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Ectothermy and the macroecology of home range scaling in snakes

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Abstract

Aim: A central question in ecology has been that of why animal home ranges scale more steeply with body size than do metabolic rates. Yet, the generality of this notion has scarcely been tested in non-model species like ectotherms, which have lower metabolic requirements than endotherms and which may, therefore, have different home range area requirements. Our aim was to examine how home range area scales with body size in snakes and to shed light on how other factors may shape home range area requirements in an understudied group of ectotherms.

Location: Global.

Time period: 1984–2018.

Major taxon studied: Serpents.

Methods: We compiled and analysed a dataset of snake home ranges from the literature to evaluate how body size, sex, climate, foraging ecology, and biogeographic factors shape home range area requirements.

Results: Home range area scaled more gradually with body size in snakes (log-linear slope of simple linear regression 0.72 with 95% confidence interval 0.48–0.96) than has been reported for mammals and birds, and instead more closely followed the scaling of metabolic rates with body size. Male snakes had larger home ranges than females and this difference increased as temperature increased at a study site, possibly from mate-searching behaviour of males and greater ease reaching optimal body temperatures in warmer areas. Finally, home range area scaled more steeply for snakes that forage actively than for those that rely on sit-and-wait ambush foraging, a reflection of their foraging ecology.

Main conclusions: Our results question the general notion that animal home range areas scale more steeply with body size than does metabolism. Key distinctions in the energy demands of endotherms and ectotherms and their responses to those demands give rise to differing home range area requirements. More attention to non-model species is needed when creating and evaluating ecological theory.

KEYWORDS

activity, body size, energetics, movement, radio telemetry, serpents, space use, spatial ecology

1 | INTRODUCTION

A central concept in ecology has been that of an animal's home range—the area an animal repeatedly traverses in search of food and mates (Burt, 1943). Home range size, like many other ecological, physiological and behavioural characteristics, has repeatedly been shown to scale with body size in an allometric relationship of the form $Y = aM^b$, where Y is the variable of interest, M is body mass, and a and b are the intercept and slope, respectively (Hendriks, 2007). As body mass increases, so too do metabolic costs, leading initially to the conclusion that home range area should scale equivalently with energetic needs (Kleiber, 1975; McNab, 1963). Indeed, McNab (1963) found that the slope of the relationship between home range area and body mass in mammals did not differ significantly from that of basal metabolic rate and body mass. Later studies in both mammals and birds, however, largely disputed this, finding that home range area requirements typically scale more steeply than the 0.75 predicted solely by metabolic costs, instead often scaling at a slope closer to 1 or even greater (Harestad & Bunnel, 1979; Kelt & Van Vuren, 1999; Schoener, 1968; Tamburello et al., 2015). What then is responsible for the discrepancy between observed slopes and that predicted solely from metabolic costs?

Perhaps the most plausible mechanism yet given for why home range area scales with body mass more steeply than do metabolic rates lies in the increasing overlap and shared home ranges of larger animals that leads to competition (Damuth, 1981). Overlap in home ranges and the loss of resources to neighbours conceivably results in lower realized rates of usable energy for any single individual (Harestad & Bunnel, 1979; Jetz et al., 2004). Such losses are predicted to be negligible at the smallest body sizes (< 100 g), but may result in as much as 90% of resources being lost to neighbours for animals > 100 kg (Jetz et al., 2004). As a result, home range area is expected to scale with body mass at a slope of 1 for most groups, and indeed there is empirical support for this mathematical prediction in mammals (Jetz et al., 2004; Tucker et al., 2014). Nevertheless, body mass is not the only factor related to energy requirements that is known to affect home range size.

Several studies have shown that other factors can shape home range area requirements. Among mammals and birds, for example, carnivores have greater mass-specific home range area requirements than do omnivores and herbivores (Jetz et al., 2004; Kelt & Van Vuren, 2001; Schoener, 1968), owing to lower food densities that result from the nature of Eltonian food pyramids (Elton, 1927). Locomotion, or the cost of movement, has also been linked to home range area requirements, with animals that move more quickly or more efficiently generally having larger mass-specific home ranges than those that do not (Tamburello et al., 2015; Tucker et al., 2014). Extrinsic factors that affect energy availability, like habitat quality or productivity, can also affect the size of home range areas. Where density of food resources is low, for example, animals tend to have larger home ranges than where such density is high (Haskell et al., 2002; Morellet et al., 2013; Schoepf et al., 2015), leading to home ranges that increase in size with decreasing productivity (Harestad & Bunnel, 1979; Lindstedt et al., 1986; Morellet et al., 2013). Ultimately, both intrinsic and extrinsic factors have been shown to influence the size of animal home ranges.

The relationships in tetrapods between energetic demands or constraints and home range size have been revealed mainly through studies of mammals and birds—endotherms that have historically received much research attention (Bonnet et al., 2002; Shine & Bonnet, 2000). Yet, there is reason to suspect that endotherms and ectotherms have differing relationships between home range size and body mass. Endotherms have greater energy needs than similarly sized ectotherms (Pough, 1980), which should translate to larger home ranges across body mass (Hendriks, 2007)—that is, a greater intercept. The slopes at which home ranges scale with body mass may also differ for endotherms and ectotherms given that field metabolic rates scale more steeply with body mass in reptiles than in birds or mammals (Nagy, 2005; Nagy et al., 1999). To date, just one study has explicitly compared patterns of home range scaling in endotherms and ectotherms, finding no support for either differing intercepts or slopes in the home range–body mass relationship when fish were included (Tamburello et al., 2015). Nevertheless, a more recent study found that home range area scales with body mass in turtles significantly < 1, with a slope of 0.57 (95% confidence interval: 0.22–0.85; Slavenko et al., 2016), far shallower than slopes reported for endotherms. Such a finding questions the generality of home range scaling in tetrapods and highlights the need for additional studies of non-model organisms.

Snakes perhaps best exemplify the moniker of non-model organisms among vertebrates (Shine & Bonnet, 2000). Notoriously difficult to study (Durso & Seigel, 2015; Willson et al., 2011), they tend to be underrepresented in ecological literature compared with mammals and birds (Bonnet et al., 2002). Decreasing size of radio-transmitters and improved battery technology have nevertheless enabled a greater range of body sizes of snakes to be tracked and thus provide more variation with which to test hypotheses. This makes possible an in-depth analysis of the factors associated with home range size in snakes that has heretofore been elusive. For instance, in the first tabular survey of snake home ranges conducted > 30 years ago, no general conclusions could be made about how home range sizes vary in snakes (Macartney et al., 1988), leaving many questions unanswered. To address this uncertainty, and to better examine the generality of how energetic factors shape home range size in tetrapods, we reviewed the literature to compile and analyse a database of snake home ranges. With this database and additional data that we obtained for each study site, we examined the relationship between home range size and body mass in snakes, and whether sex, habitat or biogeographic factors linked to productivity were associated with home range sizes. We predicted (a) that males would have larger mass-specific home ranges than females, a finding attributed to mate-searching behaviour of males in another group of squamates, the lizards (Perry & Garland, 2002); (b) that species that use many aquatic habitats, where costs of movement are low, would have larger home ranges than species that use no or few aquatic habitats (Slavenko et al., 2016; Tucker et al., 2014); (c) that factors associated with productivity at a study site, like mean annual temperature, annual precipitation or mean net primary productivity, would be negatively associated with home range size in snakes, as with other vertebrates (Morellet et al., 2013); and (d) that home range area would scale more gradually with ambush foragers than active foragers given that ‘sit-and-wait’, ambush foraging is considered a ‘low energy strategy’ compared with a costlier active foraging mode (Mushinsky, 1987; Huey & Pianka, 1981).

2 | METHODS

2.1 | Data collection

We searched peer-reviewed literature, graduate theses and unpublished technical reports using Zoological Record via ProQuest, Wildlife & Ecology Studies via EBSCO, Web of Science, and Google Scholar with the search terms ‘snake*’ AND either ‘home range’, ‘homerange’, ‘movement’, ‘telemetry’, ‘space use’ or ‘activity’. We added any studies cited in the manuscripts returned by the search results that were not found in the original search. We included studies in our analyses if they (a) tracked wild, not captive-raised and released snakes, (b) used very high frequency (VHF) radio-transmitters with weekly or more frequent resighting, and (c) tracked snakes during an active season (i.e. not just during spring migrations or winter torpor). These inclusion criteria excluded studies that relied on implanted radioactive tags to track animals, some that relied on mark-resighting at random intervals, short-term studies just days to weeks in length, and those that tracked just captive-raised and released animals. The list of references contributing data to the dataset is provided in the Appendix.

For each study, we extracted the following data: species, study location, mean mass, and mean home range for each estimator type reported. We extracted separate values for each sex where possible. We used the reported coordinates for study locations when they were provided; otherwise, we used maps, figures, and site descriptions from each study to identify their locations on Google Earth and obtain coordinates. For 23 cases, authors provided us mass data that were not reported in their studies. For 45 cases, we obtained missing mass data from publications of the same animals or we used mass–snout–vent length (mass–SVL) regressions to estimate masses from other studies of the species, following the methods of Perry and Garland (2002) and Tamburello et al. (2015). The remaining 41 cases all reported mean masses in the initial study. The home range estimates that were often reported and thus included in the final database were 100 and 95% minimum convex polygons (MCP) and 95 and 90% kernel density (KD) estimates. We tabulated mean home ranges from individual estimates provided in tables or supplementary material when means were not reported or when means were not separated by sex. Finally, we noted whether studies reported having tracked gravid females or not, and we excluded home ranges of gravid females from the mean female home range estimates when possible. Of the 109 observations from studies that met the inclusion criteria, 3 included just males, 62 did not distinguish whether gravid and non-gravid females were separated in home range estimates, 16 included gravid females in estimates of female home range size and 28 either excluded gravid females or provided estimates or data separately for gravid and non-gravid females.

We obtained elevation from Google Earth using the coordinates of each study site unless it was provided in the text of the study. We extracted mean annual temperature and total annual precipitation within a 10-km buffer around coordinates for each study site from the WorldClim dataset (Hijmans et al., 2005). We extracted net primary productivity (NPP) within the same 10-km buffer from the NASA MODIS dataset (Running et al., 2011). Following Böhm et al. (2016) and Todd et al. (2017), we counted the number of habitat types inhabited by each species reported in International Union for Conservation of Nature (IUCN) species accounts (www.iucnredlist.org) as a measure of habitat breadth. Finally, following Todd et al. (2017), we calculated an aquatic index for each species as the proportion of these habitats that was aquatic for each species.

2.2 | Statistical analysis

We analysed three subsets of the final database due to differences in which data were available and in which response variable we were interested. Because sex-specific estimates of home ranges were not available in all studies, we first analysed a dataset using mean home range size across sexes as the dependent variable for each study (107 estimates from 96 studies after dropping cases with incomplete sets of covariates). To examine differences in home range size between the sexes, we analysed a subset of studies where sex-specific home ranges could be obtained (165 estimates from 76 studies). Finally, we analysed a subset of data using as the dependent variable the natural log of the ratio of male : female home range size (78 estimates from 69 studies), using the same estimator for both sexes from a study to calculate the ratios. Taking the natural log of this ratio results in a value that, when positive, indicates males had larger home ranges than females, and when negative, indicates that females had larger home ranges than males.

Prior to all analyses, we examined correlations among predictors, whether relationships were linear, as well as variance inflation factors (all VIF < 3) using the vif function of the car package in R (Fox & Weisberg, 2019; R Core Team, 2019). Home range size and predictor variables with highly skewed distributions were log-transformed prior to analysis. For the purpose of comparing competing sets of predictors of home range size, which included body mass, ecological variables (habitat breadth and aquatic index) and biogeographic variables (elevation, mean NPP, mean annual temperature, and annual precipitation), we fit linear mixed-effects models (LMM) with varying intercepts for study and species using the lme4 package (Bates et al., 2015). This random effect structure accounted for both unmeasured, study-specific conditions and non-independence of multiple estimates for the same species. We also fit models with a random intercept for estimator type to account for differences among studies (MCP versus KD, for instance), using one estimator at random from studies where multiple types were used to calculate home range size. The variance for this intercept term was near zero (i.e. uninformative) and full models fit without estimation method had differences in corrected Akaike's information criterion (ΔAICc) < 2 compared with models that included estimation method; the random effect of estimator type was, therefore, not included in further model comparison analyses. To analyse the most inclusive subset of the data that lacked sex-specific home ranges, we fit a full model that included all predictor variables as fixed effects and we fit an intercept-only model. We next compared using AICc the full and intercept models with competing models fit with all individual-level variables (in this case, log-mass only), both ecological variables, the biogeographic variables, as well as models with each variable fit separately (Tables 1–3). We were careful to construct and compare only those models representing hypotheses we were interested in testing rather than constructing all possible models with all possible interactions, an approach that can 'uncover mainly spurious correlations' (*sensu stricto* Burnham & Anderson, 2002).

Because phylogenetically conserved traits could lead to non-independence of observations among closely related species, we compared estimates from the global LMM used in the model selection procedure above with a similar global model, but in which estimates were generated from a Bayesian implementation of a phylogenetic linear mixed effects model (PLMM). We also re-fit the best supported models from above using PLMM to examine estimates while accounting for phylogeny. To account for phylogenetic non-independence of species, we generated an inverse covariance matrix for the random intercept of species based on topologies from a fully sampled phylogenetic tree for squamates (Tonini et al., 2016). We specified an inverse-gamma prior distribution for the random intercept and ran the model with 5 million Markov chain Monte Carlo (MCMC) iterations and a burn in of 1,000 iterations using the MCMCglmm package (Hadfield, 2010). Convergence was assessed using the Gelman–Rubin statistic. Separately, we used a PLMM to compare home range scaling between the 23 active foraging species of Colubridae and the 17 ambush foraging species of Viperidae (Beaupre & Montgomery, 2007). This model included log home range size as the response and the interaction between mass and foraging mode as the fixed effect.

We followed a similar model fitting procedure with the two subsets of the data that included either sex-specific home range estimates or the ratio of male : female home range size as response variables. For the dataset with sex-specific home range estimates, the individual-level model included both log-mass and sex as predictors, and ecological and biogeographic models were each fit with and without sex as a covariate when comparing models using AICc. For the analysis using the natural log of the ratio of male : female home range size as the dependent variable, the individual-level models included the natural log of male : female mass ratio (a measure of sexual size dimorphism) and the log-mean mass for each species, and ecological and biogeographic models were each fit with and without male : female mass ratio as a covariate when comparing models using AICc. For these sex-specific and male : female home range subsets of the data, we also fit a global PLMM to evaluate effect sizes while controlling for phylogenetic relationships, as described above.

3 | RESULTS

Our literature search returned 98 studies that met the inclusion criteria, providing home range estimates for 50 species from 5

TABLE 1 Competing models explaining variation in home range size using the most inclusive dataset—without sex-specific estimates of home range

Model category	Predictors	*k*	AICc	ΔAICc	*w*
Single variable	Mass	5	181.95	0.00	.929
Global	Mass + Habitats + Aquatic + Elevation + NPP + Temp + Precip	11	187.12	5.17	.070
Null	Intercept	4	199.35	17.40	< .001
Single variable	Habitats	5	200.40	18.45	< .001
Single variable	Aquatic	5	200.76	18.81	< .001
Single variable	Temp	5	201.43	19.48	< .001
Single variable	Precip	5	201.43	19.48	< .001
Single variable	NPP	5	201.44	19.49	< .001
Single variable	Elevation	5	201.54	19.59	< .001
Ecological 1	Habitats + Aquatic	6	202.51	20.56	< .001
Biogeographic 1	Elevation + NPP + Temp + Precip	8	207.50	25.55	< .001

Note: NPP = net primary productivity; Temp = temperature; Precip = precipitation. We fit linear mixed models ($n = 107$ observations) with varying intercepts of species ($n = 49$) and study ($n = 96$). Support for a given model was based on corrected Akaike's information criterion (AICc), with the difference between the best supported model and all other models in the set shown (ΔAICc). We also report the fixed effects (explanatory variables) of each model, number of parameters (*k*) and model weights (*w*).

TABLE 2 Competing models explaining variation in home range size using the subset of data for which sex-specific estimates of home range size were available

Model category	Predictors	*k*	AICc	ΔAICc	*w*
Individual level	Sex + Mass	6	184.31	0.00	.948
Global	Sex + Mass + Habitats + Aquatic + Elevation + NPP + Temp + Precip	12	190.12	5.81	.052
Single variable	Sex	5	212.58	28.27	< .001
Ecological 1	Habitats + Aquatic + Sex	5	216.16	31.85	< .001
Single variable	Mass	7	217.81	33.50	< .001
Biogeographic + Sex	Elevation + NPP + Temp + Precip + Sex	9	218.38	34.07	< .001
Single variable	Elevation	5	242.94	58.63	< .001
Null	Intercept	4	243.26	58.95	< .001
Single variable	Habitats	5	244.64	60.33	< .001
Single variable	Precip	5	245.14	60.83	< .001
Single variable	Aquatic	5	245.18	60.87	< .001
Single variable	Temp	5	245.28	60.97	< .001
Single variable	NPP	5	245.37	61.06	< .001
Ecological 2	Habitats + Aquatic	6	246.79	62.48	< .001
Biogeographic	Elevation + NPP + Temp + Precip	8	248.91	64.59	< .001

Note: NPP = net primary productivity; Temp = temperature; Precip = precipitation. We fit linear mixed models ($n = 165$ observations) with varying intercepts of species ($n = 44$) and study ($n = 76$). Support for a given model is based on corrected Akaike's information criterion (AICc) with the difference between the best supported model and all other models in the set shown (ΔAICc). We also report the fixed effects (explanatory variables) of each model, number of parameters (k) and model weights (w).

continents (Appendix; Supporting Information Table S1, Figure S1). Two studies of one elapid species could not be analysed because the species lacked IUCN habitat use data. Of the 96 studies and 49 species included in our analyses, the greatest number of studies came from North America and Australia, followed by several in Europe (Supporting Information Figure S1). There were very few studies from Africa or Asia, and none from South America (Supporting Information Figure S1). Species from the family Colubridae (23) were the most represented, followed by Viperidae (17), Boidae (3), Elapidae (2), Pythonidae (3) and Dipsadidae (1) (Supporting Information Table S1).

Using the most inclusive dataset—without sex-specific estimates of home range—the best supported predictor set explaining variation in home range size included a model fit with mass as the only fixed effect (Table 1). Examination of estimates from both implementations of the full model (i.e. with and without phylogeny) show that estimates are consistent between these models and that mass had a significant, positive effect (p-value derived from the MCMC posterior, pMCMC < .001) and habitat breadth had a significant, negative effect on home range size (pMCMC = .031; Figure 1a). From a PLMM fit with just log-mass as a fixed effect, the posterior mean slope of the increase in home range size as a function of mass was 0.86 [95% credible interval (CRI) = 0.55–1.16, posterior mean $R^2_{\text{marginal}} = .24$, $R^2_{\text{conditional}} = .63$, pMCMC < .001; Figure 2]. For comparison with similar studies of other taxa, where phylogenetic non-independence is often not accounted for, a simple linear regression of log-home range with log-mass produced a slope of 0.72 (95% confidence interval = 0.48–0.96). The interaction between body mass and foraging mode was also significant ($\beta = 0.86$, 95% CRI = 0.02–1.78, pMCMC = .0496, $R^2_{\text{marginal}} = .30$, $R^2_{\text{conditional}} = .69$), and indicated that home range size increased with body mass at a greater rate for the active foraging species of Colubridae than for the ambush foraging species of Viperidae (Figure 3). Across models, $R^2_{\text{conditional}}$ explained most of the variation in responses, suggesting that while fixed effects were informative, much variation was also attributable to unmeasured taxon or population characteristics and study-level factors.

Using the subset of data for which sex-specific estimates of home range size were available, the best supported predictor set from LMMs was a model that included sex and mass as fixed effects associated with home range size (Table 2). A PLMM fit with sex and mass showed that, on average, males had larger home ranges than did females ($\beta_{\text{sex}} = 0.23$, 95% CRI = 0.16–0.30, pMCMC < .001), and home range size increased with mass ($\beta_{\text{mass}} = 0.78$, 95% CRI = 0.55–1.05, pMCMC < .001, $R^2_{\text{marginal}} = .22$, $R^2_{\text{conditional}} = .49$). Again, the differences in estimates from LMMs, used for comparison of predictor sets using AICc, and PLMMs, used to generate phylogenetically informed parameter estimates, were negligible (Figure 1b).

For the analysis of the ratio of male : female home range size, the best supported predictor sets from LMMs included a model with the ratio of male : female body mass and biogeographic variables—mean annual temperature, precipitation, NPP, and elevation—as fixed effects (Table 3). Home range size in males increased relative to females as the mass of males increased relative to females and as mean annual temperature at a study site increased (Figure 1c). There was competing support (< 2 ΔAICc) for a model

TABLE 3 Competing models explaining variation in of the ratio of male : female home range size

Model category	Predictors	*k*	AICc	ΔAICc	*w*
Biogeographic + Mass	Elevation + NPP + Temp + Precip + Mass ratio	9	158.71	0.00	.442
Single variable	Mass ratio	5	159.61	0.91	.281
Individual level	Mass + Mass ratio	6	161.84	3.13	.092
Ecological + Mass	Habitats + Aquatic + Mass ratio	7	162.65	3.95	.061
Global	Mass + Mass ratio + Habitats +Aquatic + Elevation + NPP + Temp + Precip	12	163.64	4.94	.037
Single variable	Elevation	5	164.53	5.82	.024
Biogeographic	Elevation + NPP + Temp + Precip	8	165.04	6.34	.019
Single variable	Temp	5	166.16	7.46	.011
Null	Intercept	4	166.56	7.85	.009
Single variable	Aquatic	5	166.59	7.88	.009
Single variable	Precip	5	168.19	9.48	.004
Ecological	Habitats + Aquatic	6	168.41	9.71	.003
Single variable	Mass	5	168.63	9.93	.003
Single variable	Habitats	5	168.77	10.06	.003
Single variable	NPP	5	168.79	10.08	.003

Note: NPP = net primary productivity; Temp = temperature; Precip = precipitation.We fit linear mixed models ($n = 78$ observations) with varying intercepts of species ($n = 41$) and study ($n = 69$). Support for a given model is based on corrected Akaike's information criterion (AICc) with the difference between the best supported model and all other models in the set shown (ΔAICc). We also report the fixed effects (explanatory variables) of each model, number of parameters (*k*) and model weights (*w*).

with the ratio of male : female body mass as the only fixed effect. A PLMM fit with male : female body mass likewise indicated that male home range size increased relative to that of females as male body size increased relative to that of females ($\beta_{\text{mass ratio}} = 0.59$, 95% CRI = 0.04–1.11, pMCMC = .038, $R^2_{\text{marginal}} = .09$, $R^2_{\text{conditional}} = .46$). In a PLMM fit with male : female body mass and biogeographic variables, mean annual temperature was the only biogeographic variable that was significant (also see Figure 1c)—male home range size increased relative to that of females as mean annual temperature increased at a study site ($\beta_{\text{temp}} = 0.22$, 95% CRI = 0.05–0.41, pMCMC = .016, posterior model mean $R^2_{\text{marginal}} = .24$, $R^2_{\text{conditional}} = .45$).

4 | DISCUSSION

Snakes are notoriously difficult to study due to their low detectability (Durso & Seigel, 2015; Durso et al., 2011; Willson et al., 2011), and, as a result, tend to be underrepresented in ecological literature compared with mammals and birds (Bonnet et al., 2002). It is thus unsurprising that a clear understanding of the factors that shape their home range area requirements has remained elusive. A previous attempt to summarize home range sizes in snakes, for example, found little evidence of any consistent patterns (Macartney et al., 1988). In contrast, we found clear evidence of a positive relationship between home range size and body size in snakes, typical of the relationship found across vertebrates (Tamburello et al., 2015). Moreover, our results shed light on how key characteristics like body size, foraging mode, temperature, and sex are associated with home range size in snakes.

As with all studies of animal home range, some cautions apply. Perhaps most importantly, critiques of the home range concept and associated metrics should be kept in mind. For instance, the MCP has been treated as one of the more spatially encompassing measures of the areal extent of an individual's ranging, but provides no information on space use within that area (Worton, 1987). It has nevertheless proven useful for comparisons among taxa in how home ranges vary with ecological characteristics (Nilsen et al., 2008). The KD and related utilization metrics, in contrast, may reflect more the time spent in different areas within a home range (Averill-Murray et al., 2020). The distinction between these types of metrics may be especially important given that reptiles are often sedentary for prolonged periods within their home range, even in an otherwise active season for them (Averill-Murray et al., 2020). We explicitly accounted for these different metrics and interpretations in our modelling approach and found little variance associated with which metric was included. The growing use of radio-telemetry to track the movements of snakes has made it increasingly possible to account for these different estimation methods while examining the factors influencing variation in home ranges among species.

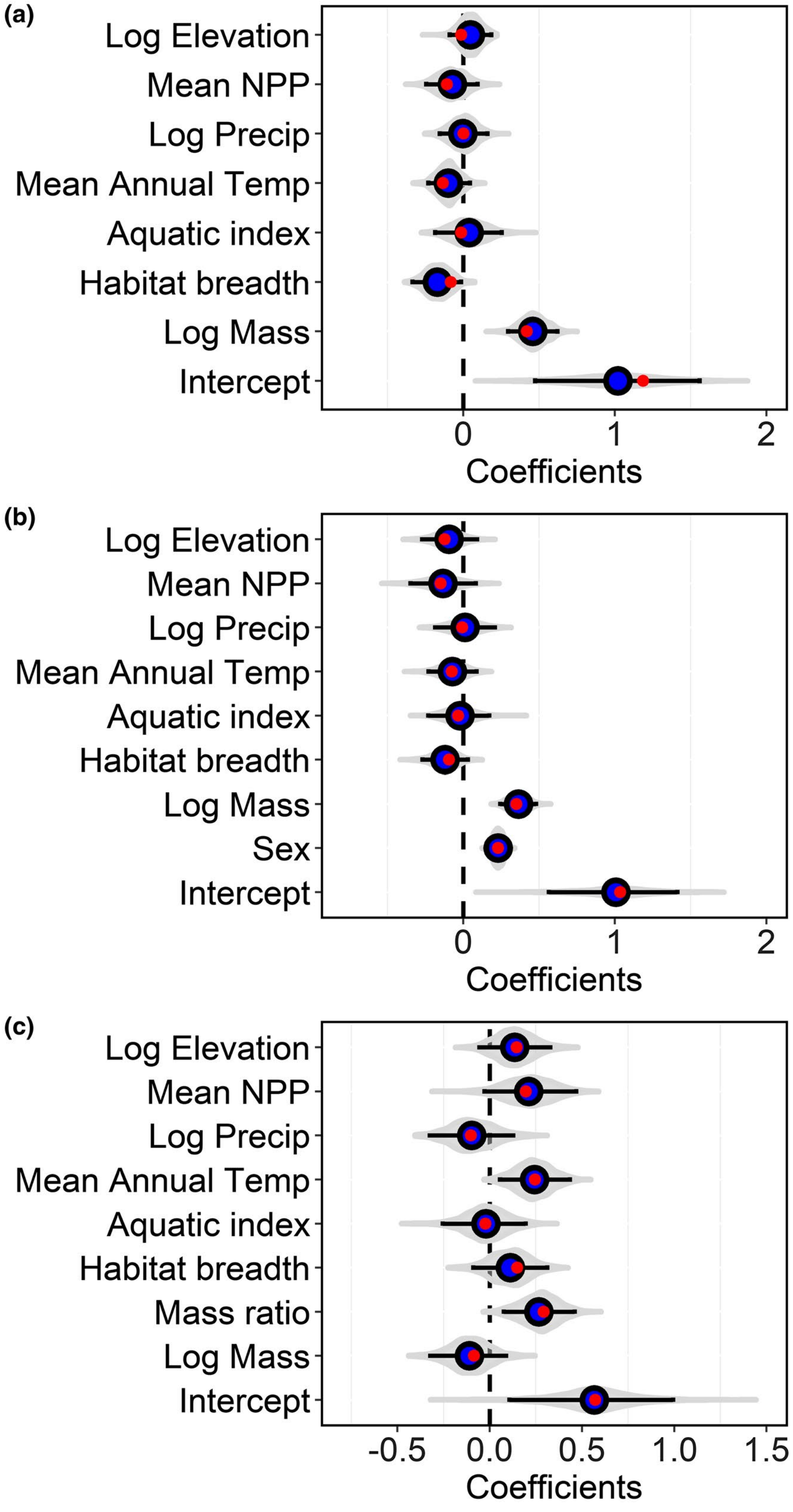

FIGURE 1 Coefficients from full models fit to each partition of the dataset, (a) the most inclusive dataset—without sex-specific estimates of home range, (b) the subset of data for which sex-specific estimates of home range size were available, and (c) models explaining variation in the ratio of male : female home range size. Blue dots represent mean estimates from a Bayesian implementation of a phylogenetic linear mixed model and error bars are 95% credible intervals. The violin plots represent 1,000 samples of the posterior distribution for each parameter. For comparison, red dots represent maximum likelihood estimates of these parameters from the full model used in the model selection procedure. NPP = net primary productivity; Precip = precipitation; Temp = temperature. [Colour figure can be viewed at wileyonlinelibrary.com]

Sex was one important determinant of home range size in snakes, with males having larger mass-specific home ranges than females, a pattern also found in the other major group of squamates, the lizards (Perry & Garland, 2002). Larger home ranges in males likely reflect key differences in how the sexes apportion energy to reproduction. For instance, whereas females apportion energy to developing embryos, males expend energy on extensive mate-searching to increase their reproductive success (Shine, 2003), a ‘cost of reproduction’ that increases their home ranges relative to those of females (Perry & Garland, 2002). The extent to which males had larger home

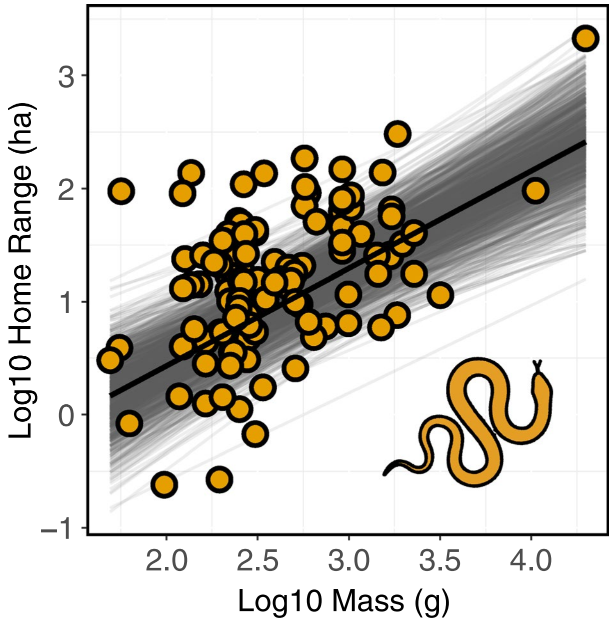

FIGURE 2 The relationship between snake home range size and body mass. The black line represents the predicted relationship based on mean estimates from a Bayesian implementation of a phylogenetic linear mixed model. The grey lines represent 1,000 samples of the posterior distribution [Colour figure can be viewed at wileyonlinelibrary.com]

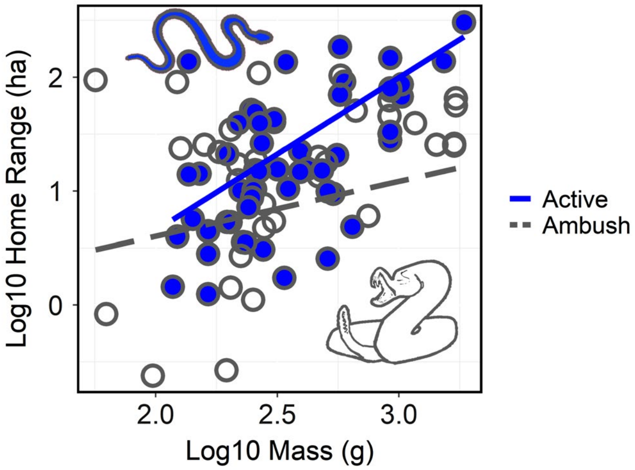

FIGURE 3 The relationship between snake home range size and body mass for active foraging Colubridae (23 species, 56 datapoints) and ambush foraging Viperidae (17 species, 35 datapoints). The lines represent the predicted relationships based on mean estimates from a Bayesian implementation of a phylogenetic linear mixed model [Colour figure can be viewed at wileyonlinelibrary.com]

ranges than females also increased with temperature, possibly a consequence of it being easier to reach optimal body temperatures in warm environments (e.g. Agha et al., 2018; Nowakowski et al., 2020). Quickly reaching optimal body temperatures would lower the opportunity cost of basking and allow males to spend more time seeking mates; few of the available studies, however, radio-tracked snakes in the tropics. Although temperate study sites ranged from cooler locales to hot deserts, additional studies from the tropics may shed light on the generality of this finding. It may be that seasonality of temperature regimes becomes an important factor associated with snake home ranges with more studies from the tropics, where seasonal temperature variation is low. Another reason females may generally have smaller home ranges than males is because being gravid reduces locomotor performance, which can lower survival (Miles et al., 2000). Consequently, females often curtail their movements when gravid and will bask more to support embryo development (Shine, 1980), actions that would shrink home ranges. Indeed, of the 18 studies where home ranges were estimated separately for gravid and non-gravid females, 15 reported gravid females having smaller home ranges than non-gravid ones, whereas just one study found the opposite.

Locomotion is another factor linked to home range size in tetrapods. Aquatic species often have larger home ranges than do terrestrial or semi-aquatic species because movement in aquatic habitats is less costly than on land (Slavenko et al., 2016; Tucker et al., 2014). We did not, however, find support for an effect of degree of aquatic habitat use on home range size in snakes. This likely stems from the fact that very few of the approximately 3,700 snake species are fully aquatic like sea snakes, limiting the opportunity to examine how home range size changes with substantial variation in locomotion. Even the highly aquatic species in our study make frequent use of terrestrial habitat with extensive upland movements away from aquatic areas (i.e. Glaudas et al., 2007; Roe et al., 2004). However, for species that use a broader range of habitats overall, they may be better able to readily obtain resources in heterogeneous landscapes by exploiting more habitat types within a smaller area in these landscapes, giving rise to the negative association between habitat breadth and home range size hinted at by our results.

Variation in diet is also frequently associated with home range size in tetrapods, with carnivores having larger home ranges than omnivores and herbivores (Tamburello et al., 2015; but see Slavenko et al., 2016). Snakes are uniformly carnivores, and species large enough to carry radio-transmitters all feed primarily on vertebrates, precluding such an evaluation for snakes. Nevertheless, foraging mode is an important diet-related aspect of snake ecology (Glaudas et al., 2019), and our results show how foraging mode may affect home range area requirements. Although more accurately viewed as a gradient rather than an explicit dichotomy, snake species generally fall into one of two local optima along a continuum from lie-in-wait, ambush foraging to active foraging (Beaupre & Montgomery, 2007). Active foraging snakes have been shown to have nearly twofold greater daily energy expenditures than ambush foraging species (Secor & Nagy, 1994). Ambush foraging snakes also have larger maximal prey sizes than active foraging species (Glaudas et al., 2019), which can curtail their movements as snakes take up to weeks to digest large meals. In both cases, greater daily energy expenditures and less sedentary time spent digesting meals would be expected to lead to larger home ranges for active foragers than for ambush foragers. Indeed, we found that home range sizes increased more steeply with body mass for the active foraging Colubridae than for the ambush foraging Viperidae, revealing an important consequence of this fundamental life history trait in snakes.

The main difference between our findings and those of previous studies lies in our estimate of the scaling of the home range–body mass relationship. Compared to slopes estimated similarly for other carnivorous taxa, our estimated slope of 0.72 [95% confidence interval (0.48–0.96)] is much lower than those reported for carnivorous mammals [1.36 (1.04–1.68) in Harestad & Bunnel, 1979; 1.23 (1.05–1.41) in Kelt & Van Vuren, 2001; 1.36 (1.18–1.54) in Tamburello et al., 2015] and carnivorous birds [1.39 (1.23–1.55) in Schoener, 1968; flightless: 1.14 (−0.45–2.73), flying: 1.50 (1.34–1.66) in Tamburello et al., 2015]. Instead, our results are in line with estimates from other groups of ectothermic tetrapods, the turtles [0.57 (0.22–0.85) in Slavenko et al., 2016, with no difference in slope among diets] and lizards [females: 0.79 (0.6–1.0), males: 1.05 (0.8–1.3) in Perry & Garland, 2002; diets not specified]. Altogether, these results suggest possible key differences among tetrapods in the scaling of the home range–body mass relationship between ectotherms and endotherms. Although this would seem to contradict a study that found no difference in scaling between ectotherms and endotherms (Tamburello et al., 2015), the inclusion of fish in that study muddied the waters due to the confounding factors that fish swim and often use three-dimensional space, which was found to greatly affect scaling. Among mammals and birds, slopes are ≥ 1 and significantly larger than the *c*. 0.67–0.75 at which their metabolic rates scale with body mass, whereas among reptiles, the slopes are more closely aligned with the *c*. 0.8 at which their metabolic rates scale with body mass (Glazier, 2005; McNab, 1963; Nagy, 2005). The discrepancy between the rates of home range and metabolic scaling with body mass in endotherms has been attributed to greater home range overlap with increasing animal size and resulting loss of food resources to neighbours, especially as animals surpass > 100 kg (Harestad & Bunnel, 1979; Jetz et al., 2004). However, there is reason to question whether ectotherms suffer similar losses, and if they do not, this may in part explain the closer estimates of the slopes of home range–body mass relationships with those of their metabolic rate–body mass relationships.

Ectotherms are ‘low energy organisms’ whose metabolic demands are affected by environmental temperatures (sensu Pough, 1980, 1983). They are consequently able to endure prolonged periods of resource scarcity by reducing activity or selecting lower temperatures that allow their metabolic rates and energy demands to fall (Lang, 1979; Lillywhite et al., 1973; Pough, 1980). Thus, for ectotherms in terrestrial habitats often characterized by thermally heterogeneous environments, loss of resources to neighbouring animals within an individual’s home range may be offset by reduced body temperatures or reduced activity. In contrast, the need of endotherms to maintain stable internal body temperatures fuelled largely by metabolic heat creates a constant demand for resources that must be met by increased foraging as resources become scarce (Pough, 1980). Also, most ectothermic tetrapods weigh < 1 kg, far below the size at which resource losses to neighbours have been shown to increase home range area requirements in mammals (Jetz et al., 2004). These differences may at least partly explain why home range sizes exceed those expected solely based on metabolic demands in endotherms, but seemingly do not in ectotherms. In support of this idea, neither the slopes reported here for snakes nor those reported recently for turtles differ significantly from those of basal or field metabolic rate–body mass relationships (Slavenko et al., 2016), which range from 0.67–0.89 (Glazier, 2005; McNab, 1963; Nagy, 2005). Consequently, we propose that the general notion that in tetrapods home range area scales more steeply with body mass than does metabolism is questionable. Instead, key differences in the ways that endotherms and ectotherms respond to energy needs likely give rise to differing home range area requirements.

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AUTHOR CONTRIBUTIONS

BDT conceived the idea and collated the data; BDT and AJN analysed the data and wrote the manuscript.

DATA AVAILABILITY STATEMENT

The annotated dataset and associated metadata can be accessed in the Dryad repository along with the R code and data subsets necessary to reproduce the analyses: https://doi.org/10.25338/B85G98.

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SUPPORTING INFORMATION

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

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APPENDIX

DATA SOURCES

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