



Factors predicting habitat use by leopards in human-altered landscapes

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Transformed landscapes caused by human activity leave remnant patches of natural habitat for wildlife. The persistence of species in the face of such transformation depends on individuals' ability to adapt to novel habitat, and to secure resources and reproductive opportunities despite habitat alterations. The leopard, *Panthera pardus*, is the last free-roaming top carnivore in South Africa whose high trophic status and wide-ranging movements make them an effective focal species in conservation planning. Using location data from leopards, we investigated key correlates of habitat selection in human-altered landscapes at two spatial scales. We compared sex-related differences and predicted how conspecific home range locations influenced habitat selection. Leopards avoided human-altered landscapes more strongly at the large spatial scale, where both sexes selected core areas near formally protected areas. Conspecific home range locations had a strong positive effect at both spatial scales for males, while for females, conspecifics explained fine-scale habitat selection by selecting areas near neighboring females. Spatial scale, sex-related differences, and conspecific location play roles in habitat selection for solitary felids and have implications for conservation planning and management. Excluding these factors may result in inappropriate species management policies.

Key words: carnivore conservation, conspecific home range location, habitat selection, leopard (*Panthera pardus*), spatial scale

Habitat loss and fragmentation leave remnant patches of habitat for wildlife. The persistence of species in the face of altered habitat depends in part on the capacity of remnant habitat patches to promote reproduction or survival, and the ability of individuals to ensure fitness by balancing resource utilization and threats despite the altered nature of remnant patches (Mysterud and Ims 1998; Hebblewhite and Merrill 2008). Habitat selection is the behavior individuals display in response to environmental cues and that determines the distribution of populations and ultimately species (Boyce and McDonald 1999). If individuals can respond to altered habitat without loss of reproductive

or survival potential, populations and species are more likely to persist in the long term. Thus, treating environmental factors as elements that make up the habitat of species can be considered in the investigation of an animal's realized niche. In turn, conservation managers may use strong correlations between environmental factors and individual animal occurrences to understand the relationships between individual distribution and factors that influence survival or reproduction (Morrison 2001; Marshal et al. 2006).

While the distribution of individuals can be described according to key resources, conspecifics also have a strong

influence on habitat selection (Elbroch et al. 2016). For example, a dominant individual can interfere with a subordinate's habitat selection, forcing it to occupy low-quality habitat (resource dispersion hypothesis; Geffen et al. 1992), or to access resources at different times (land tenure hypothesis; Hornocker 1969). Alternatively, conspecifics may choose to be near each other for benefits such as hunting success (Creel and Creel 1995), to improve the survival of kin by selecting locations near to relatives (Hamilton 1964) or, as the "habitat copying" hypothesis suggests, to learn from others where to find resources (Parejo et al. 2005). Although many hypotheses about the costs and benefits of conspecific locations exist, the positioning of individuals within populations has fitness consequences and contributes to the explanation of species distribution (Pulliam and Danielson 1991; Morris 2003).

Furthermore, an often overlooked consideration in habitat studies is that of sex-related differences. For many mammals, resources and constraints elicit behaviors that differ between sexes (Goodall 1986; Broomhall et al. 2004; Conde et al. 2010). Sexual selection theory suggests that males generally use riskier habitat than females, partly due to the larger spatial requirements necessary to find additional mates, as well as due to dispersal behavior (Trivers 1976; Schmidt et al. 1997). In polygamous, territorial felids, males generally locate themselves according to mates, while females tend to select areas that promote offspring reaching adulthood successfully; females therefore are considered more averse to human-associated features than are males (Conde et al. 2010; Colchero et al. 2011). If biologists use data attributed primarily to one sex, the results may (i) not represent the population accurately and (ii) miss important criteria for reproduction. This will result in inappropriate management policies (Colchero et al. 2011).

The selection of environmental variables by individuals takes place in a hierarchical process that may not be consistent over various spatial scales (Johnson 1980; Boyce 2006; Linden et al. 2018). However, scales of selection are interrelated, because large-scale distribution patterns result from individuals' daily interactions at the fine scale. Similarly, at the fine scale, individuals are constrained by large-scale distribution factors of the populations (Rettie and Messier 2000). At the large scale, habitat selection is considered to relate more strongly to evolutionary pressures such as reproductive success (Rettie and Messier 2000; Wilmers et al. 2013). We therefore predict that riskier environmental variables (variables that may reduce survival) would be avoided more at a large scale (Bunnfeld et al. 2006; Wilmers et al. 2013).

By considering conspecific home range locations, sex-related behavioral differences, and how animals use habitat at different spatial scales, we can gain insight into environmental and social factors that affect the biology of species (Boyce et al. 2002; Hirzel and Le Lay 2008). For leopards (*Panthera pardus*) in South Africa, this can contribute to the conservation of the species. Unlike other apex predators in South Africa, leopards are not restricted by fences and are the last truly free-roaming, large predators in South Africa (Skead et al. 2007). Much of their

range exists outside of protected areas, where human–carnivore conflict is common (Swanepoel et al. 2013; Ripple et al. 2014). The important ecological role of leopards and their vulnerability to humans raise questions as to their ability to persist in human-altered landscapes (Ripple et al. 2014; Tshabalala et al. 2021).

To develop a better understanding of habitat use by leopards, we aim to identify key factors associated with habitat selection by leopard in the Eastern and Western Cape provinces, South Africa. We investigate (i) whether conspecific home ranges play a role in where individuals place themselves, (ii) whether sexes respond differently to environmental cues, (iii) how leopards respond to anthropogenic landscape features, and (iv) how these interactions may change at large- and fine-scale habitat selection.

MATERIALS AND METHODS

Study area.—The study took place in the Eastern and Western Cape provinces, South Africa (33°11'–33°23' S and 25°53'–18°53' E), extending approximately 1,000 km along the southernmost part of South Africa (Fig. 1). Topography varies from coastal zones and low-lying valleys from sea level, to mountain peaks > 1,600 m along the Cape Fold Mountain range, which extends approximately 800 km between Port Elizabeth in the east and Cape Town in the west (Thamm and Johnson 2006). The study area hosts various biomes and vegetation types, from the semi-arid, dwarf shrublands in the northern reaches representing the semi-arid Succulent and Nama-Karoo biomes (Mucina et al. 2006) to forest in the southern cape, characterized by tall trees (> 30 m) with a shrubby understory. In the east, subtropical thicket with an average height of about 2–3 m is dense, mesic bush dominated by Spekboom (*Portulacaria afra*) and *Searsia* sp. Sandstone Fynbos is prolific in higher-altitude zones on the Cape Fold Mountain range, and commonly include *Protea* sp. and *Erica* sp. Finally, savanna elements are found in parts of the region, particularly in lower-rainfall areas along riverine zones (Mucina et al. 2006). Rainfall in the semi-arid environments averages approximately 290 mm per year. In contrast, the highest average annual rainfall in the study area occurs in the afrotemperate forests, falling year-round and averaging approximately 950 mm per year (Mucina et al. 2006). Land uses include agriculture, urban areas, and formally protected areas. Protected areas make up 9.3% of South Africa's landcover with 15% and 8% of the Western Cape and Eastern Cape formally protected, respectively (Swanepoel et al. 2013; Fig. 1).

Leopard data.—We used walk-in, fall-door cages (2 m long, 0.7 m wide, 0.8 m high) to capture leopards in the study area between 2007 and 2015 (Table 2). This research formed part of a greater predator conservation project (www.landmarkfoundation.org.za). We sampled leopards opportunistically across the Eastern and Western Cape, where leopards were present; this often was on private land adjacent to protected areas. We placed cages where leopard activity such as tracks, prey kill sites, and scrapes were found. No baits were used unless a recent livestock kill was made by a leopard, in

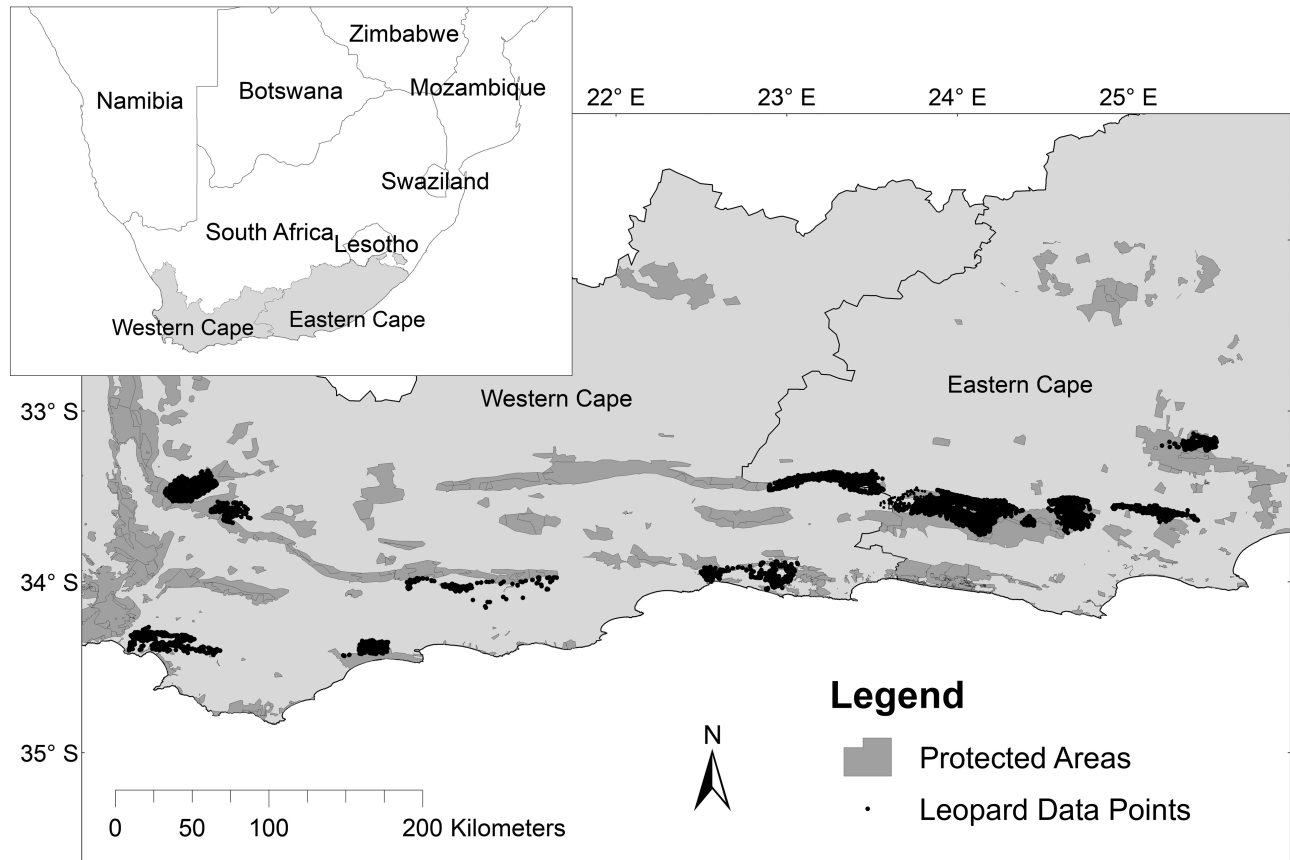


Fig. 1.—Study area of the Eastern and Western Cape, South Africa with the distribution of GPS data from sampled leopards and protected areas.

which case the carcass was used as bait. Once a leopard was captured, a veterinarian immobilized the animal with Zoletol–Medetomidine at a standard dosage (1–2 mg/kg; McManus et al. 2015a). We fitted Geographic Positioning System (GPS) or satellite collars (Vectronic-Aerospace, Berlin, Germany, or Animal Wildlife Tracking, Johannesburg, South Africa) to adult leopards. No subadults or juveniles were fitted with collars. Collars recorded locational data between 4- and 6-h intervals; data were downloaded remotely using an ultra-high frequency receiver, or by satellite transmission.

Spatial scale.—We estimated habitat selection at two spatial scales: locations within home ranges (fine scale) and the placement of home ranges within the region (large scale). We generated 10 random locations per observed location within home range boundaries of that leopard, such that we expected the random locations to adequately represent available habitat in the home range (Fig. 2; Manly et al. 2002; Marshal et al. 2011). We buffered observed locations with a 1-km radius area (average distance moved by leopards in 6 h; Fig. 2) to ensure that random points represented locations where the leopard was capable of accessing before or after a GPS point was stored (Boyce 2006; Fattbert et al. 2015). We converted spatial data to 1-km² cell size to correspond with leopard presence data. We created a “super home range” (one 100% minimum convex polygon [MCP] incorporating all individuals using Home Range Tools; Rodgers et al. 2007) to define the large-scale habitat selection assessment (Treves et al. 2011; Fattbert et al. 2015).

The super home range provided an area over which leopards potentially could move, and we hoped to incorporate residents as well as extraterritorial movements by residents in this area (Treves et al. 2011). Similarly to the fine-scale analyses, within the super MCP, we generated 10 random locations for each observed location (Manly et al. 2002; Marshal et al. 2011). We clipped habitat covariates to each observed and random location, using ArcGIS 10.1 software (ESRI, Redlands, California), as explained next.

Habitat covariates.—We developed habitat models in a geographic information system (GIS) by selecting GIS layers that represented environmental factors known or suspected to influence leopard behavior (Bothma et al. 1997; Dickman and Marker 2005; Gavashelishvili and Lukarevskiy 2008; Swanepoel et al. 2013; Table 1). Although prey distributions and abundances commonly influence carnivore distributions (Creel et al. 2001; Karanth et al. 2004), these data were not available across our study area. We used small livestock (sheep and goats) density as a correlate of leopard habitat fragmentation following Swanepoel et al. (2013). Cattle are killed rarely by leopard in the region, thus most conflict exists where small stock are farmed (Ogada et al. 2003; McManus et al. 2015b). Slope and elevation were derived from a digital elevation model originally from Shuttle Radar Topography Mission (<http://srtm.csi.cgiar.org>; Table 1). In addition, we included the influence of other leopards, both male and female, in our models by incorporating the distance from the home range centers of each

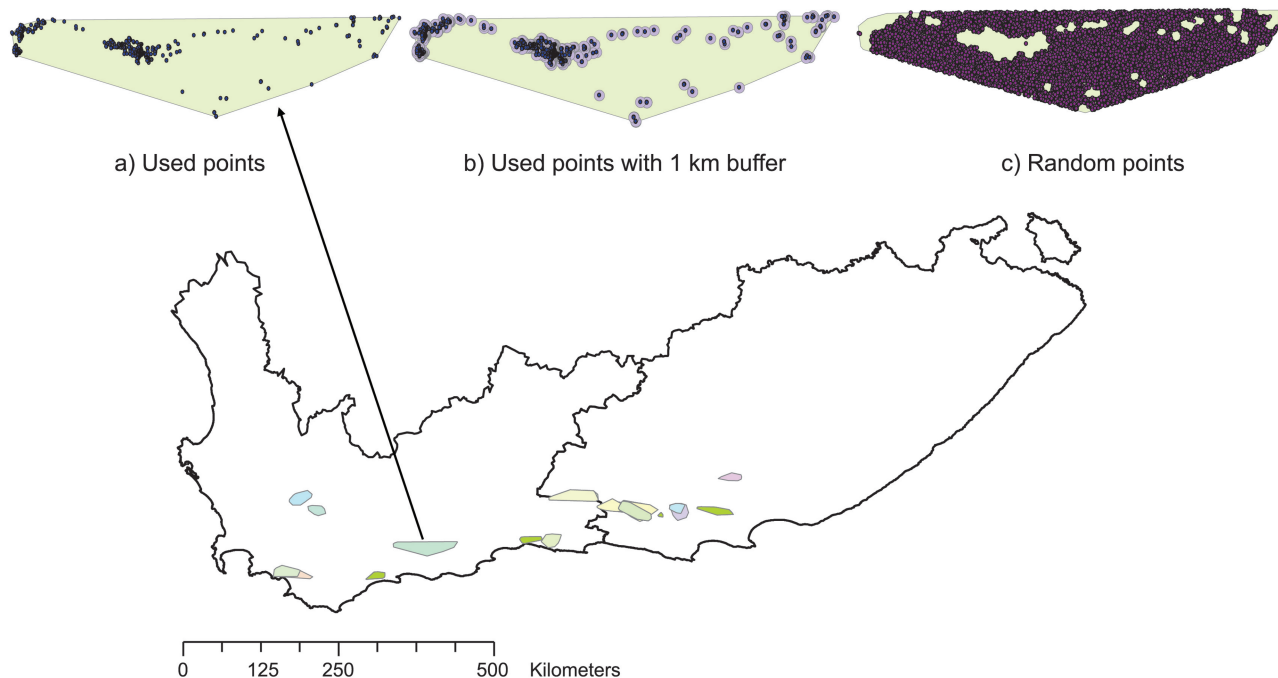


Fig. 2.—Distribution of leopard home ranges estimated from 100% minimum convex polygon (MCP). A 1-km buffer (average distance walked by male and female leopards at 6-h intervals) was placed around used locations to separate available locations from observed points within home ranges. a) Used locations, b) used points with 1-km buffer, and c) random points.

Table 1.—Environmental variables used to model leopard resource selection function in the Eastern and Western Cape.

Variable	Description	Resolution (m)	Units	Source
Roads	Euclidean distance to roads	90	km	^a
Rivers	Euclidean distance to rivers	90	km	^a
PA	Euclidean distance to protected areas	90	km	^a
Town	Euclidean distance to town	90	km	^a
Pop	Human population density/km ²	1,000	Density	^a
Farm	Euclidean distance to farms	90	km	^a
Slope	Digital elevation model	90	°	^b
Elevation	Digital elevation model	90	m	^b
Livestock	Density of small livestock/km ²	5,600	Density	^c
Female	Euclidean distance to female leopard home ranges	1,000	km	GPS data
Male	Euclidean distance to male leopard home ranges	1,000	km	GPS data

GPS, Geographic Positioning System; PA, protected area.

^aNational Geospatial Information (NGI), South Africa, Cape Town, 2010. Department of Land Affairs, South Africa. ^bJarvis et al. (2006). ^cInternational Food Policy Research Institute (IFPRI) (<http://www.ifpri.org/>).

leopard, because we expected that to reveal the probability of conspecifics' roles in habitat selection. We calculated all distances as Euclidian distances (Spatial Analyst in ArcGIS 10.1).

Analyses.—We divided half the data into a training dataset for model construction and the other half into a testing dataset to evaluate model performance (Treves et al. 2011; Fattebert et al. 2015). We used the data of each sex in the analyses and included individual identity as a random effect in the generalized linear mixed models (GLMMs) to account for repeated observations of the same individuals (Gillies et al. 2006; Koper and Manseau 2009). We used GLMM's with a probit link to evaluate relationships between observed leopard locations and landscape variables, and distance to center of leopard home ranges using package lme4 (Bates et al. 2015) in R 2.13.2 (R

Development Core Team 2014). To avoid over-fitting, inherent in analyzing large behavioral datasets (Garamszegi 2011), we used three criteria for selecting variables in models: (i) receiver operating characteristic (ROC) in package pROC (Robin et al. 2011; Treves et al. 2011), (ii) Bayesian information criterion (BIC; Conde et al. 2010; Treves et al. 2011), and (iii) the width of mean standard error (SEM; Treves et al. 2011). The ROC combines measures of sensitivity and specificity (false positives and false negatives) to reveal how well models discriminate between used and random points. We added a new predictor in a forward stepwise fashion if the ROC value increased by 1% and if the following screening steps also indicated an important effect of the added predictor. Because we were seeking informative predictors but also parsimonious

models, we also used BIC. Any BIC change of 2 or more justified inclusion of a new predictor in the multivariate model. We screened predictors in initial, univariate GLMMs, before combining them and their interactions into multivariate GLMMs (Supplementary Data SD1). Finally, we excluded any variable if the estimate of the SEM crossed zero (Treves et al. 2011). We evaluated multi-collinearity among habitat covariates with Pearson's correlation coefficient ($r > 0.6$) before including a new covariate in the forward stepwise procedure (Olea et al. 2010; Treves et al. 2011). Final models were selected based on the BIC values (Burnham and Anderson 2004).

RESULTS

Leopard data.—We obtained a total of 19,815 and 15,062 GPS locations from 14 male and 10 female leopards, respectively (Table 2).

Fine-scale habitat selection.—At the fine-scale analyses, the best model explaining male locations included the interaction between distance to center of female home ranges and distance to towns (Table 3; Fig. 3). The interaction was negative with both features, indicating that male leopards were more likely to be nearer to these features. When we tested additional predictors, no additional explanatory power in the training and testing of model fit based on the ROC was observed. Female locations were best explained by the interaction between distance to other females and distance to rivers (Table 3; Fig. 4). There

was a negative interaction with the variable distance to center female home ranges and a positive interaction with distance to rivers. This indicated that female leopards were more likely to be nearer to the centers of other females' home ranges, and further from rivers. Females selected areas nearer to rivers at both spatial scales when rivers were run as a univariate model (Supplementary Data SD1; Fig. 4).

Large-scale habitat selection.—At the large scale, male leopards were located near females and protected areas, and where human population density was low (Table 4; Fig. 5). For females, locations were associated near protected areas and roads (Table 4; Fig. 6). When testing the interaction between the variables "distance to protected areas" and "distance to roads" for females, we found that the probability of females being near a road increased when the road was nearer to protected areas (Table 4). No other landscape features improved ROC and BIC.

DISCUSSION

We found that conspecifics' home range locations explained habitat selection for leopards in the Eastern and Western Cape, and that sexes responded differently to environmental cues. Furthermore, these responses varied at different spatial scales. We further found that females selected areas nearer to female conspecifics' home ranges, more strongly at the fine spatial scale. For solitary female felids, there have been opposing findings on conspecific interactions, with Packer (1986) finding that females

Table 2.—Collar number (ID) for male and female leopards, Geographic Positioning System (GPS) location data, 100% minimum convex polygon (MCP) range sizes (km²), and the monitoring period GPS data were collected for male and female leopards in the Eastern and Western Cape, South Africa.

Number	Male ID	Monitoring period	GPS points	MCP (km ²)	Female ID	Monitoring period	GPS points	MCP (km ²)
1	1015	January 2015 / November 2015	593	656, 1	1412	September 2014 / January 2016	1232	48, 11
2	2996	January 2007 / December 2007	1874	214, 17	3704	September 2007 / February 2009	2388	184, 37
3	2997	June 2007 / October 2008	2504	54, 48	3710	July 2007 / December 2007	600	134, 85
4	29971	October 2009 / July 2010	1554	75, 68	3805	January 2009 / December 2010	3142	278, 04
5	3805	September 2012 / June 2013	1133	654, 13	3809	September 2009 / June 2010	977	135, 30
6	3809	January 2008 / May 2009	1809	770, 21	6775	April 2009 / July 2009	457	226, 62
7	6666	March 2009 / May 2010	1368	307, 37	6777	June 2009 / July 2010	2013	132, 56
8	6667	December 2008 / June 2010	2457	570, 52	8183	May 2010 / July 2011	1202	239, 55
9	6776	April 2009 / September 2010	2222	659, 19	8294	March 2011 / November 2011	1362	162, 12
10	8182	June 2010 / June 2011	1053	1068, 45	8642	April 2010 / December 2011	1691	25, 21
11	8578	October 2010 / September 2011	2147	3,150, 15				
12	8677	May 2014 / June 2014	252	224, 23				
13	9536	June 2011 / September 2011	377	474, 27				
14	9648	February 2012 / June 2012	472	396, 73				
Total			19815				15064	

Table 3.—Within-home-range selection: best models explaining female and male leopard occurrence, with receiver operating characteristic (ROC), Bayesian information criterion (BIC), *SE* of the slope coefficient (β), lower (2.5) and upper (97.5) confidence intervals (CIs). Variables included distance to female home range centers (Females), distance to rivers (Rivers), and distance to towns (Town).

Leopards	Best model	Predictors	β	<i>SE</i>	Lower CI (2.5)	Upper CI (97.5)	ROC	BIC
Females	Best model	Females	-0.003	0.0004	-0.0041	-0.00254	0.6865	47296.1
		Rivers	0.02	0.014	-0.00684	0.043611		
		Females * Rivers	-0.003	0.0002	-0.00302	-0.00222		
Males	Best model	Females	-0.009	0.0004	-0.00917	-0.00782	0.7879	52144.64
		Towns	-0.043	0.001	-0.04515	-0.0407		
		Females * Town	-0.00014	0.00002	-0.00019	-0.00009		

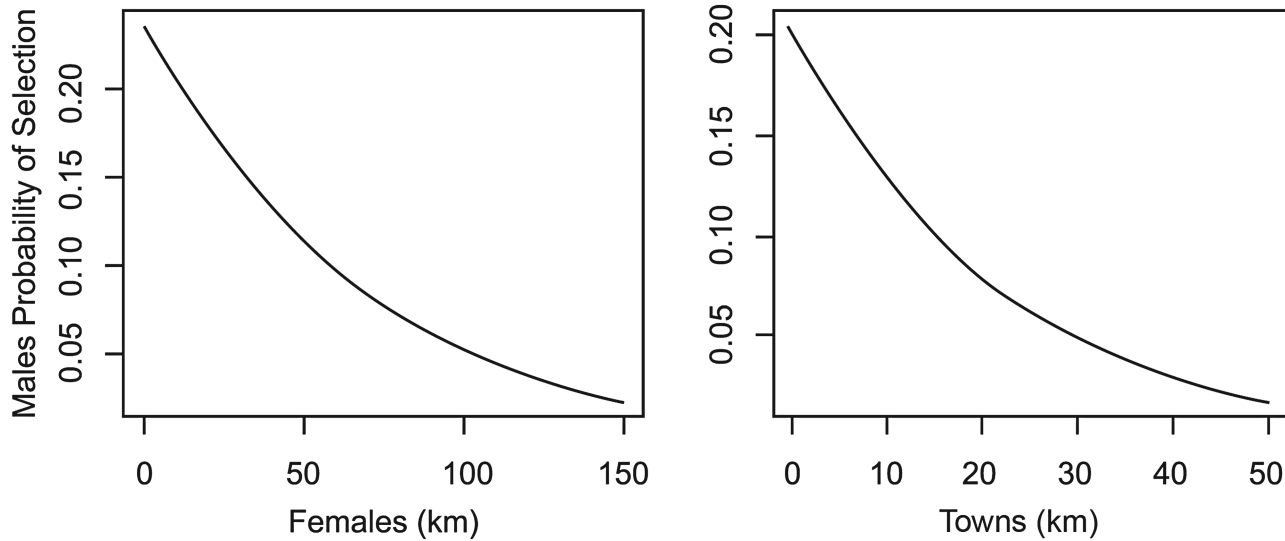


Fig. 3.—Male habitat selection within home range: predicted use based on environmental covariates from the highest ranked model (distance to females [km] and distance to towns [km]).

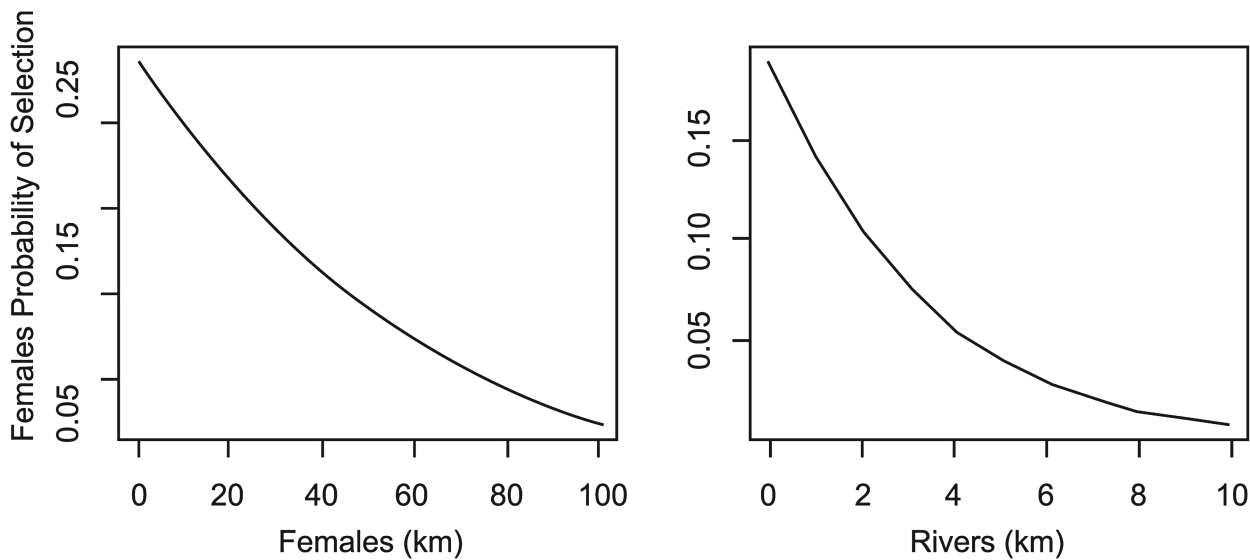


Fig. 4.—Female habitat selection within home range: predicted use based on environmental covariates from the highest ranked model (distance to females [km] and distance to rivers [km]).

Table 4.—Home range selection: best models explaining male and female leopard occurrence, with receiver operating characteristic (ROC), Bayesian information criterion (BIC), *SE* of the slope coefficient (β), lower (2.5) and upper (97.5) confidence intervals (CIs). Variables included distance to female home range centers (Females), distance to protected areas (PA), human population density (Population), and distance to roads (Roads).

Leopards	Best model	Predictors	β	<i>SE</i>	Lower CI (2.5)	Upper CI (97.5)	ROC	BIC
Females	Best model	PA	-0.14	0.002	-0.14324	-0.13439	0.81	43583.61
		Roads	-0.15	0.003	-0.15624	-0.14619		
Males	Best model	Females	-0.013	0.000	-0.013	-0.013	0.83	48586.47
		PA	-0.19	0.004	-0.198	-0.181		
		Population	-0.015	0.001	-0.017	-0.015		
		Females*PA	-0.00014	0.00002	-0.00019	-0.00009		

were intolerant of conspecifics, while others were tolerant (Seidensticker et al. 1973). We consider various theories that can explain our observation. First, the kin selection hypothesis

predicts that relatives should aggregate and thus philopatric behavior in female felids generally is expected because males disperse while mothers and daughters generally hold adjacent

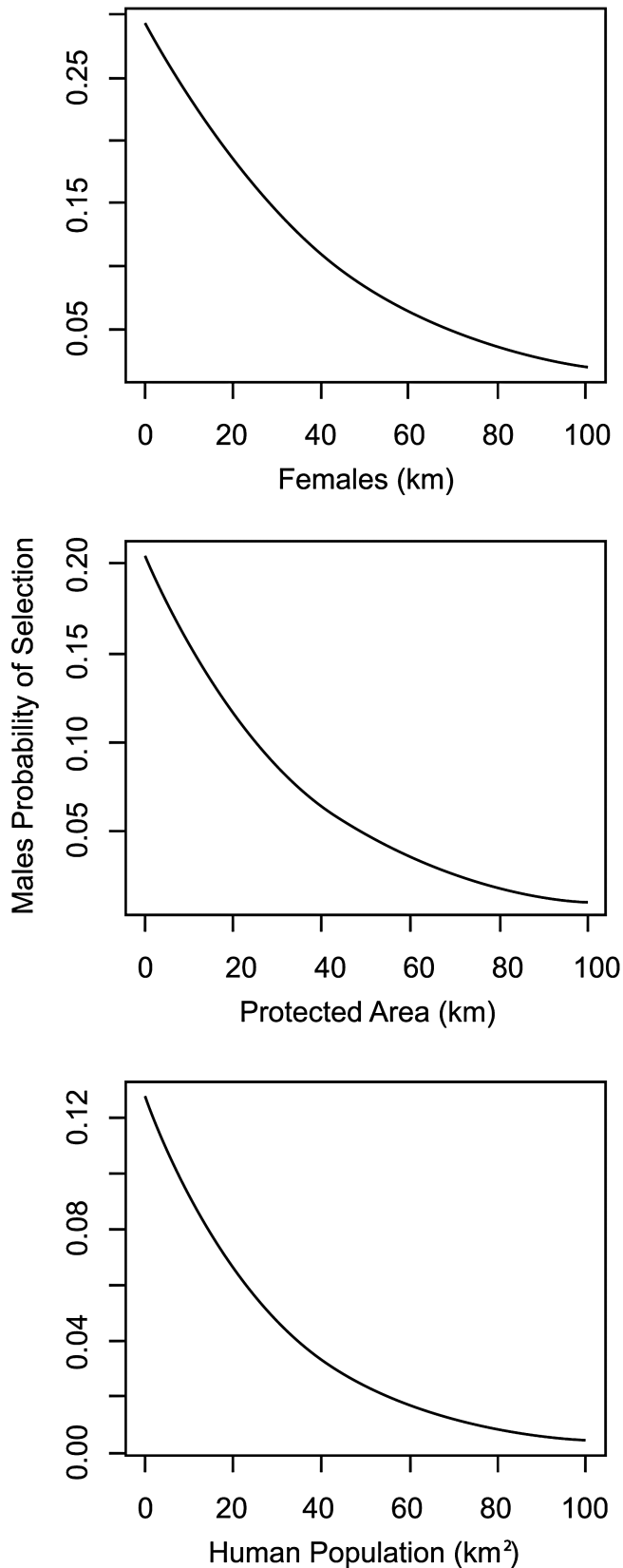


Fig. 5.—Male home range selection: predicted use based on environmental covariates from the highest ranked model (distance to females [km], distance to protected area [km], and human population density [km²]).

territories, thereby suiting our observations. However, philopatry may not occur when resources are limited and only are sufficient for the mother, resulting in female offspring dispersing from natal areas (e.g., Iberian lynx, *Lynx pardinus*; Ferreras et al. 2004). Where resources are low and females not related, conspecific attraction may be explained by the habitat copying hypothesis where conspecifics use information about habitat suitability from other individuals (Parejo et al. 2005). Finally, proximity to other females can be an infanticide avoidance strategy (Balme and Hunter 2013; Knott et al. 2019). Infanticide contributes to more than half of the mortality of juvenile leopards in protected areas, forcing females to employ various infanticidal avoidance strategies (Balme and Hunter 2013; Swanepoel et al. 2015). High rates of infanticide may reduce population viability and, therefore, influence leopard socio-spatial dynamics (Balme and Hunter 2013; Swanepoel et al. 2015). We found that female leopards were further from the centers of other females' home ranges when they were further from male leopards. Thus, being near to female counterparts may contribute to an infanticide avoidance strategy. However, this requires further investigation. Interestingly, females changed their interaction with distance to rivers from selecting areas closer to rivers at both spatial scales, to further from rivers when nearer to the centers of females' home ranges. Selecting areas near rivers may benefit individuals, as the taller riparian vegetation offers concealment from threats and better cover when hunting (Swanepoel et al. 2013). Furthermore, the predominantly annual river courses allow easier passage when traversing the landscape. This raises questions regarding the interaction females have with one another because concealment may not be required when near other female home ranges. It may be useful for future studies to investigate the causes of leopard distribution if females interact with, or avoid conspecifics that might attack her or her cubs.

As expected, male distribution was predicted by the location of the centers of females' home ranges at both spatial scales, aligning with other studies (Schmidt et al. 1997; Logan et al. 2009). The finding that both sexes' locations are correlated with the centers of females' home ranges at the fine scale has implications for leopard distribution. Generally, male leopards are predicted to have higher mortality risk due to dispersal and the cost of acquiring and defending territories (Bailey 1994). However, Swanepoel et al. (2015) did not find a bias in sex in leopard mortality. Because we found the centers of females' home ranges correlated with leopard habitat selection for both sexes, and females generally display philopatric behavior, female mortality has a greater demographic impact than male mortality (Dalerum et al. 2008; Swanepoel et al. 2015). Thus, questioning how the constellation of leopards may respond to a female who is removed from the system is not well understood, and may be important to better understand how conspecifics influence leopard distribution and metapopulation dynamics, particularly where human-wildlife conflict or hunting exist.

We found support for the hypothesis that sexes respond differently to environmental cues, and variables are selected in a hierarchical fashion in relation to spatial scale. Females showed no strong correlation to anthropogenic interaction at the fine scale,

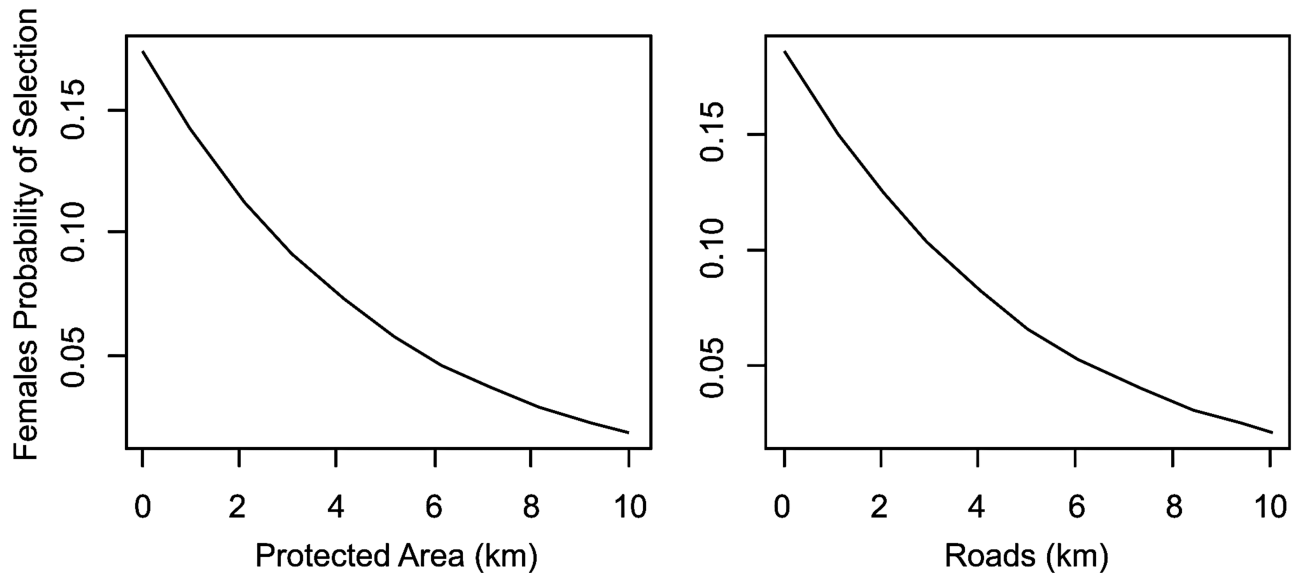


Fig. 6.—Female home range selection: predicted use based on environmental covariates from the highest ranked model (distance to protected area [km] and distance to roads [km]).

where distance to the center of females' home ranges and rivers best explained female leopard locations. We interpret this to mean that females avoided high-risk encounters with people within home ranges. At the large spatial scale, females selecting areas near to roads contradicts previous research elsewhere in South Africa (Swanepoel et al. 2013), although leopards in Kenya also approached roads (van Cleave et al. 2018). A subsequent study reported that females were more likely to be killed in road collisions than males (Swanepoel et al. 2015). Further investigation into the relationship between distance to protected areas and distance to roads showed that females were nearer to roads when roads were near protected areas, suggesting that roads may be more selected where there is less human activity, as found in wolves (Thurber et al. 1994; van Cleave et al. 2018). Investigating the effect of road characteristics (e.g., vegetation cover adjacent to roads, traffic rates) on leopard presence could further explain why female presence has a positive association with roads at this spatial scale. This can improve insights into what impact roads have on leopard distribution. In contrast with females, male leopards in our study selected areas nearer to towns at the fine scale and where low human population densities occurred at the large scale. The selection of low human population density at the large spatial scale provides support that male leopards are more negatively associated with anthropogenic features at large scale compared to finer scales. Selecting areas near to towns may be a result of larger spatial requirements by males increasing interaction with these sites (Bunnfeld et al. 2006).

Despite known sex-related differences in behavior among many large carnivores, sex-biased difference in resource selection rarely is incorporated into habitat models and could result in inappropriate conservation management actions (Palma et al. 1999; Linkie et al. 2006; Klar et al. 2008). For example, roads may not appear to be an important management consideration if data are sourced predominately from males.

An observed factor shared between sexes in the large-scale analyses was proximity of protected areas. In Southern Africa,

leopard survival rates are significantly higher inside protected areas than outside, where human-caused mortality is the predominant cause of mortality (Swanepoel et al. 2015). The selection of protected areas by leopards therefore likely relates to source–sink dynamics because protected areas have safer habitat where human activity is restricted, hunting is prohibited, and no livestock occur inside—thereby reducing human–carnivore conflict, and these areas are likely to contain more abundant wild prey. While protected areas offer higher survival, protected areas only host a small portion of leopard habitat (Swanepoel et al. 2013) and are unable to host genetically viable leopard populations with the exception of the very large Kruger National Park and Kgaligadi Transfrontier National Park (Bothma et al. 1997). Leopard territories outside of protected areas therefore are important to conserve because they contribute to population density and dynamics, and genetic connectivity in disjunct leopard populations (McManus et al. 2015a; Devens et al. 2018).

While prey is known to influence predator distribution, livestock density had a weak correlation with leopard distribution. This implies leopards do not select livestock-rich areas, and selecting grazing sites carefully could reduce human–wildlife conflict. Unfortunately, no natural prey data are available for the study area for further testing. With these data, researchers could better understand leopard habitat, and assess if and how food availability influences intraspecific interactions and the spatial distribution of individuals on the landscape.

Management implications.—We found that conspecifics, sex-related differences, and spatial scale are predictors for presence of leopards. Excluding such interactions in habitat modeling may result in incorrect habitat predictions and associated management actions.

Studies based on data predominately from one sex could result in inaccurate habitat predictions for the other sex and thereby lead to management actions that are mistargeted or biased to one

sex (Conde et al. 2010; Colchero et al. 2011). Predictions about habitat, colonization, corridors, habitat restoration, density estimates, and extrinsic mortality factors, all could be improved by incorporating data reflecting sex-specific data (Devens et al. 2018). Similarly, data collection methods that do not reveal sex of detected animals should apply caution in extrapolation from the sample. This highlights the need for species sociality to be incorporated in resource selection function models.

Most leopard habitat exists outside protected areas, where leopard survival is significantly reduced. Considering male and female resource requirements in management planning becomes important to support population genetic viability and connectivity. Reducing human-caused mortality and mitigating human–carnivore conflict becomes increasingly pertinent as a conservation focus to ensure safe breeding areas for females and stable male territories to reduce infanticide.

Unfortunately, we did not have information on the social status of sampled individuals (i.e., dominant or subdominant). While this could have provided information on how dominant and subdominant individuals interact with their environment, studies considering these parameters found that dispersing subdominant individuals used habitat in accordance with established adults (Fattebert et al. 2015). Incorporating sex, and conspecific home range locations contributes to a more dynamic approach to predicting species habitat, benefiting both research and management. Furthermore, connectivity among habitat patches is a valuable conservation tool to overcome major threats to biodiversity (Beier et al. 2011; Ripple et al. 2014). The use of RSFs can improve the identification of (i) functional corridors, (ii) areas to conserve, and (iii) suitable re-introduction sites for leopards.

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SUPPLEMENTARY MATERIAL

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

Supplementary Data SD1.—Univariate analyses results for male and female leopard occurrence probability at the fine and large spatial scales.

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