

ORIGINAL RESEARCH

Life-history attributes and resource dynamics determine intraspecific home-range sizes in Carnivora

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Body mass, carnivore, home range, NDVI, resource availability, space-use

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Abstract

Home ranges capture a fundamental aspect of animal ecology, resulting from interactions between metabolic demands and resource availability. Yet, the understanding of their emergence is currently limited by lack of consideration of the covariation between intrinsic and extrinsic drivers. We analysed intraspecific home-range size (HRS) variation with respect to life histories and remotely sensed proxies of resource dynamics for 21 Carnivora species. Our best model explained over half of the observed variability in intraspecific HRS across populations of multiple species. At the species level, median HRS was smaller for omnivorous species and increased with increasing body mass (model $R^2 = 0.66$). Here, HRS scaled with body mass at 0.80, a value much closer to the expected allometric scaling of 0.75 than previously reported. At the intraspecific level, while much variation was driven by intrinsic factors (body mass, diet, social organization and sex; $R^2 = 0.39$), inclusion of spatiotemporal variation in extrinsic factors (average resource availability and seasonality) enabled explanation of a further 13% of observed variability in HRS. We found no evidence for interactions between intrinsic and extrinsic HRS drivers, suggesting a generally ubiquitous influence of resource availability on space-use. Our findings illustrate how spatial and temporal information on resource dynamics as derived by satellite data can significantly improve our understanding of HRS variation at the interspecific and intraspecific levels, and urge caution in interpreting HRS allometry in the face of large intraspecific variation. Moreover, our results highlight the importance of considering life-history constraints in modelling intraspecific space-use and HRS.

Introduction

The home range is a fundamental ecological parameter (Burt 1943), affording fitness benefits to animals from familiarity with the environment (Stamps 1995), and providing insights into how individuals perceive and utilize their surroundings (Börger et al. 2008; Moorcroft 2012; Powell 2012). The location and size of animal home ranges across landscapes is important in structuring species interactions and broader ecological processes (Gautesstad and Mysterud 2005) as well as community structure (Buchmann et al. 2011); it moreover has important implications for wildlife conservation as a means by

which to estimate population sizes and threat exposure (Gros et al. 1996; Woodroffe and Ginsberg 1998). Gaining an understanding of how and why home-range patterns emerge, and what factors influence these, is thus crucial for understanding and predicting the potential effects of global environmental change on the spatial distribution of biodiversity.

The home range and drivers of home-range size (HRS) variation have received an enormous amount of research attention. Home-range size can vary greatly across taxonomic groups, as well as among populations and individuals within species (McLoughlin et al. 2000; Nilsen et al. 2005). Home ranges are a spatial representation of beha-

viours associated with maximizing fitness (Burt 1943), and HRS directly results from interactions between metabolic constraints (Harestad and Bunnell 1979; Lindstedt et al. 1986; Kelt and Van Vuren 2001), energetic requirements (Mysterud et al. 2001; Jetz et al. 2004) and resource availability (McLoughlin et al. 2000; Nilsen et al. 2005; Hansen et al. 2009). Home-range size variation has been described as being hierarchical in structure (McLoughlin and Ferguson 2000), owing to both intrinsic life-history constraints on metabolic costs and energetic needs at the species level (e.g. body mass, diet, social organization: Harestad and Bunnell 1979; Gittleman and Harvey 1982; Lindstedt et al. 1986; Gompper and Gittleman 1991; Dahle and Swenson 2003; Tucker et al. 2014), and to extrinsic environmental variation influencing resource supply at the individual- and population- levels (McLoughlin et al. 2000; Nilsen et al. 2005; Hansen et al. 2009). Interestingly, extrinsic and intrinsic drivers of variation in HRS are rarely considered in combination (but see Nilsen et al. 2005 and Pearce et al. 2013).

Previous investigation has indeed largely focused on examining the influence of life-history traits on HRS across species; particularly looking at the role of increased energetic requirements associated with increasing body mass on HRS. Allometric scaling relationships between body mass and HRS for mammalian species have consistently been found to be greater than that predicted solely by an increase in metabolic rate (0.75; e.g. Harestad and Bunnell 1979; Lindstedt et al. 1986; Kelt and Van Vuren

2001; Tucker et al. 2014). Noticeably, the slope of HRS allometry has been shown to vary according to the nature of the sample of populations considered (Nilsen and Linnell 2006), suggesting a potential important influence of environmental variability in driving the observed relationship between HRS and body mass. While it is clear that spatiotemporal variation in resource availability is a key driver of intraspecific HRS, with decreased resource availability and stability resulting in increased HRS (e.g. McLoughlin et al. 2000; Herfindal et al. 2005), the strength of its influence has been found to vary greatly between species (Nilsen et al. 2005; Table 1). This may suggest a potential interaction between processes occurring between intrinsic and extrinsic HRS drivers (see Table 1). Such a suggestion was recently promoted by Haskell and colleagues, who developed a mechanistic model predicting that resource availability and distribution across landscapes should influence the slope of HRS allometry, because of larger bodied animals using resources at a coarser spatial scale (Haskell et al. 2002). If this is true, it may therefore be expected that the influence of spatiotemporal variation in resource availability on intraspecific HRS across locations should be differentially greater for larger bodied species due to a decreased resource supply rate (Table 1). Variation in species level dietary differences may equally influence the response of individual HRS to resource availability; space-use of omnivorous individuals may, for example be less affected by variation in resource availability than more obligate feeders, due to increased probability of resource encoun-

Table 1. The variables hypothesized to influence home-range size (HRS) across the order Carnivora.

Variable	Hypothesis	Supporting information
Body mass	Larger species exhibit larger home ranges (H1)	Harestad and Bunnell (1979); Gittleman and Harvey (1982); Lindstedt et al. (1986)
Diet	Carnivorous species exhibit larger home ranges than omnivorous species (H2)	Gittleman and Harvey (1982); Gompper and Gittleman (1991)
Sex	Within solitary species, males exhibit larger home ranges than females (H3)	Dahle and Swenson (2003); Nilsen et al. (2005)
Productivity	Populations of given species in more productive environments exhibit smaller home ranges (H4)	McLoughlin and Ferguson 2000; McLoughlin et al. (2000); Herfindal et al. (2005); Nilsen et al. (2005); Hansen et al. (2009)
Seasonality (contingency)	Populations of given species in environments with greater seasonality exhibit larger home ranges (H5)	McLoughlin and Ferguson (2000); Herfindal et al. (2005); Nilsen et al. (2005); Powell (2012)
Inter-annual variability (constancy)	Populations of given species in environments with greater inter-annual variability in productivity (low constancy) exhibit larger home ranges (H6)	Powell (2012)
Productivity–body mass interactions	The effect of all measures of spatiotemporal variation in resource availability on HRS is greater for larger-bodied species (H7)	McLoughlin and Ferguson (2000); Haskell et al. (2002)
Productivity–diet interactions	The effect of all measures of spatiotemporal variation in resource availability on HRS is greater for obligate carnivores (H8)	Gompper and Gittleman (1991); Nilsen et al. (2005)

ter for omnivores (Gompper and Gittleman 1991; Nilsen et al. 2005; Table 1). Because such potential interactions between intrinsic and extrinsic drivers of HRS remain largely unexplored, our understanding of the relative influence of life-history constraints and spatiotemporal variation in resource availability on HRS currently remains limited. This may hinder our current ability to accurately predict intraspecific HRS across landscapes (Nilsen et al. 2005).

To fill this gap in knowledge, this study makes use of long-term satellite data and a substantial compilation of HRS data for Carnivora to develop a general model for intraspecific HRS, which incorporates for the first time both intrinsic (life histories) and extrinsic (indices of resource availability) variables. First, an initial species level model is developed, examining the influence of body mass and diet on median HRS. This species level model is then incorporated into an intraspecific model of HRS, which is then used to predict HRS for a set of independent species. The full list of hypotheses being tested in this work can be found in Table 1. Carnivora represents a suitable model taxa with which to test these hypotheses, due to the large amount of data available on HRS and large inter- and intraspecific variation in ranging behaviour (Nilsen et al. 2005; Nilsen and Linnell 2006).

Materials and Methods

Carnivore home ranges

We compiled carnivore home-range data from the published literature and that requested from unpublished studies for populations of 110 species (studies from 1970 to 2011; see Appendix A for details; Nilsen et al. 2005). Two subsets of this dataset were considered: a study dataset containing HRS for species with sufficient information (≥ 6 individual studies) upon which to develop an intraspecific population level model, and a test dataset containing HRS for the remaining species in the database to be used for model validation. For the latter, we included only species within the body mass range of the study species, to avoid predicting outside the range of the original model. In order to remove biases according to estimation method (Fieberg and Börger 2012), only HRS estimates from telemetry studies (Very High Frequency (VHF), Global Positioning System (GPS) tracking) generated by either the 95% or 100% minimum convex polygon (MCP; Powell 2000) method were included. Only annual or multi-year composite estimates from resident adults were included, in order to standardize the time-period of estimation and effects of social status (Linnell et al. 2001; Powell 2012). For solitary species, we obtained sex-specific means for each study. For group-living spe-

cies, either group-specific means were obtained, or if sex-specific information was given, the largest sex-specific mean size was used, as this estimate is more representative of true group home range (Nilsen et al. 2005). Studies in areas where the validity of productivity indices as a measure of effective resource availability is reduced (i.e. urban or wetland areas), manipulated populations (i.e. supplementary feeding, sterilization) and fenced areas smaller than the species' maximum HRS) were omitted. Studies that compiled means across multiple sites, or where no study area name or coordinates were provided, were also omitted. For sites where multiple home-range studies had been made, we considered the latest study due to recent improvements in telemetry and home-range estimation methods. The resulting study dataset comprised 496 HRS estimates for 21 Carnivora species from 284 unique study sites (Appendix A; Table A1; Fig. A1); the test dataset comprised 148 estimates for 51 species across 92 unique study sites (Appendix A; Table A2; Fig. A1).

Species level traits

Data on species average adult body mass were taken from the PanTHERIA database (Jones et al. 2009), and were supplemented for species with missing values by data from other published sources (Kodkod, *Oncifelis guigna*; Hunter and Caro 2008). Data on diet were taken from Nowak (1999), and all species were considered to be either obligate carnivores or omnivores.

The normalized difference vegetation index

We indexed primary productivity using the Normalized Difference Vegetation Index (NDVI; Pettorelli 2013), extracted from the bimonthly Global Inventory Modelling and Mapping Studies dataset (GIMMS; Tucker et al. 2005; 1982–2011). While these data are at relatively coarse spatial resolution (8 km), they comprise the longest running NDVI time-series dataset available. Data processing and spatial and statistical analyses were carried out in R v.3.0.0 (R Development Core Team 2013). For each study location, a circular buffer polygon was created around the central coordinates with an area equal to its total size. Coordinates were derived from the original study, if provided, or taken from the online Geonames database (<http://www.geonames.org>; accessed June 2013) if no coordinates but a named location was provided. Total area was either derived from the study, if provided, or was taken from the World Database on Protected Areas (IUCN and UNEP 2013). Study sites with no area information were omitted. For each polygon, NDVI values were extracted for all intersecting pixels. The time-

series data were then corrected for atmospheric noise (smoothing; Pettorelli et al. 2005), following the method outlined in Garonna et al. (2009) and English et al. (2012).

In order to index site level productivity, the average annual Integrated NDVI (iNDVI; the sum of all NDVI composites within a given year; Pettorelli 2013) was taken across all pixels for each study area. The level of seasonality (also known as contingency), and inter-annual variability (also known as constancy) in NDVI were calculated across the time-series data for each study area using the method outlined in Colwell (1974) (see Loe et al. 2005 and English et al. 2012 for recent applications). Contingency and constancy vary from 0 to 1 (Colwell 1974); higher values of contingency indicate greater seasonality in vegetation dynamics, whereas higher values of constancy indicate lower inter-annual variation. In order to calculate these, the smoothed NDVI time-series data were discretized into 10 classes (English et al. 2012). Due to the global scale of these analyses, we did not expect a loss of information associated with NDVI data discretization to impact on these results.

Statistical analyses

All analyses were carried out in R v. 3.0.0 (R Development Core Team 2013). In order to model both inter- and intraspecific variation in HRS (see Table 1), analyses were carried out at both the species- and the population levels. First, linear models (lms) were conducted at the species level in order to model the effect of species traits [body mass (kg; log-transformed) and diet (carnivorous vs. omnivorous species)] on median species level HRS variation. Three plausible candidate models were constructed at the species level: univariate models for the effects of body mass and diet on HRS, and an additive model containing these two variables. Of these three, the 'best-fitting' model was selected by ranking the AICc weights ($\Delta AICc < 4$; Burnham and Anderson 2002). It is now widely acknowledged that interspecific analyses cannot treat species-specific data as independent when phylogenetic relationships exist for the considered traits (Harvey and Pagel 1991). We therefore tested for the existence of evolutionary relationships in median HRS at the species level, in order to assess the need to control for phylogeny within subsequent analyses (see Appendix B for full methodology). No phylogenetic signal was found in median HRS. As any attempt to estimate phylogenetic signal including the populations for each species was overinflated (due to the effect of representing populations as polytomies; Appendix B; Table B1), phylogenetic effects were not further considered.

The factors included within the best-fitting species level model were then incorporated into subsequent population level models to examine the influence of spatiotemporal variation in resource availability (average primary productivity, iNDVI; and seasonality, contingency and inter-annual variation, constancy, in primary productivity) on intraspecific HRS. Pearson's correlation coefficients were calculated between all explanatory variables, and variance inflation factors (VIFs) were calculated from a full additive model; variables with VIFs > 2.5 were not considered within the same statistical models. Modelling at the population level was conducted using linear mixed effect models (lmes) with MCP contours (100% or 95%) and study area as random effects. In order to model group-living and solitary species within the same framework, group-living species' HRS estimates were duplicated to create female and male categories for each study area. The effect of sex was then assessed by considering an interaction between social organization and sex. Models with all plausible variable combinations and meaningful interaction terms were considered in the candidate set of models, and were then assessed by ranking their AIC weights (Burnham and Anderson 2002). We selected a 'best-fitting' population level model according to ranked AIC weight ($\Delta AIC < 4$; Burnham and Anderson 2002), which was used to predict population level HRS for the remaining test dataset. Furthermore, model averaging based on AIC weights was performed across all candidate models, in order to examine the effects of all variables not included within this 'best-fitting model' via multimodel inference (but see Cade in press). Moran's I was calculated via permutation tests on the residuals for the 'best-fitting' model, in order to test for the existence of spatial autocorrelation; a distance-based nearest neighbours estimation via the smallest distance at which all observations were linked and a row-standardized spatial weight matrix was used.

Results

A high level of inter- and intraspecific variation existed in carnivore HRS (Appendix A). Across study populations, HRS ranged between 0.43 km² (Eurasian badger, *Meles meles*) and 8171.00 km² (brown bear, *Ursus arctos*) (mean = 258.85; $n = 496$), iNDVI between 0.13 and 20.38 (mean = 12.07, $n = 284$), seasonality (NDVI contingency) between 0.01 and 0.68 (mean = 0.33, $n = 284$) and inter-annual variability (NDVI constancy) between 0.05 and 0.98 (mean = 0.32, $n = 284$). There was some degree of correlation between explanatory variables (Appendix C; Fig. C1). Correlation between contingency and constancy was particularly strong (Pearson's $r = -0.81$, $P < 0.01$), and the VIFs when considering these were very high (5.64

and 6.21 respectively). Consequently, these variables were not considered within the same statistical models.

At the species level, model selection revealed that the best model of HRS was an additive model including body mass and diet; this best-fitting model explained 66% of the variability in median HRS at the species level. The next best model, which only considered the effect of body mass, explained 21% less variance in HRS ($R^2 = 0.45$), and delta AICc between the first and second model was 7.12. In accordance with H1 and H2 (Table 1), body mass had a positive effect on HRS, and omnivorous species had smaller home ranges than carnivorous species (Table 2; Fig. 1).

At the population level, model averaging over all candidate models (see Table 3) revealed a significant interaction term between social organization (group-living or solitary species) and sex, with solitary males having larger HRS than females [as expected under H3; estimate = 0.90 ± 0.09 (1 SE), 95% CIs = 0.73–1.06], as well as a positive effect of body mass [estimate = 0.81 ± 0.04 (1 SE), 95% CIs = 0.72–0.89] and negative effect of diet [estimate = -1.58 ± 0.11 (1 SE), 95% CIs = -1.80 to -1.35]. Moreover, and as expected under our hypotheses H4–H6 (Table 1), across all candidate models there was a

significant negative effect of productivity [iNDVI; H4; estimate = -0.09 ± 0.02 (1 SE), 95% CIs = -0.13 to -0.06], a significant positive effect of seasonality [NDVI contingency; H5; estimate = 2.73 ± 0.45 (1 SE), 95% CIs = 1.84–3.62], and a significant negative effect of NDVI constancy on HRS [H6; estimate = -2.36 ± 0.48 (1 SE), 95% CIs = -3.30 to -1.42] (Fig. 2). Note here that higher values of NDVI constancy reflect lower inter-annual variability (Colwell 1974) and thus HRS was smaller in areas of reduced inter-annual variability. Conversely to H7, however, no support was found for an interaction between iNDVI and body mass [estimate = -0.02 ± 0.01 (1 SE), 95% CIs = -0.03–0.00]. Moreover, and contrary to all predictions under H7 and H8, no support was found for a greater influence of resource availability and variability on HRS for larger-bodied or obligate carnivores (95% CIs of model averaged estimates similarly encompassed 0).

In the interest of HRS prediction for our test dataset, two candidate models provided plausible explanations for variation in intraspecific HRS (Table 3). Both of these models included the interaction term between social organization and sex, the additive effects of body mass and diet from the 'best-fitting' species level model, and the negative effect of average productivity (iNDVI) and positive effect of seasonality (NDVI contingency; Table 3). The second-ranked model additionally contained a positive interaction term between iNDVI and NDVI contingency (Table 3). However, model averaging across all candidate models revealed no support for such an interaction between these two variables [estimate = 0.1 ± 0.1 (1 SE), 95% CIs = -0.1–0.3]. Furthermore, scaling the model variables to retrieve the beta coefficients (Murray and Conner 2009) revealed a small and highly variable effect of this interaction term within the second-ranked model [estimate = 0.03 ± 0.04 (1 SE)]. Accordingly, and in the interest of parsimony, we considered the first-ranked model without this interaction term to be the 'best-fitting' model with which to predict population level HRS for our remaining test dataset. This 'best-fitting' model included the solitary-living-sex (male) interaction, the species level variables of body mass and diet, as well as the negative effect of iNDVI and the positive effect of NDVI contingency (Tables 2 and 3; model $R^2 = 0.52$). Scaling the model variables to retrieve the beta coefficients revealed that life-history variables had strong effects on population level HRS [intercept: 0.27 ± 0.06 , body mass: $\beta = 0.56 \pm 0.03$ (1 SE); omnivore: estimate = -0.80 ± 0.06 (1 SE); solitary-living-sex (male) interaction: estimate = 0.46 ± 0.04 (1 SE)]. iNDVI and NDVI contingency then produced similar, but opposite, effects on population level HRS [iNDVI: $\beta = -0.19 \pm 0.04$ (1 SE); NDVI contingency: $\beta = 0.23 \pm 0.04$ (1 SE)]. At the

Table 2. Parameter estimates of the 'best-fitting' species level linear model (lm) of median carnivore HRS, and the selected 'best-fitting' linear mixed effects (lme) model of population level carnivore HRS.

Best-fitting species level model (lm)					
Variable	Estimate	SE	d.f.	t	P
Intercept	2.02	0.57	18	3.54	0.002
log(BM)	0.80	0.17	18	4.80	<0.001
Diet (omnivorous)	-1.75	0.52	18	-3.36	0.004
Best-fitting population level model (lme)					
Fixed effects	Estimate	SE	d.f.	t	P
Intercept	2.21	0.32	326	6.81	<0.001
Sex (male)	0.00	0.07	326	0.00	1.00
Group (solitary)	-0.48	0.11	326	-4.43	<0.001
Sex (male): Group (solitary)	0.90	0.09	326	10.36	<0.001
log(BM)	0.81	0.04	326	18.83	<0.001
Diet (omnivorous)	-1.57	0.11	326	-13.70	<0.001
Contingency	2.73	0.46	281	5.98	<0.001
iNDVI	-0.09	0.02	281	-5.13	<0.001
Random effects					Variance
Study area					0.58
MCP contours					0.81
Residual					0.27

HRS, home-range size; MCP, minimum convex polygon; NDVI, normalized difference vegetation index.

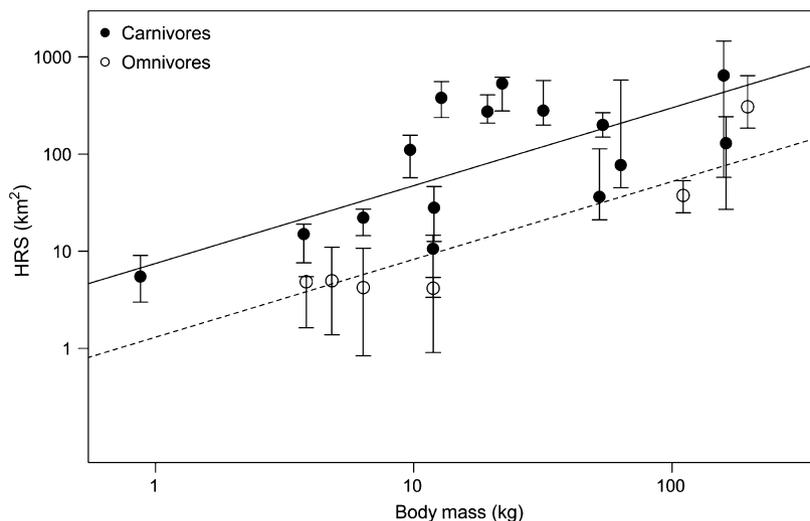


Figure 1. Median species level Carnivora home-range size (HRS) (km²; *N* = 21 species) for carnivores (black circles) and omnivores (white circles). Error bars depict the upper and lower 95% bootstrap percentile confidence intervals (*R* = 99 999 bootstrap iterations) for the median species level HRS values. The lines represent the regression in our ‘best-fitting’ model of species level traits (log-transformed body mass (kg) and diet (carnivore or omnivore) on median species level HRS (log-transformed). The solid black line represents the relationship between body mass and HRS for carnivores: $\log(\text{HRS}) = 0.80 \log(\text{body mass}) + 2.02$; the dashed black line represents this relationship for omnivores: $\log(\text{HRS}) = 0.80 \log(\text{body mass}) + 0.27$. Model *R*² = 0.66.

Table 3. The candidate set of linear mixed effects models (study area and MCP contours as random effects) considered while modelling population level home-range size (HRS) (km²; log-transformed) across the 21 study species.

Model	AIC	ΔAIC	Akaike weight	<i>K</i>	Deviance	Conditional <i>R</i> ²
Sex * Group + log(BM) + Diet + Contingency + iNDVI	1671.64	0.00	0.624	11	1649.64	0.52
Sex * Group + log(BM) + Diet + Contingency * iNDVI	1672.73	1.09	0.361	12	1648.73	0.52
Sex * Group + log(BM) + Diet + Constancy * iNDVI	1679.65	8.01	0.011	12	1655.65	0.51
Sex * Group + log(BM) + Diet + Constancy + iNDVI	1682.16	10.52	0.003	11	1660.16	0.50
Sex * Group + log(BM) + Diet + Contingency	1695.13	23.49	<0.001	10	1675.13	0.47
Sex * Group + Contingency * log(BM) + Diet	1696.10	24.46	<0.001	11	1674.10	0.47
Sex * Group + log(BM) + Diet * Contingency	1696.92	25.29	<0.001	11	1674.92	0.47
Sex * Group + iNDVI * log(BM) + Diet	1701.17	29.53	<0.001	11	1679.17	0.46
Sex * Group + log(BM) + Diet + iNDVI	1703.29	31.66	<0.001	10	1683.29	0.47
Sex * Group + log(BM) + Diet * iNDVI	1705.29	33.65	<0.001	11	1683.29	0.47
Sex * Group + log(BM) + Diet + Constancy	1726.25	54.62	<0.001	10	1706.25	0.41
Sex * Group + Constancy * log(BM) + Diet	1726.31	54.67	<0.001	11	1704.31	0.41
Sex * Group + log(BM) + Diet * Constancy	1728.25	56.61	<0.001	11	1706.25	0.41
Sex * Group + log(BM) + Diet	1730.96	59.32	<0.001	9	1712.96	0.39
log(BM) + Diet	1916.67	245.03	<0.001	6	1904.67	0.40

BM, average adult body mass (kg; Jones et al. 2009); MCP, minimum convex polygon; iNDVI, integrated NDVI.

*Indicates the presence of an interaction between two variables within the model.

population level, intrinsic factors (body mass, diet, social organization and sex) explained 39% of observed variation in HRS (Table 3). Inclusion of productivity (iNDVI) and seasonality (NDVI contingency) enabled explanation of a further 13% of observed variation in HRS (Table 3). No significant spatial autocorrelation was found in the model residuals (Moran’s *I* statistic = 0.002, *P* = 0.17).

Predicting HRS for the ‘test’ dataset (Appendix A; Table A2) using our ‘best-fitting’ model showed a high level of correlation between observed and predicted estimates ($\beta = 0.87 \pm 0.07$ [1 SE], d.f. = 146, *R*² = 0.51; Fig. 3). The difference between observed and predicted HRS within the ‘test’ dataset did not vary according to interspecific variation in body mass [$\beta = 0.07 \pm 0.05$ (1 SE), d.f. = 146, *P* = 0.14], diet [omnivore: esti-

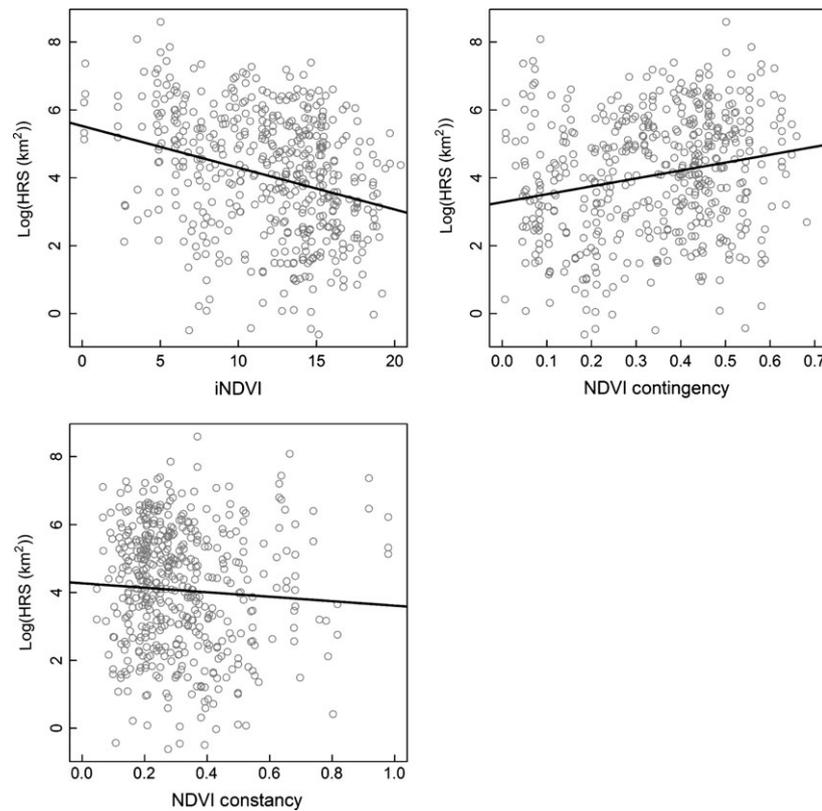


Figure 2. The effect of NDVI-based metrics (iNDVI, NDVI contingency and NDVI constancy) on carnivore HRS (km^2 ; log-transformed) for the study dataset, after controlling for the effects of social organization (group-living or solitary), sex, diet and body mass (kg ; log-transformed). iNDVI, integrated NDVI; HRS, home-range size; NDVI, normalized difference vegetation index.

mate = -0.20 ± 0.14 (1 SE), d.f. = 146, $P = 0.15$] or social organization [solitary: estimate = 0.20 ± 0.13 (1 SE), d.f. = 146, $P = 0.13$], and did not vary between sexes for solitary species [males: estimate = -0.03 ± 0.16 (1 SE), d.f. = 146, $P = 0.86$].

Discussion

This study provides the first ever modelling framework for intraspecific HRS across multiple species, combining both intrinsic and extrinsic drivers of space-use. A novel feature of our approach is that both spatial and temporal variation in resource dynamics, as assessed by satellite data, is taken into account when exploring the importance of HRS drivers. Our models were able to explain two-thirds of the variability in HRS at the species level, and over half of the observed intraspecific HRS variation across populations of multiple Carnivora species. Our ability to predict HRS at the intraspecific level was not found to vary according to species' life histories. Thus, our approach builds on previous intraspecific HRS studies for multiple species, which have found highly variable explanatory power across species where intrinsic life-his-

tory information has not been considered (Nilsen et al. 2005). We show that, while intrinsic life-history differences exert the greatest control over carnivore HRS, spatiotemporal variation in resource availability has a large and ubiquitous influence across species. We find no evidence for interactions between resource availability metrics and intrinsic life-history constraints (body mass, diet and social organization). Thus, it appears there are broad generalities in the emergence of home-range configuration across species, with HRS responding negatively to increased resource availability and positively to increasing seasonality. Overall, our study highlights (1) the importance of incorporating life-history constraints in observational and mechanistic study of intraspecific HRS, (2) that a multi-species framework for predicting intraspecific HRS is applicable for carnivores and (3) the need for caution in interpreting allometric HRS scaling relationships in the face of high intraspecific variation.

Our best model explained a relatively large amount of variation in intraspecific HRS ($R^2 = 0.52$), even when applied to independent populations ($R^2 = 0.51$). This level of explained variation is similar to those reported for some species-specific studies (McLoughlin et al. 2000; Herfindal

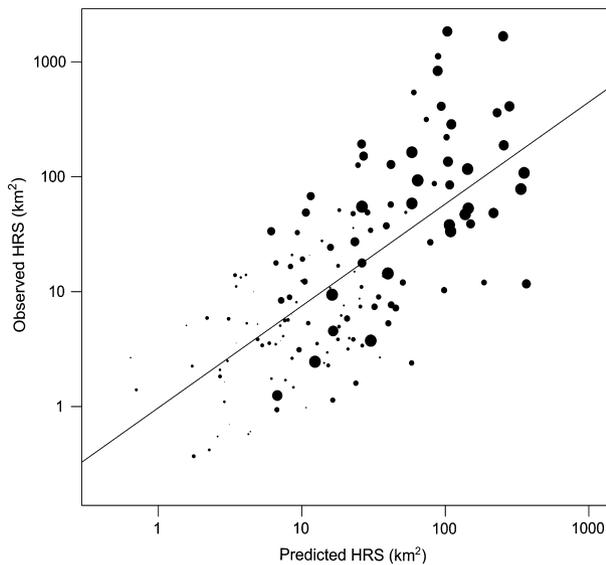


Figure 3. Log-scale plot of observed vs. model-predicted values of population level home-range size (HRS) (km^2) for the test species dataset. Carnivore species included are species which fall within the same body mass range as species the original study dataset. Point sizes are relative to the species level body mass (kg) of each population. $R^2 = 0.51$.

et al. 2005; Nilsen et al. 2005). The parameters of the best model in our analyses, as well as multimodel inference, showed that life-history traits (body mass and diet) are extremely influential in determining HRS. This provides a plausible explanation for the low explanatory power found in some previous species-specific models that failed to consider such traits (Nilsen et al. 2005), and highlights the importance of incorporating intrinsic life-history constraints in mechanistic modelling of intraspecific HRS in dynamic resource environments (see Buchmann et al. 2011). While life-history constraints had the greatest effect on HRS in our model, the influences of spatial and temporal (seasonality) variation in resource availability were found to produce strong, yet opposite, effects on HRS, and to increase explanatory power by 13%. Contrary to our predictions, we found no evidence of differences in HRS responses to spatiotemporal variation in resource availability according to differences in body mass or diet across species. Our results thus do not provide support to the notion that variation in the scale of resource utilization according to body mass may drive departures from expected scaling coefficients in carnivore HRS (Haskell et al. 2002).

Within our initial species level model, the slope of the relationship between body mass and median HRS was 0.80; much closer to the expected scaling coefficient of this relationship if determined by an increase in energetic demands according to body mass alone (0.75; McNab 1963) than previously reported (Harestad and Bunnell

1979; Gittleman and Harvey 1982; Lindstedt et al. 1986; Kelt and Van Vuren 2001). These previous studies have incorporated mean species HRS across often small intraspecific samples (Nilsen and Linnell 2006). Our model has incorporated a relatively large sample of intraspecific HRS for each species (min six studies), with a high degree of variation in resource availability across samples (Appendix A; Table A1), from which median species' HRS was determined. If the median HRS can be considered as the 'typical' home range of a species, our results then suggest that this 'typical' HRS does indeed increase with body mass as expected by an increase in metabolic rate alone (McNab 1963). Our analyses show, supported by previous species-specific studies (e.g. McLoughlin et al. 2000; Herfindal et al. 2005), that much intraspecific variation in HRS is driven by spatiotemporal variation in resource availability. We thus echo the caution urged by Nilsen and Linnell (2006) in interpreting species level allometric HRS scaling relationships in the presence of intraspecific variation in resource availability.

The success of model predictions for our test dataset was not found to vary according to interspecific differences in body size, diet or social organization, suggesting that our model performs generally well. However, some unexplained variability remained in our model estimates for both the study and test datasets (i.e. Fig. 3), suggesting that further model development and inclusion of additional parameters is necessary. Key intrinsic factors that could not be explored in these analyses were territoriality (McLoughlin et al. 2000) and population density (Jetz et al. 2004), as well as mating systems (MacDonald 1983). Territoriality in species and individuals can result in reduced HRS for those actively defending resources within the home range, while overlap between co-occurring individuals can result in shared resources and thus increased HRS (Pearce et al. 2013). Both of these factors may be controlled by population densities of co-occurring species, another important driver of HRS due to control on levels of resource sharing (Jetz et al. 2004; Pearce et al. 2013). Territoriality is difficult to measure for most carnivores (Gittleman and Harvey 1982) and can be exacerbated by variation in resource availability (McLoughlin et al. 2000; Pearce et al. 2013). Furthermore, both population densities and territoriality may be altered by human influences and persecution of carnivore populations, which may impact observed linkages between resource availability and HRS. Future studies should look towards data collation and means to incorporate information on population densities, levels of territoriality and home range overlap into studies of extrinsic resource availability influences on HRS in real systems (but see Pearce et al. 2013). Such studies may begin to enable quantification of the relative impacts of these complex processes on

intraspecific HRS across multiple species within modelling frameworks such as the one presented here. Another important consideration for HRS differences between populations is variation in the spatial distribution of resources, and in particular high-quality foraging patches (Geffen et al. 1992; Powers and McKee 1994; Powell 2000; Mitchell and Powell 2004, 2012; Buchmann et al. 2011). Spatial texture analysis of satellite imagery can provide insights into the configuration of resources across landscapes (Wood et al. 2013), and could be employed within future analyses to further elucidate intraspecific variation in HRS. Moreover, intuitively, HRS should be influenced by the preferred prey type, as movement is greater in larger prey species (Mysterud et al. 2001). This effect is likely to be particularly great for species consuming larger prey relative to their body size, where the effect of prey size is not adequately described by the relationship between body mass and HRS. Due to data availability, we here considered intrinsic variation in life-history constraints as static within species. However, individual level variation in metabolic constraints (i.e. body mass; Gompper and Gittleman 1991) can produce further intraspecific variation in HRS. In particular, dietary variation may be one of the factors causing residual variation among the populations of larger carnivores. Large carnivores are thought to exhibit wider diet breadths than smaller species (Carbone et al. 1999; Sinclair et al. 2003; Radloff and DuToit 2004), and it is thought that individual variability in prey choice may be particularly great in larger predators due to this relative generality in prey profiles (Pettorelli et al. 2011). A future avenue for exploration in space-use research further lies in elucidating the potential and relative roles of such intraspecific metabolic and behavioural differences on HRS across species.

Further causes of the unexplained variability found in this study may lie within limitations in our HRS dataset. First, variability in the HRS estimates may have been subject to telemetric sampling variation and telemetry methods in the studies considered. However, it was not possible to control for the influence of sampling variation in these analyses, as the number of telemetric fixes used in HRS estimation in many studies is not published. The number of fixes obtained in given studies may be influenced by the telemetry method employed (Börger et al. 2006; Hebblewhite and Haydon 2010). The majority of HRS estimates in our database were conducted via VHF telemetry. While VHF methods can result in a comparatively smaller number of fixes per individual, superior lifespans and cost-effective procurement over GPS and other satellite-based collars often result in increased numbers of studied individuals within populations (Börger et al. 2006; Hebblewhite and Haydon 2010). Thus, at a population level considered here, potential variation in HRS estimation according to differ-

ing telemetry methodologies is minimal. Another important consideration is the focus on MCP HRS estimator studies, as the MCP home range is heavily influenced by the amount of data used in its estimation (Powell 2000; Börger et al. 2006). However, data availability for HRS using different estimators (i.e. kernel density estimators) across carnivores are comparatively limited; thus HRS estimates using the MCP method were considered here. Finally, some of the HRS estimates considered in these analyses (1970–2011) did not align temporally with the GIMMS NDVI information (1982–2011) utilized to index productivity and predictability dynamics (32 of 292 published studies within the study dataset). Rerunning our analyses while omitting these HRS estimates, however, revealed no influence of their inclusion on all results presented here. We thus retained these HRS estimates within these analyses in order to improve statistical confidence in median study species-specific HRS calculations when developing our species level model.

We have highlighted the usefulness of macroecological approaches that combine long-term satellite data with extensive information on space-use at both inter- and intraspecific levels to explain and predict carnivore HRS. Ecologists have recently begun to combine mechanistic and statistical approaches to understand the processes determining observed movement patterns (Gautestad et al. 2013). Attempts to reproduce the variation in HRS found here using mechanistic approaches would serve to further elucidate relationships between animal movement decisions, energetic requirements and dynamic resource environments, and to increase predictive power for patterns of home-range emergence. Furthermore, development of home-range modelling frameworks such as these to include the other potentially important inter- and intraspecific factors discussed above may serve to further improve our understanding in space-use and HRS modelling. Refinement of HRS models incorporating both intrinsic and extrinsic HRS drivers will better enable prediction of the influence of changing environmental conditions and resource availability on both individual space-use and energy budgets, and changes to local community compositions (Buchmann et al. 2011).

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Conflict of Interest

None declared.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix A. Summary of the 'study' and 'test' datasets considered in these analyses.

Table A1. List of all carnivore species considered in the 'study' dataset, including the number of studies for each species, the median and median absolute deviation in home-range size (HRS), body mass, dietary category, geographical range of study locations and the range of average I-NDVI across these study locations.

Figure A1. Geographical locations of all study areas considered for the 21 carnivore species within the ‘study’ dataset listed in Table A1 (black circles) and for the 51 species within the ‘test’ dataset listed in Table A2 (grey circles).

Table A2. List of all carnivore species for which the best-fitting population level HRS linear mixed effects model was tested, including the number of studies for each species, the median and median absolute deviation in HRS, body mass, dietary category, geographical range of study locations and the range of average I-NDVI across these study locations.

Appendix B. Description of phylogenetic analyses tested in this study.

Figure B1. Species level phylogeny for the 21 study species depicting the median value of log-transformed home-range size (HRS; km²) for each species (Nyakatura and Bininda-Emonds 2012).

Table B1. AICc and AIC table for the best-fitting evolutionary model of HRS across the species level and population level phylogenies for all study species respectively.

Appendix C. Relationships among explanatory variables.

Figure C1. Correlation matrix for population level explanatory variables; average Integrated Annual NDVI (iNDVI), NDVI contingency (level of seasonality) and NDVI constancy (level of inter-annual variability).