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Human impact overrides bioclimatic drivers of red fox home range size globally

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Abstract

Aim: Identifying the variables that influence animal home range size is important for understanding the biological requirements of individuals and their social interactions. Given their often broad distributions, carnivores are model organisms for studying range-wide determinants of home range size. Here, we test predictions about environmental determinants of home range size for one of the world's most widely distributed carnivores, the red fox (*Vulpes vulpes*).

Location: Global.

Methods: We compiled a database of 70 mean home range estimates from 62 studies and four continents, which we analysed according to site-based temperature, precipitation, environmental productivity and human influence variables.

Results: We found a very strong negative effect of the Human Footprint Index (HFI), with fox home range size decreasing as the level of human impact increased. When analysing the constituent components of the HFI separately, we found that human population density was the only well-supported variable (*cf.* built environments, croplands, pasture lands, nightlights, railways, roads and navigable waterways). Predicted home range size at the highest human population densities (0.75 km^2) was 93% lower than at the lowest population densities (10.83 km^2). We also found that home range size increased as mean annual temperature and temperature seasonality increased. The analyses did not support our prediction that home ranges would be smaller in areas of higher environmental productivity or precipitation.

Main conclusions: Smaller home range sizes observed in highly disturbed areas can be attributed to increased food availability from anthropogenic sources. The lack of an effect of environmental productivity contrasts with previous studies that have shown a negative relationship with carnivore home range size. It may be that anthropogenic food sources have negated the impacts that low-productivity environments have on fox home ranges. Our results emphasize the strong potential for human activities to transform animal space use across the globe.

1 | INTRODUCTION

The home range is a fundamental concept relating to the ecological requirements of animals and their interactions with conspecifics, competitors and predators (Börger, Dalziel, & Fryxell, 2008; Powell & Mitchell, 2012). The home range can be defined as the area regularly traversed by the individual for foraging and reproduction (Burt, 1943). Because it is linked to many other important concepts, including optimal foraging theory and bioenergetics (Börger et al., 2008; Johnson, Kays, Blackwell, & Macdonald, 2002), home ranges can be used to assess and predict how natural or anthropogenic disturbances affect the behaviour and spatial distribution of animals. This is particularly important in our current era of global change as humans increasingly transform ecosystems and alter species assemblages. For instance, recent work has shown that movement rates of mammals are on average half to two-thirds smaller in areas of high human disturbance (Tucker et al., 2018). This likely represents both "winners" and "losers" of anthropogenic change (Santini et al., 2019; Wilson, Pond, Brown, & Schaefer, 2019). The drivers and consequences of these altered movement patterns include changes in resource availability, restricted gene flow, novel species interactions and human–wildlife conflict (Cosgrove, McWhorter, & Maron, 2018; Newsome et al., 2015).

Mammalian carnivores are model organisms for studying broad-scale determinants of space use because they typically roam over large areas and have wide geographic distributions that span land use gradients and bioclimatic zones. Multiple factors can influence the spatial distribution and home ranges of carnivores, both within and between species. Generally, animals with greater body mass maintain larger home ranges (Duncan, Nilsen, Linnell, & Pettorelli, 2015), primarily because they require more food to meet their energy demands (Lindstedt, Miller, & Buskirk, 1986; McNab, 1963). Diet composition also influences home range size, with omnivores having smaller home ranges than carnivores (Duncan et al., 2015; Fauvelle, Diepstraten, & Jessen, 2017). Within a species, home range size can vary between individuals depending on their metabolic requirements, which may be influenced by body size, sex and reproductive status (Henry, Poulle, & Roeder, 2005; Lindstedt et al., 1986; Nilsen, Herfindal, & Linnell, 2005). For instance, Dahle and Swenson (2003) found that male brown bears (*Ursus arctos*) had significantly larger home ranges than females, and female bears rearing cubs utilized smaller ranges than those of lone females and females with yearlings. Competition for, and defence of, resources can further affect space use, depending on whether animals actively defend their home ranges from competitors (Grant, Chapman, & Richardson, 1992). In an attempt to reduce competition for resources, smaller carnivores may preferentially use habitats that are free of larger competitors (Hernandez-Satin, Goldizen, & Fisher, 2016; de Satgé, Teichman, & Cristescu, 2017).

Home range size often varies with resource availability across a species' distribution, and prey availability is likely to be of prime importance for most, if not all, carnivore species (Herfindal, Linnell, Odden, Nilsen, & Andersen, 2005). Unfortunately, obtaining precise estimates of prey densities is impractical for carnivores with large distributions. However, several studies have found a correlation between herbivore abundance and satellite-derived productivity indices (Bawa et al., 2002; Herfindal et al., 2005). As such, environmental productivity has been revealed as a key correlate of carnivore home range size (Bengsen et al., 2016; Castañeda et al., 2018; Duncan et al., 2015; Herfindal et al., 2005; Nilsen et al., 2005). For instance, lynx (*Lynx lynx*) home range size across Europe decreased as environmental productivity increased, and this broad-scale result was supported by a local study where lynx home range size in Norway was negatively correlated with the local density of roe deer, a key prey species (Herfindal et al., 2005). Similarly, feral cat (*Felis catus*) home range size showed a similar negative relationship with environmental productivity, although the relationship did not hold for sites with high seasonality in productivity (Bengsen et al., 2016).

In addition to spatial variation, resource availability can also vary with seasonal changes in climatic conditions, including rainfall and temperature. The overall intensity of seasonality is determined by latitude, with seasons being more pronounced further away from the equator (Addo-Bediako, Chown, & Gaston, 2000; Van Schaik & Pfannes, 2005). For species with large geographic distributions, it is expected that home range size will vary according to local seasonal conditions (McLoughlin, Ferguson, & Messier, 2000; Morellet et al., 2013). For instance, Duncan et al. (2015) found that home range size of 21 carnivore species increased with seasonality in vegetation dynamics and decreased with environmental productivity. This result may relate to seasonal fluctuations in food availability, as the abundance and activity of prey species typically decreases during the harshest months of the year, forcing carnivores to roam over larger areas to find sufficient food (Metz, Smith, Vucetich, Stahler, & Peterson, 2012; Taylor, White, & Sherratt, 2013).

While environmental productivity and seasonality are clearly important determinants of carnivore home range size, anthropogenic changes to the environment may decouple this relationship. Decreases in natural vegetation cover in human-dominated landscapes—which normally lead to a reduction in natural food abundance—are often compensated by an increase in anthropogenic food sources (Bateman & Fleming, 2012). Provision of supplementary food resources, such as garbage and carcass dumps, can reduce an animal's space use requirements relative to the distances they would normally travel if relying solely on natural food (Newsome et al., 2015). For instance, Kolowski and Holekamp (2007) found that

the home range sizes of spotted hyenas (*Crocuta crocuta*) increased following the closure of a refuse pit in Kenya. Red foxes (*Vulpes Vulpes*) in arid regions of Saudi Arabia have also been observed utilizing sites containing waste materials and dumped livestock carcasses (Macdonald, Courtenay, Forbes, & Mathews, 1999). Furthermore, Bino et al. (2010) found that red fox home ranges increased more than twofold after access to anthropogenic food sources was reduced. Taken together, these studies point to a key role for both natural and anthropogenic processes in shaping carnivore space use.

Here, we use a range-wide analysis of red fox home range size to test predictions about the relative effects of environmental productivity, climate and anthropogenic disturbance on carnivore space use. Apart from the domestic dog and cat, the red fox has the largest geographic distribution of any carnivore, with an estimated range of 70 million km^2 spanning North America, Europe, Asia, North Africa and an introduced range in Australia (Hoffmann & Sillero-Zubiri, 2016). Their generalist diet and behavioural plasticity makes foxes a highly adaptable species found in a broad range of environments, ranging from deserts to tundra and urban to agricultural areas. Fox home range size varies greatly between different ecosystem types (e.g. Harris, 1980; Jones & Theberge, 1982; Newsome, Spencer, & Dickman, 2017), but the relative roles of environmental and anthropogenic variables in driving this remain unknown. We tested the following predictions:

1. Home range size will decrease as environmental productivity and annual precipitation increase due to increased resource availability (Herfindal et al., 2005; McLoughlin & Ferguson, 2000; Nilsen et al., 2005).
2. Home range size will increase in areas of greater seasonality due to greater variation in food availability (Duncan et al., 2015; McLoughlin et al., 2000).
3. Home range size will decrease as the degree of human disturbance increases due to the provision of anthropogenic food subsidies (Šálek, Drahníková, & Tkadlec, 2015; Tucker et al., 2018).

2 | METHODS

We sourced studies from Web of Science and Google Scholar using the following search terms: (red fox OR *Vulpes vulpes*) AND (home range OR habitat selection OR habitat use OR landscape OR natural OR agriculture OR peri-urban OR suburban OR urban). Additional studies were identified in the reference lists of relevant studies. Studies were included in our database if they provided home range size estimates derived from VHF or GPS tracking and the sample size was >1 animal. Studies were excluded if it was not possible to calculate mean home range size based on the data presented.

We extracted mean home range estimates from studies. Where home range sizes for male and female foxes were reported separately, a new mean was calculated as the weighted average of the individual estimates. Similarly, where a study provided multiple home range estimates for different seasons or years, we calculated

a weighted mean across all seasons or years. One study only presented minimum and maximum values (Cavallini, 1992), so we took the mid-point of those values. Some studies investigated foxes occurring in different landscape types (e.g. urban and rural), so we recorded multiple estimates for those studies. We extracted 100% or 95% minimum convex polygon (MCP) estimates from most studies because this method is considered to be comparable between studies (Harris et al., 1990). However, six studies only reported mean home range sizes derived from either kernel density (Gosselink, Van Deelen, Warner, & Joselyn, 2003; Roseatte & Allan, 2009; Tolhurst, Grogan, Hughes, & Scott, 2016; Van Etten, Wilson, & Crabtree, 2007), harmonic mean (Reynolds & Tapper, 1995) or local convex hull kernel methods (Walton, Samelius, Odden, & Willebrand, 2017). Including these studies did not affect the results, so we analysed all studies together. We excluded one data point from the Northern Boreal zone in Walton et al. (2017) because environmental productivity data (see below) were not available for that location. A list of data sources is found in Appendix S1.

2.1 | Environmental predictor variables

We quantified the environmental productivity of study locations using long-term (1980–2010) mean monthly normalized difference vegetation index (NDVI) grids (0.05° resolution) from the Vegetation Index and Phenology Lab, University of Arizona (https://vip.arizona.edu/). We calculated annual statistics by taking the mean ("NDVI_mean") and standard deviation ("NDVI_seas") of the 12 monthly layers. We also downloaded BIOCLIM data (2.5 min resolution; http://www.worldclim.org/bioclim) for mean annual temperature and precipitation ("T_mean," "P_mean") and seasonality ("T_seas," "P_seas"). Temperature and precipitation seasonality represent the standard deviation and coefficient of variation of monthly values, respectively, with higher values representing larger fluctuations across the year. Further, we downloaded layers of the Human Footprint Index (HFI) for 1993 and 2009, which represent anthropogenic influence at 1 km resolution (Venter et al., 2016). This dataset is derived from eight global data layers representing human activities: human population density, extent of built environments, cropland, pasture land, night-time lights, railways, roads and navigable waterways. We used the 1993 data for studies undertaken pre-2000 and the 2009 data for studies undertaken from 2000 onwards.

Previous studies have adopted one of two approaches for quantifying environmental variables around study locations. The first approach involves recording the study area size if it is reported by authors, or if not, estimating study area size either by multiplying mean home range size by the number of study animals, or summing all home range estimates (Herfindal et al., 2005; Nilsen et al., 2005). The second approach uses a standard buffer radius around the centre of study locations (Bengsen et al., 2016). We did not consider the first approach appropriate because it resulted in mostly very small study areas (mean = 36.2 km^2) and quantifying the environmental variables within these areas would focus on a small area that does not necessarily
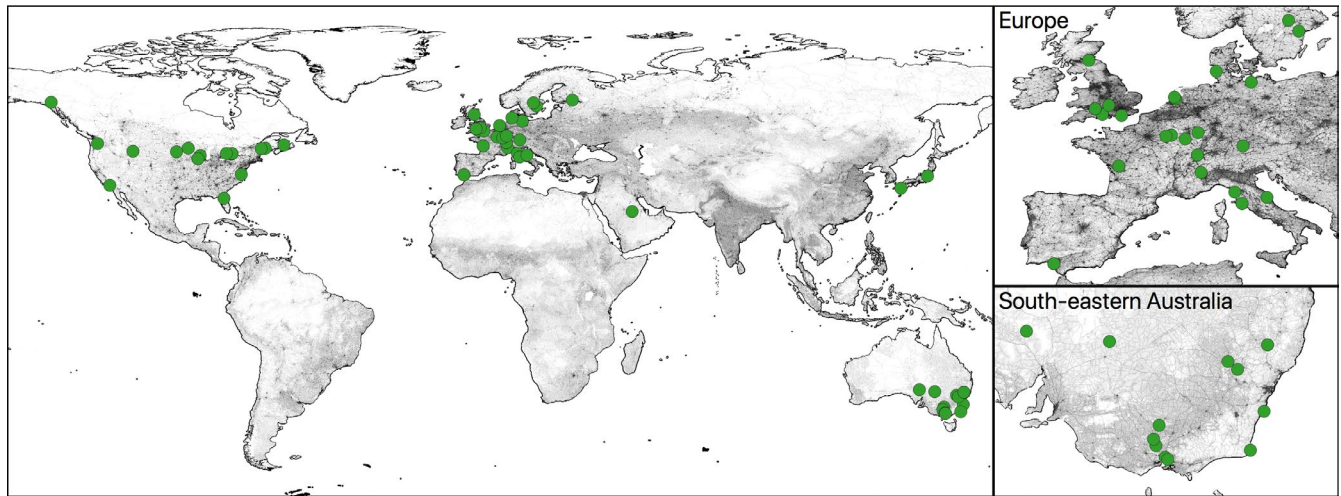
FIGURE 1 Locations of studies that provided red fox (Vulpes vulpes) home range estimates for analysis. Shading represents the Human Footprint Index, with darker areas representing higher values. The two boxes on the right-hand side show expanded maps for Europe and south-eastern Australia. Regions where studies were conducted were Europe (35 home range estimates), North America (19), Australia (13) and Asia (3)

represent the locations of fox home ranges. We instead averaged the environmental variables within a 10-km radius (~314 km^2) around each study location as this provides a more representative picture of the conditions that all study animals were likely to have experienced. We chose a 10-km radius to provide an approximation of local climatic variables and recognize that the actual area covered by the animals in each study may have been smaller or larger.

2.2 | Statistical analysis

We tested our predictions regarding the influence of climatic, environmental productivity and human influence variables on mean home range size using model selection of generalized linear mixed models. We excluded NDVI_seas from analysis as it was negatively correlated with T_mean (Pearson's $r = -.61$) and T_seas (.79). The global model contained an interaction between NDVI_mean and HFI, individual terms for the remaining variables and a random effect of Study_ID to account for multiple estimates from individual studies. We included the interaction between NDVI and HFI to determine whether the predicted importance of environmental productivity is not supported in areas of high human influence. Predictor variables were centred and scaled by subtracting the mean and dividing by the standard deviation. We log-transformed the response variable to improve model fit based on residual plots. We fitted all possible model combinations (80 in total, including the null model) and ranked them using Akaike's information criterion corrected for small sample size (AICc) (Burnham & Anderson, 2002). We considered any model with a delta AICc value (ΔAICc) < 2 to be well supported. We considered model terms statistically significant where the 95% confidence intervals did not overlap zero. We provide marginal and conditional R^2 values as measures of model fit (Nakagawa, Johnson, & Schielzeth, 2017).

Based on the results of the first analysis, we also conducted a secondary analysis to determine which components of the Human Footprint Index best predicted fox home range size. Specifically, we examined the relationship between home range size and built environments, croplands, pasture lands, human population density, nightlights, railways, major roadways and navigable waterways. We calculated mean values of each variable with a 10-km radius around each study location using the original layers from Venter et al. (2016). Following the same modelling approach as above, we fitted and ranked all combinations of variables, except we did not allow correlated variables ($r ≥ ±.5$) to occur in the same model, resulting in 48 models in total. However, the model containing only built environments and navigable waterways failed to converge, so we excluded it from model selection.

3 | RESULTS

After applying the selection criteria, 70 home range estimates from 62 studies remained for analysis (Figure 1; Table S1). Mean home range size ranged from 0.14 (Tolhurst et al., 2016) to 44.62 km^2 (Towerton, Kavanagh, Penman, & Dickman, 2016) (median = 3.25). Mixed modelling revealed no clear "best" model, with four models having ΔAICc values < 2 and model weights of 0.085–0.221 (Table 1). The null model (ΔAICc = 50.04, $w = 0$) was ranked 70 out of 80 models in total (Table S2). The Human Footprint Index and temperature seasonality featured in all models with ΔAICc < 2 and mean temperature and precipitation featured in two models each (Table 1). There was a clear negative effect of HFI on home range size across the four top models and a clear positive effect of temperature seasonality, with the 95% confidence intervals not overlapping zero in all cases (Table 1; Figure 2). There was a positive effect of mean annual temperature in the top ranked model, with confidence

TABLE 1 Generalized linear mixed models explaining the effects of environmental variables on red fox home range size

Model	AICc	ΔAICc	w	R^2_m	R^2_c	HFI	T_mean	T_seas	P_mean
HFI + T_mean +T_seas	178.5	0	0.221	0.561	0.598	**−1.39** **(−1.79, −1.00)**	**0.44** **(0.03, 0.86)**	**0.88** **(0.45, 1.31)**	– –
HFI + P_mean +T_mean + T_seas	180.1	1.56	0.101	0.567	0.609	**−1.41** **(−1.80, −1.01)**	0.37 (−0.07, 0.81)	**0.88** **(0.45, 1.30)**	−0.19 (−0.60, 0.21)
HFI + P_mean +T_seas	180.3	1.82	0.089	0.550	0.582	**−1.44** **(−1.83, −1.04)**	– –	**0.73** **(0.33, 1.13)**	−0.31 (−0.70, 0.08)
HFI + T_seas	180.4	1.91	0.085	0.533	0.550	**−1.42** **(−1.83, −1.02)**	– –	**0.70** **(0.29, 1.10)**	– –

Note: Only models with a ΔAICc < 2 are shown. Values under parameter names are models estimates with 95% confidence in parentheses. Bold text indicates model terms with confidence intervals not overlapping zero.

Abbreviations: HFI, Human Footprint Index; P_mean, mean annual precipitation; R^2_c, conditional R^2; R^2_m, marginal R^2; T_mean, mean annual temperature; T_seas, temperature seasonality; w, model weight.

intervals not overlapping zero (Table 1; Figure 2). There was a weak negative effect of annual precipitation in models 3 and 4, with confidence intervals overlapping zero (Table 1). Marginal R^2 values (the proportion of variance explained by the fixed effects) were similar for the four top models (0.533–0.567; Table 1). The remaining variables (precipitation seasonality, NDVI, NDVI × HFI) did not feature in the top models and had no detectable effects on home range size (Table S2, Figure S1).

Analysis of the individual components of the HFI showed that a model containing only human population density was well supported (AICc = 184.3, w = 0.425, R^2_m = 0.489, R^2_c = 0.491). All other models had ΔAICc > 2 and model weights of 0–0.141 (Table S3). The null model was ranked 41 out of 47 models (ΔAICc = 44.26, w = 0).

There was a strong negative effect of human population density on home range size (−1.66, −2.07 to −1.25; Figure 3). Human population density was also a better predictor than the Human Footprint Index alone (AICc = 188.8). Predicted home range size at the highest human population densities (0.75 km²) was 93% lower than at the lowest population densities (10.83 km²).

4 | DISCUSSION

Our global analysis has identified key relationships between home range size and environmental variables for one of the world's most widely distributed carnivores, the red fox. There was a 300-fold

FIGURE 2 Predicted relationships between red fox home range size and (a) the Human Footprint Index, (b) mean annual temperature, (c) temperature seasonality and (d) mean annual precipitation. Home range size on the y-axes has been log-transformed and all x-axis variables have been centred and scaled. Relationships are derived from the second model in Table 1. Grey bands represent 95% confidence bands
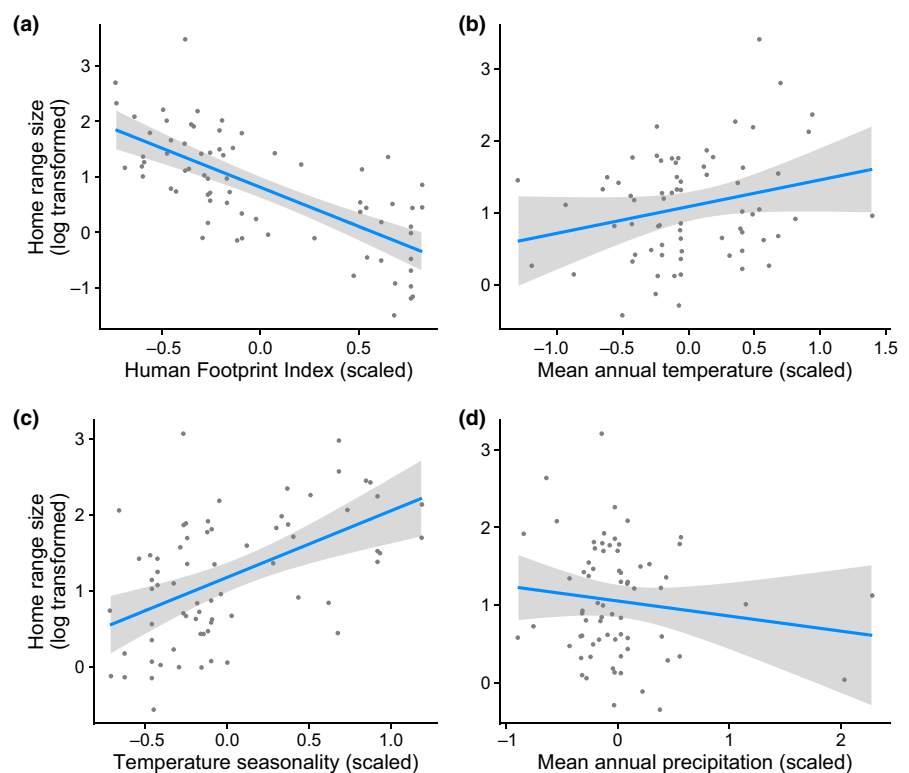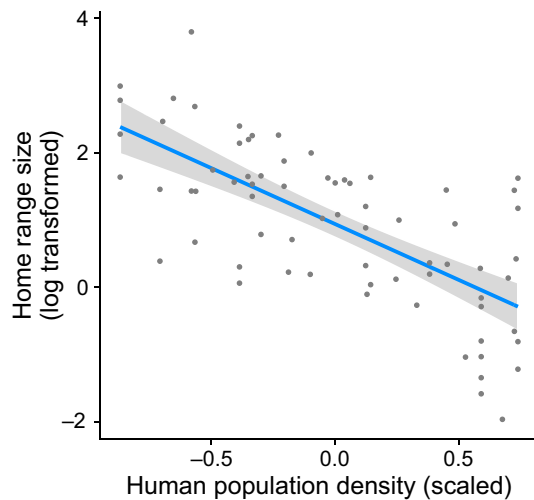
FIGURE 3 Predicted relationship between red fox home range size and human population density. Home range size on the y-axis has been log transformed and population density has been centred and scaled. Grey bands represent 95% confidence bands

difference in minimum and maximum mean home range size across four continents. Contrary to our first prediction, we did not find that fox home range size decreases with increasing environmental productivity and precipitation. We did, however, find support for our third prediction that fox home ranges would be smaller in areas of higher human disturbance, and mixed support for our second prediction that home ranges will be larger in areas of higher climatic seasonality. Further, we found that predicted home range size was 93% smaller in areas of high compared to low human population densities. There were some geographical biases in the available data, with few studies available from parts of the red fox's range in Asia and Eastern Europe. Both regions contain a similar range of landscapes and human population densities as the more well-sampled regions; thus, we do not expect there to be any serious bias in our results.

Bioclimatic variables have frequently been used to explain variation in carnivore home range sizes, but measures of environmental productivity and precipitation exhibited low explanatory power for the red fox. Instead, the degree of human disturbance at study locations proved to be a strong predictor of home range size. This finding is consistent with previous studies, where foxes inhabiting highly disturbed areas typically maintained smaller home ranges (Coman, Robinson, & Beaumont, 1991; Marks & Bloomfield, 2006; Tolhurst et al., 2016) than foxes occurring in natural environments (Šálek et al., 2015; Towerton et al., 2016; Van Etten et al., 2007; Walton et al., 2017). Further, our secondary analysis of the individual components of the Human Footprint Index revealed human population density as a stronger predictor of fox home range size than the Human Footprint Index itself. Our results lend support to a similar pattern observed for mammals globally, where movements by 57 species decreased by up to threefold in areas of high human footprint when compared to counterparts in less developed areas (Tucker et al., 2018). These relationships could also be tested for

other species that share similar ecological strategies, such as feral cats and dogs, racoons, opossums and some mustelids.

Reduced movements by foxes in highly modified areas may be due to an increase in food availability from anthropogenic sources. For instance, in Israel, the home range sizes of foxes more than doubled after anthropogenic food sources in two villages were reduced (Bino et al., 2010). Anthropogenic food sources often occur at higher quantities and in closer proximity to each other than natural food sources, thus allowing foxes to satisfy their metabolic requirements within a smaller area (Fleming & Bateman, 2018). Further, where the provision of anthropogenic food sources is highly predictable in both space and time (e.g. regular dumping of rubbish), foxes need to spend less time searching for food, thus decreasing their overall movements. On the other hand, if foxes maintain small home ranges in highly developed areas, but do not have access to adequate food resources, they may suffer fitness consequences, such as lower body condition, reproductive output and survival (White, 1978, 2008). However, multiple studies have recorded high exploitation of anthropogenic food sources by foxes in urban areas (Contesse, Hegglin, Gloor, Bontadina, & Deplazes, 2004; Doncaster, Dickman, & Macdonald, 1990; Handler, Lonsdorf, & Ardia, 2020). For instance, in the city of Bristol, food scavenged from anthropogenic sources contributed to 64% of the diet of foxes (Saunders, White, Harris, & Rayner, 1993). Further, in south-eastern Australia, red fox body mass and skeletal size increased along a land use gradient from natural to urban areas (Stepkovitch, Martin, Dickman, & Welbergen, 2019), which supports similar findings from Spain (Gortázar, Travaini, & Delibes, 2000). In Israel, red fox survival was higher when anthropogenic subsidies were available compared to when they were not (Bino et al., 2010). Taken together, this evidence supports the notion that the reduced home range size of foxes in highly developed areas is due to increased food availability.

It is also important to acknowledge that an over-reliance on anthropogenic subsidies may have negative consequences for both carnivores and their prey species. Carnivores may experience genetic drift (Wandeler, Funk, Largiadèr, Gloor, & Breitenmoser, 2003), increased human–wildlife conflict (Plumer, Davison, & Saarma, 2014) and poorer health (Murray, Edwards, Abercrombie, & St. Clair, 2015) when subsidized with anthropogenic resources. Further, prey species can experience heightened lethal and non-lethal effects because resource subsidies can support artificially high densities of predators (Newsome et al., 2015; Rodewald, Kearns, & Shustack, 2011). For instance, Shapira, Sultan, and Shanas (2008) found that gerbils were less abundant and showed higher foraging vigilance near to, compared to far from, farms where foxes were more abundant. Threatened species inhabiting urban, rural or peri-urban areas may experience hyper-predation if foxes are sustained on anthropogenic food sources, but also occasionally kill wild prey (Maeda, Nakashita, Shionosaki, Yamada, & Watari, 2019).

Another possible reason for reduced movement in highly developed areas is the impediment of movement by physical barriers, represented either by infrastructure or habitat fragmentation (Tucker et al., 2018). Roads and other barriers that disrupt habitat

connectivity can alter ranging behaviours of animals and lead to negative impacts on populations, such as increased mortality or loss of genetic diversity (Epps et al., 2005; Wilson, Farley, McDonough, Talbot, & Barboza, 2015). However, our secondary analysis of the individual components of the HFI found that models containing roads, railways and built environments had limited or no support (model weights of 0–0.003), although these variables did have moderate to high correlation with human population density. Nonetheless, given the behavioural plasticity of foxes, as well as the numerous studies reporting high abundances and distributions of fox populations in urban environments, plus their willingness to cross major highways (Baker, Newman, & Harris, 2001; Bateman & Fleming, 2012; Šálek et al., 2015), it seems unlikely that reduced home range size of red foxes in highly disturbed areas is due to movement barriers.

Home range size increased with temperature seasonality, which is comparable to previous studies that reported positive effects of seasonality on home range size of both carnivores (Herfindal et al., 2005; McLoughlin & Ferguson, 2000; Nilsen et al., 2005) and large herbivores (Morellet et al., 2013). Home range size also increased with mean annual temperature, but the relationship was weaker. The positive effects of mean annual temperature and seasonality may reflect seasonal fluctuations in food abundance (Ims & Fuglei, 2005; Soe et al., 2017). Indeed, during times of reduced prey availability, foxes have been found to increase the size of their home range to utilize alternative sources of food (Dell'Arte & Leonardi, 2005). Further, fox population densities in Eurasia are lowest in areas of higher seasonality and lower winter temperatures (Bartoń & Zalewski, 2007). This suggests that the larger home ranges of foxes in areas of high temperature seasonality reflect fundamental limitations to their survival in these areas. The warming climate of the Arctic and associated northward expansion of the red fox into the tundra provides a key opportunity to tease apart the relative roles of food availability and climatic variables in shaping red fox space use and demographics (Carricondo Sánchez, Samelius, Odden, & Willebrand, 2016; Gallant, Lecomte, & Berteaux, 2019).

We expected that fox home range size would decrease as environmental productivity increased, but this was not the case. Previous studies revealed such a pattern for lynx in Europe (Herfindal et al., 2005), feral cats globally (Bengsen et al., 2016) and many other carnivores (Duncan et al., 2015). It may be the case that provision of anthropogenic food sources has decoupled the relationship between environmental productivity and red fox home range size. However, if so, we would have expected the interaction between NDVI and HFI to be supported in the modelling, but it was not. Overall, this suggests that remotely sensed measures of environmental productivity may be a poor predictor of space use in the red fox. Indeed, Nilsen et al. (2005) found no correlation between fox home range size and another productivity index (fraction of photosynthetically active radiation) and suggested that this may be due to the red fox's flexible, omnivorous diet. Indeed, diet plasticity and prey switching are common strategies used by foxes in response to seasonal fluctuations

in food availability (Risbey, Calver, & Short, 1999; Sidorovich, Sidorovich, & Izotova, 2006).

Based on the strong relationship between human disturbance and fox home range size, we expect that the global distribution of this carnivore will continue to expand with increasing urbanization. This presents a challenge to wildlife managers and conservation agencies, as foxes become prevalent in environments that they were previously absent from. For example, invasion by the red fox into arctic regions has caused the displacement of the native Arctic fox (*Vulpes lagopus*) (Post et al., 2009). The expansion of the red fox beyond the northern limits of its geographic distribution has previously been attributed to morphology and climate-driven secondary productivity (Hersteinsson & Macdonald, 1992). However, Gallant, Slough, Reid, and Berteaux (2012) found no support for climate warming driving increased red fox abundance through bottom-up processes. Recent studies instead found that the presence of humans and associated food subsidies influence red fox expansion into these arctic regions (Elmhagen et al., 2017; Gallant et al., 2019). This could result in novel ecological interactions whereby increased competition and predation from red foxes, combined with increasing temperatures, could have detrimental impacts on Arctic foxes and other wildlife. This also applies to other landscapes where foxes have been introduced deliberately by humans (i.e. Australia).

5 | CONCLUSION

Understanding how animal space use is shaped by environmental conditions, either natural or anthropogenic, is important for predicting changes in distribution and population dynamics. Our range-wide analysis of home range size in the red fox provided mixed support for our predictions. There was no support for the prediction that fox home ranges would be larger in areas of lower environmental productivity, as neither NDVI nor precipitation had a significant influence on home range size. It is likely that foxes inhabiting low productivity environments are able to survive by employing behavioural strategies, such as diet plasticity, prey switching and exploitation of anthropogenic food sources. Future studies should investigate how the spatial distribution of foxes is influenced by differences in prey densities and anthropogenic food sources, and how these factors are influenced by seasonality and human disturbances.

CONFLICT OF INTEREST

The authors have declared that no competing interests exist.

DATA AVAILABILITY STATEMENT

Data have been deposited in the Dryad repository (https://doi.org/10.5061/dryad.5mkkwh72w).

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BIOSKETCH

The following article extends from a post-graduate thesis that is currently being undertaken by the first author, Michael Main. The current focus of Michael's research is to identify the distribution and diversity of red foxes inhabiting nature reserves within urban areas of south-west Australia and determine how anthropogenic disturbances influence movement, ranging behaviour and occupancy of the species.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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