Home range variation in leopards living across the human density gradient

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Home range size is a fundamental measure of animal space use, providing insight into habitat quality, animal density, and social organization. Human impacts increasingly are affecting wildlife, especially among wide-ranging species that encounter anthropogenic disturbance. Leopards (*Panthera pardus*) provide a useful model for studying this relationship because leopards coexist with people at high and low human densities and are

sensitive to human disturbance. To compare leopard home range size across a range of human densities and other environmental conditions, we combined animal tracking data from 74 leopards in multiple studies with new analytical techniques that accommodate different sampling regimes. We predicted that home ranges would be smaller in more productive habitats and areas of higher human population density due to possible linkage with leopard prey subsidies from domestic species. We also predicted that male leopards would have larger home ranges than those of females. Home ranges varied in size from 14.5 km^2 in India to 885.6 km^2 in Namibia, representing a 60-fold magnitude of variation. Home range stability was evident for 95.2% of nontranslocated individuals and 38.5% of translocated individuals. Leopard home range sizes were negatively correlated with landscape productivity, and males used larger areas than females. Leopards in open habitats had a predicted negative correlation in home range size with human population density, but leopards in closed habitats used larger home ranges in areas with more people.

Humans increasingly are affecting ecosystems worldwide, with well-known effects on biodiversity. Most of the focus on these impacts has been on biodiversity loss and ecosystem functioning (Koerner et al. 2017), but there also is increasing evidence that even at the individual scale, animals are altering behavior in the face of these rapid and large-scale changes (Dumyahn and Pijanowski 2011; Niemi et al. 2019). Disturbance by humans presumably worsens habitat quality for most species, causing changes in behavior (Parsons et al. 2016). Indeed, one study showed that leopard (*Panthera pardus*) density was lower in habitats adjacent to human disturbance (Havmøller et al. 2019). Nevertheless, another recent investigation of broader mammal movements found that movement was reduced in human-dominated landscapes for most terrestrial species (Tucker et al. 2018), which might be a sign of improved habitat quality for some species (Odden et al. 2014). Two primary hypotheses potentially explain the relationship between habitat quality and animal movement: fragmentation forces animals to move less, or food availability for mammals near humans is higher. For larger carnivores, increased food availability near people might be underpinned by preying on domestic animals (Athreya et al. 2016) or on wild species that thrive near people (Parsons et al. 2018). While large-scale analyses have noted the importance of humans to mammal movement patterns (Tucker et al. 2018), such analyses are limited in their focus to a simple movement measures (linear displacement), making it difficult to know whether this relationship persists for longer-term space needs of animals or the extent to which this is driven by fragmentation or food availability.

Regardless of the specific details driving human-induced changes, it is hypothesized that improved conservation planning and management across landscape and habitat scales are required to alleviate conservation challenges (Ehrlich and Pringle 2008; Di Minin et al. 2016). This is particularly important when considering large carnivore conservation because large predators perform essential ecosystem functions (Ripple et al. 2014) and serve as focus points for broader conservation efforts (Borg et al. 2016; Kittle et al. 2018).

Despite the limitations of traditional home range size descriptors, comparative studies have repeatedly identified general trends suggesting that home range size reflects fundamental ecological relationships. Across species, home range size increases with body mass (McNab 1963; Lindstedt et al. 1986; Gompper and Gittleman 1991; Haskell et al. 2002; Nilsen et al. 2005; Ofstad et al. 2016). Similarly, within species, individuals with larger body mass tend to have larger home ranges than those with smaller body mass (McNab 1963), even when exact measurement of this phenomenon is subject to underestimation (Noonan et al. 2020). In sexually dimorphic species such as leopards, adult males are larger than adult females and typically have larger home ranges than females (Marker and Dickman 2005). Males might also have larger home ranges than females because it increases their mating opportunities (Macdonald 1983; Fattebert et al. 2016). Home ranges' size also has been linked to food availability. Individuals in areas of high food availability often have smaller home ranges than individuals in areas with low food availability (Herfindal et al. 2005). This has been shown within species (e.g., brown bear, *Ursus arctos*—Mangipane et al. 2018—and African lions, *Panthera leo*—Loveridge et al. 2018) and across 21 species of carnivore (Duncan et al. 2015). Thus, broad-scale changes in home range size likely are related to changes in density, with both in turn related to resource availability (Carbone and Gittleman 2002; Hatton et al. 2015).

In human-dominated landscapes, factors predictive of home range size and movement such as resource availability can be altered due to subsides (e.g., directly or indirectly feeding on domestic animals), reductions in habitat productivity (e.g., due to changes in primary productivity), or changes in landscape structure (e.g., habitat fragmentation). Such changes influence home range size in ways that are particularly notable in larger carnivore species. Leopards occur in diverse settings across Africa and Asia (Jacobson et al. 2016), occupy a wide range of habitat types (deserts to rainforests), and coexist with humans along a spectrum of development from wilderness to habitats adjoining high human density areas (Stein et al. 2011, 2016; Rostro-García et al. 2016; Kshettry et al. 2017; Kafley et al. 2019). In some human-dominated settings inhabited by leopards, domestic prey biomass is much higher relative to natural prey biomass observed inside protected areas (Athreya et al. 2016), and as such, some leopard populations consume higher proportions of domestic species. This trend of domestic prey density vastly outnumbering wild prey occurs in many areas (Seidensticker et al. 1990; Mizutani 1999;

Babrgir et al. 2017) and can mean that large carnivores, such as leopards inhabiting human-dominated landscapes, might not need large home ranges. Rather, they might be able to persist in areas without what we understand as "natural" habitat, making them a strong candidate for comparing home range variation across their distribution. Insight gained here might be useful for exploring human–carnivore relationships for other large-bodied species living near humans such as mountain lions (*Puma concolor*), tigers (*Panthera tigris*), and bears (Lamb et al. 2020).

We examined relationships between leopard home range size and habitat variables including human density, vegetation productivity, temperature, precipitation, and habitat openness for 74 individuals in seven countries. Leopard locational data were collected using Global Positioning Satellite and local proximity Very High Frequency (VHF) tracking collars from 10 different projects between 2004 and 2016. Because intraspecific, cross-study comparisons of home range size are influenced by choices of analytic techniques (Nilsen et al. 2005), we used the same analytic technique (autocorrelated kernel density estimates; AKDEs) for all leopards to correct for autocorrelation (Calabrese et al. 2016). By applying continuous time stochastic models, AKDEs can account for autocorrelation within data sets in which consecutive points are assumed to be related by first estimating each data set's autocorrelation structure and then optimizing bandwidth estimates based on autocorrelation conditions (Noonan et al. 2019). This method also allows for comparison among studies using different sampling designs

and data collection methods because each data set is adjusted for autocorrelation individually.

We hypothesized that male leopards would have larger home range sizes than female leopards (Macdonald 1983; Fattebert et al. 2016) and that not all leopards would exhibit stable home ranging behavior, with home range following the concept defined by Burt (1943:351) as the "area traversed by the individual in its normal activities of food gathering, mating, and caring for young. Occasional sallies outside the area, perhaps exploratory in nature, should not be considered…" We also expected smaller home ranges within productive landscapes with higher precipitation, warmer temperatures, and higher Nominal Difference Vegetation Index (NDVI—Nilsen et al. 2005) values, which corresponded to being able to support higher numbers of prey. Finally, because of their use of domestic animals as food, compounded with a possible human-induced landscape of fear (Brown et al. 1999) limiting times and distances of movement (Tucker et al. 2018), we predicted that leopard home range size would decrease as human density and intensive land use increased.

MATERIALS AND METHODS

Study sites.—We used data from 10 field studies across seven countries, with tracking data from 74 leopards (Fig. 1; Table 1). Namibian study sites were located in the central band of managed livestock ranches immediately east and
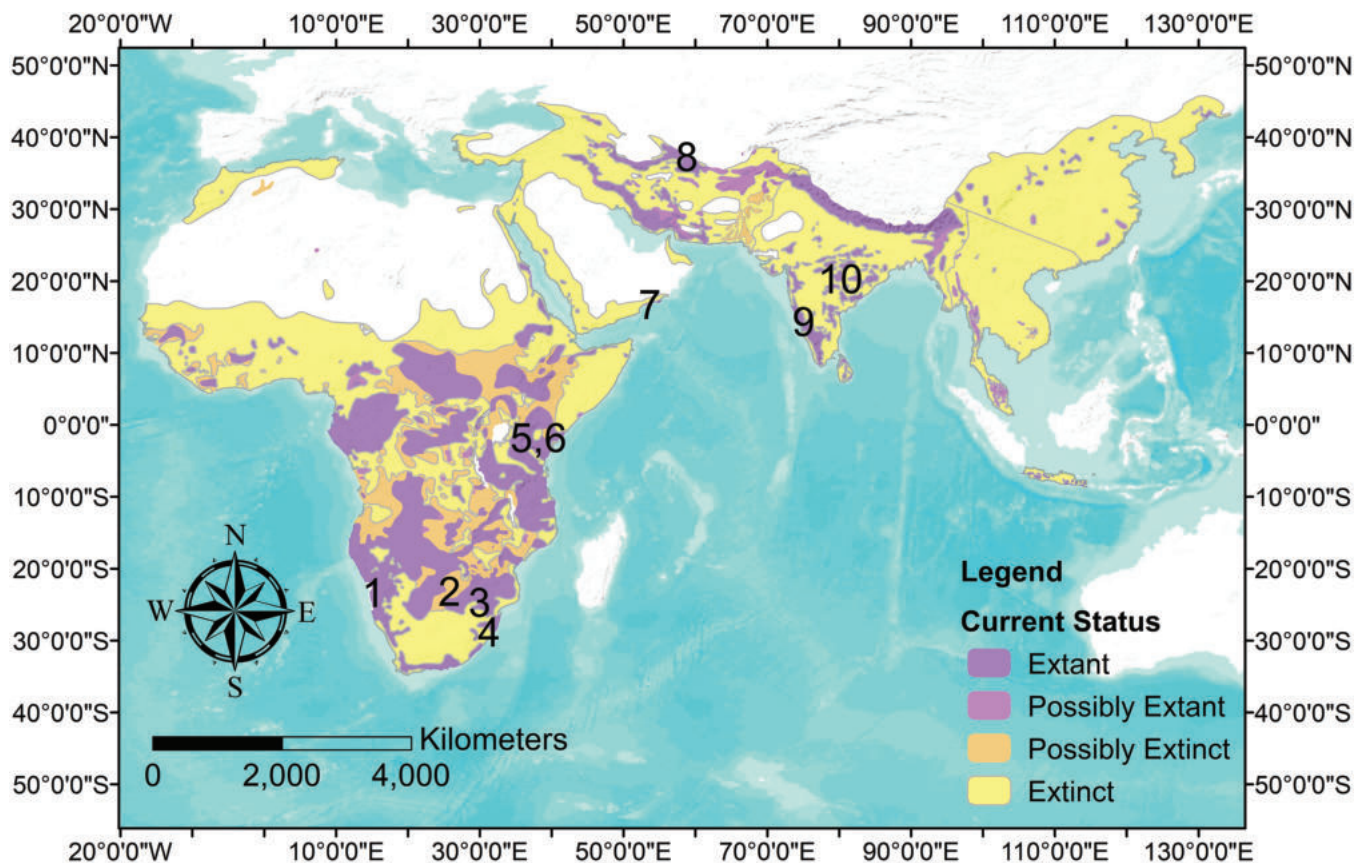

Fig. 1.—Current and historical distribution of leopards (Stein et al. 2016). Numbered locations denote leopard sites used in this study.

Table 1.—Summary of studies in our analyses; characteristics averaged across all leopard GPS locations from each study.

Location	Map study location	Sample size	Mean human pop density in study area (humans/km²)	Mean fix frequency (per day)	Coordinates
Central Namibia	1	13	0.1	1 (GPS)	21.06 S, 16.45 E to 24.56 S, 15.56 E
Tuli Game Reserve, Botswana	2	5	3.5	5 (GPS)	22.02 S, 29.02 E
Karongwe Private Game Reserve, South Africa	3	11	0.5	2 (GPS, VHF)	27.33 S, 32.06 E
Phinda Private Game Reserve and Mkhuze Game Reserve, South Africa	4	21	2.6	1–6 (VHF)	27.78 S, 32.35 E
Mpala Research Centre, Kenya	5	4	5.0	288 (GPS)	0.29 N, 36.90 E
Mpala Research Centre, Kenya	6	4	5.0	96 (GPS)	0.29 N, 36.90 E
Western Oman	7	2	2.3	10–18 (GPS)	17.12 N, 54.56 E & 16.44 N, 53.23 E
Northeastern Iran	8	7	12.7	8–24 (GPS)	36.56 N, 59.41 E
Southern India	9	5	385.2	8 (GPS)	12.40 N, 77.00 E
Northern India	10	5	224.4	8 (GPS)	19.57 N, 73.94 to 19.46 N, 74.09 E

west of Windhoek and in the arid zone between the country's central mountain range and the sandy desert environments in the west. Both areas have extremely low human and low-to-medium livestock densities, mainly due to the low primary production qualities of these landscapes, resulting in extensive range management. Botswanan leopards included in this study lived in the Northern Tuli Game Reserve of the semiarid Tuli Block region situated in southeastern Botswana (Steyn and Funston 2009). Two leopard studies were included from South Africa. The first of these took place in Limpopo Province, South Africa, with leopards living on Karongwe Private Game Reserve (Owen 2013). The second was in and around Phinda Private Game Reserve in northern KwaZulu-Natal, South Africa (Fattebert et al. 2016). Kenyan leopard data were collected at Mpala Research Centre, a wildlife conservancy and working cattle ranch located on the Laikipia Plateau in central Kenya (Isbell et al. 2018; Van Cleave et al. 2018). Leopards from Oman lived in two distinct management landscapes. The male occupied the Jabal Sahman Nature Reserve along a rocky spine of mountains jutting out of the arid landscape with very low human impact (Spalton et al. 2006); the female lived in a more heavily wooded enclave which lacked official wildlife protection along the Arabian coast and was dotted with herding villages and coastal roads. Persian leopards were studied in Tandoureh National Park, a steppe mountain landscape along the Iran-Turkmenistan border (Farhadinia et al. 2018b). We included data from two studies of leopards carried out in India. The first of these was located in the Ramanagara, Chamarajanagara, Bangalore Rural, Mandya, and Mysore districts of southern India and focused on translocated individuals from areas with high frequencies of livestock predation. The second study tracked collared leopards across a wide area of western Maharashtra centered around Ahmednagar district (Odden et al. 2014). India is characterized by dense agriculture and high human population densities, whereas Namibia had extremely low human densities and drought-adapted vegetation; all other sites fell between these extremes.

Data collection.—Leopards included in the studies described above were captured with a variety of techniques including free-darting, baited cage traps, and soft-hold foot snares as described in Balme et al. (2007). Individuals were fitted with GPS, VHF, or GPS/VHF tracking collars. Eleven movement profiles represented relocated "problem" leopards that were moved to novel environments far from their original home ranges. These included livestock predators and also leopards released from rehabilitation centers after injuries. We used these tracks to quantify their space use to evaluate establishment of home ranges by translocated individuals. Leopards that did not establish stable (extended local residence without rapid, repeated displacement to new areas) home ranges were excluded from model comparisons.

Analyses.—We uploaded all locational data to Movebank (and integrated data already accessible on Movebank) to allow for uniform data comparison of covariates across all leopard data sets (Kays et al. 2015). We used the Movebank ENV-Data system (Dodge et al. 2013) to spatiotemporally link each leopard location to the chosen covariates to test our hypotheses about the effect of habitat productivity and human disturbance. Our chosen variables were log-transformed human density from a large NASA data set detailing human development (SEDAC GRUMP 2000 Population Density Adjusted—Center for International Earth Science Information Network [CIESIN] 2018); landscape productivity based on vegetation cover (MODIS Land Terra Vegetation Indices 250 m 16-day NDVI); closed/open habitat, synthesized using satellite-derived land-cover classification of GlobCover 2009 Land-Cover Classification (Bontemps et al. 2011) included as Appendix I; elevation (ASTER ASTGTM2 Elevation); and temperature (ECMWF Interim Full Daily SFC Temperature, 2 m above ground—Dee et al. 2011). We initially considered the two following variables but later removed them due to their high (> 0.6) correlation with other variables. The first of these, satellite forecasted precipitation (ECMWF Interim Full Daily SFC-FC Total Precipitation), was strongly correlated with vegetative cover, while the second, UN mapped domestic livestock density (Gilbert et al. 2018), was highly correlated with human density. Although larger predators like African lions and tigers might affect leopard movement

(du Preez et al. 2015; Maputla et al. 2015; Mugerwa et al. 2017; Kafley et al. 2019), we omitted these apex predators as potential covariates due to a lack of data on their abundance across our study sites.

We removed GPS outliers manually when locations represented > 40 km movement in less than 12 h. In addition, the GPS histories of two individual leopards (Kaveh/M6 in Iran and Pp27 in Namibia) were split into two distinct transects denoted as their Alpha and Beta tracks (Supplementary Data SD1). This was due to their apparent displacement from their original home ranges (noted as Alpha home ranges), followed by brief exploratory movements, and subsequently establishment of a second distinct home range (designated as Beta home ranges). These Alpha and Beta home ranges were treated as separate distinct entities for analyses resulting in $n = 76$ home ranges.

We used a vegetation index (NDVI) as a proxy for landscape productivity where higher primary production likely supported higher prey densities (either wildlife or livestock) in a similar manner to how Enhanced Vegetation Index (EVI) was previously used to evaluate potential dispersal zones for young leopards (Fattebert et al. 2016).

We estimated home range sizes using the *ctmm* package in R (Calabrese et al. 2016). We plotted semivariograms to evaluate stable and nonstable home ranging behavior. These semivariograms were plots of the semivariance in locations as a function of the time lag separating observations (Noonan et al. 2019). An asymptotic smoothing of a semivariogram indicated stabilization in home range establishment (Fig. 2A: individual 5864), whereas a lack of such stabilization in the plot indicated lack of establishment of a defined home range (Fig. 2B: individual D031671).

To evaluate the relative importance of these six covariates in explaining variation in home range size, we used linear regression models and ranked these models by their corrected Akaike's Information Criterion (AICc), corrected for small sample sizes values to determine which model best fit the data with regard to our beta coefficients to determine the most important parameters (Anderson 2008). After initial data explorations, we added one interactive effect between habitat openness and human population density, to help test the hypothesis that habitat openness mediates the way leopards responded to humans. We ultimately tested six models in different combinations to assess effects the different variables on home range size and calculated R^2 values for each model.

RESULTS

Home range establishment and maintenance.—Of the 61 nontranslocated leopards, 58 (95.2%) maintained stable home ranges. Of the three (4.8%) that did not, all were males, and two were subadults in the dispersal time stage of their lives. In contrast, only five of the 13 translocated individuals (38.5%) established home ranges during the duration of their monitoring, and eight (61.5%) did not (Supplementary Data SD1). Individuals that did not establish home ranges were not included in the modeling.

Males' versus females' home range size.—We found that across their entire geographic range, mean home range size of females differed from that of males (Mann–Whitney U-test: $U = 343$; $z = 0.01$; $P = 0.008$). On average, home ranges of males (188.90 ± 34.59 SE km^2, $n = 28$) were 3.2 times larger than those of females (58.26 ± 10.52 SE km^2, $n = 31$). Leopard home range sizes showed substantial variation across countries (Fig. 3).
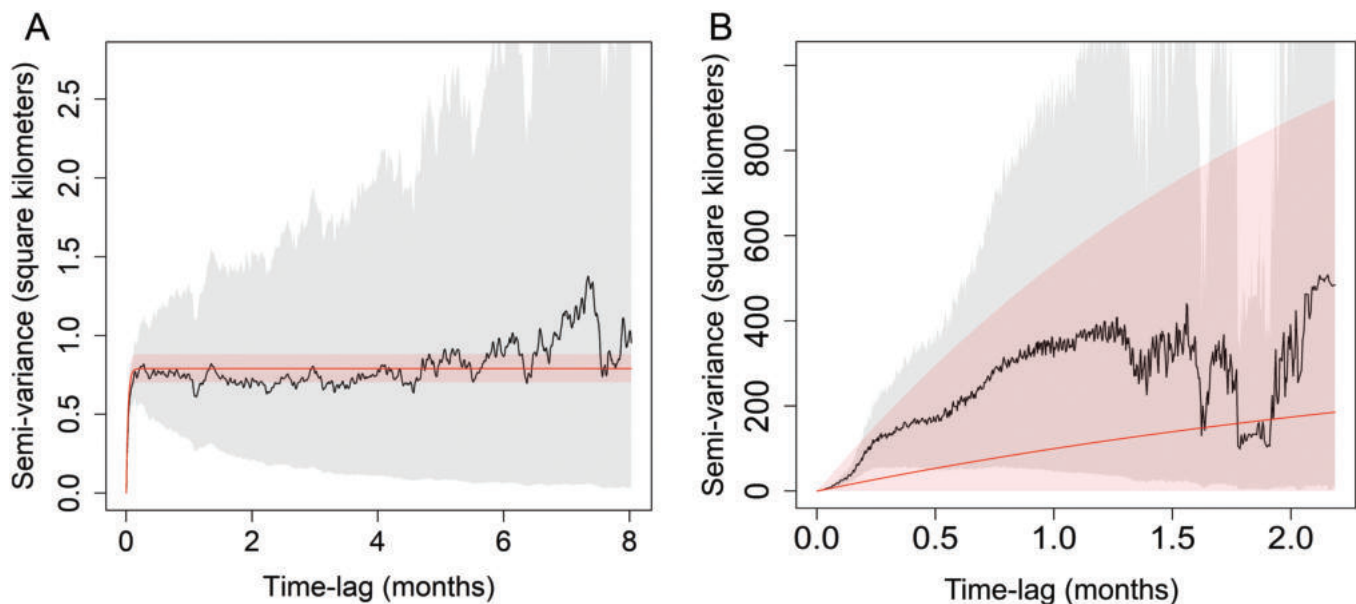
Fig. 2.—Variogram comparisons of two leopards demonstrating home range establishment through time. The gray shading represents pointwise 95% confidence intervals and the red shading represents fitted model 95% confidence intervals after accounting for autocorrelation. (A) Leopard 5864's semivariogram reaches an asymptote demonstrating that it rarely moved substantially out of an 0.8 km^2 from the location where it was originally recorded even compared to locations sampled 8 months later. (B) Leopard D031671's semivariogram does not stabilize over the 2+ months of observation; distance between points sampled 2 months apart from each other was sometimes up to 400 km and demonstrated a lack of home range establishment.
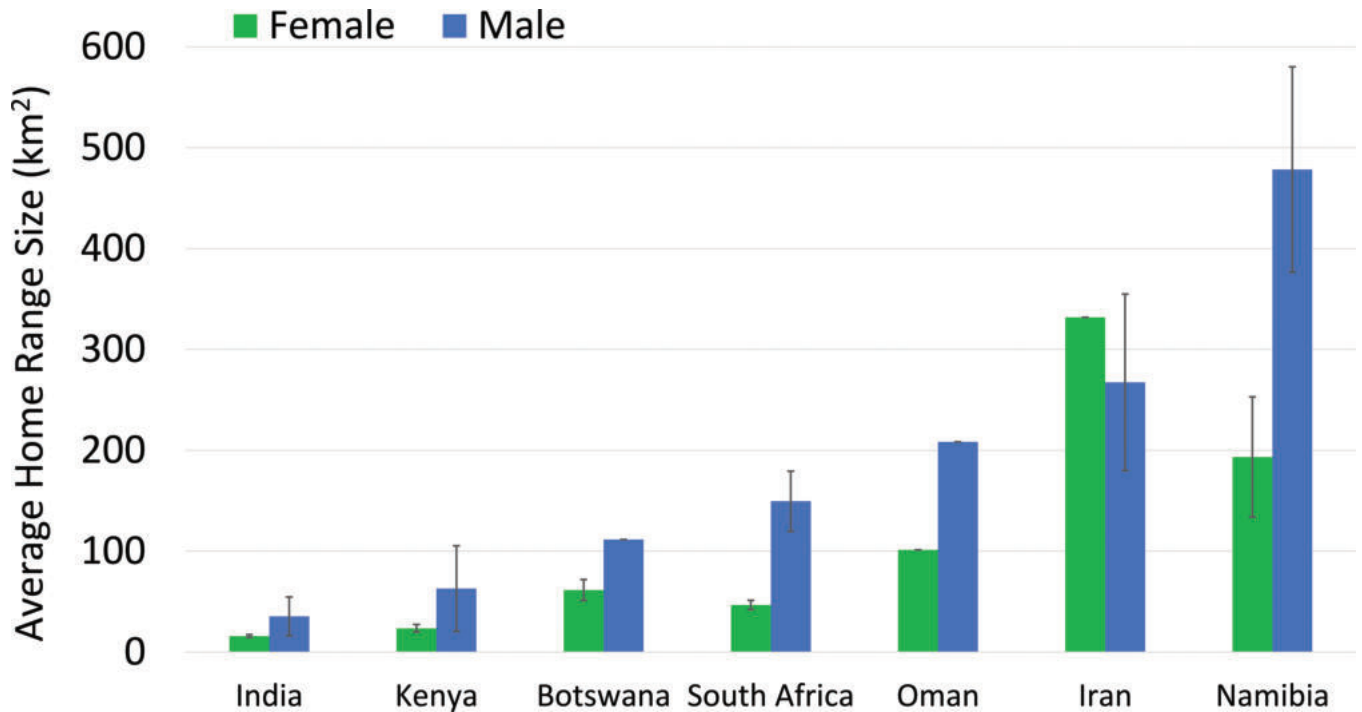
Fig. 3.—Average leopard home range size (± *SE*) by country and sex.

Model fit.—The best-fitting generalized linear model (GLM) had an adjusted R^2 of 0.64 and included the log of population density, closed/open habitat, their interactive effect, air temperature at ground level, NDVI as a proxy for landscape productivity, sex of the individual, and elevation, as the best predictors a leopard's home range size (Table 2). The beta coefficient value for each of these parameters is recorded in Table 3. Broadly, we observed that as landscape productivity increased, leopard home range size decreased (Fig. 4). During more thorough exploration of the data, we observed that vegetation did not tell the full story. When open versus closed habitat was added to the model as an interactive effect, we found that as human population density increased in open habitats, leopard home range size decreased (Fig. 5); however, as human population density increased in closed habitats, leopard home range size increased.

DISCUSSION

Generally, our hypotheses regarding factors that affect variation in leopard home range size were supported by the data. For instance, males maintained larger home ranges than females in most countries, and leopards inhabiting areas with higher habitat productivity usually resulted in smaller home ranges. Some of our results revealed deeper nuance: the relationship between leopard home range size and local human density, where leopard home range size increased as human density increased in closed habitats but home range size decreased as human density increased in open habitats.

New techniques for home range analysis and the ability to uniformly evaluate GPS and VHF tracking data enabled us to carry out one of the most extensive studies of a large terrestrial

carnivores (Hofman et al. 2019), with 74 leopards included across seven countries, and home ranges varying in size from 14.5 to 885.6 km². This represents a 60-fold variation in home range size, one of the largest known for terrestrial carnivores. This is only exceeded by red foxes (*Vulpes vulpes*) with a 200-fold variation (Macdonald et al. 2015; Walton et al. 2017) and wolves (*Canis lupus*) with a ~100-fold variation in home range size (Hefner and Geffen 1999; Walton et al. 2001). By comparison, home range size variation in leopards exceeds that of other cryptic, solitary felids; e.g., jaguars (*Panthera onca*, 36-fold—Morato et al. 2016) and puma (*P. concolor*, 8-fold—Dellinger et al. 2019), and nonfelids such as the wolverine (*Gulo gulo*, 50-fold—Persson et al. 2010). Although leopard home ranges are larger, particularly in mountainous regions such as Iran and Oman, even our large estimates might be underestimated. Planimetric estimates of home ranges without accounting for vertical relief in rugged terrain could result in 38% underestimation in home range size in leopards (Farhadinia et al. 2019).

Our measures of area used by leopards in relation to levels of human disturbance are consistent with predictions from a recent study on distance moved (Ngoprasert et al. 2017) for animals in open, protected wildlife habitats. Tucker et al. (2018) demonstrated the effects of human-restricted wildlife movement for a variety of mammalian species, but their study relied on straight-line distance moved using two different measures with two different time periods and did not include studies from the world's most densely populated areas. Our study confirmed that humans affected leopard movements over longer time periods and at the home range level. Our best-fitting model also revealed an important new detail about the leopard–human relationship where leopard home range size increases as human

Table 2.—Top-ranked linear models predicting the effects of environmental variables and human population density of leopard home range sizes. AICc = corrected Akaike's Information Criterion.

| Model covariates	AIC	Delta AICc	Model likelihood
Log of population density + closed/open habitat + (log of population density * closed/open habitat) + temperature + vegetation + sex + elevation	26.8	0	1.0
Log of population density + temperature + vegetation + sex + closed/open habitat + elevation	36.0	9.1	0
Log of population density + temperature + vegetation + sex + elevation	39.6	12.7	0
Log of population density + closed/open habitat + (log of population density * closed/open habitat) + temperature + vegetation + sex	43.7	16.8	0
Log of population density + temperature + vegetation + sex	51.2	24.4	0
Log of population density + temperature + vegetation + sex + closed/open habitat	53.7	26.8	0

Table 3.—Beta estimates for covariates from the best fit model. In open habitats, as human population density increases, leopard home range size decreased. In closed habitats, as human population density increases, leopard home range size decreased. As temperature and vegetation increase, leopard home range size decreased. Home range sizes were smaller for females than males.

Variable	Beta estimate
Log of population density	−0.699
closed/open habitat	−0.320
(Log of population density * closed/open habitat)	0.460
Temperature	−0.041
Vegetation	−1.161
Sex	−0.444
Elevation	−0.004

density increases in open habitats but home range size decreases as human density increases in closed habitats.

The mechanism behind the relationship between closed and open habitats relative to human population density is not immediately obvious, but it is possible that livestock populations are higher in open habitats, especially for smaller stock such as goats and sheep, providing more food for leopards and allowing them to use smaller home ranges near people. This hypothesis, which speaks to a common bottom-up effect impacting carnivore behavior, should be tested with additional data from leopard populations elsewhere, and with local, fine-scale estimates of livestock density. It is possible that leopards also are impacted by a top-down effect whereby they actively reduce their movement to limit exposure to potential human threats with less available concealment in open habitats; e.g., by spatiotemporally adjusting their activity to avoid encounters with humans (Odden et al. 2014). Exactly which aspects of habitat structure affect this relationship currently remains unknown, but we are aware that related generalist predators (such as mountain lions) operating in urban environments balance risk versus reward to similar landscapes of fear (Blecha et al. 2018). In less risky areas, such as closed habitats where concealment is plentiful, leopards might be freer to move more broadly around the landscape in search of areas of high food availability. Similarly, males might be able to expand their home ranges to overlap with more females if the risk of moving between these female's home ranges is reduced by higher degrees of cover and concealment.

It is important to note that our classification of open and closed habitat was necessarily coarse due to our large-scale
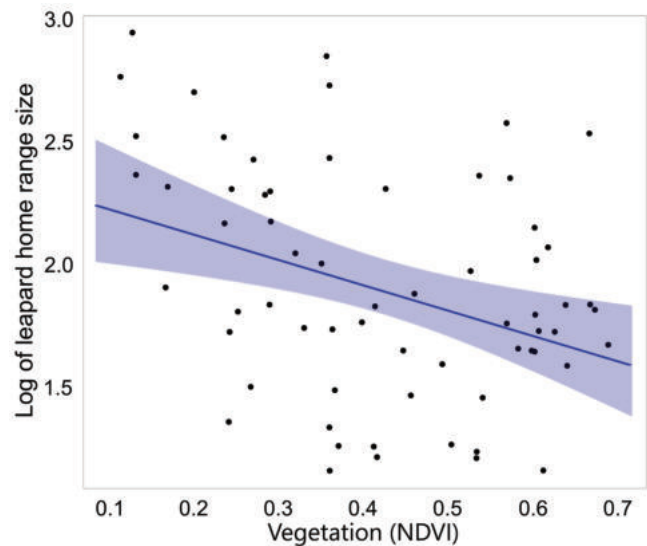

Fig. 4.—Relationship between landscape productivity (indexed as Nominal Difference Vegetation Index [NDVI]) relative to the log of leopard home range size with the 95% confidence interval shaded in blue; each dot represents an individual leopard's home range estimate.

comparisons. This suggests a need for study of higher resolution comparisons to test if trends in leopard density follow similar patterns, especially in border locations between anthropogenic and natural habitats and in dense rainforest, which are not well represented in our data set. A further consideration is that important resources in open habitat often are more widely distributed (e.g., water in the vast arid stretches of Namibia) that impact prey distribution in addition to being essential for leopards. These aspects should be a priority for future research into how habitat mediates relationships between humans and leopards at a finer-scaled resolution.

Recent comparisons of jaguar ranging behavior also indicate that a habitat-mediated response might be a general ranging characteristic of large felids living near areas of human activity, because home range size was positively correlated with human density (Morato et al. 2016). This is inconsistent with Tucker et al. (2018), who found reduced movement of mammals proximate to human development; however, many jaguars in the study by Morato et al. (2016) were located in densely vegetated areas near people, matching our result of leopards in dense habitats using larger home ranges near people.
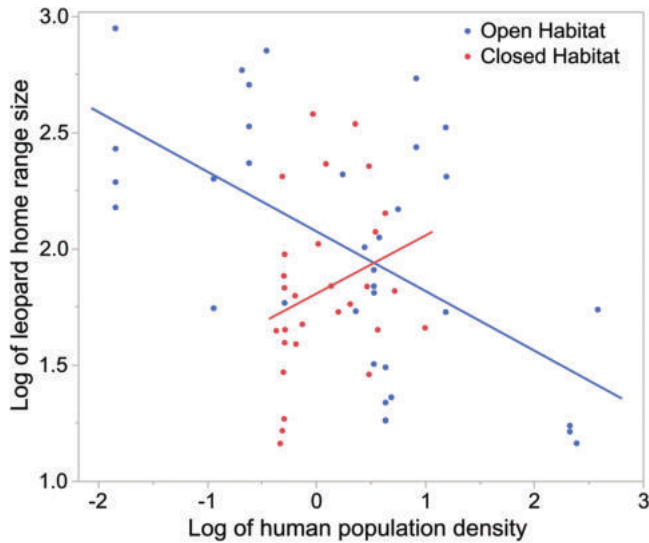
Fig. 5.—Relationship of human population density in closed versus open habitats on leopard home range size.

Variogram analysis revealed that 63 individuals (85.1%) in our study established or maintained stable home ranges during their study periods while 11 (14.9%) did not. Translocated individuals of a variety of carnivore species have been observed to move extensively after release (Fontúrbel and Simonetti 2011), and this has been shown to be partially true for leopards in India and Namibia (Odden et al. 2014; Weise et al. 2015). The tendency to move widely immediately after release is evident in our data because only five of the 13 translocated individuals (38.5%) established recognizable home ranges.

Only three of 74 nontranslocated leopards did not establish stable home ranges over the course of this study; all three were males. One was a subadult, whose collar was removed after he moved far outside of the area in which he was originally collared. Another subadult appeared to traverse between two areas of thick vegetative cover across multiple properties with different management styles, including ones with a history of large carnivore persecutions. Given that both individuals were about 3 years old, it is likely that their extensive movements signified dispersal from natal ranges. Only one adult male, from Iran, representing 1.6% of our nontranslocated sample, did not exhibit a stable home range according to our analyses, in contrast to jaguar studies in which 16.1% of adults did not establish home ranges (Morato et al. 2016).

Male leopards maintained stable, resident home ranges about three times larger than females across almost all regions. This is consistent with other predominantly solitary large felids, such as snow leopards (*Panthera uncia*—Orjan et al. 2018), jaguars (Morato et al. 2016), and pumas (Grigione et al. 2002). The single young leopard female studied in Iran constituted the only exception, but a small sample size in this region limits our inference. This sex-based pattern in home range size aligns with a general trend among solitary carnivorous mammals where females are constrained by prey availability (Owen 2013) and dietary balance needed to raise less mobile young, while males tend to range more widely to increase access to females (Macdonald 1983). On a more nuanced level, past leopard

research has found that as leopard density increased, female home range decreased independent of habitat productivity due to mothers giving space to daughters, whereas males home ranges remained large under the same conditions to maintain access to more females (Fattebert et al. 2016).

Our negative relationship between habitat productivity (indexed with NDVI) and leopard home range size is similar to results from other carnivore home range studies (Duncan et al. 2015) and presumably also is related to higher population density for these species in more productive habitats (Hatton et al. 2015). This was corroborated by previous leopard home range work in Namibia where home range size was negatively correlated with prey biomass and prey biomass was linked to rainfall (Marker and Dickman 2005).

We demonstrated the potential for broad-scale comparisons across multiple biogeographic regions to investigate large-scale ecological patterns while providing new insight into wildlife–habitat relationships, specifically how habitat type could modify the relationship between humans and large carnivores. We found that leopards used smaller areas near people in open habitat but had larger home ranges near people in dense habitats, yielding a novel insight into human–carnivore interactions. A more refined understanding of how leopards perceive risk in an environment will make conservation efforts more effective. Refugia become even more vital in riskier environments and intentionally preserving such resources make landscapes more accommodating for leopards.

Recent research involving main habitat has shown that in some regions leopards extensively forage and make 90% of their kills in core home range areas (Farhadinia et al. 2018a). Additional data, especially from areas with low livestock density but high human density, could help shed more light on the core causes of some of these relationships between risky landscapes and prey availability. Working to conserve refugia and corridors will have a significant benefit for leopards making a home in those habitats. Finally, more robust data on carnivore tolerance and leopard persecution at a local scale might enable a much more nuanced understanding of leopard behavior across different sampling landscapes.

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Supplementary Data

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

Supplementary Data SD1.—Home range size, residency, and demographic information for individual leopards by country and research project. Home range size of nonresident leopards was not calculated.

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Appendix I

GlobCover closed/open Evaluation: GlobCover values assigned different habitat types detected through satellite remote sensing. The closed/open evaluation was assigned after using Google Earth to review examples of these different land covers in the countries that were covered in the study.

GlobCover value	GlobCover label	closed/open assignment
11	Postflooding or irrigated croplands (or aquatic)	open
14	Rainfed croplands	open
20	Mosaic cropland (50–70%)/vegetation (grassland/shrubland/forest) (20–50%)	open
30	Mosaic vegetation (grassland/shrubland/forest) (50–70%)/cropland (20–50%)	open
40	closed to open (> 15%) broad-leaved evergreen or semideciduous forest (> 5 m)	closed
50	closed (> 40%) broad-leaved deciduous forest (> 5 m)	closed
60	open (15–40%) broad-leaved deciduous forest/woodland (> 5 m)	closed
70	closed (> 40%) needle-leaved evergreen forest (> 5 m)	closed
90	open (15–40%) needle-leaved deciduous or evergreen forest (> 5 m)	open
100	closed to open (> 15%) mixed broad-leaved and needle-leaved forest (> 5 m)	closed
110	Mosaic forest or shrubland (50–70%)/grassland (20–50%)	closed
120	Mosaic grassland (50–70%)/forest or shrubland (20–50%)	open
130	closed to open (> 15%) (broad-leaved or needle-leaved, evergreen or deciduous) shrubland (< 5 m)	closed
140	closed to open (> 15%) herbaceous vegetation (grassland, savannas, or lichens/mosses)	open
150	Sparse (< 15%) vegetation	open
160	closed to open (> 15%) broad-leaved forest regularly flooded (semipermanently or temporarily)—fresh or brackish water	closed
170	closed (> 40%) broad-leaved forest or shrubland permanently flooded—saline or brackish water	closed
180	closed to open (> 15%) grassland or woody vegetation on regularly flooded or waterlogged soil—fresh, brackish, or saline water	closed
190	Artificial surfaces and associated areas (urban areas > 50%)	open
200	Bare areas	open
210	Water bodies	N/A
220	Permanent snow and ice	N/A
230	No data (burnt areas, clouds)	N/A