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Trends in cheetah *Acinonyx jubatus* density in north-central Namibia

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Abstract

Assessing trends in abundance and density of species of conservation concern is vital to inform conservation and management strategies. The remaining population of the cheetah (*Acinonyx jubatus*) largely exists outside of protected areas, where they are often in conflict with humans. Despite this, the population status and dynamics of cheetah outside of protected areas have received relatively limited attention across its range. We analyzed remote camera trapping data of nine surveys conducted from 2005 to 2014 in the Waterberg Conservancy, north-central Namibia, which included detections of 74 individuals (52 adult males, 7 adult females and 15 dependents). Using spatial capture–recapture methods, we assessed annual and seasonal trends in cheetah density. We found evidence of a stable trend in cheetah density over the study period, with an average density of 1.94/100 km^2 (95% confidence interval 1.33–2.84). This apparent stability of cheetah density is likely the result of stable and abundant prey availability, a high tolerance to carnivores by farmers and low turnover rates in home range tenure. This study highlights the importance of promoting long-term surveys that capture a broad range of environmental variation that may influence species density and the importance of nonprotected areas for cheetah conservation.

KEYWORDS

Acinonyx jubatus, camera trapping, density, scent posts, spatial capture-recapture

1 | INTRODUCTION

Apex predators play a major role in ecosystem functioning (Estes et al., 2011), but worldwide most carnivore populations are rapidly declining both in distribution and abundance (Wolf & Ripple, 2017). For example, the leopard (*Panthera pardus*) now occurs in only 37% of its historical range (Jacobson et al., 2016), the lion (*Panthera leo*) in 25% (Riggio et al., 2013) and the cheetah (*Acinonyx jubatus*) in less than 10% (Durant et al., 2017; Wolf & Ripple, 2017). This reduction in cheetah range is the largest among the large carnivores of greatest conservation concern (Wolf & Ripple, 2017). Such losses can alter ecosystem functions (Ripple et al., 2014), affect humans through the loss of income from ecotourism, and changing disease dynamics (Ordiz, Bischof, & Swenson, 2013; van der Meer, Badza, & Ndhlovu, 2016). Thus, it is important to assess trends in density of large carnivores over multiple generations in order to improve our understanding of species response to temporal variation in environmental conditions (e.g., changes in prey availability or habitat structure), assigning conservation status to species, and devising comprehensive conservation strategies.

Namibia has the second largest population of cheetahs across the species range (Marker, Boast, & Schmidt-Küntzel, 2018), with approximately 95% of individuals occurring in freehold and communal farmlands, that is, areas without formal protection status (Marker-Kraus, Kraus, Barnett, & Hurlbut, 1996). As a result of human–cheetah conflict, cheetahs are killed or translocated to farms where owners are more tolerant (henceforth referred to as "removed") due to perceived or true conflict with farmers (Marker-Kraus et al., 1996), but removals are reported to have reduced significantly (Marker, Dickman, Mills, Jeo, & Macdonald, 2003). The decline in removals is primarily attributed to the growth and engagement of non-governmental organizations with farmers (e.g., Cheetah Conservation Fund, AfricCat, World Wildlife Fund, Namibia Association Community Organization), training and capacity building in local communities, and the establishment of commercial and communal conservancies (Marker & Dickman, 2003). Conservancies consist of adjacent landowners that voluntarily manage their lands sustainably as a single unit while accruing direct (e.g., trophy hunting, employment) and/or indirect (e.g., building of clinics) benefits (NACSO, 2015). Approximately 42% of the total land in Namibia is under some form of conservation, including 6 and 20% in freehold and communal conservancies, respectively (NACSO, 2015). Thus, conservancies have been critical in transforming the Namibian landscape into a conservation-oriented country, and they can play a significant role in preventing further population declines of large carnivores.

A critical aspect of conservancies is the promotion of sustainable wildlife management practices informed by long-term population monitoring. Monitoring is conducted through indices (e.g., counts at waterholes and track counts) and direct observations (e.g., distance sampling) (NACSO, 2015), but these techniques are often inappropriate for monitoring carnivores such as cheetah unless they are calibrated (Funston et al., 2010). Additionally, cheetahs are wide-ranging, elusive and occur at low densities (Marker, Fabiano, & Nghikembua, 2008) making monitoring challenging. Thus, there is a lack of information on trends in cheetah abundance and density at all spatial scales (local or regional) in Namibia and across its range (but see Durant et al., 2011).

Remote camera traps are often employed to obtain individual encounter data for species with individually identifiable pelage patterns, such as cheetahs. These data can be used to generate spatially explicit density estimates using spatial capture–recapture methods (SCR, Royle, Fuller, & Sutherland, 2018, Fabiano, Boast, Fuller, & Sutherland, 2018). To date, SCR-derived density estimates for cheetah have been reported for Botswana (Boast, Reeves, & Klein, 2015; Brassine & Parker, 2015) and Kenya (Broekhuis & Gopalaswamy, 2016) but not yet for Namibia.

In this study, we use a unique 9-year camera trapping data set collected on commercial farmlands in north-central Namibia to quantify temporal trends in cheetah density, and to investigate aspects of their spatial ecology including sex- and season-specific space use. This region is of significance for cheetah conservation in Namibia as it is considered to have the highest density in the country (Marker, Dickman, Wilkinson, Schumann, & Fabiano, 2007). Sampling this area across multiple years and seasons offers important insights into the existence, if any, of interannual or seasonal patterns in density (e.g., population trends, or transience, respectively) and space use in relation to temporal variations in environmental conditions, life history strategies (e.g., home range tenure), and indirectly, the impact of conservation interventions. Our prediction was that this population was stable given the various conservation initiatives in the study area. We discuss our findings in the context of requirements for continuing to promote effective conservation measures for carnivores, the importance of long-term monitoring, and the need to replicate this study across Namibia and elsewhere.

2 | METHODS

2.1 | Study area

Camera-trapping surveys were located in the Waterberg Conservancy in north-central Namibia in the Otjozondjupa region (20°28′56″S 17°2′24″E, Figure 1). The area is semi-arid with annual rainfall of 400–500 mm concentrated during the summer season (November to February) (Barnard, 1998). The study area is an unfenced, free-movement area characterized by thornbush and tree and woodland savanna vegetation (Geiss, 1971) where bush encroachment was prevalent (Barnard, 1998). Primary land use practices include livestock (cattle and small stock) farming and wildlife ranching, including fenced game farms, eco-tourism and trophy hunting (Marker-Kraus et al., 1996). The area supports a diversity of ungulates, most of which are included in the cheetah diet including kudu (*Tragelaphus strepsiceros*), eland (*Taurotragus oryx*), springbok (*Antidorcas marsupialis*), steenbok (*Raphicerus campestris*), scrub hare (*Lepus saxatilis*), oryx (*Oryx gazella*), red hartebeest (*Alcelaphus buselaphus*), warthog (*Phacochoerus africanus*) and springhare (*Pedetes capensis*). Carnivores in the study area sympatric with the cheetah include black-backed jackal (*Canis mesomelas*), brown hyaena (*Hyaena brunnea*), caracal (*Caracal caracal*) and leopard (*Panthera pardus*).

2.2 | Camera trapping

Between November 2005 and February 2014, we conducted nine camera trapping surveys of which five were in winter (May to October) and four were in summer (November to February) (Table 1). The trap array per survey ranged from 277 to 477 km^2 (381 ± 43; mode 384). Surveys lasted 3–5 months (90–184 days, mode 90) (Table 1). This sampling range was selected to minimize violating the geographic and demographic closure assumption (Brassine & Parker, 2015; Karanth, Nichols, Kumar, & Hines, 2006) while increasing capture–recapture events (Gerber, Ivan, & Burnham, 2014).

We placed cameras at 32 unique trap locations across the duration of the study (average 16 cameras per survey, range = 15–19, Table 1). Most camera stations were at cheetah scent-marking posts ($n = 21$), six were in close proximity to cheetah captive facilities (<3 km), and five were adjacent to roads or fence lines (≤0.1 m). The number of camera trap nights per survey averaged 1,763 (±*SD* 581). Twenty-eight percent of the 32 cameras stations ($n = 9$) were active during all eight surveys. Mean camera trap spacing was 6.91 km (±*SD* 5.69), which is smaller than the home range radius of a female cheetah in the study (Marker, Dickman, Mills, Jeo, & Macdonald, 2008). Additionally, historical daily movement ranges of cheetahs in the study area are reported to be similar to this camera spacing (Marker, 2002).

We used flash Cuddeback® DeerCam™ DC200 (DeerCam, Park Falls, WI) cameras from 2005 to 2009 and infrared Bushnell® Trophy Cam™ (Kansas) cameras from 2010 to 2014. However, in 2008, one station contained a Moultrie® M60 digital camera (GA). We placed two cameras per station, facing each other at a slight angle, mounted ~75 cm above the ground and 5 m apart. Cameras were programmed to take pictures every 30 s, with a burst of photos consisting of three 5MP images taken within 1-s. We visited camera sites every 2–7 days to check for functionality, change film/memory card and/or batteries. Cheetah photographs from developed films were logged into an excel database while photographs from digital cameras were stored following Harris, Thompson, Childs, and Sanderson (2010) using an automated software for camera trapping data management. All sampling protocols complied with the Namibian Ministry of Environment and Tourism.

2.3 | Data preparation

We identified individual cheetahs manually, based on a set of one to three unique spot patterns on any clearly visible part of either side of an animal. We discarded all

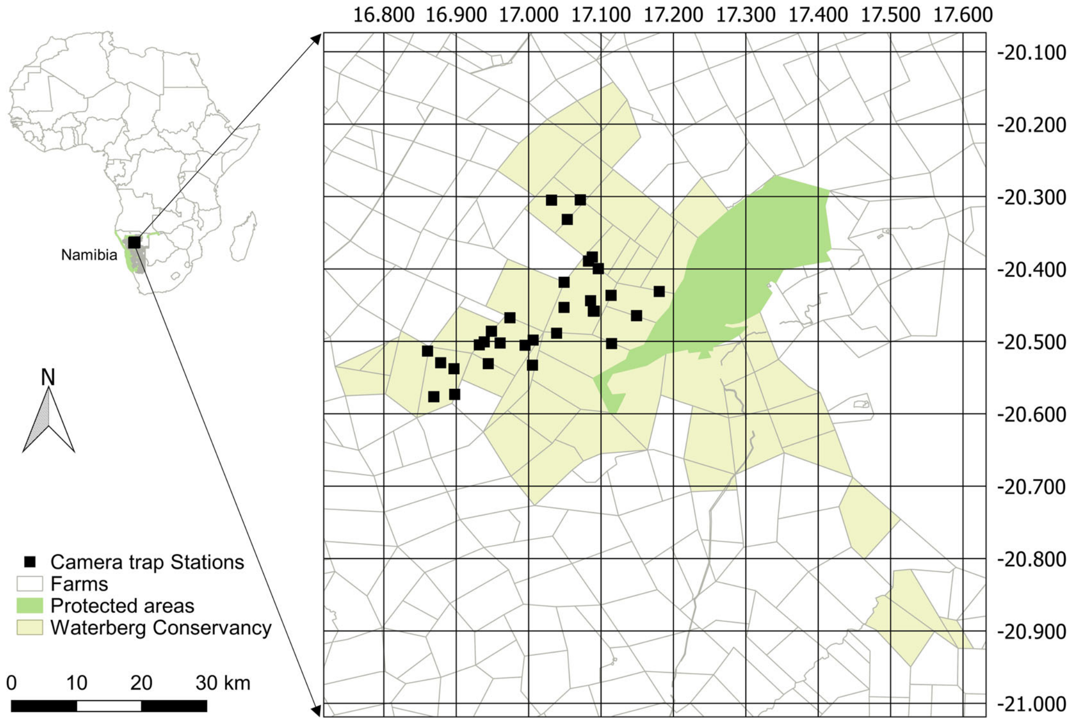

FIGURE 1 Location of camera trap stations in the Waterberg Conservancy, north-central Namibia

TABLE 1 Sampling effort for nine camera trap surveys conducted in north-central Namibia, 2005–2014, including the year of the survey, season, camera trap array size, number of camera stations, number of trap nights, number of independent cheetah photographs per 24 hr, capture rates (number of cheetah photos/100 trap nights), number of unique adult individuals detected per survey, number of observed male to female ratio whose sex could be identified, and average number of captures and spatial captures

Survey	Year of survey	Season	Trap array size (km^2)	State space (km^2)	No. of camera stations	No. of trap nights	No. of independent cheetah photographs	No. of cheetah photos/100 trap nights	No. of unique individuals	Observed male:female	Average captures	Average spatial captures
November 15, 2005–February 12, 2006	2005–2006	Summer	277	6,852	15	1,350	153	12	9	8:1	17.00	3.22
July 4 –October 1, 2007	2007	Winter	477	7,552	19	1,710	63	4	11	11:0	5.73	1.91
Jul 10–7 October, 2008	2008	Winter	370	7,052	15	1,350	71	5	9	8:1	7.89	2.78
July 6–Oct 3, 2009	2009	Winter	379	7,216	16	1,440	126	9	5	5:1	25.20	2.80
July 1–October 31, 2010	2010	Winter	123	7,268	15	1,845	149	8	7	5:2	21.29	3.29
Nov 1, 2010–April 30, 2011	2010	Summer	181	7,268	15	2,715	165	6	6	4:2	27.50	3.50
May 1–October 31, 2011	2011	Winter	184	7,268	15	2,760	146	5	9	6:1	16.22	2.22
November 17, 2011–February 15, 2012	2011–2012	Summer	384	7,268	15	1,350	59	4	4	3:0	14.75	1.75
November 17, 2013–February 15, 2014	2013–2014	Summer	384	7,268	15	1,350	195	14	10	11:1	19.5	3.2

blurry or poor-quality pictures. The identification of multiple spot patterns on both flanks was vital as patterns can be distorted based on the photo orientation or if only one side was captured. We compared all left flanks among each other and right among each other. In the event that a photo did not match any other photo, it was considered to be a new individual. Following this process, we were able to match all photos to individuals. Sex was determined using cues such as the presence of visible genitals or ear tag position (in previously physically captured cheetahs, that is, right for males and left for females) or the presence of accompanying dependents (<18 months, Marker et al., 2003). Dependents were identified based on body size or if detected with a female. Nonetheless, only adults (independent from mothers) were used for analysis. Individual cheetah identification was performed by a single individual (MN) and unidentifiable pictures were excluded (<1%, MN). This process was performed after each survey. We calculated the total number of detections over the 90-day sampling period (encounter frequencies) and the number of days cameras were operational (effort). As some studies using SCR have shown that ignoring group structure (i.e., lack of independence) does not bias density estimates (Russell et al., 2012), each male in a coalition was considered to be independent (Broekhuis & Gopalaswamy, 2016).

2.4 | Density estimation

We analyzed the spatially explicit individual encounter histories using spatial capture-recapture methods (Efford, 2004; Royle, Chandler, Sollmann, & Gardner, 2014) to estimate cheetah density (*D*), detection and space use, and to test for the existence of temporal trends in density. Treating years as "sessions" and using the information collected about the sex of the individuals, we analyzed the data using the R package oSCR (Sutherland, Royle, & Linden, 2019) that intuitively accommodates the multi-session sex-structured nature of the analysis. In this study, we assumed negligible within-session temporal variation in detectability, so we collapsed all encounters into a single count and analyzed the data using a Poisson encounter rate model and refer to detection rate as λ from henceforth.

In SCR, the individual home range, or activity centers are assumed to be randomly distributed within a defined area including all individuals that may have been exposed to detection by the cameras, known as the state-space (*S*). Estimation of the latent individual activity center locations is informed by the spatial pattern of captures via a spatial encounter model that describes the detection rate as a declining function of distance between the activity center and a trap. Specifically in our analysis, spatial encounter histories were used to estimate the parameters of a half-normal spatial encounter model: λ_0 is the detection rate at the activity center, and σ is a spatial scale parameter that determines the distance over which detectability declines to 0 (Efford, 2004). Hence, σ is related to space use. Our S was a polygon that buffered all camera locations by 35 km (area: 6,852 km^2), which was approximately four times the estimate of σ. Likelihood estimation of density typically requires the specification of a discrete representation of the state space for computational tractability; we used a resolution of 2 km (i.e., each state-space location represents a 2×2 km pixel) which was assumed to be fine enough to approximate continuous space.

To investigate temporal variation in density, and in addition to the null model (no variation in time or space), we tested for a linear trend, variation by season, by year and season additively (constant trend with season-specific intercepts) and interactively (season-specific trends), and finally, a session-specific model that allowed density to vary independently in all year-season combinations (Tables 2 and S1). This resulted in six density models. These models were motivated by previous studies that demonstrate how large carnivores including cheetah population dynamics can be sensitive to temporally varying anthropogenic and ecological factors. A primary anthropogenic factor is possible changes in tolerance as a function of levels of depredation (Harmsen et al., 2017; Marker et al., 2003). Ecological factors include prey availability, interspecific and intraspecific competition, mortality, seasonal changes in home range size, tenure and turnover due to interspecific and intraspecific competition or displacement, and the presence of dispersers (Durant, 1998; Fabiano, 2013; Kubala et al., 2017; Marker, Dickman, et al., 2008; Melzheimer et al., 2018; Swanson et al., 2014).

Similarly, like most large carnivores, cheetah behavior is often season- and sex-specific (McKnight & Ligon, 2017). As such, in addition to the null model for detection rate (λ_0), we compared models that allowed for variation by camera location type, sex, season and all additive combinations (Tables 2 and S1). This resulted in a total of eight detection models. Because camera trapping sessions varied in the number of deployment days, we included an offset in the detection rate model (log[number of trap days]), and thus, the interpretation of λ_0 is the *per day* encounter rate. Finally, in addition to the null model, we evaluated a model that also allowed for sex-specific variation in space use resulting in two models for σ. Considering all combinations of density, detection and space use models resulted in a total of 96 models (S1). Models were evaluated using Akaike's Information Criterion corrected for small sample size (AICc) and models were compared based on differences in AIC (ΔAICc). Our interpretation of the model comparisons and the importance, or lack thereof, follows recommendations outlined in Arnold (2010). Specifically, single effects are considered uninformative if they do not reduce the AIC value of the equivalent model without that effect. Finally, we note that the sex-structured "mixture model" implemented in oSCR (Sutherland et al., 2019), naturally produces estimates of the inferred sex ratio, Ψ, taking explicitly into account any sex-specific variation in detectability (Royle, Sutherland, Fuller, & Sun, 2015).

3 | RESULTS

Our camera trapping effort resulted in 15,960 trap-nights and yielded 4,943 individually identifiable cheetah photographs out of 286,556 total photos. An average of

TABLE 2 Description of the effects used to explain variation in the three SCR model components (density, detection, and space use)

Parameter	Hypothesis	Description
Density (D)	Constant	Density is constant across all years and seasons
	Season	Density different in summer and winter
	Trend	Linear trend in density over time (years)
	Session	All year-season combinations vary independently
	Year and season	Density different among years and season
	Year, season and interaction	Density different among years and season plus main effects
Detection (λ_0)	Constant	Detection rate is constant across all years and seasons
	Sex	Detection rate varies by sex
	Season	Detection rate different in summer and winter
	Location type	Detection rates at cameras placed at roads different to those placed at trees
	All combinations	Detection rate different between sex and season, location type and sex or season, and between sex, type and season
Sigma (σ)	Constant	Space use is constant across all years and seasons
	Sex	Space use varies by sex

TABLE 3 Final model table after removing models that included uninformative parameters (as per Arnold, 2010)

Density	Detection	Space use	*K*	*L*	AICc	dAICc	w_i	Σw_i
D(~1)	**p(~sex + Type)**	**sig(~sex)**	**7**	**1,473.10**	**2,961.549**	**0.000**	**0.923**	**0.923**
D(~1)	p(~sex + Type)	sig(~1)	6	1,476.84	2,966.627	5.078	0.073	0.996
D(~1)	p(~Type)	sig(~1)	5	1,476.70	2,974.412	12.863	0.001	0.997
D(~1)	p(~Type)	sig(~sex)	6	1,481.23	2,975.409	13.860	0.001	0.998
D(~1)	p(~sex)	sig(~sex)	6	1,481.44	2,975.832	14.283	0.001	0.999
D(~1)	p(~Type + Season)	sig(~1)	6	1,481.54	2,976.034	14.485	0.001	1
D(~1)	p(~Type + Season)	sig(~sex)	7	1,480.46	2,976.273	14.724	0.001	1.001
D(~1)	p(~sex)	sig(~1)	4	1,484.94	2,980.497	18.948	0.000	1.001

Notes: Models are named according to the structure of the density (*D*), detection (λ_0) and space use (σ) models and ordered according to AICc (smaller is better). In addition, we report the number of parameters (*K*), the negative log-likelihood (*L*), AICc differences (ΔAICc), AICc weights (w_i) and cumulative AICc weights (Σw_i). The model in bold was considered the "top" model and used for reporting.

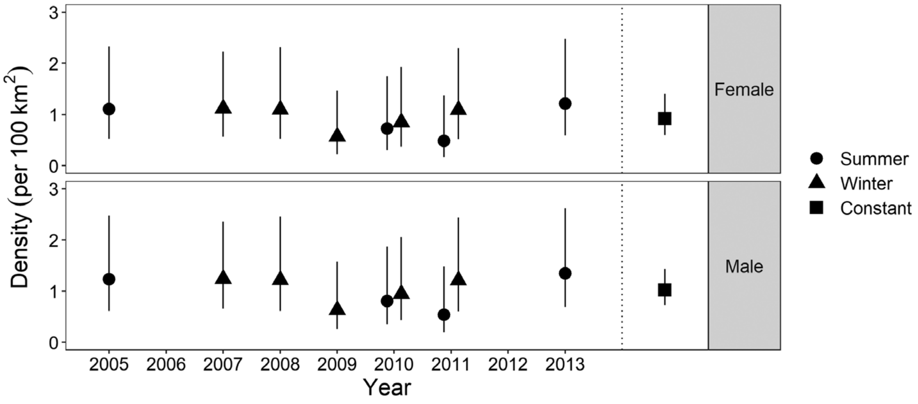

FIGURE 2 Estimated sex-specific cheetah densities. Estimates to the right of the dotted line are produced from the top model that was a constant density model. Estimates to the left of the dotted line are produced from a model with the same detection (λ_0) and space use (σ) model structure as the top model, but that allows density to vary independently across all unique year-season combinations. The black lines are the 95% confidence intervals

27 (±21) usable cheetah photographs were recorded per 100 trap-nights (i.e., photographs that allowed individual identification). We identified 77 individuals, including 62 adults (52 males, seven females and three of unidentified sex) and 15 dependents. Individuals were captured on average at 6 ± 2 (range 2–10) camera stations per survey. Of the 52 males, 67% were single and 33% occurred in coalitions (seven in coalition of two cheetahs and one in a coalition of three). Of the seven females, five were accompanied by dependents (mean litter size 3 ± 1.2, $n = 15$). Of the 74 unique individuals, nine (range: 4–11) individuals were detected in only one survey, and nine were detected in multiple surveys. Each individual was captured on average 6.5 (range: 1–102) times per survey at an average of 2 (range: 1–7) camera stations (Table 1).

A single "AIC-top" model emerged with constant sex-specific density (*D*), encounter rates that varied by sex and trap location type (λ_0), and sex-specific space use (σ) (Tables 3 and S1, Figure 2). Thus, we found no support for temporal variation in density across the nine surveys conducted over a span of 9 years or for between-season variation. We report maximum likelihood estimates of the parameters on the real scale with associated 95% confidence intervals in Table 4.

TABLE 4 Maximum likelihood estimates (MLE) and standard errors (*SE*) of the estimated parameters for the AIC-top model ($w_i = 0.923$) that had constant density: *D*(~1), detection that varied according to sex and trap location type: p(~sex + Type), sex-specific space use: sig(~sex) and the inferred sex ratio (Ψ)

Parameter	MLE	*SE*
λ_0 (Intercept: female, tree)	−2.393	0.106
λ_0 (Effect: male)	0.521	0.127
λ_0 (Effect: road)	−0.362	0.091
σ (Intercept: female)	8.885	0.061
σ (Effect: male)	−0.184	0.069
Density	−2.557	0.137
Ψ(prob[male])	0.105	0.281

Estimated density was 1.94 (95% confidence intervals [CI] 1.33–2.84) cheetahs per 100 km^2 (Table 4). The estimated probability of being a male was $\Psi = 0.53$ (95% CI 0.39–0.66) which translates to 1.02 (95% CI 0.73–1.43)

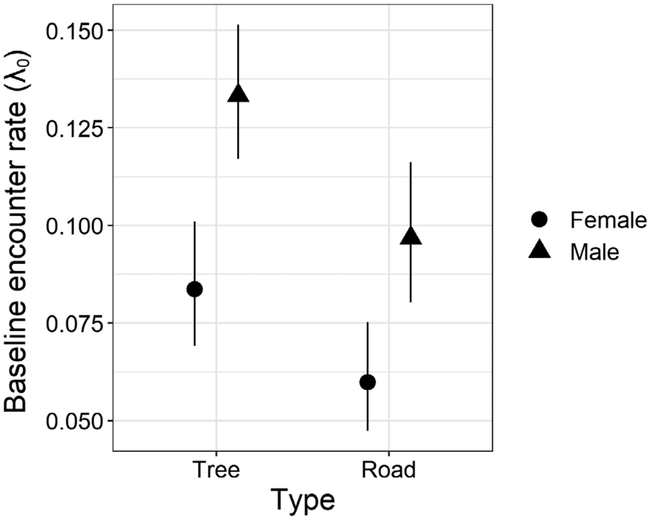

FIGURE 3 Estimated sex- and location-specific encounter rates (λ_0). These values represent the expected number of detections at a location for which the distance between the activity center of an individual (s) and the location (d), $d(s,x)$ is 0. The black lines are the 95% confidence intervals

male cheetahs per 100 km^2 and 0.92 (95% CI 0.60–1.41) female cheetahs per 100 km^2 (Table 4).

In terms of variation in baseline detection (λ_0), cheetahs were less detectable at cameras on roads than trees ($\beta_{\text{road}} = -0.36$, 95% CI −0.54 to −0.18), and male detectability was higher than for females ($\beta_{\text{male}} = 0.52$, 95% CI −0.54 to −0.18). In terms of the spatial scale parameter (σ), estimated space use was smaller for males than for females ($\beta_{\text{male}} = -0.184$, 95% CI −0.057 to 0.320). These estimates translate into σ estimates of 6.01 km (95% CI 5.66–6.39) and 7.22 km (95% CI 6.40–8.15) for males and females, respectively (Figure 3).

4 | DISCUSSION

Assessing trends in abundance and density of cheetahs is critical due to the species continued global declines. Here we investigate trends in density of an adult cheetah population using 9 years of camera trapping data collected from a landscape dominated by commercial farmlands in north-central Namibia. Cheetah density did not fluctuate substantially among the nine surveys conducted over a 9-year period. Our estimated average density of 1.94 cheetahs/100 km^2 was towards the upper end of the two previously reported estimates for this population, 0.25 and 2.3 cheetah/100 km^2 based on radio telemetry and a non-spatial capture recapture model, respectively (Marker, 2002; Marker et al., 2008). Similarly, this was the case when comparing our results to estimates of density from other populations, which ranged from 0.03 to 2 individuals/100 km^2 (Belbachir, Pettorelli, Wacher, & Belbachir-bazi, 2015; Boast et al., 2015; Brassine & Parker, 2015; Broekhuis & Gopalaswamy, 2016; Durant et al., 2011; Marnewick et al., 2014; Mills & Mills, 2017). Below we highlight a number of ecological and anthropogenic factors that may have contributed to the observed stable trend and the relatively high density observed in our study relative to previous assessments.

4.1 | Trends in density

We found no evidence of temporal variation in density over the study period. While the apparent stability we found may have been due to a lack of power to detect a trend (White, 2019), the number of individuals observed in each sampling period and the variation in estimates from a survey-specific density model were similar and showed no indication of a trend (Figure 2). It is also worth noting that our study only lasted a generation (4.9 years, Durant, Mitchell, Ipavec, & Groom, 2015), although White (2019) found no correlation between a species generation time and the sampling duration required to detect at least a linear trend. Thus, the stable trend is likely real.

Long home range tenure periods together with individual experience and ability to adapt may have promoted a stable trend. Only 15% of adult cheetahs were detected in multiple years (Fabiano, 2013). This suggests that 85% of adult cheetahs per survey were transients (i.e., they stayed in the area for less than a year) (sensu Barlow et al., 2009). The high proportion of transients justifies the inclusion of all identified individuals in our analysis, since transients can influence species viability (Lee, Reid, & Beissinger, 2017). A similar phenomenon was observed in a 9-year study of cheetahs in the Kalahari in which most males were transients (Mills & Mills, 2017). The high proportion of transients raises the possibility that either resident individuals were dominant, thus preventing home range takeover (Caro, 1994) due to numeracy advantage (coalitions versus singleton transients) (Caro, 1994; Fabiano, 2013; Melzheimer et al., 2018), or that this population is part of a larger population. The latter is likely as the study area is surrounded by farms where cheetahs are known to occur but could not be surveyed due to limited access (Marker, Fabiano, & Nghikembua, 2008; Marker-Kraus et al., 1996).

Additionally, the apparent stability in cheetah trends may suggest consistent prey availability. Trends in density of large carnivores are linked to ecosystem primary productivity and biomass of herbivores, which in turn is influenced by primary productivity (Jędrzejewski et al., 2018; Karanth, Nichols, Kumar, Link, & Hines, 2004; Kubala et al., 2017; Pettorelli, Bro-Jørgensen, Durant, Blackburn, & Carbone, 2009). The amount of forage in the study area was found to be relatively stable in all seasons from 2005 to 2015 (Hengari, 2017) and supports the assumption of associated stability in prey, and hence predator, populations. Such trends combined with the presence of permanent waterholes that are considered to have promoted a largely sedentary prey base (Marker-Kraus et al., 1996) suggest that prey availability may not have been a limiting factor for cheetahs in this study area. NACSO (2015) reports that the abundance of prey species on both freehold and communal conservancies in Namibia has in fact increased since their inception. This in turn, indirectly suggests that the management of wildlife in these conservancies has been sustainable to some extent. In addition to a stable prey base, our relatively high and stable density estimates might also be related to reduced interspecific competition due to the absence of other apex predators on farmlands (Durant, 1998, 2000 but see Swanson et al., 2014).

Farmers in conservancies may have higher tolerance levels to predators (Lindsey et al., 2013) resulting in lower rates of indiscriminate removal of cheetahs (Wolf & Ripple, 2016) and more stable carnivore populations (Proffitt et al., 2015). Changes in tolerance due to the continuous engagement of conservation organizations (e.g., Cheetah Conservation Fund, AfriCat Foundation) with farmers in the study area are reported to have led to a significant reduction in cheetah removals (Marker & Dickman, 2003). For example, these organizations assist farmers with implementing a wide array of human–wildlife mitigation measures. Additionally, the presence of conservancies may have led to stable prey bases partly through their sustainable consumptive management (e.g., hunting quotas determined based on annual wildlife surveys) and law enforcement (e.g., community-based antipoaching monitoring) approaches (Harmsen et al., 2017; NACSO, 2015; Wolf & Ripple, 2016). Similar positive impacts resultant from the implementation of conservation interventions are reported for a leopard population in South Africa (Balme, Slotow, & Hunter, 2009) and a tiger (*Panthera tigris*) population in Russia (Chapron et al., 2008). The opposite trend was observed in Zimbabwe, where land reforms implemented in 2000 caused a decline in the abundance and distribution of multiple carnivore species including the cheetah (Williams, Williams, Joubert, & Hill, 2016). It is indeed encouraging that the wildlife statutory institutions in Namibia appear to benefit cheetah populations through their support of community-based natural resource management policies, and through engaging with NGO partners.

4.2 | Cheetah space use

Our study revealed an approximately equal sex ratio in this population. Unlike observed (naïve) sex ratios that may depict a biased representation of a population due to sex-specific movement and detectability (e.g., Marker, Fabiano, & Nghikembua, 2008), our estimate explicitly accounts for these differences (Mollet, Kéry, Gardner, Pasinelli, & Royle, 2015).

Differences in detection probabilities between camera locations and sexes are likely to be related to their differential use of camera sites and roads. Male cheetahs use scent-marking sites with a higher frequency than females (Eaton, 1970; Fabiano, 2013) and use of such sites by males has been associated with patrolling territories (Broomhall, Mills, & du Toit, 2003; Caro & Collins, 1987). Furthermore, cheetahs in general do not travel continuously along roads. Other studies report similar low detection probabilities of cheetahs on roads or active game trails (Brassine & Parker, 2015; O'Brien & Kinnaird, 2011). In turn, female cheetahs are suggested to visit scent-marking sites when in estrus (Wilson, 2006). The lack of differences in female detections by season suggests that, in this study area, other factors besides estrus may influence female visitation to scent-marking sites. Furthermore, increases in detection could be expected given that movements of female cheetahs tend to increase with age of dependents (Houser, Somers, & Boast, 2009; Marker, 2002) and all but one female cheetah detected was accompanied by dependents. Given the latter, our estimates of female space use and encounter rates are likely to reflect that of females accompanied by dependents. These estimates of space use also suggest that females make use of larger ranges than males, a finding that is in agreement with previous telemetry studies in the study area (Marker, Fabiano, & Nghikembua, 2008).

4.3 | Short- and long-term monitoring

Conditional on monitoring program objectives, our study design and findings suggest that sampling during either winter or summer is effective and at least a 90-day survey duration is reasonable to acquire adequate recaptures. Similar to Brassine and Parker (2015), sampling beyond 90 days did not increase the number of unique individuals captured, but increased recaptures. Researchers should also strive to gain access to a larger number of farms, a limiting factor on this study, as this would allow for an improved understanding of the population dynamics at a landscape scale as trends in density may differ among populations under different forms of land use practices (Fuller, Sutherland, Royle, & Hare, 2015; Williams et al., 2016). Of particular concern is the recent increase in fences being erected for game farming, which could decrease landscape connectivity for cheetahs. Similarly, sampling across the species range in the country is necessary because the ecological mechanisms driving this stable trend are unlikely to be homogenous. We suggest including transients in cheetah population estimates because for long-lived species, transients may constitute a large proportion of the population (Proffitt et al., 2015) and can influence species viability (Lee et al., 2017). Even though some studies suggest excluding transients, SCR derived density estimates tend to be unbiased despite the inclusion of transients (Royle et al., 2015).

5 | CONCLUSION

The density of cheetahs in our study within a conservancy in Namibia remained stable over 9 years. This lack of variation in density is possibly driven by the continuous availability of prey, compatible land use practices including high tolerance to cheetahs by farmers, and the ability of few individuals to remain in the study area for years. This finding is a positive outlook for this population and highlights the importance of north-central Namibia for the conservation of cheetahs at the national level. Similarly, our study population occurs within a conservancy, suggesting that some conservancies may be playing a critical role in maintaining cheetah populations. We encourage national and international conservation agencies to continue supporting conservancies while promoting cohabitation of carnivores and humans through education, improved livestock management and business enterprises. Longer study periods are poised to improve our understanding of the impacts of ecosystem changes (e.g., due to climate change) on carnivores' persistence at national, regional and biogeographical scales.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of this article.

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