Convergence in trophic morphology and feeding performance among piscivorous natricine snakes

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Abstract

Piscivory has independently evolved numerous times amongst snakes, and therefore these animals provide a powerful opportunity to test for convergent evolution in a vertebrate feeding system. In this study, we integrate performance trials with comparative methods to test the hypothesis that piscivory drives convergence in trophic morphology and feeding performance among natricine snakes. Within and across species, increasing the relative length of the quadrate bone in the skull is positively and strongly linked to a reduction in the time needed to swallow large fish prey. Thus, our feeding experiments suggest that a longer quadrate bone enables snakes to better conform their head shape to the shape of the prey during swallowing. Ancestral diet reconstructions and phylogenetically corrected multiple regression analyses further reveal that evolutionary increases in piscivory are coupled to the evolution of relatively longer quadrates, and hence improved feeding performance on fish prey in these animals. The exploitation of similar dietary niches drives the evolution of convergent trophic morphologies and feeding performances in natricine snakes.

Introduction

Morphological convergence has provided some of the most compelling test cases for adaptive evolution (Schluter, 2000). The repeated independent evolutionary origins of similar trophic morphologies in eretmodine cichlids from Lake Tanganyika, e.g. is a striking example of morphological convergence in response to the occupation of similar dietary niches in animals (Winemiller *et al.*, 1995; Ruber & Adams, 2001). Theoretically, morphological convergence is predicted to evolve as a result of organisms experiencing similar functional demands on their phenotype (Schluter, 2000). Thus, if adaptive evolution underlies convergence, organisms are also expected to exhibit convergence in their performance (Arnold, 1983; Hulsey *et al.*, 2008). Alternatively, a lack

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of convergence in performance would indicate that morphological similarities among species are in fact the result of non-adaptive processes [e.g. shared evolutionary histories, etc. (Schluter, 2000; Alfaro *et al.*, 2004)]. Although examples of morphological convergence are widespread (Losos, 1992; Winemiller *et al.*, 1995; Harmon *et al.*, 2005; Stayton, 2006; Revell *et al.*, 2007; Hulsey *et al.*, 2008), relatively few studies have incorporated direct measures of whole-organismal performance capacities (but see Ackerly & Reich, 1999; Ackerly, 2004; McHenry & Patek, 2004; Hoso *et al.*, 2007). As a result, it remains unclear whether morphological convergence signals convergence in whole-organismal performance capacities as well.

Piscivory has independently evolved in almost every major extant lineage of 'macrostomatan' (enlarged gape) snakes (Savitzky, 1983; Young, 1991; Cundall & Greene, 2000; Alfaro, 2002). These animals therefore provide an excellent opportunity to test for convergent morphological and functional evolution in a vertebrate feeding

system. For example, previous authors have noted that many phylogenetically diverse piscivorous snakes have independently evolved relatively long, vertically oriented quadrate bones relative to their skull size, which is believed to be adaptive for feeding on the laterally compressed bodies of some fish species (e.g. sunfishes, trout, etc.) (Dwyer & Kaiser, 1997; Cundall & Greene, 2000). However, this hypothesis remains to be tested in a closely related group of snakes using modern phylogenetic comparative methods.

Previous functional morphological work has shown that 'functional prey size' in gape-limited snakes is typically determined by the relative sizes of a prey's various dimensions (i.e. prey shape; but see Jayne *et al.*, 2002). Specifically, relative prey width and/or height often bulge outwards at the corners of the mouth and therefore considerably slow down the swallowing process in snakes (Kardong, 1977; Greene, 1983; Vincent *et al.*, 2006a, 2007; also see Jackson *et al.*, 2004). Moreover, ecomorphological studies have shown that snake species that consume relatively tall or wide prey, and especially piscivores (Dwyer & Kaiser, 1997), often have longer quadrate bones, presumably to accommodate this functional demand (Greene, 1983; Vincent *et al.*, 2004, 2007). Thus the inclusion of irregularly shaped prey (e.g. many types of fish) into the diet of snakes should be coupled to the evolution of longer quadrate bones.

Here, we first test the hypothesis that quadrate length in European and North American natricine snakes is indicative of their feeding performance on irregularly shaped fish prey. Second, we test whether an increase in the degree of piscivory among species is coupled to the evolution of longer quadrates and shorter swallowing times on fish prey. European and North American natricines are an ideal group for such a study for several reasons including the availability of a phylogenetic framework (e.g. Alfaro & Arnold, 2001), and the fact that previous studies have shown that piscivory is widespread within this group (Hibbits & Fitzgerald, 2005; Bilcke *et al.*, 2006; Herrel *et al.*, 2008). Using this system, we experimentally test how variation in fish size/shape is linked to variation in feeding performance among five piscivorous natricine snakes. We then use ancestral state reconstruction and independent contrasts to test whether the evolution of morphological and performance traits is correlated with the evolution of extreme piscivory.

Materials and methods

Animal care and feeding experiments

Our feeding experiments were approved by the animal ethics committee at Tulane University prior to the start of the study. For the feeding experiments, we hand captured animals from nearby field sites in southeastern Louisiana and transported them back to the laboratory at

Tulane University (sample sizes per species: *Nerodia clarkii* individuals = 5; trials = 35; *Nerodia cyclopion* individuals = 5; trials = 76; *Nerodia erythrogaster* individuals = 3; trials = 35; *Nerodia fasciata* individuals = 7; trials = 54; *Nerodia rhombifer* individuals = 3; trials = 72). We used these five *Nerodia* species because they all readily feed on a common natural prey item (see below), thus facilitating comparisons on a common performance metric among species. Within the first 1–2 days after capture, we measured (in mm) the snout-vent length (SVL), head length and quadrate length of each individual. We maintained each snake separately in a 37.8-L terrarium at an average temperature of 25 °C and on a 12 h light cycle, with access to water at all times. To increase each snake's motivation to feed, snakes were fasted for up to 2 weeks prior to the experiments. A single species of killifish (*Fundulus grandis*) was used in all experimental trials because it is a natural prey item for all five snake species examined (Gibbons & Dorcas, 2004 and references therein) and approximates the true handling requirements of fish in the wild.

All feeding experiments were performed in a snake's home cage and filmed using a handheld video camera (Handycam DCR HC28, Sony, Tokyo, Japan) at 30 Hz. Prior to feeding, we measured the mass (g), standard length (mm), maximum body width (mm) and maximum body height (mm) of each fish. For these trials, we measured two aspects of swallowing performance. First, we recorded the time required to pass an entire prey item from the most anterior portion of the buccal cavity through to the anterior most part of the esophagus, which was determined by observing the external 'bulge' of the prey item as it passed into the anterior trunk. Timing was initiated once the snake aligned the prey with the long axis of its braincase and began the jaw movements of ingestion and ceased once the most posterior portion of the prey passed the anterior most portion of the esophagus. To facilitate comparisons among individuals and species, we only retained trials in which the snake consumed the fish headfirst, and when the snake's head width was aligned with the dorsoventral axis (height) of the fish's body. Timing measurements were recorded to the nearest tenth of a second. Second, we recorded the total number of jaw protraction–retraction cycles (hereafter referred to as 'jaw cycles') used to transport each prey item. We used total swallowing time and number of jaw cycles to estimate feeding performance because previous work has shown that these two measures are associated with several ecologically important issues in snakes such as predation risk and feeding rate (Pough & Groves, 1983; Shine, 1991; Vincent & Mori, 2008).

For the feeding trials, we offered only one fish per trial with a minimum of a 10-min interval between trials. Individual snakes were offered no more than three fish within a 24-h period. Each individual was tested a minimum of 30 times in the feeding experiments.

Because some individuals fed more readily than others, however, we were not able to record an equal number of usable feeding events for all individuals tested (minimum number of usable trials recorded per individual = 5; maximum = 37; mean = 12). In total, we recorded 272 usable (i.e. snakes were not disturbed during the experiments) feeding events from 23 individual snakes.

Morphometrics and taxon sampling

To examine the coevolutionary relationships between snakes and their prey, we measured each specimen's SVL, cranial length and quadrate length (Fig. 1). Skull measurements were taken (in mm) using Mitutoyo digital calipers (± 0.01 mm). Cranial length was recorded because it is an excellent indicator of overall head size in snakes (e.g. King, 2002; Vincent *et al.*, 2006a,b). Quadrate length was recorded because it is one of the primary functional determinants (along with the maximum stretch capacity of the intermandibular soft tissues; Young, 1998), of how far snakes can spread their jaws laterally over a prey's body (Vincent *et al.*, 2006a). Quadrate length has also been show to be a strong predictor of maximum prey dimensions taken in the wild (Vincent *et al.*, 2004). SVL was recorded to estimate a snake's overall body size, which is often correlated with the maximum size of prey consumed by snakes (reviewed in Arnold, 1993).

Dietary data

To characterize the diet of each species used in this study, we reviewed the ecological literature and recorded the per cent fish in the diet for each species. All species had multiple published dietary datasets available, with the exception *Thamnophis couchii* (Table 1). For species that exhibited substantial geographic variation in the amount of fish in the diet (i.e. dietary generalists that feed on prey depending solely on their relative abundance), we averaged the per cent fish in the diet across populations, within populations among seasons and/or among studies (Table 1).
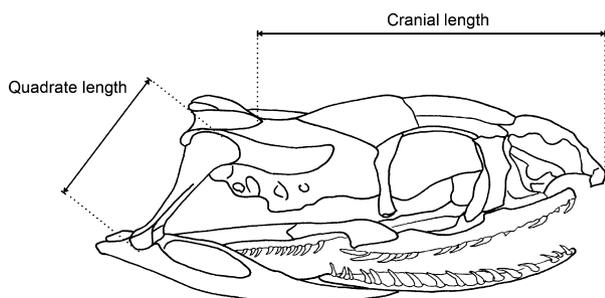
Fig. 1 Illustration of a typical natricine skull showing the linear morphometric variables recorded for each museum specimen.

Phylogenetic analysis

To construct a framework for comparative study, we performed phylogenetic analyses of the 24 species of natricine snakes for which we had both morphometric and dietary data. We conducted maximum likelihood (ML) analyses, using RAxML 7.0.3 (Stamatakis *et al.*, 2005), of a combined DNA data set consisting of Cytochrome *b* (1117 bp) and ND2 (1029 bp) mtDNA data downloaded from GenBank. Because the application of data partition specific models of nucleotide evolution is known to improve phylogenetic analysis (Castoe *et al.*, 2004; Nylander *et al.*, 2004; Brandley *et al.*, 2005), we assumed separate GTR+Γ model parameters for each codon position for each gene (six total data partitions). Because accurate independent contrasts and ancestral state reconstructions are dependent on accuracy in the phylogeny, it is important to obtain a measure of confidence in this phylogeny. We therefore performed additional partitioned Bayesian phylogenetic analyses, assuming the same partitions and models as in our ML analysis, to obtain measures of clade support. We ran a total of four Bayesian analyses using MRBAYES v.3.1.2. (Ronquist & Huelsenbeck, 2003), each consisting of 10^7 generations, using default priors, and sampling every 1000th generation. To determine convergence, cumulative posterior probability plots for each clade were constructed for several analyses using the *cumulative* function in AWTY (Nylander *et al.*, 2008). Stationarity was assumed when the cumulative posterior probabilities of all clades stabilized. These plots indicated that excluding the first 10^6 generations as burn-in was sufficient and the frequency of inferred relationships in the remaining trees represent estimated posterior probabilities. Posterior probability estimates for each clade were then compared between the four analyses using a scatter-plot created by the *compare* command in AWTY. Posterior probability estimates for clades were similar in all analyses and the results were combined (36 000 trees). Posterior probabilities ≥ 0.95 are considered statistically significant clade support (Huelsenbeck & Rannala, 2004).

Phylogenetic reconstructions

To accommodate phylogenetic non-independence in our analyses, we used COMPARE 4.6b (Martins, 2004) and the ML phylogram (Fig. 2), to calculate independent contrasts (Felsenstein, 1985) for the arcsine-transformed percentage piscivory and the three $\log_{10}$-tranformed skull measurements. To evaluate evolutionary changes in piscivory, we reconstructed ancestral states of arcsine-transformed percent fish in the diet using the ML phylogeny and squared-change parsimony in MESQUITE v2.01 (Maddison & Maddison, 2007). For clarity and ease of discussion, these variables were then untransformed into raw percentages.

Species	N	SVL (mm)	CL (mm)	QL (mm)	% fish in diet	Reference
Natrix maura	3	354.8	14.1	6	56	Santos *et al.*, 2000
Natrix natrix	3	707.9	20.9	11.2	10	Gregory & Isaac, 2004
Natrix tesselata	3	371.5	13.2	5.2	97	Luiselli *et al.*, 2007
Nerodia clarkii	3	446.7	18.6	10.7	99	Gibbons & Dorcas, 2004
Nerodia cyclopion	3	492.4	23.6	13.6	94	Gibbons & Dorcas, 2004
Nerodia erythrogaster	3	506.9	25.9	12.5	35	Gibbons & Dorcas, 2004
Nerodia fasciata	10	427.5	23.2	11.9	72	Gibbons & Dorcas, 2004
Nerodia harteri	3	430.3	18.1	7.9	99	Gibbons & Dorcas, 2004
Nerodia rhombifer	3	547.9	28.6	18.4	97	Gibbons & Dorcas, 2004
Nerodia sipedon	3	445.7	23.2	10.8	80	Gibbons & Dorcas, 2004
Nerodia taxispilota	3	538.1	26	19.5	100	Gibbons & Dorcas, 2004
Regina grahami	3	533	13.8	5.5	0	Gibbons & Dorcas, 2004
Regina rigida	3	420	13.2	6.5	0	Gibbons & Dorcas, 2004
Regina septemvittata	3	411	13.9	4.5	0	Gibbons & Dorcas, 2004
Thamnophis atratus	3	405.2	15	4.7	30	Rossman *et al.*, 1996
Thamnophis couchii	10	467.7	16.6	5.8	21	Lind, 1990
Thamnophis cyrtopsis	3	454.6	14.8	3.9	5	Rossman *et al.*, 1996
Thamnophis elegans	3	400.7	15.7	6.8	45	Rossman *et al.*, 1996
Thamnophis marcianus	3	434.9	19.1	8	0	Rossman *et al.*, 1996
Thamnophis melanogaster	3	311.4	14.1	5.1	5	Rossman *et al.*, 1996
Thamnophis ordinoides	3	311.4	16.6	6	0	Rossman *et al.*, 1996
Thamnophis proximus	3	297.4	12.2	3.4	15	Rossman *et al.*, 1996
Thamnophis radix	3	381.1	16.6	6.5	0	Rossman *et al.*, 1996
Thamnophis rufipunctatus	3	494.1	18.7	6.9	95	Rossman *et al.*, 1996

CL, cranial length; QL, quadrate length.
Note that for the dietary literature, we have attempted to cite reviews when possible, but used data from the references therein in most cases.

Statistical analysis

We used SPSS (version 11.5; SPSS Inc., Chicago, IL, USA) for all statistical analyses. We log_{10}-transformed all morphological/performance variables and arcsine-transformed the per cent fish in the diet for a species to meet the assumption of homoscedascity for analysis of variance (Sokal & Rolf, 1981; Kachigan, 1991), and tested all transformed data for normality using Lillifores tests. The mean log_{10}-transformed morphological and dietary values for each clade were used in all inter-specific statistical comparisons.

Morphology–performance relationships

To test the hypothesis that larger relative quadrate lengths lead to shorter swallowing times and fewer jaw cycles when feeding on fish, we first tested whether species differ in relative quadrate length using a one-way ANOVA. Second, we calculated the mean values for swallowing time, jaw cycles and prey mass for each individual tested in the performance trials. Using these mean values, we tested whether species differ in feeding performance after accounting for differences in prey size, using a two-way ANCOVA with species as a fixed factor, individual as a random factor and prey mass as a covariate. Finally, we tested whether species differ in feeding performance after accounting for differences in both prey size and relative

quadrate length, using a two-way ANCOVA with species as a fixed factor, individual as a random factor, and prey mass and relative quadrate length as covariates.

Phylogenetic analyses of morphology and diet

To examine the evolutionary relationships between morphology and diet, we input the phylogenetic independent contrasts (PICs) for snake morphology as the independent variables and the diet contrasts (arcsine-transformed proportion of fish in the diet) as the dependent variable in a stepwise multiple regression (backwards model) forced through the origin (Garland *et al.*, 1992). For these analyses, relative quadrate length was calculated by regressing the PIC for quadrate length (*y*-axis) against the PIC for cranial length (*x*-axis), forced through the origin, in order to generate 'size-free' residuals. These analyses were performed for both all species together (piscivores and non-piscivores), and for just piscivores alone (i.e. species that include at least 10% of fish in their diet).

Results

Swallowing performance

The one-way ANOVA testing for differences in relative quadrate length among species was highly significant
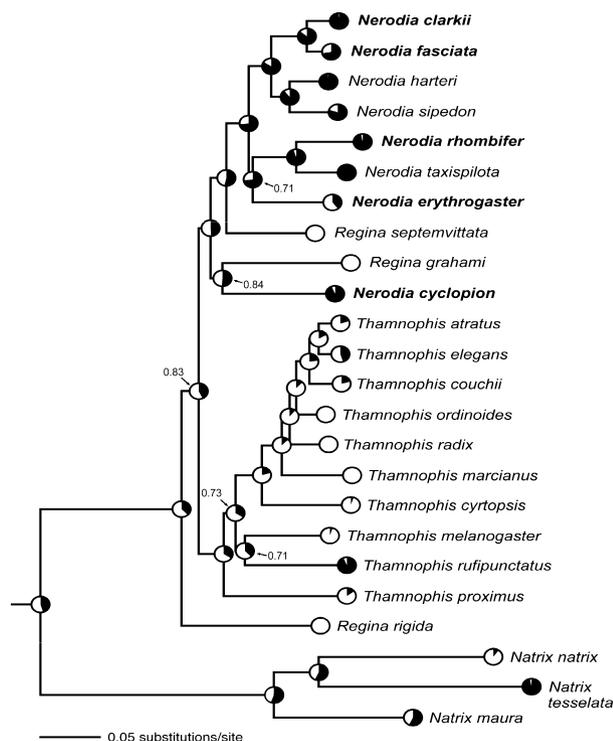
Fig. 2 Maximum-likelihood phylogram of natricine snake taxa used in this study. All relationships are strongly supported (i.e. clade posterior probabilities ≥ 0.95) unless otherwise noted with numbers. Taxa in bold represent those used in feeding performance trials. Pie charts of terminal taxa represent the per cent fish in that species' diet according to the literature. Pie charts in of internal nodes indicate squared-change parsimony reconstructions of per cent fish in the diet for that ancestor.

Fig. 3 (a) Mean ± 1 SE values for relative quadrate length for the five species of natricine snakes examined in the feeding performance trials. (b) Mean ± 1 SE prey size-adjusted (swallowing time/fish mass) for the five species of snakes examined in the feeding performance trials.

($F_{4,18} = 55.8$, $P < 0.001$). Bonferroni posthoc tests coupled with comparisons of mean values for relative quadrate length (Fig. 3a) show that *N. clarkii* and *N. fasciata* have significantly smaller relative quadrates than all other species examined ($P < 0.05$ in all comparisons), whereas *N. rhombifer* has a larger relative quadrate length than all other species examined ($P < 0.05$). Moreover, *N. cyclopion* and *N. erythrogaster* do not significantly differ from one another in relative quadrate length ($P > 0.80$). The two-way ANCOVA testing for differences in swallowing time among species, independent of prey size, was highly significant (species: $F_{4,11} = 4.75$, $P = 0.018$; individual: $F_{6,11} = 0.824$, $P = 0.574$). Bonferroni *post hoc* tests coupled with comparisons of mean prey size-adjusted swallowing time show that *N. clarkii* and *N. fasciata* take significantly longer to swallow fish than all other species ($P < 0.05$ in all comparisons) (Fig. 3b). Furthermore, *N. rhombifer* swallows fish significantly faster than all other species examined ($P < 0.05$). *Nerodia cyclopion* and *N. erythrogaster* do not significantly differ from one another in mean swallowing time ($P > 0.50$). The two-way ANCOVA testing for differences in number of jaw

cycles among species, independent of prey size, was not significant (species: $F_{4,11} = 2.56$, $P = 0.098$; individual: $F_{6,11} = 0.202$, $P = 0.969$). Finally, the two-way ANCOVA testing for differences in swallowing time among species, independent of both prey size and relative quadrate length, was not significant (species: $F_{4,10} = 2.17$, $P = 0.145$; individual: $F_{6,10} = 0.792$, $P = 0.596$). Take together, these analyses show that increasing relative quadrate length among species leads to shorter swallowing times on fish prey.

Ancestral reconstruction of diet

Squared-change parsimony reconstructions of ancestral diet show that there have been several rapid phylogenetic transitions from piscivory to non-piscivory amongst European and North American natricines, especially within the genus *Thamnophis*. Moreover, this analysis shows that extreme piscivores (species whose
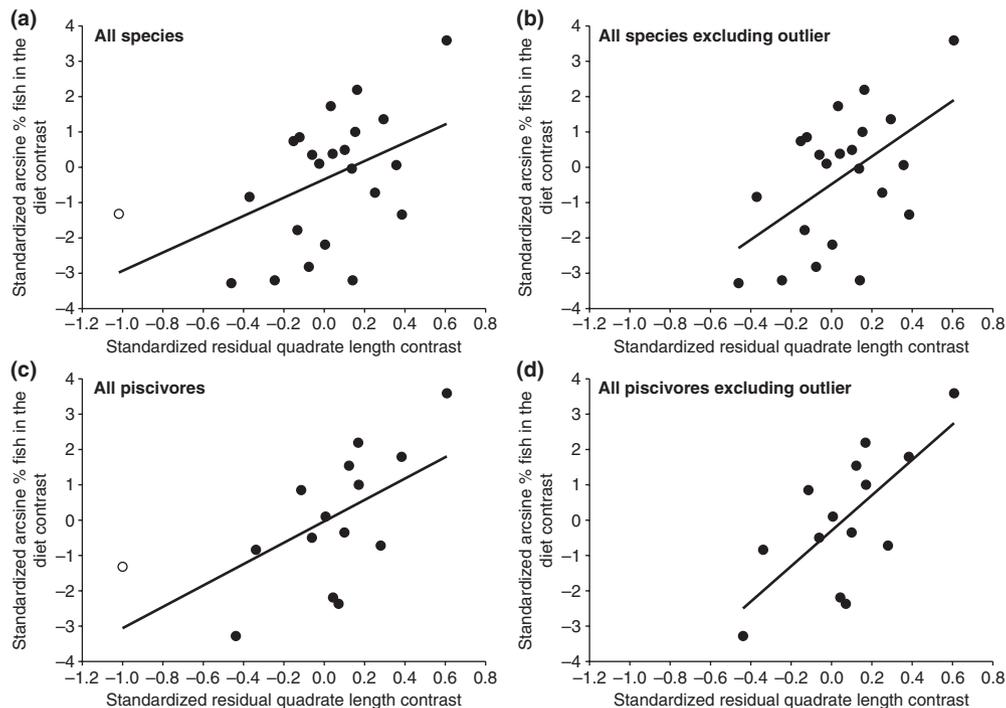
Fig. 4 Plots of the phylogenetically independent contrasts for arcsine per cent fish in the diet (*y*-axis) vs. relative quadrate length (*x*-axis). Open circle indicates the *Thamnophis atratus–Thamnophis elegans* contrast, which was shown to be a morphological outlier in the statistical analysis.

diets are composed of more than 90% of fish) have independently evolved at least six times amongst European and North American natricines (Fig. 2). Overall, this analysis shows that there have been several rapid evolutionary shifts in the degree of piscivory amongst natricines in general, and that these shifts occur across the entire clade.

Phylogenetic analysis of morphology and diet

The stepwise regression testing for correlations between the arcsine transformed per cent fish in the diet and morphology among all species retained residual quadrate length ($\beta = 0.47$, $R^2 = 0.22$, $P < 0.05$; Fig. 4a), but no other morphological variables. When restricting the analysis to piscivores (species that include a minimum of 10% of fish in their diet), the model also only retained residual quadrate length ($\beta = 0.61$, $R^2 = 0.37$, $P < 0.01$; Fig. 4c). However, visual inspection of the resulting plots, coupled with statistical tests, shows that the *Thamnophis atratus–Thamnophis elegans* quadrate contrast is a morphological outlier in both analyses (Durbin–Watson D Statistic: 2.24; Fig. 4a, c), thus potentially reducing the explanatory power of the general-linear models. To address this issue, we recalculated the PICs without *T. elegans*, and reran the stepwise regressions. This new model once again only retained residual quadrate length ($\beta = 0.44$, $R^2 = 0.19$, $P < 0.05$; Fig. 5b). In a similar

manner, the model restricted to piscivores only retained residual quadrate length ($\beta = 0.67$, $R^2 = 0.45$, $P < 0.001$; Fig. 4d). The recalculated contrasts thus confirm the original results.

Moreover, a phylogenetically corrected scaling analysis reveals that this increase in quadrate length is the result of a marked evolutionary allometry, both across all species and across a restricted data set including only piscivores (Fig. 5a–d). Specifically, reduced major axis slopes calculated for the standardized cranial length contrast (*x*-axis) vs. the standardized quadrate length contrast (*y*-axis) are approximately twice the predicted slope of 1 in all comparisons (range 1.78–2.44). However, the slopes of these regressions were much steeper in the piscivores restricted analyses compared to those using all species (Fig. 5a–d).

Discussion

Our study presents the first quantitative empirical support for the idea that the evolution of elongate quadrate bones in piscivorous snakes (Savitzky, 1983; Dwyer & Kaiser, 1997; Cundall & Greene, 2000) represents an adaptation towards handling fish. Furthermore, this study reveals a significant relationship between increasing relative quadrate length and shorter swallowing times on fish prey in natricines (Fig. 3a,b). As predicted by the convergence hypothesis, we also observed an
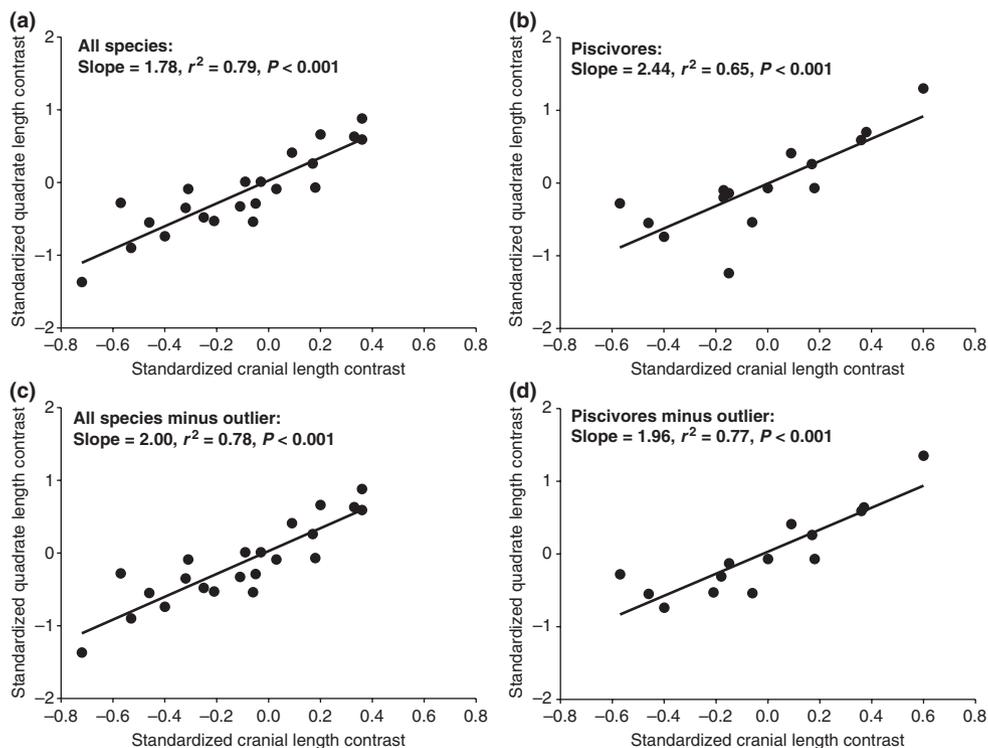
Fig. 5 Plots of the phylogenetically-independent contrasts for quadrate length (*y*-axis) vs. cranial length (*x*-axis). *P*-value was calculated for the expected slope of 1 vs. the observed slope using two-sample *t*-tests. All slopes are significantly higher than the predicted slope of 1 (see Results).

evolutionary increase in relative quadrate length in association with an increase in piscivory in a larger phylogenetic sample of natricines. Overall, we found that evolutionary increases in the degree of piscivory across this phylogenetic sample of natricine snakes is strongly associated with the evolution of similar trophic morphologies and feeding performances.

The feeding experiments show that fish size-adjusted swallowing times differ significantly among species, whereas the number of jaw cycles used to transport fish was only trending towards significance ($P = 0.098$). We suggest that the stronger evolutionary signal in swallowing time compared with jaw cycles may be due to the fact that a large component of the total energy required for ingestion is generated by glycolysis in snakes (Feder & Arnold, 1982; Cruz-Neto *et al.*, 2001; Canjani *et al.*, 2003). For example, Feder & Arnold (1982) showed that as much as 26% of the total energy required for ingestion in another natricine (*T. elegans*) comes from anaerobic respiration, resulting in a 260% increase in circulating lactate levels. Shorter swallowing times would thus enable snakes to optimize the net energy gained from a given feeding event, and avoid the possibility of fatiguing while attempting to ingest a large prey item. We suggest that a comparative study examining the energetic costs of feeding performance in snakes coupled to measurements of performance would be especially insightful.

Previous work has shown that frontally striking aquatic natricines show strong morphological convergence towards a narrow streamlined head shape designed to reduce drag and bow waves during feeding strikes (Hibbits & Fitzgerald, 2005; Herrel *et al.*, 2008). However, narrow head shapes will result in relatively small maximum gape sizes in snakes (S.E. Vincent, unpublished), and therefore small maximum ingestible prey sizes (Arnold, 1993; King, 2002). By contrast, laterally striking species do not exhibit convergence in external head form and have evolved maximum gape sizes up to 4× larger than frontally striking species (S.E. Vincent, unpublished). *Nerodia clarkii* was the only frontally striking species examined in the feeding experiments here, with all other species being lateral strikers (Bilcke *et al.*, 2006; Herrel *et al.*, 2008). A comparison of fish size-adjusted swallowing times across all individuals (swallowing time/fish mass) between *N. clarkii* and the fastest swallowing species, *N. cyclopion*, shows that the frontally striking *N. clarkii* takes approximately 18× longer to swallow a fish than the laterally striking *N. cyclopion*, which appears to be due to its relatively narrow head shape (Herrel *et al.*, 2008). This comparison therefore supports the notion of a potential functional trade-off between aquatic prey capture and swallowing. Although a larger phylogenetic sample of frontal vs. lateral strikers feeding on similar fish species is needed to show that a trade-off indeed exists, we find it

particularly interesting that lateral strikers qualitatively appear to have overcome this potential trade-off given their large head sizes and lack of streamlined head shapes. Strike kinematic studies coupled to computational fluid dynamic models and digital particle image velocimetry may help us understand why lateral strikers have failed to converge in the face of potentially stringent environmental pressures.

In conclusion, our data support the hypothesis that adaptive evolution underlies observed similarities in trophic morphology and performance in piscivorous European and North American natricine snakes. Given that piscivory has independently evolved in a wide diversity of snakes (e.g. aquatic pythons, acrochordids, homolapsines, sea snakes, etc.), we suggest that similar, and potentially even more powerful, opportunities exist in these other snake clades to test for phenotypic convergence. For example, the adaptive radiation of homolapsines has been hypothesized to be linked to their ability to feed on an impressive array of fish species that differ dramatically in their size, shape and anti-predator tactics (Voris & Voris, 1983; Alfaro *et al.*, 2008). Yet, relatively little is known about the relationships amongst trophic morphology, feeding behaviour, performance and evolutionary history within either homolapsines, or the majority of aquatically feeding snakes. Future comparative studies that integrate performance and morphology are needed to clarify how the functional demands of piscivory have influenced skull evolution in aquatic and semi-aquatic snakes.

Acknowledgments

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