Mammalian Biology
https://doi.org/10.1007/s42991-024-00429-z

SHORT COMMUNICATION

Denning and maternal behavior of caracals (*Caracal caracal*)

Laurel E. K. Serieys[1,2,3] · Gabriella R. M. Leighton[3] · Justin Merondun[4,5] · Jacqueline M. Bishop[3]

Received: 5 January 2024 / Accepted: 30 May 2024

Abstract
Knowledge of behaviors surrounding reproduction in wild species is essential to the development of effective management and conservation strategies. Many carnivores use dens to increase the safety and survival of their neonatal young while females shift to central-place foraging to meet the energetic demands of raising young. Caracals (*Caracal caracal*), a medium-size wild cat, have a widespread geographic distribution but limited information from minimal observations exists on the behaviors associated with denning and caring for young. We report observations of dens used by four caracals in the surrounds of Cape Town, South Africa, including the duration of den use, maternal home ranges, and movements away from dens. Three of four females established denning in September and one in December, suggesting a birth pulse during the Southern Hemisphere spring and summer. Of seven den sites we documented, six were in dense shrubland fynbos vegetation and one among boulders; all of which had thick overhead cover. Females and neonatal young used 1–3 primary dens for approximately six weeks, followed by the use of short-term auxiliary dens. Female maternal home ranges were approximately 31% the size of their home ranges estimated using all their data. Trips away from the dens averaged 12 h while the average maximum distances across all trips away from dens for each female was 1135 m (range = 801–1327 m). Our observations inform our understanding of the timing and physical characteristics of caracal dens and help fill research gaps on the natural history of caracal denning behavior.

Keywords Central place forager · Carnivore · Movement ecology · Home range · Reproduction

Introduction

Neonates are usually the most vulnerable life stage in mammals (Palomares et al. 2005). Many carnivores use dens to increase the safety and survival of their altricial offspring (Fernández and Palomares 2000; Trapp et al. 2008; Ross et al. 2010), as dens provide multiple benefits including thermal insulation and safety from inclement weather and predators (Beier et al. 1995; Fernández and Palomares 2000; Boutros et al. 2007; Ross et al. 2010). While there is variation in the types of dens used by mammals, felids generally use dens as temporary shelter for dependent kittens that are still nursing; dens are often abandoned once the kittens progress to primarily consuming meat (Fernández and Palomares 2000; Yovovich et al. 2020) and are sufficiently mobile to move with their mothers (O'Malley et al. 2018). Many carnivores with neonatal young shift their activity to become central-place foragers (Orians and Pearson 1979), reducing their movements and hunting efforts to smaller areas around dens (Orians and Pearson 1979; Beier et al. 1995; Yovovich et al. 2020) to meet the energetic demands of raising young (Maehr et al. 1989).

Caracals (*Caracal caracal*) are widely distributed but relatively understudied across their distribution in African and Asian ecosystems, with some subpopulations listed as threatened or endangered (Avgan et al. 2016). Caracals are generalist feeders that often feed on small prey (Leighton et al. 2020; Parchizadeh et al. 2023) and are also habitat

Handling editor: Rebecca Ray-Brambach.

✉ Laurel E. K. Serieys
Lekserieys@gmail.com

[1] Panthera, New York, NY, United States

[2] Cape Leopard Trust, Cape Town, South Africa

[3] Institute for Communities and Wildlife in Africa, Department of Biological Sciences, University of Cape Town, Cape Town, South Africa

[4] Division of Evolutionary Biology, Faculty of Biology, LMU Munich, Planegg-Martinsried, Germany

[5] Department of Ornithology, Max Planck Institute for Biological Intelligence, Seewiesen, Germany

Published online: 24 June 2024

generalists, using diverse natural and human-modified environments (Avgan et al. 2016; Ramesh et al. 2016; Serieys et al. 2023). Caracals are thought to reproduce throughout the year, with a peak in births in spring and summer in some regions (Bernard and Stuart 1987). Caracals may give birth to 1–4 kittens, but on average have litters of 2 kittens (Bernard and Stuart 1987). Collecting data on the breeding biology and behavior of felids through direct observations is usually impossible because they are secretive, typically nocturnal, and have large ranges (Fernández et al. 2002); it is thus not surprising that much of the current knowledge of caracal reproductive behavior is from minimal observations, primarily of captive caracals (e.g., Bernard and Stuart 1987). The limited understanding of caracal reproductive behaviors underscores the need for more comprehensive research to facilitate management and conservation efforts.

Here we share observational data of denning behavior by four caracals monitored with GPS-collars on the Cape Peninsula in Cape Town, South Africa. We provide observations on the natural history of caracal denning behavior, including their duration of use, seasonality, and den characteristics. Additionally, we examine home range sizes of denning females and their movement patterns from the dens.

Methods

We studied caracals in the Cape Peninsula in Cape Town, South Africa (Fig. 1), where caracals are the apex predator. The Cape Peninsula comprises 320 km^2 of largely protected open spaces (including Table Mountain National Park, 220 km^2) isolated by 860 km^2 of City of Cape Town urban matrix. Land uses within the study area includes altered open areas (e.g., golf courses), low-to-high density residential development, commercial development, vineyards, and pine plantations. Natural habitat includes coastal sand dunes, fynbos and renosterveld-dominated habitat, and wetlands.

We captured 26 caracals ($n_{male} = 15$, $n_{female} = 11$) between 2014 – 2016 using cage traps as part of a larger caracal ecology study (Serieys et al. 2023). Briefly, we fit individuals with Tellus 1C collars (Followit™, Lindesberg, Sweden) which recorded GPS locations at 3-h intervals, but also assessed fine-scale movement patterns by increasing the GPS-sample rate to 20-min intervals every 10th day. As a result, collar batteries depleted within six months. We downloaded collar data weekly via the

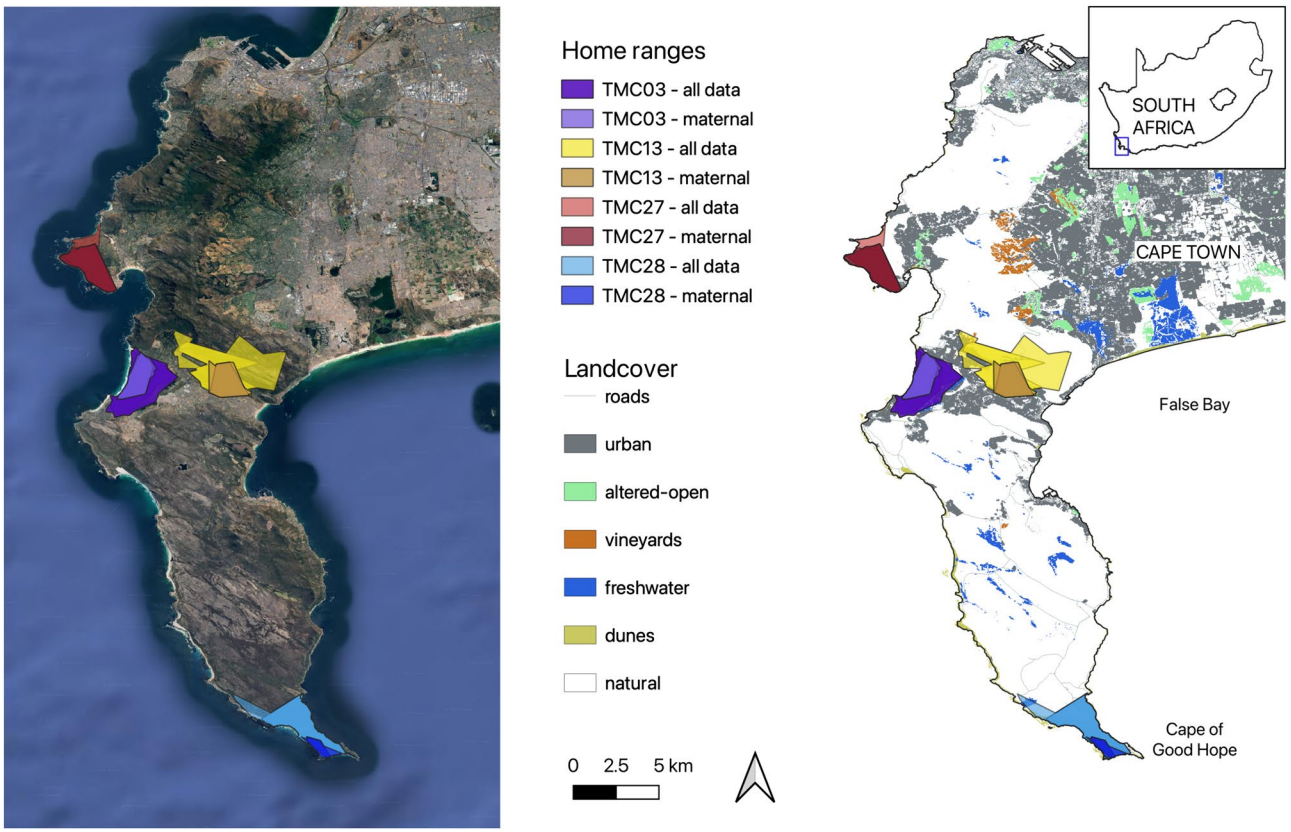

Fig. 1 Map of Cape Peninsula, South Africa, showing maternal home ranges and home ranges estimated using all their data for collared female caracals ($n = 4$)

FollowIt™ GEO web interface or obtained data directly from collars after units dropped-off.

Putative denning behavior (restricted movement within 100 m diameter for ≥ 1 week) was observed for four female caracals during an earlier study on foraging behavior (Leighton et al. 2020, 2022). If the period of restricted movements (during which movements were to and from a fixed point on the landscape) extended for ≥ 4 weeks, parturition was assumed to have occurred. In the present study, we used the R package *GPSeqClus v1.4.0* (Clapp et al. 2021) implemented in R v.4.3.2 (R Core Team 2023) to quantitatively determine denning periods and locations for four females using search parameters of a 100 m radius, a 3-day temporal window, and a minimum of 30 cluster locations. The analysis output included the cluster centroid (i.e., den), cluster date ranges, maximum cluster radius, and maximum (straight-line) distance that the female moved away from the centroid. If females moved denning locations, multiple centroids were reported. Using this approach, we detected that a"primary" period of denning in natal or maternal dens occurred over a period of roughly 6 weeks post-parturition (hereafter 'denning' period). Moriarty (2007) found that female bobcats (*Lynx rufus*, an ecologically similar species to caracals) abandoned natal or maternal dens at roughly 6 weeks post-parturition, and that between approximately 6–12 weeks post-parturition, bobcats utilized "auxiliary" dens for 48–216 h (Moriarty 2007). Therefore, we used *GPSeqClus* to assess whether female caracals also formed clusters that could represent auxiliary den sites using the same search parameters as above, except with a minimum of 10 locations, once denning ceased (hereafter 'auxiliary denning'). The den cluster centroids determined by *GPSeqClus* were within five meters (within the range of GPS error) of ground-truthed den sites, and thus for trip analyses (see below) we used the *GPSeqClus* centroids as the location of all den sites.

We also opportunistically ground-searched for den sites (at least four searchers present) by slowly and quietly approaching the den centroid from variable directions, searching an area of roughly 7800 m^2 (a circular area with a 50 m radius starting from the centroid). We looked for concealed areas with evident well-used resting beds that contained caracal hairs (from grooming). When unable to find the den, we placed cameras around the den centroid to help locate the den. Upon successful den detection, we measured dimensions and used a densiometer (Forestry Suppliers, Jackson, Missouri, USA) to determine the percent cover. We observed kittens ($n = 2$) at a den site of one female (TMC13), two weeks after denning behavior commenced. Kittens were weighed and morphometric measurements taken. We used a 3 mm biopsy punch to remove a small amount of ear tissue for genetic analysis and collected hair samples. After approximately 15 min of handling the kittens, we placed them back into their den site and quickly left the area.

We estimated 95% LoCoH-*a* home ranges implemented in the R package *t-locoh* (Lyons et al. 2013) for each female while denning and using her complete dataset as in Leighton et al. (2022). We performed a t-test to compare sizes of the two home range estimates using R v.4.3.2 (R Core Team 2023).

We examined movement distance and duration (hereafter 'trips') of the female caracals while denning to understand their activity while away from their den. We assessed variation in trip characteristics from den locations to determine if movement behavior changed as denning progressed. We calculated Haversine distance from each GPS location to the den centroid using the R package *geosphere v1.5–18* (Hijmans et al. 2022). A trip began when a caracal left the radius of 125 m from the den, and ended when it returned within this radius. This radius was chosen because it corresponds to the average maximum den radius observed across the four females from *GpsSeqClus*. For each trip, we summarized the number of GPS locations, maximum distance (m) from the den, total distance of the trip (m, summarized as the cumulative step length including the initial segments entering and exiting the den centroid), and duration of the trip (hr). Uncertainty regarding the duration of the trip exists because of the coarse nature of the data (3 h intervals), so we calculated the expected, minimum, and maximum trip duration.

Trips were statistically analyzed across the duration of the denning period with correlations. We calculated Spearman's rank correlation between the numbers of days into denning and three explanatory variables (maximum distance from den, total distance from den, and duration of trip) for each caracal ($n = 4$). We applied a Bonferroni multiple test correction based on the number of tests ($n = 12$).

Results

We documented denning behavior for four GPS-collared caracals (Fig. 1, Table 1). Females were monitored for a total average of 131 days (SD = 3.86). Denning behavior began in September for three individuals, and January for the fourth. Denning for three females for which we have complete denning data occurred over 42, 44, and 46 days (6.0, 6.3, and 6.6 weeks). The fourth female (TMC03) denned for 28 days (4 weeks) before the battery of her collar depleted and we were no longer able to monitor her movements. Two females who were undisturbed during denning used a single natal den site. One female (TMC13) moved den sites 144 m in the evening (day 15 of den use) after we sampled her two kittens. The period of her second den was approximately 27 days. The fourth female (TMC28) was more difficult to

Table 1 Denning and movement characteristics for female caracals ($n = 4$) on the Cape Peninsula, South Africa

Animal ID	Denning duration (days)	Maternal home range area (km^2)	All data home range area (km^2)	*n* trips	Average time away (h)	Max time away (h)	Average max distance away across trips (m)	Max distance away (m)	Average distance traveled during trips (m)	Max distance traveled during trips (m)
TMC03	28*	3.86	10.50	32	9.75	24	1327	3022	3039	7978
TMC13	42	4.42	18.28	35	15.51	45	1146	2136	2938	9071
TMC27	44	5.59	7.69	29	18.41	69	1267	3667	3204	11,249
TMC28	46	1.27	12.29	47	5.55	24	802	1731	1842	4898
Average	44**	3.79	12.19	37**	12.31	41	1135	2639	2756	8299

*Collar battery depleted while the individual was denning so we do not know the total time denned

**Average excludes TMC03 for which we do not have complete denning data

monitor because her collar did not regularly upload data. When we attempted to put cameras around the natal denning area to help locate TMC28's den she moved to a secondary maternal den site 180 m from the first, possibly because of our disturbance in the area. She spent roughly 9 days at the secondary site before we again attempted to locate the den site. We were unable to locate a den site and she again moved to a den site 850 m from the second site, where she remained for 11 days.

Of seven primary den sites documented, six were in dense shrubland fynbos (four in dunes). The seventh den (TMC27) was in a natural area interspersed with woodland, open bush, and large boulders; her den site was nestled within boulders. Den elevations varied between 5–150 m. We physically observed three dens. TMC13's natal den was situated in a dense fynbos bush adjacent to an old, large pile of dead invasive vegetation. The overall dimensions of the den entrance were 72.5 cm wide, 65.5 cm high, and a depth of 1.56 m to the main chamber. There was also a secondary entrance approximately 3 m from the first. The degree of cover within the den site was 95%. TMC28 also denned in thick fynbos bushes (100% cover). Her first den had two entrances (34 cm high, 25 cm wide) and leading from the entrance was a "tunnel" 230 cm long which led to the second entrance (31 cm high, and 33 cm wide). The central denning area was 29 cm long and 32 cm high. TMC27's den site was in an area with large boulders. Amongst the boulders we found what appeared to be a denning area with a length of 52 cm long, and a width of 58 cm. As the den was in a pile of boulders, there were multiple entrances into the denning area, and the boulders provided 100% cover. We did not observe feces or prey remains in any den.

We sampled TMC13's kittens (TMC14, male, 0.55 kg, body length 310 mm; TMC15 female, 0.55 kg, body length 262 mm). For two other dens we investigated, we were able to investigate them only after the sites were abandoned (TMC27 and TMC28). We were unable to investigate den sites for TMC03, TMC13's second den, or TMC28's second or third den due to logistical constraints.

While denning, the estimated size of each female's home range ($\bar{x} = 3.8$ km^2, SD = 1.8, range = 1.3 – 5.6) was approximately 31% the size of their home range estimated using their entire movement dataset ($\bar{x} = 12.2$ km^2, SD = 4.5, range = 7.7 – 18.3), indicating a significant restriction in utilized area while denning (df = 4, t = -3.48, $p = 0.026$; Table 1, Fig. 1).

We calculated between 29 and47 trips across the four females ($\bar{x} = 36$; Table 1). Trips away from the dens averaged 12.3 h, with an average maximum time away of 41 h (range = 24–69 h; Table 1). Maximum distances from the den site varied among females ($\bar{x} = 2639$ m, range = 1731–3667 m), while the average maximum distances across all trips for each female was 1135 m

(range = 801–1327 m). During forays away from the den site, the average distance females travelled was 8299 m (range = 4898–11,248 m). We did not observe a significant relationship between trips characteristics and the timing of parturition (e.g., no change in movements as kittens aged). However, caracals utilizing a single den (TMC03, TMC27) exhibited positive correlations between denning initiation and all trip characteristics (Spearman's rho (r); maximum distance traveled, $\bar{r} = 0.19$; total distance traveled, $\bar{r} = 0.24$; total hours, $\bar{r} = 0.36$) in contrast to caracals utilizing multiple dens (TMC13, TMC28) who exhibited weaker or negative correlations with larger trips as kittens aged (maximum distance, $\bar{r} = 0.11$; total distance, $\bar{r} = 0.06$; total hours, $\bar{r} =$ -0.15).

For three females for which we have data more than 6-weeks post-parturition, we observed the presumed use of auxiliary dens. Unfortunately, we have only 24 (TMC27), 30 (TMC28), and 65 days (TMC13) of movement data following the denning periods for three females (total data days since parturition: TMC13, 107 days; TMC27, 68 days; TMC28, 78 days). We observed four potential auxiliary dens for TMC27, six for TMC28, and eight for TMC13 (total $n = 17$). The last auxiliary den for TMC13 (the only female for which we have complete post-parturition movement data) was abandoned 91 days post-parturition. The average period of use of auxiliary dens was 4 days (SD = 3 days, range = 2–8 days). The average period between auxiliary dens was 2 days (SD = 2.3, range = 0–7 days). We feel confident that the clusters we observed post-denning were auxiliary dens because we did not observe the same pattern of extended clusters consecutively formed prior to denning for any female.

Discussion

For many carnivore species with altricial offspring, securing den sites with associated maternal home ranges is essential for reproduction (Gittleman and Thompson 1988; Boutros et al. 2007). Thus, understanding facets of the reproductive biology of species can be instrumental in promoting their management and conservation. Little is known about the breeding ecology of free-ranging felids, particularly patterns of breeding den use and kitten development (Fernández et al. 2002; White et al. 2015) with most of the knowledge of reproductive behavior of wild felids centering on landscape characteristics of selected den sites (e.g., resource selection,White et al. 2015; Yovovich et al. 2020). Here we leveraged GPS collar data to report observations of caracal reproductive ecology; while these observations are limited by our sample size, they represent a step towards a better understanding of caracal denning behavior.

In the literature, caracals are reported to sometimes reproduce throughout the year (Bernard and Stuart 1987). However, three of our females birthed in the Southern Hemisphere spring, and one in summer. In the Eastern Cape of South Africa, a caracal birth pulse was also noted in spring and summer (Bernard and Stuart 1987). In our study area we receive frequent caracal sighting reports (through urbancaracal.org), and typically observations of females with young (at least 3 months of age) occur through fall and winter, suggesting that at least in the Cape Peninsula, there is a pulse birth that occurs during the spring and summer. Similar spring and summer birth pulses have been documented for bobcats (Moriarty 2007) and Iberian lynx (*Lynx pardinus*, Palomares et al. 2005), with parturition date of Iberian lynx coinciding with an increase in abundance of their primary prey.

The use of GPS data allowed us to make accurate measurements of the duration of the denning period (excluding auxiliary denning). Post parturition, amongst our three females with full datasets, there was a remarkably consistent pattern of utilizing primary den sites for a period of roughly 6 weeks. Highly similar timelines for denning have been observed in bobcats (Moriarty 2007), mountain lions (*Puma concolor*, Beier et al. 1995; O'Malley et al. 2018), and snow leopards (*Panthera uncia*, Palsson 2022). While two undisturbed females used single natal den sites, our attempts to find the den sites for the two other females (successful in one case) seemed to disturb the females sufficiently to prompt den relocation. Human intervention also caused bobcats (Moriarty 2007), Iberian lynx (Fernández et al. 2002), and snow leopards (Palsson 2022) to move den sites. It is possible that female caracals typically maintain single natal den location, moving only when experiencing extreme disturbance. Simultaneous to denning, females established maternal home ranges that were a fraction (approximately 30%) of the size of their full home range estimates. These findings establish that like other felids including Eurasian lynx (*Lynx lynx*), bobcats, black-footed cats (*Felis nigripes*), mountain lions and tigers (*Panthera tigris*) (Molteno et al. 1998; Moriarty 2007; Krofel et al. 2013; Yovovich et al. 2020; Klevtcova et al. 2021), caracals are central place foragers while denning. The use of substantially smaller home ranges is likely to meet the high nutritional demands (lactation and increased hunting effort) to support their developing young (Maehr et al. 1989).

Utilizing the GPS-collar data, we were also able to document what appeared to be a period of auxiliary denning, where females used temporary den sites between 6–13 weeks post-parturition. In Iberian lynx, auxiliary den use is thought to accommodate the kittens' developing motor skills (Fernández et al. 2002) while in mountain lions, home range expansion post-denning also likely reflected increased mobility in kittens (Maehr et al. 1989). Iberian lynx auxiliary

dens were in bushes and thickets (Fernández et al. 2002). Both types of (primary and auxiliary) dens appear to play an important role in the protection of kittens against temperature fluctuations and predators (Fernández and Palomares 2000; Moriarty 2007). Approximately 12 weeks post-parturition, bobcats abandon dens altogether and kittens begin to follow the female (Moriarty 2007). Given the apparent similarities between bobcat and caracal denning patterns and our auxiliary denning observations of TMC13 (the only female for which we have a complete post-parturition dataset), it is likely that caracals also abandon dens altogether around 12-weeks post-parturition, following the mother during her daily movements.

We found that females primarily used areas with thick fynbos vegetation to establish dens that protected their kittens, and while the locations themselves were relatively accessible, finding the exact den location was exceptionally difficult given the density of the vegetation. Den sites in rocky outcrops and with dense vegetation are used by Eurasian lynx in Norway, and the locations are thought to be chosen to reduce human interference, the primary threat to lynx in Europe (White et al. 2015). Den sites for other species are also often located in difficult-to-access areas with a high degree of cover (Ross et al. 2010; Yovovich et al. 2020). Although in theory, utilizing GPS-collar data of reproductive females could make it easier to locate den sites, we struggled nonetheless to locate dens demonstrating the ability of caracal females to effectively hide their kittens.

We also documented substantial movements away from dens by females (averaging 12 h and about 2 km) while their kittens stayed at the den. These movements are necessary for foraging to sustain the mother during this period of substantial energy investment in young (Maehr et al. 1989; Beier et al. 1995). Lactation is considered the most energetically expensive component of reproduction with mean caloric intake increasing in mammals by as much as 190% during lactation (Gittleman and Thompson 1988). Two females had surprisingly lengthy times away from their dens (TMC13 maximum time = 45 h; TMC27 maximum time = 69 h). However, we verified these extended periods away from their den by manually visualizing and inspecting the telemetry data and noting the distances from the den making undetected return visits unlikely. In the case of TMC27's extended period away, she was primarily located at a cormorant colony; cormorants are an important component of caracal diet in the study area (Leighton et al. 2020). After TMC27's 69 h trip, she returned to the den site and continued to den for roughly one month, suggesting that at least one of her kittens survived her extended period away. A long absence of up to 36 h from the den was observed for a female leopard that was guarding a kill against scavengers (Seidensticker 1977) while the average period away from dens for mountain lions was 19 h while the females foraged (O'Malley et al. 2018). Movements away from dens are likely an important aspect of energetics of denning felids, and extended periods of absence from the den may reflect extended periods of foraging by females. Ultimately, we found sparse literature on the movements of females while denning and we encourage other studies to investigate this in more depth.

We expected to see movements increase as neonatal young grew older but did not find a significant relationship. Increased movement distances as kittens aged was observed for mountain lions (Maehr et al. 1989; Beier et al. 1995), bobcats (Moriarty 2007), and Eurasian lynx (Krofel et al. 2013). Of interest, however, is that females that were disrupted and changed denning locations had the lowest correlation between distance and time away from the den site and time since den initiation while females maintaining a singular den location throughout the observation period demonstrated stronger correlations. With a larger sample size of undisrupted females, it is possible that as kittens mature, caracal females do move further for more extended periods as seen with other felids.

In conclusion, our findings contribute to a better understanding of reproductive behavior of caracals. Studying the reproductive behavior of elusive felids is difficult; finding the den sites and kittens alone can be a rare incident for felid ecologists, even during long-term studies (Boutros et al. 2007). We encourage felid researchers from across their range to publish den characteristics and the movements of GPS-collared females while denning, so these features can be better understood. An understanding of reproductive requirements of species is essential to promote their conservation and management. This study is a first step to providing key information to local conservation and management agencies.

Acknowledgements We are grateful for the logistical support of SANParks. We thank M. Allen for support during manuscript preparation. We are grateful for J. Broadfield's and numerous volunteer interns field assistance. Essential project veterinarians were Drs. B. Stevens, A. Knight, E. Jordan, T. Hepburn. We thank the Claude Leon Foundation, the University of Cape Town Research Council, Cape Leopard Trust, Botanica Wines, Stellenbosch University, the National Research Foundation, Wildlife ACT, CoCT, Experiment, Big Cat Rescue, and numerous private donors for funding. We thank R. Ray-Brambach and an anonymous reviewer for comments which helped to improve the manuscript.

Author Contributions LEKS conceived the study, collected, and analyzed data, and wrote and edited the manuscript. GRML and JM analyzed data and edited the manuscript. JMB edited the manuscript. All authors approved the final version of the manuscript.

Funding Claude Leon Foundation, University of Cape Town Research Council, Cape Leopard Trust, Universiteit Stellenbosch, National Research Foundation (ZA), Botanica Wines, Widlife ACT, Experiment, City of Cape Town, Big Cat Rescue

Declarations

Conflict of interest The authors declare no conflict of interest.

Ethical approval Animal handling was approved by the University of Cape Town Animal Ethics Committee (2014/V20/LS), Cape Nature (AAA007-0147–0056), and SANParks (2014/CRC/2014–017, 2015/CRC/2014–017, 2016/CRC/2014–017, 2017/CRC/2014–017).

Consent to participate All authors agreed to participate in this study and all contributed to its content and current version.

Consent for publication All authors agreed to submit this manuscript to Mammalian Biology for publication.

Data availability Full movement datasets are available: doi.org/https://doi.org/10.5441/001/1.317.

Trip analysis script and files are available: https://doi.org/10.5281/zenodo.11048374.

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