track survey 2012: 1021.6 km, 95 individuals.	9.57	2.94 (2.16–3.71)
Southern CZ	2.1.4 Khutse	100	Central Kalahari Game Reserve Khutse including boundaries	G. Maude	Track survey 2012: 396.9 km, 17 individuals.	4.50	1.38 (0.76–2.00)
Southern CZ	2.2.1 KTP	100	KTP and KTP Buffer KTP and KD1, KD2 combined	Keeping (2014)	Track survey with FMP formula, 634 km, CV 10%.	-	2.30 (1.60–2.80)
Southern CZ	*2.2.1 KTP*	100	*KGNP*	*Mills (1990)*	*Radio collar*	-	1.70 (1.60–1.80)
Southern CZ	*2.2.1 KTP*	*100*	*Dune Savanna*	*Funston, P.J. et. al. (2001)*	*Track survey 2000: 3480.6 km, 129 individuals, Track Frequency 27.6.*	*3.7*	1.13
Southern CZ	*2.2.1 KTP*	*100*	*Tree Savanna*	*Funston, P.J. et. al. (2001)*	*Track survey 2000: 6128 km, 433 individuals, Track Frequency 14.3.*	*7.1*	2.17
Southern CZ	*2.2.1 KTP*	*100*	*Tree and Dune combined*	*Funston, P.J. et. al. (2001)*	*Track survey 2000: 9608.6 km, 562 individuals, Track Frequency 5.85).*	*5.8*	1.79
Southern CZ	2.3.1 Central Kalahari Game Reserve Buffer	100	-	Keeping (2014)	Assume = KTP buffer.	-	2.30 (1.60–2.80)
Southern CZ	2.3.2 Western corridor	100	-	Keeping (2014)	Assume = KTP buffer.	-	2.30 (1.60–2.80)
Southern CZ	2.3.3 KTP buffer	100	KTP and KD1, KD2 combined	Keeping (2014)	Track survey with FMP formula, 634 km, CV 10%.	-	2.30 (1.60–2.80)
Southern CZ	*2.3.3 KTP buffer*	100	*Kgalagadi WMA Survey combined*	*Mudongo and Dipotso (2010)*	*Track survey 2010: 900 km, 86 individuals, Track Frequency 11.4.*	*9.56*	2.93 (2.60–3.27)
Southern CZ	*2.3.3 KTP buffer*	100	*Kgalagadi WMA KD 15*	*Mudongo and Dipotso (2010)*	*Track survey 2010: 300 km, 38 individuals, Track Frequency 9.1.*	*12.70*	3.90 (3.16–4.64)
Southern CZ	*2.3.3 KTP buffer*	100	*Kgalagadi WMA KD 12*	*Mudongo and Dipotso (2010)*	*Track survey 2010: 150 km, 16 individuals, Track Frequency 10.7.*	*10.70*	3.28 (2.47–4.10)
Southern CZ	*2.3.3 KTP buffer*	100	*Kgalagadi WMA KD 2*	*Mudongo and Dipotso (2010)*	*Track survey 2010: 350 km, 29 individuals, Track Frequency 12.5.*	*8.30*	2.55 (2.15–2.94)
Southern CZ	*2.3.3 KTP buffer*	100	*Kgalagadi WMA KD 1*	*Mudongo and Dipotso (2010)*	*Track survey 2010: 300 km, 23 individuals, Track Frequency 14.3.*	*7.70*	2.36 (1.91–2.82)
Southern CZ	2.3.4 KTP buffer west	100	-	Keeping (2014)	Assume = KTP buffer.	-	2.30 (1.60–2.80)
Southern CZ	2.3.5 Eastern corridor 1	100	-	-	Assume high density.	-	0.58 (0.15–1.00)
Southern CZ	2.3.6 Eastern corridor 2	100	-	-	Assume high density.	-	0.58 (0.15–1.00)
Southern CZ	2.3.7 Eastern corridor 3	100	-	-	Assume high density.	-	0.58 (0.15–1.00)
Xaixai CZ	3.1.1 Xaixai Core	100	-	-	Assume high density.	-	0.58 (0.15–1.00)
Xaixai CZ	3.1.2 Xaixai Perifery	100	-	-	Assume high density.	-	0.58 (0.15–1.00)
Tuli CZ	4.1.0 Tuli GR	100	Mashatu, Northern Tuli Game Reserve	Snyman pers. comm., n.d.	Estimate 4 total.	-	0.31 (0.01–0.60)
Central Agric	5.1.0 Central Tuli farms	100	-	Thorn et al. (2011)	Assume medium density.	-	0.13 (0.10–0.15)
Central Agric	5.2.0 Central Agric Molalatau	100	-	Thorn et al. (2011)	Assume medium density.	-	0.13 (0.10–0.15)
Central Agric	5.3.0 Central Agric East	100	-	Thorn et al. (2011)	Assume medium density.	-	0.13 (0.10–0.15)
Central Agric	5.4.0 Central Agric North	100	-	Thorn et al. (2011)	Assume medium density.	-	0.13 (0.10–0.15)
Central Agric	5.5.0 Central Agric Pans	100	-	Thorn et al. (2011)	Assume medium density.	-	0.13 (0.10–0.15)
Central Agric	5.6.0 Central Agric Mopipi	100	-	Thorn et al. (2011)	Assume medium density.	-	0.13 (0.10–0.15)
Central Agric	5.7.0 Central Agric West	100	-	Thorn et al. (2011)	Assume medium density.	-	0.13 (0.10–0.15)
Ngami Agric	6.1.0 Ngami East	100	-	-	Assume low density.	-	0.09 (0.07–0.10)

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CZ, Conservation Zone; GR, Game Reserve; CV, coefficient of variance; NP, National Park; SE, South East.

Table 1-A1 continued on the next page →

TABLE 1-A1:(Continues...) Summary of reference data to estimate density of brown hyaenas (*Parahyaena brunnea*) in Botswana.

Zone	Sub-stratum	Range (% of unit)	Location	Reference	Method and year	Mean track dens	Density
Ngami Agric	6.2.0 Ngami Thamalakane Boteti	69	-	-	Assume low density.	-	0.09 (0.07–0.10)
Ngami Agric	6.3.0 Ngami South	100	-	-	Assume low density.	-	0.09 (0.07–0.10)
Ngami Agric	6.4.0 Ngami Panhandle	51	-	-	Assume low density.	-	0.09 (0.07–0.10)
Ngami Agric	6.5.0 Ngami Tsodilo	100	-	-	Assume high density.	-	0.58 (0.15–1.00)
Ngami Agric	6.6.0 Ngami North West	100	-	-	Assume low density.	-	0.09 (0.07–0.10)
Ngami Agric	6.7.0 Ngami North East	0	-	-		-	0.00
Ghanzi Agric	7.1.0 Ghanzi farms	100	Surveys combined	Boast and Houser (2012)	Track survey 2007–2008: 3535 km, 257 individuals, Track frequency 13.76 ± 1.18 (8.6% CV).	7.27	2.23 (1.91–2.68)
Ghanzi Agric	*7.1.0 Ghanzi farms*	*100*	*East of Ghanzi (Game plus livestock)*	*Boast and Houser (2012)*	*Track survey 2007–2008: 1026 km, 81 individuals, Track frequency 12.67 ± 1.69 (CV = 13%)*	*7.89*	*2.42 (1.91–3.30)*
Ghanzi Agric	*7.1.0 Ghanzi farms*	*100*	*North West of Ghanzi: game*	*Boast and Houser (2012)*	*Track survey 2007–2008: 1268.8 km, 78 individuals, Track frequency 16.27 ± 2.60 (CV = 16%)*	*6.15*	*1.89 (1.44–2.75)*
Ghanzi Agric	*7.1.0 Ghanzi farms*	*100*	*South West of Ghanzi: livestock*	*Boast and Houser (2012)*	*Track survey 2007–2008: 1240 km, 98 individuals, Track frequency 12.65 ± 1.90 (CV = 15%)*	*7.9*	*2.42 (1.87–3.43)*
Ghanzi Agric	*7.1.0 Ghanzi farms*	*100*	*North West of Ghanzi: game*	*Kent (2011); Kent and Hill (2013)*	*Track survey 2008 -2009: 1023 km, 90 individuals, Track frequency 12.634 ± 0.297*	*8.795*	*2.70 (0.00–0.00)*
Ghanzi Agric	*7.1.0 Ghanzi farms*	*100*	*South West of Ghanzi: livestock*	*Kent (2011); Kent and Hill (2013)*	*Track survey 2008 -2009: 990 km, 100 individuals, Track frequency 9.970 ± 0.181*	*10.101*	*3.10 (0.00–0.00)*
Ghanzi Agric	*7.1.0 Ghanzi farms*	*100*	*South West of Ghanzi: livestock*	*Kent (2011); Kent and Hill (2013)*	*Camera trap 2009: 3187 camera trap days at 56 stations on three sites*	-	*2.30 (0.00–0.00)*
Ghanzi Agric	7.2.0 Ghanzi community	100	-		Assume high density.	-	0.58 (0.15–1.00)
Kgalagadi Agric	8.1.0 Kgalagadi Kweneng	100	-	Thorn et al. (2011)	Assume medium density.	-	0.13 (0.10–0.15)
Kgalagadi Agric	8.2.0 Kgalagadi Dithopo	100	-	Thorn et al. (2011)	Assume medium density.	-	0.13 (0.10–0.15)
Kgalagadi Agric	8.3.0 Kgalagadi Gaborone	100	-	Thorn et al. (2011)	Assume medium density.	-	0.13 (0.10–0.15)
Kgalagadi Agric	8.4.1 Kgalagadi Kane 1	100	-	Thorn et al. (2011)	Assume medium density.	-	0.13 (0.10–0.15)
Kgalagadi Agric	8.4.2 Kgalagadi Kane 2	100	-	Thorn et al. (2011)	Assume medium density.	-	0.13 (0.10–0.15)
Kgalagadi Agric	8.5.0 Kgalagadi Molopo	100	-	Thorn et al. (2011)	Assume medium density.	-	0.13 (0.10–0.15)
Kgalagadi Agric	8.6.0 Kgalagadi Tsabong	100	-	Thorn et al. (2011)	Assume medium density.	-	0.13 (0.10–0.15)
Kgalagadi Agric	8.7.0 Kgalagadi Middelpits	100	-	Thorn et al. (2011)	Assume medium density.	-	0.13 (0.10–0.15)
Kgalagadi Agric	8.8.0 Kgalagadi Bokpits	100	-	Thorn et al. (2011)	Assume medium density.	-	0.13 (0.10–0.15)
Kgalagadi Agric	8.9.1 Kgalagadi Kang 1	100	-	Thorn et al. (2011)	Assume medium density.	-	0.13 (0.10–0.15)
Kgalagadi Agric	8.9.2 Kgalagadi Kang 2	100	-	Thorn et al. (2011)	Assume medium density.	-	0.13 (0.10–0.15)
Kgalagadi Agric	8.9.3 Kgalagadi Kang 3	100	-	Thorn et al. (2011)	Assume medium density.	-	0.13 (0.10–0.15)
Kgalagadi Agric	8.10.1 Kgalagadi Hukuntsi 1	100	-	Thorn et al. (2011)	Assume medium density.	-	0.13 (0.10–0.15)
Kgalagadi Agric	8.10.2 Kgalagadi Hukuntsi 2	100	-	Thorn et al. (2011)	Assume medium density.	-	0.13 (0.10–0.15)
Kgalagadi Agric	8.10.3 Kgalagadi Hukuntsi 3	100	-	Thorn et al. (2011)	Assume medium density.	-	0.13 (0.10–0.15)

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