

APPENDIX S1. SITE INFORMATION. FOR EACH SITE, THE NUMBERS OF INDIVIDUALS OF EACH SEX, AND THE DATES OF THEIR LOCATION DATA.

Country	Site	Lions			Leopards			Location	
		Males	Females	Dates	Males	Females	Dates	°Latitude	°Longitude
Botswana	Kgalagadi 3		17	1996- 2001, 2013- 2015	-	-	-	-25.6624	20.8674
Botswana	Kgalagadi Southern					1	2008- 2009	-24.7389	23.342
Botswana	Okavango Delta	4	8	2007- 2011	4	2	2007- 2010	-19.4808	23.6174
Botswana	Tuli	-	-	-		3	2005- 2007	-22.0922	29.0539
Cameroon	Benoue	-	-	2006- 2009	-	-	-	8.17415	13.8196
Cameroon	Waza	1	1	2007- 2009	-	-	-	11.2577	14.7062
IvoryCoast		-	-	-	1	1	1993- 1994	5.85627	-7.33509
Kenya	Amboseli	3	7	2007- 2013				-2.66842	37.2268
Kenya	Laikipia	22	23	1998- 2015		3	2014- 2015	0.422264	36.8547
Kenya	Rift Valley		4	2008- 2011	-	-	-	-1.90696	36.0869
Kenya	Tsavo	2	1	2002- 2002, 2005- 2007	-	-	-	-3.81381	38.8973
Mozambique	Niassa	5	-	2005- 2015	1		2008- 2009	-12.1845	38.0784
Namibia	Site #4	-	-	-	5	10	2008- 2017	-22.7233	16.9544

Namibia	Site #5	-	-	-	1	6	1996-1998, 2014-2016	-20.6791	17.1118
Namibia	Site #6	-	-	-	1	1	2013-2014	-19.3361	15.8401
Namibia	Site #7	-	-	-	8	5	2012-2017	-22.5257	18.0051
South Africa	Addo	7	5	2003-2015	1	-	2004-2005	-33.4856	25.762
South Africa	Blue Canyon		2	2010-2013	1		2009-2011	-24.4533	30.9818
South Africa	Cederberg 1	-	-	-	2	3	2006-2014	-32.4014	19.3249
South Africa	Cederberg 2	-	-	-	4	1	2005-2014	-32.4807	19.1596
South Africa	Gouritz	-	-	-	2		2010-2012	-33.6535	21.583
South Africa	Karongwe		1	2000-2005	3	8	2001-2005	-24.2168	30.5875
South Africa	Karoo	1	1	2014-2015	-	-	-	-32.2926	22.4063
South Africa	Kruger National Park 1	-	6	2010-2013	1	1	2011-2012	-25.1523	31.4512
South Africa	Kruger National Park 2	-	3	2010-2013	-	1	2012-2013	-25.2199	31.8887
South Africa	Kruger National Park 3	2	5	2009-2014	-	-	2011-2011	-24.4659	31.365
South Africa	Kruger National Park 4	4	5	2005-2011	-	-	2008-2009, 2012-2013	-24.3337	31.8048
South Africa	Kruger National Park 5	-	1	2011-2012	-	-	-	-24.0141	31.3108
South Africa	Kruger National Park 6	-	2	2010-2012	-	-	-	-23.58	31.3715

South Africa	Kruger National Park 7	-	7	2010-2013	-	-	-	-22.955	31.1345
South Africa	Kwandwe	2	1	2003-2003	-	-	-	-33.1421	26.532
South Africa	Mkhuze	-	-		3	4	2005-2009	-27.6742	32.2492
South Africa	Mountain Zebra National Park	2		2013-2015	-	-	-	-32.1856	25.446
South Africa	NW Province 1	-	-	-		1	2015-2015	-25.672	26.3568
South Africa	NW Province 2	-	-	-		1	2015-2015	-25.8381	27.4776
South Africa	NW Province 3	-	-	-		1	2014-2015	-25.2079	27.61
South Africa	Phinda	1	2	1993-1996	11	11	2002-2012	-27.7969	32.3423
South Africa	Shamwari		13	2001-2007	2	2	2003-2008	-33.446	26.0862
South Africa	Waterberg	-	-	-	1	2	2004-2007	-23.9818	28.2942
South Africa	Welgevonden	-	-	-		2	2010-2016	-24.3095	27.8325
Tanzania	Selous	-	5	1996-1999	-	-	-	-7.6581	38.0707
Tanzania	Serengeti	-	26	1984-1990	-	-	-	-2.58911	34.9403
Zimbabwe	Bubye Valley Conservancy	5	3	2010-2013	6	5	2010-2013	-21.6869	30.0492
Zimbabwe	Mangwe	-	-	-		1	2010-2010	-20.8744	28.0599
Zimbabwe	Shangani	-	-	-	1	1	2014-2015	-19.6175	29.2602

APPENDIX S2. INTUITIVE EXPLANATION OF THE AUTOCORRELATED KERNEL DENSITY ESTIMATOR.

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). Traditionally, home ranges have been estimated using geometric methods such as minimum convex polygons or some variation of a KDE (Fleming et al., 2015). These methods are dependent on sample sizes, and the KDE assumes that locations are independent of each other. If locations are not independent, the KDE underestimates home range size, sometimes severely (Noonan et al., 2019). AKDE minimizes these limitations in that it is insensitive to sample size and considers spatial and velocity correlations among locations. Thus, if there are no correlations, then the AKDE converges towards the traditional KDE. In effect, the AKDE uses movement data while the KDE uses location data. Consequently, our home range size estimates are larger than those reported in the literature for study sites that have used KDE for correlated data. Since the AKDE is a newer method 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 traditional fixed kernel density estimate (KDE) model was fitted. Home range and core areas were estimated using 95% and 50% isopleths.

The commonly-used kernel density estimator (KDE) assumes that all locations are independent of each other – i.e. that there is no relationship from one location to the next. The autocorrelated kernel density (AKDE) that we used allows for correlations among locations, and uses that information to estimate home range size.

Fig 1 shows a couple of examples. It is clear that LPF4 has lower correlations among locations than L17. Thus, for LPF4 the ADKE produces a similar home range size estimate as does KDE. However, for L17, AKDE estimates a much large home range size than KDE. The following explains this. The plot in Fig 2A is the movement track of L17. The plot in Fig 2B shows the same points, but in random order. Since the KDE assumes that all locations are independent, it effectively sees the data (wrongly) as in the right plot – i.e. that the animal can go from any one point to any other in one time step.

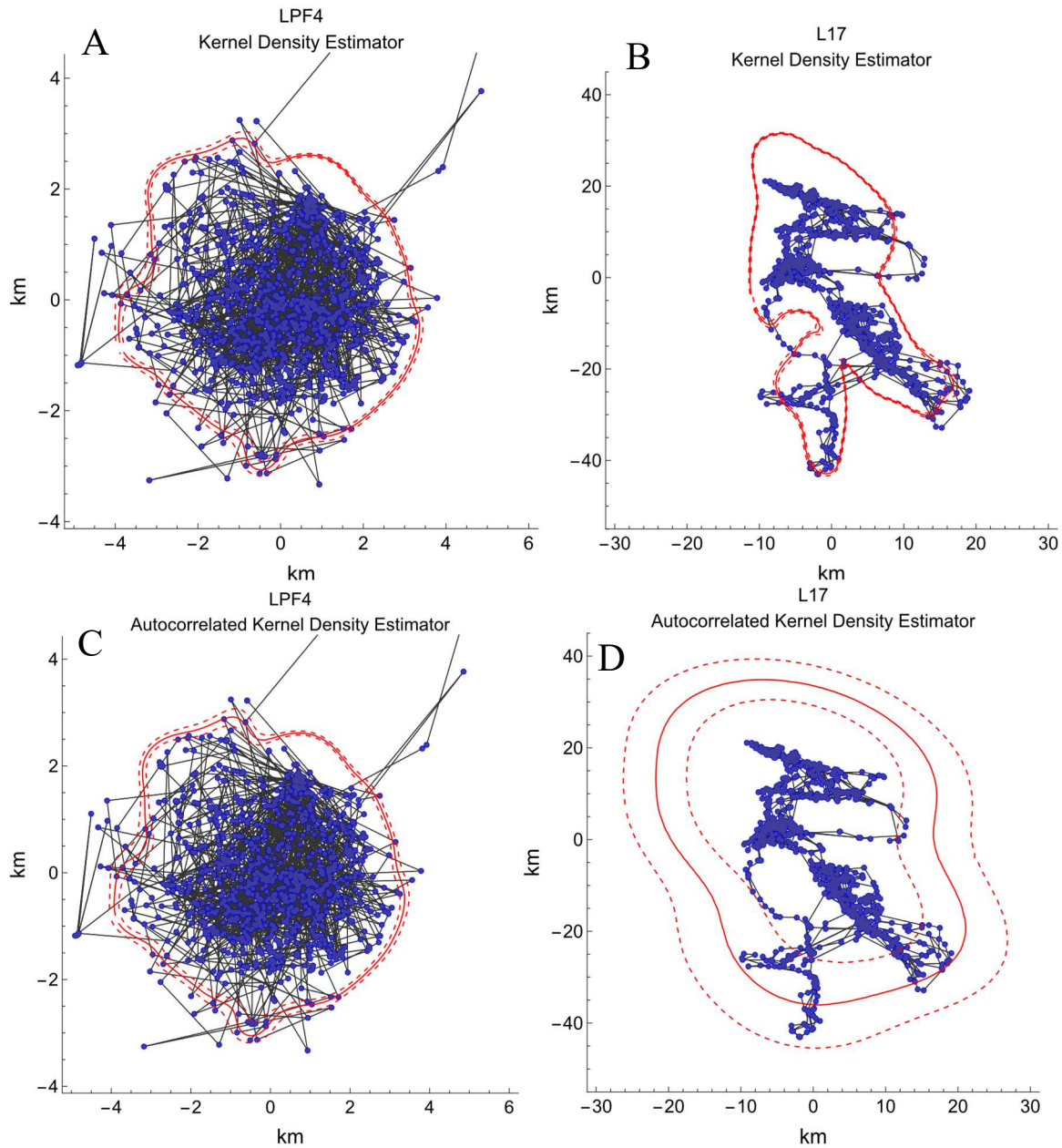


Figure 1 shows two leopard datasets from Cederberg, South Africa (left) and Namibia (right). The top are the KDE and the bottom are the AKDE home range estimates. The left is female LPF4, and the right is male (L17). The solid lines are the 95% home range, and the dashed lines are confidence intervals for that home range. Table 1 gives the statistics.

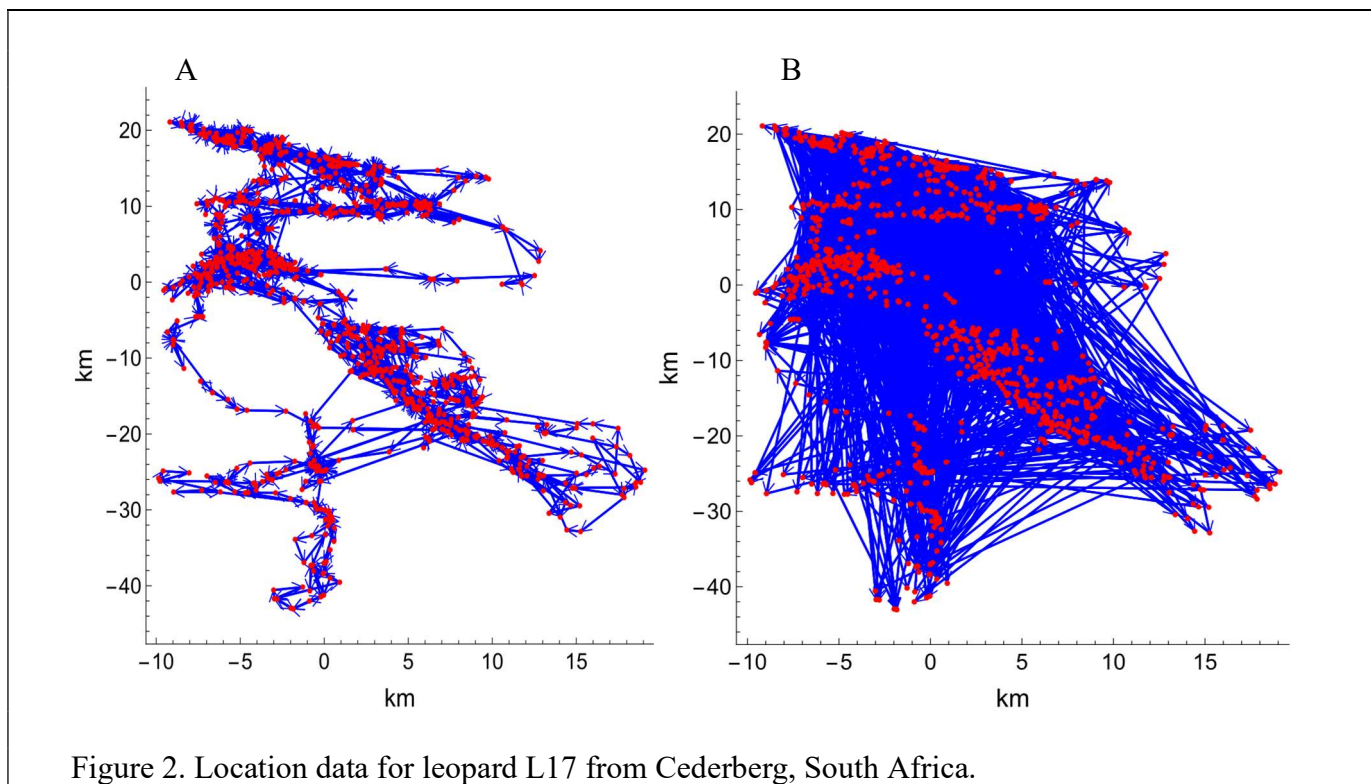


Figure 2. Location data for leopard L17 from Cederberg, South Africa.

The plot in Figure 2B gives you more confidence that the whole home range is sampled than the one in Figure 2A. In Figure 2A, the animal has visited many parts of its home range only once, so you have little confidence in the boundaries of the home range. The KDE thus, inappropriately, estimates a small and precise home range. Likely, if you tracked the animal for several more years, it would go outside of the area it covered in the last year.

The AKDE takes into account the correlations among locations and thus estimates both a larger home range but also gives wider confidence intervals for that estimate (Table 1). However, for leopard LPF4 (Figure 1A, C), the original movement pattern already shows that most of the home range is visited many times. Thus, you have more confidence in the boundaries, and the KDE results are the same as the AKDE.

We can also think about this in terms of the numbers of locations. Since locations are correlated with each other, we can calculate the effective sample size – this is how many locations the dataset would contain if all locations were independent (which is what KDE assumes; Table 1). For LPF4, the effective sample size is 397, which is still quite large. But for L17 the effective sample size is only 11! That means that KDE thinks there are 1785 independent locations, but there are actually only 11.

Table 1. Home range analyses results for two leopards, using different analysis procedures.

	Home Range Area (km ²)		# of locations	Effective Sample Size
	mean (95% confidence intervals)			
	KDE	AKDE		
LPF4	30 (28, 32)	30 (28, 32)	1172	397
L17	1082 (1032,1133)	2240 (1343, 3361)	1785	11

These two estimators have been compared in the following paper, using many real datasets and simulated ones. The study shows that the kernel estimator underestimates home range area when locations are correlated.

Noonan, Michael J., Marlee A. Tucker, Christen H. Fleming, Thomas S. Akre, Susan C. Alberts, Abdullahi H. Ali, Jeanne Altmann, et al. "A Comprehensive Analysis of Autocorrelation and Bias in Home Range Estimation." *Ecological Monographs* 89, no. 2 (May 1, 2019).

<https://doi.org/10.1002/ecm.1344>.

APPENDIX S3. SOURCES OF DENSITY DATA.

Country	Site	Source
Botswana	Ghanzi, Kgalagadi, Kweneng	Lions: (Beukes, 2016; Beukes et al., 2017; Boast & Houser, 2012; Funston et al., 2010; Mills, 2015; Winterbach & Maude, 2015) Leopards: (Mills, 2015)
Botswana	Okavango Delta	Leopards: (ODMP, 2006) Lions: (Cozzi et al., 2013)
Botswana	Tuli	Leopards: (Steyn, 2008)
Cameroon	Benoue	Both: (Croes et al., 2011)
Cameroon	Waza	Lions: (Bauer et al., 2008; Tumenta, 2015)
IvoryCoast		Leopards: (Jenny, 1996)
Kenya	Amboseli	Lions: (Huqa, 2015)
Kenya	Laikipia	Lions, Leopards: (T. G. O'Brien & Kinnaird, 2011)
Kenya	Rift Valley	Lions: (Schuette, Wagner, et al., 2013)
Kenya	Tsavo	Lions: (Patterson et al., 2004)
Mozambique	Niassa	Lions: (Begg & Begg, 2012) Leopards: (Jorge, 2012)
Namibia	All sites	Leopards: (Hanssen & Stander, 2004; Richmond-Coggan, 2019; Stander & Hanssen, 2012; Stein et al., 2011)
South Africa	Addo	Both: (Hayward et al., 2007) and South African National Parks aerial census data.
South Africa	Blue Canyon	Lions: Blue Canyon census data (T. Parker, unpublished) Leopards: (Bissett et al., 2011)
South Africa	Cederberg Sites	Leopards: (Martins, 2010)
South Africa	Gouritz	Leopards: (Mann, 2014)
South Africa	Karongwe	Both: (Vanak et al., 2013)
South Africa	Karoo	Lions: South African National Parks census data
South Africa	Kruger National Park Sites	Lions: (Ferreira & Funston, 2010) Leopards: (Maputla et al., 2013)
South Africa	Kwandwe	Both: (Bissett, 2008)
South Africa	Mkhuze	Leopards: (Fattebert et al., 2015)
South Africa	Mountain Zebra National Park	Both: South African National Parks census data
South Africa	NWProvince sites	Leopards: (Power & Venter, 2020)
South Africa	Phinda	Lions: (Hunter et al., 2007) Leopards: (Fattebert et al., 2015)

South Africa	Shamwari	Both: (J. O'Brien, 2012)
South Africa	Waterberg	Leopards: (Swanepoel et al., 2015)
South Africa	Welgevonden	Leopards: (Swanepoel et al., 2015)
Tanzania	Selous	Lions: (Spong, 2002)
Tanzania	Serengeti	Both: (Swanson et al., 2014)
Zimbabwe	Bubye Valley Conservancy	Both: BVC census data (B du Preez, unpublished data)
Zimbabwe	Mangwe	Leopards: (Grant, 2012)
Zimbabwe	Shangani	Leopards: (Nyoni, 2015)

APPENDIX S4: MATHEMATICAL MODIFICATIONS OF JETZ ET AL.'S (2014) OVERLAP EQUATION.

We elected to use the relationship between home range size and density (Ov) (Damuth, 1981; Efford et al., 2016; Fashing & Cords, 2000). 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 (Jetz et al., 2004) equation:

$$Ov = H \times D, \quad (1)$$

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 will call this estimate "density overlap". This estimate does not require tracking data from all individuals only home range size and density estimates.

Although we can estimate overlap in this way, we cannot use this directly to investigate the relationship between overlap, and home range size and density, because the dependent variable (density overlap) is calculated from the two independent variables. Thus, we used a modified version of this relationship, as follows. Many species show a linear relationship between $\log(D)$ and $\log(H)$ (Efford et al., 2016; Jetz et al., 2004), as follows:

$$\log(D) = k_1 + k_2 \log(H), \quad (2)$$

where k_1, k_2 are fitted parameters. Combining equations (1) and (2) we get that

$$\log(Ov) = k_1 + (1+k_2) \log(H). \quad (3)$$

Overlap varies monotonically with home range size if $(1+k_2) \neq 0$ (i.e., the slope between $\log(D)$ and $\log(H) \neq -1$), and the effect of home range size on density overlap is given by $(1+k_2)$. Thus we use equation (3) to test for a monotonic relationship between overlap and home range size.

To test for a \cap -shaped relationship, we fit the parabolic equation:

$$\log(D) = k_1 + k_2 \log(H) + k_3 \log(H)^2, \quad (4)$$

where k_3 is a fitted parameter that measures curvilinearity. Combining equations (1) and (4) we get that

$$\log(Ov) = k_1 + (1+k_2) \log(H) + k_3 \log(H)^2. \quad (5)$$

If k_3 is significantly positive, then the minimum value of $\log(Ov)$ will occur at,

$$\log(H)_{\min} = -\frac{(1+k_2)}{2 k_3}, \quad (6)$$

and the relationship is \cap -shaped if this value lies within the observed range of $\log(H)$ values.

Note that this analysis considers overlap as a function of home range size. One could similarly consider overlap as a function of density, with similar results – the choice is arbitrary.

Density overlap is affected not only by geometrical overlap but also by nomadicity and group sizes. If some individuals are nomadic (i.e., there is no home range estimate for them), and group sizes are greater than one, then we can partition density overlap as follows:

$$O_v = (G O_{vn})/P_h. \quad (7)$$

where P_h = the proportion of animals that have home ranges (i.e., are not nomadic),

G = size of groups using each home range, and

O_{vn} = net density overlap - overlap due only to geometrical overlap of home ranges.

Thus, nomadicity and group size need to be estimated to estimate net density overlap from density overlap.

The rate of change of net density overlap can be estimated as follows:

$$\log(G) = c_1 + c_2 \log(O_v), \quad (8)$$

If nomadicity does not vary with home range size and there is no curvilinear relationship between overlap and home range size, then we can combine equations (2), (7), and (8) to determine the relationship between O_{vn} and H :

$$\log(O_{vn}) = (k_1(1-c_2) - c_1 + \log(P_h)) + ((1-c_2)(1+k_2)) \log(H), \quad (9)$$

The first term is constant. Thus, the effect of home range size on net density overlap is given by the second term: $((1-c_2)(1+k_2))$. To make this statistic easier to interpret, we transformed this to the doubling rate, which is the amount that O_{vn} increases when H doubles. Parameters c_2 and k_2 are estimated by regressions using equations (8) and (2).

We tested the density overlap estimator by computer simulations, comparing it to geometric overlap. Geometric overlap measures the proportion of an animal's home range that is used by other individuals, and ranges from 0 to 1. Density overlap measures the number of individuals using each home range and is positive. If each part of a home range is used by only one or two individuals, then density overlap can be estimated directly from geometric overlap. However, when geometric overlap is high, then it is likely that some parts of the home range are used by more than two individuals, and then the relationship between geometric and density overlap depends on the shapes of the home ranges. Figure 1 shows the results of overlap estimations with simulated home ranges of different shapes. The general relationship between geometric and density overlap is similar for many shapes. A curve of best fit describing this relationship is:

$$\text{Geometric overlap} = \frac{O_{vn}^4 - 1}{O_{vn}^4 + 1}, \quad (10)$$

As geometric overlap approaches 1, density overlap can be very large, denoting that many individuals are using each home range. Note that density overlap can also measure the effects of home range spacing: if there are gaps between home ranges then density overlap is less than 1, whereas geometric overlap remains at 0.

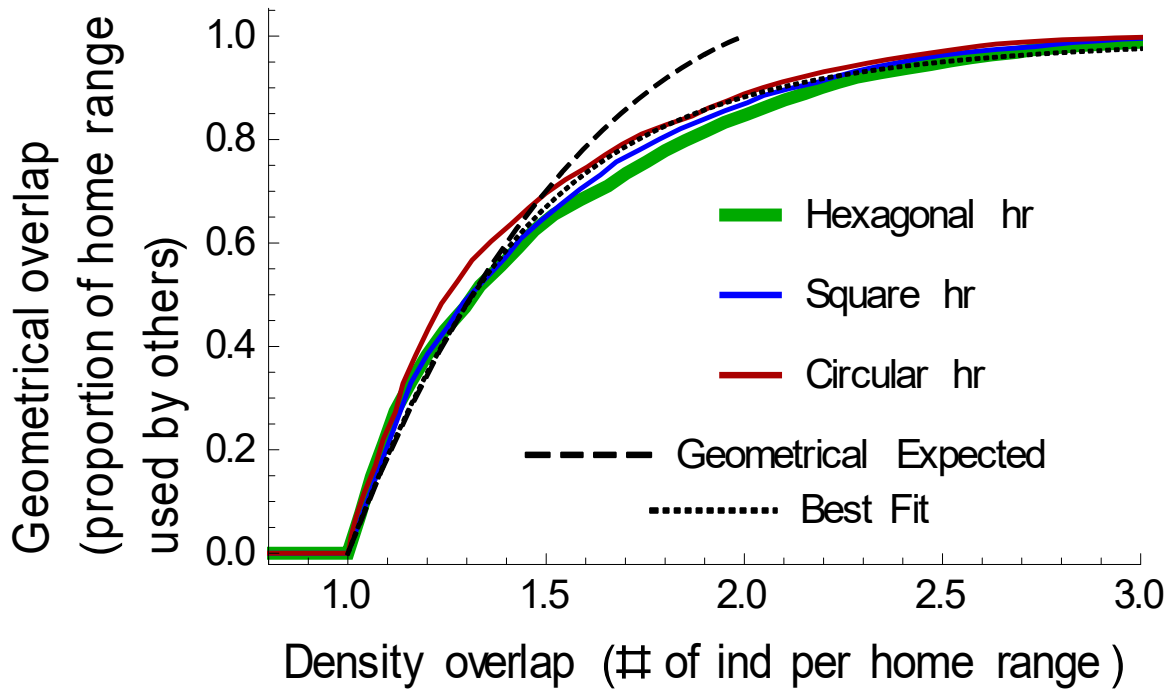


Figure 1. Geometric overlap vs. density overlap of various of home range shapes. The dashed line shows the expected density overlap calculated from the geometric if we assume that each part of a home range is used by only one or two individuals. The dotted line shows the curve of best fit. Geometric overlap reaches a maximum value at 1 while there is no maximum value for density overlap.

APPENDIX S5. LION PRIDE SIZE DATA. MEAN NUMBERS OF ADULTS, AND NUMBERS OF FEMALE ADULTS, IN PRIDES.

Country	Site	# of Adults	# of Female Adults	Source
Botswana	Kgalagadi Site #3	11.3	4.2	(Funston, 2011)
Botswana	Okavango Delta	8.5	6.1	(Kotze et al., 2018)
Cameroon	Benoue	-	3.	(Bauer et al., 2003)
Cameroon	Waza	-	3.	(Bauer et al., 2003)
Kenya	Amboseli	2.5	1.7	(Huqa, 2015)
Kenya	Laikipia	-	-	Laikipia census data (L. France, unpublished)
Kenya	RiftValley	-	5.5	(Schuette, Creel, et al., 2013)
Kenya	Tsavo	11.4	7.4	(Kays & Patterson, 2002)
Mozambique	Niassa	4.6	2.9	(Begg & Begg, 2007)
South Africa	Addo	2.5	-	(Hayward & Hayward, 2007)
South Africa	Blue Canyon	-	-	Blue Canyon census data (T. Parker, unpublished)
South Africa	Karongwe	5.	2.	(Vanak et al., 2013)
South Africa	Karoo	2.4	1.4	(Vorster, 2011)
South Africa	Kruger National Park Site #1	7.9	4.	(Maruping, 2015)
South Africa	Kruger National Park Site #2	7.5	4.	(Maruping, 2015)
South Africa	Kruger National Park Site #3	10.2	3.5	(Maruping, 2015)
South Africa	Kruger National Park Site #4	11.3	4.7	(Maruping, 2015)
South Africa	Kruger National Park Site #5	9.5	3.7	(Maruping, 2015)
South Africa	Kruger National Park Site #6	9.3	4.	(Maruping, 2015)
South Africa	Kruger National Park Site #7	9.1	3.9	(Maruping, 2015)
South Africa	Kwandwe	2.	2.	(Bissett, 2008)
South Africa	Mountain Zebra National Park	3.	1.	(Van de Vyver, 2017)
South Africa	Phinda	10.	3.8	(Turner, 2005)
South Africa	Shamwari	4.5	1.5	(J. O'Brien, 2012)
Tanzania	Selous	-	3.6	(Spong, 2002)
Tanzania	Serengeti	-	6.1	(Borrego et al., 2018; Mosser, 2008)
Zimbabwe	Bubye Valley Conservancy	-	-	BVC census data (B de Preez, unpublished)

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