Morphological and ecological convergence in two natricine snakes

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Similar morphologies between species may be due to shared ancestry or convergent evolution. Understanding instances of morphological and ecological convergence is central to evolutionary ecology because they help us understand the fit between organism and environment. Two species of stream-dwelling natricine snakes, *Thamnophis rufipunctatus* and *Nerodia harteri* present a model system for studying ecological and morphological convergence and adaptation. The species are allopatric and both live in shallow riffles in streams and forage visually for fish. We studied morphological similarity, trait evolution and functional significance of ecologically relevant traits in these and related species, and used mitochondrial DNA sequences for the ND4 gene to estimate their phylogenetic relationships. Character mapping of head length and head width supported the hypothesis of independent evolution of head shape in *T. rufipunctatus* and *N. harteri*. The elongate snout is a derived trait in these two taxa that is associated with reduced hydrodynamic drag on the snakes' heads when in a swift current, compared to other species with the ancestral blunt snout. We hypothesize that lower hydrodynamic drag facilitates prey capture success in these species that are known to forage by holding their position in currents and striking at fish prey. The elongate snout morphology has also resulted in a diminished binocular vision field in these snakes, contrary to the hypothesis that visually orientated snakes should exhibit relatively greater binocular vision. Convergent evolution of the long snout and reduced hydrodynamic drag in *T. rufipunctatus* and *N. harteri* are consistent with the hypothesis that the long snout is an adaptation to foraging in a swift current.   © 2005 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2005, **85**, 363–371.

ADDITIONAL KEYWORDS: adaptation – binocular vision field – convergent evolution – hydrodynamic drag – *Nerodia* – *Thamnophis* – whole organism performance.

INTRODUCTION

Similarities among species in morphology and ecology may be the result of either shared common ancestry or convergent evolution to common environmental conditions. Instances of convergent evolution present opportunities for testing the adaptive significance of specific traits (Mooney & Dunn, 1970; Cody & Mooney, 1978; Luke, 1986; Losos, 1990; Winemiller & Adite, 1997); they are central to evolutionary ecology because they help us understand the processes of diversification and the fit between organism and environment.

A thorough consideration of ecomorphological convergence requires information on ecologically relevant characters, performance functions for those traits, environments experienced by the species and a phylogenetic framework. Similarities among taxa may be inherited from a common ancestor (Dobson, 1985; Greene, 1986; Winterbottom & McLennan, 1993). A phylogeny is necessary to demonstrate independent origins of the focal traits; it also reveals the sequence of character-state changes in both morphology and performance (Greene, 1986; Coddington, 1988; Wanntorp *et al.*, 1990; Baum & Larson, 1991). If changes in organismal performance occur prior to a shift in morphology, then it is unlikely that the morphological change was directly associated with performance, and there is little support for a hypothesis of adaptive convergence.

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Most examples of convergence involve similar patterns of morphology and ecology in unrelated organisms that inhabit similar environments. However, similarity in morphology does not necessarily mean animals perform similarly (Miles, 1994). Thus, studies of convergence should determine that similarity in morphology also results in similarity in ecologically relevant measures of performance.

In this paper we present an analysis designed to compare performance in two species that inhabit similar environments and capture prey in similar ways. First, we measure morphological similarity among traits likely to have a role in prey capture in aquatic environments. Second, we focus on the functional significance of traits by estimating performance in several ecologically relevant tasks. By placing our results in a phylogenetic context, we are able to examine the sequence of character state changes and hypothesize about the contribution of convergent traits to performance of organisms in an ecologically relevant context.

The aquatic natricine snakes, *Thamnophis rufipunctatus* Cope, 1875 and *Nerodia harteri* Trapido, 1941, present an opportunity to study the evolution of adaptive convergence. Both inhabit rocky streams in the south-western United States and western Mexico; however, they are allopatric in distribution (Scott *et al*., 1989; Tanner, 1990). Both species forage visually for fish in stream riffles. These species, both of medium size (500–700 mm adult SVL), have similarly shaped heads, relatively thin bodies and spotted dorsal coloration (Rossman, Ford & Seigal, 1996; Werler & Dixon, 2000). The phenotypic similarities are so great that the holotype of *N. harteri* was described as a range extension of *T. rufipunctatus* (Trapido, 1942).

Several herpetologists have argued that *T. rufipunctatus* should be re-classified into the genus *Nerodia* (Lowe, 1955; Chiasson & Lowe, 1989). Recent work, however, has clearly demonstrated that these snakes are not closely related and do belong in distinct genera (de Queiroz & Lawson, 1994; de Queiroz, Lawson, & Lemos-Espinal, 2002). The availability of a phylogeny for the group facilitates comparisons among taxa and makes these natricine genera a good case study for morphological and ecological convergence (Felsenstein, 1985a; Lawson, 1987; de Queiroz & Lawson, 1994; de Queiroz *et al*., 2002). As there is no published phylogeny that includes both *T. rufipunctatus* and *N. harteri*, we have reconstructed one in order to position the relationship of *N. harteri* within this group. This has allowed us to map the evolution of head shape and associated measures of function and performance.

The morphological similarities in these snakes are accompanied by similar habitat use, foraging mode and diet. Most natricine species typically use an open-mouth foraging mode, employing lateral strikes to capture fish swimming in schools (Drummond, 1983). In contrast, *T. rufipunctatus* and *N. harteri* both orientate visually toward individual prey and strike forward for prey capture. (Drummond, 1980; Alfaro, 2002; de Queiroz, 2003). They crawl along the bottom of streams in search of prey (Alfaro, 2002; de Queiroz, 2003; pers. observ.) and commonly anchor their tails around rocks to hold their position in a current (Werler & Dixon, 2000; pers. observ.). We have observed them holding position in a current, with their head and neck exposed to the force of the water and the body unanchored on the substrate to allow for forward directed strikes (pers. observ.). The striking morphological and behavioural similarities suggest an example of convergent evolution.

We hypothesize that the narrow head shape in *T. rufipunctatus* and *N. harteri* evolved independently, and is associated with a concurrent shift in habitat to stream riffles and to visually orientated foraging. Support for the hypothesis would be evidence of convergent evolution in morphological and ecological traits.

Our primary objectives were to use phylogenetic character mapping to determine whether the narrow head shape in these two snakes evolved independently, and to evaluate the performance consequences of head shape. We predicted that similar head shape would result in decreased hydrodynamic drag, enhancing the snakes' ability to hold position in a current and make rapid forward strikes at prey. Binocular vision is widely associated with visually orientated predators, because it increases depth perception and is presumed to enhance foraging success. Thus we also predicted that *T. rufipunctatus* and *N. harteri* would have an increased binocular vision field (BVF) relative to their congeners. Increased BVF has also been hypothesized as an agent for the evolution of the head shape of many arboreal snakes (Vitt, 1987; Lillywhite & Henderson, 1993).

METHODS

Garter, ribbon and water snakes of the genera *Thamnophis* and *Nerodia* include over 40 species that demonstrate a variety of morphological and ecological variations correlated to habitat and foraging mode (Greene, 1997). We chose a suite of natricine taxa to include in our comparison of *T. rufipunctatus* and *N. harteri* based on the current phylogeny for the group (Lawson, 1987; de Queiroz *et al*., 2002).

Thamnophis proximus (Say, 1823) was chosen as a basal member of the genus and *T. marcianus* (Baird & Girard, 1853) as a member of the 'widespread' clade (*T. rufipunctatus* is a member of the 'Mexican' clade). *T. proximus* is generally associated with the edges of

permanent water, where it feeds mainly on fish and amphibians (Rossman *et al.*, 1996). *T. marcianus* is associated with permanent and ephemeral water, but is commonly found over 1 km from water; it preys on a wide variety of animals including earthworms, fish and lizards, but seem to prefer amphibians (Rossman *et al.*, 1996).

Nerodia fasciata (L., 1766) was chosen as a close relative and *N. erythrogaster* (Forster, 1771) as a more distant relative to *N. harteri*. *N. fasciata* is an inhabitant of creeks, rivers and swamps (Hebrard & Mushinsky, 1978). As a juvenile it feeds primarily on fish, shifting to a diet dominated by anurans as an adult (Mushinsky, Hebrard & Vodopich, 1982). *N. erythrogaster* inhabits permanent and ephemeral streams and rivers as well as permanent ponds and lakes (Keck, 1998); it goes through a similar shift in diet to *N. fasciata* (Mushinsky *et al.*, 1982).

All experiments and analyses included these six species. The species chosen represented the dominant morphotypes in their clades.

MOLECULAR PHYLOGENY

Tissue samples were obtained from one specimen of each of the following species: *N. harteri, N. erythrogaster, N. fasciata, N. cyclopion* (Duméril, Bibron & Duméril, 1854*), T. rufipunctatus, T. marcianus, T. proximus, Storeria dekayi* (Holbrook, 1842) and *Elaphe guttata* (L., 1766). We also used a DNA sequence from *N. taxispilota* (Holbrook, 1838) (GenBank U49322; Kraus & Brown, 1998). We added *N. cyclopion* and *N. taxispilota* to the phylogeny to reduce the risk of systematic error in a small dataset (Graybeal, 1998).

DNA was extracted using a DNeasy kit (Qiagen). A 996 bp fragment of mtDNA encompassing an 867 bp portion of the 3′ end of the mitochondrial ND4 gene and a 129 bp section of three transfer ribonucleic acid (tRNA) genes (tRNA[His], tRNA[Ser], tRNA[Leu]) was amplified using primers labelled ND4 and Leu (Arévalo, Davis & Sites, 1994).

PCR reactions were conducted in 100 μL volumes consisting of 2 μL template (50 ng), 69.5 μL H_2O, 5 μL dNTPs (8 mM), 4 μL $MgCl_2$ (25 mM), 1 μL primers (2 μL), 1 μL 5% DMSO, 16 μL *Taq* polymerase buffer (15 mM $MgCl_2$) and 0.5 μL *Taq* polymerase (Boehringer Mannheim). PCR conditions included an initial denaturation of 3 min at 95 °C, followed by 35 cycles 95 °C denaturation for 1 min, 50 °C annealing for 45 s and 72 °C extension for 1 min with a final 72 °C extension for 20 min. Sequencing reactions were conducted in 10 μL volumes consisting of 4.5 μL H_2O, 0.5 μL 5% DMSO, 0.7 μL template, 0.5 μM primer, 1.8 μL 5X sequence buffer and 2 μL Big Dye termination reaction mix. These reactions were run for 30

cycles at the conditions suggested by the sequencer manufacturer (Perkin Elmer).

All fragments were sequenced for both strands on an ABI 377 automated sequencer (Perkin Elmer, Applied Biosystems). Sequences were edited in Sequencer version 3.1.1 (Gene Codes Corporation, 1998) and multiply aligned with Clustal V (Higgins & Sharp, 1988). The default settings in Clustal V were used and indels in the tRNA segments were deleted. The alignments were verified according to GenBank sequence number U49322.

Trees were reconstructed using parsimony with PAUP version 4 (Swofford, 1999). All characters were equally weighted. Two outgroups, *Storeria dekayi* and *Elaphe guttata*, were used. *S. dekayi* was chosen because it is a close relative to both *Thamnophis* and *Nerodia*, but is not in either clade (R. Lawson, A. de Queiroz & J. A. Lemos-Espinal, pers. comm.). *E. guttata* is a more distantly related species used to root the tree. All trees were obtained with the exhaustive search option. Bootstrap values were calculated using a branch and bound search with 1000 replications (Felsenstein, 1985b)

MORPHOLOGY

Morphological measurements (to the nearest 0.01 mm) were made on at least 30 museum specimens per species. Six variables measured on the head were used to characterize head shape of each species: head length (HL), length from nostril to eye (NE), length from nostril to snout (NS), width between nostrils (BN), width between eyes (BE) and width across parietals (AP). We also measured snout–vent length (SVL) and tail length (TL). Continuous characters were natural-log transformed to normalize the data and homogenize group variances. To remove the effects of head size, the five head measurements were regressed against head length (all species pooled) and the residuals used as size-adjusted variables in a principal component analysis (PCA) using PROC PRINCOMP (SAS Institute, 1999).

BINOCULAR VISION FIELD

The BVF measures the overlap, in degrees, in the field of vision of each eye. Larger BVF results in a larger field where both eyes can focus simultaneously on the same object. The BVF for 30 museum specimens of each species was calculated according to the equation,

$$2\sin\theta = \frac{be/2 - bn/2}{ne}$$

where BE, BN and NE corresponded to the named morphometric variables. This formula yields a conservative estimate of BVF because it does not incorporate

the size of the eye or shape of the pupil. We tested the hypothesis that mean BVF differed according to species using ANOVA. Differences among group means were assessed using Tukey's post hoc tests (SPSS, 1999).

HYDRODYNAMIC DRAG

To quantify the effect of head shape on hydrodynamic drag for the different species, we measured the force of a current of water on the heads of museum specimens of five representative individuals of each species, with the exception of *N. fasciata*, which had a sample size of six. Only adult specimens were used. The apparatus consisted of a pump circulating water at 0.75 m/s through a 7.62 cm PVC pipe. A piece of steel 1 m long was bent at 45 ° and attached to the 7.62 cm pipe with hose clamps. A 30 cm length of 1.9 cm PVC pipe was cut in half longitudinally and attached to the angled end of the steel piece with hose clamps supporting a spring scale (Hibbitts, 2000). The force of water flowing against the snake head specimen registered the amount of hydrodynamic drag on the spring scale in 0.1 g increments. Because all snake heads were inserted into a water column moving at the same speed variation in the readings on the spring scale can be attributed to drag.

Snake heads were removed from museum specimens that were fixed in 10% formalin and stored in 70% ethanol. Each head was removed three ventral scales posterior to the edge of the lower jaw. A 10 cm length of 3.6 kg monofilament line was attached to the snout of the snake head and to the scale. The snake heads were inserted into the outflow area of the water column. Hydrodynamic drag was always measured at the same place in the water column. A reading was taken from the scale after the head was allowed to hold a steady position in the water column. The head was then removed from the column and reinserted at least two more times to verify the reading. After log transformation to normalize the data set, drag was regressed against SVL and the residuals were retained as size-adjusted variables. To examine the relationship between hydrodynamic drag and head shape, we plotted residual drag vs. relative snout length (PC 2); and calculated linear regressions using relative snout length (PC 2) as the independent variable and residual drag as the dependent variable.

IDENTIFYING CONVERGENT TRAIT EVOLUTION

Comparisons between species were employed to show differences in head shape, BVF and hydrodynamic drag. A gap coding method (Thorpe, 1984) was used to create character states from our continuous charac-

ters. The formula for this method is discussed in Archie (1985). Characters were mapped on the phylogeny to visualize associations between features and performance traits, and to visualize the numbers of times these traits have evolved within this group of snakes (Miles & Dunham, 1993).

RESULTS

PHYLOGENETICS

Of the 795 bp that were usable, 266 characters were variable and 135 were parsimony informative. The maximum parsimony analysis resulted in one most-parsimonious tree, 469 steps long, with a consistency index of 0.67 and a retention index of 0.42 (Fig. 1). Overall bootstrap values were low, except for the *Thamnophis* clade.
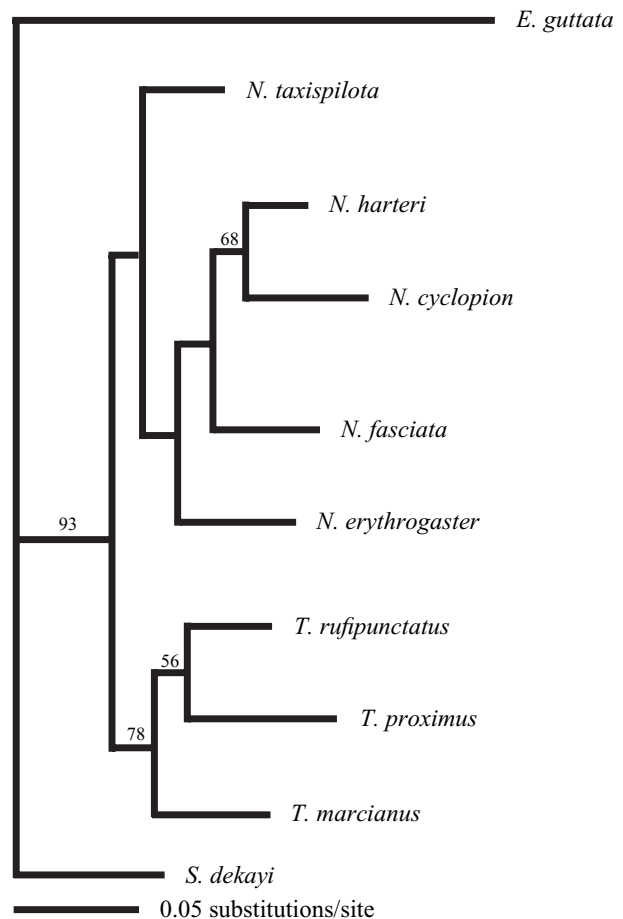

Figure 1. Maximum parsimony phylogeny for NDH4, tRNA[His], tRNA[Ser], tRNA[Leu] genes of the mtDNA. An exhaustive search was used for tree building with all characters weighted equally. Bootstrap values were obtained with a branch and bound search with 1000 replications, and those > 50% are shown.

MORPHOLOGY

Scree plot analysis identified two axes from the PCA that were readily interpretable. PC 1 explained 46% of the variance in size-adjusted head morphology, and described an overall gradient of head width with the three head width variables (BN, BE and AP) loading positively. PC 2 explained an additional 27% of the variance and described a gradient in snout length with the two length variables (NS and NE) loading positively (Table 1). Other PC axes each described < 12% of the remaining variation.

Thamnophis rufipunctatus occupied distinct morphospace due to negative values on the head width axis (Fig. 2); the other five species clustered near zero. The majority of data points for *N. harteri* and *T. rufipunctatus* were on the positive side of the snout length axis while those for the other four species fell predominantly on the negative end. There was a significant difference among species in mean multivariate head width ($F_{5,245} = 80.93$, $P < 0.0001$) and mean multivariate snout length ($F_{5,245} = 11.39$, $P < 0.0001$, Table 2). Tukey's post hoc comparisons showed *T. rufipunctatus* had a significantly narrower head, on average, than all other species ($P < 0.05$). *T. proximus* and *N. harteri* were similar in mean head width ($P > 0.05$), but formed a subset with significantly narrower head width than the subset of *N. fasciata*, *N. erythrogaster* and *T. marcianus* ($P < 0.05$). *T. rufipunctatus* and *N. harteri* had similar mean snout lengths ($P > 0.05$) that were significantly longer than those of the other four species ($P < 0.05$).

BVF AND HYDRODYNAMIC DRAG

There were significant differences among species with respect to their BVF ($F_{5,174} = 30.09$, $P < 0.001$, Table 2). Tukey's post hoc comparisons determined *T. rufipunctatus* had significantly less mean BVF than all other species ($P < 0.05$). *N. harteri* also differed significantly from the other species ($P < 0.05$) in having the second narrowest BVF; the other four species clustered more closely together in a subset with a broader BVF (Table 2, Fig. 3A).

Mean relative hydrodynamic drag was also significantly different among species ($F_{5,30} = 2.598$; $P = 0.05$, Table 2). *T. rufipunctatus* and *N. harteri* had lower mean relative hydrodynamic drag values than the other species (Fig. 3B).

TRAIT EVOLUTION

Two morphological traits, head width and snout length, and the corresponding functional consequences of these traits, BVF and hydrodynamic drag, were classified as characters using Thorpe's (1984) methods for coding continuously variable morphological features, and mapped onto the molecular phylogeny. *T. rufipunctatus* was the only species to possess the narrow-head character state. *T. rufipunctatus* and *N. harteri* shared the long snout character. The gap coding method produced four character states of BVF. *T. rufipunctatus*, *N. harteri* and *N. fasciata* were the only species in each of their respective character

Table 1. Factor loadings for the first two PC axes on size-adjusted head morphology of six species of *Nerodia* and *Thamnophis*. PC 1 describes a gradient of overall head width, PC 2 a gradient of snout length

Variable	PC 1	PC 2
Nare to eye	−0.2872	0.8097
Nare to snout	0.3606	0.7817
Between nares	0.7962	0.2160
Between eyes	0.8632	−0.1558
Across parietals	0.8315	−0.1045
Proportion of variance explained	0.46	0.27

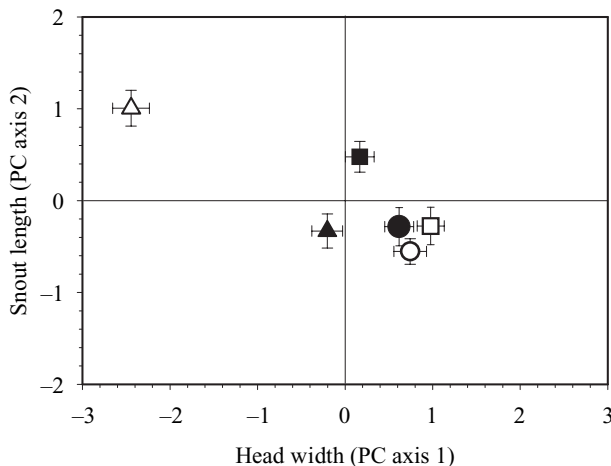**Figure 2.** Plot of species means ± 1 SE on PC axes 1 and 2. (△) *T. rufipunctatus*; (▲) *T. proximus*; (□) *T. marcianus*; (■) *N. harteri*; (○) *N. fasciata*; (●) *N. erythrogaster*.

Table 2. Results of ANOVAs on head width (PC 1), snout length (PC 2), binocular vision field and hydrodynamic drag

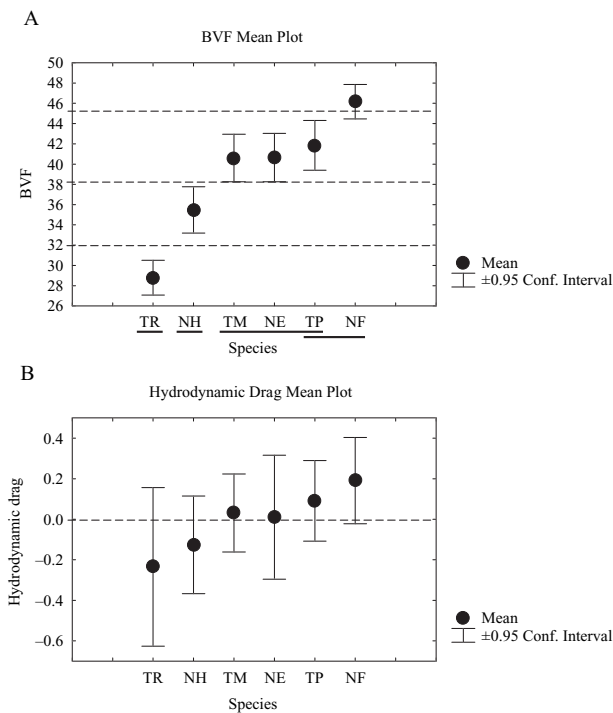|	d.f.	F	P
Head width (PC 1)	5,245	80.93	<0.0001
Snout length (PC 2)	5,245	11.39	<0.0001
BVF	5,174	30.09	<0.001
Hydrodynamic drag	5,25	2.598	0.05

A

B

Figure 3. A, plot of mean BVF ± 1 SE by species. Dashed lines denote values of BVF that correspond to character state changes according to the coding method described by Thorpe (1984). Bold lines beneath species abbreviations indicate significantly distinct subsets ($P < 0.05$) according to Tukey's post hoc comparisons following ANOVA. B, plot of mean hydrodynamic drag ±1 SE by species. The dashed line denotes values of hydrodynamic drag that correspond to character state changes.

states for BVF. However, *N. erythrogaster*, *T. proximus* and *T. marcianus* all coded similarly for BVF. Gap coding produced two character states for hydrodynamic drag. *T. rufipunctatus* and *N. harteri* were grouped in their own character state and all other species formed the other group. (Fig. 4)

DISCUSSION

Thamnophis rufipunctatus and *N. harteri* are visual predators (de Queiroz, 1992; T. Hibbitts, unpubl. data), in contrast to the other four natricines (Drummond, 1983, 1985; A. de Queiroz, pers. comm.; Mushinsky *et al.*, 1982). *T. rufipunctatus* and several other natricine species have independently evolved mechanisms for increased underwater visual acuity (Schaeffel & de Queiroz, 1990). The evolution of these mechanisms emphasizes the importance of vision in the foraging behaviour of highly aquatic natricine snakes. We predicted these visually orientated predators would exhibit large values for BVF because they would benefit from increased depth perception.
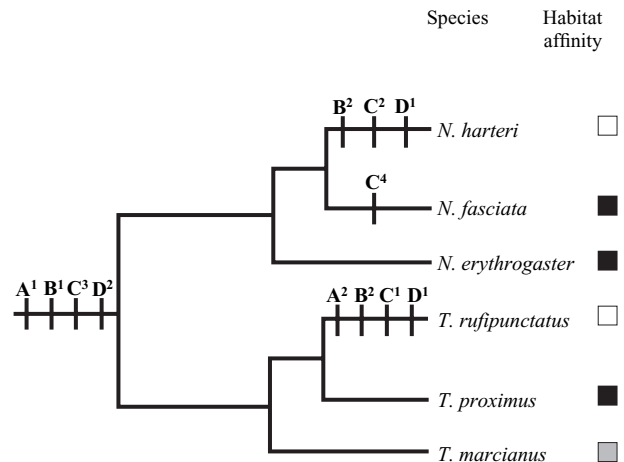

Figure 4. Cladogram of the focal species showing convergence in morphological traits of the head, functional performance measures of those traits and habitat affinity of the species. The characters head width and snout length are represented by A and B. C and D represent the functional measures of BVF and hydrodynamic drag. Superscripts denote states of those characters (Thorpe, 1984). Habitat affinity is shown for each species: open box equals stream riffle specialization, black box equals any permanent water bodies and grey box equals terrestrial and ephemeral aquatic habitats.

However, our results showed BVF was reduced in *T. rufipunctatus* and *N. harteri*, contradicting the expectation for visually hunting predators. Reduced BVF was a functional consequence of narrow head width and long snout length in these snakes, because the relatively small distance between the eyes and the relatively long snouts resulted in low angles of overlap in the field of vision of each eye. Because the visually orienting foragers in this study each had a small BVF that was independently derived, we presume there was neither a performance advantage nor disadvantage to this trait as it relates to foraging.

Hydrodynamic drag was also clearly a consequence of head morphology. The experimental trials showed elongate snouts were more hydrodynamic while facing forward in a current. *T. rufipunctatus* and *N. harteri* wait in ambush for fish by anchoring their bodies and holding their position in a current to strike at prey underwater (de Queiroz, 1992; T. Hibbitts, pers. observ.; Werler & Dixon, 2000). It is reasonable and likely that for aquatic snakes a hydrodynamic head shape enhances their ability to hold position while facing into a current. It also may allow for faster forward striking speeds underwater.

Young (1991) discussed in detail hydrodynamic flow around the head while striking frontally and laterally. He determined that during a frontal strike, turbulence

increased in line with gape and hydrodynamic advantages conferred by head shape were quickly overwhelmed when the mouth opened. Interestingly, Alfaro (2002) found that in *T. rufipunctatus* peak head acceleration coincided with peak gape, suggesting that it may have evolved a way to overcome the turbulence involved during a frontal strike. In a lateral strike, turbulence around the snake's head was greater than during a frontal strike with the mouth closed, but did not increase with the mouth open. This helps explain the prevalence of lateral sweeps in aquatic foraging organisms such as natricine snakes, gar (*Lepisosteus* spp.) and crocodilians. *N. harteri* and *T. rufipunctatus* are therefore unusual in their use of forward strikes underwater.

Young (1991) also predicted the ideal head characteristics for aquatic snakes would be minimum surface area and minimal amount of drag. This could be accomplished by achieving small head size or a long narrow head. However, the former constrains prey size in snakes (Shine, 1991) while the latter is less optimal for handling captured prey due to the relatively limited lateral movements of the jaws (Young, 1991). The evolution of a more frontally hydrodynamic head shape, as in *T. rufipunctatus* and *N. harteri*, may be important for foraging effectiveness in aquatic feeding specialists that employ quick strikes in currents.

Drummond (1983) noted that among garter snakes aquatic specialists tended to use forward strikes, a finding consistent with our observations and published reports on *N. harteri* and *T. rufipunctatus* (de Queiroz, 1992; T. Hibbitts, pers. observ.; Werler & Dixon, 2000). Alfaro (2002) determined that during forward strikes *T. rufipunctatus* and *T. couchii* (Kennicott, 1859) were able to strike at speeds up to 1.2 m/s. The more general lateral sweep, open-mouth foraging mode would not benefit from frontally decreased hydrodynamic drag, and species that use lateral sweeps are not expected to evolve a frontally hydrodynamic head shape.

Our aim was to clarify a similar pattern of evolution in two morphologically similar species, and we observed this pattern. Due to the location of the narrow head morphology in the *Thamnophis* clade (Fig. 4), we consider head width less important than snout elongation as a means of reducing hydrodynamic drag and BVF. Recent research on *Thamnophis* and *Nerodia* systematics based on DNA sequence of the ND1, ND2, ND4 and cyt *b* genes (de Queiroz *et al.*, 2002) places *T. rufipunctatus* and *T. marcianus* closer to each other than either is to *T. proximus* with high bootstrap support for that relationship. Data provided by R. Lawson, A. de Queiroz and A. L. Lemos-Espinal (pers. comm.) concerning the relationships within *Nerodia* support our results. Changes in relationships within the *Thamnophis* or *Nerodia* clades would not affect the results or conclusions presented here because *T. rufipunctatus* and *N. harteri* are each very different from all their congeners.

If environments impose constraints on the adaptations of organisms, and they are expressed simultaneously in their morphology and their ecology, then predictions can be made as to which morphological attributes are associated with a specific ecology and vice versa (Kerr & James, 1975). For instance, in studies of flea morphology, Traub (1980) found that the various modifications to the species' hairs, bristles and spines were convergent specializations for living on the same mammalian or avian hosts. These specializations were so profound that by analysing a flea's hairs, bristles and spines, one could make correct statements about attributes of the host (Traub, 1980).

Similarly, our finding that ecomorphological specializations in *T. rufipunctatus* and *N. harteri* for life in rocky flowing streams are due to convergence allows us to make predictions about the morphology of other natricine species occupying similar ecological niches. The natricine snakes are a widely ranging, speciose group and other cases of ecomorphological convergence may exist in the clade that have not been explored. It is likely, for example, that *T. couchii*, an aquatic garter snake in California, and *Natrix tessellata* (Laurenti, 1768), an aquatic species in Europe, also have independently evolved head shapes similar to those of *N. harteri* and *T. rufipunctatus*. Additional research will help improve our understanding of the complex relationships between traits, their functions, performance consequences and adaptive value. The addition of more taxa will better elucidate the occurrence of convergence in morphological and functional adaptations in species occurring in similar environments.

Thamnophis rufipunctatus and *N. harteri* are allopatric and inhabit similar ecological niches. The elongate snout morphology evolved twice in these natricine snakes, and it is doubtful that the convergent evolution in morphology and ecology was due to chance. Therefore, we suggest the elongate snout and resultant function to reduce hydrodynamic drag is consistent with the hypothesis that these features are an adaptation for maintaining position in swift water and for foraging. The elongate snout morphology was determined not to be an adaptation for increased BVF. Future research that measures effectiveness of striking prey in swift water could reveal more about the performance advantages of snout length in aquatic snakes.

ACKNOWLEDGEMENTS

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