

Correlated evolution of aquatic prey-capture strategies in European and American natricine snakes

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The evolution of aquatic prey-capture strategies in snakes has been suggested as a model system for the study of convergence. However, hypotheses of correlated evolution of prey-capture strategy with different aspects of foraging niche have never been tested quantitatively. Whereas a considerable amount of data is available for North American species, data for European species are scarce. In this study we combine original data on prey-capture strategies and strike velocities for European natricines with data for North American Natricinae obtained from the literature. We did not find any evidence for correlated evolution between prey-capture strategy and strike velocity with diet, but there was a significant correlation with prey density. Thus, our study suggests that prey density, rather than diet, played an important role in the evolution of the different prey-capture strategies and strike velocities of natricine snakes. © 2006 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2006, 88, 73–83.

ADDITIONAL KEYWORDS: diet – foraging behaviour – *Natrix maura* – *Natrix tessellata* – prey density – strike velocity.

INTRODUCTION

Aquatic feeding in snakes has been suggested as a model system with which to study evolutionary convergence and divergence (Alfaro, 2002, 2003). More than 300 snake species, belonging to six snake families, feed on aquatic prey (e.g. Kofron, 1978; Greene, 1997; May & Farrell, 1998; Pough *et al.*, 2001). The invasion of the aquatic niche has been achieved most successfully within the group Natricinae. More than 100 natricine species have invaded the aquatic niche to varying degrees, some feeding almost exclusively on aquatic prey (i.e. specialists), whereas others also exploit terrestrial prey like frogs, toads, worms and slugs (i.e. generalists; see Table 1 for references).

This difference in diet within the Natricinae appears to be associated with a difference in prey-capture strategy (Table 1): specialists seem to forage predominantly by pursuing actively prey and/or by waiting motionless until prey passes by ('sit-and-wait' strategy). Additionally, they tend to orientate visually

towards the prey before attacking it. They perform mostly fast frontal strikes, characterized by movement of the head forward, i.e. parallel to the long axis of the snake. Generalists, on the other hand, tend to forage by sweeping the head from side to side through the water with jaws opened widely ('open-mouth searching' (Drummond, 1983; cf. 'fishing' in Evans, 1942). When they strike, they move their head sideways, i.e. perpendicular to the long axis of the snake. These strikes tend to be slow and seem to be initiated predominantly by tactile cues. The latter implies that generalist snakes typically do not orientate visually to the prey prior to striking (for references see Table 1).

The apparent association between diet (specialist/generalist) and prey-capture strategy within the Natricinae has been suggested to reflect the correlated evolution of these two traits (Drummond, 1983; Alfaro, 2002, 2003). The sit-and-wait and active-pursuit behaviour, visual orientation and fast frontal strike of specialists are thought to enhance the chances of successful prey capture in water. Some piscivorous snakes have been demonstrated to possess a narrow elongated head (Marx & Rabb, 1972). Such a head shape is thought to be hydrodynamically advantageous, and

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Table 1. Diet, prey-capture strategy, average peak strike velocity and prey density of North American and European natricine snakes

Species	Diet	Prey-capture strategy	Average peak strike velocity (cm/s)	Prey density	References
<i>Nerodia clarkii</i>	Fish	Sit and wait and pursuit; frontal strike	89* ($N = 5$)	Feed on prey in low densities	Mullin & Mushinsky (1995); A. Herrel & S. E. Vincent (pers. comm.)
<i>Ne. cyclopion</i>	Fish	Open-mouth searching; lateral strike	24* ($N = 4$)	Feed on concentrated prey in shallow water and land–water interface	Mushinsky & Hebrard (1977); Kofron (1978); Vincent (pers. com.)
<i>Ne. erythrogaster</i>	Mainly frogs (toads, tadpoles, fish)	Open-mouth searching; lateral strike		Feed on concentrated prey in shallow water and land–water interface	Evans (1942); Mushinsky & Hebrard (1977); Kofron (1978); Mushinsky, Hebrard & Vodopich (1982)
<i>Ne. fasciata</i>	Fish and frogs (tadpoles)	Open-mouth searching; lateral strike	67 ($N = 4$)	Feed on concentrated prey in shallow water and land–water interface	this study; Mushinsky & Hebrard (1977); Kofron (1978); Miller & Mushinsky (1990)
<i>Ne. harteri</i>	Fish	Frontal strike		Feed on benthic prey in riffles; the majority of strikes is aimed at individual prey	Scott et al. (1989); Greene et al. (1994); Hibbits (2000)
<i>Ne. rhombifer</i>	Fish	Open-mouth searching and sit and wait; no visual orientation; lateral strike	84 ($N = 3$)	Feed on concentrated prey in shallow water and land–water interface	Mushinsky & Hebrard (1977); Kofron (1978); Alfaro (2003)
<i>Ne. sipedon</i>	Mainly fish (amphibians)	Open-mouth searching, sit and wait and pursuit; no visual orientation; lateral strike		Feed on schools of fish in shallow water	Evans (1942); Brown (1958); Drummond (1983); King (1993)
<i>Thamnophis couchii</i>	Mainly fish and tadpoles (frogs, aquatic salamanders)	Sit and wait and pursuit; visual orientation; frontal strike	114 ($N = 6$)	Feed in bodies of permanent water; low prey density	Drummond (1983); Alfaro (2002), (2003); M. E. Alfaro & A. Herrel (pers. comm.)

<i>T. elegans</i>	Slugs and fish	Open-mouth searching, sit and wait and pursuit; lateral strike	46† ($N = 3$)	Feed often on fish and tadpoles trapped in drying pools, but also on lake fish	Arnold (1977); Gregory (1978); Drummond (1983); Gregory (1984); Alfaro (2003)
<i>T. marcianus</i>	Mainly amphibians and their larvae (fish, earthworms, slugs)	Frontal strike		Feed on prey in high densities	Woodward & Mitchell (1990); Rossman, Ford & Siegel (1996); Werler & Dixon, 2000; Stebbins, 2003; A. Herrel & S. E. Vincent (pers. comm.)
<i>T. melanogaster</i>	Fish, tadpoles and leeches	Sit and wait and pursuit; frontal strike			Drummond (1983); Garcia & Drummond (1990)
<i>T. rufipunctatus</i>	Fish	Sit and wait and pursuit; visual orientation; frontal strike	79 ($N = 3$)	Forage in stream riffles; the majority of strikes is aimed at individual prey	Hibbits (2000); Alfaro (2002)
<i>T. sirtalis</i>	Amphibians and worms (invertebrates, fish, birds, mammals)	Open-mouth searching, sit and wait and pursuit; no visual orientation; lateral strike	20† ($N = 4$)	Feed on fish and tadpoles overcrowded and trapped in drying pools, in shallow pools and shorelines	Gregory (1978); Drummond (1983); Gregory (1984); Gregory & Nelson (1991); Alfaro (2002)
<i>Natrix maura</i>	Frogs, fish, tadpoles and worms	Sit and wait and pursuit (and open-mouth searching); visual orientation; frontal strike	102 ($N = 6$)	Permanent bodies of still and moving water; dispersed prey	this study; Galan (1988); Pleguezelos & Moreno (1989); Santos & Llorente (1998); Schätti (1999); Santos et al. (2000); J. Billeke & A. Herrel (pers. observ.)
<i>Na. tessellata</i>	Fish	Sit and wait and pursuit (and open-mouth searching); visual orientation; frontal strike	93 ($N = 8$)	Permanent bodies of slow and fast moving water; dispersed prey	this study; Luiselli & Rugiero (1991); Filippi et al. (1996); Gruschwitz et al. (1999); J. Billeke & A. Herrel (pers. observ.)

*Maximum peak strike velocities. †Average peak strike velocities of frontal strikes.

presumably allows for fast strikes under water (Young, 1991; Hibbits, 2000), which may increase the chances of prey capture (Drummond, 1983; Alfaro, 2002). Moreover, some natricine specialists possess a visual system adapted to seeing under water (Schaeffel & De Queiroz, 1990). This might allow them to visually locate prey either when using a sit-and-wait strategy or when in active pursuit (Drummond, 1983), thus increasing the chances of successful capture. Generalists, on the other hand, may lack such adaptations to the aquatic environment, because potentially they are disadvantageous for capturing terrestrial prey. For instance, a long and narrow head is likely to be unsuitable for swallowing large and bulky terrestrial prey such as frogs. Moreover, some generalists have been shown not to possess a visual system adapted to seeing under water (Schaeffel & De Queiroz, 1990). Open-mouth searching may therefore be an alternative strategy for capturing aquatic prey, based on tactile, rather than visual, cues.

Another hypothesis presented in the literature is that the different prey-capture strategies within the Natricinae are correlated with the density of prey on which the snakes feed (Drummond, 1983; Alfaro, 2003). Several snakes feed almost exclusively on prey that occurs in extremely high densities, for example, large numbers of fish trapped in drying pools (Table 1). Open-mouth searching may have evolved to forage under such conditions, since the chances of prey contact are high and thus a strategy that maximizes prey contact is efficient. However, for snakes that forage in rivers and lakes where fish are more dispersed, it is likely that the effort to sweep the head from side to side becomes too high compared with the chances of touching the prey. In such circumstances it may be more efficient to sit and wait for prey, a strategy that demands less energy, or to (visually) locate prey and then actively pursue it. Moreover, a fast strike enhances the chances of successful capture (Drummond, 1983; Alfaro, 2002), which can be important when the prey encounter rate is low.

However, neither of these hypotheses has been tested quantitatively to date. Such a test requires multiple independent evolutionary events (Savitzky, 1983). Whereas a considerable amount of information on prey-capture strategies is available for the *Thamnophiini* (i.e. North American Natricinae; genera *Thamnophis* and *Nerodia*) (Table 1), few data are available for the European Natricinae of the genus *Natrix*. However, including the European natricine snakes in a comparative analysis would make such a test more powerful, as this group of snake species has evolved independently of their North American counterparts (Fig. 1). Moreover, the European Natricinae include both generalized species such as *Na. maura* (Linnaeus 1758), which feed on fish, amphibians and

their larvae (Galan, 1988; Pleguezuelos & Moreno, 1989; Santos & Llorente, 1998; Schätti, 1999; Santos, González-Solis & Llorente, 2000), and specialized piscivores such as *Na. tessellata* (Laurenti 1768) (Luiselli & Rugiero, 1991; Filippi *et al.*, 1996; Gruschwitz *et al.*, 1999). Both species feed on prey in low densities. Until now, however, only data on the foraging behaviour of *Na. maura* have been reported (Hailey & Davies, 1986a, b).

The goal of this study was to test for correlated evolution of aquatic prey-capture strategies and performance with diet and prey density in natricine snakes. To do so, we first documented the prey-capture strategies and performance employed by the two species of European Natricinae known to capture prey in water (*Na. maura* and *Na. tessellata*). We also tested whether the two species differ significantly from each other in these characteristics. Second, we tested for a correlation between prey-capture strategy and strike velocity with diet and prey density, while taking into account phylogenetic relationships among the species used in the study. Data on prey-capture strategies and strike velocities of North American Natricinae were obtained from the literature and combined with the data for the European Natricinae described here. Additionally, we determined the strike velocity for *Ne. fasciata* (Linnaeus 1766), an American natricine for which no performance data were available in the literature.

MATERIAL AND METHODS

EUROPEAN NATRICINAE: PREY-CAPTURE STRATEGY AND PERFORMANCE

Study organisms and husbandry

Six *Na. maura* (three males and three females; mean \pm SE snout–vent length (SVL): 368 \pm 18 mm) and eight *Na. tessellata* (three males, four females and one individual of unknown sex; mean \pm SE SVL: 404 \pm 37 mm) were used in the experiments. Animals were housed in glass terraria (100 \times 50 \times 40 cm) containing a sandy substrate, shelter, vegetation and a tub filled with water. Snakes were fed weekly with goldfish *Carassius auratus* (Linnaeus 1758). A 100-W light bulb suspended 20 cm above the substrate provided heat and light for 9 h a day.

Feeding experiments

At the beginning of the experiments two to three goldfish of a similar relative prey mass (i.e. mean \pm SE prey mass/snake mass: 10.3 \pm 0.4%) were placed in a plexiglass vivarium (120 \times 42 \times 22 cm). The vivarium was divided into a terrestrial section (55 \times 22 cm) with shelter and an aquatic section (65 \times 22 \times 15 cm) kept at 25 °C (average temperature at which *Na. maura*

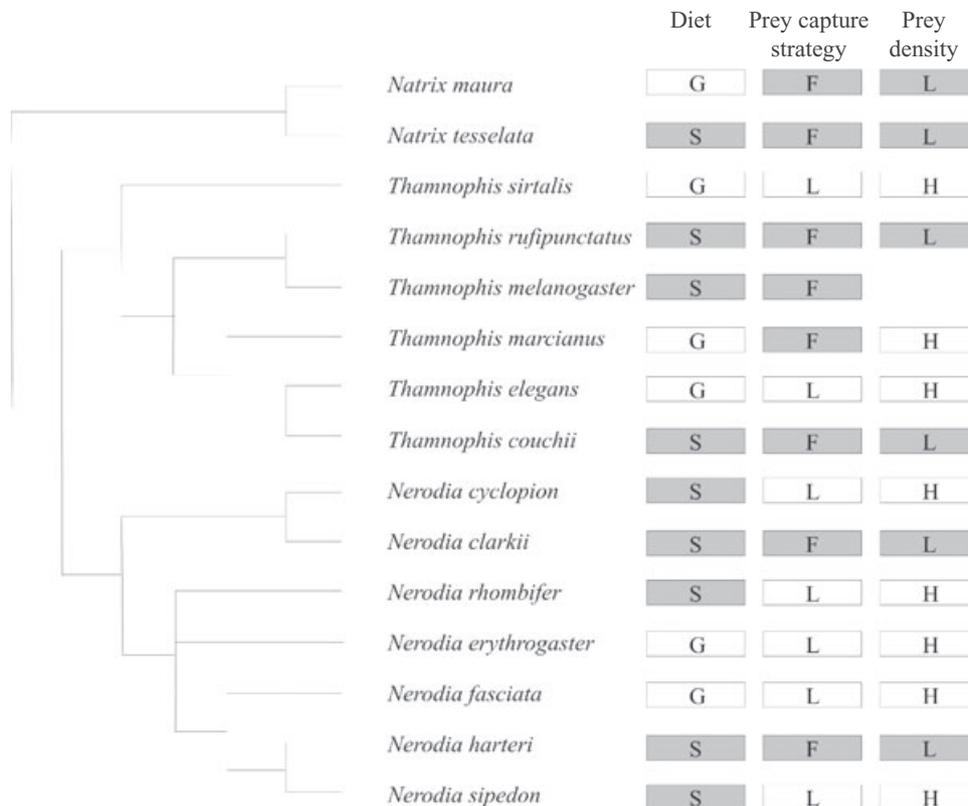


Figure 1. Phylogenetic relationships of the Natricinae considered in this study. The tree is consistent with both maximum parsimony and maximum likelihood trees recovered by Alfaro & Arnold (2001). Under maximum parsimony analysis, the placement of *Nerodia erythrogaster* as sister to *Ne. rhombifer* is equally parsimonious with its position as the sister group to *Ne. fasciata*, *Ne. sipedon* and *Ne. harteri*, whereas under maximum likelihood, this latter topology is preferred (Alfaro & Arnold, 2001). The *Thamnophis* species *T. rufipunctatus*, *T. melanogaster* and *T. couchii* were added to the tree, based on their positions as shown in De Queiroz, Lawson & Lemos-Espinal (2002). Next to each species its diet (Specialist/Generalist), prey-capture strategy (Frontal-striking/Lateral-striking) and prey density (Low/High) are shown. Traits expected to have evolved in a correlated fashion are shown in similar colours (white/grey). See text for the definition of the different categories used.

forages in nature; see Hailey & Davies, 1986b; Schätti, 1999). Subsequently, a snake was introduced into the experimental cage and filmed until all the fish had been eaten, using a Panasonic F15 ccd video camera (Matsushita, Osaka, Japan; 50 Hz). A mirror was placed at an angle of 45° relative to the bottom of the vivarium. This allowed simultaneous recording of lateral and ventral views, from which three-dimensional information could be obtained (see below). The cage with the snake stood in an undisturbed room (i.e. without experimentors). If a snake did not attempt to strike at a fish within 2 h, the trial was finished and repeated on the following day(s). Trials were conducted until all snakes had performed at least five successful strikes. A strike was regarded as successful when the fish was captured. A strike was considered as unsuccessful when the snake missed the fish or released it within 1 s after capture. Video sequences were used to describe qualitatively the prey-capture

strategies of the two species and were analysed to obtain quantitative data on their foraging behaviour, strike performance and capture success.

Foraging behaviour: As quantitative measures of foraging behaviour, we noted for each snake the proportion of its total foraging time that it spent performing each of the following behaviours: 'sit and wait', i.e. the snake waited motionless until prey passed by; 'pursuit', i.e. the snake actively chased prey; 'open-mouth searching', i.e. the snake swept its head from side to side through the water with jaws opened wide (Drummond, 1983). The total foraging time for each snake was calculated as the sum of the foraging bouts during all sequences (mean \pm SE: 3242 \pm 1100 s).

Strike performance: Each strike sequence was digitized frame-by-frame using a NAC X-Y coordinator. The beginning of a strike was defined as the frame preceding any noticeable head movement (Alfaro, 2002). The end of a strike was defined as the frame

after prey contact (Alfaro, 2002), or, in the case of a miss, the frame in which the displacement of the head declined noticeably from one frame to the next. Video coordinates were transformed to real-world data and the snout tip of the snake in lateral (x - and y -coordinates) and ventral (x - and z -coordinates) views was digitized. From these two sets of coordinates, the three-dimensional positions (x -, y - and z -coordinates) from the snout tip of the snake were obtained. For each strike, the snake's strike velocity and average strike acceleration were determined. The latter was calculated as the difference between maximum strike velocity and velocity at the beginning of a strike, divided by the time elapsed between the beginning of the strike and the moment at which the snake reached maximum strike velocity.

Capture success: The capture success of each snake was calculated as the percentage of successful strikes and was the total number of strikes over all sequences.

Statistics

Shapiro–Wilks tests were used to check the continuous data (foraging behaviour, strike performance variables and capture success) for normality, and data were \log_{10} transformed when appropriate. If the distribution of the data remained skewed after \log_{10} transformation, nonparametric tests were used. To test for differences in foraging behaviour (% sit and wait and percentage pursuit) and capture success between *Na. maura* and *Na. tessellata*, the nonparametric Mann–Whitney U -test was used. The strike performance variables (average peak strike velocity and average mean strike acceleration) were analysed using a nested ANOVA (individual nested within species). SVL was not included as a covariable in the latter analysis, because the species did not differ significantly in SVL ($t_{12} = 0.69$, $P = 0.51$).

NERODIA FASCIATA: STRIKE VELOCITY

We filmed the strikes of four *Ne. fasciata* (mean \pm SE SVL: 528 ± 38 mm) to obtain peak strike velocities. Husbandry and the experimental set-up were similar to those used for *Natrix*, except for the small differences reported hereafter. The experimental vivarium was slightly smaller ($45 \times 22 \times 20$ cm), with a terrestrial section 11 cm in width. *Ne. fasciata* were filmed using a Redlake MotionPro high-speed video camera (San Diego, USA; 250Hz) and each strike was digitized using the Midas digitizing routine.

COMPARATIVE ANALYSIS

We used a comparative method to test for an evolutionary association between prey-capture strategy and performance with diet and with prey density. Data on

diet, prey density, foraging and strike behaviour and strike velocities of *Thamnophiine* snakes were obtained from the literature (see Table 1) and to these were added the data on *Na. maura*, *Na. tessellata* and *Ne. fasciata* described in this study. Species were categorized as having a specialist ('S', i.e. feeding mainly on aquatic prey) or generalist ('G', i.e. feeding on aquatic and terrestrial prey) diet (Fig. 1). With regard to prey density, we distinguished species that generally feed on aquatic prey dispersed in large bodies of open water ('L', i.e. at low prey densities) and species that feed on aquatic prey in extremely high densities ('H') (Fig. 1, Table 1). In the latter case, snakes typically foraged in drying pools or shallow water containing large numbers of fish. Species were also divided into one of two categories of prey-capture strategy: (1) mainly sitting and waiting and/or pursuing, orientating visually to the prey and then striking frontally, henceforth referred to as the 'frontal-striking' strategy ('F'); (2) predominantly open-mouth searching resulting in a lateral strike without visual orientation towards the prey, henceforth referred to as the 'lateral-striking' strategy ('L') (Fig. 1). Average peak strike velocities of natricine snakes were also taken from the literature. When we found different values for a single species, the highest value was used (Table 1).

Statistics

We tested for a correlation between prey-capture strategy and strike velocity with diet and prey density both using the conventional statistical methods and using phylogenetically based statistical analyses. The phylogenetic tree used for the latter is represented in Figure 1. The position of *Ne. erythrogaster* is still unclear: placement of it as sister to *Ne. rhombifer* is equally parsimonious with its position as the sister group to *Ne. fasciata*, *Ne. sipedon* and *Ne. harteri* (Alfaro & Arnold, 2001). Because of this uncertainty, we performed all phylogenetical analyses with the two possible positions of *Ne. erythrogaster*. As all analyses rendered similar results, we only report the results from the phylogenetic analyses based on the tree in which *Ne. erythrogaster* is positioned as the sister group of *Ne. fasciata*, *Ne. sipedon* and *Ne. harteri*.

Differences in prey-capture strategy according to diet and prey density within natricine snakes were nonphylogenetically tested using a χ^2 -test. Differences in strike velocity between species with different diets and prey density conditions were tested using a conventional ANOVA. Strike velocity data were first \log_{10} transformed to obtain a normal distribution. SVL was not included as a covariable in this analysis, because there was no significant association between SVL and strike velocity ($F_{1,8} = 1.50$, $P = 0.26$).

Taking phylogeny into account, we tested for correlated evolution of the binary traits prey-capture

strategy (frontal/lateral striker) with diet (specialist/generalist) and prey density (high/low) using the program Discrete (Pagel, 1994). This program compares the fit (likelihood) of two evolutionary models with the data. In the first model the two binary traits in consideration are allowed to evolve independently (independent evolution model). For the independent evolution model, the program estimates transition rate parameters (p_i) to characterize the evolution of the traits. These parameters give the rates at which a trait (e.g. diet) changes from one state to another along the branches of the phylogenetic tree (e.g. specialist evolves towards generalist). For this model, four transition rate parameters are sufficient to characterize the evolutionary possibilities of the two traits: each trait evolves independently of the other, in a forward or backward manner (as shown in Fig. 2A). The program calculates the four parameters that render the model which best fits the actual data (i.e. the model with the highest log-likelihood value). This maximum log-likelihood value is then compared with the value of the second model, the correlated evolution model, which presumes the two traits to evolve in a correlated (dependent) fashion. That is, the transition rate from one state to another for trait 1 (e.g. diet) depends on the state of trait 2 (e.g. prey-capture strategy). Thus, this model considers four possible states that the two traits can adopt jointly [(specialist, frontal) (specialist, lateral) (generalist, lateral) and (generalist, frontal)]. Then it allows one of the variables to change state in any branch of the tree, yielding eight possible transitions to be estimated (as shown in Fig. 2B). The program calculates the eight-parameter dependent evolution model with the maximum log-likelihood. Subsequently, the program compares the two models by calculating the likelihood ratio statistic (as the difference between the log likelihoods of the

two evolution models) and its P -value (for d.f. = 4 = the difference in number of parameters estimated between the two models). Evidence for a correlation between the two traits in consideration is found if the eight-parameter model of correlated evolution fits the data significantly better than does the four-parameter model of independent trait evolution.

To get some indication of how much better the best model was compared with the alternative model, we calculated the ratio of Akaike weights of the two models [based on their Akaike Information Criterion correction (AICc) values (Sugiura, 1978; Hurvich & Tsai, 1989)].

To test if the average peak strike velocity differed according to diet and prey density within natricine snakes we ran a phylogenetically corrected ANOVA using the program PDAP (Garland *et al.*, 1993). First, we entered the phylogenetic tree of the natricine species for which peak strike velocity was obtained, in the PDTREE program (branch lengths set to unity; Garland, Midford & Ives, 1999), with average peak strike velocity as tip variable. Next, this tree was entered into the PDSIMUL program (Garland *et al.*, 1993). This program computed 1000 simulations of average peak strike velocity to the tips of the phylogenetic tree for the gradual Brownian motion model of evolutionary change. These 1000 simulated values for the average peak strike velocity were then entered into the PDANOVA program (Garland *et al.*, 1993), which then computed 1000 F -statistics for each simulation. If the F -statistic from the ANOVA of the real data (nonphylogenetic analysis) exceeds the critical F -value of the simulated data (i.e. the F -value for $\alpha = 0.05$, thus the 950th largest value), there is evidence for correlated evolution of average peak strike velocity with the trait in consideration (diet or prey density).

RESULTS

EUROPEAN NATRICINAE: PREY-CAPTURE STRATEGY AND PERFORMANCE

Foraging and strike behaviour

The prey-capture strategies of *Na. tessellata* and *Na. maura* were very similar. Below is a general description that applies to both species.

Upon detecting a fish, snakes initiated a sit-and-wait strategy or started pursuing the prey by moving their head (and body) towards it, mostly in an unsteady manner (i.e. in short, discrete bouts of movement). Both behaviours were performed on land as well as in water and snakes frequently switched from one type of behaviour to the other.

Na. tessellata and *Na. maura* did not differ significantly in overall foraging behaviour ('sit and wait', $U = 22.00$, $N = 14$, $P = 0.80$; 'pursuit', $U = 22.00$,

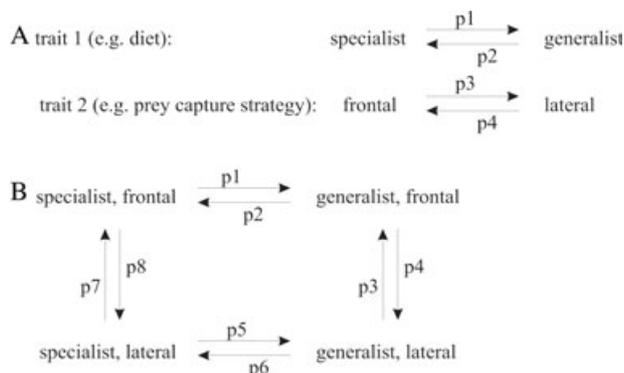


Figure 2. Schematic representation of the evolutionary transition possibilities of two binary traits that evolve (A) independently and (B) dependently. p_1 – p_8 represent the transition rate parameters.

$N = 14$, $P = 0.80$). They both spent more than half of the foraging time 'sitting and waiting' (mean \pm SE: *Na. tessellata*: $59 \pm 11\%$; *Na. maura*: $66 \pm 10\%$). The third type of foraging behaviour, open-mouth searching, was observed seldom, and was only used after unsuccessful strikes. Most unsuccessful strikes, however, were followed by recoiling, a renewed orientation towards the prey and a new strike. Except for the few lateral strikes following open-mouth searching, all strikes were frontal and made either from air into the water (42%) or while fully submerged (58%).

Strike performance

Strike initiation involved rapid acceleration of the head towards the prey item. *Na. maura* and *Na. tessellata* did not differ in average peak strike velocity ($F_{1,12.5} = 0.42$, $P = 0.53$; mean \pm SE: *Na. tessellata*: 0.93 ± 0.03 m/s; *Na. maura*: 1.02 ± 0.03 m/s), or in average strike acceleration ($F_{1,13.0} = 0.01$, $P = 0.93$; mean \pm SE: *Na. tessellata*: 8.3 ± 0.4 m/s²; *Na. maura*: 9.0 ± 0.4 m/s²). However, interindividual variation existed in both average peak strike velocity ($F_{12,305} = 8.80$, $P < 0.001$) and average strike acceleration ($F_{12,272} = 4.10$, $P < 0.001$).

Capture success

Significantly more strikes of *Na. tessellata* compared with *Na. maura* ended in successful captures (mean \pm SE: $35 \pm 8\%$ and $20 \pm 3\%$, respectively; $U = 9.00$, $N = 14$, $P = 0.05$). However, again there was considerable interindividual variation, with individual capture success varying from 10% to 82%.

NERODIA FASCIATA: STRIKE VELOCITY

As described previously in the literature (Mushinsky & Hebrard, 1977), *Ne. fasciata* foraged on fish by employing open-mouth searching behaviour almost exclusively. Peak strike velocities during lateral sweeping reached an average of 67 cm/s.

COMPARATIVE ANALYSIS

We categorized seven species as diet specialists and eight as diet generalists. Of these 15 species, we characterized two *Nerodia* species, four *Thamnophis* species and the two *Natrix* species as 'frontal strikers', and five *Nerodia* and two *Thamnophis* species as 'lateral strikers'. For ten of these natricine species the average peak strike velocities were available. The SVL of these species ranged from 37 cm (*Na. maura*) to 63 cm (*Ne. rhombifer*) (Fig. 1 and Table 1).

Diet-prey-capture strategy

The prey-capture strategy of natricine snakes is not correlated with diet, as suggested by both nonphylo-

genetic analyses ($\chi^2 = 2.29$, d.f. = 1, $P = 0.13$) and phylogenetic analysis. In the latter case, the model of correlated evolution (final likelihood = -18.26) did not fit the data better than did the model of independent evolution (final likelihood = -19.07) (likelihood ratio = 0.82, $P = 0.94$). The model of independent evolution (AICc = 50.14) fitted the data 535044 (= ratio of Akaike weights) times better than did the model of correlated evolution (AICc = 76.52).

Diet-strike velocity

Piscivorous snakes do not strike significantly faster than do more generalist snakes, as indicated by both conventional ANOVA ($F_{1,8} = 1.11$, $P = 0.32$) and phylogenetically based analysis [the F -value of the conventional analysis was lower than was the critical F -value (= 4.46) obtained using the phylogenetic analysis ($P = 0.31$)]. Dietary specialist and generalist Natricinae reached mean \pm SE peak velocities of, respectively, 81 ± 12 m/s and 59 ± 17 m/s.

Prey density-prey-capture strategy

Non-phylogenetic analysis showed that snakes feeding on fish in low densities use a 'frontal-striking' strategy, whereas snakes feeding on fish in high densities use the 'lateral-striking' strategy ($\chi^2 = 10.5$, d.f. = 1, $P = 0.001$). However, taking phylogenetic relationships into account, the model of correlated evolution (final likelihood = -11.21) did not fit the data better than did the model of independent evolution (final likelihood = -17.88) (likelihood ratio = 6.67, $P = 0.15$). The model of independent evolution (AICc = 48.20) fitted the data 13494 times better than did the model of correlated evolution (AICc = 67.22).

Prey density-strike velocity

Snakes that feed on fish in low densities strike significantly faster than do snakes that feed on fish in high densities (mean peak strike velocity \pm SE: 95 ± 6 m/s and 48 ± 12 m/s, respectively). This was indicated by both nonphylogenetic analysis ($F_{1,8} = 11.96$, $P = 0.01$) and phylogenetically based analysis [the F -value of the conventional analysis was larger than was the critical F -value (= 5.35) in the phylogenetic analysis ($P = 0.01$)].

DISCUSSION

The goal of this study was to test for correlated evolution of aquatic prey-capture strategy with (1) diet and (2) prey density. Specifically, we tested the hypotheses that dietary specialists and/or snakes foraging on prey in low densities, evolved sit-and-wait and/or pursuit-foraging behaviour, orientating visually towards prey before performing a fast frontal strike ('frontal-striking' strategy). Dietary generalists and/or species

foraging on prey in high densities were expected to have evolved an open-mouth searching foraging behaviour and to strike laterally and slowly, without prior visual orientation towards the prey ('lateral-striking' strategy). Consistent with what we would expect from both hypotheses, we found the specialized piscivore *Na. tessellata* to use a sit-and-wait and pursuit-foraging strategy. Furthermore, this species orientated visually towards prey before performing a fast frontal strike. Although the generalized species *Na. maura* sporadically shows open-mouth searching behaviour (this study; Hailey & Davies, 1986b), it behaves and performs largely similarly to *Na. tessellata*. This is in contrast to the predictions of the first hypothesis (correlated evolution of prey-capture strategies with diet), but is in accordance with the second hypothesis (correlated evolution of prey-capture strategies with prey density) as both species feed on prey in low densities. Moreover, the specialized piscivores *Ne. cyclopion*, *Ne. rhombifer* and *Ne. sipedon* use a 'lateral-striking' strategy despite their specialist diets, but all feed on prey in relatively high densities (Fig. 1). Thus, within natricine snakes there appears to be a better association of prey-capture strategy with prey density than there is with diet (Fig. 1). This suggests that the different prey-capture strategies evolved in conjunction with foraging at different prey densities rather than differences in diet *per se*.

This view is also supported by our quantitative comparative analyses: whereas we did not find evidence for correlated evolution between prey-capture strategy and strike velocity with diet, we did find a significant correlation of prey density with strike velocity and prey-capture strategy.

Fast strikes thus appear to have evolved in natricine snakes that exploit prey in low densities. Fast striking enhances the probability of a successful capture (Drummond, 1983; Alfaro, 2002), which is likely important when the prey encounter rate is low. Natricine snakes feeding on prey in high densities are found to be slow strikers. However, exceptions from this general pattern seem to exist. For instance, the generalist *Ne. rhombifer* reaches rather high velocities with a lateral strike (Alfaro, 2003), suggesting the occasional occurrence of specialization within sideways attacks.

Our nonphylogenetic analyses showed a significant correlation between prey-capture strategy and prey density. Snakes that foraged on low-density aquatic prey used the frontal-striking strategy, whereas snakes that foraged on prey in very high densities used the lateral-striking strategy. However, when taking into account phylogenetic relationships in order to test for an adaptive component, the correlation between capture strategy and density disappeared. Possibly, the different prey density conditions did not result in different prey-capture strategies within the

Natricinae, but rather in overall flexible foraging and striking behaviour. Indeed, the North American natricine snake *T. validus* shows a shift from open-mouth searching towards more specialist behaviour when prey density decreases (De Queiroz, 2003). Moreover, *Na. maura* has been reported to show open-mouth searching behaviour when foraging in drying pools crowded with fish (Hailey & Davies, 1986b). Thus, the foraging and strike behaviour of some generalist natricine snakes appears to be rather flexible, whereas specialists like *Ne. harteri* and *Na. tessellata* use almost exclusively one type of prey-capture strategy, i.e. frontal-striking behaviour (T. Hibbits, pers. comm.; this study). This appears to suggest an alternative hypothesis: generalist predators display a more variable capture strategy than do specialists. However, some generalist species switch only rarely from one type of prey-capture strategy to another. For instance, rarely have the North American generalist species *T. sirtalis* and *T. elegans* been observed to change their typically lateral prey-capture strategy to strike frontally and orientate visually towards prey before striking (Drummond, 1983; Alfaro, 2002). On the other hand, it has been demonstrated that the aquatic specialist *Ne. clarkii* does change its foraging behaviour according to the density of the vegetation within which it forages: whereas in dense vegetation snakes use a sit-and-wait strategy, when vegetation density decreases, snakes start to pursue their prey actively (Mullin & Mushinsky, 1995). There are other aspects of the feeding niche of snakes that are also likely to influence the prey-capture strategies used, such as seasonal differences in river flooding and prey availability and differences in prey type (tadpoles, worms, fish and frogs could be captured by different foraging methods). For instance, to feed on sedentary prey, a sit-and-wait strategy will be less efficient than will an open-mouth searching or an active pursuit strategy (Pough *et al.*, 2001). So, various characteristics of the foraging niche of the Natricinae seem to influence the prey-capture strategy used and the (flexibility of) prey-capture strategies of the Natricinae appear to be rather variable. To better understand the relationship between prey-capture strategies and prey density, and its adaptive significance, a more quantitative representation of foraging behaviour for a larger sample of aquatically foraging Natricinae is clearly needed.

Nevertheless, our study suggests that prey density, rather than diet, played an important role in the evolution of the strike velocity in natricine snakes. More detailed quantitative information on various aspects of the feeding niche and prey-capture strategies of natricine and other aquatic snakes should provide us with a better insight into the adaptive significance of these strategies.

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