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Repeated dietary shifts in elapid snakes (Squamata: Elapidae) revealed by ancestral state reconstruction

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Identifying the traits of ancestral organisms can reveal patterns and drivers of organismal diversification. Unfortunately, reconstructing complex multistate traits (such as diet) remains challenging. Adopting a 'reconstruct, then aggregate' approach in a maximum likelihood framework, we reconstructed ancestral diets for 298 species of elapid snakes. We tested whether different prey types were correlated with one another, tested for one-way contingency between prey type pairs, and examined the relationship between snake body size and dietary composition. We demonstrate that the evolution of diet was characterized by niche conservation punctuated by repeated dietary shifts. The ancestor of elapids most likely fed on reptiles and possibly amphibians, with deviations from this ancestral diet occurring repeatedly due to shifts into marine environments and changes in body size. Moreover, we demonstrate important patterns of prey use, including one-way dependency—most obviously the inclusion of eggs being dependent on a diet that already included the producers of those eggs. Despite imperfect dietary data, our approach produced a robust overview of dietary evolution. Given the paucity of natural history information for many organisms, our approach has the potential to increase the number of lineages to which ancestral state reconstructions of multistate traits can be robustly applied.

ADDITIONAL KEYWORDS: ancestral state reconstruction – diet evolution – ecological niche evolution – Elapidae – maximum likelihood models – natural history analysis – trophic ecology.

INTRODUCTION

Insights into the phenotypic and ecological traits of ancestral organisms can elucidate patterns and drivers of modern organismal diversification (Kraft *et al.*, 2007; Ricklefs *et al.*, 2007; Colston *et al.*, 2010). The reconstruction of ancestral phenotypic and ecological traits through ancestral state reconstruction has thus become a widely utilized tool to infer these otherwise unobservable traits (Cunningham *et al.*, 1998; Pagel, 1999; Pagel *et al.*, 2004; Gomes *et al.*, 2011; Jondelius *et al.*, 2011; Kim *et al.*, 2011; King & Lee, 2015; Joy *et al.*, 2016; Strickland *et al.*, 2016). However, the accuracy of reconstructions can vary, with model performance influenced by features of the phylogeny, the choice of mathematical model, and properties of the traits being reconstructed (Litsios & Salamin, 2012; Duchêne & Lanfear, 2015). In particular, the reconstruction of complex, multistate ecological traits has remained problematic (Grundler & Rabosky, 2020), hindering our ability to reliably reconstruct their evolutionary history.

Complex ecological and phenotypic traits cannot always be adequately summarized as simple continuous or discrete variables for use in ancestral state reconstructions. In order to reconstruct the ancestry of such traits, each species in the phylogeny is typically allocated to one of several discrete trait clusters which are then treated in the analysis as discrete traits (Mitchell *et al.*, 2014; Rainford & Mayhew, 2015; Kim *et al.*, 2016; Goodheart *et al.*, 2017). Ancestral reconstruction of organismal diet offers an example of this, and studies that have sought

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to reconstruct ancestral diets have usually done so through an 'aggregate, then reconstruct' approach by assigning each taxon to a designated dietary cluster based on an aggregation of the different food resources used, with those clusters then being reconstructed over the phylogeny (Leschen & Buckley, 2007; Portillo *et al.*, 2019; Naik *et al.*, 2021).

The diet of an organism is best described as the relative frequency at which different food types are consumed. However, the distal shift from one dietary state to another is the likely the result of a more proximal process that results from selection for or against the inclusion or exclusion of a particular prey type in an animal's diet through time. Moreover, the selective pressures for the inclusion or exclusion of different prey types in the diet of an organism might differ among prey. Unfortunately, the 'aggregate, then reconstruct' approach to multistate reconstruction fails to account for this complexity. Additionally, dietary clusters can overlap in an aspect of resource utilization or be nested within one another (e.g. Portillo *et al.*, 2019) meaning that imperfect natural history data can result in species being assigned incorrectly to dietary clusters, rather than simply impacting the apparent dynamics of a single prey type. Lastly, the dietary clusters being reconstructed need to reflect sufficient phylogenetic signal to be informative (Litsios & Salamin, 2012), which might not always be the case if diets are defined *a priori*. These attributes make it difficult to aggregate multistate traits into meaningful clusters that can be interrogated with traditional comparative techniques.

In this paper, we use and recommend a simple and flexible alternative approach to reconstructing multistate traits. We propose that the appropriate way to reconstruct multistate traits is to partition resource utilization information into its component resources, reconstruct those individual resource types across a phylogeny (using one of several established, optimizable modelling approaches including parsimony, maximum likelihood or Bayesian inference; Joy *et al.*, 2016), and then aggregate the resultant model outputs at each internal node of the phylogeny. By fitting separate models for each prey type, our approach allows for (1) heterogeneity in the transition rates for each prey type rather than transitions between aggregated diets, (2) the use of different modelling frameworks and (3) the use of different response variables (count data vs. ordinal data vs. presence-absence data) as dictated by the overall quality of the available natural history data.

To demonstrate the utility of our 'reconstruct, then aggregate' approach, we reconstructed the ancestral diets of elapid snakes. In snakes, diet is known to impact phenotype (Martins *et al.*, 2002; Heinicke *et al.*, 2020; Rajabizadeh *et al.*, 2021), habitat use (Plummer, 1981), reproductive strategy (Forsman, 1991), sexual dimorphism (Shine, 1991), venom biochemistry (Daltry *et al.*, 1996), and ultimately, the abundance and distribution of species (Slip & Shine, 1988). Thus, interpretation of the phylogenetic natural history (Colston *et al.*, 2010) of snake diet can provide important context to understanding snake diversity.

The family Elapidae (Reptilia: Squamata) comprises ~380 species of ecologically and morphologically diverse snakes (Greene, 1997; Uetz *et al.*, 2020). The clade has a large global geographic distribution characterised by (1) an Asian origin and rapid diversification during the Oligocene, (2) colonization of the Americas and subsequent diversification by New World coral snakes, (3) repeated faunal exchanges between Africa and Asia, (4) colonization of Australia and subsequent spectacular diversification and (5) two independent transitions to marine lifestyles [see Kelly *et al.* (2009) for biogeographic review]. Elapids range in body size by more than an order of magnitude, from diminutive species with a maximum recorded total length ~300 mm to black mambas (*Dendroaspis polylepis*), coastal typans (*Oxyuranus scutellatus*) and king cobras (*Ophiophagus hannah*) that each regularly exceed 3 m in length (Lee *et al.*, 2016; Maritz *et al.*, 2016). Moreover, elapid snakes consume a remarkable diversity of prey (Greene, 1997). Taken together, these attributes make elapid snakes an ideal study system in which to explore the evolution of diet.

We performed maximum likelihood ancestral state reconstructions for the presence or absence of individual prey types across a phylogeny of 298 elapid species. We used this approach to infer which components of current-day diets were included in the diets of ancestral elapid snakes at key evolutionary and biogeographically notable nodes in the phylogeny. We also examined patterns of correlation between the different prey types across the phylogeny. Among these patterns, we were particularly interested in the hypothesis that the inclusion of bird eggs and squamate reptile eggs followed phylogenetically from the consumption of birds and squamate reptiles, respectively (de Queiroz & Rodriguez-Robles, 2006). We therefore tested the hypotheses that the consumption of bird eggs, reptile eggs and fish eggs is preceded evolutionarily by a diet that already includes birds, reptiles and fish, respectively. Finally, clades of prey potentially share gross morphological attributes that influence ease of ingestion by snakes, thereby influencing the likelihood of that prey type being incorporated into the diet of snakes of different sizes. We therefore tested for differences in average maximum body length between snake species that do or do not consume each prey type.

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MATERIAL AND METHODS

Dietary and phylogenetic data

We gathered data on the diet of elapid snakes from peer-reviewed journals, books, field guides and online resources (Supporting Information, Data S1) for 298 species (~76 %) of extant elapids (Uetz *et al.*, 2020). For each species, we recorded the presence of the consumption of amphibians, mammals, birds, bird eggs, reptiles, reptile eggs, fish, fish eggs, terrestrial invertebrates and marine invertebrates. We recognize that aggregating diet into these prey types and reducing them down to presence-absence measures results in the loss of important information about dietary variation but do so here because detailed reports of prey in the diets of elapids are limited. For example, in Africa, studies providing detailed dietary information for elapid snakes are limited to a small number of well-studied species (Branch *et al.*, 1995; Pauwels & Ohler, 1999; Luiselli & Angelici, 2000; Shine *et al.*, 2007; Maritz *et al.*, 2019) and even these are often not comprehensive (see Layloo *et al.*, 2017). Thus, we frequently had to rely on relatively broad descriptions of diet, such as those found in field guides. However simplified, our approach allowed us to access a wider scope of literature, and trade-off dietary resolution against phylogenetic coverage to better reveal broad patterns of diet evolution. Fortunately, the approach we adopt can be refined as dietary data with increased taxonomic resolution become available. As a demonstration of this flexibility, we additionally partitioned reptile prey type into separate lizard and snake prey sub-types and examined how the consumption of these co-varied.

Because of its coverage, we based our phylogeny on the maximum credibility tree for elapids published by Tonini *et al.* (2016). However, we made several edits to the overall topology of the tree [following Lee *et al.* (2016), Figueroa *et al.* (2016) and Maryan *et al.* (2020)] to account for obviously anomalous relationships (see Supporting Information, Data S2.1). After removing species for which we did not have diet data from the phylogeny, our tree (Supporting Information, Data S3) was restricted to 298 species. We achieved excellent coverage, including representation of 50/53 genera, with full genus coverage (all known species represented) for 32 genera, and the remaining 18 genera being represented by between 50% and 91% of their constituent species (Supporting Information, Data S2.2).

Statistical analyses

Statistical analysis and graphing was conducted in R v.4.0.3 (R Core Team, 2020) using the following packages: *ape* v.5.5 (Paradis & Schliep, 2019), *caper* v.1.0.1 (Orme *et al.*, 2018), *coda* v.0.19.4 (Plummer *et al.*, 2006), *ggtree* v.3.1.2 (Yu *et al.*, 2017) and *phytools* v.0.7.70 (Revell, 2012). We confirmed the presence of phylogenetic signal in the data for each of our prey types by calculating D (Fritz & Purvis, 2010). We considered any value of D that was significantly less than 1 (where $D = 1$ represents random dispersion of traits across the phylogeny) to indicate that a given prey type showed phylogenetic signal. Next, taking a maximum likelihood approach, we reconstructed the likely presence or absence of each prey type at each internal node of our phylogeny using the 'ace' function in the package 'ape'. We chose a maximum likelihood approach over alternative analytical approaches (Joy *et al.*, 2016) because of its ease of implementation and because it is the only method available within 'ape' for discrete data such as ours (Paradis & Schliep, 2019). As is standard practice, for each prey type we ran two models: an equal rates model (Mk1) in which the forward and reverse transition rates between presence and absence of the prey type in the tree were constrained to be equal, and an all rates different model (Mk2) in which the forward and reverse rates were allowed to differ from each other. However, like King & Lee (2015), we found that our Mk2 models produced highly inaccurate reconstructions and we thus chose to only report equal rates model results (see Supporting Information, Data S2.3). In all cases, the joint likelihood for each tree was estimated. For each prey type, we estimated the scaled likelihood of the presence of that prey type at each internal node.

Next, we aggregated the model outputs for all prey types at each node and visually inspected nodes that represent either important biogeographic transitions, ancestors of notable radiations or important shifts in snake body size. Specifically, we inspected the reconstructed diets at the following nodes: the most recent common ancestor (MRCA) of elapid snakes (Node B); the MRCA of New World coral snakes (Node D) and their Old World closest relatives (Node C); the MRCA of the Afro-Asian 'cobra/mamba' clade of large-bodied elapids which includes the cobras (*Naja*), mambas (*Dendroaspis*) and the king cobra (*Ophiophagus*) (Node E), the MRCA of *Dendroapsis* and *Ophiophagus* (Node F), and the MRCA of true cobras (*Naja;* Node G); the MRCA of sea kraits (*Laticauda*; Node H) and the MRCA of true sea snakes (Node J); the MRCA of the spectacular Australasian radiation (Node I); and finally the MRCA of the Australian radiation (Node K) that combines the diminutive *Suta* group (Node L) and the diminutive *Simoselaps* group (Node M) (Fig. 1A).

Next, we examined the degree to which dietary traits were phylogenetically correlated with each other. Specifically, we tested for correlated evolution of discrete binary traits in BayesTraits v.3.0.2 (Meade & Pagel, 2016) via the *R* package *btw* v.2 (Griffin, 2018).

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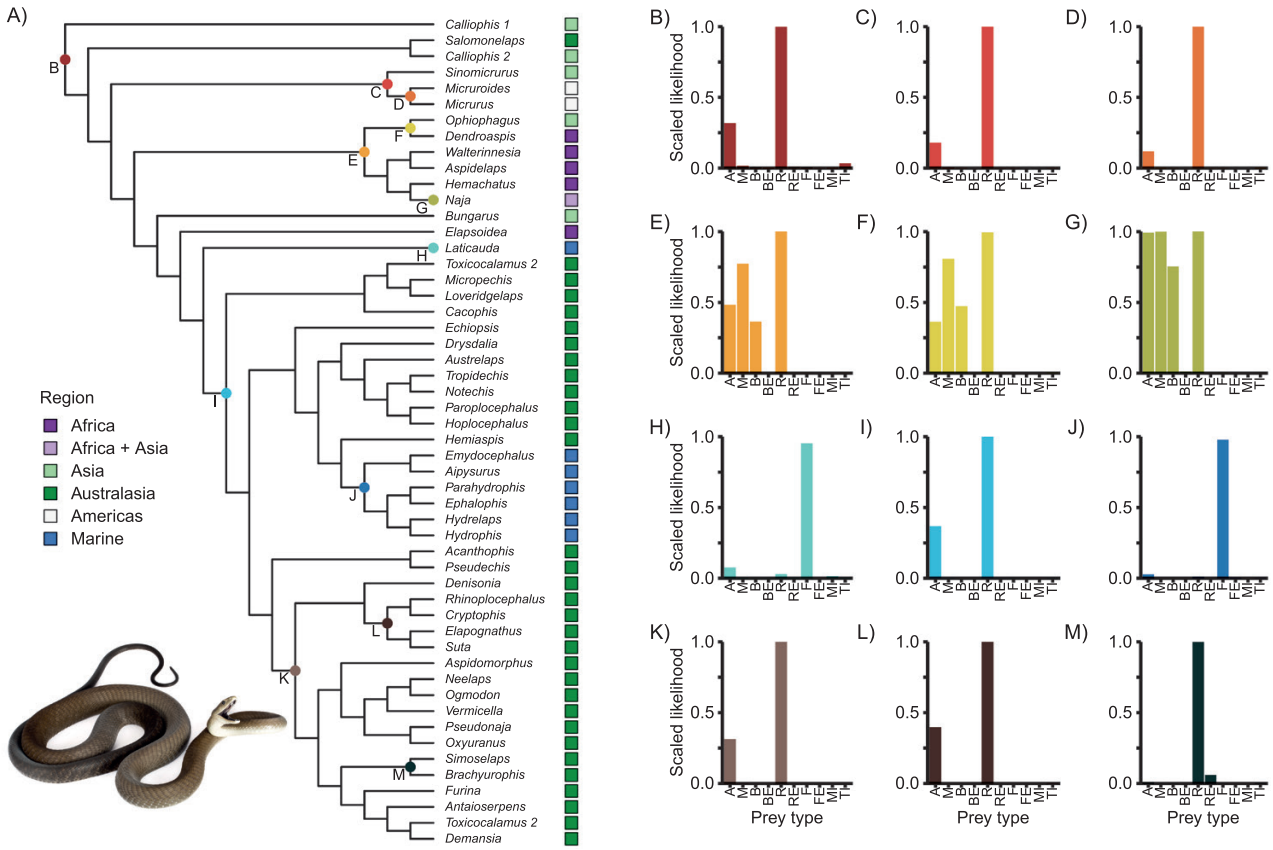

Figure 1. Genus-level phylogenetic tree (A) summarizing phylogenetic relationships between 298 species used in analyses. Bar graphs (B–M) show scaled likelihood of occurrence for different prey types (A = Amphibians; B = Birds; BE = Bird Eggs; R = Reptiles; RE = Reptile Eggs; F = Fish; FE = Fish Eggs; MI = Marine Invertebrates; TI = Terrestrial Invertebrates) in the diets at 12 nodes reflected on the tree (Node B: MRCA of elapids; Node C: MRCA of New World coral snakes and their Old World closest relatives; Node D: MRCA of New World coral snakes; Node E: MRCA of Afro-Asian cobra/mamba lineage; Node F: MRCA of king cobras and mambas; Node G: MRCA of true cobras (*Naja*); Node H: MRCA of sea kraits; Node I: MRCA of Australasian radiation; including Node J: MRCA of true seas snakes; Node K: MRCA of terrestrial Austalian clade; Node L: *Suta* group and Node M: *Simoselaps* group). Photograph: black mamba (*Dendroaspis polylepis*) by L. Verburgt and the African Snakebite Institute.

For these analyses, we ran at least two independent MCMC chains for both the independent and dependent continuous-time Markov models for 2×10^7 iterations and sampled every 1000 iterations after discarding an initial 500 000 iterations as burn-in. A reversible-jump MCMC with an exponential hyperprior (mean and variance seeded from uniform distribution from 0 to 100) was used to select priors for the analyses. Visual inspections of trace and density plots were conducted to ensure adequate mixing and convergence. Single-chain diagnostics (Geweke, Heidelberger–Welch and estimated effective sampling size) were used to assess chain stationarity, convergence and autocorrelation. A multi-chain diagnostic (Gelman–Rubin) was calculated for each set of chains to verify that inter-chain variation did not exceed intra-chain variation. For models that failed to converge, the generation time was extended to 40–100 million with a burn-in of 1–1.5 million. Only after failing under this extensive sampling were models considered to have failed to converge. Marginal likelihood was calculated using a steppingstone sampling (Xie *et al.*, 2011): 200 stones at 1000 iterations per stone. Average values for each model were used to calculate a BayesFactor score (lnBayesFactor) calculated as: 2 [(ln marginal likelihood [dependent model]) – (ln marginal likelihood [independent model])]. BayesFactor values of 2–5 were regarded as weak evidence for correlation, values of 5–10 as strong evidence for correlation and values greater than 10 as very strong evidence.

To test whether the consumption of bird eggs, reptile eggs and fish eggs were preceded by the consumption of birds, reptiles and fish, respectively, we examined the instantaneous rate transitions (q_{ij}) which are estimated

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from the aforementioned dependent continuous-time Markov models. Instantaneous rate transitions (q_{ij}) are the rate of change between character states of one trait (present or absent) given a character state of a second trait. Each estimated rate coefficient was averaged across all sampled iterations for each diet pair. Z-scores were calculated as the number of times a parameter was assigned to zero in all sampled models and divided by the number of samples for a given diet pair. Thus, a small Z-score indicates that the rate is infrequently equal to zero. We explicitly examined whether the transition to include the dependent prey type in the diet is more likely to occur in the (i) presence or (ii) absence of an independent prey type (i.e. q_{34} vs. q_{12}).

Finally, to contextualize our results, we examined the effect of body size on diet. For each prey type, we tested the hypothesis that average maximum body length does not differ between species that do or do not consume a given prey type. Body size data were gathered from the literature (Lee *et al.*, 2016; see Supporting Information, Data S1). We compared average log-transformed maximum body length [see Maritz *et al.* (2016) for justification of this measure of body size] of species that do, or do not consume a given prey type while correcting for the effects of phylogenetic autocorrelation by using the 'phylANOVA' function in *phytools*. We also examined the relationship between log-transformed maximum body length and log-transformed dietary breadth (calculated as the count of all consumed prey types) separately for terrestrial and marine species, while controlling for the effects of phylogeny. We achieved this by sub-setting our data and phylogenies into marine and non-marine elapid species and running a linear model using 'nlme' (Pinheiro *et al.*, 2016) allowing for Brownian phylogenetic structure.

RESULTS

Estimates of D averaged −0.088 (max D = 0.52; min D = −1.04). Importantly, all prey types exhibited significant phylogenetic signal (all D estimates significantly smaller than expected by random dispersion of traits across the phylogeny; Table 1) although to varying degrees. Average transition rate (i.e. the instantaneous probability of a shift in prey use) derived from these equal rates models for each prey type was 0.0086 although rates ranged from 0.0013 (fish eggs) to 0.0258 (amphibians) (Table 1). Plots of the reconstructions for each prey type are available in Supporting Information (Data S4).

Our 'reconstruct, then aggregate' approach produced evidence that the MRCA of all elapids consumed a diet that unambiguously included other reptiles, and possibly included amphibians (Fig. 1B). Additionally, this diet was conserved in early elapids, including in the MRCA of the New World coral snakes and their Old World relatives (Fig. 1C) and subsequently in the MRCA of New World coral snakes themselves (Fig. 1D). This reptile and (possibly) amphibian diet was additionally reconstructed at the nodes representing the MRCA of the speciose Australasian clade (Fig. 1I), and the nodes representing the origins of the diminutive Australian *Suta* and *Simoselaps* groups (Fig. 1K–M). The evolutionary conservation of diet was however punctuated with several diet shifts and expansions. For example, we found evidence for two independent shifts toward diets dominated by fish at the nodes representing the MRCA of sea-kraits (*Laticauda*; Fig. 1H) and the MRCA of true sea snakes (Fig. 1J). Moreover, we found evidence of an expansion of diet in the Afro-Asian 'cobra/mamba lineage' (Fig. 1E–G) that was conserved in modern cobras (*Naja*—generalist

Table 1. Phylogenetic signal estimates and associated statistical tests, and ancestral state reconstruction models for ten prey types included in the diet of elapid snakes. D is estimate of phylogenetic signal (Fritz & Purvis, 2010)

Prey type	D ($P_{D=0}$; $P_{D=1}$)	Phylogenetic signal	Transition rate (± SE)
Amphibians	0.09 (0.31; < 0.001)	Moderate	0.0258 ± 0.0034
Mammals	-0.37 (0.97; < 0.001)	Strong	0.0088 ± 0.0014
Birds	-0.06 (0.62; < 0.001)	Strong	0.0078 ± 0.0013
Bird eggs	-0.01 (0.51; < 0.001)	Moderate	0.0041 ± 0.0009
Reptiles	-0.50 (0.99; < 0.001)	Strong	0.0053 ± 0.0010
Snakes	-0.15 (0.80; < 0.001)	Strong	0.0145 ± 0.0020
Lizards	0.05 (0.39; < 0.001)	Moderate	0.0235 ± 0.0030
Reptile eggs	0.31 (0.08; < 0.001)	Moderate	0.0096 ± 0.0015
Fish	-0.27 (0.91; < 0.001)	Strong	0.0082 ± 0.0013
Fish eggs	-1.04 (0.98; < 0.001)	Strong	0.0013 ± 0.0005
Terrestrial invertebrates	0.52 (0.01; < 0.001)	Weak	0.0108 ± 0.0016
Marine invertebrates	0.37 (0.18; 0.001)	Moderate	0.0037 ± 0.0008

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diets), but differentially restricted in modern mambas (*Dendroaspis*—specialized endothermic prey diet) and modern king cobras (*Ophiophagus*—specialized reptile prey diet).

Because of their prevalence in the phylogeny, amphibians and reptiles were correlated with most other prey types (Fig. 2). Additionally, trait evolution was very strongly correlated (BayesFactor > 10) for several pairs of prey types. These included mammals and birds, mammals and bird eggs, birds and bird eggs, fish and fish eggs, fish and marine invertebrates, and fish eggs and marine invertebrates. Within the reptile prey type we found that the consumption of snakes and lizards were strongly correlated. Unfortunately, models representing several pairs of prey types failed to converge prohibiting further analysis (Fig. 2).

Examination of the instantaneous transition rate Q-matrices revealed that the transition to the consumption of bird eggs occurred more frequently in the presence bird consumption ($q_{34} = 1.6$) than in the absence of bird consumption ($q_{12} < 0.001$) (Fig. 3). This pattern was also evident for the transition to the consumption of reptile eggs relative to reptile consumption ($q_{34} = 0.0086$; $q_{12} = 0.001$), and the transition to the consumption of fish eggs relative to fish consumption ($q_{34} = 0.0086$; $q_{12} = 0$; Fig. 3). Across these contrasts, $q_{34} > q_{12}$ in 85%, 98% and 100% of models for the evolution of bird eggs, reptile eggs and fish eggs, respectively.

Phylogenetic ANOVA revealed that, on average, species that consumed mammals (F = 95.64, P = 0.002), birds (F = 63.13, P = 0.005), bird eggs (F = 39.03, P = 0.009) and amphibians (F = 29.47, P = 0.02) were all significantly larger-bodied than species that did not consume those respective prey types. Together, these results lead to a significant, positive relationship between body size and dietary breadth in terrestrial elapids (t = 4.72, P < 0.001), but not marine elapids (t = 0.87, P = 0.39) which cannot easily access these novel prey types, and for which finer taxonomic resolution of the fish prey type likely obscures a similar trend for different size and shape fish. The remaining diet types did not show statistically significant differences in average body size of the species that did or did not consume them (range: F = 0.55–28.59; P = 0.16–0.78; Fig. 4), nor did body size

	Amphibians	Mammals	Birds	Bird eggs	Reptiles	Snakes	Lizards	Reptile eggs	Fish	Fish eggs	Marine invert.
Mammals	47.8										
Birds	26.5	40.3									
Bird eggs	6.9	27.9	34.1								
Reptiles	16.7	5.8	5.6	4.8							
Snakes	16.4	< 2	< 2	< 2	47.2						
Lizards	16.4	19.6	-	5.2	81.4	24.9					
Reptile eggs	37.7	< 2	< 2	14.0	7.1	-	24.1				
Fish	-	< 2	< 2	< 2	< 2	6.6	23.9	< 2			
Fish eggs	-	< 2	2.4	-	14.0	-	-	< 2	16.7		
Marine invert.	8.4	2.9	< 2	-	11.3	-	-	-	18.8	23.7	
Terrestrial invert.	< 2	< 2	-	4.0	22.3	< 2	3.2	< 2	< 2	-	-

Figure 2. Log BayesFactor score matrix showing pairwise correlations between each prey type. Scores of > 2 represent weak evidence for correlated evolution, scores > 5 show strong support for correlated evolution and scores > 10 show very strong support for correlated evolution.

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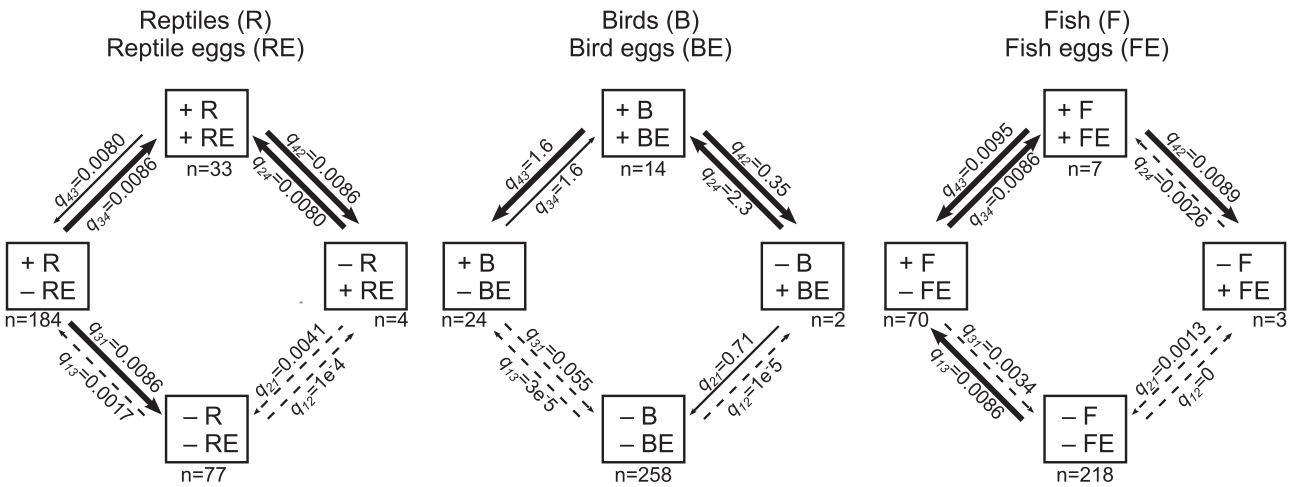

Figure 3. Transition rates (q) estimated from Reverse-Jump MCMC models of correlated evolution of discrete traits. Line thickness represents likelihood of transition (Z-scores: proportion of models sampled that assigned q to zero bin). Dashed lines: Z > 0.30; solid thin lines: Z < 0.30; solid thick lines: Z < 0.1.

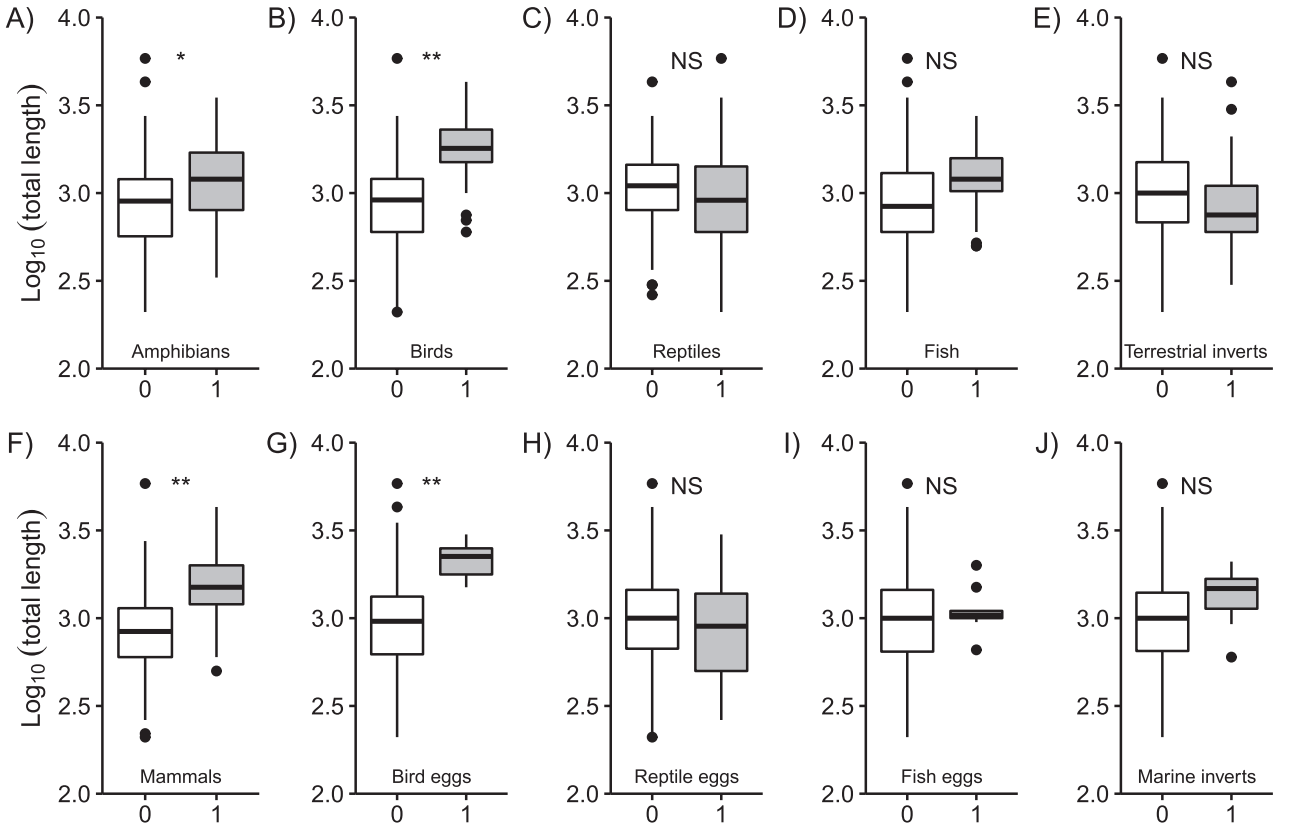

Figure 4. Phylogenetically-uncorrected bar plot contrast of log-transformed maximum total length for species that do not (0) or do (1) include a given prey type in their diet. Figures A–J refer to: (A) Amphibians; (B) Birds; (C) Reptiles; (D) Fish; (E) Terrestrial invertebrates; (F) Mammals; (G) Bird eggs; (H) Reptile eggs; (I) Fish eggs; (J) Marine invertebrates. Statistical comparisons are phylogenetic ANOVA results (NS = $P > 0.05$; *$P < 0.05$; **$P < 0.01$). Overall sample size $N = 298$; $N = 177$ consume amphibians; $N = 38$ consume birds; $N = 217$ consume reptiles; $N = 77$ consume fish; $N = 37$ consume terrestrial invertebrates; $N = 83$ consume mammals; $N = 16$ consume bird eggs; $N = 37$ consume reptile eggs; $N = 10$ consume fish eggs; $N = 12$ consume marine invertebrates.

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differ significantly between species that consumed or did not consume snakes ($F = 6.55$, $P = 0.59$) or lizards ($F = 0.55$, $P = 0.78$).

DISCUSSION

Our 'reconstruct, then aggregate' approach revealed that diet evolution in elapid snakes has been phylogenetically non-random and is characterized by niche conservation, with repeated context-specific shifts and expansions. The patterns that we identified are intuitively credible, adding confidence to our approach. We demonstrated that the ancestor of all elapid snakes likely consumed a diet consisting primarily of reptiles and possibly amphibians. Additionally, we demonstrated important generalized patterns of dietary shift and correlated evolution of prey types across the phylogenetic tree including (1) dietary expansion to include and sometimes specialize on endothermic prey for the larger-bodied lineages, (2) evolutionary predisposition for the consumption eggs of prey subsequent to the inclusion of those prey types in the diet and (3) shifts to fish-dominated diets following invasion of marine environments. Thus, we contend that our approach to ancestral reconstruction of diet provides a realistic and credible assessment of the evolution of diet in the Elapidae and recommend this approach for ancestral reconstruction of diet in other clades of snakes, as well as other multistate traits across the tree of life.

Our analyses reveal that species that consume mammals, birds, bird eggs or amphibians are significantly larger-bodied than those that do not consume those prey types. These results point to an important role for larger body size in the consumption of certain prey types. We propose that for a given cross-sectional diameter, elongate squamate reptiles are likely to offer greater digestible mass than other tetrapod prey (Close & Cundall, 2012; Wiseman *et al.*, 2019). Thus, endothermic prey shapes might be sub-optimal for smaller-bodied snakes, but are easily consumed by larger-bodied snakes, which, because of their size can potentially digest several prey items in quick succession. Thus, the challenge of consuming sub-optimal endothermic prey might explain the widespread consumption of comparatively slender reptiles across the clade. Subsequent deviation from a diet of reptiles has happened either when elapids invaded marine environments (in which case terrestrial prey types are dropped from the diet and replaced by fish and sometimes fish eggs or marine invertebrates), or when increased body size has facilitated the consumption of mammal and bird prey. This body size trend is not without exception, as our results reveal that two lineages of very large-bodied elapids, mambas (*Dendroaspis*) and king cobra (*Ophiophagus*), have shown subsequent dietary restriction since their divergence from the MRCA with true cobras (*Naja*) and one of these (*Ophiophagus*) now excludes mammals and birds from its diet (Jones *et al.*, 2020). Conversely, we found that the evolution of smaller body sizes in the *Suta* and *Simoselaps* groups (Lee *et al.*, 2016) resulted in phylogenetic conservation of the hypothesized reptile-dominated ancestral diet, possibly with the latter becoming so small so as to exclude amphibians.

By examining the presence of birds and their eggs, as well as squamates and their eggs in the diets of a number of snake lineages, de Queiroz & Rodriguez-Robles (2006) showed that a diet of eggs is more likely to arise in lineages that already consume the organisms responsible for producing those eggs. Our analyses provide support for the inclusion of bird eggs into the diet of lineages that are inferred to already include birds and show that species that consume birds or their eggs are typically larger-bodied than those that do not. We also find evidence for the inclusion of reptile eggs in the diets of lineages that already consume reptiles. Given the widespread consumption of reptiles across our phylogeny, this finding is expected. However, the absence of any difference in body size between species that do, or do not, consume reptile eggs lends support to the idea that reptile eggs (specifically squamate eggs) are functionally easier to ingest than bird eggs (de Queiroz & Rodriguez-Robles, 2006). Additionally, this finding suggests that the predisposition to consume reptile eggs may be linked to ecological opportunity or shared chemical stimuli rather than changes in body size. Unsurprisingly, we find support for the incorporation of fish eggs into the diets of snakes that arise in lineages that already consume fish—once in the ancestor of *Aipysurus*+*Emydocephalus*, and once in the ancestor of *Ephalophis greyae*.

The shift from a terrestrial to a marine environment drives several obvious changes in the diets of elapid snakes. In both marine lineages, diets shifted from being reptile-dominated to fish-dominated, providing the ecological opportunity to evolve a diet that includes fish eggs or marine invertebrates. The shift into marine habitats and the concomitant changes in sea snake diets has had dramatic impacts on the venoms of these animals (Fry *et al.*, 2003; Li *et al.*, 2005).

In order to maximize phylogenetic coverage, we chose to model the presence of broadly-defined taxonomic prey types. However, when appropriate data are available, analyses of prey usage should be conducted using (1) narrowly-defined taxonomic prey classification and (2) data that reflect the relative

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frequency with which different prey types are consumed. The impact of prey taxonomic aggregation is well-established in trophic ecology (Greene & Jaksić, 1983), and the use of finer resolution prey data can be instructive. For example, by partitioning our reptile prey type into separate lizard and snake prey types, we resolved important differences in the likely diets of the MRCAs of the New World coral snake radiation and the Australian radiation, with strong evidence for the consumption of snakes in the former but not the latter (Supporting Information, Data S4). In cases where high quality dietary data are available, our approach allows for diet responses to be modelled either as ordinal responses or even continuous count responses reflecting the relative frequency with which prey are utilized. The resulting analysis would, in such cases, offer a relatively simple to implement alternative to the approach of Grundler & Rabosky (2020) which assigns species to functional feeding clusters on the basis of their phylogenetic relatedness and similarities in their dietary records, explicitly accounting for their potential incompleteness, and reconstructs those clusters.

Assessing the ability of any ancestral state reconstruction to accurately reconstruct trait states, particularly in deep history, is challenging (Royer-Carenzi *et al.*, 2013; Gascuel & Steel, 2014; Joy *et al.*, 2016). The maximum likelihood models that we have used assume that (1) the underlying phylogeny is correct, and that (2) traits are evolving neutrally across that phylogeny (Holland *et al.*, 2020). By using a phylogeny that accurately reflects at least broad-scale relationships within the family, we trust that our analyses are reproducing broadly accurate dietary dynamics and that our findings will be robust to minor corrections in the relationships of species. Unfortunately, the assumption of neutrality is unlikely to be met, with several important evolutionary nodes likely being characterized by changes in selective regimes (Lee *et al.*, 2016). These rate changes are most likely why the attempted Mk2 models produced seemingly spurious results (Supporting Information, Data S2). However, by reconstructing prey types separately, non-neutral evolutionary dynamics (such as high transition rates) that are likely to reduce reconstruction accuracy (Holland *et al.*, 2020) can be restricted to inference around a single prey type, without impacting inference around the reconstruction of other prey types. Our analyses revealed that reconstruction of amphibian and lizard prey types showed very high transition rates. For amphibians, this high lability is potentially a result of the rapid digestion in the guts of snakes, making them more difficult to detect, and might explain the intermediate scaled likelihood of occurrence of amphibians in the diets of deep nodes in the tree. Alternatively, these prey types may genuinely exhibit high lability in elapid snake diets. Fortunately these do not impact the more robust reconstruction of reptile-dominated diets at those nodes.

Our results provide several opportunities for future investigation. For example, it is unclear to what degree taxonomic aggregation of prey types has over-simplified the true complexity of diet evolution, especially when aggregated prey groups incorporate animals with disparate body shapes (e.g. snakes vs. lizards; caecilians vs. anurans; eels vs. other fish). This question should be pursued within subclades for which precise taxonomic data already exist, or ideally across all elapids when taxonomically-precise data become available for most subclades. Ultimately, the issue of poor-quality snake dietary data will only be solved with improved study and publication of natural history observations. Fortunately, the study of snake diets (and the use of a wide range of techniques) is gaining renewed popularity (e.g. Brown *et al.*, 2014; Durso & Mullin, 2017; Lee *et al.*, 2018; Wiseman *et al.*, 2019; Maritz & Maritz, 2020; Pauwels & Brecko, 2020). In this context we foresee an overall improvement in the quality and detail of snake dietary information and a concomitant increase in our knowledge of the downstream effects of those diets, be they ecological functionality, organismal diversification, or snake venom evolution.

CONCLUSION

Our 'reconstruct, then aggregate' approach offers an intuitive and flexible approach to reconstructing complex multistate traits. We have chosen to illustrate its efficacy using the diets of elapid snakes and revealed dietary niche conservation punctuated with repeated dietary shifts associated with invasion of novel environments and changes in body size. However, our approach has far wider application in macroevolutionary studies, especially of traits for which information for the use of resource types is imperfect. Given the paucity of natural history knowledge and basic ecological information for so many organisms, especially in biodiverse, economically under-developed regions, our approach has the potential to dramatically increase the number of lineages to which ancestral state reconstructions of multistate traits can be applied, advancing the study of macroevolutionary dynamics and promoting global representation within the field.

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DATA AVAILABILITY

All data (10.6084/m9.figshare.15028470) and R code (10.6084/m9.figshare.15028449) required to reproduce our findings are available via Figshare.

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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:

Data S1. Excel spreadsheet reflecting diet data (and associated references), body size data and habitat assignment.
Data S2. Supplementary methods including (S2.1) description of edits that were made to the phylogeny published by Tonini *et al.* (2016), (S2.2) summary of taxon coverage and (S2.3) justification for exclusion of ARD (Mk2) models.
Data S3. Phylogeny in Newick format.
Data S4. Dietary reconstructions for each prey type with circle shading reflecting scaled likelihood of prey presence between 0 (white) and 1 (black).

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