Habits and characteristics of arboreal snakes worldwide: arboreality constrains body size but does not affect lineage diversification

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Received 14 March 2018; revised 19 June 2018; accepted for publication 20 June 2018

Arboreal lifestyles represent common and major habitat shifts among snakes. Major habitat shifts are often facilitated by particular traits that confer advantages in the new environment. Although studies have examined the habits and characteristics of arboreal snakes at the level of individual species or small clades, a broad survey has never been performed across all snakes. We surveyed the literature to identify all known arboreal snakes and summarize their general characteristics. We then tested for associations between diversification rates and arboreal habits and reconstructed ancestral states using the hidden state speciation and extinction (HiSSE) approach. Finally, we tested for an association between body size and arboreality by fitting multi-peak Ornstein–Uhlenbeck models. We expected that transitions to an arboreal lifestyle might open new ecological opportunities, leading to increased diversification rates, and that different selective pressures for arboreal snakes might lead to changes in body size evolution. We found that generally, arboreal snakes are most frequently nocturnal, oviparous, reptile-eating, brown/banded/patterned snakes inhabiting the Neotropics (assessing each trait individually, not jointly) and that arboreality has no effect on rates of diversification. Ornstein–Uhlenbeck models showed that arboreal snakes tend to be longer than non-arboreal snakes, that rates of body size evolution are generally lower in arboreal snakes, and that arboreal body sizes are pulled more strongly towards their optimum than in non-arboreal snakes. These results suggest that morphological evolution is more constrained in arboreal snakes than in non-arboreal snakes.


INTRODUCTION

Major shifts in habitat usage have occurred in many tetrapod clades. These shifts include the invasion of the land by early tetrapod ancestors, re-invasion of aquatic niches by several subsequent lineages (e.g. turtles, whales, sea snakes) and adaptation to arboreal lifestyles across lineages (e.g. frogs, snakes, primates). Habitat shifts are often accompanied by morphological adaptations that facilitate survival and locomotion in the new environment (Moermond, 1979; Wikramanayake, 1990; Uhen, 2007). However, the limbless nature of snakes means that they handle adaptation to new environments in a different manner compared with limbed vertebrates. Rather than modifying limbs into flippers for swimming or elongating digits to facilitate climbing, morphological evolution in the body form of snakes is generally restricted to changes in proportional length, height and width of the body and tail (Guyer & Donnelly, 1990; Lillywhite & Henderson, 1993; Brischoux & Shine, 2011, Alencar et al., 2017). One of the most common habitat shifts in snakes is the transition to an arboreal lifestyle.

Arboreal snakes, including those that are semi-arboreal, comprise > 600 species, totalling ~17% of extant snake diversity (Uetz & Hošek, 2017; Supporting
Characteristics of select species and clades of arboreal snakes are known from detailed studies on small numbers of species. These studies have found that many arboreal snakes have an overall more laterally compressed and more slender body compared with terrestrial taxa (Guyer & Donnelly, 1990; Martins et al., 2001; Pizzatto et al., 2007; Alencar et al., 2017). This suggests that arboreal and non-arboreal snakes evolve under different selective pressures, potentially leading to different optimal body sizes or body proportions and different rates of trait evolution. These differences in evolutionary modes, rates and optima can be captured by the fitting of morphological models (e.g. using the R package OUwie; Beaulieu et al., 2012), and a recent study using such an approach to examine vipers found that rates of body size evolution are constrained in arboreal taxa such that snout–vent lengths evolve more slowly and are pulled more strongly towards the optimal trait value in arboreal vipers compared with terrestrial vipers, and also that arboreal species have longer optimal tails, although with similar rates of evolution to terrestrial taxa (Alencar et al., 2017).

However, there have been no large-scale comparisons of general habitats and traits across all arboreal snakes, including how body size varies with arboreal habits across snakes or how arboreal snakes are distributed globally. Shifts to arboreality may open up ecological opportunities for newly arboreal lineages as these lineages move into environments that may be less occupied by related competitors and contain prey bases not available to terrestrial species. Ecological opportunity has long been hypothesized to lead to increased rates of diversification (Simpson, 1953; Schluter, 2000; Yoder et al., 2010), and if arboreal habitats do represent increased ecological opportunity, they may also be correlated with increased rates of diversification. Increased rates of diversification in association with arboreality have been shown across squamate reptiles generally, and specifically within snakes (Bars-Closel et al., 2017). However, at a smaller phylogenetic scale (within vipers), no link between arboreality and diversification was found (Alencar et al., 2017).

To gain a better understanding of the distribution of arboreality among and within snake lineages and determine what traits are shared and disparate among them, we performed a literature survey to provide a characterization and summary of the general habits and characteristics of arboreal snakes worldwide. We then used geographic hidden state speciation and extinction (GeoHiSSE) models (Beaulieu & O’Meara, 2016; Caetano et al., 2018) to test whether arboreality influences rates of diversification and to reconstruct ancestral states while accounting for diversification rate heterogeneity. This relationship has been demonstrated before using different methods (Bars-Closel et al., 2017), and we sought to determine whether these findings could be corroborated using GeoHiSSE, which directly estimates transformations of speciation and extinction rates for lineages in different character states. Finally, we combined our data on arboreal habits with published data on snake body sizes (Feldman et al., 2016) to determine whether arboreality is associated with different modes of body size evolution in snakes.

**MATERIAL AND METHODS**

We initially performed a literature survey to identify all known arboreal or semi-arboreal snake species, and we classify these snakes here as either primarily arboreal or semi-arboreal. During this literature survey, we also gathered information on the general distributions and characteristics of each species classified as primarily arboreal or semi-arboreal. Owing to the high diversity across snakes (> 3500 species in total), we gathered these data for arboreal/semi-arboreal snakes only, with the goal of characterizing the habits of arboreal snakes specifically rather than comparing these characters between arboreal and non-arboreal snakes. We classified snakes as arboreal and semi-arboreal if multiple sources indicated that these snakes were likely to be found off the ground in trees, bushes or shrubs when encountered. Single occurrences of a snake found in a shrub or bush, when other sources did not indicate arboreality, were ignored. Once arboreal taxa were identified, we determined from additional literature searches the following characteristics for each species: zoogeographical region (based on Proch & Ramdhani, 2012), diel activity (nocturnal, diurnal or polyphasic), diet (characterized as mammals, birds, bird eggs, amphibians, frog eggs, reptiles, reptile eggs, non-molluscan invertebrates, molluscs or fish), parity mode (oviparous or viviparous), predominant dorsal colour (brown, black, green or other) and predominant dorsal pattern (uniform, banded/blotched/patterned or striped). See the Supporting Information (Appendix S1) for all details and citations for these data.
To determine whether there is a relationship between rates of diversification and arboreality, we fitted several models using the HiSSE package (v. 1.8.7; Beaulieu & O’Meara, 2016) in R v. 3.5.0 (R Core Team, 2018). The HiSSE package implements hidden state speciation and extinction (HiSSE) models that are extensions of the binary state speciation and extinction (BiSSE) model (Maddison et al., 2007) in addition to GeoHiSSE models (Caetano et al., 2018) that implement hidden state extensions of geographic state speciation and extinction (GeoSSE) and multistate speciation and extinction (MuSSE) models (Goldberg et al., 2011; FitzJohn, 2012). The state-dependent speciation and extinction (SSE) models allow speciation and extinction rates to vary along a phylogenetic tree dependent on a given character that is hypothesized to influence diversification rates. The HiSSE and GeoHiSSE models extend SSE models by allowing diversification rates to vary with the character state and according to the state of an unobserved, hidden character. This accommodates additional diversification rate heterogeneity that is independent of the character of interest, therefore relaxing the assumption of the standard SSE models that all diversification rate heterogeneity is exclusively influenced by the character of interest.

We fitted six different GeoHiSSE models, including some that did not include hidden states and models with varying numbers of character transition rates permitted among states (including hidden states). We constrained all models to reflect an ordered MuSSE-type model that included three ordered states: non-arboreal, semi-arboreal and primarily arboreal. Although we constrained models without and with hidden states to reflect MuSSE-like models, we refer to these throughout as GeoSSE and GeoHiSSE models for better consistency with Caetano et al. (2018) and to avoid introducing further jargon for these models. Simply note that these models have been constrained so that they permit state changes only along branches, and transitions among the three states are decoupled from extinction in areas; these models are summarized in Table 1. We compared the fit of character-dependent models with models in which rates of diversification do not vary at all (a simple birth–death model) and with models in which diversification rates vary according to the hidden character states only and are thus independent of the observed character [character-independent (CID) models]. The CID models consisted of models with three hidden states possessing distinct diversification rates (thus serving as CID alternative models for GeoSSE-like models; CID GeoSSE in Table 1) or five (thus serving as CID alternative models for GeoHiSSE models with hidden states; CID GeoHiSSE in Table 1). No model permitted simultaneous transitions in observed and hidden states.

In addition to the standard CID GeoHiSSE model with five transition rates (CID GeoHiSSE 1), we included a similar model with nine transition rates to alleviate concerns raised by Harrington & Reeder (2017) that a character-dependent HiSSE (or GeoHiSSE) model might outperform a CID model simply as a result of an increased number of character transition rate parameters. The transition rate matrix for this model was designed in a similar manner to the nine-rate null-four model of Harrington & Reeder (2017), such that we assume that two hidden states are further subdivided into lower-level hidden states (two for one higher-level hidden state and three for the other), such that state 0A is split into state 0a, 0b and 0c, and state 0B is split into states 0d and 0e. We then specified a single transition rate for transitions among lower-level states within the same higher-level hidden states, and independent rates for all transitions among higher-level hidden states, to result in a model that has the same number of parameters as the character-dependent GeoHiSSE model. Code used to specify all models and run all analyses in R is included as Supporting Information (File S1).

We fitted these models using the phylogeny of Zheng & Wiens (2016), which is a supermatrix tree generated from

<table>
<thead>
<tr>
<th>Model</th>
<th>Hidden states</th>
<th>CD</th>
<th>Number of diversification rates</th>
<th>Number of transition rates</th>
<th>AIC</th>
<th>AIC weight</th>
</tr>
</thead>
<tbody>
<tr>
<td>CID GeoHiSSE 2</td>
<td>Y</td>
<td>N</td>
<td>5</td>
<td>9</td>
<td>10203</td>
<td>1</td>
</tr>
<tr>
<td>CID GeoSSE</td>
<td>Y</td>
<td>N</td>
<td>3</td>
<td>5</td>
<td>10271</td>
<td>0</td>
</tr>
<tr>
<td>CID GeoHiSSE 1</td>
<td>Y</td>
<td>N</td>
<td>5</td>
<td>5</td>
<td>10330</td>
<td>0</td>
</tr>
<tr>
<td>GeoHiSSE</td>
<td>Y</td>
<td>Y</td>
<td>6</td>
<td>9</td>
<td>10501</td>
<td>0</td>
</tr>
<tr>
<td>GeoSSE</td>
<td>N</td>
<td>Y</td>
<td>3</td>
<td>4</td>
<td>10510</td>
<td>0</td>
</tr>
<tr>
<td>Birth–death</td>
<td>N</td>
<td>N</td>
<td>1</td>
<td>4</td>
<td>10544</td>
<td>0</td>
</tr>
</tbody>
</table>

The description includes whether models include hidden states, are character dependent (CD), the number of distinct diversification rates, and the number of transition rates among hidden and observed states. AIC, Akaike information criterion; N, no; Y, yes; CID, character independent; GeoSSE, geographic state speciation and extinction; GeoHiSSE, geographic hidden state speciation and extinction.

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DNA sequence data that includes 1262 snakes, roughly one-third of extant snake diversity. We pruned the tree to exclude duplicate taxa, an unnamed species in the family Typhlopidae, and several species that we suspect may be arboreal but which lack data in the literature (i.e. duplicates specified by a “2” in the original tree, including ‘Pareas margaritophorous2’, ‘Apostolepis cearensis2’, ‘Crotalus atrox2’, ‘Platyceps karelini2’ and ‘Vipera berus2’, Typhlopidae sp. Sri Lanka’, Zamenis pulchra, Lycodon rufozonatus, Lycodon semicarinatus and Trimeresurus tibetanus). We accounted for incomplete sampling in HiSSE analyses by dividing the number of species in each state in the tree by the total number of snakes exhibiting that state. Numbers of semi-arboreal and primarily arboreal species were calculated directly from our data, whereas the number of non-arboreal snakes was calculated as the total number of snakes on the Reptile Database as of 7 December 2017 (Uetz & Hošek, 2017) minus the number of primarily and semi-arboreal snakes.

After fitting HiSSE models to the data, we inferred the ancestral states under each model. HiSSE allows ancestral state reconstructions and inferred diversification rates to be model-averaged and plotted such that displayed ancestral states and inferred diversification rates to each state in the tree by the total number of snakes exhibiting that state. Numbers of semi-arboreal and primarily arboreal species were calculated directly from our data, whereas the number of non-arboreal snakes was calculated as the total number of snakes on the Reptile Database as of 7 December 2017 (Uetz & Hošek, 2017) minus the number of primarily and semi-arboreal snakes.

For all OUwie analyses, we set the scaleheight option to false so that branch lengths remain in units of millions of years. We examined the eigenvalues from the Hessian matrix of all OUwie analyses to ensure that all parameters were optimized and discarded any models that contained any negative eigenvalues.

RESULTS

GENERAL CHARACTERISTICS OF ARBOREAL SNAKES

We identified a total of 634 snake species as primarily or semi-arboreal. Of these, slightly more than half were determined to be primarily arboreal (for details, see Supporting Information, Appendix S1). Most arboreal species are found in the speciose subfamily Colubrinae (291 species), followed by Dipsadinae (118 species), then Viperidae (93 species; Crotalinae specifically 76 species; Table 2). Some species-poor clades contain a high proportion of arboreal species, including Pareidae, Boidae and Pythonidae, but contribute relatively little to the overall richness of arboreal snakes (e.g. 90% of pareids are identified as arboreal but that is only 18 species in total; Table 2).

Geographically, the largest proportion of arboreal snakes are found in the Neotropical region (38%; including Central America), followed by the Indo-Malaysian region (27%) and the Afrotropical region (21%), with the Nearctic region contributing the lowest numbers of arboreal snake taxa (1%; Table 3). The majority of arboreal snakes are nocturnal, although nearly 40% are diurnal (Table 3).

Most prey upon reptiles and/or amphibians (52 and 43%, respectively), followed by mammals (31%) and birds (29%; Table 3). They are often dorsally brown/black (70%) and/or patterned (67%), although many are green (24%) and/or uniformly coloured (27%), with stripes being uncommon for arboreal snakes (< 10%; Table 3). More arboreal snakes feed on molluscs (12%) than they do on other invertebrates or the eggs of any other taxonomic group, e.g. bird eggs (6%), frog eggs (1%) etc. Most arboreal snakes are oviparous (79%; Table 3). See Tables 2 and 3 and the Supporting Information (Appendix S1) for additional details on characteristics. As a broad generalization, a ‘typical’ arboreal snake is a Neotropical, nocturnal, oviparous, reptile-eating, brown/banded/patterned snake (e.g. the dipsadine snakes of the genus Imantodes).

DIVERSIFICATION AND BODY SIZE ANALYSES

The HiSSE model that provided the best fit to the data was the CID GeoHiSSE 2 model, which fitted considerably better than any other model and carried to determine whether patterns differ at different analytical scales. Subclades included Booidea, Viperidae, Elapidae + Lamprophiidae, Dipsadinae and Colubrinae. For all OUwie analyses, we set the scaleheight option to false so that branch lengths remain in units of millions of years. We examined the eigenvalues from the Hessian matrix of all OUwie analyses to ensure that all parameters were optimized and discarded any models that contained any negative eigenvalues.

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The percentage arboreal is the percentage of primarily or semi-arboreal species out of the total number of species within a family/subfamily (total number of species within family/subfamily in parentheses), whereas the percentage for primarily and semi-arboreal is out of those identified as arboreal species. Subfamilies were included when many arboreal species were found across different subfamilies containing high diversity. Numbers of total species per family/subfamily used in calculations were obtained from the Reptile Database in 2017. For the arboreal taxa within each family/subfamily, general characteristics/traits were taken as follows. Generalized zoogeographical regions: Af, Afrotropical; Au, Australian; I, Indo-Malaysian; N, Nearctic; Neo, Neotropical; P, Palearctic. Diel pattern: D, diurnal; N, nocturnal; P, polyphasic. Parity: O, oviparous; V, viviparous. Diet: A, amphibians; AE, amphibian eggs/larvae; Ar, arthropods; B, birds; BE, bird eggs; F, fish; M, mammals; Mo, molluscs; R, reptiles; RE, reptile eggs. Colour/pattern: Bp, banded/blotched pattern; Bc, black/brown color; G, green; O, other/multicolour; S, striped; U, uniform. Whether species from the families/subfamilies can be characterized as venomous is included. The order of the abbreviations for each category roughly corresponds from the majority to the minority of occurrences for each category. For detailed information on all traits, see the Supporting Information (Appendix S1). *Diet type was recorded for only one species for a family/subfamily.

<table>
<thead>
<tr>
<th>Family/subfamily</th>
<th>Percentage arboreal (primarily/semi-arboreal)</th>
<th>Zoogeographical regions</th>
<th>Diel</th>
<th>Parity</th>
<th>Diet</th>
<th>Colour/ pattern</th>
<th>Venomous</th>
</tr>
</thead>
<tbody>
<tr>
<td>Boidae (61)</td>
<td>46 (36/64)</td>
<td>Neo, Au, Af</td>
<td>N, P</td>
<td>V</td>
<td>M, B, R, A</td>
<td>Bc, O, G/Bp, U</td>
<td>None</td>
</tr>
<tr>
<td>Psammophiinae (8)</td>
<td>15 (0/100)</td>
<td>Af, I, P</td>
<td>D</td>
<td>O</td>
<td>R, A, RE</td>
<td>Bc, O/Bp, U, S</td>
<td>All</td>
</tr>
<tr>
<td>Pseudoxyrhophiinae (90)</td>
<td>43 (69/31)</td>
<td>Af</td>
<td>N, D, P</td>
<td>O, V</td>
<td>R, A, AE, B, M*, Mo*</td>
<td>Bc, O/Bp, U</td>
<td>Some</td>
</tr>
<tr>
<td>Pareidae (20)</td>
<td>90 (100/0)</td>
<td>I, P</td>
<td>N</td>
<td>O</td>
<td>Mo</td>
<td>Bc/Bp</td>
<td>None</td>
</tr>
<tr>
<td>Pythonidae (40)</td>
<td>38 (69/94)</td>
<td>Au, I</td>
<td>N, P</td>
<td>O</td>
<td>M, B, R, A</td>
<td>Bc, G/Bp, U</td>
<td>None</td>
</tr>
<tr>
<td>Tropidophiidae (34)</td>
<td>29 (100/0)</td>
<td>Neo</td>
<td>N</td>
<td>V</td>
<td>A, R, M, B</td>
<td>Bc, O/Bp</td>
<td>None</td>
</tr>
<tr>
<td>Viperidae (342)</td>
<td>27 (66/34)</td>
<td>I, Neo, Af, P</td>
<td>N, P, D</td>
<td>V, O</td>
<td>M, A, R, B, Ar, Mo*</td>
<td>G, Bc, O/Bp, U</td>
<td>All</td>
</tr>
<tr>
<td>Crotalinae (240)</td>
<td>32 (59/41)</td>
<td>I, Neo, P</td>
<td>N, D, P</td>
<td>O, V</td>
<td>M, A, R, B, Ar</td>
<td>G, Bc, O/Bp, U</td>
<td>All</td>
</tr>
<tr>
<td>Viperinae (100)</td>
<td>17 (94/6)</td>
<td>Af, P</td>
<td>N, P</td>
<td>O, V</td>
<td>M, A, R, B, Mo*</td>
<td>G, Bc, O/Bp, U</td>
<td>All</td>
</tr>
</tbody>
</table>

The percentage arboreal is the percentage of primarily or semi-arboreal species out of the total number of species within a family/subfamily (total number of species within family/subfamily in parentheses), whereas the percentage for primarily and semi-arboreal is out of those identified as arboreal species. Subfamilies were included when many arboreal species were found across different subfamilies containing high diversity. Numbers of total species per family/subfamily used in calculations were obtained from the Reptile Database in 2017. For the arboreal taxa within each family/subfamily, general characteristics/traits were taken as follows. Generalized zoogeographical regions: Af, Afrotropical; Au, Australian; I, Indo-Malaysian; N, Nearctic; Neo, Neotropical; P, Palearctic. Diel pattern: D, diurnal; N, nocturnal; P, polyphasic. Parity: O, oviparous; V, viviparous. Diet: A, amphibians; AE, amphibian eggs/larvae; Ar, arthropods; B, birds; BE, bird eggs; F, fish; M, mammals; Mo, molluscs; R, reptiles; RE, reptile eggs. Colour/pattern: Bp, banded/blotched pattern; Bc, black/brown color; G, green; O, other/multicolour; S, striped; U, uniform. Whether species from the families/subfamilies can be characterized as venomous is included. The order of the abbreviations for each category roughly corresponds from the majority to the minority of occurrences for each category. For detailed information on all traits, see the Supporting Information (Appendix S1). *Diet type was recorded for only one species for a family/subfamily.

essentially 100% of the AIC weight (Table 1). This model includes diversification rate heterogeneity, but only heterogeneity that is independent of arboreality. Estimated net diversification rates for all three states have similar, overlapping distributions and similar mean values (Supporting Information, Fig. S1).

The model-averaged ancestral state reconstruction recovers the most recent common ancestors of all snakes and of most major clades of snakes as having been ancestraly non-arboreal, as expected (Fig. 1; for a version with tip labels and probabilities of each state at nodes, see Supporting Information, Fig. S2). Origins of arboreality are spread across the snake phylogeny, with at least one origin within Tropidophiidae, one or more within Pythonidae, at least one within Boidae, one in Pareidae, probably seven within Viperidae, five within Lamprophiidae (exclusive of Elapidae, although these groups are not reciprocally monophyletic in this tree), five within Elapidae, probably five or more within Colubrinae, and eight or more within Dipsadinae. We also recover several reversals from arboreality back to non-arboreality, most notably within Colubrinae, with reasonably strong support.

When we fitted models of body size evolution to the full tree using OUwie, we found that the OUM model, and OU_{MA} and OU_{MV} models returned nonsensical results and returned negative eigenvalues in the Hessian matrix, indicating failure to optimize parameters in the models; therefore, we discarded these models. Of the remaining models, we found that the OU_{M} model, with regimes defined according to ancestral state reconstructions of arboreality, provided the best fit to the body size data across all snakes (Supporting Information, Table S1). Multi-peak OU models strongly outperformed the single-peak OU model and both BM models for all snakes and three of five subclades. The OU_{MVA} model provided the best fit to Viperidae and Colubrinae, whereas the OU_{M} model provided the best fit to Dipsadinae. Boididae was best fitted by the BM_{M} model, and Elapidae + Lamprophiidae was best fitted by the single optimum OU_{M} model. Across all snakes, we found that the body size optima for primarily and semi-arboreal snakes were larger than that for non-arboreal snakes (Table 4). We found the same pattern within Viperidae, Colubrinae and Dipsadinae, although we note that the means for

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Viperidae are similar across states and are within one standard error of each other. We found that for Viperidae, Colubrinae and Dipsadinae, rates of body size evolution ($\sigma^2$) were highest in non-arboreal lineages and lower in semi- and primarily arboreal lineages. In contrast, for Booidea, we found that the rate of evolution was highest for semi-arboreal snakes. The pull towards the optimal value in Viperidae is higher in semi-arboreal and primarily arboreal lineages than in non-arboreal lineages. The $\alpha$ parameter was also allowed to vary in the best-fit model for Colubrinae, but values are all very small and near zero, thereby effectively collapsing the multi-peak OU model to a multi-mean, multi-rate Brownian motion model. For all snakes, estimated $\sigma^2(0.438)$ and $\alpha(2.771)$ values seem excessively high, which might be a result of the model inadequately accounting for additional rate heterogeneity that is likely on such a large tree; however, $\theta$ estimates appear reasonable and are similar to those estimated for smaller clades; therefore, we focus our discussion for all snakes only on differences in optima.

**DISCUSSION**

**General characteristics of arboreal snakes**

Arboreality is not evenly distributed among the snake clades of the world. Well over half of the arboreal species are found in the colubrid subfamilies Colubrinae and Dipsadinae. The remaining large subfamily within Colubridae, Natricinae, lacks any arboreal species, as do several other families [e.g. Homalopsidae, Typhlopidae (although for reports of typhlopids in trees, see Das & Wallach, 1998), Uropeltidae]. In clades that lack any arboreal species, it seems that specializations for aquatic (e.g. Natricinae, Homalopsidae, Acrochordidae) or fossorial (e.g. Typhlopidae, Uropeltidae) habitats preclude the evolution of arboreality. Geographical contingency may also play a role in limiting transitions to arboreality in some clades. As might be expected, a large majority of arboreal species are found in the tropics (Table 3). Clades that have radiated primarily in regions with fewer forests, such as the Australian radiation of elapids, may be presented with fewer potential arboreal habitats, which is likely to drive the paucity of arboreal species in such lineages.

Arboreal snakes eat a wide range of prey, with most species consuming reptiles, amphibians, mammals and/or birds in the highest proportions (Table 3), and there does not appear to be any consistent specialization on a single prey type. However, it is worth noting that a fairly large number of arboreal snakes consume molluscs; although only 12% of arboreal snakes eat molluscs, it is a specialization for pareids, and

Table 3. Characteristics across 634 snakes identified as either primarily arboreal or semi-arboreal

<table>
<thead>
<tr>
<th>Percentage primarily/semi-arboreal</th>
<th>Zoogeographical regions</th>
<th>Diet</th>
<th>Colour</th>
<th>Pattern</th>
</tr>
</thead>
<tbody>
<tr>
<td>54%/46%</td>
<td>Neotropical = 38%</td>
<td>Reptiles = 52%</td>
<td>Brown/black = 70%</td>
<td>Banded/blotched = 67%</td>
</tr>
<tr>
<td></td>
<td>Indomalayan = 21%</td>
<td>Amphibians = 43%</td>
<td>Green = 24%</td>
<td>Uniform = 27%</td>
</tr>
<tr>
<td></td>
<td>Afrotropical = 21%</td>
<td>Mammals = 31%</td>
<td>Other/multi = 14%</td>
<td>Striped = 7%</td>
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<tr>
<td></td>
<td>Palaearctic = 5%</td>
<td>Fish = 1%</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Australian = 4%</td>
<td>Birds = 6%</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Neartic = 1%</td>
<td>Reptile eggs ≤ 1%</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Multiple regions = 4%</td>
<td>Amphibian eggs = 2%</td>
<td></td>
<td></td>
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<tr>
<td></td>
<td></td>
<td>Other/multi = 14%</td>
<td></td>
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<tr>
<td></td>
<td></td>
<td>Striped = 7%</td>
<td></td>
<td></td>
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<tr>
<td></td>
<td></td>
<td>Banded/blotched = 67%</td>
<td></td>
<td></td>
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<tr>
<td></td>
<td></td>
<td>Uniform = 27%</td>
<td></td>
<td></td>
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</table>

Note that percentages may not add up to 100 if species consumes multiple prey items or has multiple colour patterns etc.
molluscs are included in the diets of many dipsadines (e.g. Sibon). Surprisingly, at least one arboreal snake, Ahaetulla fronticincta, is a fish specialist, catching fish by hanging over the water from bushes or vegetation (Das, 2010).

Related to diet, we also note that a large proportion of arboreal snakes are venomous. These include the sole-noglyphous Viperidae, which are ancestrally venomous, and many ophistoglyphous colubrids. Although we did not formally categorize this owing to the vagaries in what qualifies as a ‘rear-fanged’ or venomous snake in the literature, there are many examples of ophistoglyphous arboreal snakes globally, including many colubrines (e.g. Ahaetulla, Dispholidus, Oxybelis) and dipsadines (e.g. Imantodes, Philodryas, Uromacer). As we also did not code the presence of venom in non-arboreal snakes, we cannot be sure whether venom evolved selectively in arboreal colubrid lineages or if these lineages are members of larger clades that are ancestrally rear-fanged venomous (as may be the case for dipsadine snakes). However, it is possible that the evolution of venom in colubrid snakes either facilitates or evolves in response to shifts to an arboreal lifestyle. Capturing and handling prey in the branches of trees offers special challenges, and being able to subdue prey more quickly through the use of venom might be especially beneficial in an arboreal setting.

Parity mode for arboreal snakes parallels what is found across snakes generally, with ~21% of arboreal snakes categorized as viviparous here (Table 3); this is comparable to a recent study on the reproductive modes of non-marine/non-scolecodophian snakes globally (21.5% of snakes are viviparous globally; Feldman et al., 2015).

With respect to coloration and body patterns for arboreal snakes, the most striking result is the paucity of longitudinally striped snakes recorded (7%), with blotched/banded and uniformly coloured snakes being found in much higher proportions (67 and 27%, respectively; Table 3). Stripes (and to some extent uniform coloration) have been hypothesized to aid snakes in escape by making it harder for predators to determine the location of the moving snake accurately because of optical illusions provided by the stripes. This hypothesis was supported by Jackson et al. (1976), who found that predator-avoidance behaviour (flight or defense) best predicted colour pattern, with striped snakes being associated with fleeing behaviour; an additional study found support for this relationship when taking into account phylogeny (Allen et al., 2013). Given that the predators of an arboreal snake might not be viewing it from the same angles as those of a terrestrial snake, the lack of striped arboreal species could be attributable to the habitat making this escape behaviour or the stripe illusion less effective. However, both of the aforementioned studies focused on Australian and/or North American species, and these are regions that have the lowest numbers of arboreal snakes globally (Table 3) and therefore do not represent cohesive sampling for arboreal taxa. A future study that also includes behaviour (flight/defensive) would allow for a better understanding of whether and how colour patterns relate to these behaviours in arboreal snakes specifically. After brown/black variations, green body colour was most common among arboreal taxa, with many of these being uniformly coloured green (Supporting Information, Appendix S1). We expect that green coloration aids these snakes in camouflage from both predators and prey. Previous work also finds that uniform coloration has been correlated with snakes that are active hunters rather than ambush predators, although again, this was not specific to arboreal taxa (Allen et al., 2013).

**Diversification of Arboreal Snakes**

We found no signal of arboreality-dependent diversification in snakes, as indicated by a CID model carrying essentially 100% of the model weight and the nearly identical diversification rates returned from model averaging over...
all models. Looking at diversification rates in the model-averaged ancestral state reconstruction and the plotted distribution of diversification rates (Fig. 1; Supporting Information, Fig. S1), we see considerable variation in diversification rates across snakes, consistent with the findings of Harrington & Reeder (2017), but it is clear that this variation is largely independent of arboreality. These findings are inconsistent with the results of Bars-Closel et al. (2017), who found that diversification rates were higher for arboreal snakes. We used an explicit

Figure 1. Model-averaged ancestral state reconstruction of arboreality from hidden state speciation and extinction (HiSSE). Branches are coloured from white, denoting non-arboreality, to yellow, indicating semi-arboreality, to black, indicating primary arboreality, along a gradient according to the probability of each state. Outline colours of branches indicate net diversification rates, with cooler colours denoting slower rates. For the distribution of diversification rate values for each state, see the Supporting Information (Fig. S1). For tip labels on ancestral state reconstruction, see the Supporting Information (Fig. S2).
modelling approach that estimated diversification rates for each character state and we included CID models in our model set, whereas Bars-Closel et al. (2017) correlated estimated proportions of arboreal snakes with clade-wide estimates of diversification or used a MuSSE approach without incorporating CID models (which were unavailable at the time). We expect that these analytical differences are the driver of our different findings, highlighting the potential sensitivity of diversification rate analyses to methodology.

Ancestral state reconstructions of arboreality (for the purposes of discussion here considering both semi- and primarily arboreal snakes as arboreal in a broad sense) show multiple independent origins of arboreality in Tropidophiidae, Pythonidae, Boidae, Pareidae, Viperidae, Lamprophiiidae, Elapidae, Colubrinae and Dipsadinae. Dipsadinae features the greatest number of origins of arboreality and contains the second highest number of arboreal species, although fewer than half as many as are present in Colubrinae. Dipsadinae diversity is centered in the Neotropics (Greene, 2000), possibly presenting more opportunities for the evolution of arboreality in this clade than in Colubrinae. However, the most complex series of transitions between arboreality and non-arboreality occurs within Colubrinae. Within this clade, there is a large subclade that is recovered as having been ancestrally arboreal, followed by multiple reversals to non-arboreality. This may suggest that colubrines possess traits that make transitions between arboreal and non-arboreal habitats relatively easy evolutionarily.

Primarily arboreal and semi-arboreal snakes were inferred to have larger optimal body sizes than non-arboreal snakes in all cases in which a multiple-optimum OU model was the best fit, although this difference was relatively small for Viperidae. We also found evidence for increased constraint on body sizes in arboreal lineages. For Viperidae, Dipsadinae and Colubrinae, estimated rates of evolution were highest for non-arboreal lineages and considerably lower in semi- and primarily arboreal lineages. In Viperidae, α values were much higher for semi- and primarily arboreal lineages than non-arboreal lineages, further suggesting possible constraint. The increased constraint and lower rates of body size evolution in arboreal snakes are consistent with similar findings for vipers using more detailed metrics of size (Alencar et al., 2017).

Our findings therefore indicate that arboreal snakes may be generally constrained to be longer than non-arboreal snakes. This is consistent with studies that have shown that arboreal snakes tend to be more elongated and slender than terrestrial snakes (Guyer & Donnelly, 1990; Martins, 2001; Pizzatto et al., 2007). Our initial expectation was that although arboreal snakes are less heavily bodied than non-arboreal snakes, perhaps arboreal snakes might still be shorter in absolute terms. However, given our findings, it may be that the elongate body form of arboreal snakes is achieved by elongation with relatively stable cross-sectional areas, rather than by narrowing of the body to achieve a slender form. Brischoux & Shine (2011) showed that the laterally compressed bodies of sea snakes are the result of an increase in the height of the body, rather than a decrease in the width. If arboreal snakes simply become longer without proportionate increases in body width and height, then the end result would be snakes that are longer but proportionally more slender than their terrestrial ancestors.

This study relied on the accumulation and collation of large amounts of natural history data for thousands of species, and we would like to emphasize the utility of these data in exploring broad evolutionary patterns across snakes (or other clades). The continued collection of basic natural history data for individual species will be essential for future studies exploring additional aspects of snake diversification and trait evolution. New data may also help to refine findings from the present study, because some of the classifications we made are necessarily based on very few observations for poorly known species (e.g. most members of Lamprophiiidae).

CONCLUSIONS

Arboreality has evolved independently in several distinct lineages of snakes. Arboreal snakes are predominately found in the tropical regions of the world, which are likely to present more arboreal niche space for these snakes potentially to invade. Colubridae, specifically the subfamilies Colubrinae and Dipsadinae, contribute the greatest number of arboreal species to the global snake community. As a broad summary, arboreal snakes are likely to be nocturnal, oviparous snakes that primarily consume reptiles and amphibians and are often coloured in shades of brown or black, typically with the dorsum having a blotched/banded, rather than a striped, pattern. Arboreal habits have no effect on diversification rates, which are highly heterogeneous among snakes. Arboreal snakes are, in general, longer than non-arboreal snakes, and there is some evidence that the length of arboreal snakes is more constrained than that of non-arboreal species.

ACKNOWLEDGEMENTS

We would like to thank members of the Reeder laboratory for providing helpful insight on analyses for this manuscript. We thank three anonymous reviewers for their helpful comments that greatly improved this manuscript.
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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher’s web-site:

**Figure S1.** Model-averaged distribution of net diversification rates for tips, as estimated from HiSSE analyses, for primarily arboreal (black; mean shown by black vertical line), semi-arboreal (yellow; mean shown by yellow vertical line) and non-arboreal (white; mean shown by grey vertical line) snakes.
Figure S2. Model-averaged ancestral state reconstruction of arboreality from hidden state speciation and extinction (HiSSE). Pies at nodes show the probability that each node is non-arboreal (white), semi-arboreal (yellow) or primarily arboreal (black). Branches are coloured by net diversification rates, with blue branches indicating low net diversification and red indicating high net diversification.

Table S1. Akaike information criterion values for morphological models fitted in OUwie. Models listed with NA failed to yield reliable results and have been excluded. Best-fit models are in bold.

Appendix S1. Full list of arboreal species and characteristics for each. See other tab for literature cited for this appendix.

File S1. Zip archive containing all code and data to run HiSSE and OUwie analyses.

**SHARED DATA**

Data and R code used for diversification and body size analyses are available in the Supporting Information (File S1).