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Rewilding landscapes with apex predators: cheetah (*Acinonyx jubatus*) movements reveal the importance of environmental and individual contexts

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Rewilding landscapes through species or population restoration is an increasingly applied practice in biological conservation. There is expanding interest in wildlife release projects for apex predator population augmentation or reintroductions in historical ranges. Cheetahs (*Acinonyx jubatus*) are an IUCN Vulnerable-listed species with a declining global population facing major threats, which in southern Africa primarily include lethal persecution on livestock farms and bush encroachment transforming open habitats to woody areas. We used GPS radiocollars to monitor ten adult cheetahs from 2007 – 2018 in the Central Plateau of Namibia encompassing an area restored as an open savanna field (13.7 km²) located in a matrix of woodland savanna affected by bush encroachment. We generated a set of a priori hypotheses that tested the effects of various factors on cheetah movements indexed by step length. We compared cheetah movement metrics based on their history as wild, rehabilitated, and/or translocated individuals. Day/night activity, habitat type, and habitat edges were significant predictors of cheetah movement. Wild resident cheetahs displayed significantly longer steps than the other cheetah classes, possibly suggesting increased territorial behaviour in response to the presence of introduced cheetahs. Some cheetahs temporally segregated by moving extensively during daytime, but most individuals were primarily active during crepuscular periods. Small prey remained constant across time, whereas large prey declined over the study period. Cheetahs appeared to adjust behaviourally by increasing movements in years when large prey were scarce. Cheetahs appeared to be ecologically adaptable and behaviourally flexible in response to varying prey populations and when translocated to new environments,

specifically at the interface between bush-encroached woodland and open savanna. Environmental settings and animal history need to be carefully considered in rewilding and ecosystem restoration, and monitoring of released and resident individuals, if present, is important to understand ecological dynamics at release sites.

KEYWORDS

behavioural adjustments, bush encroachment, ecosystem restoration, large carnivore, movement ecology, restoration ecology, translocation, wildlife rehabilitation

1 Introduction

Habitat loss, illegal killing, declining prey, and human-wildlife conflicts threaten the survival of apex predators globally (Woodroffe, 2006; Ripple et al., 2014; Lennox et al., 2022). Terrestrial apex predators confront challenges that extend beyond ecological realms, impacting economic and political dimensions of conservation (Jhala et al., 2020). In Africa, many large carnivores are classified by IUCN as endangered (e.g., the Ethiopian wolf [*Canis simensis*] and African wild dog [*Lycaon pictus*] or vulnerable (e.g., cheetahs [*Acinonyx jubatus*], lions [*Panthera leo*]), requiring conservation action for persistence or recovery (Durant et al., 2017; Marneweck et al., 2019; Seid et al., 2022).

Cheetahs face alarming population fragmentation and decline, with an approximate count of 7,100 adults and subadults remaining across Africa predominantly outside protected areas (Durant et al., 2017; Marker et al., 2018a). While we cumulatively know much about baseline cheetah ecology (Caro, 1994; Durant et al., 2007; Marker et al., 2018b), information on cheetah movement ecology is sparse. Insights from movement analysis of carnivores hold the potential to inform human-wildlife conflict mitigation and bolster critical ecosystem services by maintaining carnivores on the landscape (Odden et al., 2014; Van der Weyde et al., 2017; Loveridge et al., 2022; Teichman et al., 2023).

The world's primary cheetah population stronghold is in southern Africa (Durant et al., 2017; Marker et al., 2018a), but cheetahs therein are subject to lethal persecution on livestock farms and in many areas must contend with bush encroachment, which can alter both predator and prey behaviours (Marker and Dickman, 2004; Nghikembua et al., 2021; Atkinson et al., 2022a; Nghikembua et al., 2023). Habitat change to woody vegetation potentially affects the cheetah's hunting strategies and energy acquisition, given their preference for open landscapes (Caro, 1994; Atkinson et al., 2022b). While both human-wildlife conflict and habitat change can be tackled with management and education, in some areas the cheetah populations are low or extinct, and restoration requires translocations for population recovery. In such contexts, rewilding provides a pathway to restore populations that underwent

extinction or significant declines (Fritts et al., 1997; Hayward et al., 2007; Jhala et al., 2021). Human interventions involving translocation, rehabilitation, and reintroduction are instrumental in this endeavour (Odden et al., 2014; Naha et al., 2021; Walker et al., 2022).

We assessed potential differences in movement patterns and ecological correlates associated with movement, comparing wild cheetahs and those subjected to human intervention through translocation and/or rehabilitation. Understanding movement characteristics and variability according to cheetah history and

TABLE 1 Definition of the four cheetah classes in the study.

Class	Description
Wild Local	<ul style="list-style-type: none"> Local to the area of CCF property. Individuals that were not captive raised, but were collared for research purposes and released at capture site.
Rehabilitated Local	<ul style="list-style-type: none"> Local to the area of CCF property. Individuals were taken into captivity temporarily due to injury or being orphaned. If injured, this was caused by intraspecific competition, interspecific competition (leopards), or from human-wildlife conflict. If orphaned, tracked mother had been killed in human-wildlife conflict, or cubs were attempted to be smuggled.
Rehabilitated Translocated	<ul style="list-style-type: none"> Not local to the area of CCF property. Individuals that were taken into captivity due to injury or being orphaned, or were born in captivity. If injured, this was caused by intraspecific competition (other cheetahs), interspecific competition (leopards, lions, hyenas), or from non-fatal human-wildlife conflict. If orphaned, tracked mother had died due to human-wildlife conflict or died due to natural causes, or cubs were attempted to be smuggled. Translocated to CCF property from farms where captured in human-wildlife conflict incidents.
Wild Rehabilitated Translocated	<ul style="list-style-type: none"> Translocated from farms where they were captured in human-wildlife conflict incidents. Not captive raised, but entered captivity temporarily due to injury.

Rehabilitated individuals were those that were either placed temporarily into captivity at a young age when acquired as cubs, or received veterinary care due to injury. Local individuals were those born in or nearby to CCF property, whereas translocated animals were moved from their home location to CCF property. Wild individuals had minimal human contact and were not placed into temporary captivity.

human-mediated management can assist conservation strategies and apex predator population management on African landscapes (Marker et al., 2018a; Fabiano et al., 2020). When linked to habitat conditions and prey information, apex predator movement data can allow insights into connectivity considerations and predator-prey dynamics respectively (Broekhuis et al., 2021; Loveridge et al., 2022).

Using GPS radiocollar data on cheetahs and prey information spanning 15 years, we studied movement rate (i.e., step length) (Turchin, 1998; Thurjell et al., 2014), investigated relationships between multiple variables and movement, and examined associations with prey availability (Broekhuis et al., 2019, Broekhuis et al., 2021; Rodriguez-Recio et al., 2022) in a period with declining prey (Bandyopadhyay et al., submitted). Our cheetah data were categorised among four different classes (Wild Local, Rehabilitated Local, Rehabilitated Translocated, and Wild Rehabilitated Translocated; for full description, see Table 1). We tested the following hypotheses:

1. Cheetah movement patterns differ between individuals according to history and human intervention. Wild local individuals would move slower than translocated cheetahs due to greater familiarity with their surroundings requiring less energy expenditure. Translocated individuals are unlikely to possess the same ecological knowledge of the area, and we expected them to exhibit longer movements associated with exploratory behaviour (Walker et al., 2022).
2. Marking trees and waterholes significantly influence cheetah movement patterns as exhibited by shorter movements when in the vicinity of these landscape features. Cheetahs may claim these key resources with territorial exclusivity (Marker-Kraus and Kraus, 1997), wherein marking trees are used to advertise presence to territory contesters, and

waterholes are prime hunting areas with predictable prey presence (Nghikembua et al., 2016; Broekhuis et al., 2021).

3. Cheetahs will move greater distances over time to encounter prey due to a steep decline in prey density (Bandyopadhyay et al., submitted). Although this process may also be influenced by interspecific competition and changes in habitat quality, this will not be tested in this study.
4. Cheetahs exhibit more diurnal activity than nocturnality, as a mechanism to temporal segregate from other, dominant large carnivores (leopard [*Panthera pardus*] in our system) and to maximise visibility during prey pursuits (Hayward and Slotow, 2009).

2 Materials and methods

2.1 Study area

The study took place in the Central Plateau of Namibia on farmlands that are Cheetah Conservation Fund (CCF) property. The property covers 577 km² and is managed as a wildlife reserve as well as mixed-use land for wildlife and livestock. The area has an average temperature of 19.2°C (+/- 2.4°C) and an annual rainfall of 400-450 mm (Marker et al., 2008). The predominant habitat type is semi-arid thornbush woodland savannah (Marker et al., 2008; Nghikembua et al., 2021), with dominant tree genera including: *Boscia*, *Combretum*, *Dichrostachys*, *Grewia*, *Senegalia*, *Terminalia*, and *Vachellia* (Nghikembua et al., 2021; Bandyopadhyay et al., submitted).

The focal study site for analysis centred around the 'Big Field' section of the broader property and is operated exclusively as a wildlife reserve (Lat -20.4839°, Long 17.0317°; Figure 1). 'Big Field'

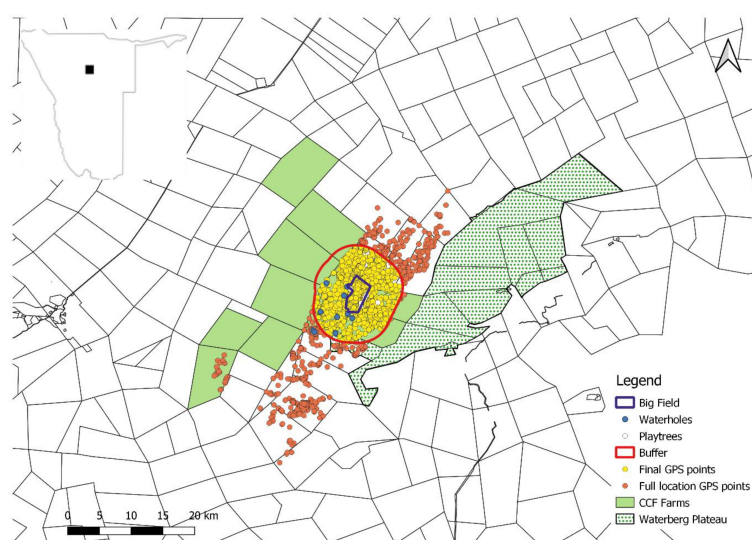


FIGURE 1

Map showing the location of the focal study area (red) in the broader landscape of North-central Namibia. The area included a large field (Big Field) managed as open savanna in a matrix of bush encroached woodland savanna. Yellow points are the cheetah GPS radiocollar locations included in the analysis.

is managed as an open savanna area covering approximately 13.7 km², while the remaining property is woodland savanna that is heavily bush-encroached, with bush cover >90% in some areas (Nghikembua et al., 2016). Big Field is of significant relevance as one of the largest open areas in north-central Namibia within a predominantly bush-encroached landscape.

2.2 Data collection

Cheetah data were collected via GPS radiocollars (Sirtrack – Havelock North, New Zealand, ATS – Minnesota, USA, or AWT – Pretoria, South Africa) on 17 adult cheetahs (11 females and 6 males) that were either captured on site by CCF for research and released at the capture location, or were captured on other properties by private farmers and translocated and released on the CCF property as part of human-wildlife conflict mitigation at the origin site, and cheetah population recovery at CCF. Cheetahs were captured by CCF or farmers through human-wildlife conflicts using double door (walk-through) cage traps, often at preferential cheetah marking sites. Cheetahs were anaesthetised with drug combinations including Telazol®, Ketamine-Medetomidine, or Ketamine-Midazolam (Marker et al., 2008). The capture and handling of animals adhered to approved procedures and were conducted in compliance with relevant regulations and permits (NCRST AN202101032). Additionally, some animals arrived at CCF as orphan cubs from human-wildlife conflict of livestock farms and were held in captivity in large enclosures on CCF property as part of a rehabilitation and release programme (Walker et al., 2022). All cheetahs were adult at the time of collaring and monitoring.

The available GPS location data covered the period September 2007 to May 2022, and included cheetah ID, individual history, sex, age class, reproductive class (solitary male, coalition male, solitary female, female with cubs), type of collar used, date and timestamp

for each GPS location, latitude, longitude, release date, and release location.

Prey data were collected in the same timeframe as the cheetah collar data via road transects that were repeatedly driven to record ungulate observations visually. We classified prey into small (common duiker [*Sylvicapra grimmia*], dik-dik [*Madoqua kirkii*], springbok [*Antidorcas marsupialis*], steenbok [*Raphicerus campestris*]) and large categories (eland [*Taurotragus oryx*], greater kudu [*Tragelaphus strepsiceros*], oryx [*Oryx gazella*], red hartebeest [*Alcelaphus buselaphus*]).

Transects covered the entire CCF property and no habitat stratification was applied as the property can be classified as woodland savanna (Bandyopadhyay et al., submitted; Supplementary Table S1). Prey data were also collected along dedicated short transects in the Big Field section. Transects were driven at a speed of maximum 20 km/h and whenever an animal was detected, the vehicle was stopped and observers recorded the perpendicular distance from the transect to the animal for subsequent analysis in a distance sampling framework (Buckland et al., 2001). The total annual transect sampling effort was 2,382 km.

2.3 Data processing

Prior to computing movement metrics, we refined the cheetah GPS radiocollar data to focus on Big Field and a buffer region around it. GPS fix acquisition rates for the deployed collars varied along the 15-year dataset. We inspected the data and found that 3-hour fix rates were used most extensively, therefore we constrained our analysis to this fix rate. While this refinement resulted in dropping seven individuals which either had different fix rates or sparse data, using variable fix rate would have affected our inferences on animal movements from collar data (Cristescu et al., 2015). Our final sample size was ten cheetahs (weight range at release – 25 to 57 kg) across four distinct classes: Wild Local,

TABLE 2 Final data of 4,965 GPS points used to investigate factors associated with movement in a GLM analytical framework.

Class	Sex	Unique cheetah ID	Range of data collection	Number of fixes
Wild Local	Male	AJU1533	Sep 2007 – May 2008	1,529
		AJU1543	Aug – Nov 2009	120
Rehabilitated Local	Female	AJU1666	Mar 2018	66
	Male	AJU1664	Mar – May 2018	120
Rehabilitated Translocated	Female	AJU1510	Dec 2013 – Feb 2014	378
		AJU1512	Dec 2013 – Sep 2014	411
		AJU1608	Aug 2014	30
		AJU1615	Apr – Jul 2014	479
		AJU1619	Jun 2014 – Feb 2016	1,401
Wild Rehabilitated Translocated	Female	AJU1606	Mar – Jul 2011	431
Total				4,965

Rehabilitated individuals were either temporarily placed into captivity at a young age due to being orphans, or as older individuals due to injury necessitating veterinary care. Local individuals were those born in or nearby to CCF property, whereas translocated cheetahs were moved to CCF property from farms of origin where they were captured in human-wildlife conflict incidents. Wild individuals are those that had minimal human contact and did not experience captivity.

Rehabilitated Local, Rehabilitated Translocated, and Wild Rehabilitated Translocated, which contributed 4,965 data points for the analysis during 2007–2018 (Tables 1, 2). We calculated step length (movement rate) for all ten cheetahs and established the buffer size around Big Field as the 95th percentile of step length of the ten individuals pooled.

For each cheetah step we calculated distances to the closest marking tree (known from long-term monitoring to be used by cheetahs for marking), waterhole, and habitat edge of the open savanna (Big Field)-woodland savanna interface, using the distance matrix function in Q-GIS. We defined day/night cycles for each season (Cold-Dry [May–August], Hot-Dry [September–December] and Hot-Wet [January–April]; Nghikembua et al., 2021), assigning day, night or crepuscular period for each GPS radiocollar point from automated time zones (NST) using the ‘suncalc’ package in R (Core Team, 2021). We categorised steps as intersecting habitat edge (open savanna-woodland savanna interface), inside Big Field, or outside Big Field.

We estimated prey encounter likelihood separately for small and large prey, using the effective strip width model (ESW) and prey density estimates in a distance sampling framework (Bandyopadhyay et al., submitted). We further categorised prey by foraging strategy (browsers, grazers, and mixed feeders) when calculating prey encounter rate. Because the number of prey observations along the Big Field transects was too small to derive density estimates, we combined these monthly collected data with annual CCF property-wide transects to obtain density estimates. The property-wide estimates also had few observations of prey, therefore similarly to Bandyopadhyay et al. (submitted), we pooled the data into four-year intervals (2009–2012, 2013–2016, and 2017–2020) to relate to daily distance moved by cheetahs stratified by the same intervals. One cheetah (AJU1533) with data points in 2007 and 2008 was excluded from the predator-prey

analysis due to a lack of yearly prey data for 2007–2008, attributed to staffing constraints.

Environmental influences on the cheetahs’ movements other than those tested in our analyses were minimised because GPS radiocollar locations occurred in the same land use type (wildlife reserve) and the same rainfall class as derived from the Atlas of Namibia (<https://atlasofnamibia.online/>).

2.4 Data analysis

Step length and turning angles for the collared cheetahs were calculated using the ‘move’ package in R (v4.2.4) (Turchin, 1998; Thurfjell et al., 2014; Core Team, 2021). We used ANOVA, t-tests and post-hoc Tukey tests to check for significant differences in step length among class, sex, and season.

We used a Generalised Linear Model (GLM) approach with covariate combinations to determine associations of ecological factors and cheetah step length. We ran a correlation analysis to identify covariates that might induce multicollinearity, and covariate combinations with $|r| > 0.6$ were excluded from the same model structure (Supplementary Table S2). For each of the four cheetah classes, we used the same candidate model set to identify fixed-effects covariates associated with step length as the dependent variable (Table 3). We excluded prey density from the GLMs because prey density was a non-spatial estimate. For each cheetah class, we ranked models in the candidate set using the Akaike Information Criterion (AIC) corrected for small sample sizes (AICc), and considered models to be supported if their $\Delta AICc < 2$. Additionally, we ran two sets of mixed-effects models with the same fixed-effects covariates, using cheetah class and individual cheetah ID respectively as random intercepts. We ranked models in these two sets using AIC (Supplementary Tables S11–S16).

TABLE 3 Table of multiple hypotheses tested with GLM models to investigate factors associated with cheetah movements.

Hypotheses	Covariates included	Model name	Rationale
1	Intersection + Waterhole + Edge + Edge ² + Time of day	Global Model (no marking tree)	Exploring potential influences on movement decisions
2	Null	No Covariates	Baseline reference for comparison
3	Waterhole + Time of day	Hunting Habitat	Investigating waterhole as a key resource
4	Marking tree + Time of day	Territoriality	Examining the role of marking trees in defining territories
5	Edge + Edge ² + Time of day	Hunting Habitat edge	Analysing movement decisions along habitat edges
6	Intersection + Time of day	Habitat Use	Assessing how intersections affect movement choices and differences in step length
7	Waterhole + Marking tree + Time of day	Resource Utilisation	Studying the relationship between movement and resource utilisation
8	Waterhole + Marking tree + Intersection + Time of day	Global model (no edge) - Resource Movement	Comprehensive understanding of resource-driven movement
9	Edge + Edge ² + Waterhole + Time of day	Hunting Behaviour	Exploring movement patterns relating to hunting

We analysed the variability in prey density over time using Wilcoxon-tests separately for large and small prey. We contrasted the empirical prey estimates with symmetrical distributions to independently test if prey density fluctuated significantly from 2009 to 2020, using the 4-year intervals mentioned above. Finally, we determined the prey encounter rates by dividing the encounter rate per day per prey species by the total number of independent observations made during the effort. Results were split into prey foraging categories (browsers, grazers, and mixed feeders). We then contrasted them with the daily distance travelled by each cheetah class.

We used Q-GIS (v3.2.8), ArcGIS (v10.8.2), R Studio (v4.2.1) and R packages *dplyr*, *lubridate*, *suncalc*, *move*, *lme4*, and *ggplot2* for analyses.

3 Results

3.1 Movement metrics

Wild Local cheetahs had the highest average step length (1,164 m), followed by Rehabilitated Local (601 m), with both local groups displaying longer movements than Rehabilitated Translocated and Wild Rehabilitated Translocated (400 m and 278 m respectively) (Figure 2). The difference was statistically significant for Wild Local compared to all other classes ($p < 0.05$) (Supplementary Table S3).

Cheetahs moved the shortest distances in the Cold-Dry season (405 m) compared to Hot-Dry (675 m) and Hot-Wet (632 m) periods ($p < 0.05$) (Supplementary Table S4). Males (903 m) exhibited longer step lengths on average than females (364 m) ($p < 0.001$) (Supplementary Table S5).

Cheetahs mostly moved in the buffer outside of the Big Field (proportion of steps 0.80) but when therein they took shorter steps (488 m). While spending less time inside Big Field, they moved faster in the open area (799 m). In contrast, steps intersecting the open savanna-woodland savanna habitat edge produced long-range movements (1618 m), but these steps were proportionally lowest compared to steps within and outside Big Field (Supplementary Table S6).

All analyses found the day, night, and crepuscular covariates to be significant, but for the mixed-effects models using pooled data, no other fixed-effects covariates were significant (Supplementary Tables S11 – S16). Cheetahs did not show a specific preference for directionality, with turning angles appearing relatively evenly distributed (Supplementary Figure S1).

3.2 Factors associated with movements

3.2.1 Wild Local

Only the Global Model (no marking tree) was supported for Wild Local individuals (Table 4; Supplementary Table S7). Wild Local cheetahs moved shorter distances during the day and night compared to crepuscular periods, and steps that intersected habitat edge were longer compared to steps inside Big Field.

3.2.2 Rehabilitated local

Four models were supported ($\Delta AICc < 2$): Global Model 2 (Resource Movement), Habitat Use model, Hunting Habitat model, and Global Model (No marking tree), but the Resource Movement model received the most support (Table 4; Supplementary Table S8). Rehabilitated Local cheetahs moved

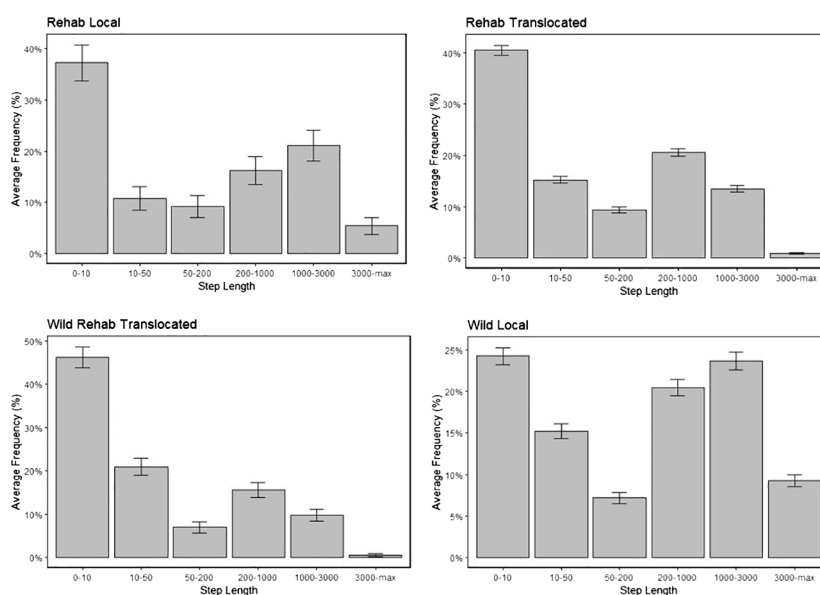


FIGURE 2 Histograms for step lengths of the four classes of cheetah. Average frequencies of step length represented as percentages, with error bars included for each class.

longer distances during the day and shorter distances during the night compared to crepuscular periods. Cheetahs moved shorter distances when far from waterholes.

3.2.3 Rehabilitated translocated

Only the Global Model (no marking tree) was supported for Rehabilitated Translocated individuals (Table 4; Supplementary Table S9). Results for steps intersecting habitat edge, day and night showed the same trend as Wild Local cheetahs. In addition, distance to edge and quadratic distance to edge were associated with

step length, indicating that step length varied non-linearly with edge habitat.

3.2.4 Wild rehabilitated translocated

Only the Global Model 2 (Resource Movement) was supported (Table 4; Supplementary Table S10). These cheetahs moved longer distances during the day compared to crepuscular periods. Additionally, the cheetahs moved shorter distances when far from marking trees. Steps intersecting habitat edges were longer compared to those confined by the Big Field boundaries.

TABLE 4 Covariates associated with cheetah movements based on supported models ranked in an AICc framework ($\Delta AICc < 2$).

Hypothesis	Covariate	Cheetah class							
		Wild Local (n=2)		Rehabilitated Local (n=2)		Rehabilitated Translocated (n=5)		Wild Rehabilitated Translocated (n=1)	
		Estimate (SE)	p-value	Estimate (SE)	p-value	Estimate (SE)	p-value	Estimate (SE)	p-value
1	Intersection	0.74 (+/- 0.08)	<0.001*	0.60 (+/- 0.45)	0.18	1.07 (+/- 0.08)	<0.001*		
	Outside	-0.09 (+/- 0.07)	0.19	-0.21 (+/- 0.37)	0.57	-0.10 (+/- 0.05)	0.052		
	Waterhole	-0.03 (+/- 0.02)	0.29	-0.15 (+/- 0.07)	0.043*	-4.9e-3 (+/- 0.02)	0.80		
	Edge	-0.06 (+/- 0.08)	0.47	-0.16 (+/- 0.29)	0.57	0.25 (+/- 0.08)	<0.001*		
	Edge^2	0.13 (+/- 0.08)	0.09	0.19 (+/- 0.28)	0.52	-0.25 (+/- 0.07)	<0.001*		
	Day	-0.65 (+/- 0.05)	<0.001*	0.32 (+/- 0.16)	0.049*	-0.14 (+/- 0.04)	0.001*		
	Night	-0.28 (+/- 0.06)	<0.001*	-0.59 (+/- 0.18)	0.001*	-0.30 (+/- 0.05)	<0.001*		
3	Waterhole	-0.04 (+/- 0.02)	0.08						
	Day	-0.89 (+/- 0.05)	<0.001*						
	Night	-0.40 (+/- 0.06)	<0.001*						
6	Intersection	0.74 (+/- 0.08)	<0.001*						
	Outside	-0.06 (+/- 0.07)	0.42						
	Day	-0.66 (+/- 0.05)	<0.001*						
	Night	-0.27 (+/- 0.06)	<0.001*						
8	Waterhole	-3.2e-3 (+/- 0.02)	0.89					-0.08 (+/- 0.04)	0.077
	Marking tree	3.2e-3 (+/- 0.03)	0.88					-0.12 (+/- 0.05)	0.014*
	Intersection	0.74 (+/- 0.08)	<0.001*					1.74 (+/- 0.36)	<0.001*
	Outside	-0.06 (+/- 0.07)	0.43					-0.05 (+/- 0.24)	0.83
	Day	-0.66 (+/- 0.05)	<0.001*					0.52 (+/- 0.11)	<0.001*
	Night	-0.27 (+/- 0.06)	<0.001*					-0.20 (+/- 0.11)	0.080

Estimates for which confidence intervals did not overlap zero are highlighted with an asterisk.

3.3 Cheetah-prey relationship

Small prey did not vary significantly over time, whereas large prey did ($W=36$, $p=0.029^*$) (Figure 3). In years of higher prey availability, including both grazer and browser ungulate species, cheetahs moved shorter distances (2013-2016) (Figure 4).

4 Discussion

The releases of cheetahs in our study system were carried out to augment a local population that persisted at low densities thought to be below carrying capacity, while simultaneously mitigating human-wildlife conflict at the sites where the released animals originated from. The releases of translocated individuals took place within existing cheetah range on CCF property which functioned as wildlife reserve, and contributed to the enhancement of the local population and presumably to ecosystem services therein (Fabiano et al., 2020). Some of the cheetahs released had initially been brought to CCF as orphaned cubs when their mothers were killed as part of human-wildlife conflicts, therefore post-release monitoring provided an ideal opportunity to compare the movement ecology of rehabilitated individuals to wild ones. We justify our categorisation of cheetahs through ecological rationale and variables included in our methodology, but acknowledge that large carnivores exhibit individual behavioural variability (Cristescu and Boyce, 2013; Shaw, 2020). Our sample size was insufficient to build individual models and to directly assess individual differences as well as influence of age within a given reproductive class. However, we did account for individual and reproductive class variability using a mixed-effects modelling approach (Supplementary Tables S14 – S16).

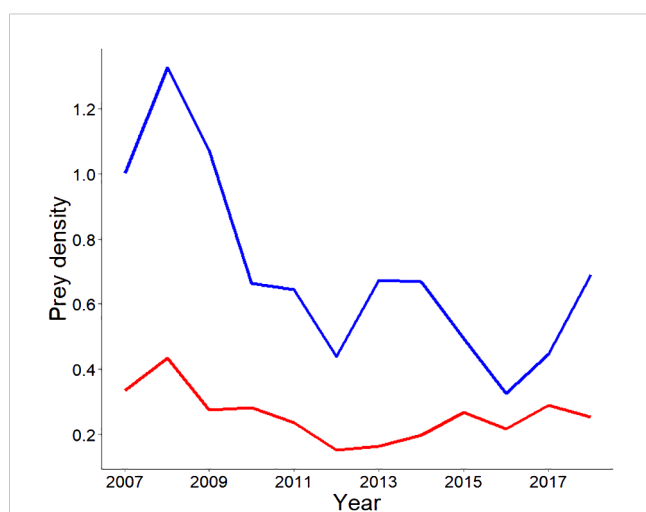


FIGURE 3

Prey density (per km²) for small and large ungulate prey, calculated over time. The blue line represents large prey, and the red line represents small prey. Giraffe was excluded due to low likelihood of cheetah hunting this species, and Leporids, ostrich and secretary birds excluded due to few observations precluding calculation of the estimated strip width from distance sampling.

4.1 Movement metrics

Wild Local cheetahs exhibited significantly longer steps than other classes, which is contrary to our expectation that they would have shortest movements because of familiarity with the area and absence of exploratory movements. The extensive movement rates of Wild Local individuals might be attributed to enhanced territorial behaviour with the release of conspecifics in the same system. Cheetah releases occurred throughout the study duration, including releases when the wild local cheetahs were monitored (2007-2009). However, some of the releases involved VHF radiocollars and therefore could not be included in this study due to lack of GPS data for movement analysis. The large movement rates of Wild Local individuals could also reflect a hunting strategy that focuses on large prey which are present at low density and require extensive searches for movements.

Also contrary to expectations, released cheetahs that were unfamiliar with the area having been translocated displayed shorter movements, which might be suggestive of cautious exploratory behaviour. The difference in movement rates among cheetah classes suggest possible behavioural changes that may be triggered by environmental factors but also possibly by conspecific interactions, pointing to the need to understand the effects of releases on resident and introduced individuals in rewilding and reintroduction efforts. Differences in movement rates were recorded among sexes also, with male cheetahs having significantly longer step lengths than females, despite females maintaining larger home ranges in this species (Marker et al., 2007). Extensive movements by males may be a strategy for territorial defence (Weise et al., 2015).

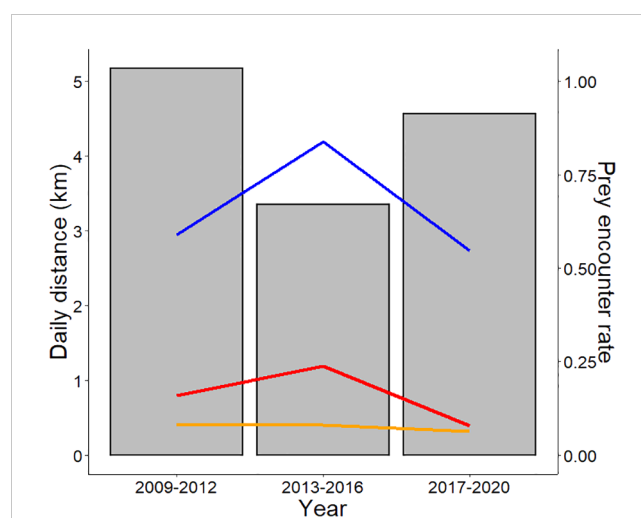


FIGURE 4

Daily distance (km) moved by cheetahs in four-year increments: 2009-2012 ($n=2$), 2013-2016 ($n=5$), 2017-2020 ($n=2$). The prey encounter rate (prey per km²) is displayed on the secondary y-axis, with results represented by lines split into three prey categories. Ungulate prey according to foraging strategy included mixed feeders ($n=2$), grazers ($n=5$), and browsers ($n=3$). The blue line represents grazers, the red line represents browsers and the orange line represents mixed feeders.

4.2 Factors associated with movements

Although classically considered to be diurnal hunters, with bouts of crepuscular activity (Hayward and Slotow, 2009; Nghikembua et al., 2016), cheetahs have been demonstrated to be flexible in activity patterns and can have nocturnal movements where dominant large carnivores are absent or where they are heavily persecuted by humans. Cheetahs can be particularly active during lunar cycles with increased moonlight, a strategy thought to increase nocturnal hunting efficiency (Broekhuis et al., 2014; Searle et al., 2021). Our findings on cheetah movements show a predominance of long movements during the crepuscular period, which might place them at risk of encountering a dominant competitor, the leopard (Verschuere et al., 2021).

Rehabilitated Local individuals were the only ones for which movements were associated with waterhole proximity, but in the opposite pattern than we had anticipated. When close to waterholes, this class of cheetahs moved greater distances than when far from waterholes, possibly indicating that proximity to waterhole may not be desirable. Although waterholes are key resources for many large carnivores (Jhala et al., 2021) for hydration and hunting opportunities, they may especially be sought after by ambush predators (Crosmary et al., 2012). The cheetahs in this category were solitary and familiar to the area, thereby presumably that waterholes increase the likelihood of encountering leopards (Krag et al., 2023). Leopards are the dominant predator and are highly abundant in this system (Cheetah Conservation Fund, unpublished data). Wild local cheetah individuals may not have shown the same pattern due to being part of male coalitions, which are at lower risk from leopards due to group living. Nonetheless, ungulates in our study system appear to adjust their waterhole visitation patterns with cheetah presence (Ruble et al., 2022), suggesting a potential response to perceived predation risk. For rehabilitated local individuals, the movements here may be determined by prey distribution as certain species of prey are more water-dependent than others (Kihwele et al., 2020), but for this study we lacked the information to confirm spatial prey availability by cheetahs.

Distance to confirmed marking trees was associated with step length of the one Wild Rehabilitated Translocated cheetah included in the study, which moved longer distances when close to the marking tree. As a translocated cheetah, this female was unfamiliar with the area and minimising the time spent around marking trees might have been part of a strategy of risky conspecific avoidance involving resident male(s). Cheetahs, particularly males use marking trees repeatedly for territorial and reproductive advertising (Marker-Kraus and Kraus, 1997), whereas in leopards both sexes often scent mark (Cornhill and Kerley, 2020). Cheetahs and leopards often choose the same marking trees but exhibit temporal segregation to avoid conflict (Rafiq et al., 2020; Verschuere et al., 2021).

The movements of Rehabilitated Translocated cheetahs in relation to the hard edge between human-managed open savanna and bush encroached woodland savanna revealed a non-linear relationship. Habitat edges are often favoured by prey and also

provide concealment, which can assist in hunting (Bissett and Bernard, 2007; Atkinson et al., 2022b).

4.3 Cheetah-prey relationship

Our study system experienced a decline in large prey over time and we were able to detect an adjustment in movement rates by cheetahs particularly in relation to the variability in browser and grazer ungulates. As resource availability fluctuates, cheetahs must adapt their ecological and behavioural processes (Broekhuis et al., 2019, Broekhuis et al., 2021; Rodriguez-Recio et al., 2022). Our data support the resource dispersion hypothesis, which predicts that large carnivores will expand their ranging patterns as resource availability becomes dispersed, resulting in increased movements (Macdonald, 1983; Farhadinia et al., 2016; Rodriguez-Recio et al., 2022).

4.4 Recommendations and conservation applications

Post-release monitoring of the behaviour of apex predators released as part of rewilding or reintroductions remains challenging and has rarely been compared with behaviours of locally resident animals. Based on a dataset of released and resident GPS radiocollared cheetahs and prey populations monitored over >10 years, we were able to draw inferences on factors that affect apex predator movements and began to explore the complexity of predator-prey relationships. We found extensive differences among cheetahs regarding their movement rates in relation to their familiarity with the area, rehabilitation, and ecological factors. We recommend that rewilding and reintroduction programmes monitor individuals closely using GPS tracking technology to understand movements and, for population augmentation projects, the potential effects on the resident population.

High movement rates in males suggest that it would be beneficial to rewild female cheetahs initially as they have shorter movements, and those females may encourage residency in future releases of males. Less expansive movements can be beneficial for cheetah survival in unprotected areas (Sievert et al., 2022; Cristescu et al., submitted). For example, roads pose a dynamic threat to individuals that cover extensive distances, and road density and type become paramount during the selection of individuals for release. This is due to the fact that roads contribute significantly to the mortality of wild individuals (Mohammadi et al., 2018; Mohammadi and Kaboli, 2016). Cheetahs that move longer distances, particularly through extensive exploratory behaviour, are most vulnerable to encountering risky situations through human-wildlife conflict. Our study highlighted that males in coalitions undertake longest movements, and territorial males will repeatedly use specific areas to advertise their presence and mark their territory in communication hubs (Caro, 1994; Melzheimer et al., 2020). We recommend farmers remove their livestock from these known areas, and that livestock should not be free-ranging

during crepuscular or night-time periods, to avoid the most frequent activity periods of large carnivores such as cheetahs, leopards, and hyenas (Puls et al., 2021; Vissia et al., 2021, Vissia et al., 2022). Removing livestock late afternoon and releasing them again in the morning would be a good strategy for conflict mitigation. Because the success of release projects for apex predators relies heavily on prey abundance and accessibility, research could benefit from incorporating observations of diet composition and prey preference, as well as kill frequencies and kill intervals by predator age and sex class (Cristescu et al., 2022).

Although focal studies such as ours are informative behaviourally by incorporating detailed parameters such as location of marking sites and waterholes and detailed knowledge of habitats, conducting movement analyses on a broader landscape scale has its own set of advantages. A great opportunity is the availability of remote sensing data, which can be used to relate animal movement trajectories to landscape characteristics over extensive regions.

Rewilding landscapes through the restoration of species that either went locally extinct or experienced significant declines is an increasingly applied practice in biological conservation. We encourage researchers to continue to investigate the post-release movement ecology of apex predators and the effects of released animals on the food webs and ecosystems at the release sites, while not neglecting resident individuals that might be present at the sites.

Data availability statement

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

Ethics statement

The animal study was approved by National Commission on Research, Science and Technology, Government of Namibia. The study was conducted in accordance with the local legislation and institutional requirements.

Author contributions

JD: Conceptualization, Formal analysis, Investigation, Methodology, Writing – original draft. BC: Conceptualization, Methodology, Resources, Supervision, Writing – review & editing.

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KB: Formal analysis, Methodology, Writing – review & editing. NR: Conceptualization, Supervision, Writing – review & editing. LM: Resources, Supervision, Writing – review & editing.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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Supplementary material

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fcosc.2024.1351366/full#supplementary-material>

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