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PREDICTIVE REVIEW

Spatial patterns of large African cats: a large-scale study on density, home range size, and home range overlap of lions *Panthera leo* and leopards *Panthera pardus*

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ABSTRACT

1. Spatial patterns of and competition for resources by territorial carnivores are typically explained by two hypotheses: 1) the territorial defence hypothesis and 2) the searching efficiency hypothesis.
2. According to the territorial defence hypothesis, when food resources are abundant, carnivore densities will be high and home ranges small. In addition, carnivores can maximise their necessary energy intake with minimal territorial defence. At medium resource levels, larger ranges will be needed, and it will become more economically beneficial to defend resources against a lower density of competitors. At low resource levels, carnivore densities will be low and home ranges large, but resources will be too scarce to make it beneficial to defend such large territories. Thus, home range overlap will be minimal at intermediate carnivore densities.
3. According to the searching efficiency hypothesis, there is a cost to knowing a home range. Larger areas are harder to learn and easier to forget, so carnivores constantly need to keep their cognitive map updated by regularly revisiting parts of their home ranges. Consequently, when resources are scarce, carnivores require larger home ranges to acquire sufficient food. These larger home ranges lead to more overlap among individuals' ranges, so that overlap

in home ranges is largest when food availability is the lowest. Since conspecific density is low when food availability is low, this hypothesis predicts that overlap is largest when densities are the lowest.

4. We measured home range overlap and used a novel method to compare intraspecific home range overlaps for lions *Panthera leo* (n = 149) and leopards *Panthera pardus* (n = 111) in Africa. We estimated home range sizes from telemetry location data and gathered carnivore density data from the literature.
5. Our results did not support the territorial defence hypothesis for either species. Lion prides increased their home range overlap at conspecific lower densities whereas leopards did not. Lion pride changes in overlap were primarily due to increases in group size at lower densities. By contrast, the unique dispersal strategies of leopards led to reduced overlap at lower densities. However, when human-caused mortality was higher, leopards increased their home range overlap. Although lions and leopards are territorial, their territorial behaviour was less important than the acquisition of food in determining their space use. Such information is crucial for the future conservation of these two iconic African carnivores.

INTRODUCTION

The home range is the area traversed by an individual as it fulfils its typical needs of food gathering, mating, and caring for young (Burt 1943). Home range size, and the amount of overlap between home ranges of neighbouring individuals or groups, varies according to factors such as habitat quality and resource availability (Riley et al. 2003). Understanding the factors that underlie variation in home range size and overlap for large, terrestrial carnivores is important for their conservation and management. For example, understanding spatial patterns can help researchers to identify key habitat types and dispersal corridors (Riley et al. 2003, Kaszta et al. 2020). In addition, for species with larger home ranges that are susceptible to human–carnivore conflict (Woodroffe & Ginsberg 1998), understanding spatial patterns can help us to predict and mitigate conflict.

In the absence of other conspecifics, the area that an animal uses is determined by available resources (Loveridge et al. 2009), suitable habitat (Gese et al. 1988), and the spatial (Geffen et al. 1992) and temporal (Fleming et al. 2014) distribution of the habitat. However, other individuals that use the same resources may limit the quantity and quality of resources and how they are distributed. Therefore, to limit the impact of other individuals, individuals of many species defend parts of their home ranges to exclude competitors – that is, they demonstrate territorial behaviour (Packer et al. 2005). For terrestrial carnivores, territoriality affects the total amount of space used. If space use becomes exclusive (through territory defence), then more resources become available within the home range of the animal, and a smaller area is needed. Thus, space use for terrestrial carnivores is influenced by both the available resources and the extent of their territoriality.

Despite substantial variation in the home range sizes of two of Africa's largest territorial carnivores, lions *Panthera leo* and leopards *Panthera pardus* (Funston et al. 2003, Hayward et al. 2009, Loveridge et al. 2009, Balme et al. 2010, Davidson et al. 2011, Fattebert et al. 2016), it is unclear whether this variation is due to resource use or territory defence.

Lions live in groups of varying sizes, depending on factors such as resource value (Mosser & Packer 2009) and prey dispersion (Valeix et al. 2012). Females live in prides consisting of one or more related adults and their offspring (Packer et al. 1990). Prides are strongly territorial (Funston et al. 1998, Packer et al. 2005) and territory size varies with food supply during the dry season, but not with group size (Mbizah et al. 2019). However, the spatial behaviour of males varies. For example, in the Kruger National Park, South Africa, prides live separately from male coalitions and are territorial, but male and female home ranges overlap (Funston et al. 1998). Contrastingly, in the Serengeti, Tanzania, some males live in female territories while others are nomadic, living singly or as coalitions (Borrego et al. 2018). Female group size is mainly affected by food and internal competition (Packer et al. 1990). Similarly, lion home range overlap shows some plasticity. In Selous Game Reserve, Tanzania, about half of female home ranges are exclusive (Spong 2002). In Hwange

National Park, Zimbabwe, lion density increased after the termination of lion trophy hunting, but home ranges decreased, and home range overlap increased for females but decreased for males (Davidson et al. 2011).

Leopards are also territorial (Fattebert et al. 2016), but their territories are not exclusive (Stander et al. 1997), and some animals are transients (Bailey 1993). Furthermore, females may form matrilinear clusters and tolerate each other (Fattebert et al. 2016). Males and females react differently to changes in food and conspecific density but typically live singly in their own home ranges, with related females normally adjacent to one another (Fattebert et al. 2016). Leopard home range overlap varies throughout Africa, ranging between 25% and 60% for neighbouring males (Jenny 1996, Steyn & Funston 2009), although instances of zero home range overlap have also been recorded (Mizutani & Jewell 1998). Nevertheless, mother–daughter associations appear to have the highest levels of home range overlap (Naude et al. 2020), presumably because of their relatedness. Leopard spatial patterns are also affected by human-induced mortality. For example, after leopard trophy hunting was stopped in Phinda Game Reserve, South Africa, leopard densities increased, home range sizes decreased, and overlap increased for females but not for males (Fattebert et al. 2016).

Two hypotheses that may explain lion and leopard spatial patterns are the territorial defence hypothesis and the search efficiency hypothesis.

Territorial defence hypothesis

Where food resources are abundant, animal densities are high and home ranges are small (Kittle et al. 2015). Animals can maximise energy intake with minimal territorial defence, and, in some cases, competitor density increases so much that territorial defence is impossible (Carpenter & MacMillen 1976). Thus, there is high overlap of home ranges and little sharing of resources (Mcloughlin et al. 2000). At medium resource levels, larger ranges are needed to acquire the necessary resources, and it is energetically more feasible to defend them against a lower density of competitors. Thus, there is minimal overlap of home ranges and the sharing of resources. By contrast, at low resource levels, animal densities are low and home ranges are large, but the resources available are so scarce that is it not beneficial to defend such a large territory. Consequently, there is much overlap of home ranges and sharing of resources.

The territorial defence hypothesis therefore predicts that decreased resource quality will result in larger home range sizes and lower predator densities, and also a ∩-shaped response in territoriality with increasing resource quality, and a U-shaped response in home range overlap with increasing resource quality (Fig. 1a). This hypothesis also predicts a U-shaped relationship between home range overlap and both home range size and predator density. In addition, territorial behaviour affects the statistically defined (e.g. 50% isopleth) core home range size more than searching behaviour. Thus, since variation in resources affects territoriality, the size of the defended core home range should vary more than that of the entire home range (95%). Therefore, the shape of the relationship between overlap and size and density should be different for the entire home range and core areas: specifically, overlaps of the core areas should vary more than overlaps of the home range areas.

Searching efficiency hypothesis

Animals need to know where resources, dangers, and potential mates are within their home ranges (South 1999, Powell & Mitchell 2012), and therefore visit parts of their home ranges regularly to update their cognitive map (Powell & Mitchell 2012). For example, striped skunks *Mephitis mephitis* retain search images from feeding sites and apply those search images when visiting those sites in the future (Nams 1997). When resources are scarce, animals require larger home ranges to acquire sufficient food, which leads to increased overlap between the home ranges of individuals. Thus, the searching efficiency hypothesis predicts a decrease in conspecific density and an increase in home range overlap at low resource levels (Fig. 1b). The hypothesis also predicts an increase in home range overlap with increasing home range size and decreasing density. While the searching efficiency hypothesis does not include territoriality, this does not mean that it only applies to non-territorial animals. Rather, it states that searching efficiency ultimately drives home range size. Consequently, at certain resource levels and/or home range sizes, some species will develop territorial behaviours to defend the available resources. Under this hypothesis, territorial behaviour derives from the space use, rather than determines it. Furthermore, the defended, statistical core home range would vary similarly to the entire home range. Thus, this hypothesis also predicts that the shape of relationship between overlap and size and density is similar for the entire home range and for core areas.

Testing the hypotheses

We test the territory defence and search efficiency hypotheses of space use using a comparative approach with lions and leopards. Although both species are large terrestrial carnivores that live in similar habitats in Africa (Maputla et al. 2015), and feed on similar prey (Hayward & Kerley 2008), they have different social systems – lions

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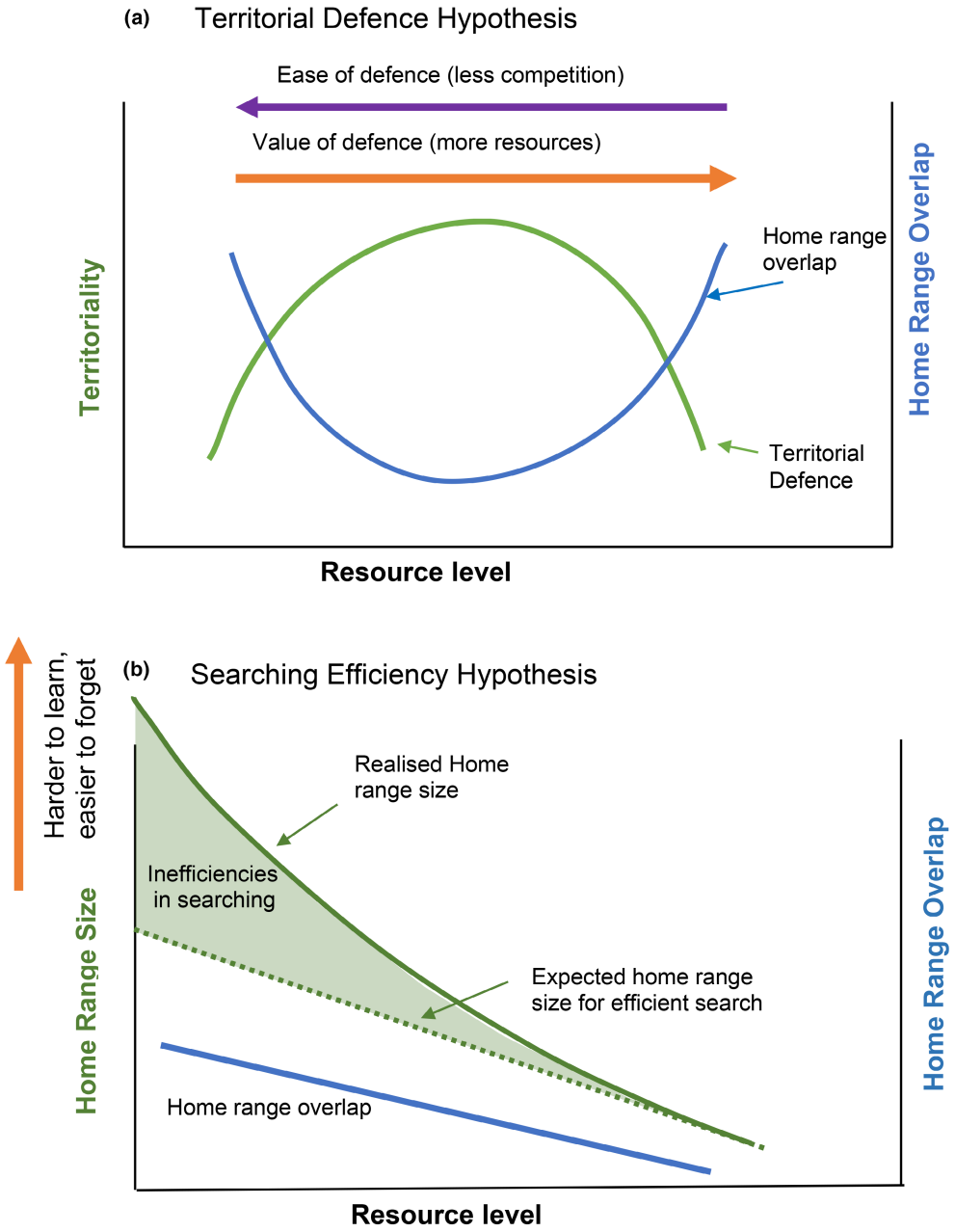

Fig. 1. Idealised diagram of (a) territorial defence and (b) searching efficiency hypotheses.

being social and leopards mostly solitary. Nevertheless, for both species, densities (Hayward et al. 2007) and home range sizes (Hayward et al. 2009) vary with resources. We therefore aimed at comparing home range overlap across a wide variety of densities and home range sizes. We also wanted to investigate the factors that may affect home range overlap, such as group size and nomadicity.

For the territorial defence hypothesis, we predicted that: 1a) there would be a U-shaped relationship between home range overlap, and home range size and conspecific density; and 1b) the shape of the relationship between home range overlap and size and density would be different for the entire home range and for the core home range – specifically, overlaps of core home ranges would vary more than overlaps of entire home ranges.

For the searching efficiency hypothesis, we predicted that: 2a) home range overlap would increase with decreasing conspecific density and increasing home range size; and 2b) the shape of the relationship between overlap and size and density would be similar for the entire home range and for the core home range.

METHODS

Movement datasets

We used telemetry movement data from collared lions and leopards to estimate home range sizes at 45 sites across Africa, with lion data collected from 26 sites and leopard data from 27 sites (Appendix S1). Data were from 149 lions (all female) and 111 leopards (48 males, 63 females). We only used data from female lions because they represent movements of entire prides (Packer et al. 1990, Loveridge et al. 2009), and because the relationship of male coalitions to prides varies among sites (Bouley et al. 2018). The telemetry data for both lions and leopards were collected by the authors during their site-specific research projects (Appendix S1). Sampling areas were designated as separate sites if the movements of the study animals in each area did not overlap.

Home range size

Our datasets varied immensely in terms of the numbers of data points, type of sampling (Global Positioning System and Very High Frequency radio tracking), sampling intervals, location accuracy, temporal variation in sampling intervals, and correlations among locations. Thus, the method of home range size estimation needed to be flexible. We used the autocorrelated kernel density estimator (AKDE; Fleming et al. 2015) using the R package 'ctmm' (Calabrese et al. 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 using the small-sample size corrected Akaike's Information Criterion (AICc; Burnham et al. 2011). The models incorporated various combinations of position autocorrelation, velocity correlation, and restricted space use.

The AKDE is a recent method that results in more accurate home range estimates than previous methods when velocity and locations are correlated (Noonan et al. 2019). Previously, home ranges were estimated using geometric methods such as minimum convex polygons or some variation of a kernel density estimator (Fleming et al. 2015). These methods are dependent on sample sizes, and the kernel density estimator assumes that locations are independent of each other. If locations are not independent, the kernel density estimator underestimates home range size, sometimes severely (Noonan et al. 2019). AKDE minimises these limitations, in that it is insensitive to sample size and considers spatial and velocity correlations among locations. If there are no correlations, then the AKDE converges towards the kernel density estimator. In effect, the AKDE uses movement data while the kernel density estimator uses location data. Consequently, our home range size estimates are larger than those reported in the literature for study sites that have used kernel density estimator for correlated data. Since the AKDE is a newer method that is fundamental to our study, we give an intuitive explanation of it in Appendix S2. However, if our model selection showed that velocities and locations were not correlated, then a fixed kernel density estimate model was fitted. Entire home ranges and core home range areas were estimated using 95% and 50% isopleths.

Nomadicity

We use the term 'nomadic' to describe lions and leopards that do not have stable home ranges. The AKDE estimates variograms, which represent the variability in distance between two locations, as a function of time between these locations (Fleming et al. 2014). If an animal has an established home range, then the variogram has an asymptote. Thus, we used the slope of the variogram over the time-scale of data as a measure of nomadicity. If the slope of the variogram was >0.4 of the home range (selected by visually evaluating a series of variograms), then we designated that animal as nomadic, meaning that either the individual was not monitored for long enough, or was not resident. From this, we estimated the proportion of nomadic animals in each study site.

Densities

Predator density estimates (number of adult individuals km^{-2}) were obtained from various sources, depending on the site (Appendix S3). Most sites had a single density estimate, but some had different estimates for subregions within the site. If so, then for each individual animal, conspecific density within the surrounding area was estimated by the density within an area twice the size of the home range (measured by the minimum convex polygon). Density was then a mean of the subregion densities, weighed by the proportion that each subregion overlapped the polygon. If sites had estimates taken at several times, then conspecific density estimates for each animal were estimated for each year of available location data. If the year of location data fell between the times of density estimates, we used a linear interpolation. If year of location data was outside of the range of time of density estimates, then we used the estimate closest in time. Of the locations that lay within the times that density data were collected, over half were within four months of the density times. Of the locations that lay outside, over half were within three years.

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Overlap

Home range overlaps have been estimated in two ways: the geometric area of overlap (Fieberg & Kochanny 2005, Steyn & Funston 2009, Fattebert et al. 2016), and the relationship between home range size and conspecific density (Fashing & Cords 2000, Efford et al. 2016). It has been shown that geometric overlap is biased, with the bias depending on the amount of overlap, the shapes of home ranges and the proportion of the population being tracked (Fieberg & Kochanny 2005). Thus, we elected to use the relationship between home range size and density (Ov; Fashing & Cords 2000, Efford et al. 2016). If there is no overlap, and there are no spaces between home ranges, then home range size and density are inversely related. If there is some overlap, then home range size is larger than we would expect from the inverse of density. Thus, we can estimate overlap by using a modification of Jetz et al.'s (2004) equation:

$$\mathrm{Ov} = H \times D,$$

where H = home range size; D = density.

This measure of overlap estimates the mean numbers using each home range. Thus, an overlap of 1 means that an individual has exclusive use of its home range and that all space is occupied with non-overlapping home ranges. We denote this estimate of overlap as 'density overlap'. This estimate does not require tracking data from all individuals, only home range size and density estimates (Appendix S4). To compare relationships between species, we estimated the doubling rate, which is the proportional change in overlap for each doubling of home range size.

Group sizes

Group size estimates were obtained from various sources, depending on the site. Lion pride size was not reported consistently, with some sources reporting the numbers of adult females and some the numbers of adults (Appendix S5), and thus, we tested each. Group size estimates were only available on a site basis. Thus, for each site, overlap was estimated using Jetz et al.'s (2004) overlap equation, and then group size was compared with overlap, on a per site basis (Appendix S4). We then statistically removed the effect of group size from our estimate of density overlap, to estimate geometrical overlap (Appendix S4).

Analyses

We fitted a linear and quadratic model between log(density) and log(home range size). Typical parametric models assume that the independent variable has no error, because errors in the independent variable yield biased estimates of the parameters (Draper & Smith 2014). Since our analysis required estimates of these parameters and not just tests for significant relationships, we used the more general total least squares, which allows for error in both dependent and independent variables (van Huffel & Lemmerling 2013). This analysis uses error estimates for each data point. Sampling errors in home range size were estimated from the AKDE algorithm (Fleming et al. 2015). Sampling errors in density were taken from the literature (Appendix S3). However, if error estimates were not available for a site, then we used the overall mean variance for the species. The appropriate models were chosen using significance tests rather than model likelihood, because AICc is not valid for total least squares models.

We also tested whether group size and nomadicity varied with overlap. These analyses were carried out using means for each site, not each individual. This process was done for group size, because the literature estimates of group sizes were only available for entire sites. The process was also carried out for nomadicity because it is a population measure – that is, the proportion of individuals. For each site, we estimated overlap using Jetz et al.'s (2004) overlap equation. For tests of the relationships between group size and nomadicity and overlap, we did not have error estimates for individual data points and thus used the orthogonal regression variant of total least squares (van Huffel & Lemmerling 2013), with bootstrapping to estimate errors.

Table 1. Parameters for total least squares fit of log(density) vs. log(home range size), for 95% and 50% home range size isopleths. The values are as follows: mean ± standard error. Tests for significance were used because AICc is not valid for total least squares analysis. Effect of home range size on overlap is $1 + k_2$

Isopleth	Parameter	Female lions	All leopards
95%	Intercept (k_1)	0.50 ± 0.11	0.59 ± 0.17
	Slope (k_2)	−0.71 ± 0.05**	−1.0 ± 0.092
50%	Intercept (k_1)	0.040 ± 0.08	−0.13 ± 0.12
	Slope (k_2)	−0.72 ± 0.05**	−0.93 ± 0.09

**The slope is significantly different from −1, at $\alpha = 0.01$.

RESULTS

Overlap relationships differed between species and between sexes. Density overlap increased significantly for lions at larger home ranges and lower densities, but there was no significant relationship for leopards (Table 1, Figs 2 and 3). Neither of the species showed significant curvilinearity (lions: $t(148) = 0.01$, $P = 0.99$, leopards: $t(134) = 0.000$, $P = 0.99$). There was no significant difference in the slope between

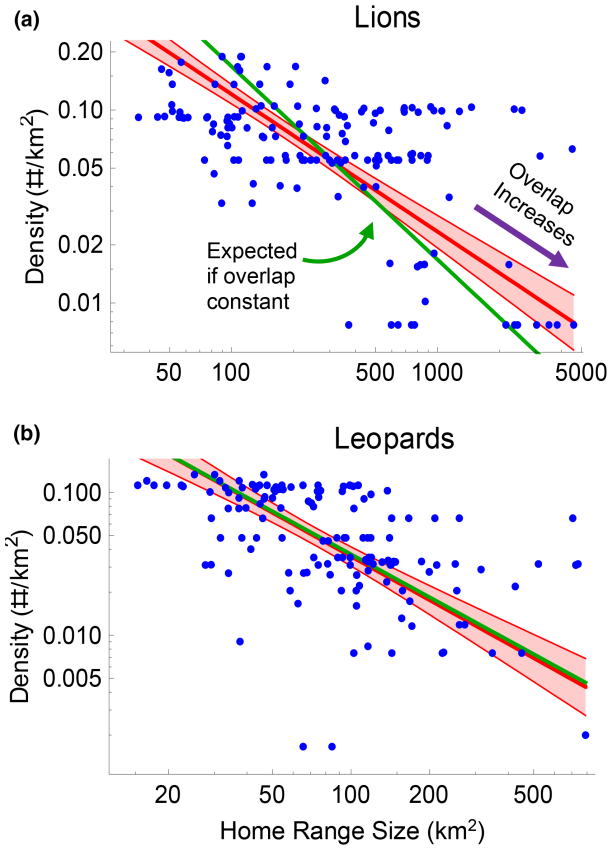

Fig. 2. Density vs. home range size for (a) lions *Panthera leo* and (b) leopards *Panthera pardus*. The wide red band is the 95% confidence band, with the central line being the line of best fit (using total least squares fit). The solitary green line is the expected relationship if overlap is constant. The dots represent individual animals. For lions, overlap increases as home range size increases.

sexes of leopards ($t(75) = 1.07$, $P = 0.28$). Thus, both sexes of leopards showed no significant relationship between overlap with conspecific density and home range size (Table 1).

The partitioning of overlap also differed between species and sexes. The proportion of nomadic individuals showed no significant relationship with overlap for either of the species (lions: $t(17) = 0.34$, $P = 0.73$; leopards: $t(11) = 0.69$, $P = 0.50$). Lion pride size, measured by both the number of adult females ($t(21) = 2.2$, $P = 0.037$) and the number of adults ($t(21) = 2.0$, $P = 0.058$), significantly increased with increasing overlap (Fig. 4).

Doubling rate (proportional change in overlap for each doubling of home range size) for lions was 1.22; for leopards, it was constant at 1.0. To estimate net overlap, the effects of increasing group size were removed, with the lion doubling rate decreasing to 1.12 (Table 2). Lion pride size (numbers of adult females) increased with overlap by a doubling rate of 1.36. Thus, removing the effect of changes in pride size (Appendix S4), and setting the effects of nomadicity to zero, we found that lion net overlap increased with home range size by a doubling rate of 1.12 (Table 2, Fig. 3).

The same analyses were run using home range sizes of 50% isopleths, rather than 95% entire home ranges. All results were like those of 95% isopleths (Table 1, Fig. 3). Thus, overlaps of core home range areas responded in similar ways to changes in size and density, as did overlaps of entire home ranges.

DISCUSSION

Density overlap changed at varying degrees for both species. Since the curvilinear term was not significant for either species, there was no U-shaped response in home range overlap with respect to home range size and conspecific density. Thus, prediction 1a was not supported. Lions showed a significant increase in home range overlap with decreasing density and increasing home range size, whereas leopards showed no change in home range overlap (Fig. 3). Therefore, prediction 2a was supported for lions but not for leopards. Both species showed similar relationships for the 95% and 50% home range sizes (Fig. 3). Therefore, prediction 1b was not supported but 2b was supported for both species. Our results support the searching efficiency hypothesis for lions, but neither hypothesis for leopards.

Our study would not be a valid test of the territorial defence hypothesis if our sites did not include the highest levels of resources. However, we included regions of Africa with the highest reported densities of leopards (Chase Grey et al. 2013, Fattebert et al. 2016) and lions (Bauer et al. 2015), which are therefore likely to have the highest levels of resources found in nature. In addition, some of the sites were small, fenced reserves that sometimes enrich prey to higher levels than found in nature (McEvoy et al. 2022); thus, our study included the highest levels of resources. While it is possible that at our small, fenced sites ($n = 7$) home ranges were physically constrained, they constituted a relatively small proportion of all lion sites.

The overall patterns in lion overlap could be construed as a result of, within one region, large home ranges overlapping more than small home ranges. However, our results do not compare individuals within study sites. Our results compare among sites, showing that at smaller home ranges and higher densities, individuals' home ranges have less overlap than at larger home ranges and lower densities.

Sampling issues

It is important to examine how methodological issues may have affected our results. There is much heterogeneity among our sites, both in natural conditions and in sampling

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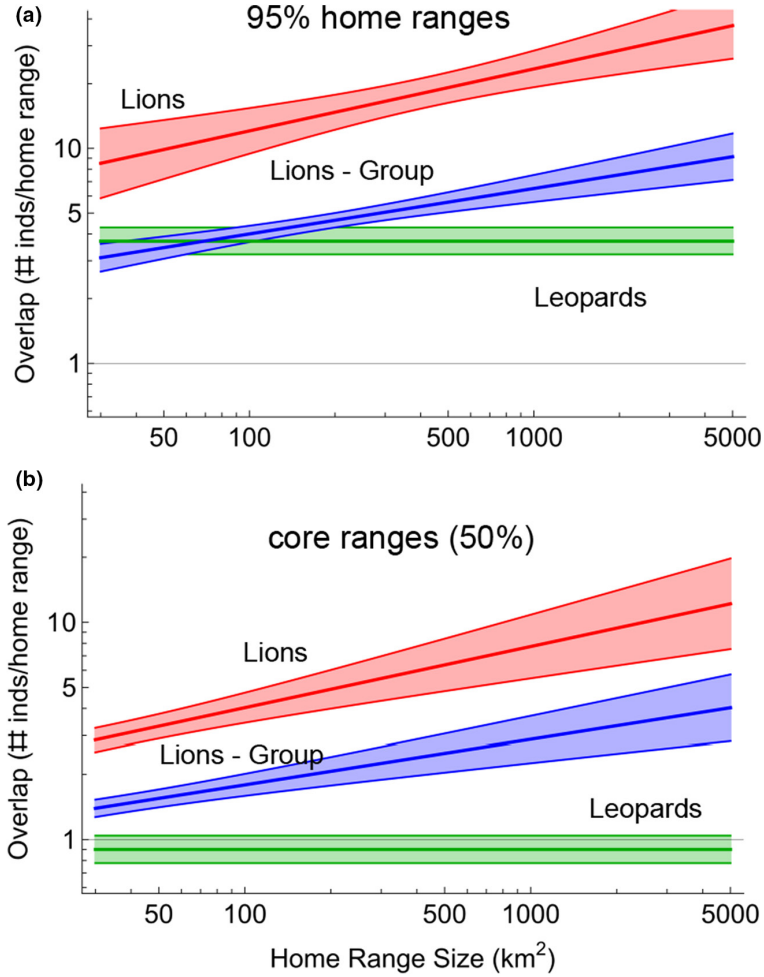

Fig. 3. Overlap vs. home range size for (a) lions *Panthera leo* and (b) leopards *Panthera pardus*, for 95% and 50% home range isopleths. 'Lions-Group' represents overlap with the effects of lion group size removed. The bands are the 95% confidence bands. The horizontal line at 1.0 represents a baseline of one individual per home range.

methods. The effects of heterogeneous sampling were minimised by our use of AKDE to estimate home range size. Unlike other techniques, AKDE is insensitive to sample sizes, sampling frequencies, precision of locations, and correlations among locations (Fleming et al. 2015, 2019, Noonan et al. 2019). Thus, accuracies of home range sizes were not affected by the different types of field protocols and types of collars among study sites. In fact, the natural heterogeneity among study sites is a strength of our study. Our hypotheses about spatial patterns are general ones and should therefore be tested in sites that vary in densities, resources, and habitats, like the sites we included. In other words, we asked whether the effects were larger than background variation. In addition, the heterogeneity makes our analyses more conservative, giving more confidence in the significant results.

Our method to estimate overlap is also a strength. Unlike the method of geometric overlap, accuracy of density overlap is not affected by the number of individuals at each site. Precision is affected by the number of individuals, but that effect is minimised by the large numbers of sites. Our study also avoids the difficulties encountered in other studies of these hypotheses (Mcloughlin et al. 2000, López-Bao et al. 2014), either because the correct resources were not measured, or because the resource range was not wide enough. We avoided these difficulties in two ways. First, we did not measure a specific resource, but compared overlap for different levels of conspecific density. Second, we used data from sites across Africa, covering the entire range of resources available for these two terrestrial carnivores.

Partitioning overall overlap

Lion home range overlap increases with home range size, with a doubling rate of 1.22. The three components of density overlap are nomadicity, group size, and net overlap. However, changes in nomadicity are a minor component

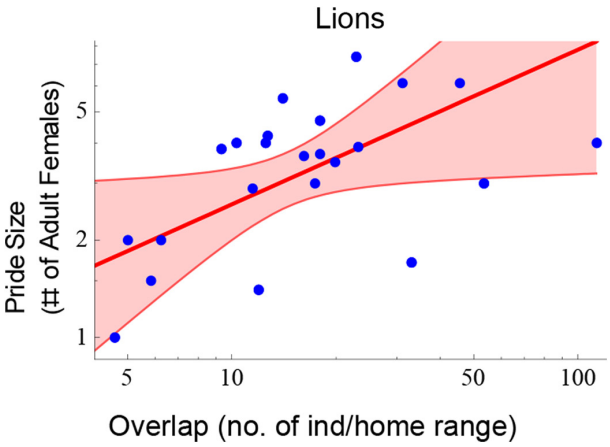

Fig. 4. Pride size vs. home range overlap for lions *Panthera leo*. The thick line is the line of best fit (averaging, via AICc, the constant and linear models), and the band is the 95% confidence band. Each dot represents mean values for one site. Pride size increases as overlap increases.

Table 2. Effect of home range size on gross and net overlaps, and effect of gross overlap on group size. Slope measures the rate of change in linear log regressions. The mean slopes are shown ± the standard errors. Doubling rate is the amount of change in the dependent variable when the independent variable doubles

Variable	Isopleth	Statistics	Female lions	All leopards
Gross Overlap[1]	95%	Slope	0.29 ± 0.05**	0 ± 0.092
		Doubling	1.22	1.00
	50%	Slope	0.28 ± 0.05**	0.07 ± 0.091
		Doubling	1.21	1.00
Group Size[3]		Slope	0.48 ± 0.21[2,*]	–
		Doubling	1.39	
Net Overlap[4]	95%	Slope	0.15 ± 0.09	–
		Doubling	1.11	1.00
	50%	Slope	0.14 ± 0.09	–
		Doubling	1.10	1.00

[1]Log(Gross Overlap) vs. log(Home Range Size).
[2]For lions, this refers # of adult females in prides.
[3]Log(Group Size) vs. log(Gross Overlap).
[4]Log(Net Overlap) vs. log(Home Range Size).
*Mean significantly different from 0, at α = 0.05.
**Mean significantly different from 0 at α = 0.01.

of density overlap. Non-territorial adult lions are primarily males in coalitions. However, their behaviour differs among regions. Only two studies have measured the proportion of nomadic individuals. In the Serengeti, coalitions of non-territorial males form into nomadic coalitions. Being nomadic, they travel widely and thus the proportion of non-territorial individuals varies from year to year, with an overall mean average of 0.165 (Borrego et al. 2018). In Kruger National Park, non-territorial male coalitions do not become nomadic, but remain close to their natal territories. They do not travel widely and thus the proportion of non-territorial individuals varies very little from year to year, with an overall mean of 0.152 (Funston et al. 2003). Using our data, we can estimate density overlap in these two sites using home ranges and densities (see 'Results' and Appendices S1–S4). In the Serengeti, mean home range size is 455 km^2, lion density is 0.100 ind km^{-2}, with a resulting density overlap of 45.5 ind/home range, and pride size is 6.2 adult females. In Kruger National Park, mean home range size is 129 km^2, density is 0.0911 ind km^{-2}, with a resulting density overlap of 12 ind/home range, and pride size is 4.0 adult females. The difference in density overlap from Kruger to Serengeti is large (3.8×), yet the difference in density of nomadic animals is small (1.1×). This difference suggests that most of the density overlap increase over the range of home range sizes is due to a change in net density overlap, not due to changes in nomadicity.

Leopards do not show a significant increase in density overlap with changes in home range size. The precision of density overlap estimates was similar between species (see the confidence bands in Fig. 3). Thus, density overlap for leopards is constant, compared to that in lions. Nomadicity does not change significantly with overlap. Thus, group size and net density overlap are either constant, or both vary. Leopards are usually solitary (Bailey 1993), but females may occasionally be accompanied by their dependent young (Fattebert et al. 2015). Thus, overall group size (irrespective of sex) shows little variation from low to high home range sizes. Therefore, we can conclude that density overlap is also constant, and that group size, net density overlap, and nomadicity are constant with respect to home range size and leopard density.

Responses to resources

Each species responds to changes in conspecific density and resources in a different way, but both reduce their home range size with increasing resources (Hayward et al. 2009). Lions adjust to resource scarcity by increasing group size and home range overlap (Loveridge et al. 2009). About half of the change in overlap was due to changes in pride sizes (Loveridge et al. 2009). Larger prides often break into smaller hunting groups that can cover more area, while smaller prides are forced to travel as one group in defence of attack by neighbouring prides (Packer et al. 1990). Thus, larger prides can defend larger territories and potentially search for food more efficiently. However, larger lion prides are capable of capturing larger prey, effectively increasingly prey availability in some systems (Loveridge et al. 2006). Nevertheless, this finding is the opposite of the territorial defence hypothesis, which predicts that at lower

resource levels territorial behaviour becomes too costly. Territorial defence drives wolf *Canis lupus* space use in North America, where, unlike lions, wolves adjust their territory size and not their group size in response to changes in resource quality (Kittle et al. 2015). It may be that the unique social structure of lions, where males are frequently not resident with female prides and practice infanticide, forces females to form larger prides to protect their cubs and not necessarily to search for food (McEvoy et al. 2022).

Leopards do not change overlap with changes in conspecific density or home range size. Density overlap is 3.5, meaning that 3.5 individuals use each home range, and this is constant throughout the range of densities and home range sizes. The home range of one male leopard typically overlaps with the home ranges of two to five females (Balme & Hunter 2013, Fattebert et al. 2016).

We suggest that the constant overlap for leopards occurs for two reasons. First, both dispersal strategies and human hunting would affect overlap, but in different directions. Dispersal strategies lead to smaller overlaps at low densities, and dispersal strategies differ between males and females. Male dispersal is driven mostly by mate competition (Fattebert et al. 2015, Naude et al. 2020), and thus young males tend to emigrate. Female dispersal is affected mostly by philopatry, where, in favourable conditions, the benefit of daughters staying outweighs the cost to the mothers (i.e. the resident fitness hypothesis; Naude et al. 2020). For example, at high densities, mean overlap between all individuals (both sexes) was between 18% and 20%, but within kin-groups it was as high as 60% (Naude et al. 2020). Thus, at high densities we would expect higher overlap among females than at low densities. By contrast, human-caused mortality leads to higher overlaps at low densities. While leopards are sometimes viewed as being adaptable and resilient, their world-wide range loss of ~70% is greater than the loss for the world's other large carnivores (Jacobson et al. 2016). Leopards are declining for three reasons: loss of prey, loss of habitat, and mortalities from humans (Jacobson et al. 2016). Leopards are heavily persecuted in farmland areas, with retaliatory killing having an even greater effect on numbers than sport hunting (Swanepoel et al. 2015). Even protected areas do not completely protect leopards – hunting outside of protected areas decreases leopard numbers in protected areas, even when there is enough prey (Balme et al. 2010). In areas where leopards are heavily persecuted, home ranges are larger and more unstable, resulting in less territoriality and more overlap (Fattebert et al. 2016). Such a response to human-induced mortality has also been reported for cougars *Puma concolor* (Maletzke et al. 2014). Thus, those leopard populations exposed to high persecution should show lower density and larger overlaps than those in areas with low pressure.

Second, leopards search more efficiently than lions. Leopards are more generalised predators (Hayward & Kerley 2008) and have a smaller range of home range sizes than lions (a maximum size of 800 km^2, as compared to 4800 km^2 for lions). At low resource levels, leopards may not have to increase search areas as much as lions, leading to smaller home range sizes than lions. Perhaps at even lower resource levels than observed in nature, overlap might increase. Lions show a consistent change in overlap, not just at the extremes – a reanalysis of our lion overlap relationships but using the same narrow breadth of ranges of home range sizes as evident for leopards, did not change the results (details not shown).

CONCLUSION

Being top predators means that lions and leopards can play important roles in the structuring of ecosystems, and in the survival of other species (Ripple & Beschta 2004). However, top predators are also among the most vulnerable components of biodiversity in any system. Although both lions and leopards are territorial, their territorial behaviour does not appear to drive the scale of space use in our study. For lions, space use appeared to be driven by variations in search efficiency, governed by different aspects of their social behaviour. By contrast, for leopards, space use seemed to be driven by dispersal strategies, external mortality, and their flexible predatory behaviour. Thus, even though lions and leopards live in similar habitats, often together, and feed on similar prey items, their social structures appear to determine how they respond to variations in resource abundance. Our findings are significant, because understanding the space use of large carnivores is crucial for their future conservation (Johansson et al. 2016). Although numerous site-specific assessments of these two species have been conducted, our study is one of the first to bring together data from multiple sites throughout the African continent, to begin to understand the drivers behind the use of space in these important terrestrial carnivores.

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at the publisher's website.

Appendix S1. Site information.
Appendix S2. Intuitive explanation of the autocorrelated kernel density estimator.
Appendix S3. Sources of density data.
Appendix S4. Mathematical modifications of Jetz et al.'s (2014) overlap equation.
Appendix S5. Lion pride size data.