Running Header: Leopard space use

The implications of large home range size in a solitary felid, the Leopard (*Panthera pardus*)

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The size of the home range of a mammal is affected by numerous factors. However, in the normally solitary, but polygynous, Leopard (*Panthera pardus*), home range size and maintenance is complicated by their transitory social grouping behaviour, which is dependent on life history stage and/or reproductive status. In addition, the necessity to avoid competition with conspecifics and other large predators (including humans) also impacts upon home range size. We used movement data from 31 sites across Africa, comprising 147 individuals (67 males and 80 females) to estimate the home range sizes of leopards. We found that leopards with larger home ranges, and in areas with more vegetation, spent longer being active and generally travelled faster, and in straighter lines, than leopards with smaller home ranges. We suggest that a combination of bottom-up (i.e., preferred prey availability), top-down (i.e., competition with conspecifics), and reproductive (i.e., access to mates) factors likely drive the variability in leopard home range sizes across Africa. However, the maintenance of a large home range is energetically expensive for leopards, likely resulting in a complex evolutionary trade-off between the satisfaction of basic requirements and preventing potentially dangerous encounters with conspecifics, other predators, and people.

Key words: Africa, bottom-up, competition, Leopard, *Panthera pardus*, top-down

Teaser text: Bringing all the boys to the yard. Male leopards travel further and faster to find females and to avoid other males. Whereas females are more concerned with food than other leopards. See Fig. 3.

Over the last 50 years, humans have had a greater impact on natural ecosystems than any other time period in human history (Hassan et al. 2005). Large carnivores face anthropogenic threats worldwide—specifically persecution, habitat degradation, and habitat fragmentation (Groom et al. 2014; Ripple et al. 2014). Because large carnivores often occupy high trophic levels, their presence may influence species at lower levels through trophic cascades (Ripple et al. 2014; but see MacNulty et al. 2016). Significantly, large predators provide fundamental ecosystem and economic services that help maintain healthy and diverse ecosystems—thus, in their absence, ecosystem functionality may be at risk (Ripple et al. 2014). Fundamental to our efforts to conserve large carnivores globally is an understanding of their use of space and their movements (Welch et al. 2015). The spatial utilisation of a large predator reflects the interactions between itself and a range of other resources and environmental conditions, such as cover for hunting and concealment, prey distribution and abundance, human influences, the presence of competitors, and access to water (Bailey 1993; Marker and Dickman 2005; Vanak et al. 2013; Snider et al. 2021). In addition, overall behaviour—including movement within home ranges—is also regulated by the sociality of the species in question (Macdonald 1983; Henschel 1986). For example, solitary foragers and pair-living animals may need to maintain a relatively larger home range to encounter potential mates and to acquire food compared to more gregarious species (Macdonald 1983; Klug 2018). Moreover, seasonality—particularly shifts in day length and the amount of nocturnal light available—are also important drivers of space use for some large carnivores (Rafiq et al. 2020). However, the relative importance of these factors is variable and are more important for smaller members of the large carnivore guild (Rafiq et al. 2020).

Leopards (*Panthera pardus*) are solitary felids, and like other felids there may be associations such as a female with her dependent offspring or courting males when mating

(Tilson et al. 1987; Bailey 1993; Macdonald and Loveridge 2010). However, patterns of individual home range overlap in leopards are sufficient to suggest that some form of social congruency exists (Rafiq et al. 2020)—often referred to as a species having individual ‘spatial groups’ (Macdonald and Loveridge 2010)—suggesting a continuum of sociality where the ranges of some cats will be highly congruent and clearly falling within a spatial group, while the ranges of others will be incongruous (Macdonald and Loveridge 2010). For felids like leopards, spatial groups can be characterized by the extent of overlap within and between the home ranges of females and males, adults, and sub-adults alike (Bailey 1993; Macdonald and Loveridge 2010). Within the Felidae more broadly there are species that are truly social (i.e., lions; *Panthera leo*), those that form male coalitions but where females are solitary (i.e., cheetahs; *Acinonyx jubatus*), and those that show extended consortship with more than one female defended against other males (i.e., leopards; Macdonald and Loveridge 2010). Thus, felids are ideal study animals for understanding the importance of sociality and/or social systems on movement and home range use.

Bailey (1993) characterized the spatial organisation of leopards in the Kruger National Park, South Africa by investigating the degree of overlap among adult males, adult females, and transients—there was little overlap between neighbouring home ranges of resident adult males. However, like tigers (*Panthera tigris*) that are also solitary pantherine felids (Tilson et al. 1987), the range of a single adult male usually overlapped with three or four, and occasionally up to six smaller female home ranges (Bailey 1993). Although such monopolization of reproduction appears to influence the space use of leopards and tigers, recent research on pumas (*Puma concolor*) and snow leopards (*Panthera uncia*) suggests that such an ecological driver is not necessarily applicable to all solitary felids (Johansson et al. 2018). Transient (sub-adult or old adult) leopards generally have the largest home ranges (Bailey 1993).

As with most felids, the spatial organisation of female leopards is dictated by food supply and high-quality habitats needed to successfully raise young (Bailey 1993; Mizutani and Jewell 1998; Le Roex et al. 2022). Indeed, 72% of the variability in leopard home range size is explained by the biomass of their preferred prey (Hayward et al. 2009). By contrast, the spatial organization of males is dictated by access to and successful breeding with multiple females, without interference from neighbouring males (Bailey 1993; Mizutani and Jewell 1998; Le Roex et al. 2022). Moreover, male leopards practice infanticide, where an incoming male that takes over the territory of the current dominant male will kill any cubs present to bring the mother into oestrus sooner and replace them with his own offspring (Bailey 1993).

Because large carnivores kill comparatively large prey relative to their metabolic requirements, they generally have large home ranges and low population densities (McNab 1963; Gittleman and Harvey 1982; Macdonald and Loveridge 2010). Such prey requirements likely explain why both male and female leopard home range sizes increase in arid areas where prey are scarcer (Simcharoen et al. 2008) and decrease in the more mesic prey rich habitats (Bailey 1993; Stander et al. 1997; Marker and Dickman 2005; Odden and Wegge 2005; Simcharoen et al. 2008). Other factors that may influence home range sizes and movements therein include competition with conspecifics, intra-guild competition, and whether leopards are persecuted (Marker and Dickman 2005; Fattebert et al. 2016; Comley et al. 2020; Le Roex et al. 2022). For example, previous studies have shown that leopard trophy hunting, and the subsequent removal of individual leopards, can result in the expansion of the home ranges of any remaining leopards and, in some cases, increase overlap of territories (Marker and Dickman 2005; Fattebert et al. 2016).

We explore the means with which leopards, as generally solitary felids, with some social congruency, move within and maintain their home ranges. Specifically, for leopards with large home ranges (relative to other leopards, see below) we asked whether—compared with leopards that have small home ranges—they spend more time being active, travel faster, travel more directionally with intent, or shift home range use over time. Since male leopards have larger home ranges than females, and males also tend to patrol their boundaries, we also included leopard sex in our analysis. Moreover, because prey availability is a key driver of home range size in predators and generally scales with habitat quality, we included a proxy for habitat quality and structure in our analysis. We use the relationship between GPS collar-derived activity, speed, path tortuosity, seasonality (ratio of seasonal:lifetime home range), and log home range area to assess the drivers of home range size in leopards. We predicted that as home range size increases, activity and/or speed will also increase but that these increases will be contingent on path tortuosity, season, and habitat quality.

MATERIALS AND METHODS

Movement datasets.—We used movement data to estimate home range sizes for leopards. Movement data were obtained from 31 sites across Africa (Supplementary Appendix 1). We used data from 147 individuals: 67 males and 80 females. Data were cleaned to remove obviously erroneous data points (e.g., if speeds from one sampling point to another were biologically impossible; see Supplementary Data SD1 for the temporal scales of the datasets).

Home range size.—We estimated home range size using the auto-correlated kernel density estimator (AKDE) (Fleming et al. 2015; Nams et al. 2023) estimated with the R package 'ctmm' (Calabrese, Fleming, and Gurarie 2016), which fits a continuous-time, correlated-velocity movement model to describe the movement data. We used model-selection to fit the best movement model, employing the small-sample size corrected Akaike's Information Criterion (AICc). Models incorporated various combinations of position autocorrelation, velocity correlation, and restricted space use. If model selection showed that velocities and locations were not correlated, then a traditional fixed kernel density estimate (KDE) model was fitted. Home range areas were estimated using the 95% isopleth. Our analysis did not include animals whose home ranges were not stable.

Activity and speed.—We estimated activity and speed at a timescale of 15 minute (the shortest possible from our datasets). To classify active vs inactive 15-minute intervals, we noted that there was a bimodal distribution of log (net distances) travelled in 15 minutes (Supp. Fig. 1). We thus fitted a normal mixture distribution, with the following parameters: m1, m2 = means of the two normal distributions; s1, s2 = standard deviations of the two normal distributions; (1-p2), p2 = the weightings of the two normal distributions. These parameters also estimate the proportion of active vs inactive intervals.

To classify intervals, we used the minimum value of the probability density function of the normal mixture distribution (Supp. Fig. 1). This threshold value depends on the errors of the locations, which depend on the type of transmitters on the animals and the local topography. These values tend to differ among sites, and thus we estimated a different threshold value for each site.

Speed was estimated using the mean distance travelled during active intervals. Thus, speed was speed while the animal was active. The procedure we followed would thus exclude locations when the leopards were invariably inactive such as at rest or feeding on kills (Swanepoel 2008). We could only estimate activity and speed for that subset of datasets with a time between locations of at most 15 minutes.

Tortuosity.—We estimated path tortuosity by the ratio of gross/net distance travelled. This estimation was done at time scales of 15-30 minutes, 1-2 days, 1-2 weeks, and 1-2 months. For example, at the scale of 15-30 minutes, the net distance travelled was the distance travelled in 30 minutes, and the gross distance was the distance travelled in two 15-minute intervals (Supp. Fig. 2). Thus, we estimated path tortuosity following Gillis & Nams (1998): (2 * (Mean step length at a scale of 15 minutes)) /(Mean step length at a scale of 30 minutes). This measure is 1 for a straight line and 1.57 for a completely random walk. Values larger than 1.57 indicate that the animal tends to turn back towards the starting point. Datasets were included in each time scale analysis based on their frequency of data collection. Thus, all 147 datasets were analysed for the 1–2-month time scale, and 51 datasets for the 15–30-minute time scale.

Seasonality.—We measured by the ratio of seasonal/overall home range sizes. We determined both the numbers of seasons and the season start and end dates, as follows. Starting with daily rainfall measurements from 1980-2015, data were smoothed to mean weekly estimates using a Loess smoothing function. Then, for each combination of number of seasons, and season start and end dates, the ratio of rainfall variation among seasons:within seasons (this is analogous to the F-statistic) was estimated. Finally, the optimum number of seasons and season dates were selected by using the maximum rainfall variation ratio. We only used those animals with at least a year of data collection. This period provided a sufficiently long sampling time because even those animals with only one year of data had lifetime home range estimates that were stable.

Habitat.—We measured habitat in two ways: the amount of vegetation and the connectivity of habitat. The amount of vegetation was estimated using satellite imagery from NASA, with data downloaded from ftp.glcf.umd.edu. The Moderate Resolution Imaging Spectroradiometer is a satellite-based sensor used for earth and climate measurements and gathers data in 36 spectral bands. While various indices are then estimated, we used the Landsat Enhanced Vegetation Index (EVI), which is like the more traditionally used Normalized Difference Vegetation Index (NDVI). However, EVI corrects for some atmospheric conditions and canopy background noise and is more sensitive in areas with dense vegetation, and basically measures the amount of greenness. Habitat connectivity was estimated as the proportion of adjacent pairs of pixels with the same habitat. This information was then scaled to remove the dependence on the amounts of each type of habitat.

Relationships to home range size and sex.—We related activity, speed, tortuosity, and seasonality to leopard sex, the log of the home range area, EVI, and habitat connectivity. We carried out a General Linear Model (GLM) analysis, using Akaike weights corrected for small sample sizes (AICc; Johnson and Omland 2004) for models with all combinations of constant, area, and sex. Leopard sex was treated as a categorical variable. The chosen best models were those within five of the minimum AICc values. We then used model averaging to estimate the means and standard errors of each fitted parameter. Each parameter was tested for significant deviation from zero, using a t-statistic = mean/se, and df = *n*-1.

RESULTS

Sex effects.—For each dependent variables tested, all chosen models contained a term for sex and an interaction between sex and area (Table 1). Thus, male and female leopards with large home ranges moved differently than those with smaller ranges. However, the difference between sexes was small compared to the main effect of area (Figs. 1-4). Importantly, the slopes of the male and female relationships differed slightly as compared to the overall slope (Figs. 1-4). Thus, males and females responded in biologically similar ways to changes in home range area. As such, the remainder of our analyses combined the sexes.

Habitat effects.—Habitat connectivity did not have a significant effect on any of the dependent variables. EVI had a significant effect on activity, tortuosity at a scale of 15 minutes, and seasonality. Although EVI is a continuous variable, to display all the information for each variable on one figure, the effect of EVI was displayed by showing models at two levels of EVI: the 25 and 75% quantiles (Figs. 1 and 4).

Activity and speed.—Those leopards with larger home ranges, and in habitats with more vegetation (large EVI values), spent a greater proportion of time being active (Table 1, Fig. 1). In addition, leopards with larger home ranges also travelled faster when they were active (Table 1, Fig. 2).

Since energy used scales linearly with travelling speed (Kram and Taylor 1990), multiplying the increase due to more activity and due to a faster speed will give an increase in energy use. For instance, going from a home range size of 10 to 900 km^2 increases the proportion of time spent traveling from 8 to 18 hours (2.5 x), and the speed from 0.55 to 1.9 km/hr (3.8 x).

Thus, energy use for leopards with larger home ranges while being active would increase by 9.5 x.

Path tortuosity.—There were statistically significant decreases in path tortuosity at the scales of 15 minute, day-to-day, and week-to-week, but not month-to-month (Table 1, Fig. 3). Note that although EVI had a significant effect on tortuosity at the 15-minute scale, the overall change in tortuosity was so small that it was negligible (Fig. 3). The decrease in tortuosity for the day-to-day scale was much larger than the others. This finding suggests that from one day to the next, leopards with larger home ranges generally travelled in straighter lines. The difference was substantial—e.g., at the largest home range sizes paths from one day to the next were almost completely straight.

Seasonality.—If leopards shift home ranges seasonally, then seasonal home ranges would be smaller than lifetime home ranges. If leopards with larger home ranges shift seasonally more than for smaller home ranges, it would be expected that this ratio would decrease with home range size. Leopards in our study significantly shifted their home ranges seasonally (Table 1, Fig. 4). Specifically, seasonal home ranges were on average 0.4 the size of lifetime home ranges. This shift decreased significantly with home range size, and in habitats with less vegetation (small EVI). Thus, leopards with larger home ranges and in areas of less vegetation shifted seasonally less than leopards with small home ranges or in areas of more vegetation.

DISCUSSION

While it is self-evident that leopards with larger home ranges will travel longer distances, it is important to emphasize how this occurs. Our data show that leopards with larger home ranges travel faster, spend more time traveling, and travel in straighter paths from day-to-day. Had the only change been path tortuosity then leopards could conceivably increase their home range size without any increase in energy use. However, since we have shown that leopards also travel faster, and spend more time traveling, it is likely costing them much more to have larger home ranges.

Leopards generally have larger home ranges and travel farther daily in more arid areas, presumably because of lower preferred prey densities (Stander et al. 1997; Hayward et al. 2009; Simcharoen et al. 2008). Similarly, leopards with smaller reported home ranges sizes have smaller daily displacements (i.e., distance moved from one day to the next; Hamilton 1976; Bailey 1993). The primary motivation for leopards to travel is to satisfy their prey requirements, and preferred prey catchability essentially structures the spatial ecology of leopards (Balme, Hunter, and Slotow 2007). This longer-term factor appears to be more important for females than males (Le Roex et al. 2022), ostensibly because males mark their territory boundaries while females mark throughout their territories (Rafiq et al. 2020). Males traverse their ranges to assess the reproductive state of the females within their ranges (Bailey 1993; Mizutani and Jewell 1998) and are unimpacted by competitors and intraguild predators at certain scales (Rafiq et al. 2020). Therefore, in areas with high leopard densities (i.e., greater biomass of preferred prey; Hayward, O’Brien, and Kerley 2007), males may travel shorter distances to access these females. However, for a polygynous species such as the leopard, competition between conspecifics is also a crucial driver of male home range size and maintenance (Le Roex et al. 2022). For example, in the Sabi Sand Game Reserve adjacent to the Kruger National Park, South Africa, high overall male leopard densities drove smaller male home ranges (Le Roex et al. 2022). Because this site has one of the highest recorded leopard densities on the continent, leopards are likely to encounter conspecifics more frequently than at other sites, resulting in intense competition for space (Le

Roex et al. 2022). Such findings underscore the important role played by social factors in leopard home range size and maintenance, even when prey density is high.

Other research in the southern Kruger National Park, which is also known for its high available preferred prey biomass and overall leopard density (Bailey 1993), has shown that leopards have smaller daily displacement distances than leopards in more arid areas (e.g., the Kalahari; Bothma and Le Riche 1984) where prey densities and leopard densities are significantly lower. Thus, leopards in arid habitats are forced to travel further to encounter prey and other leopards (Bailey 1993; Swanepoel 2008). However, Snider et al. (2021) suggested that leopards living in open habitats generally had smaller home ranges when human density was high but were able to expand their home ranges in closed habitats, even when human density was high. The significant effect of EVI (amount of vegetation as a proxy for prey availability) on activity and seasonality supports findings (Snider et al. 2021), further highlighting the complex suite of interacting factors that ultimately shape home range sizes in leopards.

The maximum distance that a leopard can travel is also influenced by other leopards in the area, where encounters with other leopards are generally avoided, thus normally confining travels to within the territory of each animal, except perhaps in the case of transient animals (Bailey 1993; Le Roex et al. 2022). Where encounters do occur, it may be due to incomplete information by the instigator of the interactions (Rafiq et al. 2020). Ranges of males are usually larger, as they patrol territory boundaries, scent-marking and calling, often travelling at speeds of about 2.9 km/hour (Bailey 1993; Rafiq et al. 2020). By contrast, while capable of also travelling large distances daily, females generally tend to move relatively short distances, moving the minimum distance that it takes to obtain prey and rear their young (Mizutani and Jewell 1998; Le Roex et al. 2022). We found that for leopards to maintain a large home range, they likely needed to expend up to approximately 10x more energy than leopards with smaller home ranges. Thus, to balance their foraging and reproductive needs against the potential for agonistic encounters with other leopards it is likely that, dependent on individual site conditions, there may be an energetic threshold beyond which leopards can no longer maintain a large home range. Although work in relation to energetic thresholds has been completed for territorial birds (Myers et al. 1979), we recommend further research in this field for leopards.

Some of the most complex terrestrial carnivore communities are found in African savannas, where morphological, behavioural, and life history adaptations have minimized the cost of inter-specific competition and promoted co-existence through resource partitioning, and spatial and temporal partitioning (Fedriani et al. 2000; Owen-Smith and Mills 2008; Hayward and Slotow 2009; Vanak et al. 2013). Throughout most of the savanna systems in Africa, lions (*P. leo*) and spotted hyaenas (*Crocuta crocuta*) are the largest and often most abundant carnivores (Périquet et al. 2015). Consequently, these two large carnivores can have profound effects on other, normally smaller, carnivores through either exploitative (i.e., indirect negative effects due to shared resources, usually food; Donadio and Buskirk 2006) or interference competition (i.e., direct aggression for resources; Vance 1984; Périquet et al. 2015)). Such effects can include behavioural responses, changes in activity patterns (Hayward and Slotow 2009) or space and habitat use (Vanak et al. 2013), declines in population size through predation or inter-specific killing (Palomares and Caro 1999; Donadio and Buskirk 2006) and, in extreme cases, local extinction (Creel et al. 2001; Fortin et al. 2005; Hayward and Kerley 2008). Our results indicated that although leopards with larger home ranges were active for longer, especially where vegetation was thicker, they also tended to travel faster and in more direct and seemingly straighter lines when active. Such findings may point towards exploitative competition from more dominant lions and spotted hyaenas forcing leopards to be more efficient (i.e., travel faster) when maintaining larger home ranges to reduce agonistic interactions with these larger competitors (Vanak et al. 2013). However, it is more likely that our findings are driven by conspecific density, particularly for males, that need to move across their territory boundaries quickly to deter/avoid conspecifics and maintain access to females or because of anthropogenic impacts. Such rapid movement across and within territories is akin to the streaking behaviour that has been observed in African elephants (*Loxodonta africana*) when they are forced to move through human-dominated corridor areas (Jachowski et al. 2013). In addition, Fattebert et al. (2016) showed that leopard home ranges tended to be larger, and not directly adjacent to one another, when conspecifics had been removed from the population through trophy hunting. Moreover, at some of our sites, particularly those that are more arid, the scarcity of prey may have forced leopards to expand their home ranges (Stander et al. 1997; Hayward et al. 2009).

Approximately half of our study populations (Supplementary Appendix 11) did not have other large carnivores present, especially those sites in Namibia. In addition, like pumas (Johansson et al. 2018), leopards in our study shifted their home ranges seasonally, especially where EVI values were lower, suggesting that factors other than inter-specific competition are driving the maintenance of larger home ranges in leopards. In fact, leopards appear to be generally unaffected by lions at most scales and seem to be able to coexist with them (Balme et al. 2017) by using a variety of cues to avoid interactions (Rafiq et al. 2020). For example, in woodland habitats, leopards hoist their kills into trees to avoid kleptoparasites (Balme et al. 2017), and protect themselves from harm by ascending into trees (Bailey 1993). Thus, it is most likely that nuanced trade-offs between ecological factors are important in shaping the maintenance of large home ranges in leopards.

Prey abundance has long been considered a key, bottom-up driver of home range size in leopards (Bailey 1993), and vital to the co-existence of large carnivores (Périquet et al. 2015; Balme et al. 2017). In highly productive ecosystems where large and medium prey species are abundant, large predators can attain high densities, promoting co-existence (Périquet et al. 2015) and generally have smaller home ranges (Bailey 1993). However, it is also important to consider the influence of site-specific contexts on leopard home range size. For example, the recent work of Le Roex et al. (2022) highlights that in some populations, particularly those that are in highly productive systems, social factors may supersede resource availability for both male and female leopards. The effect of EVI in our study supports such a scenario since, in general, we found that leopards with larger home ranges were also most often in habitats with denser vegetation (i.e., increased prey availability).

Rather than a single factor being important, it is far more likely that the complex interplay among the suite of ecological drivers of home range shape the maintenance of large home range size in leopards. For example, leopards in the Western Cape, South Africa occur at low densities, where they have infrequent contact with conspecifics, and prey availability is low (Martins and Martins 2006). It is possible that that smaller body size of Cape leopards (Martins and Martins 2006) is a manifestation of the greater energetic costs of maintaining a large home range in such a system or because the evolutionary pressure to grow larger is less since agonistic interactions with other leopards is rare. By contrast, in more productive savanna systems, competition amongst conspecifics tends to be more intense (Le Roex et al. 2022) and so a larger body size may be more advantageous but not necessarily result in larger home ranges. By contrast, leopards in the arid Kalahari, where prey and conspecific density are also low (Bothma et al. 1997), tend to be quite large (Bothma and Le Riche 1984) unlike those in the Western Cape. It is possible that although the prey species in the Kalahari are just as widely dispersed as in the Western Cape, the prey that are available is generally larger and allows leopards in the Kalahari to also be larger. However, more research is needed to confirm such a contention.

In conclusion, we have shown that leopards with larger home ranges spent more time being active, generally travelled faster, spent more time travelling, and in straighter lines, than leopards that maintained smaller home ranges—likely expending significant energy in the process. Thus, leopards in areas of lower prey densities not only have to travel further to find prey and other leopards but they also likely expend more energy, and thus need to eat more food than in areas of lower prey densities. We believe that a combination of bottom-up (i.e., preferred prey availability), top-down (i.e., competition with other leopards), and reproductive (i.e., access to mates) factors likely drive the variability in leopard home range sizes across Africa. However, the maintenance of a large home range is energetically expensive for leopards, likely resulting in a complex evolutionary trade-off between the satisfying basic resource requirements and preventing potentially dangerous encounters with other leopards and humans at some sites.

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CONFLICT OF INTEREST

The authors declare they have no conflict of interest.

AUTHOR CONTRIBUTIONS

DMP and VON conceived the idea, VON conducted the analyses. All other authors provided data and provided constructive input into the writing of the manuscript.

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DATA AVAILABILITY

All raw data is available from the corresponding author upon reasonable request.

SUPPLEMENTARY DATA

Supplementary Data are available at *Journal of Mammalogy* online.

Supplementary information.—two additional figures and a detailed appendix of site locations are provided.

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Figure legends

Fig. 1.—Activity vs home range size, for males and females, at high and low EVI values. Each dot represents one individual leopard. Activity was measured at 15-minute intervals. The lines are the lines of best fit and the bands are the 95% confidence bands. For simplicity, confidence bands are only shown for large EVI values—the band widths for small EVI values are similar.

Fig. 2.—Speed while being active, for males and females. Each dot represents one individual leopard. Speed was measured at 15 minute intervals. The lines are the lines of best fit and the bands are the 95% confidence bands.

Fig. 3.—Path tortuosity at various temporal scales, for males and females. Tortuousity is measured by gross distance / net distance. 3A (above graphs) gives an example of tortuosity estimation, at a scale of 15 minutes. Thus, a value of 1 means the path is completely straight. The red angle symbols to the right of the y-axis show the amount of turning corresponding to the tortuousity values on the y-axis. Each dot represents one individual leopard. The lines are the lines of best fit and the bands are the 95% confidence bands. The red dotted line represents a correlated random walk—tortuosity values below this represent travel outwards, and values above this represent returning towards the center.

Fig. 4.—Relative seasonal home range size vs overall home range size, for males and females, at high and low EVI values. Seasonality is measured by the ratio of seasonal/lifetime home range areas—thus, 1 means that the seasonal home range is the same size as the lifetime home range. Each dot represents one individual leopard. The lines are the lines of best fit and the bands are

the 95% confidence bands. For simplicity, confidence bands are only shown for large EVI values —the band widths for small EVI values are similar.

Table 1.—Parameter estimates from GLM model selection for each dependent variable. Models with habitat EVI and connectivity, and all combinations of area and sex and were tested. Only models within five of the minimum AICc value were chosen. Parameter estimates were obtained by averaging among models, using weights based on AICc. "Figure" refers to the figure number showing the relationship. "*P*-value" tests for a non-zero value for the model parameter. Since sex is a categorical variable, model parameters are estimated separately for each type (i.e. males and females).

Dependent Variable	Model Parameter	Figure	Mean	s.e.	*n*	*P*-value
Proportion of Time Active	const (male)	1	0.845	0.161	28	0
	const (female)		0.773	0.186	28	0
	EVI		-2.72	0.586	28	0
	area(male)		0.059	0.0179	28	0.003
	area(female)		0.0554	0.0218	28	0.019
Speed	const (male)	2	2.11	0.0425	98	< 0.001
	const (female)		2.09	0.0537	98	< 0.001
	area (male)		0.00202	0.00696	98	0.77
	area (female)		-0.0247	0.0106	98	0.02
Tortuosity: 15 min	const (male)	3	0.93	0.0548	90	0
	const (female)		0.948	0.0618	90	0
	EVI		1.07	0.182	90	0
	area(male)		-0.00913	0.00651	90	0.17
	area(female)		-0.00812	0.0085	90	0.32
Tortuosity: day-to-day	const (male)	3	1.96	0.0564	185	< 0.001
	const (female)		2.2	0.106	185	< 0.001
	area (male)		-0.0949	0.0106	185	< 0.001
	area (female)		-0.158	0.0172	185	< 0.001
Tortuosity: week-to-week	const (male)	3	2.06	0.0365	174	< 0.001
	const (female)		2.13	0.0497	174	< 0.001
	area (male)		-0.0173	0.00705	174	0.015
	area (female)		-0.0277	0.00841	174	0.001
Tortuosity: month-to-month	const (male)	3	2.11	0.0425	98	< 0.001
	const (female)		2.09	0.0537	98	< 0.001
	area (male)		0.00202	0.00696	98	0.77
	area (female)		-0.0247	0.0106	98	0.02
Seasonality	const (male)	4	0.903	0.119	98	0
	const (female)		0.797	0.14	98	0
	EVI		-0.618	0.182	98	0.001
	area(male)		-0.0647	0.017	98	0

area(female)	-0.0653	0.0203	98	0.002
area(female)	-0.0653	0.0203	98	0.002