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## Research

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# Trophic divergence despite morphological convergence in a continental radiation of snakes

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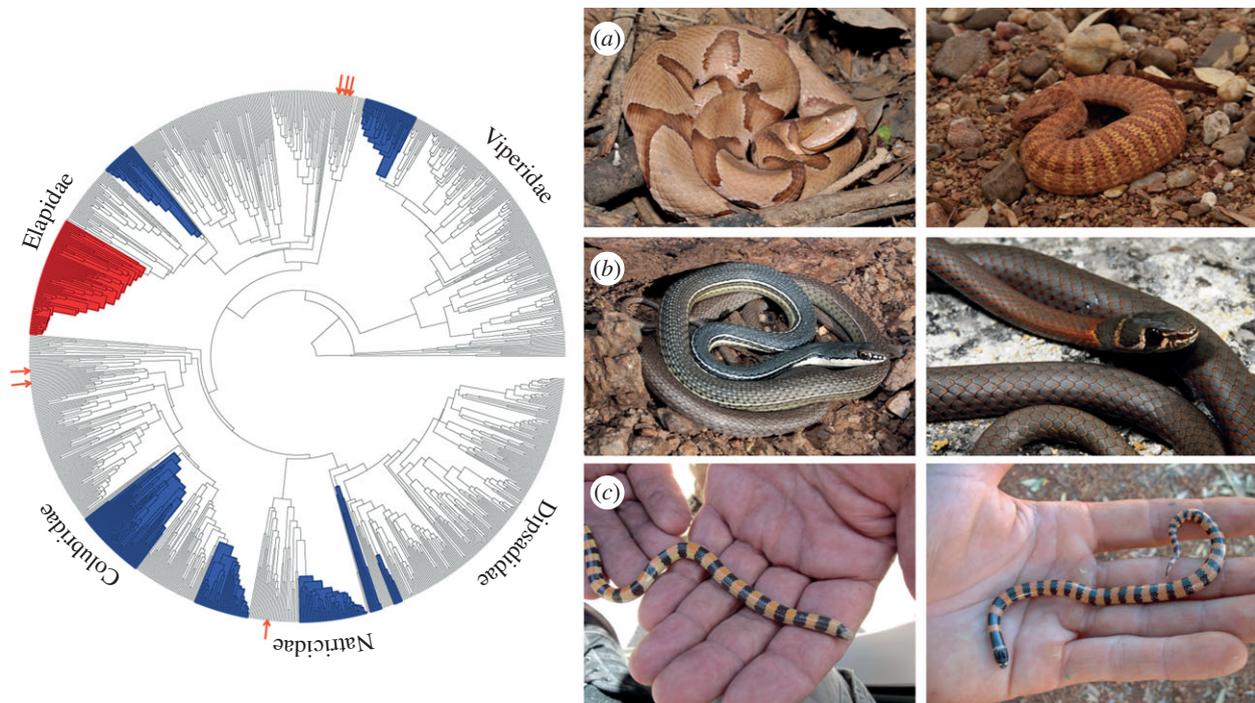
Ecological and phenotypic convergence is a potential outcome of adaptive radiation in response to ecological opportunity. However, a number of factors may limit convergence during evolutionary radiations, including interregional differences in biogeographic history and clade-specific constraints on form and function. Here, we demonstrate that a single clade of terrestrial snakes from Australia—the oxyuranine elapids—exhibits widespread morphological convergence with a phylogenetically diverse and distantly related assemblage of snakes from North America. Australian elapids have evolved nearly the full spectrum of phenotypic modalities that occurs among North American snakes. Much of the convergence appears to involve the recurrent evolution of stereotyped morphologies associated with foraging mode, locomotion and habitat use. By contrast, analysis of snake diets indicates striking divergence in feeding ecology between these faunas, partially reflecting regional differences in ecological allometry between Australia and North America. Widespread phenotypic convergence with the North American snake fauna coupled with divergence in feeding ecology are clear examples of how independent continental radiations may converge along some ecological axes yet differ profoundly along others.

## 1. Introduction

Evolutionary convergence is a widespread pattern that occurs when separate lineages independently evolve similar phenotypes in response to similar ecological conditions. Traditionally, convergence between pairs of species has been used as evidence for adaptation by natural selection [1]. More recently, convergence has been identified at the scale of entire evolutionary radiations and used as evidence for the predictable nature of the evolutionary process [2–5]. These efforts constitute a departure from earlier investigations of radiation-wide convergence, which emphasized differences among radiations and the importance of biogeographic and phylogenetic history in determining their outcome [6–8].

Biogeographic and phylogenetic history may exert large effects on the morphological and ecological trajectories of diversifying clades [8]. In some cases, convergence in morphology and ecology is detectable despite the imprint of these historical factors [4,9]. In other cases, phenotypic and ecological convergence in some traits is complemented by divergence in others [10]. Despite the potential ubiquity of convergence with divergence in nature, these patterns are poorly documented in the literature [11]. Many, perhaps most, organisms that show convergence in one or several traits are likely to show divergence in other traits because of the multidimensional nature of the niche [12].

In this study, we report a striking pattern of convergence with divergence during the evolutionary assembly of Australia's terrestrial snake fauna. We studied patterns of morphological and ecological diversification during the radiation of Australia's colubroid ('advanced', or 'typical') snakes. Colubroids dominate terrestrial snake assemblages on nearly every landmass where they occur and account for approximately 80% of global snake diversity [13]. In most biogeographic regions, colubroid snake faunas are drawn from a number of phylogenetically



**Figure 1.** Left: Phylogeny of colubroid snakes from [15] illustrating ‘core’ North American radiations (blue) and the Australian elapid radiation (red). Arrows denote ‘singleton’ non-elapid colubroid lineages that colonized Australia but failed to radiate. Some members of North American radiations also occur in South America. Right: Matched pairs of North American colubroids (left column) from three distinct radiations and an example of a phenotypically similar Australian elapid snake (right column). Photo credits (from left to right): (a) *Agkistrodon contortrix* (Chris Williams), *Acanthophis pyrrhus* (Dan Rabosky); (b) *Coluber bilineatus* (Todd Pier-son), *Demansia torquata* (Eric Vanderduys) and (c) *Chilomeniscus stramineus* (Kate Jackson), *Simoselaps anomalus* (Dan Rabosky).

disparate lineages [14] (figure 1). For example, North America’s colubroid fauna (approx. 125 species; [16]) comprises at least five distinct evolutionary radiations [17], and local ecological communities may contain representatives from each of these radiations [18]. By contrast, the approximately 100 species of terrestrial colubroids from Australia are largely the result of a single evolutionary radiation that occurred sometime after the colonization of Australia by a colubroid lineage approximately 10–18 Ma [19]. This clade—the oxyuranine elapids—includes forms that collectively occupy nearly all terrestrial habitats within Australia [20]. Only two other extant snake clades (Pythonidae; Typhlopidae) have diversified to any extent within Australia; neither clade is a colubroid and both are highly distinct from the elapids in general ecology and morphology. These observations suggest the possibility that the diversity of species and forms among Australia’s elapids is an outcome of ecological opportunity that can be attributed to the general absence of other colubroid snake lineages.

Anecdotal evidence indicates that Australia’s elapid snakes may occupy the morphological and ecological spaces filled by multiple distinct colubroid lineages (e.g. viperids, colubrids; figure 1) that are widespread on other major landmasses [20]. Several instances of convergence between Australian elapids and North American colubrids, elapids and viperids have been suggested in the literature [21–24]. An outstanding question is whether or not these purported convergences are part of a larger pattern of radiation-wide convergence between Australian elapids and the phylogenetically disparate North American snake fauna. More generally, this system represents an important test of the extent to which a single evolutionary radiation occurring in isolation can replicate the morphological and ecological diversity observed in similarly species-rich but phylogenetically diverse continental communities elsewhere.

We tested the extent to which the Australian elapid radiation has converged and diverged on phenotypic and ecological modalities observed across a diverse set of co-radiating lineages from North America. We assembled morphological and ecological data for a range of colubroids from North America, Australia and elsewhere. Our results reveal substantial morphological and functional diversity among Australian elapids with widespread morphological convergence to distantly related snakes in North America. However, convergence in morphology is matched by an equally striking level of divergence in trophic ecology. Morphologically convergent snakes from North America and Australia may be highly distinct in diet, and a number of significant feeding niches from North America are lacking entirely from the Australian elapid fauna. These two patterns stand in sharp relief and are clear examples of how independent continental evolutionary radiations may converge along some ecological axes yet differ profoundly along others.

## 2. Material and methods

### (a) Phenotypic data

We collected phenotypic data from preserved snake specimens housed in the natural history collections of the University of Michigan Museum of Zoology (UMMZ), the Field Museum of Natural History (FMNH) and the Western Australian Museum (WAM). The morphological dataset consisted of terrestrial elapid snakes from Australia and elsewhere (e.g. cobras, coralsnakes and kraits), and a phylogenetically disparate set of colubroid snakes, principally from North America. We included species not present in Australia or North America to distinguish convergent phenotypes unique to the two groups from convergent phenotypes that occur elsewhere, including generalized elapid phenotypes from South America, Africa and Asia (e.g. cobras, kraits, mambas, coralsnakes).

For each specimen, we measured its snout-vent-length and tail length (TL) using a wetted thread laid out first along the specimen's spine and subsequently along a ruler. In addition, we used digital calipers with 0.01-millimetre precision to take 10 measurements of head and body dimensions (12 variables total; provided in the electronic supplementary material) specifically chosen to capture major axes of functional variation. In total, we have data from 786 specimens representing 248 species. Each species is represented by a median of three specimens (mode: five specimens, range: one to eight specimens). Phylogenetic data were available for 166 of these species. We used species means for the analyses described below. We used the geometric mean of the 12 linear body dimensions measured for a species as an estimate of body size and obtained size-independent shape variables by standardizing each measurement by body size [25]. We conducted a principal components analysis on the covariance matrix of log-transformed shape variables. For the analyses below, we use the first two principal components of body shape (PC1 and PC2) and the body size variable, which together account for 70% of the variance in the data.

### (b) Ecological data

We surveyed the published literature for quantitative data on the feeding habits of as many species in Australia and North America as possible. We placed diet observations in eight prey categories: invertebrates, fishes, amphibians (including larvae), squamate reptiles, squamate reptile eggs, birds, bird eggs and mammals. This coarse categorization enabled us to pool dietary studies from many different researchers into a single ecological matrix. A cell in the diet matrix corresponded to the fraction of a certain prey category in the diet of a particular species. We used studies that examined stomach contents by dissection of museum specimens as well as studies that examined stomach contents of snakes in the field by palpation or scat analysis. Typically, studies reported either the number of recovered items in specific prey categories or the number of snakes that had a specific prey category in their stomach. We treated these as the same measurement in order to generate prey frequency distributions for each snake species using as much information as possible. If a study reported both measurements, we used the former because that was the measurement we most commonly encountered in the literature. Snakes typically have only a single food item in their gut but occasionally gorge themselves (e.g. an individual feeding on frog metamorphs or on small minnows). The number of prey items, in such cases, will overestimate the number of individual snakes that used a particular prey category. The two measurements are therefore not always equivalent. Our diet data are based on specimens collected over large geographical areas, time periods and individual ages, and therefore provide a general characterization of diet over time, space and ontogeny. The final diet matrix included 92 North America colubroids (median prey records per species: 58, range: 1–1278) and 71 Australian elapids (median prey records per species: 21, range: 1–296). A subset of 58 North America colubroids and 33 Australian elapids had matching phenotypic and phylogenetic data.

### (c) Phylogenetic tests for phenotypic convergence

To evaluate phenotypic convergence between radiations of Australian and North American snakes, we used a recent time-calibrated phylogeny for squamates (lizards and snakes), pruned to include only the 166 species (North America: 74, Australia: 34, Other: 58) in common with our morphological dataset [15]. We first tested whether the phenotypes of Australian elapids are exceptionally similar to those found in North American colubroids relative to patterns expected under multi-rate Brownian motion models of phenotypic evolution. For each elapid snake in the Australian radiation we found the Euclidean distance to its phenotypic nearest neighbour in the North

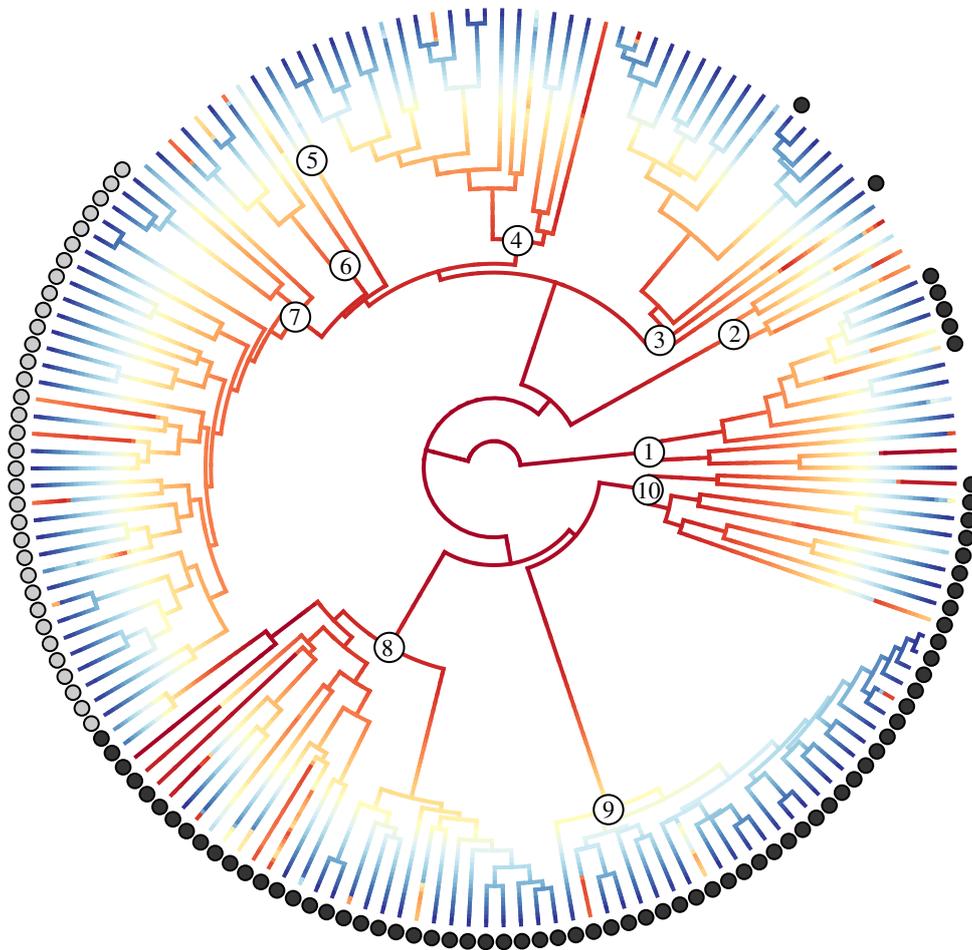
American radiation and recorded the average of these distances. To evaluate significance, we generated null distributions of phenotypes for snakes under a complex multi-process Brownian motion model that explicitly allows rates of phenotypic evolution to vary through time and among clades. The model and associated implementation (BAMM; [bamm-project.org](http://bamm-project.org)) can infer mixtures of time-dependent and clade-specific phenotypic rate regimes on phylogenetic trees [26–28]. Specifically, the model assumes that phylogenetic trees are shaped by a countably distinct set of time-varying evolutionary processes. The number of such processes, as well as their location and associated rate parameters, are inferred from the data using reversible jump Markov chain Monte Carlo (MCMC). We used BAMM to estimate marginal densities of phenotypic rates on each branch of the time-calibrated colubroid phylogeny for each of the three morphological variables. We used the mean marginal rate configuration across the colubroid phylogeny to generate 999 simulated datasets, combining the results of the three separate trait simulations into a null three-dimensional morphospace. Our simulation protocol thus generated species-specific distributions of phenotypes conditional on the observed level of heterogeneity in evolutionary rates through time and among clades. We tested whether the mean observed phenotypic distance between Australian elapids and North American colubroids was less than that expected under the multi-rate simulations.

To identify species or groups of species with convergent phenotypes, we used a stepwise model fitting procedure known as SURFACE that automatically detects shifts and convergence in phenotypic optima [5,29]. Each optimum, here termed a 'regime', contributes a parameter to an Ornstein–Uhlenbeck (OU) process of trait evolution. The SURFACE model involves two phases, corresponding to a 'forward' and a 'backward' step. In the forward step, the algorithm finds the maximum-likelihood estimate of the number and location of phenotypic optima under the OU model, using a stepwise model-selection procedure that is similar to the widely used MEDUSA model of diversification rate variation [30]. The algorithm then sequentially collapses all pairwise optima, retaining only the set of phenotypic regimes that can be justified under a specified information-theoretic criterion (e.g. corrected Akaike Information Criterion (AICc)). Phenotypic convergence is diagnosed when independent lineages share a common optimum. We found that the SURFACE algorithm can occasionally lead to incorrect inference of phenotypic regimes for certain lineages on account of the order dependence induced by the forward stepwise procedure. In the electronic supplementary material, we describe a modification of the forward phase of SURFACE that makes the inferences less prone to misclassification. As before, we assessed whether or not the two continental radiations are phenotypically more or less similar than expected by simulating trait data under the optimal OU model of trait evolution using the R package *ouch* [31] and performing the convergence test described above.

### (d) Visualizing morphological and ecological spaces

Two-dimensional projections of three-dimensional data lose a significant amount of information and three-dimensional plots can be difficult to interpret without the ability to dynamically rotate the viewing angle. A subtler problem with traditional two- and three-dimensional morphospace plots is that by emphasizing Euclidean distances among species they fail to emphasize how species covary in morphospace. For example, species may be far apart on some axes of morphospace yet they may all deviate in the same direction from the origin. The direction of deviation is biologically more meaningful than the magnitude of separation when comparing groups of distantly related species in a common morphospace.

To address this problem, we use a novel technique called a 'morphospace wheel plot' to make an image of the three-dimensional morphospace in two dimensions. Each point in the three-dimensional morphospace has three descriptors: its angle in the



**Figure 2.** Phylorate plot showing BMM-estimated rates of phenotypic evolution during the global radiation of colubroid snakes plotted on a time-calibrated tree of 166 species [15]. Inference model explicitly allows rates of trait evolution to vary through time and among lineages. Warmer (red) colours indicate faster rates than cooler (blue) colours. Australian terrestrial elapids and North American snakes included in our sample are labelled with light grey and dark grey dots, respectively. Despite several accelerations in rates, the dominant pattern is one of temporal slowdown in the rate of morphological evolution. Rates shown here are for the first principal body shape component, but the same pattern is obtained for the second principal body shape component and for body size. Numbered clades are: (1) Viperidae, (2) Homalopsidae, (3) Elapidae: coralsnakes, (4) Elapidae: cobras and mambas, (5) Elapidae: African gartersnakes, (6) Elapidae: kraits, (7) Elapidae: Australia, (8) Colubridae: USA, (9) Natricidae: USA and (10) Dipsadidae: USA. See the electronic supplementary material for tree with labelled tips.

$xy$ -plane, its angle above the  $xy$ -plane, and its distance from the origin. We can represent these three descriptors in two dimensions by using polar coordinates and setting the polar coordinate equal to the angle of the point in the  $xy$ -plane and the radial coordinate equal to the angle above the  $xy$ -plane. The size of the point is then made proportional to the point's distance from the origin. Because the angle of the point above the  $xy$ -plane is constrained to be in the interval  $[\pi/2, -\pi/2]$  the radial coordinate is constrained to lie within an annulus centred on the origin of the polar coordinate system. A point on the outer circle of the annulus is  $\pi/2$  radians above the  $xy$ -plane; a point on the inner circle is  $\pi/2$  radians below the  $xy$ -plane; a point in the middle of the annulus is directly on the  $xy$ -plane. The Euclidean distances between points in the new coordinate system do not equal the Euclidean distances in the original coordinate system (although these could be reconstructed). However, the new coordinate system emphasizes the relative bearing of points to one another in three-dimensional space and therefore identifies groups of species that covary positively or negatively. Further information regarding the construction of morphospace wheel plots is given in the electronic supplementary material.

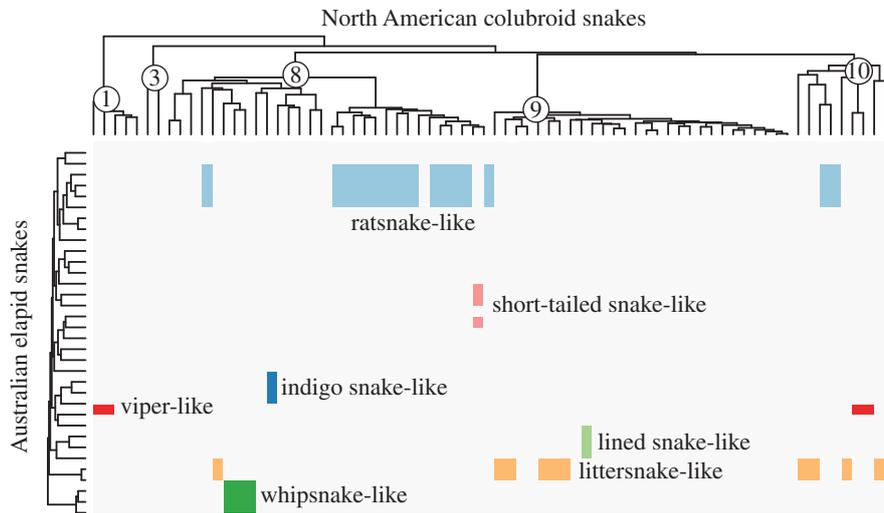
To visualize variation in feeding biology of North American colubroids and Australian elapids, we converted the ecological diet matrix to a graphical representation of the relationships between species and the component prey types that make up their diets. In a diet graph, prey categories and species are represented as vertices and trophic relationships are represented as

edges. Each cell in the diet matrix represents an edge in the diet graph and the value of a cell is used to weight the corresponding edge in the diet graph. To assess how morphology and diet are correlated, we regressed logit-transformed diet proportions against body size using phylogenetic generalized least squares (PGLS). We included the phylogenetic signal parameter  $\lambda$  in our PGLS regressions [32,33]. We performed PGLS regressions in R [34] using the caper package [35].

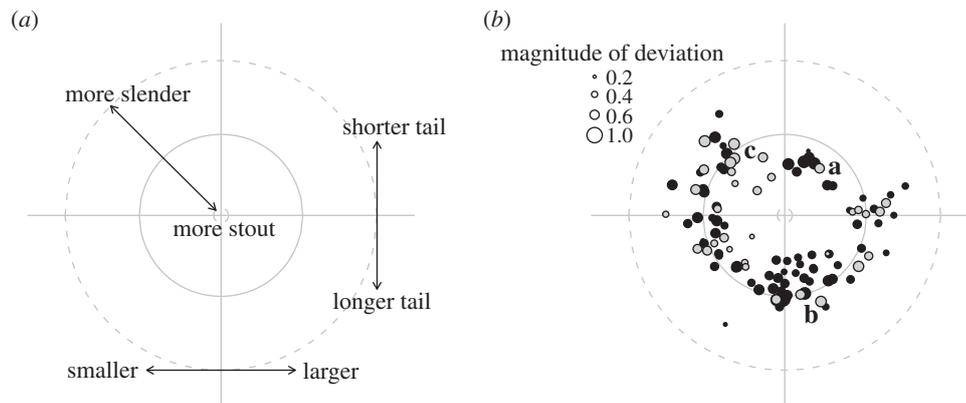
## 3. Results

### (a) Phenotypic convergence

We find little support for a shift to a higher rate of phenotypic evolution at the base of the Australian elapid radiation or any other clade. Although certain lineages stand out for having higher mean rates of phenotypic evolution than the mean background rate, we find highest posterior support for a model with just a single process of time-varying phenotypic evolutionary rates for each of the three traits examined (figure 2). A model with just a single time-varying process of trait evolution was preferred for body size (posterior probability = 0.76, Bayes factor relative to the next best model = 2.65), PC1 (0.60, 1.27) and PC2 (0.79, 3.48). However, despite a lack of detectable overall among-clade heterogeneity in phenotypic rates, we found



**Figure 3.** Pairwise convergence matrix of Australian elapids (left margin) and North American colubroid snakes (top margin). Node labels reference the clades in figure 2. A coloured cell at the intersection between species indicates a convergent phenotypic regime identified through the SURFACE analysis. Labels ascribe a generalized morphology to convergent lineages. The full analysis included a diversity of non-Australian and non-North American colubroid lineages that are not pictured.



**Figure 4.** (a) Simplified interpretation of the morphologies characteristic of different regions in the morphospace wheel plot. Points in the left and right hemispheres are, respectively, smaller or larger than the average body size. Points in the lower and upper hemispheres have, respectively, longer and shorter tails than the average relative TL. Points in the inner and outer annulus are, respectively, stouter or more slender than the average relative body width. (b) Morphospace wheel plot showing ordination of snake species in three-dimensional space defined by body size and the first two principal components of body shape. The size of a point corresponds to the relative magnitude of that point's deviation from the global average (e.g. smaller points are closer to the average). Dark grey points represent North American colubroid snake species and light grey points represent Australian elapid snake species. Inset letters reference positions of phenotypically similar species illustrated in figure 1. The single radiation of Australian elapids exhibits the same phenotypic breadth as multiple distinct radiations of North American colubroids.

that the average nearest neighbour distance between Australian elapids and North American colubroids is significantly smaller than expected under the fitted model ( $p = 0.001$ ). This indicates that, despite no difference in overall dynamics of phenotypic evolution, Australian elapids are significantly more similar in phenotype to North American snakes than expected under the multi-rate Brownian motion model.

Using SURFACE, we inferred at least 15 distinct phenotypic regimes and 40 shifts in phenotypic modality across the full set of 166 colubroid snake species in our dataset. A striking pattern of convergence was detected between Australian elapids and North American colubroids. A model with multiple independent regimes and no convergence ( $AICc = -774.5045$ ) was a substantial improvement over a model with a single regime ( $AICc = -651.9029$ ). However, a model with multiple convergent regimes ( $AICc = -945.5062$ ) generated substantial improvement over the model with independent regimes and

no convergence ( $\Delta AICc = 177$ ). The Australian elapid snakes include a number of major phenotypes that are highly distinct from stereotypical elapid phenotypes (e.g. cobras, kraits and coralsnakes) and were found to converge on such distantly related lineages as rattlesnakes and colubrine whipsnakes (figures 3 and 4). Convergent morphologies observed among Australian elapids include stout-bodied ambush predators (e.g. *Acanthophis*), slender fast-moving active foragers (e.g. *Demansia*) and small burrowing snakes (e.g. *Furina*, *Simoselaps*).

Among Australian elapids SURFACE inferred 10 phenotypic regimes and all but three are convergent with phenotypic regimes among North American colubroids. Out of 12 shifts in phenotypic modality within Australian elapids, eight represent shifts to phenotypic regimes shared with North American colubroids (table 1). The four shifts to phenotypic regimes not represented among North American colubroids include three regimes present in other elapid lineages. Average

**Table 1.** Convergence parameters identified by the stepwise OU model-selection algorithm for the radiation of oxyuranine elapids in Australia. The number of unique phenotypic regimes as well as the number of regime shifts is listed first, followed by the number of regimes and regime shifts that are convergent on phenotypic regimes of North American colubroids. The number of regime shifts is not equal to the number of regimes due to two instances of intra-radiation convergence. The convergence fraction is the number of regime shifts that are convergent on regimes in North America divided by the total number of regime shifts.

phenotypic regimes	10
phenotypic regime shifts	12
convergent phenotypic regimes	7
convergent phenotypic regime shifts	8
convergence fraction	0.67

nearest neighbour distances among species of the two continental radiations as predicted by the multi-optima OU model are not appreciably different from the observed average nearest neighbour distance ( $p = 0.073$ ). The variance of trait data simulated under the multi-optima OU model was approximately equal to the variance of the observed data, averaging only 0.006 times smaller. By contrast, the variance of trait data simulated under the multi-rate Brownian motion model was on average 1.4 times larger than the variance of the observed data. This indicates that incorporating convergence into the model of trait evolution significantly improves its ability to simulate phenotypic distributions of Australian elapids and North American colubroids.

### (b) Ecological divergence

The diet graph reveals several major differences in feeding habits between Australian elapids and North American snakes (figure 5). Invertebrates and fishes are used heavily or exclusively by numerous species in North America. By contrast, very few terrestrial Australian elapids include invertebrates or fishes as important components in their diets. Elapid diets in Australia are dominated by a single prey category: squamate reptiles. While a number of snakes in North America also feed on squamates, fewer rely on them to the same extent as many Australian elapids.

Major divergences in diet between the two faunas are associated with body size (figure 6). Among Australian elapids the proportion of squamate reptiles in the diet is negatively correlated with body size ( $r = -0.50$ ,  $p = 0.002$ ). Among North American colubroids, this allometric trend is weak and reversed ( $r = 0.06$ ,  $p = 0.28$ ). Instead, the proportion of invertebrates in the diet is negatively correlated with body size ( $r = -0.52$ ,  $p < 0.001$ ). This pattern is driven by the radiations of non-lampropeltine colubrids, natricids and dipsadids (cf. figure 1). When these radiations are excluded, the proportion of squamates in the diet is also negatively correlated with body size ( $r = -0.57$ ,  $p = 0.004$ ;  $r = -0.87$ ,  $p < 0.001$  when *Cemophora coccinea*, a specialist squamate egg predator, is excluded). In both the Australian and North American snake fauna, mammals and birds are consumed only by larger species ((Australia) mammals:  $r = 0.66$ ,  $p < 0.001$ ; birds:  $r = 0.59$ ,  $p < 0.001$ ; (North America) mammals:  $r = 0.59$ ,  $p < 0.001$ ; birds:  $r = 0.42$ ,  $p < 0.001$ ).

## 4. Discussion

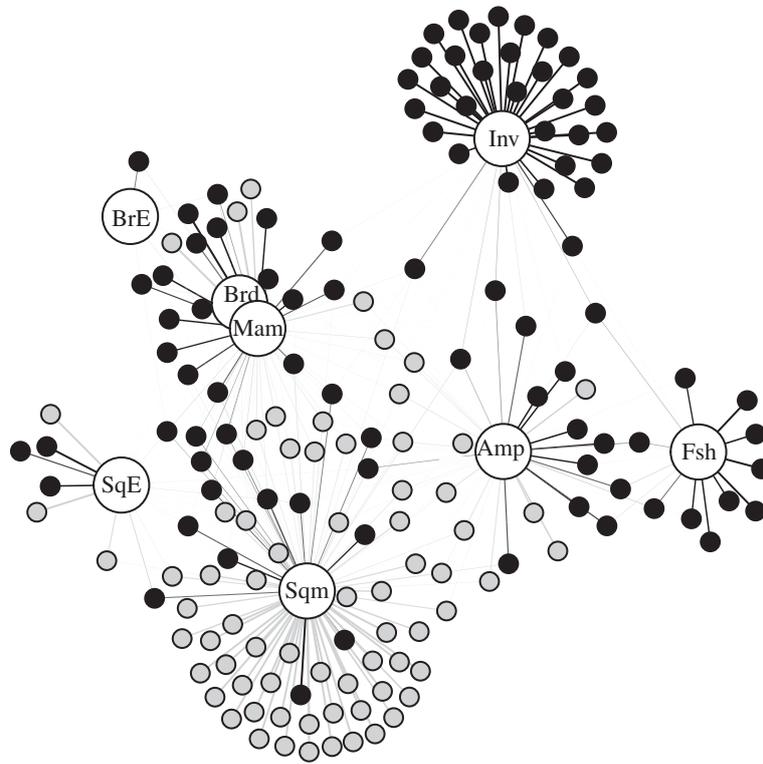
### (a) Phenotypic convergence

The widespread phenotypic convergence among Australian elapids and a phylogenetically disparate set of North American colubroid snakes challenges the notion that evolutionary radiations are unlikely to be replicated among continental landmasses [36]. It is true that the Australian snake fauna bears a large imprint of biogeographic history: Australia is the only continent where colubroid snake communities are dominated by elapids. However, the 10 phenotypic regimes identified by SURFACE among the Australian elapids encompass an enormous breadth of morphological and functional diversity, and all but three of these regimes have counterparts among North American colubroids. By using an explicit model of evolutionary convergence, our study offers the first quantitative evidence to support previous anecdotal evidence that phenotypically convergent species exhibit convergent ecology [20–24]. Consistent associations between ecology and morphology indicate that at least some of these phenotypic regimes are adaptive for specific foraging modes or habitat use. For example, Australian shovel-nosed snakes (*Brachyuropsis* and *Simoselaps*) and North American sand snakes (*Chilomeniscus*, *Chionactis*) are small arenophilic snakes that live in loose, sandy substrates and frequently locomote in the undersand environment. A wedge-shaped head and a lower jaw that is countersunk against the upper jaw facilitate moving in sandy substrates, and these same traits occur independently in many other squamate reptiles living in sandy regions of the Earth [37,38]. Australian death adders (*Acanthophis*) are stout-bodied sit-and-wait predators with cryptic coloration, large triangular heads and slender necks. Methods of prey capture and their morphological correlates in death adders resemble those observed in several viperid species and facilitate rapid prey strike behaviour and ingestion of large prey [39–41].

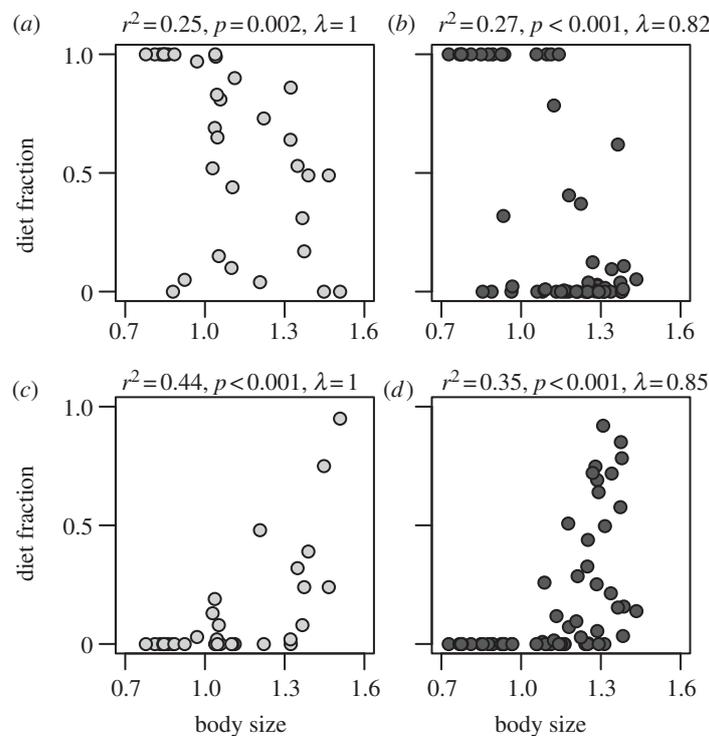
The presence of such widespread phenotypic convergence in the absence of any strongly supported shifts in the rate of phenotypic evolution is notable. Simulated trait data from the multi-rate Brownian motion process have larger variance than observed trait data. By contrast, variance of simulated trait data from the multi-optima OU process of trait evolution is comparable to observed trait data. This indicates that the observed convergence and divergence of species in morphospace are characterized better by shifts in phenotypic modality than by shifts in the rate of phenotypic evolution. This is also consistent with the observation that many of the observed phenotypes have functional consequences in terms of locomotion, foraging or prey handling. Because of their functional consequences, we expect such traits to experience greater constraint, and a model of unconstrained rate variation will fail to capture observed patterns of convergence and divergence. It is also possible that clades do differ in their phenotypic evolution rate dynamics but that our test for detecting such differences lacked power because it operated on only a single trait at a time.

### (b) Ecological divergence

Each major clade of colubroid snakes in North America contains species that will occasionally consume invertebrates, but specialized invertebrate predators are limited to the Colubridae, Natricidae and Dipsadidae. Natricid invertebrate predators generally feed on earthworms, molluscs and occasionally crustaceans [42,43]. Similar feeding modes are



**Figure 5.** Diet connectivity graph for Australian elapids (light grey) and North American colubroids (dark grey). Each small point represents a species, and species are connected to one or more primary diet categories (white). Thickness of connecting lines denotes relative importance of dietary variables for each species. Australian species overwhelmingly consume other squamate reptiles (Sqm), and few if any species specialize on invertebrates (Inv) or fish (Fsh), both of which are widely consumed by North American snakes. Collectively, the dietary breadth of North American snakes is far greater than that of Australian elapids. Other diet categories: Amp, amphibians; SqE, squamate eggs; Brd, birds; BrE, bird eggs; Mam, mammals.



**Figure 6.** Allometric patterns in the diet of Australian elapids and North American colubroids. Proportions of prey types on the  $y$ -axis are plotted against the logarithm of body size on the  $x$ -axis. Major divergences in diet between Australian elapids (light grey) and North American colubroids (dark grey) are associated with body size. Squamate reptiles form the dominant dietary component of small elapid snakes in Australia (a). By contrast, invertebrates replace squamates as the dominant component in the diets of small North American colubroids (b). Mammals are represented predominantly in the diets of larger snakes in both faunas (c,d). Data were fitted using PGLS with Pagel's correlation structure. Graph legends indicate the prey type, maximum-likelihood estimate of Pagel's  $\lambda$ , model  $r^2$  and  $p$ -value.

present in some natricids living in Asia [44,45]. Dipsadid lineages typically occupy more mesic habitats and invertebrate predators prey mainly on earthworms and molluscs [8]. By contrast, invertivorous colubrid lineages are found in more arid habitats where they eat mainly arthropod prey [46] (P. A. Holm 2008, unpublished PhD dissertation). Among elapids, we are aware of only a single genus that specializes on invertebrates: the earthworm-eating snakes of the genus *Toxicocalamus* endemic to New Guinea. Australia's elapids derive from a single colonization of the landmass by a Melanesian ancestor, and no extant Melanesian elapids other than *Toxicocalamus* feed heavily on invertebrates. Given the rarity of invertivory among elapids, it is reasonable to suppose that invertebrates were an unimportant component in the diet of the ancestral Australian elapid. Why invertivory did not later evolve, especially considering the great morphological diversity that arose subsequently, is puzzling. This is especially interesting because in arid Australia numerous mammals and non-elapid squamates are invertivorous, and the abundance of invertebrate prey has been proposed as an explanation for the exceptional species richness of Australian squamate communities [47,48].

Allometric patterns in the feeding ecology of snakes are widespread and are not particularly surprising [49]. What is notable, however, is that the component prey types contributing to the allometry of snake diets are quite distinct between the elapid snake fauna of Australia and the colubroid radiations of North America. Among North American colubroids a major allometric pattern in snake feeding ecology is an increasing proportion of invertebrates in the diets of small-bodied snake species. This is driven by the North American radiations of non-lampropeltine (lampropeltines include the ratsnakes, kingsnakes and pinesnakes) colubroids. Similarly, strong allometric patterns are documented in the diet of Australian elapids, except that squamate reptiles replace invertebrates as the prey of small-bodied snake species [50]. The preponderance of squamate reptiles, particularly scincid lizards, in the diets of Australian elapids may be due to the impressive diversity and abundance of that prey in Australia [20,51]. Selection to eat or avoid one prey type will have consequences for how a snake responds to other prey types because of genetic correlations in feeding behaviour [52]. If the ancestor of Australia's elapids had a diet similar to many extant species, perhaps because of selection to feed on abundant squamate prey, we may not observe invertivorous snakes in Australia today because evolutionary transitions from a diet of squamates to a diet of invertebrates are rare, even when invertebrate prey is abundant, due to negative genetic correlations in feeding responses to these two prey types. In other geographical regions, however, some snake species feed heavily on both invertebrate and squamate prey and exhibit equally strong feeding responses to each prey type [53]. Additionally, several of North

America's invertivorous snake clades are closely related to clades that feed heavily on squamate prey, suggesting that feeding shifts between these prey types may occur. Snakes are strongly gape-limited predators and an alternative explanation is that Australia's squamate prey communities contain a diversity and abundance of small prey species, which has permitted the evolution of small-bodied snake predators without requiring a shift in feeding strategy to accommodate the smaller gape imposed by a reduction in body size. Previous work also indicates that North American colubroids are unusual in their degree of invertivory, and a complementary question to why invertivory is rare among Australian elapids is why invertivory is so common among North American colubroids [51].

Finally, it is notable that many of the phenotypic and ecological modalities that are rare or absent among Australian elapids, including arboreal and semi-aquatic forms, do occur among the small number of non-elapid colubroid snakes inhabiting the more mesic environments of Australia's northern and eastern coasts. At least 10 such lineages colonized Australia, comprising arboreal (e.g. Colubridae: *Dendrelaphis punctulatus*), freshwater semi-aquatic (e.g. Natricidae: *Tropidonophis mairii*) and invertivorous (e.g. Homalopsidae: *Fordonia leucobalia*) forms. None of these species, however, is endemic to Australia and fossil evidence suggests that their arrival occurred well after the core radiation of Australian elapids [54].

## 5. Conclusion

We demonstrated that a single lineage of colubroid snakes from Australia—the terrestrial oxyuranine elapids—has converged on a range of distinctive morphologies that are found in a much more phylogenetically disparate snake fauna from North America comprising multiple distinct evolutionary radiations. However, the snake faunas of these regions are highly differentiated in diet, and the observed morphological patterns appear largely to reflect convergence in habitat and foraging mode. These results are consistent with recent work on squamate reptiles demonstrating relatively high lability of morphological traits [2,55–57], yet highly conserved patterns of trophic niche divergence [58–60]. More generally, our results indicate that interregional convergence in morphology cannot be assumed to reflect a general signal of ecological convergence.

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## References

- Harvey PH, Pagel MD. 1991 *The comparative method in evolutionary biology*. Oxford, UK: Oxford University Press.
- Losos JB, Jackman TR, Larson A, de Queiroz K, Rodríguez-Schettino L. 1998 Contingency and determinism in replicated adaptive radiations of island lizards. *Science* **279**, 2115–2118. (doi:10.1126/science.279.5359.2115)
- Gillespie R. 2004 Community assembly through adaptive radiation in Hawaiian spiders. *Science* **303**, 356–359. (doi:10.1126/science.1091875)
- Melville J, Harmon LJ, Losos JB. 2006 Intercontinental convergence of ecology and morphology in desert lizards. *Proc. R. Soc.*

- Soc. B* **273**, 557–563. (doi:10.1098/rspb.2005.3328)
5. Mahler DL, Ingram T, Revell LJ, Losos JB. 2013 Exceptional convergence on the macroevolutionary landscape in island lizard radiations. *Science* **341**, 292–295. (doi:10.1126/science.1232392)
  6. Ricklefs RE, Travis J. 1980 A morphological approach to the study of avian community organization. *The Auk* **97**, 321–338.
  7. Pianka ER. 1986 *Ecology and natural history of desert lizards*. Princeton, NJ: Princeton University Press.
  8. Cadle JE, Greene HW. 1993 Phylogenetic patterns, biogeography, and the ecological structure of Neotropical snake assemblages. In *Species diversity in ecological communities: regional and historical perspectives* (eds RE Ricklefs, D Schluter), pp. 281–293. Chicago, IL: University of Chicago Press.
  9. Stayton CT. 2006 Testing hypotheses of convergence with multivariate data: morphological and functional convergence among herbivorous lizards. *Evolution* **60**, 824–841. (doi:10.1111/j.0014-3820.2006.tb01160.x)
  10. Mares MA. 1993 Desert rodents, seed consumption, and convergence. *Bioscience* **43**, 372–379. (doi:10.2307/1312045)
  11. Langerhans RB, DeWitt TJ. 2004 Shared and unique features of evolutionary diversification. *Am. Nat.* **164**, 335–349. (doi:10.1086/422857)
  12. Harmon LJ, Kolbe JJ, Cheverud JM, Losos JB. 2005 Convergence and the multidimensional niche. *Evolution* **59**, 409–421. (doi:10.1111/j.0014-3820.2005.tb00999.x)
  13. Uetz P (ed.) 2014 *The reptile database*. See <http://www.reptile-database.org> (accessed 2 February 2014).
  14. Greene HW. 1997 *Snakes: the evolution of mystery in nature*. Berkeley, CA: University of California Press.
  15. Pyron RA, Burbrink FT. 2014 Early origin of viviparity and multiple reversions to oviparity in squamate reptiles. *Ecol. Lett.* **17**, 13–21. (doi:10.1111/ele.12168)
  16. Ernst CH, Ernst EM. 2003 *Snakes of the United States and Canada*. Washington, DC: Smithsonian Books.
  17. Pyron RA, Burbrink FT, Wiens JJ. 2013 A phylogeny and revised classification of Squamata, including 4161 species of lizards and snakes. *BMC Evol. Biol.* **13**, 93–146. (doi:10.1186/1471-2148-13-93)
  18. Tuberville TD, Willson JD, Dorcas ME, Gibbons JW. 2005 Herpetofaunal species richness of southeastern national parks. *Southeast. Nat.* **4**, 537–569. (doi:10.1656/1528-7092(2005)004[0537:HSROSN]2.0.CO;2)
  19. Sanders KL, Lee MSY, Leys R, Foster R, Keogh JS. 2008 Molecular phylogeny and divergence dates for Australasian elapids and sea snakes (hydrophiinae): evidence from seven genes for rapid evolutionary radiations. *J. Evol. Biol.* **21**, 682–695. (doi:10.1111/j.1420-9101.2008.01525.x)
  20. Shine R. 1994 *Australian snakes: a natural history*. Ithaca, NY: Cornell University Press.
  21. Shine R. 1980 Ecology of the Australian death adder *Acanthophis antarcticus* (Elapidae): evidence for convergence with the Viperidae. *Herpetologica* **36**, 281–289.
  22. Shine R. 1980 Ecology of eastern Australian whipsnakes of the genus *Demansia*. *J. Herpetol.* **14**, 381–389. (doi:10.2307/1563694)
  23. Shine R. 1989 Constraints, allometry, and adaptation: food habits and reproductive biology of Australian brownsnakes (*Pseudonaja*: Elapidae). *Herpetologica* **45**, 195–207.
  24. How RA, Shine R. 1999 Ecological traits and conservation biology of five fossorial 'sand-swimming' snake species (*Simoselaps*: Elapidae) in south-western Australia. *J. Zool.* **249**, 269–282. (doi:10.1111/j.1469-7998.1999.tb00764.x)
  25. Mosimann JE. 1970 Size allometry: size and shape variables with characterizations of the lognormal and generalized gamma distributions. *J. Am. Stat. Assoc.* **65**, 930–945. (doi:10.1080/01621459.1970.10481136)
  26. Rabosky DL, Santini F, Eastman J, Smith SA, Sidlauskas B, Chang J, Alfaro ME. 2013 Rates of speciation and morphological evolution are correlated across the largest vertebrate radiation. *Nat. Commun.* **4**, 1–8. (doi:10.1038/ncomms2958)
  27. Rabosky DL. 2014 Automatic detection of key innovations, rate shifts, and diversity-dependence on phylogenetic trees. *PLoS ONE* **9**, e89543. (doi:10.1371/journal.pone.0089543)
  28. Rabosky DL, Donnellan S, Grundler M, Lovette I. 2014 Analysis and visualization of complex macroevolutionary dynamics: an example from Australian scincid lizards. *Syst. Biol.* (doi:10.1093/sysbio/syu025)
  29. Ingram T, Mahler DL. 2013 SURFACE: detecting convergent evolution from comparative data by fitting Ornstein–Uhlenbeck models with stepwise Akaike Information Criterion. *Methods Ecol. Evol.* **4**, 416–425. (doi:10.1111/2041-210X.12034)
  30. Alfaro MA, Santini F, Brock C, Alamillo H, Dornburg A, Rabosky DL, Carnevale G, Harmon LJ. 2009 Nine exceptional radiations plus high turnover explain species diversity in jawed vertebrates. *Proc. Natl Acad. Sci. USA* **106**, 13 410–13 414. (doi:10.1073/pnas.0811087106)
  31. King AA, Butler MA. 2009 *Ornstein–Uhlenbeck models for phylogenetic comparative hypotheses (R package)*.
  32. Pagel M. 1999 Inferring the historical patterns of biological evolution. *Nature* **401**, 877–884. (doi:10.1038/44766)
  33. Blomberg SP, Garland T, Ives AR. 2003 Testing for phylogenetic signal in comparative data: behavioral traits are more labile. *Evolution* **57**, 717–745. (doi:10.1111/j.0014-3820.2003.tb00285.x)
  34. R Core Team. 2013 *R: a language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing.
  35. Orme D, Freckleton R, Thomas G, Petzoldt T, Fritz S, Isaac N, Pearse W. 2013 *caper: comparative analyses of phylogenetics and evolution in R. R package version 0.5.2*.
  36. Losos JB. 2010 Adaptive radiation, ecological opportunity, and evolutionary determinism. *Am. Nat.* **175**, 623–639. (doi:10.1086/652433)
  37. Mosauer W. 1932 Adaptive convergence in the sand reptiles of the Sahara and of California: a study in structure and behavior. *Copeia* **1932**, 72–78. (doi:10.2307/1435888)
  38. Maladen RD, Ding Y, Li C, Goldman DI. 2009 Undulatory swimming in sand: subsurface locomotion of the sandfish lizard. *Science* **325**, 314–318. (doi:10.1126/science.1172490)
  39. Pough FH, Groves JD. 1983 Specializations of the body form and food habits of snakes. *Am. Zool.* **23**, 443–454. (doi:10.1093/icb/23.2.443)
  40. Deufel A, Cundall D. 2006 Functional plasticity of the venom delivery system in snakes with a focus on the poststrike prey release behavior. *Zool. Anzeiger* **245**, 249–267. (doi:10.1016/j.jcz.2006.07.002)
  41. Young BA. 2010 How a heavy-bodied snake strikes quickly: high-power axial musculature in the puff adder (*Bitis arietans*). *J. Exp. Zool. A Ecol. Genet. Physiol.* **313A**, 114–121. (doi:10.1002/jez.579)
  42. Rossman DA, Ford NB, Seigel RA. 1996 *The garter snakes: evolution and ecology*. Norman, OK: University of Oklahoma Press.
  43. Gibbons JW, Dorcas ME. 2004 *North American watersnakes: a natural history*. Norman, OK: University of Oklahoma Press.
  44. Wall F. 1907 Notes on snakes collected in Fyzabad. *J. Bombay Nat. Hist. Soc.* **18**, 101–129.
  45. Smith MA. 1943 *The Fauna of British India: Reptilia and Amphibia III: Serpentes*. London, UK: Taylor and Francis.
  46. Stafford PJ. 2005 Diet and reproductive ecology of the Yucatán cricket-eating snake *Symphimus mayae* (Colubridae). *J. Zool.* **265**, 301–310. (doi:10.1017/S0952836904006338)
  47. Morton SR. 1985 Granivory in arid regions: comparison of Australia with North and South America. *Ecology* **66**, 1859–1866. (doi:10.2307/2937381)
  48. Morton SR, James CD. 1988 The diversity and abundance of lizards in arid Australia: a new hypothesis. *Am. Nat.* **132**, 237–256. (doi:10.1086/284847)
  49. Arnold SJ. 1993 Foraging theory and prey-size–predator-size relations in snakes. In *Snakes: ecology and behavior* (eds RA Seigel, JT Collins), pp. 87–115. New York, NY: McGraw-Hill.
  50. Shine R. 1994 Allometric patterns in the ecology of Australian snakes. *Copeia* **1994**, 851–867. (doi:10.2307/1446709)
  51. Shine R. 1977 Habitats, diets, and sympatry in snakes: a study from Australia. *Can. J. Zool.* **55**, 1118–1128. (doi:10.1139/z77-144)
  52. Arnold SJ. 1981 Behavioral variation in natural populations. I. Phenotypic, genetic and environmental correlations between chemoreceptive responses to prey in the garter snake, *Thamnophis elegans*. *Evolution* **35**, 489–509. (doi:10.2307/2408197)
  53. Cooper WE, Burghardt GM, Brown WS. 2000 Behavioural responses by hatchling racers (*Coluber constrictor*) from geographically distinct populations to chemical stimuli from potential prey and

- predators. *Amphibia-Reptilia* **21**, 103–115. (doi:10.1163/156853800507318)
54. Greer AE. 1997 *The biology and evolution of Australian snakes*. Chipping Norton, UK: Surrey Beatty and Sons.
55. Vitt LS, Caldwell JP, Zani PA, Titus TA. 1997 The role of habitat shift in the evolution of lizard morphology: evidence from tropical *Tropidurus*. *Proc. Natl Acad. Sci. USA* **94**, 3828–3832. (doi:10.1073/pnas.94.8.3828)
56. Herrel A, Huyghe K, Vanhooydonck B, Backeljau T, Breugelmans K, Grbac I, Van Damme V, Irschick DJ. 2008 Rapid large-scale evolutionary divergence in morphology and performance associated with exploitation of a different dietary resource. *Proc. Natl Acad. Sci. USA* **105**, 4792–4795. (doi:10.1073/pnas.0711998105)
57. Aubret F, Shine R. 2009 Genetic assimilation and the postcolonization erosion of phenotypic plasticity in island tiger snakes. *Curr. Biol.* **19**, 1932–1936. (doi:10.1016/j.cub.2009.09.061)
58. Vitt LJ, Pianka ER. 2005 Deep history impacts present-day ecology and biodiversity. *Proc. Natl Acad. Sci. USA* **102**, 7877–7881. (doi:10.1073/pnas.0501104102)
59. Colston TJ, Costa GC, Vitt LJ. 2010 Snake diets and the deep history hypothesis. *Biol. J. Linn. Soc.* **101**, 476–486. (doi:10.1111/j.1095-8312.2010.01502.x)
60. Rabosky DL, Cowan MA, Talaba AL, Lovette IJ. 2011 Species interactions mediate phylogenetic community structure in a hyperdiverse lizard assemblage from arid Australia. *Am. Nat.* **178**, 579–595. (doi:10.1086/662162)