



# Phylogenetic analysis of macroecological patterns of home range area in snakes

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Received: 7 June 2020 / Accepted: 10 December 2020 / Published online: 1 January 2021  
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## Abstract

A home range is the area animals use to carry out routine activities such as mating, foraging, and caring for young. Thus, the area of a home range is an important indicator of an animal's behavioural and energetic requirements. While several studies have identified the factors that influence home range area (HRA), none of them has investigated global patterns of HRA among and within snake species. Here, we used a phylogenetic mixed model to determine which factors influence HRA in 51 snake species. We analysed 200 HRA estimates to test the influence of body mass, sex, age, diet, precipitation, latitude, winter and summer temperature, while controlling for the duration of the study and sample size. We found that males had larger HRA than females, that adults had larger HRA than juveniles, and that snake species with fish-based diets had smaller HRA than snake species with terrestrial vertebrate-based and invertebrate-based diets. We also found that HRA tended to increase as mean winter temperature decreases and tended to decrease with precipitation. After accounting for these factors, the phylogenetic heritability of HRA in snakes was low ( $0.21 \pm 0.14$ ). Determining the factors that dictate macroecological patterns of space use has important management implications in an era of rapid climate change.

**Keywords** Activity · Energetic constraints · Phylogenetic mixed model · Squamates · Temperature

## Introduction

Movement is an essential part of the life cycle of the vast majority of animals as most animals move at least to find food and mates. These routine activities are performed within an area coined the home range by Burt (1943). Ecologists have devoted much effort to estimate home range area (HRA) in a wide range of animals because this relatively straightforward metric can shed light on critical aspects of a species' ecology such as foraging behaviour, population density, spacing patterns, resource distribution, and habitat

selection (Harris et al. 1990) as well as inform conservation actions (Fauvelle et al. 2017).

The growing availability of data has allowed ecologists to search for general predictors of HRA in animals. Starting with McNab's (1963) seminal analysis, most of this work has been done in mammals (Mace and Harvey 1983; Reiss 1988; Kelt and Van Vuren 1999; Myserud et al. 2001; Tucker et al. 2014; Albuquerque et al. 2015; Ofstad et al. 2016; Boratyński 2019). To date, only two studies have controlled for phylogeny to simultaneously test the effects of multiple factors on HRA in reptiles (Lizards: Perry and Garland, 2002; Turtles: Slavenko et al. 2016). Both studies found HRA to be influenced by habitat type and diet. Sex influenced HRA in lizards, but not in turtles. Tamburello et al. (2015) examined patterns in HRA in snakes as part of their exhaustive analysis of HRA in vertebrates, but did not attempt to explain variation in HRA within this group.

Snakes reside on all continents (with the exception of Antarctica and New Zealand) and in a wide range of habitats, including aquatic and terrestrial environments. Across species, body mass can vary from 0.6 g to 150 kg (Fredriksson 2005; Hedges 2008). Snakes are different in many respects from the taxa studied to date with respect to

Communicated by Jean-François Le Galliard.

**Supplementary Information** The online version contains supplementary material available at <https://doi.org/10.1007/s00442-020-04832-4>.

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HRA, including lizards (even though snakes are included in the lizard clade). Snakes are highly specialised lizards with enough marked differences from other lizard clades to prompt Perry and Garland (2002) to exclude snakes from their analysis of lizard HRA. Snakes are also secretive, making it nearly impossible to obtain estimates of HRA without the help of radio-telemetry. Fortunately, the exact location of individuals can usually be determined with radio-telemetry without resorting to triangulation (Blouin-Demers and Weatherhead 2001). Estimates of HRA in snakes are thus expected to be accurate and the variation between studies attributable to methodology to be minimal. We acknowledge that HRA estimated from short-term radio-telemetry studies, however, may underestimate the real home range area of long-lived species (Ballouard et al. 2020). Collectively, these biological and methodological attributes should help us identify the factors shaping HRA in snakes.

We compiled data from the literature to explain the inter- and intra-specific variation in HRA in snakes. Specifically, we tested for the effects of body size, sex, age, diet, and environmental factors (precipitation, temperature) on HRA while accounting for phylogeny. We can make alternative predictions regarding the effect of sex on HRA in snakes. The energetic cost of gamete production is generally higher in females than in males (Hayward and Gillooly 2011) so, all else being equal, females may have to travel further than males to obtain the resources necessary to gamete production, and may thus have larger HRA than males (Madsen et al. 1993; Glaudas et al. 2020). Males, on the other hand, are generally under stronger sexual selection than females for behaviours such as mate searching, territory defense, and combat that may translate into larger HRA. For instance, Perry and Garland (2002) found males of both territorial and non-territorial species of lizards to have larger HRA than females and suggested that the availability and distribution of females have a greater influence on males' HRA than the energetic cost of gamete production has on females' HRA. The same could be true in snakes.

Broad feeding guilds (e.g., herbivores, carnivores, omnivores) may also explain some of the variation in HRA as it does in mammals (Tucker et al. 2014), lizards (Perry and Garland 2002), and turtles (Slavenko et al. 2016). All snakes are exclusively predators, but prey type varies enough between species to make predictions on the effects of diet on HRA. Smaller animals tend to occur at greater densities (Damuth 1981) than larger ones and aquatic animals occur at higher densities than terrestrial ones (Cyr et al. 1997). Animals feeding on sparse prey should need to cover more ground to meet their energetic requirements. We thus predicted species feeding on invertebrates to have the smallest HRA for their size and the species feeding on terrestrial vertebrates to have the largest HRA for their body size.

Piscivorous species are predicted to have intermediate HRA for their body size.

Finally, we considered the productivity (i.e. the biomass produced by an ecosystem by unit of time) of the study area in our analysis. Productivity can also affect HRA because it dictates the minimum area required to sustain the energetic needs of animals (Harestad and Bunnell 1979). Regions with higher productivity should favour smaller HRA because more resources are available in a smaller area. Productivity can be approximated from measures of water and energy (Hawkins et al. 2003) such as average precipitation, average summer temperatures, and latitude. Areas with low precipitation, cooler active seasons, and higher latitudes generally have lower productivity, which, everything else being equal, should result in larger HRA.

## Materials and methods

### Data collection

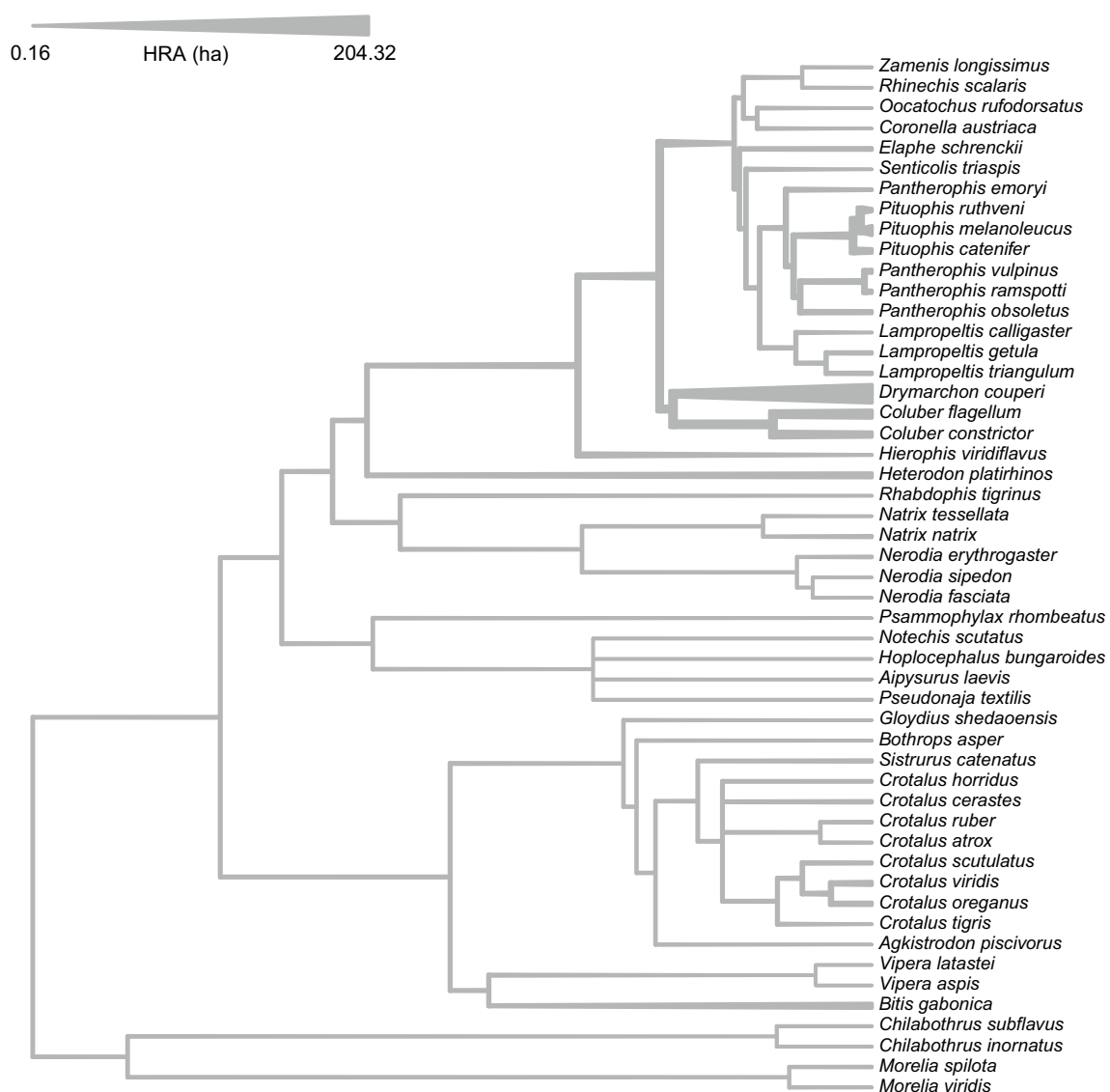
We found articles by combining various keywords in ISI Web of Science and Google Scholar and through cited reference searches. We compiled HRA data from 223 peer-reviewed articles on 51 species of snakes (Online Resource 2). HRA estimates were taken from articles that reported HRA averaged across the number of individuals of each sex studied via radio-telemetry. For each study, we recorded the study species, HRA, the geographical coordinates of the study area (latitude and longitude), as well as the sex, snout-vent length (SVL), total length (TL), body mass, and age (adult/juvenile). All HRA included in the analysis ( $n=200$ ) were estimated with 100% minimum convex polygons (MCP). MCPs are estimated using locations where the animal was present to form the smallest polygon where no internal angles exceed  $180^\circ$  (Burgman and Fox 2003) and are commonly used in studies of reptiles (Row and Blouin-Demers 2006). Our compilation of HRA estimates reflects the data currently available, but this data is likely biased towards species large enough to be implanted with radio-transmitters. The smallest snake species in our dataset has a SVL of 40.9 cm. According to a review of 25% of all snake species (Boback and Guyer 2003), about 13% of species are smaller than 40 cm.

We obtained dietary information for each species from a combination of scientific articles and field guides. The diet of each species was classified into three categories: invertebrates, terrestrial vertebrates, and fish. The dietary category 'fish' included species who rely solely on fish as well as species who rely on a combination of fish and terrestrial vertebrates. We also assigned each species a foraging mode (active, ambush, or mixed strategy). Foraging mode was determined and assigned to each species based on published

data and, on occasion, personal experience. Using the geographical coordinates recorded for each of the studies, we downloaded the monthly temperature and precipitation data averaged over 1970–2000 with a 10 min (340 km<sup>2</sup>) spatial resolution from WorldClim2 (Fick and Hijmans 2017). With the mean monthly precipitation data, we calculated mean annual precipitation. We included two sets of mean temperatures in the analysis: June, July, and August, and December, January and February. Mean winter temperature (December, January and February—in the Northern Hemisphere and June, July, and August in the southern hemisphere) is a proxy for the length of the activity season; regions with colder winters should have a shorter active season.

## Snake phylogeny

To account for the relatedness among species, we used a recent, fully sampled phylogeny of squamates (Tonini et al. 2016; see Online Resource 3) that we pruned to the species included in this study (Fig. 1). We used the all-compatible consensus of the 10,000 trees produced by Tonini et al. (2016), which integrates over phylogenetic uncertainty by collapsing poorly known clades into polytomies (e.g., *Crotalus*; Fig. 1). We used the package MCMCglmm (Hadfield 2010; Hadfield and Nakagawa 2010) to create a phylogenetic covariance matrix (relatedness matrix) from the phylogeny (Hadfield and Nakagawa 2010).



**Fig. 1** Phylogeny used in this study, based on Tonini et al. (2016) and pruned to represent the 51 snake species for which home range area was available. Using R package phytools (Revell 2012), branch thick-

ness was made proportional to the mean home range area (HRA in ha) in each tip species (the mean HRA values of parent–daughter species were used to reconstruct HRA values in ancestor species)

## Analyses

We analysed inter- and intra-specific variation in HRA using a weighted phylogenetic mixed model in ASReml-R version 4 (Butler et al. 2018). All code are available as supplementary materials (Online Resource 4). Observations were weighted by the number of individuals sampled in the original HRA study. The model included sex, age, body mass, foraging mode, diet, mean annual precipitation, latitude, an interaction between mean annual precipitation and latitude, mean winter temperature, mean summer temperature, and duration of study as fixed effects. The interaction between precipitation and latitude was included to account for precipitation falling as snow, which occurs at higher latitudes, and would not necessarily have the same effect on productivity as rain occurring at lower latitudes. The length of a study typically corresponds with larger HRA because individuals usually travel more over a longer span of time. Adults could travel more than juveniles because they engage in reproductive behaviour and because they are larger. In general, larger snakes travel further than smaller snakes (Tamburello et al. 2015). Finally, sit-and-wait species should travel less than active foragers (Beaupre and Montgomery 2007; Reilly et al. 2014).

All continuous variables were standardised to a mean of 0 and a variance of 1. Continuous and categorical variables were moderately correlated (Online Resource 1). The distribution of HRA and body mass were strongly skewed to the left (Fig. 2), so they were  $\log_{10}$  transformed. Most studies did not report all three measurements of body size (body mass, SVL, and TL). Thus, we used clade specific equations from Feldman and Meiri (2013) to estimate snake mass from SVL and TL in 43 cases from 19 species. There were some studies for which there were no measurements of body mass, SVL, or TL provided. To include these HRA data into the model, we first centred the  $\log_{10}$  transformed body mass variable, and then assigned a value of zero to the missing body mass data (Butler et al. 2018). Similarly, sex

and age were not reported in 33 and 51 cases, respectively. To include these observations in the analyses, we created an additional level ('missing') for these two variables.

The phylogenetic covariance matrix and species identity were included as random effects to partition the phenotypic variance into the phylogenetic variance ( $V_{\text{phylo}}$ ), among-species variance ( $V_{\text{sp}}$ ), and residual variance ( $V_e$ ). The significance of  $V_{\text{phylo}}$  and  $V_{\text{sp}}$  was estimated using a likelihood ratio test (LRT) by comparing the log-likelihoods of the full model to a model that excluded the component of interest. The LRT statistic was assumed to follow a  $\chi^2$  distribution with an equally weighted mixture of 0 and 1 degree of freedom (Snijder and Bokser 2012, p. 98). Phylogenetic heritability ( $h^2_{\text{phylo}}$ ) in HRA was calculated as the proportion of variance attributed to the relatedness among the taxa:  $h^2_{\text{phylo}} = V_{\text{phylo}} / (V_{\text{sp}} + V_{\text{phylo}} + V_e)$  (Housworth et al. 2004). Approximate standard error for  $h^2_{\text{phylo}}$  was calculated using the delta method. The conditional  $R^2$  (variance explained by the entire model) and marginal  $R^2$  (variance explained by fixed effects) for linear mixed models were calculated following Nakagawa and Schielzeth (2013).

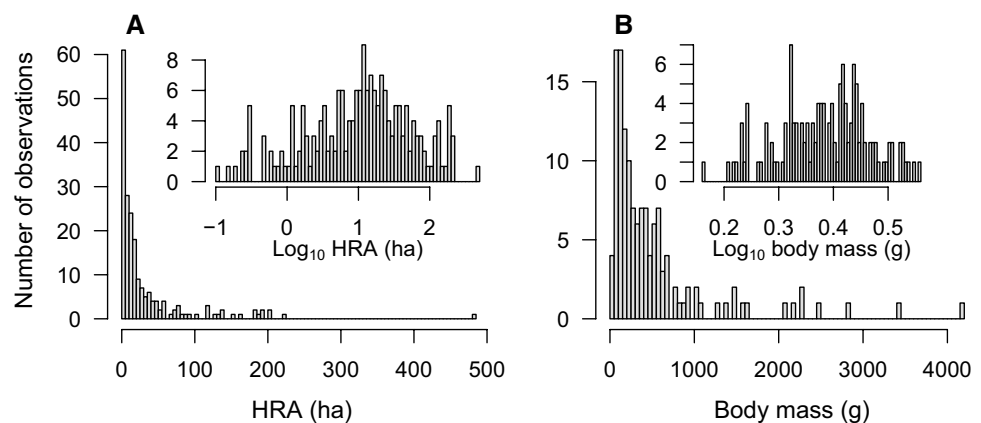
## Results

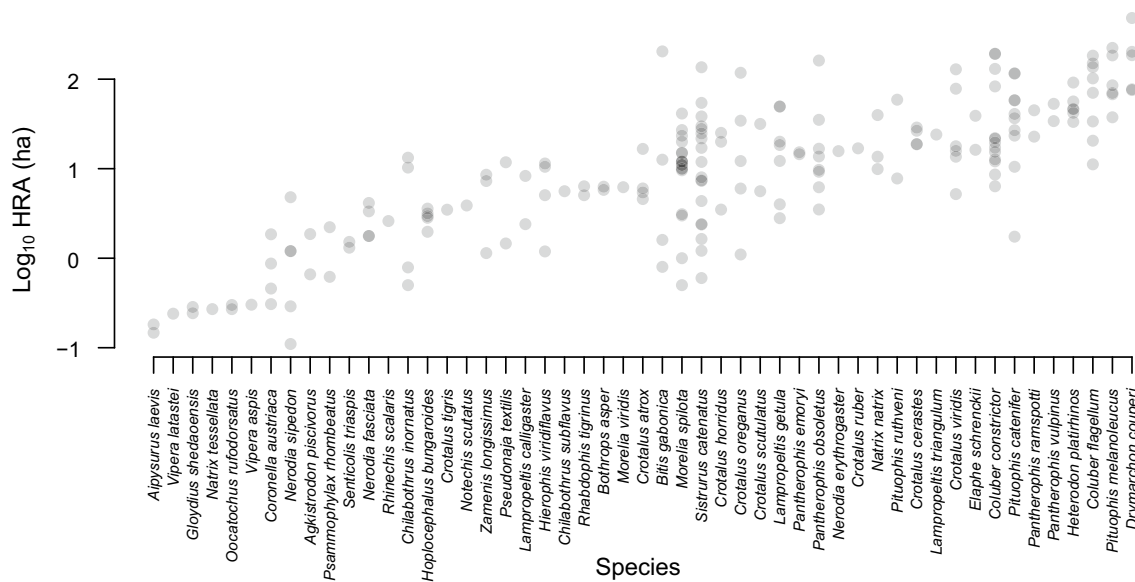
### Database

For each of the 51 species included in the analysis, there were 1–18 estimates of HRA with a mean ( $\pm$  sd) number of HRA estimates per species of  $3.9 \pm 3.8$ . The number of individuals sampled varied greatly between species, from 2 to 273 individuals, with a mean of  $41 \pm 52$  individuals. HRA also varied greatly between and within species (Fig. 3), ranging from 0.2 to 1021.6 ha with a mean of  $126.5 \pm 225.3$  ha.

The available data on HRA include snakes living over a wide geographic area under various climatic conditions (Fig. 4). Nevertheless, 90% of the home range studies were conducted in temperate regions between  $25^\circ$  and  $50^\circ$

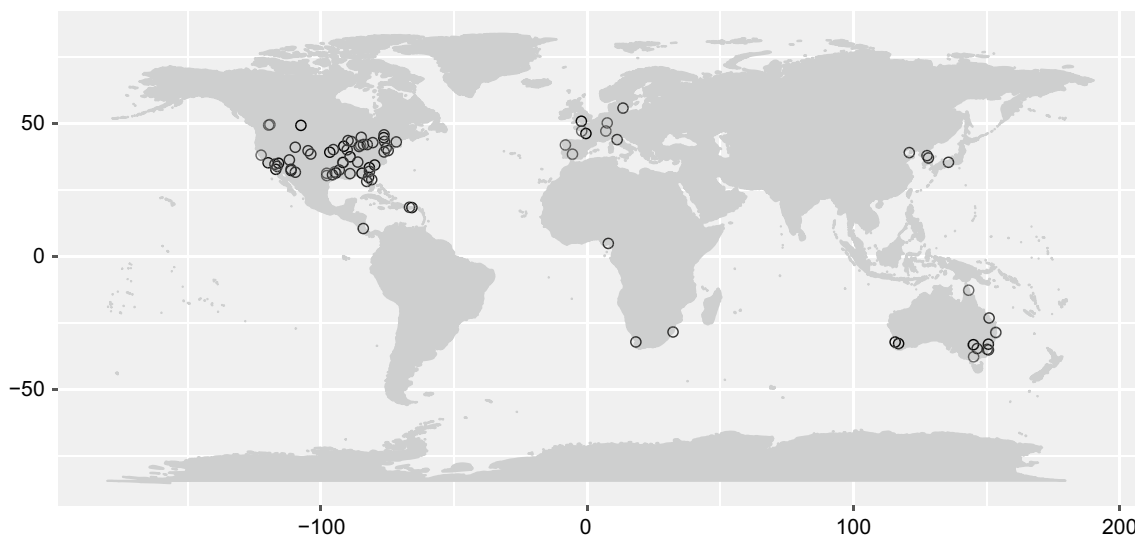
**Fig. 2** Frequency distribution of **a** body mass (g) and **b** mean home range area (HRA; calculated as minimum convex polygon) in 51 snake species





**Fig. 3** Among- and within-species variance in home range area (HRA, calculated as minimum convex polygon;  $\log_{10}$  transformed) in 51 snake species. To show sampling distribution and raw variation in

HRA among and within species, the data points were not phylogenetically corrected. Species are ordered along the x-axis according to their mean HRA values



**Fig. 4** Geographic distribution of home range data in the 51 snake species included in this study

latitude, and the majority of these took place in the United States of America. HRA data are sorely lacking for snakes living in regions such as South America and Asia (Fig. 4). Moreover, HRA data are also lacking for very small and very large snake species (Fig. 2a), arboreal species, and most sea snakes (only one species included in the dataset). Given the fragmented nature of the available data (i.e. many lineages and life styles are not well represented), we consider the results below as preliminary yet as the first important step in understanding the factors influencing HRA in snakes.

### Factors influencing HRA

The phylogenetic mixed model explained 32% of the variance (conditional  $R^2$ ) in HRA. Fixed effects accounted for 11% (marginal  $R^2$ ) with significant effects of sex, age, diet, and study duration (Table 1). HRA was larger for males than for females (Table 1; Fig. 5a) and for adults than for juveniles (Table 1; Fig. 5b). Fish consumers had significantly smaller home ranges than both invertebrate consumers (Table 1; Fig. 5c) and terrestrial vertebrate consumers

**Table 1** Estimates, standard errors (se),  $z$  ratios, and  $P$  values extracted from a phylogenetic mixed model of 200 estimates of home range area calculated as minimum convex polygons in 51 snake species

| Fixed effects                                | Estimate $\pm$ se                      | $z$ ratio                   | $P$                |
|--|--|-----------------------------|--------------------|
| Intercept                                    | $-1.9138 \pm 0.5539$                   | $-3.4550$                   | 0.0006             |
| Sex <sub>[male vs female]</sub>              | <b><math>0.2671 \pm 0.0894</math></b>  | <b>2.9877</b>               | <b>0.0028</b>      |
| Age <sub>[juvenile vs adult]</sub>           | <b><math>-0.9141 \pm 0.2364</math></b> | <b><math>-3.8668</math></b> | <b>0.0001</b>      |
| Body mass                                    | $0.0681 \pm 0.0841$                    | 0.8097                      | 0.4181             |
| Diet <sub>[vertebrate vs fish]</sub>         | <b><math>1.7704 \pm 0.3561</math></b>  | <b>4.9724</b>               | <b>&lt; 0.0001</b> |
| Diet <sub>[invertebrate vs fish]</sub>       | <b><math>2.1026 \pm 0.4529</math></b>  | <b>4.6428</b>               | <b>&lt; 0.0001</b> |
| Diet <sub>[vertebrate vs invertebrate]</sub> | $-0.3322 \pm 0.3562$                   | $-0.9327$                   | 0.3510             |
| Winter temperature                           | $-0.3249 \pm 0.1811$                   | $-1.7939$                   | 0.0728             |
| Summer temperature                           | $0.1759 \pm 0.1451$                    | 1.2121                      | 0.2255             |
| Precipitation                                | $-0.2124 \pm 0.1141$                   | $-1.8622$                   | 0.0626             |
| Latitude                                     | $-0.1747 \pm 0.2171$                   | $-0.8049$                   | 0.4209             |
| Precipitation $\times$ latitude              | $-0.0593 \pm 0.0518$                   | $-1.1430$                   | 0.2530             |
| Study duration                               | <b><math>0.1982 \pm 0.0809</math></b>  | <b>2.4491</b>               | <b>0.0143</b>      |
| Foraging mode <sub>[mixed vs active]</sub>   | $0.1712 \pm 0.4381$                    | 0.3908                      | 0.6959             |
| Foraging mode <sub>[ambush vs active]</sub>  | $-0.4516 \pm 0.3427$                   | $-1.3178$                   | 0.1876             |
| Foraging mode <sub>[mixed vs ambush]</sub>   | $0.6236 \pm 0.5033$                    | 1.2390                      | 0.2153             |
| Random effects                               | Variance $\pm$ se                      | $\chi^2_{1:0}$              | $P$                |
| $V_{\text{phylo}}$                           | $0.8201 \pm 0.5346$                    | 2.51                        | 0.0731             |
| $V_{\text{sp}}$                              | $0.0949 \pm 0.1214$                    | 0.59                        | 0.1858             |
| $V_e$  | $3.0854 \pm 0.3627$                    |                             |                    |

Sources of variation (fixed effects) include sex (male vs female), age (juvenile vs adult), body mass, diet (vertebrate vs fish vs invertebrate), mean winter temperature (December, January, and February), mean summer temperature (June, July, and August), mean annual precipitation, latitude, a precipitation  $\times$  latitude interaction, study duration, and foraging mode (active vs ambush vs mixed). Also shown are the variance estimates associated with the random effects of phylogenetic relatedness ( $V_{\text{phylo}}$ ), species ( $V_{\text{sp}}$ ), and the residual variance ( $V_e$ ). Significance of  $V_{\text{phylo}}$  and  $V_{\text{sp}}$  was tested using a log-likelihood ratio test following a Chi-square distribution with an equal mixture of 0 and 1 degree of freedom ( $\chi^2_{1:0}$ ). All significant sources of variance are bolded ( $P < 0.05$ ).

(Table 1; Fig. 5c). The HRA of invertebrate consumers and of terrestrial vertebrate consumers was not significantly different. Foraging mode did not influence HRA (Table 1; Fig. 5d). Larger species of snakes had larger home ranges (Table 1; Fig. 5c). Home ranges tended to be larger where winters were cold (Table 1; Fig. 5e). The effect of winter temperature remains marginally non-significant ( $P = 0.08$ ) when restricting the analyses to North American snakes. Mean summer temperature, precipitation, latitude, and the interaction between latitude and precipitation did not have significant effects on HRA (Table 1). Note that the non-significant effect of latitude is not due to collinearity with temperature because latitude remained non-significant even after we removed winter and summer temperatures from the model (Table 1;  $P = 0.45$ ).

### Phylogenetic heritability

Accounting for the fixed effects above, the  $V_{\text{phylo}}$  component was low and not significant (Table 1). Accordingly, phylogenetic heritability in HRA was low ( $h^2_{\text{phylo}} = 0.205 \pm 0.136$ ),

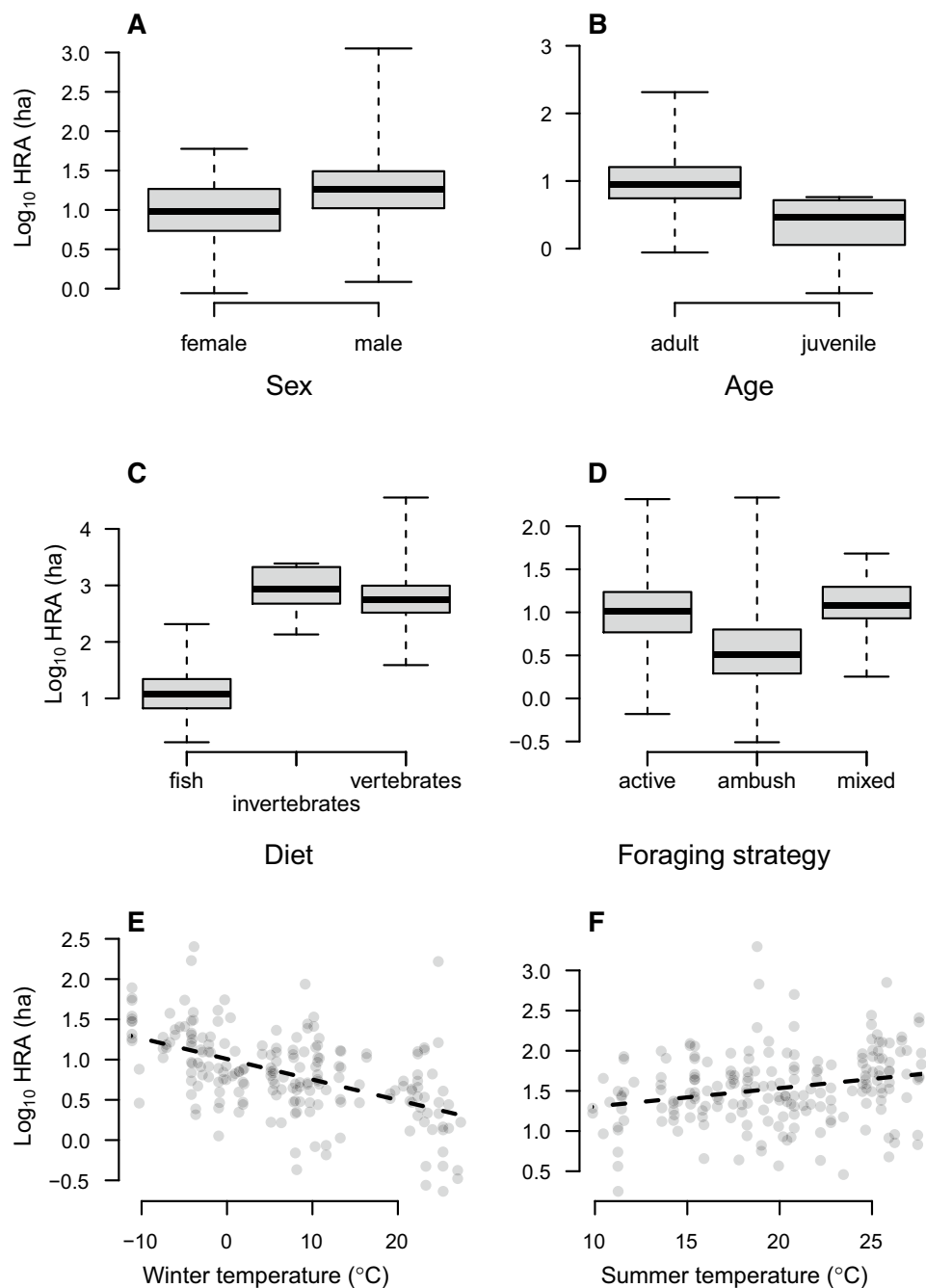
suggesting that closely related species do not necessarily have similar sized home ranges.

### Discussion

After accounting for sex, diet, body mass, age, foraging mode, precipitation, latitude, temperature, sampling effort, and phylogeny, there was little variance left in HRA at the among-species level, as indicated by a low and nonsignificant  $V_{\text{sp}}$  component ( $V_{\text{sp}} = 0.09 \pm 0.12$ ; Table 1). Most of the variance occurred at the residual level ( $V_e = 3.09 \pm 0.36$ ; Table 1), indicating that there was substantial variability in HRA for the same species of snakes compared to the variability of HRA between species (Fig. 3). Moreover, phylogenetic heritability was low ( $h^2_{\text{phylo}} = 0.205$ ) and the phylogenetic variance was not significant ( $V_{\text{sp}} = 0.82 \pm 0.53$ ; Table 1), indicating that HRA has not been phylogenetically conserved with speciation events. This result is consistent with other studies showing that closely related species do not occupy home ranges of similar size (Perry and Garland Jr 2002; Stelatelli et al. 2016), and that behavioural traits are



**Fig. 5** Home range area (HRA, calculated as minimum convex polygon;  $\log_{10}$  transformed) as a function of **a** sex, **b** age, **c** diet, **d** foraging strategy, **e** mean winter temperature, and **f** mean summer temperature in 51 snake species. Shown are partial residuals calculated from the phylogenetic mixed model in Table 1 run on unstandardized variables. The median, 25–75th percentiles, and range are indicated by the black line, box, and the whiskers, respectively



generally more labile than other types of traits (Blomberg et al. 2003).

Like in lizards (Perry and Garland 2002), male snakes had significantly larger home ranges than females. This finding is consistent with previous studies that have documented larger home ranges in male snakes than in female snakes (Webb and Shine 1997; Blouin-Demers and Weatherhead 2002) and suggests that males may need to travel more than females to reproduce successfully. Contrary to the general pattern we found here, larger home ranges in females than in males have been reported in some snakes and attributed to

the movement of females to suitable egg-laying sites (Bull et al. 1991; Bertram 2004; Ovaska and Sopuck 2004). While such egg-laying movements may contribute to the larger HRA in females of some species, it clearly does not account for the general pattern observed in our dataset, potentially because nearly 30% of all species of snakes are viviparous and nearly 51% of species from North America, where most of our samples came from, are viviparous (Feldman et al. 2015). Sexual selection operating on male snakes is possibly a stronger driver of mobility (i.e., HRA) than natural selection on female snakes.

We predicted that snakes feeding on invertebrates would have smaller HRA than snakes feeding on terrestrial vertebrates based on the relationship between animal size and density (Damuth 1981). HRA did not differ between snakes that consumed predominantly invertebrates and terrestrial vertebrates, but piscivorous species had smaller home ranges than both invertebrate and terrestrial vertebrate consumers. Perhaps differences in energy content between vertebrate and invertebrate prey offset the effect of prey abundance, but there is no evidence that invertebrate prey systematically yield lower assimilable energy per unit of mass than vertebrate prey (Bessler et al. 2010). Our sample is limited to HRA estimated with radio-telemetry and is thus biased towards larger species. Small snake species are more likely to feed on invertebrates so the absence of difference between terrestrial vertebrate and invertebrate consumers may be an artefact of the size bias in the available data. Within some snake species, prey abundance can influence movement and space use (Taylor et al. 2005), but not in others (Glaudas and Alexander 2017).

Snakes feeding on fish had the smallest HRA, a result that is in striking contrast with those obtained in turtles (Slavenko et al. 2016) and mammals (Tucker et al. 2014). The smaller HRA in snakes feeding on fish may reflect the generally higher abundance of prey in aquatic ecosystems compared to terrestrial ecosystems (Cyr et al. 1997). It should be noted, however, that most piscivorous species in our dataset are semi-aquatic colubrids that tend to be associated with wetlands. Thus, our results may not be generalizable to all aquatic snakes. In particular, our dataset includes a single species of sea snake. Space use in the marine environment may differ from that in freshwater wetlands for a variety of reasons including the physical environment itself, prey density, and the cost of locomotion. We note, however, that while food manipulation studies in snakes showed that food supplementation can affect movement, it has no effect on snake HRA. Glaudas and Alexander (2017) studied free-ranging male puff adders (*Bitis arietans*), a “sit-and-wait” ambush-foraging snake species, and found that supplementally fed individuals spent less time foraging and travelled shorter distances compared to control snakes, but did not differ in movement frequency and home range area. (Taylor et al. 2005) also found that supplementally fed female Western diamond-backed rattlesnakes (*Crotalus atrox*) did not differ in surface activity and HRA compared to control females.

Of the variables related to productivity we tested, none were significant predictors of HRA. Our sample included snake species occupying a wide range of productivity, from deserts to temperate forests with a few species sampled in tropical forests. We thus expected to find an effect of productivity on HRA. It is possible that our indirect metrics of productivity did not capture enough of the

variation in productivity for us to detect an effect. Alternatively, productivity may not have a strong impact on HRA in snakes. Snakes have relatively low metabolic requirements compared to most vertebrates and feed infrequently (Secor and Diamond 2000). Certain species will go for months without eating (Secor and Diamond 2000). In snakes, low productivity may thus not translate in longer distances travelled in search of food, and thus in larger HRA. A non-mutually exclusive possibility is that highly productive regions also support higher snake densities, which would increase competition for resources and hence, counteract the negative effect of productivity on HRA.

Mean winter temperature had a notable but non-significant effect on HRA; cooler temperatures tended to be associated with a larger HRA. At least in the northern hemisphere, snakes may spend several months of the year brumating underground (Sperry et al. 2010). Suitable brumation sites may be limited at northern latitudes as suggested by the tendency of snakes to brumate communally (Blouin-Demers et al. 2000). Limited brumation sites may translate in longer movements and thus could lead to larger HRA. Given the trend detected, more studies are needed to test the possibility that the length of the active season influences HRA.

We showed that HRA in snakes is not strongly phylogenetically conserved. In addition to age, HRA is affected by sex, diet, and mean winter temperature. Collectively these results add to our understanding of the macroecological determinants of space use in animals and explain some of the variation in home range area not previously examined. Determining what dictates macroecological patterns of space use has important management implications in an era of rapid climate change.

**Acknowledgements** We are grateful to Chris Love and to Vanessa Gagnon-Chantreau for help building the database of snake home ranges. AF, GBD, and VC were supported by the University of Ottawa; GB was supported by Carleton University.

**Author contribution statement** GB conceived the project. GBD, GB, and AF designed the project. AF completed the home range data base. AF and VC analyzed the data. AF wrote the first draft of the manuscript, and VC, GB and GBD edited it. All authors edited the final version of the manuscript and approved its submission.

**Data accessibility** When the manuscript is accepted for publication, we will make the data (Online Resource 2) available in Dyad.

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