

Energy and the Scaling of Animal Space Use

Natascia Tamburello,* Isabelle M. Côté, and Nicholas K. Dulvy

Earth to Ocean Research Group, Department of Biological Sciences, Simon Fraser University, Burnaby, British Columbia V5A 1S6, Canada

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ABSTRACT: Daily animal movements are usually limited to a discrete home range area that scales allometrically with body size, suggesting that home-range size is shaped by metabolic rates and energy availability across species. However, there is little understanding of the relative importance of the various mechanisms proposed to influence home-range scaling (e.g., differences in realm productivity, thermoregulation, locomotion strategy, dimensionality, trophic guild, and prey size) and whether these extend beyond the commonly studied birds and mammals. We derive new home-range scaling relationships for fishes and reptiles and use a model-selection approach to evaluate the generality of home-range scaling mechanisms across 569 vertebrate species. We find no evidence that home-range allometry varies consistently between aquatic and terrestrial realms or thermoregulation strategies, but we find that locomotion strategy, foraging dimension, trophic guild, and prey size together explain 80% of the variation in home-range size across vertebrates when controlling for phylogeny and tracking method. Within carnivores, smaller relative prey size among gape-limited fishes contributes to shallower scaling relative to other predators. Our study reveals how simple morphological traits and prey-handling ability can profoundly influence individual space use, which underpins broader-scale patterns in the spatial ecology of vertebrates.

Keywords: allometry, home range, metabolic theory, prey handling, prey size, spatial ecology.

Introduction

Many animals travel daily across discrete home range areas in the pursuit of sustenance, shelter, and prospective mates, and home-range size represents a key species trait with important implications for the distributions of animals across landscapes and the spatial structuring of community and ecosystem processes (Greenwood and Swingland 1983; Stamps 1995; Holyoak et al. 2008). Understanding the factors that influence home-range size is important both for understanding spatial processes in ecological communities and for predicting home-range size in order to evaluate extinction risk, determine minimum reserve size, or forecast the influence of invasive species (Haskell et al. 2002; Moffitt

et al. 2009; Freiwald 2012; Hastings 2014). While we have a good understanding of the determinants of bird and mammal home-range sizes, whether these mechanisms apply to the wider diversity of vertebrate ecologies is an open question (Haskell et al. 2002; Jetz et al. 2004; Makarieva et al. 2005; Tucker et al. 2014). Thus, while existing hypotheses can accurately predict the home-range size of a snowy owl on the tundra or a lynx in the boreal forest, we cannot yet say whether they hold for a rattlesnake in the desert or a grouper on a coral reef. Moreover, there is little understanding of the relative importance of the various mechanisms hypothesized to influence home-range scaling. Given that knowledge of home-range size is an integral component of conservation planning to mitigate the threats facing all vertebrate species, the relative support for proposed drivers of home-range scaling should be evaluated across the full breadth of vertebrate diversity.

The principal determinant of home-range size is considered to be body size. Larger animals have larger home ranges, which in turn must be large enough to meet metabolic energy needs that scale positively with mass. Home-range area (HRA) is thus expected to scale positively with body mass M according to the power law $HRA = a \cdot M^b$, where a represents a taxon-specific normalization constant, with greater values indicating larger home range for a given body size, and b represents the scaling exponent, the rate at which HRA increases with body size (West et al. 1997; Jetz et al. 2004; Hendriks 2007). In theory, mean home-range size of a species is expected to scale with body size similarly to metabolic rate (i.e., with an exponent of approximately $M^{3/4}$), but in practice, empirical estimates of a and b range widely across taxa, which suggests that additional mechanisms are at work (Hendriks 2007).

Five main hypotheses have been advanced to explain the observed variation in home-range scaling across birds and mammals. Working under the reasonable assumption that a home range must be large enough for an organism to meet its energetic needs (McNab 1963), these hypotheses range along a continuum from intrinsic mechanisms influencing energy needs to extrinsic mechanisms influencing the distribution of energy (i.e., food resources) in the environment. The mechanisms invoked include thermoregulation

* Corresponding author; e-mail: ntambure@sfu.ca.

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tion strategy (Hendriks 2007); rate of movement (Haskell et al. 2002), which varies with locomotion strategy (Bejan and Marden 2006); foraging dimension (Haskell et al. 2002); trophic guild and prey size (Makarieva et al. 2005); and differences in productivity across realms (Harestad and Bunnell 1979; Boudreau and Dickie 1992; Hendriks 2007).

Thermoregulation strategy is an intrinsic mechanism that might be expected to influence home-range scaling through its direct effects on metabolism. Homeotherms have greater intrinsic energy needs than similarly sized poikilotherms, as reflected by consistently higher metabolic rates, because of the energy they must expend to maintain a constant body temperature (White et al. 2006). Greater metabolic costs per unit mass in homeotherms are expected to translate into larger home ranges for a given body mass (Hendriks 2007), but similarities in the metabolic-rate allometries of homeotherms and poikilotherms suggest that thermoregulation strategy should have little influence on the slope of home-range allometry.

Additional intrinsic traits such as movement rate, foraging dimension, trophic guild, and prey handling can influence home-range size through their impact on resource encounter rates and thus the effective density and distribution of resources available to animals at the landscape scale.

Movement rate determines how far an animal can travel in a given day and thus constrains the size of the area that is regularly used (Haskell et al. 2002). The most energetically efficient or optimal movement rate increases with body mass with a similar slope for all animals, but its relative magnitude varies with locomotion strategy. For a given body mass, animals that fly move slightly faster than those that run, and both are roughly an order of magnitude faster than animals that swim (Bejan and Marden 2006), while slithering snakes fall somewhere between runners and swimmers (Hu and Shelley 2012). This is consistent with the theoretical prediction that velocity should influence the intercept but not the slope of home-range scaling relationships (Haskell et al. 2002), and it suggests that the faster fliers and runners should have larger home ranges than slitherers or swimmers of a similar size. Although the cost of transport also varies across locomotory strategies, it accounts for only an estimated 1%–6% of the daily energy budget in running animals, which have the costliest mode of transport (Baudinette 1991). Thus, the influence of locomotory costs on home-range scaling is expected to be negligible compared to that of velocity.

Three-dimensional foragers such as flying or swimming animals encounter lower effective resource densities because these resources are generally distributed over a larger search area than those of two-dimensional foragers (Pawar et al. 2012). This effect is amplified at larger body sizes because larger animals are capable of “sampling” or perceiving a larger volume of habitat while foraging, according to

principles of the fractal scaling of resources (Haskell et al. 2002). Note that although previous studies have considered foraging dimension equivalent to the dimension occupied by food resources (Pawar et al. 2012), home ranges are not used exclusively for feeding. We argue that animals also effectively “forage” for nonfood resources such as mates, breeding sites, or shelter, which may be distributed differently than food resources. For example, predatory birds foraging for ground-dwelling prey distributed in two dimensions may still depend on arboreal resting or nesting sites distributed in three dimensions. As a result, the distribution of all types of resources should be considered when determining dimensionality for the purpose of home-range estimation. Because lower resource densities require animals to forage over a larger area to acquire a given amount of resources, three-dimensional foraging is expected to increase both the intercept and the slope of home-range allometry (Haskell et al. 2002).

Trophic guild also has a strong influence on resource distributions. Carnivores naturally experience much lower resource densities than herbivores, which feed on generally abundant and widespread vegetation (Haskell et al. 2002). Thus, the home ranges of carnivores are expected to be larger than those of herbivores. Moreover, resource density for carnivores depends strongly on the size of prey exploited, as smaller animals generally occur at higher densities than larger ones (Damuth 1981; Makarieva et al. 2005). The largely overlooked implication is that the faster prey size increases with predator size, the faster predator home ranges should expand to keep pace (Makarieva et al. 2005).

Finally, home-range size could also be influenced by differences in the timing, pattern, and scale of local production between realms (Nixon et al. 1986; Boudreau and Dickie 1992). Although life may be sparsely distributed in the open ocean, aquatic organisms in coastal marine and freshwater ecosystems can reach biomass densities 6–60 times greater than those observed in terrestrial ecosystems (Cyr et al. 1997). As higher biomass densities often reflect higher environmental productivity (Boudreau and Dickie 1992), this suggests that certain aquatic environments can be more productive than terrestrial ones. Given that animals can meet their metabolic needs more quickly in more productive environments with higher resource densities (Haskell et al. 2002), we might expect aquatic home ranges to be systematically smaller than terrestrial home ranges.

In addition to potential differences in productivity, terrestrial and aquatic realms also present contrasting trophic patterns that might be expected to influence home-range allometry but have not been fully appreciated (Yvon-Durocher et al. 2011; Keith et al. 2012). One key difference is that trophic interactions in aquatic realms are much more strongly size-structured than those on land (Webb et al.

2011; Webb 2012; Trebilco et al. 2013). This difference can be attributed in part to ontogenetic change in body size and in part to the widespread prevalence of suction feeding in predatory fishes, which constrains them to eating prey small enough to be swallowed whole (Peters 1983; Webb 2012; Trebilco et al. 2013). Terrestrial carnivores, on the other hand, can escape this constraint on prey size by using their limbs or coils to grasp and hold down larger prey while using their teeth or beaks to tear it into bite-sized pieces (Schwenk and Rubega 2005). Anticipated differences in the mean prey size of dominant terrestrial and aquatic consumers could have profound effects on the distribution and density of predators across these contrasting realms, given that relative consumer body size influences foraging behavior, food-web dynamics, and the scaling of species distributions at the population scale (Brose et al. 2004; McCann et al. 2005; Brose 2010). Importantly, systematic cross-realm differences in relative prey size suggest that terrestrial predators should have larger home ranges than their aquatic counterparts and that the slope of home-range allometries may differ systematically with cross-realm differences in the scaling of prey size to predator size (Makarieva et al. 2005).

Here, we take advantage of the recent proliferation of home-range estimates for fish and reptile species made possible by evolving tracking technologies to derive new home-range allometries representative of poikilotherm taxa (Pittman and McAlpine 2003; Dorcas and Willson 2009). Combining these new data with published home-range allometries for birds and mammals, we use a model-selection strategy to evaluate mechanistic hypotheses of home-range scaling across the full breadth of diversity in body sizes, thermoregulation strategies, and trophic ecologies of vertebrate groups in both terrestrial and aquatic realms. We find that locomotion strategy, dimensionality, trophic guild, and prey size exert the greatest influence on home-range allometry across vertebrates, while thermoregulation strategy and realm contribute relatively little.

Methods

To compare home-range scaling relationships across taxa and realms, we assembled estimates of home-range size for birds, mammals, reptiles, and fishes from the literature. We first subset the data to assess the variation in home-range allometry within taxa and then constructed global models corresponding to each proposed home-range scaling mechanism to assess how well each hypothesis explains the observed cross-taxon variation in home-range allometry.

Literature Search

We first obtained existing databases of home-range estimates for birds (Schoener 1968; Ottaviani et al. 2006),

mammals (Kelt and Van Vuren 1999, 2015; Jones et al. 2009), and freshwater fishes (Minns 1995) from previous home-range allometry studies. We augmented this data set through a literature search to compile additional home-range estimates for mammals and birds and to generate new home-range data sets for flightless birds, marine fishes, snakes, turtles, tortoises, and lizards.

We searched the peer-reviewed and gray literature, using the Web of Science and Google Scholar and employing various combinations of the following keywords: (fish, marine, reef, demersal, benthic) or (snake) or (lizard) or (turtle) or (bird) and (movement, home range, territory, tracking, tagging, mark-recapture, telemetry, kernel density, minimum convex polygon). Relevant citations within identified publications were also examined. We retained studies that provided, at minimum, a mean home-range area and mean length or weight estimate for the specimens examined. Studies were excluded when the area measured (1) pertained to juveniles of a species, (2) was exclusively related to breeding activity, (3) was obtained from displacement and homing experiments, (4) approached or surpassed the boundaries of the detection area searched for tracked individuals (in the absence of area-time relationships; Pittman and McAlpine 2003), or (5) was biased because of other methodological limitations (e.g., studies in artificial environments). Where more than one tracking study was available per species, only one study was selected for analysis, with a preference toward studies carried out more recently, with a larger sample size, and using telemetry.

Data Selection

For each study, we extracted the study location, tracking method (direct observation, mark-recapture, or telemetry), study detection area (m^2), and mean home-range area (m^2), as well as body mass (g). For existing data sets on mammals and birds where tracking method was not reported, we assumed that all or most home-range estimates for these terrestrial species were acquired with telemetry. Where body mass was not reported, it was calculated from total length (cm) for fishes and snout-vent length for reptiles (cm) with published length-weight relationships (Froese and Pauly 2011; Feldman and Meiri 2012) or, for a handful of species, with the estimated mean weight from other published studies specified in the full data set, which is publicly available in the Dryad digital data repository: <http://dx.doi.org/10.5061/dryad.q5j65> (Tamburello et al. 2015).

We estimated the mean home-range size and mean body mass across multiple specimens in each study, reflecting standard practice in the allometry literature (Yvon-Durocher et al. 2011). Individuals sampled were expected to be representative of the mean body size of individuals in those populations, assuming size-independent sampling.

Few studies included equal representation of both sexes, so we were unable to conduct a sex-specific analysis. Each species was categorized as either an exclusive herbivore or exclusive carnivore on the basis of the source study or, for fishes, from the presence of either exclusively plant or animal material in the gut-contents data reported in FishBase (Froese and Pauly 2011).

We excluded several groups from our analysis to simplify comparisons and minimize the occurrence of extreme outliers in our data set. We focused on solitary, generalist species because home ranges for a given body mass can be exceptionally large in highly social animals (e.g., lions and starlings), as a result of substantial home-range overlap (Haskell et al. 2002), or exceptionally small in large, highly specialized large animals that show high site fidelity toward specific resource-rich locations (e.g., anteaters closely associated with large insect nests). Omnivores from all taxa were also excluded because of their highly variable diet composition. Carnivorous lizards were excluded because few species are strictly carnivorous and few home-range estimates are available for these species (Perry and Garland 2002). We also excluded large pelagic fishes because they often form large schools and exhibit highly migratory Lévy flight-like movements that preclude the simple definition of a distinct home range (Humphries et al. 2010). We instead limited our analyses of marine fishes to benthic (seabed-associated) species, given that the benefits afforded by a home range are thought to depend largely on familiarity with surrounding habitat structure (Stamps 1995). Although some of the reptiles in our data set spend part of their time foraging in water (e.g., freshwater turtles), we excluded reptiles that are primarily swimmers and spend the majority of their time underwater (i.e., sea snakes or sea turtles). Finally, arboreal reptiles were also excluded from this analysis because of broad variability in habitat dimension and the scarcity of home-range estimates for these species.

Our literature search ultimately yielded home-range estimates for 569 terrestrial and aquatic vertebrate species spanning 380 genera, 152 families, and 53 orders, and these data and their sources are available in full in the Dryad digital data repository: <http://dx.doi.org/10.5061/dryad.q5j65> (Tamburello et al. 2015). Data for flying birds were drawn primarily from two studies of avian home-range allometry (Schoener 1968; Ottaviani et al. 2006), while data for flightless birds were gathered individually from the literature, resulting in data for 140 avian species spanning 99 genera, 48 families, and 20 orders. Data for mammals were drawn primarily from three published data sets of mammalian home ranges (Kelt and Van Vuren 1999, 2015; Jones et al. 2009; Tucker et al. 2014), augmented with several species-specific studies from the literature. We compiled home-range estimates for 238 carnivorous and herbivorous spe-

cies representing 155 genera, 54 families, and 19 orders, but we did not include flying mammals (i.e., bats). Data on reptile home ranges were compiled from individual studies. Our literature search yielded 34 studies on snake home ranges, resulting in home-range data for 41 species representing 27 genera, 5 families, and 1 order. We found 26 studies on home-range sizes in turtles and tortoises, yielding mean home-range estimates for 13 herbivorous tortoises and 14 carnivorous turtles spanning 22 genera, 8 families, and 1 order. We also found 11 studies on lizard home ranges, yielding mean estimates of home range and body mass for 11 herbivorous species in 1 order, 5 families, and 9 genera. Data for freshwater fishes were drawn from a previous study of home-range allometry in this group representing 9 lake species and 14 river species, all carnivores, spanning 7 orders, 9 families, and 15 genera (Minns 1995). Home-range data for marine benthic fishes were compiled individually from 63 studies, primarily on coral-reef and temperate rocky-reef species, yielding data for 90 carnivorous and herbivorous species across 4 orders, 23 families, and 53 genera.

Data Analysis

Deriving Taxon-Level Home-Range Scaling Relationships. All analyses were carried out with the statistical software R, version 2.14.1 (R Development Core Team 2008), and the code used to carry out these analyses is publicly available in the Dryad digital data repository: <http://dx.doi.org/10.5061/dryad.q5j65> (Tamburello et al. 2015). To facilitate comparisons with previous studies, we subset taxa within each class by trophic guild (herbivorous or carnivorous), foraging dimension (two-dimensional for flightless birds, marine, and river fishes; three-dimensional for flying birds and lake fishes), locomotion strategy (flying for birds; running for mammals, flightless birds, lizards, tortoises, and turtles; slithering for snakes; and swimming for fishes). We \log_{10} -transformed home ranges and body masses and, for each subset, obtained new estimates of intercepts $\log(a)$ and slopes b for each taxon with simple linear or linear mixed-effects models fitted via maximum likelihood to allow for comparisons between models with different fixed effects (Crawley 2007; Kerkhoff and Enquist 2009). For taxa where home-range estimates were derived entirely or primarily using a single tracking method, log-log linear models followed the R syntax form $\log_{10}(\text{HRA}) \sim \log_{10}(M)$, and 95% confidence intervals (CIs) were calculated numerically from the standard errors of the estimates with the `fit.se` argument in the “`lm`” function. For taxa where home-range estimates were derived with more than one tracking method, we accounted for tracking method as a random effect with a log-log linear mixed-effects model taking the form $\log_{10}(\text{HRA}) \sim \log(a) + b \cdot \log_{10}(M) + (1|\text{tracking})$

method), because tracking method is known to bias estimates of home-range size (Nash et al. 2015). As most home-range estimates within each subset came from a single class and/or order, there was insufficient taxonomic diversity to account for phylogenetic effects within subsets. Mixed-effects models were fitted via the “lmer” function, and their 95% confidence bands were derived from the model’s variance-covariance matrix as described in the R code.

In our log-log models, the intercepts lie outside the range of the data (at $M = 1$ g) and are hence correlated with the slope (Quinn and Keough 2002; Anderson-Teixeira et al. 2009). To more easily compare intercept effects on absolute home-range size across taxa, we also report the height of scaling relationships, defined as the estimated home range for a 1-kg animal ($HRA_{1\text{ kg}}, \text{ m}^2$).

Comparing Support for Home-Range Scaling Hypotheses across Taxa. We evaluated how well each proposed mechanism of home range explained variation across taxa in our full data set by constructing a series of nonnested models for each hypothesis and comparing model support and fit. For each hypothesis, we constructed two models incorporating the variable of interest as (1) an additive term to assess the intercept effect (e.g., $HRA \sim M + X$) and (2) an additive and an interaction term to assess effects on both the intercept and slope of the body mass–home range relationship (e.g., $HRA \sim M + X + M : X$, annotated as $M \times X$). In addition to the fixed effects of interest, each model accounted for systematic heterogeneity in home-range size due to methodological differences (continuous tracking vs. point estimates) and phylogenetic nonindependence by incorporating tracking method and taxonomic class as random effects (Pittman and McAlpine 2003; Isaac and Carbone 2010).

The default output of these R models yields parameter estimates expressed as departures from an arbitrary baseline level of each categorical fixed factor. To make the interpretation of parameter estimates more intuitive, we added the term -1 to each individual factor model. This does not influence model fit but yields absolute rather than relative coefficient values for each categorical factor level (Schielzeth 2010). This approach is not possible for models that include multiple categorical factors. Therefore, the coefficients of our full models are presented as the default contrasts that show the departure of each categorical variable from the specified baseline combination of factor levels.

We assessed the relative support for each model by using the small sample–unbiased Akaike information criterion (AICc), where lower AICc scores represent increasing model support while accounting for the trade-offs between model complexity and fit (Johnson and Omland 2011). Here, ΔAICc represents support for the model under investigation above and beyond the theoretical baseline model,

that is, where HRA is a function of M alone. We also described model fit by using the marginal and conditional R^2 for mixed-effects models via the “r.squaredGLMM” function in version 1.10.0 of the MuMIn package in R (Nakagawa and Schielzeth 2013; Bartoń 2014; Johnson 2014). The marginal R^2 describes the proportion of variation explained by fixed effects alone, while the conditional R^2 describes the proportion of variation in the data explained by both fixed and random effects (Nakagawa and Schielzeth 2013). To construct our final global models, we included only terms with a ΔAICc less than -2 and included interaction terms only when they were better supported (i.e., had a lower ΔAICc) than the corresponding additive model. In all cases, the inclusion of random effects improved model fit, as reflected by both a lower ΔAICc and a higher R^2 .

Because the prey-size hypothesis pertains only to carnivorous species, our global analysis was followed by a restricted analysis using the subset of carnivorous species in our data set for which estimates of prey size were reported or could be calculated from existing species-specific estimates of predator-prey mass ratio (PPMR) available in the literature. Because predator mass and prey mass are generally highly correlated (Vézina 1985), it would be inappropriate to include an interaction term between these variables in our carnivore home-range models. To assess how systematic differences in prey-predator size scaling might affect home-range allometry, we instead created simple linear models of prey size against predator size for each taxonomic class. We then used these predator-prey mass relationships to predict appropriate prey sizes over the range of mammalian and fish predator sizes in our data and used our predicted prey-size data in the final carnivore-only model to visualize how differences in prey-size scaling across realms affected the slope of predicted home-range allometries.

Results

Taxon-Level Vertebrate Home-Range Scaling Relationships

Here, we summarize home-range allometry across 569 terrestrial and aquatic vertebrate species spanning 6 orders of magnitude of body mass from the rusty goby (*Priolepis hipoliti*), at 0.2 g, to the African bush elephant (*Loxodonta africana*), at 4,000 kg, and corresponding home-range sizes spanning 7 orders of magnitude, from less than 1 m^2 to more than 3,500 km^2 .

Carnivorous-bird home ranges scaled higher and more steeply than those of herbivorous birds (fig. 1). Within trophic guilds, the home ranges of flying birds scaled more steeply than those of flightless birds (fig. 1). Importantly, the parameter estimates for flightless carnivorous birds and both flying and flightless herbivorous birds have large















SYMBOL	TAXON	R	T	L	D	TG	N	SOURCE	$\log_{10}(a)$ 95% CI range	b [95% CI range]	HRA _{1kg}	R ²
	Birds	Terrestrial	Homeotherm	Flying	3D	Carnivores	106	1,2	2.79 [1.99, 3.59]	1.50 [1.34, 1.66]	49,421,691	0.84
	Birds	Terrestrial	Homeotherm	Flying	3D	Herbivores	9	2,3	1.63 [-1.68, 4.94]	1.77 [0.18, 3.36]	87,84,892	0.41
	Birds	Terrestrial	Homeotherm	Running	2D	Carnivores	10	3	2.69 [-1.62, 7.00]	1.14 [-0.45, 2.73]	1,268,991	0.20
	Birds	Terrestrial	Homeotherm	Running	2D	Herbivores	15	3	2.31 [-0.2, 4.82]	1.13 [0.37, 1.89]	511,463	0.39
	Mammals	Terrestrial	Homeotherm	Running	2D	Carnivores	80	4	1.66 [1.11, 2.21]	1.36 [1.18, 1.54]	568,576	0.77
	Mammals	Terrestrial	Homeotherm	Running	2D	Herbivores	158	5	1.32 [0.97, 1.67]	1.09 [0.99, 1.19]	37,721	0.75
	Snakes	Terrestrial	Poikilotherm	Slithering	2D	Carnivores	41	3	1.99 [1.19, 2.79]	1.22 [0.87, 1.57]	458,350	0.55
	Turtles	Terrestrial	Poikilotherm	Running	2D	Carnivores	14	3	2.67 [0.83, 4.51]	0.73 [0.08, 1.38]	75,588	0.28
	Tortoises	Terrestrial	Poikilotherm	Running	2D	Herbivores	12	3	2.26 [0.22, 4.30]	0.93 [0.26, 1.60]	112,924	0.43
	Lizards	Terrestrial	Poikilotherm	Running	2D	Herbivores	11	3	0.67 [-0.45, 1.79]	1.07 [0.70, 1.44]	7,677	0.77
	River Fish	Aquatic	Poikilotherm	Swimming	2D	Carnivores	14	5	1.33 [0.92, 1.74]	0.63 [0.41, 0.85]	1,767	0.72
	Lake Fish	Aquatic	Poikilotherm	Swimming	3D	Carnivores	9	5	1.85 [0.13, 3.57]	0.99 [0.28, 1.70]	68,180	0.52
	Marine Fish	Aquatic	Poikilotherm	Swimming	2D	Carnivores	70	3	1.1 [-0.12, 2.32]	0.82 [0.55, 1.09]	42,625	0.65
	Marine Fish	Aquatic	Poikilotherm	Swimming	2D	Herbivores	20	3	-0.03 [-2.6, 2.54]	1.21 [0.84, 1.58]	42,105	0.91

Figure 1: Parameter estimates of home-range scaling relationships for individual vertebrate taxa, based on linear models of the form $\log_{10}(\text{HRA}) \sim \log_{10}(a) + b \times \log_{10}(M)$. R = realm; T = thermoregulation; L = locomotion strategy; D = dimensionality (two- or three-dimensional); TG = trophic guild; N = number of species used to derive the relationship; a = normalization constant; b = slope; 95% CI = 95% confidence interval; HRA_{1kg} = predicted home-range size (in m²) at M = 1 kg. Sources: (1) Schoener (1968); (2) Ottaviani et al. (2006); (3) this study; (4) Kelt and Van Vuren (1999, 2015); (5) Minns (1995).

Table 1: Relative support for mechanisms proposed to influence home-range scaling across vertebrates

Hypothesis	References ^a	Predicted effect			Model	Formula: HRA ~ (version)	$\log_{10}(a)$ (95% CI)	b (95% CI)	ΔAIC_c	k	R^2_M	R^2_C
		a	b									
Body mass (M)	1	...	↑		A	M	1.87 (.81, 2.93)	1.05 (.97, 1.13)	0	5	.44	.77
Thermoregulation (T)	2, 3	Hom: ↑; poik: ↓	Hom: ↑; poik: ↓		B1	$M + T$ (hom)	2.48 (1.3, 3.66)	1.05 (.97, 1.13)	.06	6	.56	.78
					B2	$M \times T$ (poik)	1.27 (.11, 2.43)	1.05 (.97, 1.13)				
Locomotion (L)	4, 5	HV: ↑; LV: ↓	None		C	(hom)	2.39 (1.19, 3.59)	.9 (.72, 1.08)	-1.31	7	.55	.79
						(poik)	1.56 (.34, 2.78)	1.08 (1, 1.16)				
						$M + L$ (flying)	3.21 (2.37, 4.05)	1.09 (1.01, 1.17)	-54.77	6	.60	.77
Dimensionality (D)	4	3D: ↑; 2D: ↓	3D: ↑; 2D: ↓		D1	(running)	1.62 (.84, 2.4)	1.09 (1.01, 1.17)				
						(slithering)	2.31 (1.47, 3.15)	1.09 (1.01, 1.17)				
						(swimming)	.72 (-.38, 1.82)	1.09 (1.01, 1.17)	-35.55	6	.48	.74
						$M + D$ (2D)	1.59 (.73, 2.45)	1.07 (.99, 1.15)				
Trophic guild (TG)	6, 7, 8, 9	Carn: ↑; herb: ↓	None		D2	(3D)	2.72 (1.82, 3.62)	1.07 (.99, 1.15)	-40.75	7	.48	.74
						$M \times D$ (2D)	1.69 (.81, 2.57)	1.03 (.95, 1.11)				
					E1	(3D)	2.18 (1.18, 3.18)	1.34 (1.12, 1.56)				
						$M + TG$ (carn)	1.99 (1.01, 2.97)	1.13 (1.07, 1.19)	-127.48	6	.48	.80
						(herb)	.99 (-.01, 1.99)	1.13 (1.07, 1.19)				
					E2	$M \times TG$ (carn)	1.82 (.82, 2.82)	1.21 (1.11, 1.31)	-130.80	7	.49	.80
						(herb)	1.22 (.20, 2.24)	1.07 (.99, 1.15)				

Realm (RI)	3, 8	Terr: ↑; aq: ↓	None	F	M + RI (terr) (aq)				
Full model ^b							1.96 (.92, 3.00)	1.04 (.96, 1.12)	.37
							.72 (-.91, 2.35)	1.05 (.97, 1.13)	
				G	M + L + D +		.13 (-.87, 1.13)	1.06 (.98, 1.14)	-152.53
					D: M + TG +				12
					TG: M				.68
					(baseline)				.80
					(flying)		+2.06 (.9, 3.22)		
					(running)		+1.29 (.29, 2.29)		
					(slithering)		+1.49 (.45, 2.53)		
					(swimming)		...		
					(3D)		-.29 (-1.02, .44)	+ .27 (.05, .49)	
					(2D)		
					(carn)		+.55 (.14, .96)	+ .12 (-.02, .26)	
					(herb)		

Note: Comparison of linear mixed-effects models of the effects of body mass (M , g) on home range area (HRA, m^2) across vertebrate species ($N = 569$). All models include the random effect of tracking method and taxonomic class. "Predicted effect" indicates the direction of the effect of the hypothesized mechanism on the intercept and/or slope, where ↑ indicates an increase and ↓ a decrease compared to a baseline model based on mass alone. In models A–F, we provide slope and intercept estimates as absolute values for each factor level. In the full model G, where combinations of levels must be specified, the sign of the $\log_{10}(a)$ and b values indicates the departure from the overall baseline model scenario of a herbivore swimming in two dimensions. a = normalization constant; AIC_c = Akaike information criterion corrected for small sample sizes; aq = aquatic; b = slope; $carn$ = carnivore; ΔAIC_c = difference between AIC scores of the target model and the baseline model (HRA $\sim M$); $herb$ = herbivore; hom = homeotherm; HV = higher velocity (flying, running, slithering); k = number of parameters; LV = lower velocity (swimming); $poik$ = poikilotherm; R^2_c = conditional R^2 and R^2_{adj} = marginal R^2 (see "Methods"); $terr$ = terrestrial; $2D$ = two-dimensional; $3D$ = three-dimensional; 95% CI = 95% confidence interval.

^a References: (1) Damuth (1981); (2) White et al. (2006); (3) Hendriks (2007); (4) Haskell et al. (2002); (5) Bejan and Marden (2006); (6) McNab (1963); (7) Schoener (1968); (8) Harestad and Bunnell (1979); (9) Kelt and Van Vuren (1999).

^b The full model includes the baseline intercept and slope for a herbivore swimming in two dimensions.

margins of error, as a result of low sample size, and should be interpreted with caution.

Carnivorous-mammal home ranges scaled more steeply (b [lower and upper 95% CI] = 1.36 [1.18, 1.54]) than those of herbivorous mammals (b = 1.09 [0.99, 1.19]; fig. 1). At a mass of 1 kg, carnivores had home ranges roughly 14 times larger than those of herbivores (fig. 1).

Snake home-range size increased faster than body size, scaling with a slope significantly greater than 3/4 in the final model (b = 1.22 [0.87, 1.57]; fig. 1). Carnivorous turtles accrued home-range area more slowly (b = 0.73 [−0.08, 1.38]) than did herbivorous tortoises (b = 0.93, [0.26, 1.60]; fig. 1). Herbivorous-lizard home range scaled positively and proportionately with body mass in the final model, with a slope slightly greater than but not significantly different from 1 (b = 1.07 [0.70, 1.44]; fig. 1). As above, parameter estimates for turtles, tortoises, and lizards have large margins of error, as a result of low sample size, and should be interpreted with caution.

Lake fish scaled with a larger intercept and a steeper slope (b = 0.99, [0.28, 1.70]) than river fish (b = 0.63, [0.41, 0.85]; fig. 1). Carnivorous marine fishes accrued home range area more slowly (b = 0.82, [0.55, 1.09]) than did herbivores (b = 1.21 [0.84, 1.58]; fig. 1) and generally exhibited smaller home ranges than freshwater fish, as reflected by smaller intercepts (fig. 1).

Evaluating Support for Mechanisms Driving Variation in Home-Range Allometry

Locomotion strategy, dimensionality, and trophic guild emerge as the main factors influencing home-range scaling across taxa, as reflected by the relative support for these individual models (ΔAICc ; table 1; fig. A1; figs. A1, A2 available online). Along with body mass, these fixed effects explained 68% of the variation in home-range size across vertebrates, and accounting for phylogenetic relationships and tracking method as random effects drives this figure up to 80% (model G: marginal R^2 = 0.68, conditional R^2_c = 0.80; table 1). The relationships predicted by our global model for each combination of factors closely resemble observed relationships for the corresponding taxa (fig. A2). Closer examination of scaling relationships among carnivores revealed that prey mass is also an important determinant of home-range scaling (table 2). Carnivores of similar mass pursuing larger prey have larger home ranges, and a more rapid increase of prey size in relation to predator size can drive steeper home-range scaling relationships. We explore these results in greater detail below.

Thermoregulation. Differences in thermoregulation strategy explain little additional variation in home-range allometry beyond that explained by mass alone, as highlighted

by substantial overlap in the height and scaling of home-range relationships across these groups (models B1 and B2: ΔAICc = 0.06 and −1.31, respectively; table 1; fig. A1B). Moreover, scaling relationships vary substantially within poikilotherms and are not consistent across representative groups such as reptiles and fishes (figs. 1, 2).

Locomotion Strategy. Accounting for locomotion strategy explained substantially more variation in home-range size than did mass alone (model C: ΔAICc = −54.77; table 1; fig. A1C). Among the locomotory strategies, swimming is associated with the lowest home-range intercept by far ($\log_{10}(a)$ [lower and upper 95% CI] = 0.72 [−0.38, 1.82]; table 1). Flying animals and running animals are thus predicted to have home ranges roughly 100 times larger and 10 times larger, respectively, than those of swimming animals (flying: $\log_{10}(a)$ = 3.21 [2.37, 4.05]; running: $\log_{10}(a)$ = 1.62 [0.84, 2.40]; table 1).

Foraging Dimensionality. Home-range scaling models that incorporate foraging dimensionality had nearly as much support as those incorporating locomotion strategy, with relatively more support for an interaction model (models D1 and D2: ΔAICc = −35.55 and −40.75, respectively; table 1; fig. A1D), suggesting that dimensionality influences both the intercept and the slope of home-range allometry. This is further supported by the fact that birds foraging in three dimensions had larger home ranges that increased more steeply with body size, compared with those foraging in two dimensions, both within and across trophic guilds (figs. 1, 2). Similarly, lake fishes, which tend to access a greater proportion of the three-dimensional water column, had a higher and steeper home-range allometry than marine fishes and river fishes in our data set, which are more closely associated with two-dimensional bottom features (fig. 1).

Trophic Guild. Trophic guild emerged as having the greatest support as a predictor of home-range size and affected both the intercept and the slope of home-range allometry (models E1 and E2: ΔAICc = −127.48 and −130.80, respectively; table 1; fig. A1E). Herbivores scaled similarly across taxa, but while carnivorous birds, mammals, and reptiles generally scaled higher and steeper than herbivores in the same class, carnivorous fish scaled shallower than did herbivorous fish (figs. 1, 2).

Realm. There was no systematic difference between the home-range allometries of terrestrial and aquatic organisms (model F: ΔAICc = 0.37; table 1; fig. A1A).

Predator-Prey Body Mass Relationships. Closer examination of the unexpected variation in scaling relationships

Table 2: Relative support for the influence of prey size on home-range scaling among carnivores

Hypothesis	Reference	Predicted effect		Model	Formula: HRA ~ (version)	log ₁₀ (a) (95% CI range)	b (95% CI range)	ΔAICc	k	R _{adj} ²	R _c ²
		a	b								
Full model ^a	Makarieva et al. 2005	H	M + L + D + D : M (baseline) (flying) (running) (slithering) (3D)	1.29 (.37, 2.21) +2.58 (1.33, 3.83) +2.68 (2.03, 3.33) +1.46 (.95, 1.97) -1 (-2.02, 2.22)	.81 (.54, 1.08) +22 (-.43, .87)	0	10	.83	.85
		Larger RPM: ↑; smaller RPM: ↓	...	I	M + L + D + D : M + PM (baseline) (flying) (running) (slithering) (3D) (PM)	2.59 (1.41, 3.77) +1.83 (.58, 3.08) +2.13 (1.44, 2.82) +73 (.10, 1.36) -.02 (-1.96, 1.92) +.51 (.22, .80)	.20 (-.25, .65) +32 (-.27, .91) ...	-6.91	11	.86	.87

Note: Comparison of full linear mixed effects models of the effects of body mass (M , g) on home range area (HRA, m²) across carnivores ($N = 67$ species), with and without prey mass (PM, g) as an additive fixed effect. Both models include the random effect of tracking method and taxonomic class. "Predicted effect" indicates the direction of the effect of the hypothesized mechanism on the intercept and/or slope, where ↑ indicates an increase and ↓ a decrease compared to the baseline model, H. In these models, where combinations of levels must be specified, the sign of the log₁₀(a) and b values indicates the departure from the overall baseline model scenario of a carnivore swimming in two dimensions. L = locomotion; D = dimensional; a = normalization constant; b = slope AICc = Akaike information criterion corrected for small sample sizes, ΔAICc = difference between AICc and that for the full model, k = number of parameters; RPM = relative prey mass; R_{PM} = conditional R² and R_{adj}² = marginal R² (see "Methods"); 3D = three-dimensional; 95% CI = 95% confidence interval.

^a The full model includes the baseline intercept and slope for a carnivore swimming in two dimensions.

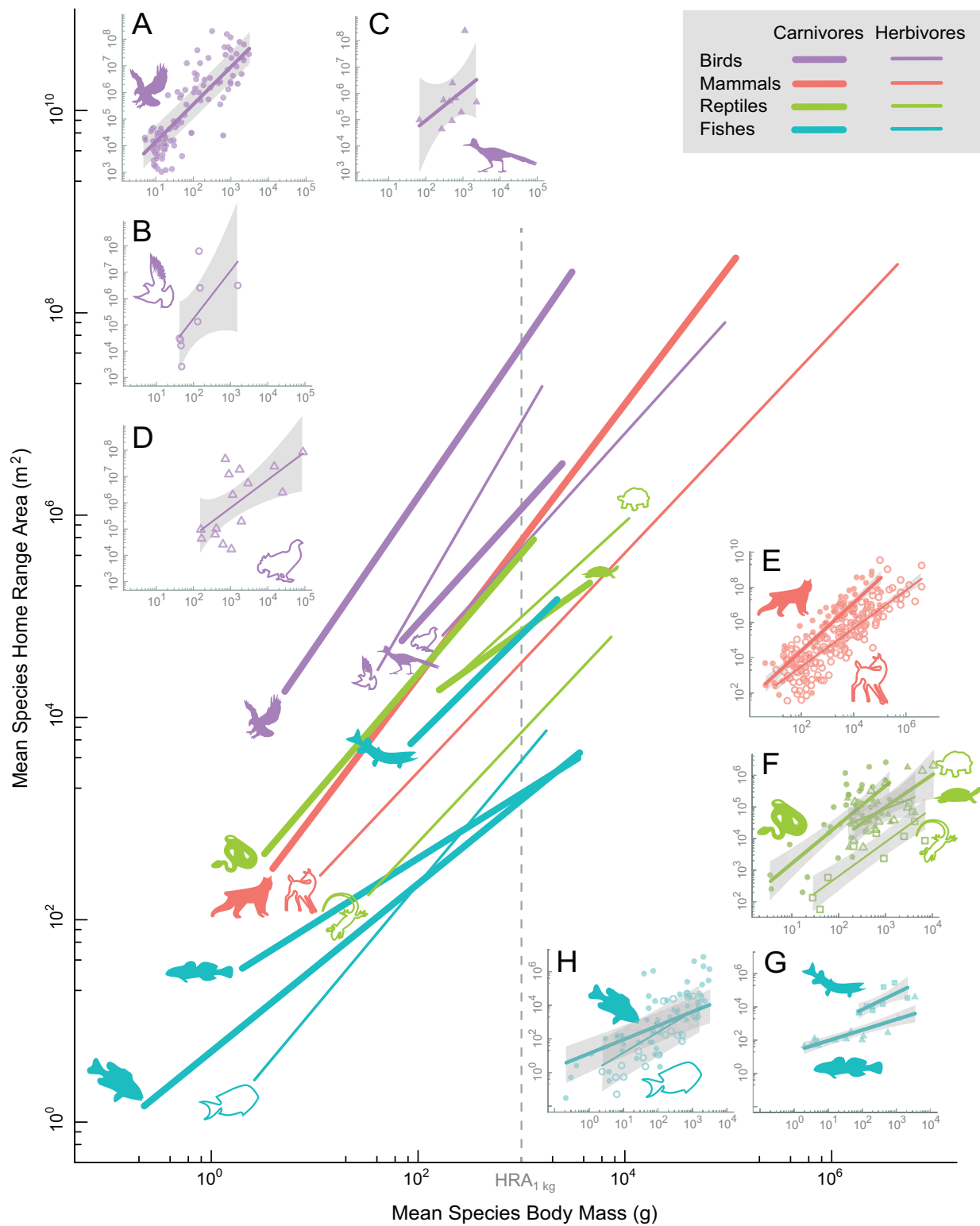


Figure 2: Home-range allometry across 569 terrestrial and aquatic vertebrate species spanning body masses from 0.2 g to 4,000 kg and home-range sizes from less than 1 m² to more than 3,500 km². Each regression line is based on the taxon-specific log-log relationship between home-range size and mean species body mass of the form $\log_{10}(\text{HRA}) \sim \log_{10}(a) + b \times \log_{10}(M)$. Lines and symbols are color-coded by taxonomic class (pink for mammals, purple for birds, green for reptiles, and blue for fish) and diet (thick lines and filled symbols for carnivores,

among carnivores revealed that prey mass is also an important determinant of home-range scaling in predators (table 2). We found that prey size scales more steeply with predator size in mammals, birds, and snakes than in fishes (fig. 3A). Incorporating the predicted mean prey size as an additive fixed effect yields a model with slightly improved fit but much stronger support than the model without prey mass (table 2). This suggests that prey size does influence home-range size. Plotting the predicted allometries of carnivore home-range models that either exclude or include prey mass further illustrates how shallower prey-predator mass scaling in fishes results in home-range allometries shallower than those of carnivorous mammals and explains the discrepancy between home-range predictions in the global and carnivore-only models (figs. 3B, A2).

Discussion

Until recently, ecologists understood less about the allometric scaling of home-range size than about the dependence on size of almost any other anatomical, behavioral, or ecological variable (Kelt and Van Vuren 1999; Holyoak et al. 2008). Here, we quantitatively evaluated the relative support for six hypotheses advanced to explain observed variation in home-range allometry over the largest and most diverse set of empirically measured species home ranges yet assembled. Neither realm nor thermoregulation explained substantial systematic variation in home-range sizes, suggesting that although homeotherms have a consistently higher metabolic rate (White et al. 2006), this does not result in consistently larger home ranges. Our analysis shows that home-range allometry is instead driven by locomotion strategy and by mechanisms influencing the effective density of food, specifically, foraging dimension, trophic guild, and prey size. Importantly, accounting for each of these factors and controlling for tracking methodology and taxonomic relatedness allows us to explain 80% of the observed variation in home-range size among vertebrates.

In line with theoretical predictions (Haskell et al. 2002), locomotion emerged as an important factor influencing home-range size, as reflected in the largest intercept effect sizes of any home-range scaling predictor. For a given body mass, home-range sizes across locomotion strategies increased in tandem with the optimal velocities of each strategy (Bejan and Marden 2006), yielding the intuitive result that, all other things being equal, the fastest-moving animals generally had the largest home-range sizes. The home-range sizes of snakes, however, are much more sim-

ilar to those of running animals than might be expected, given that their optimal locomotion speed appears to be well below that of runners (Hu and Shelley 2012). The fact that snake locomotion speeds have been largely measured in laboratory settings may account for some of this discrepancy.

Foraging dimension plays a smaller but still important role in determining home-range size across vertebrate taxa, supporting the hypothesis that three-dimensional foraging dilutes the fractal scaling of resource distribution (Haskell et al. 2002). We found that flying birds scaled higher and more steeply than flightless birds within the same trophic guild. A similar pattern is apparent in fishes, where lake carnivores that have access to a tall water column scale more steeply than river carnivores, which are constrained by the shallower depth and hence more two-dimensional nature of rivers, or marine carnivores, which are represented largely by species strongly associated with the seabed (e.g., coral-reef and rocky-reef fishes; Kramer and Chapman 1999). We hypothesize that fishes foraging higher in the water column but still maintaining fidelity to home ranges, such as coral-reef planktivores, should demonstrate steeper home-range allometries resembling those of lake carnivores. However, home-range estimates for such fishes are currently too scarce to test this prediction.

Trophic guild also had an important influence on home-range size. Carnivores' home ranges scaled higher and steeper than those of herbivores, supporting the notion that carnivores generally encounter lower resource densities than herbivores (Haskell et al. 2002). However, this tendency does not, apparently, extend to fishes. Although herbivorous-fish home ranges scale similarly to those of other herbivorous taxa, carnivorous-fish home ranges scale more shallowly than those of any other group of carnivores. A closer investigation of variation in home-range allometry among carnivores revealed that these differences are likely to be driven by systematic differences in relative prey size as a result of prey size–predator size scaling among these taxa (fig. 3A).

Relative prey size is a key determinant of differences in body size distributions and species- versus size-based interactions between marine and terrestrial biomes (Andersen and Beyer 2006; Reum et al., forthcoming). Prey size is constrained by gape size in all carnivores. However, some predators circumvent this limitation through morphological or behavioral adaptations that increase their ability to handle large prey and thus the energy obtained per prey item. Most terrestrial carnivores escape the constraints of gape limitation by holding down and fragmenting their prey and

thin lines and open symbols for herbivores). Each line is further distinguished by the silhouette corresponding to the taxon-specific characteristics and parameter estimates reported in figure 1. Insets A–H show the raw data and regression lines, with 95% confidence intervals, for each taxon of interest: flying carnivorous birds (A), flying herbivorous birds (B), flightless herbivorous birds (C), flightless carnivorous birds (D), mammals (E), reptiles (F), freshwater fish (G), marine fish (H).

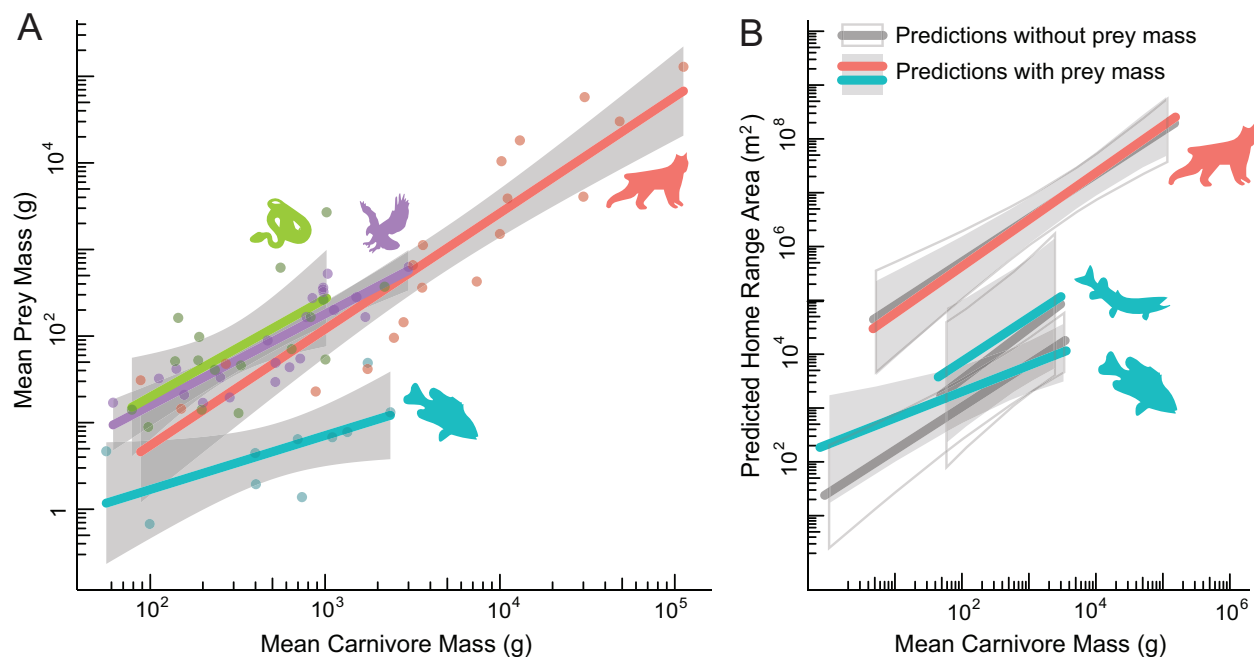


Figure 3: A, Prey size–predator size relationships among carnivorous taxa for which both home-range area estimates and prey size estimates were available in the literature. B, Home-range areas of carnivorous mammals and fishes predicted from models of the form $HRA \sim M + L + D + M:D$ or $HRA \sim M + L + D + M:D + PM$ over a range of prey sizes predicted from linear models of taxon-specific prey size–predator size relationships shown in A. D = dimensionality; HRA = home-range area; L = locomotion strategy; M = mean body mass (g); PM = mean prey mass (g); see figure 1 for symbols.

can thus target larger prey sizes relative to predator size (Schwenk and Rubega 2005). Predatory birds and mammals are typically only marginally heavier than their prey: predatory birds have a median predator-prey mass ratio (PPMR) of 4:1 (range 1.2–28:1; Jaksic and Carothers 1985) and predatory mammals a median PPMR of 8:1 (range 0.3–200:1; Vézina 1985; Carbone et al. 1999). In contrast, suction-feeding aquatic carnivores can eat only what can be swallowed whole (Jennings and Mackinson 2003; Yvon-Durocher et al. 2011). Consequently, carnivorous fishes are typically 2–3 orders of magnitude heavier than their prey, with a median PPMR of approximately 285:1 (range: 0.005– 1.95×10^{15} :1, with extremely high values characteristic of planktivores such as whale sharks or manta rays, which were not included in our analyses; Jennings and Mackinson 2003; Brose et al. 2004). Lacking limbs, snakes might be considered terrestrial analogs to predatory fishes and might demonstrate similar home-range scaling. However, snakes are able to overcome the prey-handling limitations of fishes by coiling their body around their prey and through further adaptations such as constriction, venom, and dislocating jaws, which help them to subdue and ingest large prey (Beaupré and Montgomery 2007). These adaptations are reflected in snake PPMRs, which are more similar to those of mammalian carnivores, with a typical

mean of 5:1 (overall range: 0.6–200:1; Greene 1983; Martins et al. 2002; Shine and Thomas 2005; Beaupré and Montgomery 2007).

In addition to experiencing stronger constraints on prey size, carnivorous fishes exhibit a scaling of prey-to-predator size ratios markedly different from that of other carnivores. Prey sizes generally increase with predator size as increasingly large predators drop smaller prey items from their diet (Arnold 1993; Carbone et al. 1999; Riede et al. 2011). However, excluding small prey from the diet is more common among terrestrial predators; gape-limited fishes tend to broaden the range of prey sizes exploited at larger sizes rather than drop small prey from the diet (Brandl et al. 1994; Scharf et al. 2000; King 2002; Tucker and Rogers 2014). In our data set, mean prey size does indeed increase more slowly in carnivorous fishes than in other carnivorous taxa and is reflected in the shallower scaling of home-range allometry in fishes. Field biologists are well placed to undertake the first empirical tests of the importance of PPMR in determining home-range size, for example, by combining acoustic-array technology with stable-isotope and gut-contents analysis to track how range size covaries with prey size and distribution.

Although we chose to focus on metabolic and trophic correlates of home-range scaling, home-range size can also

be influenced by behavioral factors. For example, males often maintain larger home ranges than females in order to attract more mates or defend an existing harem (Harestad and Bunnell 1979). In addition, animals that are more vulnerable to predation may have smaller home ranges, reflecting their need to remain closer to a familiar shelter (e.g., Mather and O'Dor 1991). A more systematic exploration of behavioral factors influencing home-range size would be a promising area for future work, and behavioral factors may explain some of the residual variation not accounted for by our model.

Our comparative analysis reveals the general importance of locomotion, dimensionality, trophic guild, and prey size for shaping the allometry of home-range size across the diversity of vertebrate species. This represents an important step in narrowing the recognized gap between movement biology and ecology and evolution (Holyoak et al. 2008). We have shown how the energetic costs and benefits of morphological constraints can influence the spatial ecology of individual species and contribute to broader-scale patterns in the distributions of vertebrates across landscapes and seascapes. This work underscores the importance of basic research on the spatial ecology of underrepresented taxa, highlights the value of a spatial approach to predator-prey relationships, and opens the door to a rich line of inquiry investigating the ways in which metabolic ecology interacts with individual space use to generate emergent patterns at the largest scales.

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Most aquatic predators, like this crocodile fish (*Cymbacephalus beauforti*), caught in the middle of a meal in Malaysian Borneo, differ from their terrestrial counterparts in a big way: they can eat only what can be swallowed whole. This simple constraint contributes to smaller home-range sizes among fishes, in contrast to other animal groups. Photograph by Natascia Tamburello.