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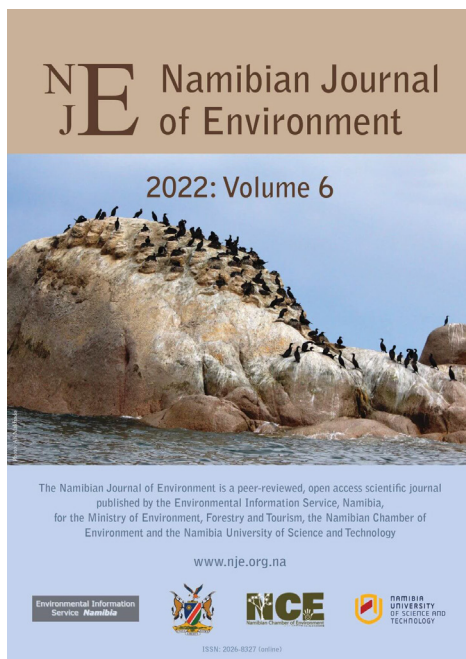
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## SECTION A: RESEARCH ARTICLES

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## At home or passing through? Leopard population and spatial ecology on a private game reserve

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### ABSTRACT

Estimating large carnivore population size and understanding how individuals share space is crucial for their conservation, even more so now they are increasingly restricted to small, fenced game reserves where active management is often required. Combining data from GPS collars and camera traps, we estimated population size for leopards (*Panthera pardus*) on Ongava Game Reserve, northern Namibia, and investigated their spatio-temporal use of waterholes. Over three years of camera trapping, we identified a total of 29 individuals (including 12 adult or sub-adult females and 15 adult or sub-adult males). Based on the time interval over which they were observed, we defined 10 of these individuals as resident (four adult or sub-adult males and six adult or sub-adult females). The remaining 19 individuals (66%) were classified as transient. During the same period, we deployed two GPS collars, one on a resident adult male, the other on a resident adult female. Home range sizes from GPS data were estimated at 193 km<sup>2</sup> for the male and 122 km<sup>2</sup> for the female. Based on home range overlap found in the literature, we estimated Ongava's resident population to be composed of 2-4 males and 3-6 females. We found no evidence of exclusive use of waterholes by individuals, suggesting an absence of spatial avoidance. Our work highlights the importance of taking social status (resident vs transient) into account and of using multiple methods when estimating population size of leopards.

**Keywords:** camera trap, GPS collar, home range, leopard, Namibia, overlap, *Panthera pardus*, spatial ecology

### INTRODUCTION

Estimating and monitoring the population sizes of carnivores is increasingly important in the current context of their global decline and even more so in small fenced game reserves where intensive management of predator populations is often required (Miller *et al.* 2013). Large carnivores are notoriously difficult to census due to their wide-ranging behaviour, elusive and nocturnal activities and their low density (Balme *et al.* 2009). However, as most large carnivore species are territorial at least to some extent, it is possible to use home size and overlap of a few individuals to produce an estimate of population size and/or density in a given area (e.g. Devens *et al.* 2018). In addition, for species in which individuals can be identified based on natural markings (e.g. stripes or spots), camera trapping has been used extensively to estimate carnivore population size (e.g. tigers, *Panthera tigris*, Karanth *et al.* 2004, cheetahs, *Acinonyx jubatus*, Broekhuis & Gopalaswamy 2016). The leopard (*Panthera pardus*) is a highly secretive and adaptable species, capable of living in landscapes with high anthropogenic disturbance levels, including near large towns such as Mumbai, India (Odden *et al.* 2014) and Johannesburg, South Africa (Kuhn 2014). However, leopard populations are decreasing throughout their

range (Jacobson *et al.* 2016), for example by more than 30% in Southern Africa in the past 22 years (Stein *et al.* 2016). Due to their climbing abilities, leopards are not easily constrained by fences (Balme *et al.* 2007, du Preez *et al.* 2015) and thus cannot be effectively restricted within protected areas. These protected areas are often seen as sources for large predator populations, from which sub-adults disperse across neighbouring lands (sometimes across very long distances, such as the ~200 km reported by Fattebert *et al.* 2015a) in search of free space to establish their own territory.

In this study, we focus on estimating population size and density of leopard on the Ongava Game Reserve bordering Etosha National Park in northern Namibia. Given that we might expect leopard populations to be composed of resident individuals (with established territories) and transients (either sub-adults looking to establish a territory or sub-dominant adults displaced from their territory), we also assess resident versus transient status. The reserve is dedicated to non-consumptive tourism, but despite intensive use for game-viewing tourism (as many as 15 safari vehicles driving through the reserve on a daily basis), leopards are rarely seen. However, Ongava represents a prime habitat for leopards, being mostly covered by rocky hills providing numerous caves and

refuges from competitors (namely lions, *Panthera leo*) and harbouring a high density of leopards' preferred prey (Hayward *et al.* 2006). We used camera traps deployed at waterholes over a 3-year study period and identified individual leopards based on their coat patterns to produce estimates of population size. In addition, we investigated the potential for intraspecific competition which might be manifested in spatio-temporal avoidance in the use of waterholes.

**METHODS**

**Study area**

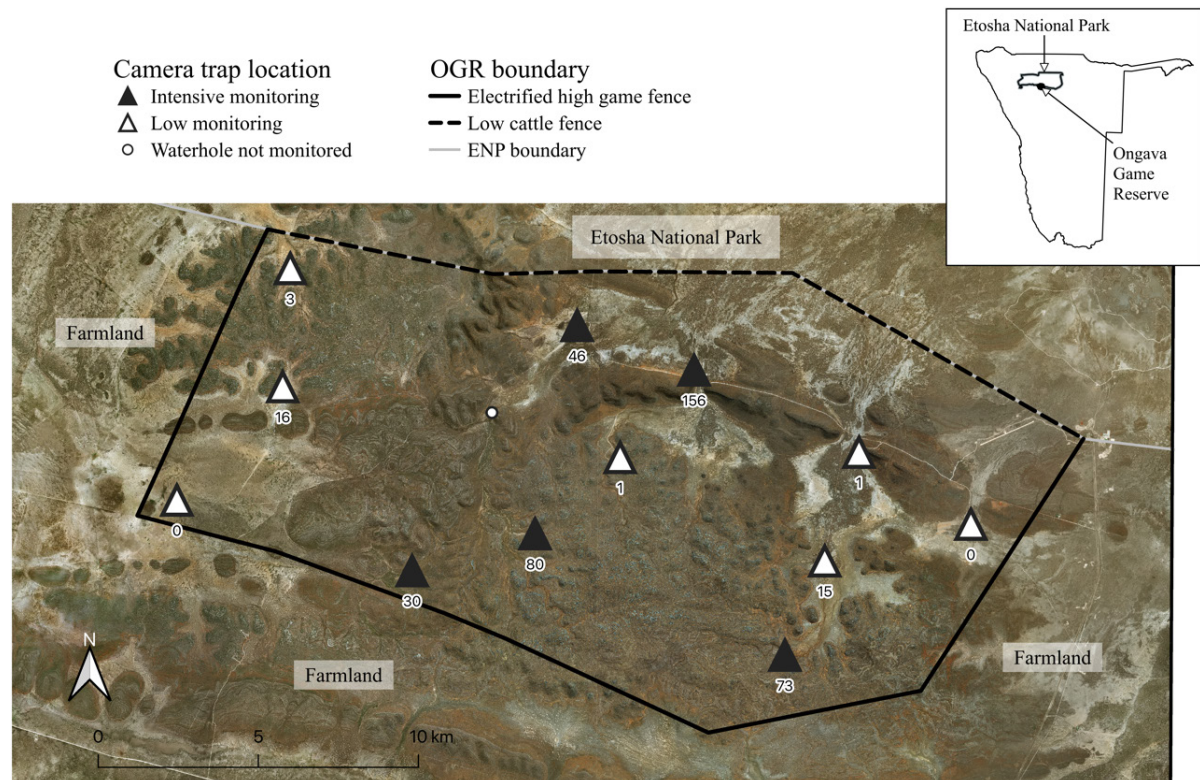
Ongava Game Reserve (Ongava hereafter) borders the south of Etosha National Park (Figure 1), covering an area of approximately 300 km<sup>2</sup>. At the time of the study, the boundary with Etosha was a low non-electrified cattle fence permeable to carnivores, but not to medium and large-sized herbivores, whereas all other fences were electrified high game fences. The habitat is termed Karstveld, with vegetation primarily (up to 70%) *Colophospermum mopane* shrub and woodland, with some savanna-like areas (about 30%). Ongava's relief is mostly dolomite hills, with an open plain area in the southeast corner (~11 km<sup>2</sup>) and a well-defined ridge and small mountain covering about 6 km<sup>2</sup> in the northern part of the reserve. The weather zone for the reserve is typical for semi-arid northern Namibia,

with an average annual rainfall of 380 mm (see Stratford & Stratford 2011 for further details). There are several natural dams on the reserve, although most of these only contain water during the rainy season (January - March). Water is accessible all year at 12 waterholes spread across the reserve. We defined the wet season as the period from January to April during which water was still available in natural dams and ephemeral pans and the dry season as the period from May to December when water was only available at artificial waterholes where herbivores congregate.

Ongava supports a range of mammalian herbivores that are candidate prey species for leopards such as common duiker (*Sylvicapra grimmia*), black-faced impala (*Aepyceros melampus petersi*), springbok (*Antidorcas marsupialis*) and rock hyrax (*Procavia capensis*; Hayward *et al.* 2006) with an overall herbivore density of about 10.4 animals per km<sup>2</sup> (Stratford and Stratford 2011).

**Data collection**

We used two methods to estimate the number of leopards on Ongava. First, we computed home range (HR) size from GPS data of two collared individuals (one adult male and one adult female) and used HR overlap metrics from the literature to calculate how many resident males and females would be predicted to have permanent HRs on Ongava. Second, we used



**Figure 1:** Location of camera traps deployed at 10 waterholes in Ongava Game Reserve, northern Namibia showing intensive (black triangles) and low (white triangles) monitoring locations. Figures indicate the number of leopard records at each location, including unidentified individuals.

camera traps deployed at waterholes across the reserve to identify individual leopards and estimate their number. Based on individual capture histories, we classified each individual as resident or transient and characterised their spatio-temporal overlap in waterholes usage.

#### *Leopard collaring*

We captured leopards in 2013 (February for the female, October for the male) in steel box traps deployed close to waterholes on suspected leopard trails. We baited traps with remains of carcasses and the trap door release was triggered by a conventional pressure plate. We monitored each trap using camera traps and implemented a remote alert system with a signal being triggered when the door was released allowing for a rapid response to minimise the time that animals were captive. Leopards were immobilised in the trap by a professional team using a CO<sub>2</sub> dart gun (Dan Inject, www.dan-inject.com) with an induction dose of 350 mg of Zoletil (Vibrac RSA, Halfway House, RSA). Once sedated, we removed the animals from the trap to take measurements and fit a collar. Each individual received a 50 mg Zoletil IM top-up at some point in the procedure to keep the immobilisation stable. We then transferred the animals to a padded and ventilated recovery crate (1 x 1 x 2 m) close to the capture site and kept them enclosed until fully recovered from the anaesthetic, upon which they were released.

We fitted each leopard with a GPS radio-collar (Vectronic, Berlin) of weight adjusted to fit an adult male and adult female; 550 g and 280 g respectively. Both collars were equipped with VHF beacons, as well as automatic drop-offs (programmed to activate 12 months after deployment) to ensure collar recovery after the study period. Due to battery size difference (smaller for the female) to provide a full year of monitoring, we programmed the collars to record GPS locations every 3 h for the male and every 6 h for the female.

#### *Camera trap survey*

We deployed camera traps (Reconyx RC-55 and HC-500) at 12 waterholes spread across the reserve (Figure 1) from January 2012 to December 2014 (see Appendix 1 for operation table of camera traps). Some waterholes (n = 5, see Figure 1) were part of an intensive monitoring programme, while the rest were monitored during shorter periods across the three years. To provide the best coverage of the waterhole area, we deployed multiple (2-5) camera traps simultaneously at a given waterhole, and pooled their data together, resulting in a single set of images defined as a single observation. We mounted each camera inside a stainless-steel protection case that had been bolted to a tree and additionally secured using a locking steel cable. We set the cameras to

record a sequence of 10 images separated by one second with a delay of 15 seconds between successive triggers. For some remote waterholes, we used a 30 second delay between sequences to extend the interval between trap servicing.

We identified individual leopards based on their unique coat patterns. Pattern comparisons were manually performed over several areas of the body, as small changes in posture, light, and picture quality between images complicate the process. Identification was helped by the fact that images recorded at night using infrared flash provide an enhanced contrast between dark spots and light coat. We developed a reference database for individual leopards, with a minimum of one picture for each side available for each individual. When possible, we determined the sex of each individual based on based on body size, size of dewlap, and the presence of external genitalia (Balme *et al.* 2012). From the camera trap images, it was not possible to accurately age individuals, and animals of adult size were therefore classified as adults or sub-adults.

#### **GPS data analysis**

##### *Home range size and overlap*

To allow for comparison with other studies, we defined HR and core for each leopard as 95% and 50% location based kernel respectively (Worton 1989). We used a fixed kernel density estimator using the reference smoothing factor *href* as recommended by Hemson *et al.* (2005). We calculated HR and core sizes using the whole dataset for each individual.

We computed HR and core overlap between the two individuals using percentage overlap to allow comparison with other studies. We also provided a measure of three-dimensional utilisation distribution overlap index (UDOI, Fieberg & Kochanny 2005). UDOI values range from 0 (no overlap) to 1 when uniformly distributed utilisation distributions (UDs) overlap completely.

##### *Prediction of the number of leopards present*

Similarly to Devens *et al.* (2018), we estimated the resident leopard population size using HR size and overlap obtained from the literature (Table 1) to predict the number of possible HRs, *N*, for both sexes separately on Ongava using the following formula:

$$N = \frac{\text{Ongava area}}{\text{HR size} - (\text{overlap} \times \text{HR size})}$$

where *Ongava area* = 300 km<sup>2</sup>, *HR size* is the size of the 95% kernel computed in this study and *overlap* is the value of percentage overlap taken from the literature. For each sex, we used the minimum and maximum overlap values taken from the literature to produce a resident leopard population size range for

Ongava. Density was calculated as the number of resident leopards per 100 km<sup>2</sup>.

**Camera trap data**

*Resident versus transient individuals*

We estimated the number of resident and transient leopards based on each individual’s capture history from camera trapping. Residents were defined as individuals having a stable HR on Ongava that would lead to consistent captures over time, while transients were individuals with no defined HR and are thus passing through, spending an unpredictable amount of time on Ongava. Based on capture histories, we therefore defined residents as individuals captured at least twice per year for at least two consecutive years.

*Spatio-temporal overlap in waterhole use*

For each waterhole, we computed the number of identified leopards seen during each dry season for each sex separately. We restricted our analyses to the dry season as this was when most of the observations occurred (see Results).

For each identified individual observation, we computed the time elapsed since the last visit of another identified individual. If the previous individual was not identified, we discarded the observation. We calculated the time since the last visit for the overall dataset of identified leopards (i.e. time since the last visit by any other known individual irrespective of its sex) and each sex (i.e. time since last visit by a known male and a known female) separately.

**Table 1:** Leopard home range size and overlap as reported in published scientific literature. Numbers in brackets give the range of estimates and n is the number of individuals used in each case.

Study area	Average home range size in km <sup>2</sup> (range, number of animals)		Home range estimation method	% Overlap (range)		Reference
	Adult male	Adult Female		Between males	Between females	
Waterberg farmland, Namibia	229 (125-312, n = 3)	179 (52-394, n = 4)	95% MCP	24	22	Marker & Dickman (2005)
Khaudum Game Reserve, Namibia	451 (210-1164, n = 6)	188 (183-194, n = 3)	95% MCP	46 (18-59)	35 (28-51)	Stander <i>et al.</i> (1997)
Hobatere Concession, Namibia	94.9 (n = 1)	171.1 (84.5-285.4, n = 5)	95% Kernel		27.8	Stander (2001)
Waterberg farmland, Namibia	109 (n = 1)	50 (46-53, n = 2)	95% Kernel		Existent but not quantified; no core overlap	Stein (2008), Stein <i>et al.</i> (2011)
Okonjima Nature Reserve, Namibia	100.2 (71.4-221.5, n = 6)	72 (70.8-73.2, n = 2)	95% Kernel	26 Males overlap females by 31%	4 Females overlap males by 38%	Stander & Hanssen (2000)
Okonjima Nature Reserve, Namibia	21.7 ± 10.1 (n = 14) 15.6 ± 13.4 (n = 9)	8.9 ± 4.3 (n = 14) 7.8 ± 1.3 (n = 9)	100% MCP From camera trap data	Extensive overlap with dispersing sub-adult males. All male HRs overlapped with at least one female home range	Limited overlap	Noack (2016)
Phinda Game Reserve, South Africa	74 (n = 11)	30 (n = 10)	95% Kernel	23	18	Fatteberg <i>et al.</i> (2016)
Cederberg, South Africa	51 (40-69, n = 3)		95% MCP	10-57		Norton & Henley (1987)
Eastern and Western Cape, South Africa	179.5 (71.7-690, n = 12)	72.5 (34.8-150, n = 9)	95% Kernel	15 (n = 4)	0 (n = 2)	Devens <i>et al.</i> (2018)

We used R software (R Core Team 2022) to extract and analyse data using the packages *adehabitatHR* (Calenge 2006) and *oSCR* (Sutherland *et al.* 2019). Means are given  $\pm$  their standard error (SE) unless mentioned otherwise.

**RESULTS**

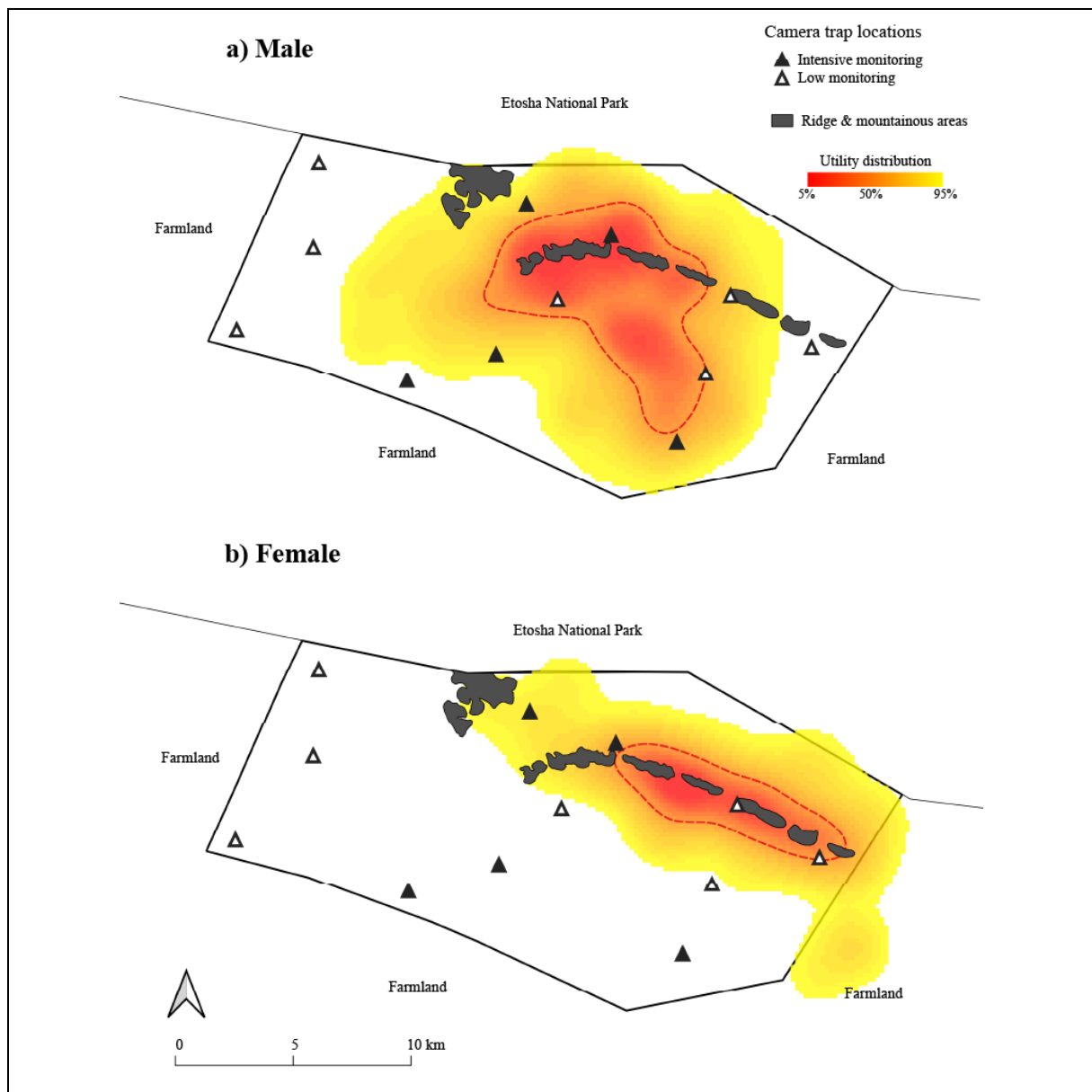
**Spatial ecology from GPS data**

GPS data were collected for 365 days (November 2013 to October 2014, 2 790 locations) for the male and 314 days (March to December 2013, 1 125 locations) for the female. Both individuals established spatially and temporally stable HRs and we thus classified them as resident. While the male was never recorded outside the reserve, 5.6% (n = 63)

of the female GPS locations were outside the reserve fence. The male had both a larger HR (192.8 km<sup>2</sup> versus 121.8 km<sup>2</sup>) and a larger core than the female (51.7 km<sup>2</sup> versus 22.1 km<sup>2</sup>, Figure 2). From the male's perspective, 40% of its HR and 18% of its core was overlapped by the female HR and core respectively. From the female's perspective, 64% of its HR and 41% of its core was overlapped by the male HR and core respectively (Figure 2). UDOI was 0.39 for HR and 0.05 for cores, showing different space use of the area shared by the two individuals.

**Camera trapping**

Camera traps were deployed for the three-year study period (from January 2012 to November 2014) with trapping effort varying across waterholes from four



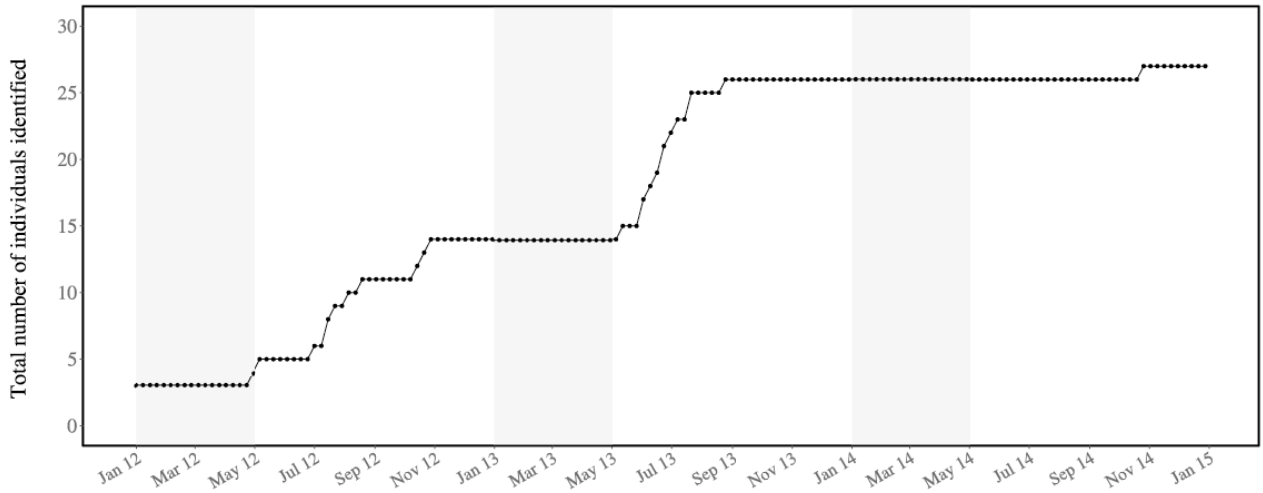
**Figure 2:** a) Male and b) female leopard home ranges (HRs) computed using location-based fixed kernels showing utility distribution. Core areas (50% kernel isopleth) are shown as red dashed lines. Dark grey polygons represent ridges and mountainous areas.

days to 915 days (Figure 1, Appendix 1). Across all waterholes, traps were operational for a total of 5 283 days.

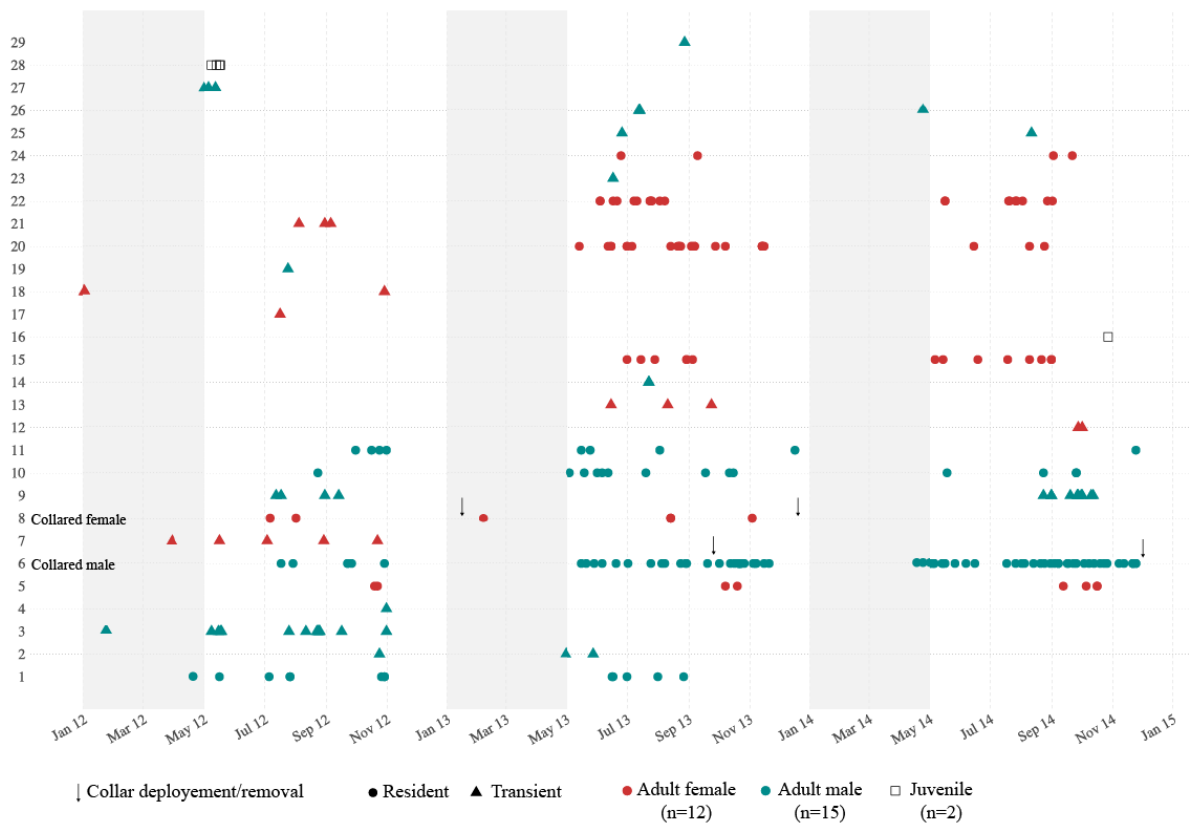
We collected 407 independent observations of leopards across 10 of the 12 waterholes surveyed (Appendix 2, Figure 1). Trapping rate, defined as the percentage of active trap nights on which leopards were observed, was low and averaged  $6.2 \pm 4.8\%$  (range: 0.3-13.1). Most of the observations (96.3%) occurred during the dry seasons, with only 15

observations during the wet seasons across the three years (Figures 3 and 4).

Leopards were observed alone on 396 occasions, and in pairs on 11 occasions. We identified 29 individuals (12 adult or sub-adult females, 15 adult or sub-adult males and two juveniles of unknown sex) from 245 observations (i.e. individual identification was possible for 60% of the sightings across the whole study period). Among the 11 pairs observed, four were of a male and a female, three involved at least



**Figure 3:** Acquisition rate of new individuals during the study period (three years) of camera trapping on Ongava Game Reserve. Shaded areas represent wet seasons.



**Figure 4:** Individual leopard capture histories and status. Transient individuals are represented by triangles and resident individuals by circles. Collar deployment and removal are shown with vertical arrows. Shaded areas represent wet seasons.

one female with an unknown individual, three involved at least one male and in the last case we could not identify either of the individuals.

Known individuals were observed between one and 75 times during the three-year study period with eight individuals seen more than 10 times and 16 seen five times or fewer (Figure 4 and Appendix 2). We classified four males and six females as resident, resulting in 66% of the population being composed of transients.

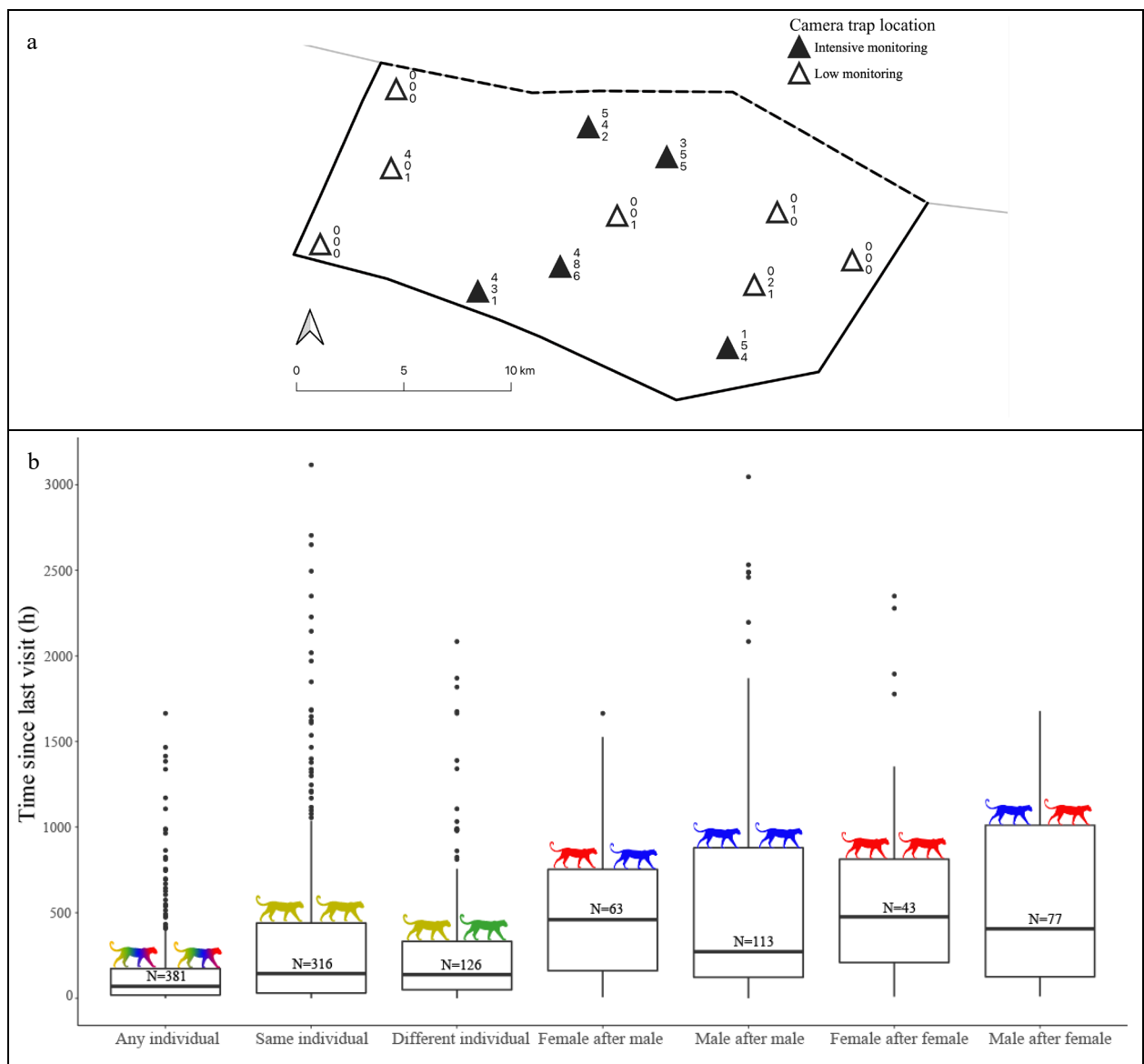
**Population size predictions**

In the literature, within-sex HR overlaps for resident individuals range from 20% to 60 % (Table 1) with

no core overlap. Therefore, we would predict 2-4 resident males (HR size estimated at 193 km<sup>2</sup>) and 3-6 resident females (HR size estimated at 121 km<sup>2</sup>) on the 300 km<sup>2</sup> of Ongava Game Reserve. This would result in a density of 1.7-3.3 leopards/100 km<sup>2</sup>.

**Spatio-temporal overlap in waterhole use**

Based on the 12 individuals (six males and six females) observed more than five times during the study period, leopards used on average  $2.7 \pm 1.9$  waterholes (range: 1-8). Males tend to use a higher number of waterholes ( $3.0 \pm 2.5$ , 1-8) compared to females ( $2.0 \pm 0.6$ , 1-3). A maximum of eight individuals were observed using the same waterhole within a given dry season (Figure 5a).



**Figure 5:** Spatio-temporal overlap in waterhole visitation by individual leopards. a) Number of identified leopards at each camera trap location for each year (top to bottom 2012, 2013 and 2014) of trapping. Black triangles show intensely monitored waterholes while white triangles represent waterholes monitored less intensively. b) Time (in hours) since the last visit of a given waterhole by another identified leopard for resident and transient females and resident and transient males. Error bars represent standard errors, N gives the sample size over which the mean was computed.



On most of the nights (94.4%,  $n = 204$ ) during which leopards could be seen and identified, only one individual was observed at any given waterhole. On 4.6% ( $n = 10$ ) and 1% ( $n = 2$ ) of nights, two and three leopards were observed at the same waterhole respectively.

Time elapsed between the visit of any leopard at a given waterhole (same individual or not) averaged 6.5 days  $\pm$  12.8 hours (12 minutes to 69 days, Figure 5b). A given individual would revisit the same waterhole with an average interval of 14.9 days  $\pm$  1.2 hours (12 minutes to 129.9 days) while visits between different individuals were separated by 13.1  $\pm$  3.2 days on average (51 min to 18.3 days). Females visited a waterhole on average 25.5  $\pm$  3.6 days after another female and 25.0  $\pm$  2.6 days after a male (Figure 5b). Males visited a waterhole on average 25.2  $\pm$  2.8 days after another male and 22.1  $\pm$  2.2 days after a female (Figure 5b).

## DISCUSSION

### Resident leopard space use

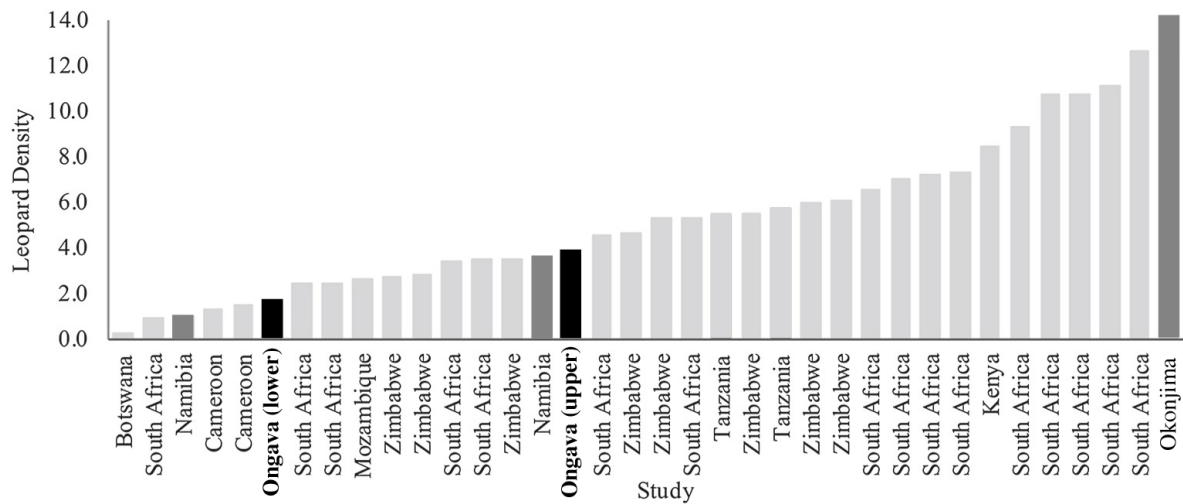
We found that leopard HR sizes on Ongava were well within the known range for the species and that the male had a larger HR than the female, as reported elsewhere (e.g. Snider *et al.* 2021, Rodríguez-Recio *et al.* 2022, and see Table 1). The female had a HR size larger than the average reported for Africa overall but confirms that leopards in Namibia have larger HRs than in other African countries (Snider *et al.* 2021, Rodríguez-Recio *et al.* 2022). Leopards on Ongava were not significantly constrained by fences (as the female repeatedly crossed the eastern boundary fence, even though it was an electrified high game fence), which has been observed in other areas such as Phinda Game Reserve, South Africa (Fattebert *et al.* 2015b). HR overlap between the male and the female was high. This has been reported in other areas (e.g. Odden & Wegge 2005, du Preez 2014, Fattebert *et al.* 2016) and is typical in species with a polygynous mating system, where females defend exclusive territories and male HRs overlap with several females, therefore accessing more mating opportunities (e.g. cougar, *Puma concolor*, Elbroch *et al.* 2016). The UDOI was low, especially for cores, which suggests some extent of resource partitioning between the male and female. This might be due to difference in diet as female leopards have been shown to have a wider and more opportunistic diet (Voigt *et al.* 2018). This could also result from females trying to avoid males to avoid infanticide which is common in this species, with up to 40% of cub mortality caused by males (Balme *et al.* 2012, Balme & Hunter 2013). HR cores were mainly located over the northern ridge, which highlights the importance of this habitat for leopards. In South Africa, leopards have also been shown to select for

habitat of intermediate ruggedness and make use of steep slope areas (Fattebert *et al.* 2015b, Mann *et al.* 2020). Ridges most probably provide ideal habitat for hunting and resting (dense vegetation and rocky outcrops) and are rich in leopards' preferred prey such as rock hyrax and small antelopes (e.g. common duiker or Kirk's dik-dik, *Madoqua kirkii*, Hayward *et al.* 2006). Ridges could also provide refuges from competitors like lions and spotted hyaenas (*Crocuta crocuta*). Leopards have also been shown to react less strongly to lions in closed habitats such as are found on Ongava's ridges (du Preez 2014). However, since ridges only cover a small proportion of Ongava, the availability of this optimal habitat could restrict the number of leopards that could establish stable HRs in Ongava, despite the abundance of prey.

### Leopard population on Ongava

There was an apparent discrepancy between the number of individuals that we predicted might reside in Ongava based on HR overlap and camera trap data. While HR overlap has been used elsewhere to estimate leopard density (Devens *et al.* 2018), it can only be applied to estimate the resident population size, and therefore might underestimate the total number of individuals that can be present on the reserve at any given time. On the other hand, not examining capture histories from camera trap surveys in detail (e.g. number of observation and temporal distribution of these observations) would lead to an overestimation of population size (i.e. a total of 29 adults or sub-adults in the population, while only a subset of these were actually residing on the reserve). HR overlap predicts 5-10 resident leopards on Ongava, and this is in agreement with the number of residents that were identified from the capture history (a maximum of four resident males and six resident females). The resulting density of 1.7-3.3 leopards/100 km<sup>2</sup> falls within the range of density estimates across their range (Allen *et al.* 2020) and in Namibia (Richmond-Coggan 2019; see Figure 6). Leopard density on Ongava is far lower than that estimated for Okonjima Nature Reserve in Namibia (estimated at 14.5 leopards per 100 km<sup>2</sup>, Noack *et al.* 2019), where the surrounding 2.4 m high electrified fences do appear to effectively constrain leopard movement.

Transients might be young adults or sub-adults dispersing across the landscape in search of a territory. These individuals might find it difficult to displace mature resident animals. That our collared male was still recorded with very good body condition in 2019 (pers. obs.), some six years after he was collared, suggests that resident leopards on Ongava may have long tenures.



**Figure 6:** A comparison of leopard densities adapted from Allen *et al.* (2020) showing Ongava’s lower and upper estimates (black) and an estimate for Okonjima Game Reserve, central Namibia (dark grey).

**Relationships between individuals**

We did not find any evidence of spatial partitioning in the use of waterholes since several individuals made use of the same waterhole within a few hours of each other. This suggests that there is little competition for access to water and that multiple residents can use common waterholes in overlapping zones of their HRs. Social large carnivores such as lions and spotted hyaenas usually have exclusive use of waterholes within their territories (e.g. Valeix *et al.* 2011, Périquet 2014), which represent prey hotspots and prime hunting grounds. However, permanent waterholes might not be as important for leopards who can find their preferred prey elsewhere and meet their water requirements from other water sources. Leopards on Ongava were rarely seen together, which is characteristic of this solitary species (Bailey 1993) but does not necessarily result from temporal partitioning in activity patterns. Several studies (e.g. Havmøller *et al.* 2020, Rouse *et al.* 2021) have shown leopards to be mainly nocturnal and not to display significant differences in activity between males and females, despite some fine scale differences in time of activity peaks. Nevertheless, the very low number of simultaneous observations of multiple individuals, but the short time span between visits from different individuals suggests that subordinate individuals might wait for dominant ones to leave the waterhole before coming to drink. Such a fine-scale spatio-temporal avoidance has also been suggested for leopards in Iran (Rouse *et al.* 2021).

**Limitations and way forward**

It is clear from the GPS data that fences did not constrain leopard movement within the reserve boundaries, and we did not account for individuals having only part of their HR on the reserve.

Therefore, our prediction of the resident population size may be an underestimate. We also had a very small sample size for collared individuals, and it would be beneficial to equip leopards with GPS collars in other parts of the reserve to better understand their spatial ecology.

We found that many camera trap images failed to yield positive identification of animals and that capture rate was low, especially during the wet season. The camera traps were not deployed specifically to capture leopards but to survey waterholes in a more general way. Additionally, since leopards were observed drinking at other water sources (e.g. leaks in pipes, sewage overflows) during the study, our reported trapping frequency did not reflect drinking frequency. We would therefore recommend that future studies use camera trapping to concentrate efforts in the dry season (when capture rate will be the highest) and employ the traps in ways that maximise the potential for individual identification. Placing two camera traps facing each other has successfully been used for tigers and leopards along trails (e.g. Karanth *et al.* 2004, Chapman & Balme 2010), although this might be difficult to implement at waterholes.

We found that identifying resident and transient individuals from their capture histories can be misleading. For instance, while the female’s GPS data clearly showed that she was resident, she was only captured on camera trap three times during the entire tracking period (Figure 4), and would have therefore been naively classified as transient. This also suggests once more that leopard drink from sources other than waterholes. Baiting camera trap stations has also been found to significantly increase capture rates (e.g. du Preez *et al.* 2014, Tarugara *et al.* 2019).

This study raises many questions about the transient part of the leopard population, which on a yearly basis can represent 20-70% of the population. Despite having a sizable lion population, Ongava provides an optimal environment for leopard with high habitat suitability and high prey availability. Due to its location between private farmlands where leopards might be trophy hunted and/or persecuted over livestock losses, and the sub-optimal habitat in the neighbouring area of Etosha, we argue that Ongava is highly attractive to leopards, hence the high number of individuals observed on camera traps. At this stage, we do not know where transients come from or go to once leaving Ongava, and we encourage further work to investigate these questions, most probably via tracking devices.

Our work highlights the importance of taking into account the social status of individuals when estimating and presenting population size estimate. This has already been demonstrated in cheetahs (Edwards *et al.* 2018) and failure to do this might yield highly biased estimates. We also call attention to the value of using multiple methods to approach population estimates for species as elusive as leopard.

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## REFERENCES

- Allen ML, Wang S, Olson LO, Li Q, Krofel M (2020) Counting cats for conservation: seasonal estimates of leopard density and drivers of distribution in the Serengeti. *Biodiversity and Conservation* 29(13): 3591–3608. <https://doi.org/10.1007/s10531-020-02039-w>.
- Bailey T (1993) *The African Leopard: Ecology and Behavior of a Solitary Felid*. Columbia University Press, New York, USA.
- Balme GA, Batchelor A, Britz N de W, Seymour G, Grover M, Hes L, Macdonald DW, Hunter LTB (2012) Reproductive success of female leopards *Panthera pardus*: the importance of top-down processes. *Mammal Review* 43(3): 221–237. <https://doi.org/10.1111/j.1365-2907.2012.00219.x>.
- Balme GA, Hunter LTB (2013) Why leopards commit infanticide. *Animal Behaviour* 86(4): 791–799. <https://doi.org/10.1016/j.anbehav.2013.07.019>.
- Balme GA, Hunter LTB, Slotow R (2007) Feeding habitat selection by hunting leopards *Panthera pardus* in a woodland savanna: prey catchability versus abundance. *Animal Behaviour* 74(3): 589–598.
- Balme GA, Hunter LTB, Slotow R (2009) Evaluating methods for counting cryptic carnivores. *Journal of Wildlife Management* 73(3): 433–441. <https://doi.org/10.2193/2007-368>.
- Broekhuis F, Gopalaswamy AM (2016) Counting cats: spatially explicit population estimates of cheetah (*Acinonyx jubatus*) using unstructured sampling data. *PLoS ONE* 11(5): e0153875. <https://doi.org/10.1371/journal.pone.0153875>.
- Calenge C (2006) The package “adehabitat” for the R software: A tool for the analysis of space and habitat use by animals. *Ecological Modelling* 197(3–4): 516–519. <https://doi.org/10.1016/j.ecolmodel.2006.03.017>.
- Chapman S, Balme GA (2010) An estimate of leopard population density in a private reserve in KwaZulu-Natal, South Africa, using camera-traps and capture-recapture models. *South African Journal of Wildlife Research* 40(2): 114–120. <https://doi.org/10.3957/056.040.0202>.
- Devens C, Tshabalala T, McManus J, Smuts B (2018) Counting the spots: The use of a spatially explicit capture-recapture technique and GPS data to estimate leopard (*Panthera pardus*) density in the Eastern and Western Cape, South Africa. *African Journal of Ecology* 56(4): 850–859. <https://doi.org/10.1111/aje.12512>.
- Edwards S, Fischer M, Wachter B, Melzheimer J (2018) Coping with intrasexual behavioral differences: Capture-recapture abundance estimation of male cheetah. *Ecology and Evolution* 8: 9171–9180. <https://doi.org/10.1002/ece3.4410>.
- Elbroch LM, Lendrum PE, Quigley H, Caragiulo A (2016) Spatial overlap in a solitary carnivore: support for the land tenure, kinship or resource dispersion hypotheses? *Journal of Applied Ecology* 85(2): 487–496. <https://doi.org/10.1111/1365-2656.12447>.
- Fattebert J, Balme GA, Dickerson T, Slotow R, Hunter LTB (2015a) Density-Dependent natal dispersal patterns in a leopard population recovering from over-harvest. *PLoS ONE* 10(4): e0122355. <https://doi.org/10.1371/journal.pone.0122355.s001>.
- Fattebert J, Balme GA, Robinson HS, Dickerson T, Slotow R, Hunter LTB (2016) Population recovery highlights spatial organization dynamics in adult leopards. *Journal of Zoology* 299(3): 153–162. <https://doi.org/10.1111/jzo.12344>.
- Fattebert J, Robinson HS, Balme GA, Slotow R, Hunter LTB (2015b) Structural habitat predicts functional dispersal habitat of a large carnivore: how leopards change spots. *Ecological Applications* 25(7): 1911–1921. <https://doi.org/10.1890/14-1631.1.sm>.
- Fieberg J, Kochanny CO (2005) Quantifying home-range overlap: the importance of the utilization distribution. *Journal of Wildlife Management* 69(4): 1346–1359. <https://doi.org/10.2193/0022-541X>.
- Havmøller RW, Jacobsen NS, Scharff N, Rovero F, Zimmermann F (2020) Assessing the activity pattern overlap among leopards (*Panthera pardus*), potential prey and competitors in a complex landscape in Tanzania. *Journal of Zoology* 311: 175–182. <https://doi.org/10.1111/jzo.12774>.
- Hayward MW, Henschel P, O'Brien J (2006) Prey preferences of the leopard (*Panthera pardus*). *Journal of Zoology* 270: 298–313.

- Hemson G, Johnson P, South A, Kenward RE, Ripley R, Macdonald DW (2005) Are kernels the mustard? Data from global positioning system (GPS) collars suggests problems for kernel home-range analyses with least-squares cross-validation. *Journal of Animal Ecology* 74(3): 455–463. <https://doi.org/10.1111/j.1365-2656.2005.00944.x>.
- Jacobson AP, Gerngross P, Lemeris Jr JR, Schoonover RF, Anco C, Breitenmoser-Würsten C *et al.* (2016) Leopard (*Panthera pardus*) status, distribution, and the research efforts across its range. *PeerJ* 4(1): e1974-28. <https://doi.org/10.7717/peerj.1974>.
- Karanth KU, Chundawat RS, Nichols JD, Kumar NS (2004) Estimation of tiger densities in the tropical dry forests of Panna, Central India, using photographic capture–recapture sampling. *Animal Conservation* 7(3): 285–290. <https://doi.org/10.1017/S1367943004001477>.
- Kuhn BF (2014) A preliminary assessment of the carnivore community outside Johannesburg, South Africa. *South African Journal of Wildlife Research* 44(1): 95–98. <https://doi.org/10.3957/056.044.0106>.
- Mann GKH, O’Riain MJ, Parker DM (2020) A leopard’s favourite spots: Habitat preference and population density of leopards in a semi-arid biodiversity hotspot. *Journal of Arid Environments* 181: 104218. <https://doi.org/10.1016/j.jaridenv.2020.104218>.
- Marker LL, Dickman AJ (2005) Factors affecting leopard (*Panthera pardus*) spatial ecology, with particular reference to Namibian farmlands. *South African Journal of Wildlife Research* 35(2): 105–115. <https://journals.co.za/content/wild/35/2/EJC117223>.
- Miller SM, Bissett C, Burger A, Courtenay B, Dickerson T, Druce DJ *et al.* (2013) Management of reintroduced lions in small, fenced reserves in South Africa: an assessment and guidelines. *South African Journal of Wildlife Research* 43(2): 138–154. <http://www.bioone.org/doi/abs/10.3957/056.043.0202>.
- Noack J (2016) *The assessment of leopard (Panthera pardus) density and population size via a capture – recapture framework in an island bound conservation area in Namibia*. Unpublished report: AfriCat Namibia. [https://africat.org/wp-content/uploads/2018/10/africat\\_foundationprogress\\_report\\_leopard\\_density\\_study\\_1.pdf](https://africat.org/wp-content/uploads/2018/10/africat_foundationprogress_report_leopard_density_study_1.pdf).
- Noack J, Heyns L, Rodenwoldt D, Edwards S (2019) Leopard density estimation within an enclosed reserve, Namibia using spatially explicit capture–recapture models. *Animals* 9(10): 724. <https://doi.org/10.3390/ani9100724>.
- Norton PM, Henley SR (1987) Home range and movements of male leopards in the Cedarberg Wilderness Area, Cape Province. *South African Journal of Wildlife Research* 17(2): 41–48. [https://journals.co.za/content/wild/17/2/AJA03794369\\_3497](https://journals.co.za/content/wild/17/2/AJA03794369_3497).
- Odden M, Athreya V, Rattan S, Linnell JD (2014) Adaptable neighbours: Movement patterns of GPS-collared leopards in human dominated landscapes in India. *PLoS ONE* 9(11): e112044-9. <https://doi.org/10.1371/journal.pone.0112044>.
- Odden M, Wegge P (2005) Spacing and activity patterns of leopards *Panthera pardus* in the Royal Bardia National Park, Nepal. *BioOne* 11(2): 145–152. <https://doi.org/10.2981/0909-6396>.
- Périquet S (2014) *Sharing the top: How do spotted hyaenas cope with lions? Apex predator coexistence in a wooded savanna*. PhD, Université Claude Bernard, Lyon 1, Lyon, France.
- du Preez BD (2014) *The impact of intraguild competition with lion Panthera leo on leopard Panthera pardus behavioural ecology*. PhD, University of Oxford, Oxford, UK.
- du Preez B, Hart T, Loveridge AJ, Macdonald DW (2015) Impact of risk on animal behaviour and habitat transition probabilities. *Animal Behaviour* 100(C): 22–37. <https://doi.org/10.1016/j.anbehav.2014.10.025>.
- du Preez BD, Loveridge AJ, Macdonald DW (2014) To bait or not to bait: A comparison of camera-trapping methods for estimating leopard *Panthera pardus* density. *Biological Conservation* 176(C): 153–161. <https://doi.org/10.1016/j.biocon.2014.05.021>.
- R Core Team (2022) R: A language and environment for statistical computing. R Foundation for Statistical Computing.
- Richmond-Coggan L (2019) *National Leopard Census Project*. Unpublished report.
- Rodríguez-Recio M, Burgos T, Krofel M, Lozano J, Moleón M, Virgós E (2022) Estimating global determinants of leopard home range size in a changing world. *Animal Conservation*. <https://doi.org/10.1111/acv.12777>.
- Rouse S, Behnoud P, Hobeali K, Moghadas P, Salahshour Z, Eslahi H *et al.* (2021) Intraspecific interactions in a high-density leopard population. *Ecology and Evolution* 11(23): 16572–16584. <https://doi.org/10.1002/ece3.8227>.
- Snider MH, Athreya VR, Balme GA, Bidner LR, Farhadinia MS, Fattebert J *et al.* (2021) Home range variation in leopards living across the human density gradient. *Journal of Mammalogy* 102(4): 1138–1148. <https://doi.org/10.1093/jmammal/gyab068>.
- Stander PE (2001) *Predator Research Programme Research Progress Report May 2001*. pp. 1–18.
- Stander PE, Haden PJ, Kagece, Ghau (1997) The ecology of asociality in Namibian leopards. *Journal of Zoology* 242: 343–364.
- Stander PE, Hanssen L (2000) *Predator Research Programme Research Progress Report October 2000*. Unpublished report: pp. 19.
- Stein AB (2008) *Ecology and conservation of the leopard (Panthera pardus linnaeus 1758) in northcentral Namibia*. PhD, University of Massachusetts Amherst.
- Stein AB, Athreya V, Gerngross P, Balme GA, Henschel P, Karanth U *et al.* (2016) *Panthera pardus*. <http://www.iucnredlist.org/details/15954/0>.
- Stein AB, Fuller TK, DeStefano S, Marker LL (2011) Leopard population and home range estimates in north-central Namibia. *African Journal of Ecology* 49(3): 383–387. <https://doi.org/10.1111/j.1365-2028.2011.01267.x>.
- Stratford KJ, Stratford SMC (2011) Fine-scale movements and use of space by spotted hyaena (*Crocuta crocuta*) on Ongava Game Reserve, Namibia. *African Journal of Ecology* 49(3): 343–352. <https://doi.org/10.1111/j.1365-2028.2011.01270.x>.
- Sutherland C, Royle JA, Linden DW (2019) oSCR: A spatial capture-recapture R Package for inference about spatial ecological processes. *Ecography*: 42(9): 1459–1469. <https://doi.org/10.1111/ecog.04551>.
- Tarugara A, Clegg BW, Gandiwa E, Muposhi VK (2019) Cost-benefit analysis of increasing sampling effort in a baited-camera trap survey of an African leopard (*Panthera pardus*) population. *Global Ecology and Conservation* 18: e00627. <https://doi.org/10.1016/j.gecco.2019.e00627>.

- Valeix M, Chamaillé-Jammes S, Loveridge AJ, Davidson Z, Hunt JE, Madzikanda H, Macdonald DW (2011) Understanding patch departure rules for large carnivores: lion movements support a patch disturbance hypothesis. *The American Naturalist* 178(2): 269–275. <https://doi.org/10.1086/660824>.
- Voigt CC, Krofel M, Menges V, Wachter B, Melzheimer J (2018) Sex-specific dietary specialization in a terrestrial apex predator, the leopard, revealed by stable isotope analysis. *Journal of Zoology* 306(1): 1–7. <https://doi.org/10.1111/jzo.12566>.
- Worton BJ (1989) Kernel methods for estimating the utilization distribution in home-range studies. *Ecology* 70(1): 164–168. <http://www.esajournals.org/doi/abs/10.2307/1938423>.

*Appendix 1: Trapping effort at each waterhole. Grey shading indicates intensively monitored waterholes.*

Waterhole	Session	Start	Stop	Trapping Days	
Andersson's AND	1	17/09/2013	28/09/2013	11	27
	2	01/10/2014	17/10/2014	16	
Bobbejaan's Pos BOB	1	02/10/2014	18/10/2014	16	16
	1	22/10/2012	01/11/2012	10	
Lodge LOD	2	11/05/2013	17/06/2013	37	69
	3	05/09/2014	11/09/2014	6	
	4	01/10/2014	17/10/2014	16	
Margo MAR	1	10/01/2012	05/11/2012	300	915
	2	24/04/2013	30/12/2014	615	
Onduri OND	1	17/07/2012	01/11/2012	107	566
	2	27/04/2013	28/09/2013	154	
	3	05/03/2014	04/01/2015	305	
Ongarangombe ONG	1	27/09/2012	01/10/2012	4	359
	2	07/05/2013	28/09/2013	144	
	3	20/03/2014	17/10/2014	211	
OTC	1	01/01/2012	01/10/2012	274	405
	2	17/09/2013	25/09/2013	8	
	3	15/06/2014	19/06/2014	4	
	4	21/08/2014	18/12/2014	119	
Rainer's Pos RAI	1	10/01/2012	02/11/2012	297	405
	2	14/05/2013	22/05/2013	8	
	3	17/09/2013	27/09/2013	10	
	4	31/07/2014	18/10/2014	79	
	5	06/12/2014	17/12/2014	11	
Roland's Pos ROL	1	05/01/2012	03/11/2012	303	914
	2	04/05/2013	05/01/2015	611	
Sonop SON	1	27/09/2012	02/11/2012	36	134
	2	08/05/2013	22/05/2013	14	
	3	17/09/2013	27/09/2013	10	
	4	05/08/2014	18/10/2014	74	
Suiderkruis SUI	1	01/01/2012	02/11/2012	306	675
	2	30/04/2013	24/09/2013	147	
	3	10/03/2014	18/10/2014	222	
Tiervlei TIE	1	30/04/2012	31/10/2012	184	798
	2	24/04/2013	29/12/2014	614	
Total				5 283	

**Appendix 2:** Capture histories of individual leopards by waterhole. Grey shading indicates intensively monitored waterholes. Two waterholes (SON and AND) did not yield any leopard pictures. Waterholes are represented by the first three letters of their name; see Figure 1 for their location.

Individual	Sex	BOB	LOD	MAR	OND	ONG	OTC	ROL	RAI	SUI	TIE	Total
L1	Male	-	-	6	-	-	-	2	2	3	-	13
L2	Male	-	-	2	-	-	-	1	-	-	-	3
L3	Male	-	-	-	-	-	-	-	-	-	14	14
L4	Male	-	-	-	-	-	-	-	-	-	1	1
L5	Female	-	-	-	-	-	-	6	-	-	2	8
L6 (collared)	Male	-	1	34	17	4	1	-	6	6	6	75
L8 (collared)	Female	-	-	4	-	-	-	-	-	1	-	5
L10	Female	-	-	4	-	-	-	-	-	2	-	6
L11	Male	-	-	13	-	-	-	-	1	-	-	14
L12	Male	-	-	11	2	-	-	-	-	1	-	14
L13	Male	-	-	4	-	-	-	-	-	-	5	9
L14	Female	-	-	2	-	-	-	-	-	-	-	2
L15	Female	-	-	-	3	-	-	-	-	-	-	3
L16	Male	-	-	-	2	-	-	-	-	-	-	2
L17	Female	-	-	-	11	3	-	-	-	-	-	14
L18	Juvenile	-	-	-	1	-	-	-	-	-	-	1
L19	Female	-	-	-	-	-	-	1	-	-	-	1
L20	Female	-	-	-	-	-	-	-	3	-	-	3
L21	Male	-	-	-	-	-	-	-	1	-	-	1
L22	Female	-	-	-	-	-	-	-	13	12	1	26
L23	Female	-	-	-	-	-	-	-	-	3	-	3
L24	Female	-	-	-	-	-	-	-	-	20	-	20
L25	Male	-	-	-	-	-	-	-	-	1	-	1
L26	Female	-	-	-	-	-	-	-	-	4	-	4
L27	Male	-	-	-	-	-	-	-	-	2	-	2
L28	Male	-	-	-	-	-	-	-	-	3	-	3
L29	Male	-	-	-	-	-	-	-	-	-	3	3
L30	Juvenile	-	-	-	-	-	-	-	-	-	4	4
L31	Male	-	-	-	-	-	-	-	-	-	1	1
Unknown	NA	3	-	72	37	8	-	6	4	23	9	162
TOTAL		3	1	152	73	15	1	16	30	81	46	418