Estimating global determinants of leopard home range size in a changing world

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Abstract

Movement is a fundamental process in animal ecology. For many species, such as large carnivores, movement patterns are greatly shaped by a combination of ecological and anthropogenic factors. Understanding how these factors impact the roaming capacity of large carnivores is essential to forecast risks and design long-term conservation strategies. The leopard (*Panthera pardus*) is a generalist predator broadly distributed over varied and different environments, but global leopard populations are declining at a concerning rate and conservation actions are pressing. This scenario makes the leopard a suitable species to understand how global ecological and anthropogenic drivers affect the spatial behaviour of large carnivores and how these should inform conservation efforts. We compiled data from local studies worldwide and used macroecological (climatic, productivity, and human footprint), and intra- and interspecific (conspecifics, competitors and prey) predictors to model the roaming requirements of leopards based on home range sizes. Male home range size was largely and positively related to the range sizes of local females and inversely to vegetation productivity. For females, higher seasonal variations in temperature like the observed in arid areas were associated with larger home ranges, while increased human impact resulted in smaller home ranges likely due to concentrated food resources such as domestic species. These predictors are linked to threatening global change processes due to anthropogenic activities that will likely impact the roaming behaviour of leopards in the coming decades with potential consequences for their populations worldwide. Our results provide crucial information towards the development of integrative research linking macroecological and local variables with global change predictions that can inform conservation programmes addressing future risks of degradation, endangerment and human-leopard conservation conflicts.

Introduction

Movement is a fundamental property of non-sessile animals that implies continuous decisions on why, when and where to move in order to maximise reproduction and survival (Nathan *et al.*, 2008). Movement decisions shape emergent patterns of a species' space use and thus ecosystem structure and functioning; therefore, understanding this behaviour is of paramount ecological, evolutionary and conservation importance (Swingland & Greenwood, 1983; Tucker *et al.*, 2018). A broadly used concept and estimator to summarise the space use of individual animals is the home range (hereafter HR), which location, size and shape are moulded by movement choices (Börger *et al.*, 2008). Initially defined as the

space where animals perform their normal activities to survive and reproduce (Burt, 1943), a recent definition considers HR as the spatial expression of a cognitive map of the environment that individuals keep up-to-date (Powell & Mitchell, 2012). Hence, animals move and shape their HR according to the physical characteristics of the environment and the distribution, aggregation and predictability of resources (e.g. food, shelter and potential mates; Macdonald, 1983; Mitchell & Powell, 2007; Macdonald & Johnson, 2015). Additionally, threats such as agonistic interactions with conspecifics and other species, including humans, influence the selection of HRs (Newsome *et al.*, 2017; Melzheimer *et al.*, 2020). Hence, disentangling the drivers of HR size and shape resulting from animal movements is paramount to understanding

ecological patterns including species' distribution, abundance and habitat selection (Rhodes *et al.*, 2015), predator–prey dynamics (Lewis & Murray, 1993), population regulation (Gautestad & Mysterud, 2005) and community structure and function (Fagan *et al.*, 2007). Research efforts in this direction are currently pressing, considering the increasing constraints to animal movements due to anthropogenic ecosystem changes (Tucker *et al.*, 2018). This threat is considered particularly severe for terrestrial species that exhibit long-range roaming behaviour, such as large mammalian carnivores (Chapron, 2014; Ripple *et al.*, 2014; Tucker *et al.*, 2018).

There is considerable empirical evidence of how individual features, such as sex, age and body mass shape HR sizes in carnivore species, which are strongly influenced by environmental constraints; as predicted by the Resource Dispersion Hypothesis (RDH; and other theoretical frameworks; Macdonald, 1983; Macdonald & Johnson, 2015). The resulting compromise between the benefits and costs of maintaining an HR (i.e. net-resource value) determines its size (Mitchell & Powell, 2012), which is commonly inverse to local food availability (Mitchell & Powell, 2007). To date, most HR studies on carnivores have been conducted at small and intermediate spatial scales (e.g. Mizutani & Jewell, 1998; Hayward *et al.*, 2009). Nevertheless, the role of macroecological factors on HR size has been rarely evaluated over the global range of widely distributed carnivore species (Gompper & Gittleman, 1991; Ferguson & McLoughlin, 2000; Nilsen *et al.*, 2005; Macdonald & Loveridge, 2010). Although macroecological research cannot completely explain the variations in HR size and replace intensive small-scale studies, it can reveal valuable information about the general processes that affect the behavioural traits of species at a global scale and can assist related conservation efforts.

Among large carnivores, the leopard (*Panthera pardus*) is one of the most widespread; however, leopards have recently experienced a dramatic reduction in their global distribution (Fig. 1), existing today over only 25–37% of their historical range (Ripple *et al.*, 2014; Jacobson *et al.*, 2016). Consequently, the species is listed as vulnerable by the IUCN, with several of the nine subspecies classified as critically endangered (Jacobson *et al.*, 2016; Stein *et al.*, 2020). The main factors contributing to the decline of the leopard are habitat destruction, prey depletion, human-wildlife conflict (resulting in retaliatory killings), trophy hunting and poaching (Jacobson *et al.*, 2016). The leopard is a generalist apex predator considered the most adaptable among the big cats (Sunquist & Sunquist, 2002). It preys upon a broad range of species and can live in a remarkable array of environments as varied as deserts, savannahs, tropical and temperate forests, high-mountain regions and even densely populated urban areas (Athreya *et al.*, 2020; Stein *et al.*, 2020). This adaptability enabled the leopard to maintain a broad distribution across Africa, Asia and even Europe during the Pleistocene (Sommer & Benecke, 2006; Jacobson *et al.*, 2016). For most felids, there is limited data on intraspecific variation in HR sizes (Macdonald & Loveridge, 2010), but numerous

telemetry studies on leopards at a local scale have been conducted across its global distribution. These studies reveal HR size in leopards is among the most variable known within the large carnivores. Leopards are solitary, territorial animals and males defend an exclusive territory that typically contains the territories of several females. Male HRs differ in size up to two orders of magnitude across bioclimatic regions (Sunquist & Sunquist, 2002; Stein & Hayssen, 2013). The existence of such striking variation makes the leopard a useful model species to identify the fundamental macroecological drivers of felids' HRs at a global scale and across broad environmental gradients. Furthering our knowledge about the HR size of leopards across their distribution could provide insights into drivers determining carnivore movements and spatial requirements at the global scale. Such understanding can contribute to improve the quality of long-term conservation strategies of leopards and other similar predators in addition to the valuable local-scale studies.

Studies aiming to understand general patterns of carnivore HR size at a global scale require the use of indirect macroecological predictors linked to prey. These predictors can include proxies on seasonality, primary productivity and aridity (Ferguson & McLoughlin, 2000; Nilsen *et al.*, 2005; Hayward *et al.*, 2009). This is especially important for species such as the leopard, which hunts and scavenges a wide variety of species in a wide range of environmental conditions (Matthew W. Hayward *et al.*, 2006). Previous research incorporating 10 sites in Africa and Asia identified ecosystem productivity as inversely related to home-range size (Snider *et al.*, 2021). However, in addition to prey, leopards often coexist with other large carnivores, including larger competitors such as tigers (*Panthera tigris*), lions (*Panthera leo*) and spotted hyenas (*Crocuta crocuta*). Interspecific interactions can have a major influence on large carnivore ecology and survival (Palomares & Caro, 1999), with the potential to shape their movements and HRs. High prey availability in productive environments can relax competition and reduce the HR size of predators (Santos *et al.*, 2019). Moreover, vulnerable carnivore species can seek refuge in areas with a low abundance of larger competitors to avoid agonistic encounters, which can result in spatial segregation (Kafley *et al.*, 2019). Ultimately, local displacement (Newsome *et al.*, 2017) and a reduction in resource availability due to exploitative competition (Caro & Stoner, 2003) influence carnivore HR size. Local-scale studies have shown inconsistent results regarding the role of dominant carnivores on leopard population density and activity (Steinmetz *et al.*, 2013; Vanak *et al.*, 2013; Balme *et al.*, 2017). However, no attempt has been made so far to understand general trends on how the presence of different competitors influences the HR behaviour of leopards on a global scale.

We compiled research on leopard home-range size collected from 1968 to 2018 over 34 sites and used a multipopulation and macro-scale approach that combined climatic and anthropic factors with biotic intra- and inter-specific drivers to estimate how the HR sizes of leopards (indicating their roaming capacity) vary across their global distribution. We accounted for important variables for feline behaviour
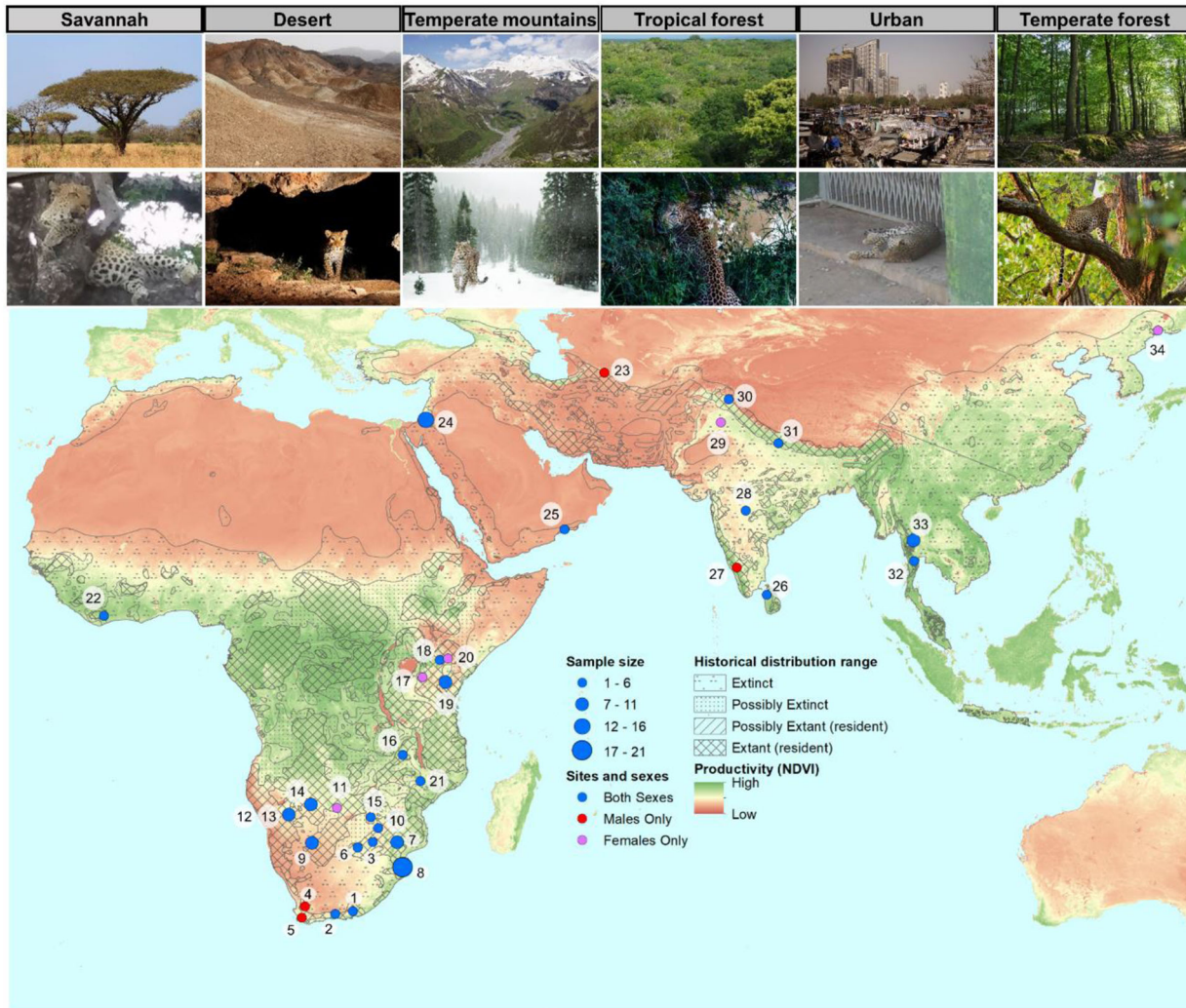
Figure 1 Global distribution of leopard (NatureServe and IUCN, 2019). The study sites used to collect information on home ranges from studies published between 1968 and 2018 are shown by coloured points. Sample size is given as the number of resident adults. A complete list of the numbered study sites and the research there conducted is included in the Supporting Information (Table S1.1). Photo credits from left to right (top; bottom).- savannah (Sebastian Justicia; Luis Miguel González); desert (both by Miha Krofel); temperate mountains (Miha Krofel; pexels.com); tropical forest (Marcos Moleón; DenRousezet / Unsplash); urban (Nicolas Vigier / flickr.com; Coolboyshiv / commons. wikimedia.org); temperate forest (Jorge Lozano; Jeremy Bishop/Unsplash).

related to mate availability, competition with other carnivores and prey diversity. Given the considerable sexual dimorphism in leopards relating to body size and resulting in sex-specific dietary preferences (Voigt *et al.,* 2018), we conducted analyses separately for males and females. This approach enabled us to evaluate whether the HR size ratio between sexes varies across the leopard's distribution. This also enabled us to test the hypothesis made by Bailey (2005), who suggested that beyond a certain threshold of decreasing landscape productivity, the HR of both sexes might converge in size. The incorporation of global indicators of human impacts may also inform our view of plausible responses of leopard populations to anthropogenic global-change scenarios. Lastly, we discuss how variations in

crucial macroecological factors could impact leopard ecology and conservation in the future, which requires particular attention in international strategies for the conservation of leopards and other endangered species.

Materials and methods

Study areas

We covered the global distribution of the leopard and included a total of 34 study areas across Africa (*n* = 22) and Asia (*n* = 12, including three in the Middle East) with published information on the home-range size of the species (Fig. 1; Table S1.1).

Datasets

Leopards.

We searched for scientific articles, books and technical reports that contained information on the HR size of leopards tracked with either VHF or GPS collars, or both within the same research. We selected 30 studies published between 1968 and 2018, from which we compiled HR information of 158 resident adult leopards (83 males and 75 females) (see Appendix S1). We excluded non-adult and non-resident individuals data to avoid inflated estimations on HR size due to dispersal and nomadic behaviour. We also discarded seasonal estimates and only used the final HR size values derived from the entire tracking period conducted in each reviewed study. Home-range size was estimated in these publications using 100% and/or 95% minimum convex polygon ($n = 24$ study areas) (Mohr, 1947), kernels ($n = 11$) (Worton, 1989) or both estimators ($n = 10$). The estimator was not mentioned in three publications, as these were older publications. Thus, we assumed that 100% MCP was used, as reporting this estimator has been standard practice and is broadly used in the literature. For subsequent analyses, we used estimations based on the 95% MCP. Although different home-range estimators produce different results, we identified a strong linear relationship between the 95% and 100% MCP home ranges in the studied leopard dataset ($R^2 = 0.99$ males, 0.98 females and 0.98 for all leopards). We also identified a linear relationship between 95% MCP and kernels ($R^2 = 0.76$ males, 0.93 females and 0.83 for all leopards). Thus, we assumed the resulting linear models were suitable for our leopard study to convert home-range sizes to their equivalent 95% MCP (Appendix S2, Table S2.1, Fig. S2.1, Fig. S2.2).

Predictors

We collected variables of vegetation productivity, climate, human footprint (Venter *et al.,* 2016), competitors, leopard body mass, prey size and prey group size. For vegetation productivity, we used global rasters (0.05 degrees or 5600 m pixels) on the average mean annual NDVI (Normalised Digital Vegetation Index; Didan & Barreto, 2016) from 1981, 1993 and 2010. These were the middle years of the three equal periods. We divided the study window into (1968–2018) to account for potential changes in productivity over this time. Climate variables were obtained from the CHELSA database (Climatologies at high resolution for the Earth's land surface areas; Karger *et al.,* 2017). They included aridity, annual precipitation, annual mean temperature, temperature seasonality, the maximum temperature of the warmest month, and precipitation seasonality. Most of the reviewed articles did not provide information on the home range size of each individual tracked, nor the spatial datasets of their spatial location and distribution necessary to quantify the values of the local environmental variables they individually contained. Thus, for each study area, we used

ArcGIS software (ESRI, Redlands, California) to extract the mean value of each predictor within a buffer equal to the average HR size reported in the area multiplied by the number of studied individuals. We considered this buffered area characterised a scale encompassing the region where leopards chose to place their home range (Johnson, 1980). When these buffers were smaller than the average HR size of all the studied leopards (111 km^2), we used the global value as the buffer instead. Additionally, we also extracted the standard deviation of each variable within the buffers to account for spatial heterogeneity.

The number of potential prey species present in each study area (determined from literature and internet search) was incorporated in the analyses, as well as the presence of major competitors, that is lion, spotted hyena, tiger, dhole (*Cuon alpinus*) and grey wolf (*Canis lupus*) as dummy variables. For prey, we included the mean group size of the main three leopard prey species at each site and the mean adult (male and female) weight of these species according to published data (Hayward *et al.,* 2019; Encyclopedia of Life, n.d.). In addition, we incorporated the average body weight of male and female leopards in each study area, as reported in the source studies used for this research or according to Castelló (2020) when this information was not provided in these sources.

Modelling

Before implementing models, we checked for multicollinearity between our predictors and discarded variables that showed a high correlation ($|r| > 0.7$) and variance inflation factor (VIF <4) (Zuur *et al.,* 2010). Based on these analyses, we removed annual mean precipitation from the predictors modelled. We also discarded wolf presence because models failed to produce coefficients for this factor, likely due to the low number of sites with wolves ($n = 3$). Thus, we included 12 predictors in our model procedures (Table 1).

We regressed predictors (scaled) against a logarithmic transformation of the HR size as the response variable using linear models in R Software (R Core Team, 2020). Considering the limited sample size, we iteratively tested all the models that resulted from all possible combinations of up to 5 of any of the 12 predictors in each model (Burnham & Anderson, 2002). All the models were ranked based on Akaike's Information Criterion (AIC) applied to small sample size (AICc) and averaged the top-ranked most plausible models with ΔAICc <2 (Burnham & Anderson, 2002). We conducted this procedure separately for males, females and both sexes combined. Because females are considered an important driver on the space use of male felids (Sunquist & Sunquist, 2002), including the leopard (Bailey, 2005), we incorporated in the male modelling procedure the size of female HRs. Additionally, we also calculated the ratio between male and female HR size per site. Then, we regressed it against the predictors used in the previous model procedure for all leopards to identify which environmental variables affect the male/female HR size ratio. In the

Table 1 Final predictors used to model home-range size patterns in leopards across their global distribution

Predictors	Description	Source
Climatic		
TempSeason	Standard deviation of mean temperature seasonality within the study site buffer (i.e. spatial variation)	https://chelsa-climate.org/
mTemp	Standard deviation of the annual mean temperature within the study site buffer	https://chelsa-climate.org/
PrecipSeason	Standard deviation of mean precipitation seasonality within the study site buffer	https://chelsa-climate.org/
Productivity		
mNDVI	Mean normalised digital vegetation index within the study site buffer	https://lpdaac.usgs.gov/products/vipphen_ndviv004/
sdNDVI	Standard deviation of the Normalised Digital Vegetation Index within the study site buffer	https://lpdaac.usgs.gov/products/vipphen_ndviv004/
Humans		
mHF	Mean Human Footprint within the study site buffer	https://wcshumanfootprint.org/
sdHF	Standard deviation of the Human Footprint within the study site buffer	https://wcshumanfootprint.org/
Competitors		
NComp	Number of main competitor predators identified in each study site	Literature
Lion	Binomial predictor on lion's presence.	Literature
Tiger	Binomial predictor on tiger's presence.	Literature
Hyena	Binomial predictor on hyena's presence.	Literature
Dhole	Binomial predictor on dhole's presence.	Literature
Prey		
mWeightPrey	Mean weight of the main prey in each study size	Literature
mGroupSize	Mean group size of the main prey in each study size.	Literature

modelling procedures, we assumed no spatial correlation between locations. We confirmed our assumption by testing the spatial autocorrelation of the residuals of each final model using a Moran I test. These tests rejected the alternative hypotheses that autocorrelation existed in the all leopards model ($P = 0.34$) and in the models on males ($P = 0.75$) and females ($P = 0.65$), which confirmed the suitability of our analyses. Finally, we performed a t-test to identify significant differences between continents in mean home range size per site and the male/female size ratio per site.

Results

The average HR size (mean $\pm$ SE) of leopards in the species' global distribution was 113.1 ± 20.1 km^2 (males = 161.1 ± 39.2 km^2, females = 68.1 ± 12.7 km^2). Home range size varied up to 80-fold between the study sites (7.6 km^2 in Sri Lanka and 613.6 km^2 in the Khalahari in southern Africa). The average HR size was larger in Africa (138.7 ± 30.3 km^2, males = 206.0 ± 56.7 km^2, females = 74.7 ± 15.8 km^2) than in Asia (65.5 ± 14.7 km^2, males = 75.8 ± 20.0 km^2, females = 56.1 ± 22.0 km^2), although not significantly different ($t(32) = 1.62$; $P = 0.12$). The average HR size in Asia further decreased to 46.5 ± 12.7 km^2 (males = 60.3 ± 21.4 km^2, females = 32.7 ± 13.2 km^2) after excluding the three study areas in the Middle East. In this case, the HR size of Asian leopards (after excluding the Middle East locations) were significantly

smaller to those in Africa ($t(15.93) = 2.52$; $P = 0.02$). The average HR size in the Middle East was 126.13 ± 37.6 km^2 (males = 137.9 ± 14.0 km^2, females = 118.3 ± 67.7 km^2). The average ratio of male/female HR size (mean $\pm$ SE) was fairly consistent across the study sites and was largest in the Middle East (2.80 ± 0.65), followed by Africa (2.77 ± 0.43) and Asia (2.05 ± 0.26). However, we found no significant differences between the ratios in Africa and Asia ($t(1.11, P = 0.28)$) even after discarding the three Middle East locations ($t(1.43, P = 0.17)$) (Appendix S3, Fig. S3.1).

The female-only modelling yielded 11 most plausible models (i.e. ΔAICc <2) with an adjusted R^2 ranging from 0.52 to 0.63 (Appendix S4, Table S4.1). The averaged model included human, climatic, prey and competitor related variables (Table 2). For female leopards, larger HR sizes were significantly related to increasing temperature seasonality (Fig. 2) and not significantly related to the spatial variation of annual mean temperature and human footprint variability within the study site (Fig. 3). Conversely, smaller HRs were significantly associated with higher productivity and average human footprint (Fig. 2), and not significantly with tiger and dhole's presence, mean prey group size and lower female's weight (Fig. 3).

The male-only modelling resulted in the three most plausible models with an R^2 of the top-ranked models between 0.72 and 0.75 (Appendix S4, Table S4.2). The averaged model contained four predictors showing a significant positive relationship between male HR size and those of females

Table 2 Coefficients including standard errors (SE) and 95% confidence intervals (CI) of the final averaged models (ΔAICc <2) resulting from each of the modelling analyses on home range size of leopards

Predictor	Females			Males			All			Male:Female HR		
	β	SE	CI	β	SE	CI	β	SE	CI	β	SE	CI
TempSeason	0.71	0.17	[0.36, 1.06]*	–	–	–	0.53	0.17	[0.19, 0.89]*	–	–	–
mTemp	0.05	0.13	[−0.10, 0.68]	–	–	–	–	–	–	–	–	–
PrecipSeason	–	–	–	–	–	–	–	–	–	–	–	–
mNDVI	−0.03	0.12	[−0.79, −0.09]*	−0.35	0.14	[−0.64, −0.06]*	−0.04	−0.03	[−0.60, 0.13]	–	–	–
sdNDVI	–	–	–	0.03	0.08	[−0.12, 0.39]	–	–	–	–	–	–
mHF	−0.49	0.19	[−0.89, −0.10]*	–	–	–	−0.71	0.20	[−1.13, −0.28]*	–	–	–
sdHF	0.11	0.22	[−0.13, 0.94]	–	–	–	0.58	0.20	[0.16, 1.00]*	–	–	–
NComp	–	–	–	–	–	–	–	–	–	−0.40	0.40	[−1.23, 0.44]
Lion	–	–	–	−0.12	0.23	[−0.44, 0.09]	–	–	–	−0.60	0.60	[−1.85, 0.66]
Tiger	−0.91	1.05	[−3.45, 0.52]	–	–	–	−0.18	0.44	[−1.62, 0.20]	–	–	–
Dhole	−0.18	0.99	[−3.69, 2.64]	–	–	–	−0.13	0.41	[−1.48, 0.23]	–	–	–
Hyena	–	–	–	–	–	–	0.03	0.03	[−0.37, 1.03]	–	–	–
mWeightPrey	–	–	–	–	–	–	–	–	–	−0.07	0.07	[−0.02, 0.01]
mGroupSize	−0.10	0.21	[−0.86, 0.17]	–	–	–	–	–	–	–	–	–
Female HRsize	×	×	×	0.77	0.18	[0.48, 1.05]*	×	×	×	×	×	×
Female's weight	−0.01	0.06	[−0.54, 0.15]	×	×	×	×	×	×	×	×	×
Male's weight	×	×	×	–	–	–	×	×	×	×	×	×

(×) indicates the predictor was not part of that modelling procedure. (−) Indicates the predictor was used in the modelling procedure but was absent from the top-ranked models to average. (*) Indicates a significant relationship between the predictor and the response variable (i.e. CI excludes zero). Variable descriptions are included in Table 1.

and increasing variability in productivity (Table 2; Fig. 2). Conversely, lion presence was not significantly associated with the smaller HR size of males (Table 2; Fig. 3).

Combined (i.e. males and females together) modelling resulted in a total of five most plausible models and an adjusted R^2 range of 0.46 to 0.51 (Appendix S4, Table S4.3). The resulting averaged model from these top five models included human, climate, prey and competitor-related variables (Table 2). This model indicated that larger HRs were significantly associated with increasing temperature seasonality and the human footprint over the study area and non-significantly with hyena's presence. Conversely, smaller HRs were significantly related to increasing averaged human footprint and non-significantly to high vegetation productivity (increasing NDVI) and dhole and tiger presence (Table 2).

Modelling to determine the environmental variables that most influenced male:female HR size ratio resulted in an averaged model that showed a negative but non-significant relationship between this ratio and the mean weight of prey, lion presence and the number of competitors (Table 2).

Discussion

This study aimed to estimate the global drivers of home range size of a widely distributed but threatened large carnivore, the leopard. Our approach combined predictors traditionally applied in macroecological research with variables reflecting dynamics between leopards and other species (i.e. intra- and interspecific relationships). We found that climatic factors and human pressure combined were the most informative predictors of the home range size of leopards across their global distribution. Our results provide valuable insights, informing decision-making in leopard conservation. Temperature seasonality, mean productivity and human footprint were the most important drivers of HR size in female leopards. In contrast, the home-range size of male leopards was mostly driven by the size of female home ranges and vegetation productivity. Considering the scope of these variables, our results suggest that global warming and human presence and activities will have a significant negative impact on leopards through impacting their use of space. Consequently, leopards will likely face reduced abundance and distribution worldwide, especially in their distribution's aridest regions due to increased anthropogenic impacts.

With regard to our abiotic predictors, larger HRs were associated with spatial heterogeneity in annual temperatures and high average maximum temperatures, as well as low vegetation productivity. Due to inconsistent prey availability under these harsh environmental conditions, foraging leopards likely require broader and larger movements. Previous research on leopards and other medium and large felids, such as the Eurasian lynx (*Lynx lynx*) in Europe, identified the importance of vegetation productivity on HR size (Herfindal et al., 2005; Snider et al., 2021), suggesting that this could be a general pattern among widely distributed felids (see also Nilsen et al., 2005). Thus, global warming might have
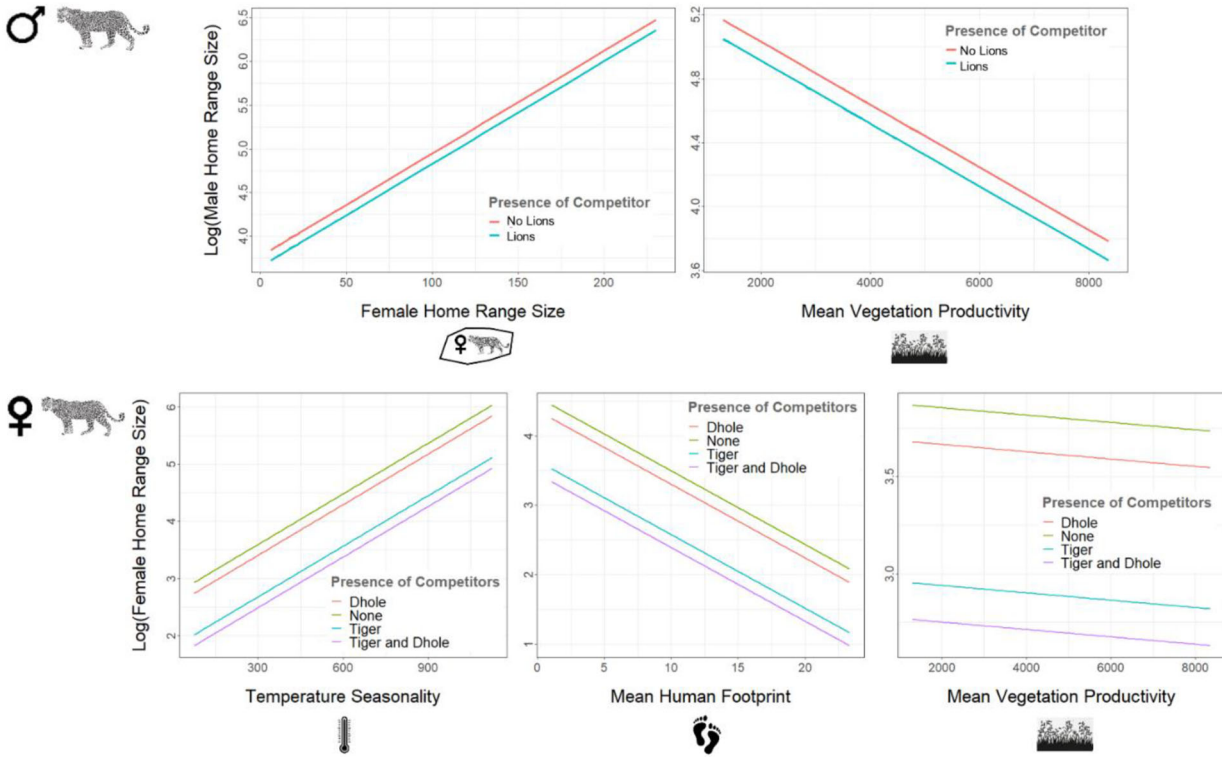
Figure 2 Identified global leopard home range responses to the significant variables identified in the models. These trends account for the categorical predictors in the models on the presence of interspecific competitors.
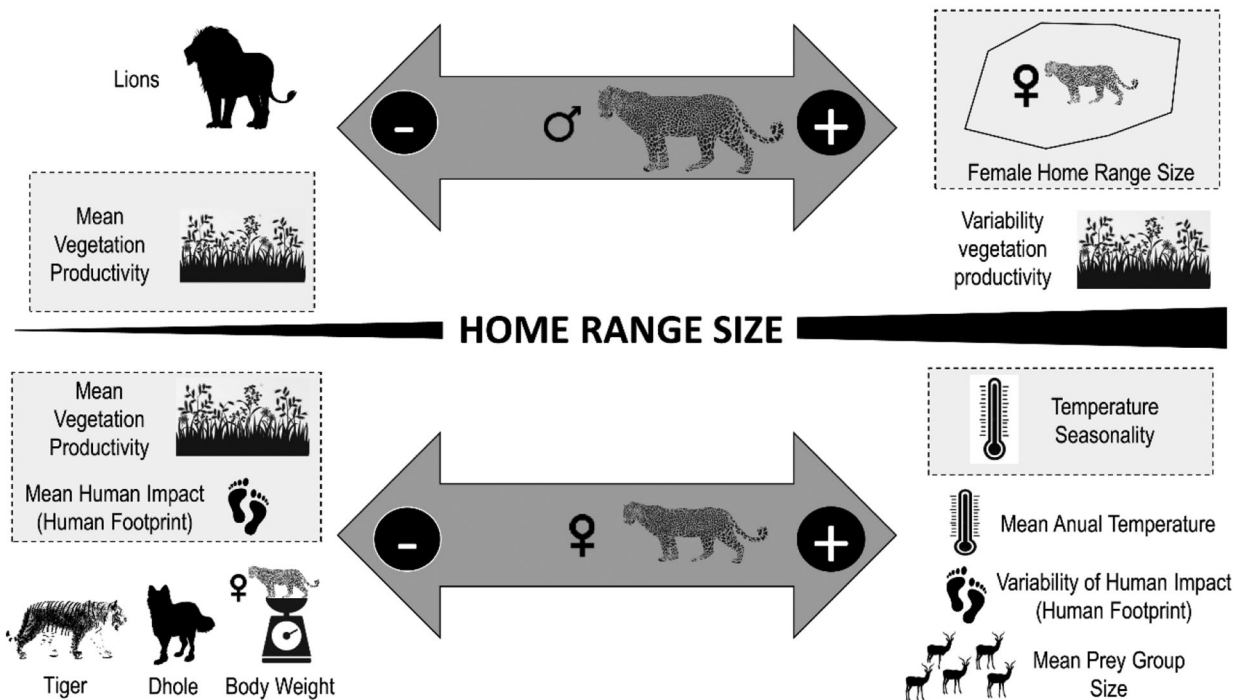

Figure 3 Conceptual illustration of factors driving home range size in male and female leopards globally. Predictors in dashed frames represent the statistically significant variables resulting from the models. Increasing Mean Vegetation Productivity and Mean Human Impact drive smaller home range sizes in male and female leopards. Increasing female home range size drives larger home ranges of males. Increasing temperature seasonality drives larger home ranges of female leopards.

important consequences for the space use of large felids and thus, for their population densities and dynamics, which must be considered in felid conservation programmes. Savannas and arid regions are the areas where climate change is predicted to have the most negative influence on vegetation productivity (Parton *et al.,* 1995; Ostberg *et al.,* 2013; Berdugo *et al.,* 2020; Nath *et al.,* 2021). These habitats are a major part of leopard's global distribution, including several of the endangered and critically endangered populations. Consequently, any further modification of the roaming behaviour of leopards in these regions, resulting in increased HR sizes, could lead to a critical decline in abundance. Reductions over such a broad area would have implications for leopard conservation status at a global level. Nevertheless, as identified by our models, an increasing human footprint results in smaller home ranges. Thus, the expected large size of HRs in increasing arid regions could be attenuated in those particular areas of increasing human impact where leopards could concentrate their search of human-related resources but at risk of being killed. All these potential scenarios are undesirable for the conservation of the species.

In addition to the indirect effects of climate change, humans and their activities strongly shape the roaming behaviour of animal species worldwide through habitat modification and destruction (Tucker *et al.,* 2018). Our results suggest that sites with a high and spatially heterogeneous human footprint are significantly associated with smaller HRs, particularly in female leopards. This finding could reflect leopards shift their foraging behaviour into humanised areas and prey upon livestock (Khorozyan *et al.,* 2017). Thus, leopards inhabiting regions of intense human use and population density might focus their activities on a few available habitats that provide a surplus of food resources, including domestic species (Snider *et al.,* 2021). Furthermore, large competitors (e.g. tigers and lions) are more sensitive to human presence than leopards, so they are often absent from human-dominated areas. Therefore, more resources may be available for leopards and less need to find refugia from antagonistic encounters with competitors, which might result in smaller HR sizes, as identified in our models. This modification of roaming behaviour and space use in leopards often leads to hunting raids into human settlements, resulting in increased conflicts with people and retaliatory persecution (see a global review in Lozano *et al.,* 2019). This is already the case in India's highly human-modified and densely populated areas (Odden et al., 2014; Athreya *et al.,* 2020), a trend that ultimately results in poaching and indiscriminate killing leopards (Jacobson *et al.,* 2016).

With regard to intraspecific patterns in HR size, female HR size was a chief driver of HR selection for males. Previous local studies support this finding, asserting the importance of female HRs for male leopards (Bailey, 2005; Snider *et al.,* 2021) and felids in general (Macdonald & Loveridge, 2010; Hunter, 2015). The ratio of male:female HR size was relatively stable over the global range (Appendix S3, Fig. S3.1) and was related to sex-specific interactions with prey and competitors. Thus, we found no support for converging male and female HR size in areas of low vegetation productivity, as had been previously suggested by Bailey (2005) in times where such large-scale analyses were not possible. Instead, male HRs seemed to encompass several females even when female HR size increased substantially (in the least productive areas). Moreover, none of the climate or vegetation productivity variables was included in top models explaining changes in the male–female HR size ratio.

Interspecific interactions are major drivers shaping the structure of ecological communities (Hardin, 1960; Krebs, 2014), and local-scale studies have revealed a variable influence of intraguild competition on leopard abundance (Steinmetz *et al.,* 2013; Vanak *et al.,* 2013; Balme *et al.,* 2017). At a global scale, our models showed a non-significant effect of competitors on HR size. This result might be because the response of leopards to competitors is to displace their home range to competitor-free areas. Also, the competitor species considered are only present at a continental level, with lions in Africa and tigers and dhole in Asia. Therefore, further continental-scale analyses considering these species are encouraged. Concerning prey species, our models only showed a non-significant relationship between the mean group size of prey and female HR size. Overall, the lack of clear general patterns in our results indicate that understanding HR sizes in leopards across their global distribution is not enhanced by including the information of local faunal communities we considered for this research. In particular, we included indicators of wild prey diversity rather than data on prey abundance or density because this information was lacking in most of the studies we considered (but for areas of India) and for the years they were conducted. We discarded the herd size of domestic prey due to its large variability, although we acknowledge leopards could prey heavily on livestock in these sites. Also, we considered wild prey diversity as a proxy for prey choice. However, conclusions and discussions derived from future macroecological research involving space use of leopards could benefit from more detailed information on intra- and interspecific relationships at local scales to account for the complexity and variability of these interactions.

The important macroecological variables identified in our models can assist managers and conservationists in predicting the spatial requirements of leopards, particularly in regions lacking local empirical data (Sutherland *et al.,* 2004). Such information could be beneficial for reintroduction programmes aiming to expand the distribution of leopards through recolonization of areas within their historical distribution from which they have been lost (Seddon *et al.,* 2007). In conjunction with models predicting future global changes (e.g. climate, habitat degradation and human activity), predictions using the relationships identified in our models can help to identify areas likely to be at risk in the future. Such areas are where conservation actions should be developed and focused on maintaining suitable leopard habitats in the future. Multidisciplinary efforts to combine predictions of future human activity with information on local societal aspects can also assist in producing sustainable socio-ecological suitability and coexistence models (Behr *et al.,* 2017). The combination of such data can

reveal specific risks of human-leopard conflicts resulting from an increasing overlap of human and leopard activity centres. Considering the expected negative trajectory of global change processes due to anthropogenic influences, international regulations and programmes need to step up. This effort involves reinforcing transboundary efforts, policies and commitments to mitigate the effects of pervasive global threats and the expected dramatic consequences for the leopard. Combining efforts at a global scale with local programmes and commitments to ameliorate conflicts with leopards in human-dominated areas are needed to ensure the long-term persistence of this iconic threatened species. Our study also confirms the importance of large-scale macroecological studies in providing an overview of global drivers of animal space use. Such studies can also reveal critical regions threatened by anthropogenic global changes for many at-risk species that otherwise may be difficult to identify.

ACKNOWLEDGMENTS

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Supporting information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Appendix S1. Bibliographic search and study sites.

Appendix S2. Relationships between reported leopard home range size using different estimators.

Appendix S3. Male:Female home-range size ratio.

Appendix S4. Model results on drivers of leopard's home-range size.

Fig. S2.1. Equivalence between the 95% MCP (minimum convex polygon) and 100% MCP home range size (Km2) reported for the leopard.

Fig. S2.2. Equivalence between the 95% MCP (minimum convex polygon) and 95% Kernels home range size (Km2) reported for the leopard.

Fig. S3.1. Comparison of the male:female home range size ratio (Mean ± 95% Confidence intervals) of the leopard between continental regions.

Table S1.1. Locations and main prey species where research reported information on home range size (HR source column) and diet in leopards (Diet source column). Numbered references are included at the end of this document.

Table S2.1. Number of leopards tracked using telemetry methods in each of the 34 sites. The baseline was 95% minimum convex polygon (MCP) because this was the most used method. Transformation to other estimations was applied according to the relationship identified in Figures S2 and S3.

Table S4.1. Top-ranked models (ΔAICc < 2) obtained from model dredging analysing the drivers on home range size of female leopards at a global scale.

Table S4.2. Top-ranked models (ΔAICc < 2) obtained from model dredging analysing the drivers on home range size of male leopards at a global scale.

Table S4.3. Top-ranked models (ΔAICc < 2) obtained from model dredging analysing the drivers on home range size of male and female leopard together at a global scale.