

Head Morphology and Diet in the Dice Snake (*Natrix tessellata*)

JONATHAN BRECKO, BART VERVUST, ANTHONY HERREL & RAOUL VAN DAMME

Abstract. In aquatic natricine snakes, piscivorous species tend to have narrow streamlined heads, while species that prey on frogs have broader heads. This pattern is thought to reflect the antagonistic design requirements of fast underwater striking on the one hand and the consumption of bulky prey on the other. Here we test whether a similar correlation between head shape and diet exists at the intraspecific level, by quantifying head shape and diet in the frontal striking aquatic natricine snake *Natrix tessellata*. Our results show that museum specimens with fish in their stomachs had significantly narrower and more streamlined heads than individuals with frogs in their stomachs. Given that diet is strongly determined by local abundance of potential prey, these results suggest strong population-level divergence in head size and shape in this species. Future studies need to establish whether the observed differences in head shape have a genetic basis, or result from phenotypic plasticity.

Key words. *Natrix tessellata*, feeding, fish, frogs, prey capture, trade-off.

Introduction

Aquatic natricine snakes have recently become a model system for studies of evolutionary convergence (VINCENT et al. 2006a, 2009, HERREL et al. 2008). Previous studies have demonstrated convergent evolution of narrow streamlined heads in species of piscivorous natricines that use a frontal strike to capture prey (ALFARO 2002, HIBBITS & FITZGERALD 2005, HERREL et al. 2008). As the hyoid bone is strongly reduced in snakes as a result of the specialization of the tongue for chemoreception (MCDOWELL 1972, SCHWENK 1994), snakes cannot use suction feeding to capture prey underwater. Consequently, it is predicted that frontally striking aquatic snakes should have streamlined heads to minimize drag and bow-waves induced by the forward movement of the predator (VOGEL 1981, YOUNG 1991, HERREL et al. 2008). Conversely, species specializing on bulky prey such as frogs and toads are often characterized by broad and wide heads (FORSMAN & LINDELL 1993, VINCENT et al. 2006b, VINCENT & MORI 2008). As snakes cannot reduce their prey (but see JAYNE et al. 2002), the maximum size of the prey eaten is a direct function of the size of the head of the snake (POUGH & GROVES 1983, RODRIGUEZ-ROBLES et al. 1999, CUNDALL & GREENE 2000, VINCENT et al. 2006b) thus putting strong selective pressures on the evolution of wide heads. A trade-off between the ability of snakes to capture prey underwater using a forward strike mode and their ability to eat large, bulky prey is thus predicted (HERREL et al. 2008).

While there is ample evidence for a relationship between prey type (fish versus frogs) and head shape across aquatic snake species, it is unclear whether a similar connection exists within a species (SNELL et al. 1988, LOSOS & IRSCHICK 1994, HERREL et al. 2001). Indeed, although an essential component of micro-evolutionary theory, empirical evidence for functional trade-offs at the intraspecific level is scarce on the whole (VAN

DAMME et al. 2002). Here, we quantify head shape and diet in the aquatic dice snake, *Natrix tessellata*. The dice snake seems an appropriate study species because it is a piscivore (LUISELLI & RUGIERO 1991, FILIPPI et al. 1996, GRUSCHWITZ et al. 1999, LUISELLI et al. 2007, GHIRA et al. 2009, GÖÇMEN et al. 2011) that uses frontal strikes to capture prey underwater (BILCKE et al. 2006). And it has a well adapted visual system allowing it to better focus while submerged than in its congener *N. natrix* (SCHAEFFEL & MATHIS 1991). Moreover it is also known to eat frogs and other amphibians across parts of its range, although it is still unclear whether this happens frequently (GRUSCHWITZ et al. 1999, BRECKO & HERREL pers. obs.). Our personal observations on Greek Islands, e.g. Serifos, show that they probably consume almost exclusively amphibians due to annually drying up of streams and puddles, rendering the aquatic habitat not suitable for fish. We predict that individuals, whose diet predominantly consists of fish, will have narrower and more streamlined heads than individuals from populations including frogs in their diet.

Materials and Methods

Study Animals

We measured snakes of the species *Natrix tessellata* contained in the following museums: Musée Nationale d'Histoire Naturelle in Paris, France; Forschungsmuseum Alexander Koenig in Bonn, Germany; Natural History Museum in London, UK; California Academy of Sciences in San Francisco, USA; The Field Museum in Chicago, USA; and the Senckenberg Institute in Frankfurt, Germany (see Appendix I). This resulted in a database with a total of 576 snakes. Specimen catalog numbers and locality data are listed in Appendix I. The animals measured were both juveniles and adults of both sex, however the specimens with a prey in their stomach

(and used for this paper) were all adults. We determined the sex of a subset of the animals by dissection of the cloacal region.

Morphometrics

We measured the snout-vent length (SVL) and tail length of all specimens using a measuring tape and a piece of string. Additionally, we measured the following characteristics of the head displayed in Figure 1: (1) head length, as the distance from the back of the skull (posterior edge of the parietal bone as determined by palpation) to the tip of the snout; (2) head width, measured at the widest part of the posterior cephalic region; (3) lower jaw length, as the distance between the posterior end of the compound bone and the tip of the dentary bone; (4) the distance from the corner of the mouth to the tip of the dentary bone; (5) head height, measured at the highest point of the head; (6) and quadrate length, defined as the length from the quadrate-lower jaw joint to the anterior dorsal most aspect of the quadrate at the quadrate-supratemporal joint. All these characteristics were measured using digital calipers (Mitutoyo; 0.01 mm).

We also took digital pictures of the head in dorsal, ventral, lateral and frontal views on all specimens. A background grid was included for scaling purposes. The pictures were used to measure the surface area of the head in dorsal, ventral, lateral and frontal view with

the aid of the surface measurement tool in TpsDig 2.10 (Sunny at Stony Brook). The lateral surface area was calculated by summing left and right side measurements and dividing by two, unless one of the sides showed any kind of unnatural deformation, in which case the measurement was based on one side only. On the pictures we also measured the inter-ocular and inter-nostril lengths, as the distance between the eyes and the distance between the nostrils (no. 7 and 8 on Figure 1, respectively).

Diet

We evaluated the presence of prey in the stomach by palpation. If prey were detected, a small incision through the abdominal scales and muscles was made to expose the stomach at the level of the prey. The stomach was opened and prey items were removed and stored in a 70% aqueous ethanol solution. After removing the prey from the stomach, pictures were taken of all prey for subsequent identification.

Statistics

We used SPSS (version 13.0, SPSS Inc., Chicago, IL, USA) for statistical analyses. All morphometric variables were Log_{10} transformed before analyses to ensure normality by eliminating the effect of allometric growth. To reduce the dimensionality, e.g. remove the effect of different size classes in the dataset, and to explore shape variation within species, unstandardized residuals of the regression of the cranial traits on SVL were used as input for a principal component analysis with varimax rotation. Factors with eigenvalues greater than 1 were extracted and used as input for subsequent analyses of variance testing for differences in head shape between snakes that had eaten frogs *versus* fish. Finally, Spearman rank correlations were used to test for associations between head shape and the number of prey retrieved from the stomach of each snake. We used discriminant analysis to predict the sex of the animals that were not dissected for sex determination. However we failed to obtain a large enough subset of animals with known/predicted sex and with prey in their stomach. This made it impossible to statistically look for differences in head morphology between the sexes with ingested prey.

Results

Fifty-two out of the total 576 snakes examined had detectable prey in their stomachs. Of the individuals with prey in their stomachs, 19 had eaten frogs and 33 had eaten fish. The number of prey items per stomach varied between 1 and 9. Most of these specimens ($n = 34$) had one prey item in their stomach, 12 snakes contained remains of 2 or 3 prey items, and the others had swallowed 5, 6, 7, 8 and even 9 prey items. In the latter cas-

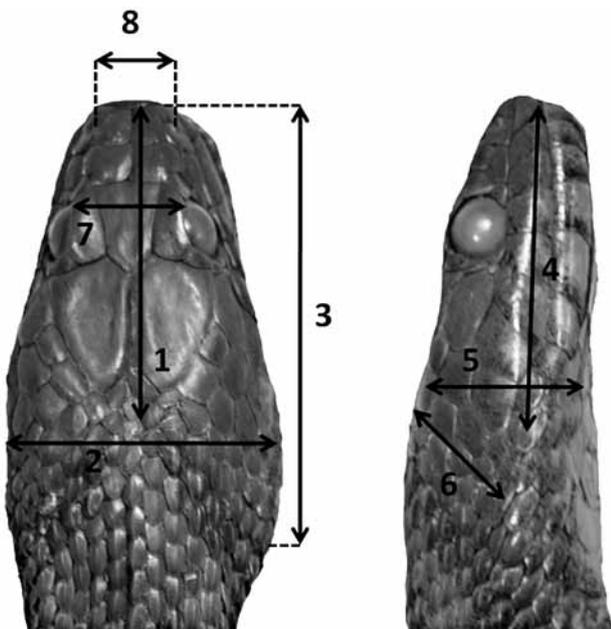


Fig. 1. Dorsal and lateral view of the head of a *Natrix tessellata* specimen, illustrating the morphometric variables determined on each specimen (see also text): (1) head length, (2) head width, (3) lower jaw length, (4) distance from corner of mouth to tip of dentary bone, (5) head height, (6) quadrate length, (7) inter-ocular length, (8) inter-nostril length.

es, prey typically consisted of small fish, tadpoles, and froglets, but occasionally also included small adult frogs and newts. None of the specimens examined contained both, amphibious and fish prey. Table 1 reports head and body characteristics of snake specimens that had eaten fish and amphibians, respectively.

A principal component analysis on the regressed craniometric data produced two new composite axes that jointly explained approximately 75% of the total variation in the data set. Whereas the first axis was highly and positively correlated with the relative length of the head, the second axis was highly and positively correlated with the relative frontal surface area and the relative distance between the eyes and nostrils (Tab. 2). A plot of the individuals in multivariate space composed of the first two factors shows clear separation of individuals that had fish or frogs in their stomachs (Fig. 2).

Head shape differed only between fish-eating and frog-eating individuals on the second axis (Univariate F-tests: Axis 1: $F_{1,50} = 2.53$, $P = 0.12$; Axis 2: $F_{1,50} = 6.85$, $P = 0.012$); individuals that had fish in their stomachs re-

Tab. 2: Results of a factor analysis performed on the head morphometric data. Loadings greater than 0.8 are in bold.

	factor 1	factor 2
% variation explained	44.49	30.54
eigenvalue	7.64	1.36
residual head length (mm)	0.80	0.38
residual head width	0.70	0.36
residual head height	0.72	0.32
residual lower jaw length	0.87	0.29
residual jaw outlever	0.85	0.23
residual quadrate length	0.84	0.05
residual dorsal surface area	0.69	0.54
residual frontal surface area	0.39	0.83
residual lateral surface area	0.43	0.49
residual ventral surface area	0.51	0.57
residual interocular distance (mm)	0.25	0.87
residual internasal distance (mm)	0.12	0.87

Tab. 1. Descriptive data representing head measurements in snakes with either fish or frogs in their stomach. Both absolute and relative (residuals of the regression of head lengths on SVL) dimensions are indicated.

Descriptive Statistics	Prey	Absolute		Relative	
		Mean	SE	Mean	SE
Head length (mm)	Fish	14,11	0,72	-0,006	0,007
	Frog	15,54	1,15	-0,014	0,010
Head width (mm)	Fish	9,58	0,61	-0,017	0,010
	Frog	12,27	1,08	0,023	0,013
Head height (mm)	Fish	7,13	0,46	-0,008	0,009
	Frog	8,95	0,94	0,012	0,017
Lower jaw length (mm)	Fish	19,28	1,16	0,002	0,008
	Frog	21,67	1,71	-0,004	0,011
Mouth-tip (mm)	Fish	11,05	0,69	-0,004	0,010
	Frog	12,34	1,00	-0,014	0,014
Quadratum (mm)	Fish	5,66	0,45	-0,006	0,014
	Frog	6,70	0,77	-0,024	0,016
Dorsal surface (mm ²)	Fish	159,64	19,70	-0,025	0,015
	Frog	240,13	42,87	0,011	0,028
Frontal surface (mm ²)	Fish	82,86	10,94	-0,041	0,019
	Frog	135,70	23,91	0,020	0,034
Lateral surface (mm ²)	Fish	106,58	13,37	-0,027	0,015
	Frog	143,63	25,89	-0,036	0,028
Ventral surface (mm ²)	Fish	139,37	19,23	-0,060	0,020
	Frog	209,83	39,71	-0,031	0,028
Distance nostrils (mm)	Fish	4,43	0,31	-0,022	0,010
	Frog	5,34	0,47	-0,002	0,019
Distance eyes (mm)	Fish	6,46	0,41	-0,030	0,009
	Frog	8,04	0,66	0,007	0,016
SVL (cm)	Fish	39,06	3,08		
	Frog	45,16	3,74		
Tail length (cm)	Fish	10,41	0,90		
	Frog	10,69	1,15		

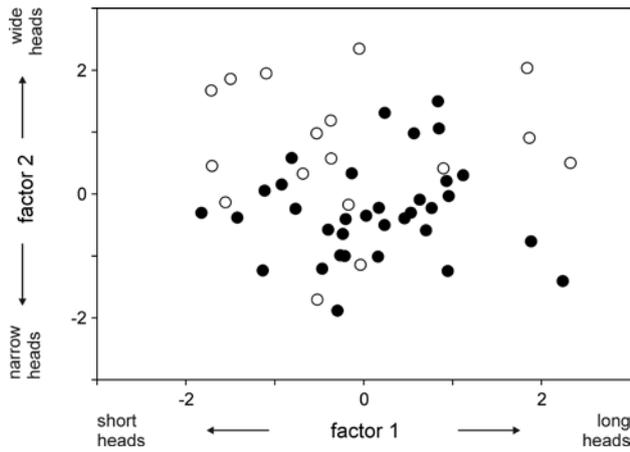


Fig. 2. Graph illustrating the results of a factor analysis performed on the size-corrected craniometric data. Note that individuals with fish in their stomachs (closed circles) exhibit relatively narrower snouts than individuals with frogs in their stomachs (open circles).

vealed narrower snouts (smaller distance between the eyes and nostrils) and a reduced frontal surface area (Figs. 2, 3). Scores on the first principal component axis correlated with the number of prey found in the stomach (Spearman $r = -0.413$; $P = 0.001$). Thus snakes that had more prey in their stomachs had relatively shorter heads.

We do not have enough data to statistically test for differences in head morphology between populations of which the diet is known. But we placed the data for the head morphology (PCA axis 2, Fig. 4) against the population information together with the known diet of individuals for that region. The two out of five populations with on average the widest head shape and four

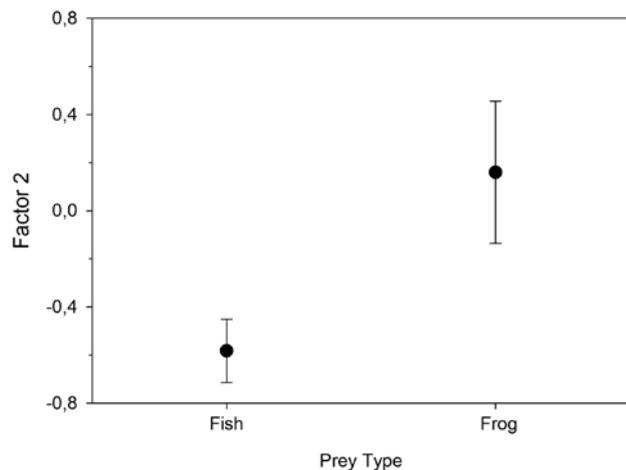


Fig. 3. Plot illustrating the difference in head shape between snakes that had fish and frogs in their stomachs. Snakes feeding on fish have significantly narrower snouts than snakes feeding on frogs. Illustrated are means \pm standard errors.

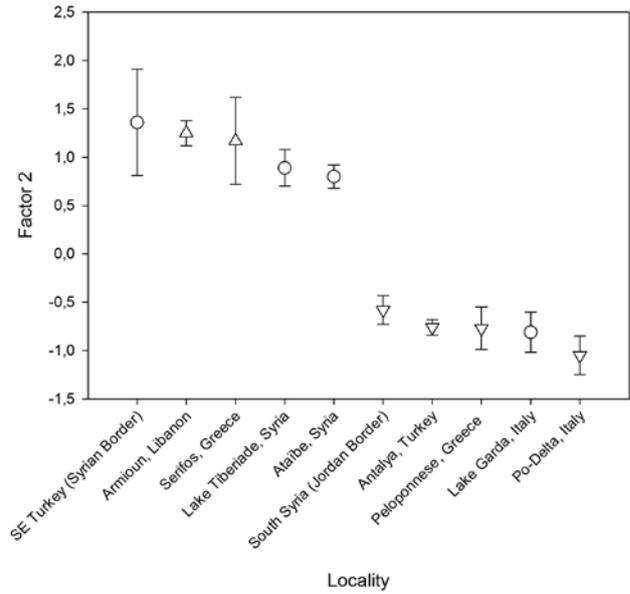


Fig. 4. Graph illustrating the results of the second axis of the factor analysis performed on the craniometric data against the locality data. Illustrated are the top five populations with the on average largest frontal head shape and the on average smallest frontal head shape. The triangles with the top upward are populations that have fed on frogs. The downward positioned triangles are populations that have fed on fish. The circles represent populations without a known diet. There is a trend that populations with on average a larger frontal head shape feed on frogs, whereas the populations with the smallest frontal head shape feed on fish.

out of five populations with the most narrow head shape appear to be feeding on frog and fish respectively. The other populations had no individuals with any stomach contents, so their diet remains unclear.

Discussion

Our results show that individuals that consumed fish had more streamlined heads than individuals with frogs in their stomachs (see Fig. 5). These data thus confirm prior suggestions that striking at prey frontally under water may impose a constraint on the evolution of head shape in these snakes. Although we predicted that individuals who consumed frogs would have a larger relative head width as principal determining factor, our results show that inter-ocular length and projected frontal surface play a more important role. The larger projected frontal surface of the head may increase drag during striking and swimming of the frog eating specimens. It would therefore be interesting to compare the underwater striking performance and gape distance of dice snakes selecting between the two types of prey, as well as their habitat use and behavior. If these intraspecific differences in morphology mirror those found among Natricine species, we predict that specimens with relatively large frontal surfaces will be found in drier habi-

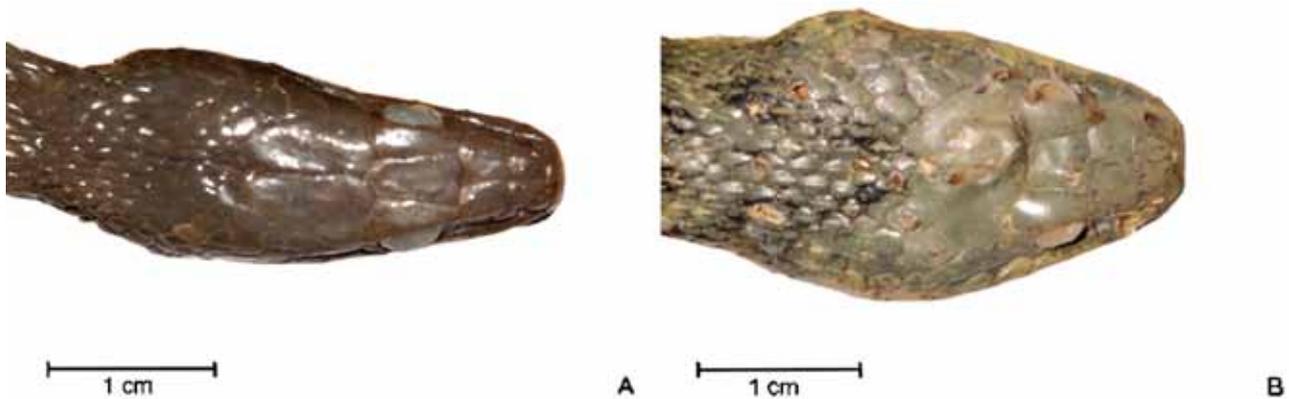


Fig. 5. Illustration of the two extreme head morphologies observed in *Natrix tessellata* utilizing different prey. Specimen A with only fish in its stomach differs significantly in head shape from specimen B which had eaten only frogs.

tats and engage less in swimming than their streamlined conspecifics.

Further investigations using geometric morphometric techniques based on pictures taken from live animals may be especially insightful in determining differences in shape. Overall, projected frontal surface may be constrained in aquatic snakes for energetic reasons as narrow heads may improve a snake's hydrodynamic profile and minimize drag while swimming under water (see HIBBITS & FITZGERALD 2005). If so, this may explain why aquatic snakes are generally characterized by an extreme elongation of the quadrate as this would provide them with a performance advantage for eating large prey (VINCENT et al. 2009) and at the same time would allow them to maintain a streamlined head shape. However, measurements of the energetic cost of locomotion in snakes with different head shapes are needed to explicitly test this hypothesis.

Despite the fact that our data for *Natrix tessellata* suggest a constraint on head shape in snakes that use frontal strikes to capture prey underwater, it is known that other species characterized by much wider heads do also prey on fish (e.g. *Natrix maura*: PLEGUEZUELOS & MORENO 1989, SANTOS & LLORENTE 1998, SCHÄTTI 1999, SANTOS et al. 2000, *Agkistrodon piscivorus*: VINCENT et al. 2004a, b, 2005). Previous works on aquatic prey capture in snakes have suggested an important role of behavioral strategies that may mitigate the constraints imposed by striking at prey in a dense medium like water (DRUMMOND 1983, HAILEY & DAVIES 1986, ALFARO 2002, BILCKE et al. 2006). Alternatively, snakes with wide heads may just suffer from a highly reduced strike performance (VINCENT et al. 2005, BILCKE et al. 2007) and only prey on small fish when present in high densities (HAILEY & DAVIES 1986) as observed in drying water bodies during the summer (SAVITZKY 1992, SCHÄTTI 1999).

Our dietary dataset was not large enough to take into account differences between the sexes and look statistically at population differences in diet and head shape. However there appeared to be no difference between

the number of females and males with frog or fish in their stomach as they preyed upon fish and frogs in equal numbers, but the overall number was too small to statistically determine differences between the sexes. Other work on a larger morphological dataset of *Natrix tessellata* did not show any differences between the sexes (BRECKO et al., submitted). However, significant intersexual differences in prey composition, with the females taking more anurans than males have been found at three sites in central Italy (LUISELLI et al. 2007, CAPULA et al. 2011). Preliminary results on population differences show a trend of populations with a large mean frontal surface and distance between the eyes and nostrils feeding on frogs, whereas those with a small overall frontal surface tend to feed on fish (Fig. 5). This conclusion is supported by further observations. For example, ESTERBAUER (1985, 1994) observed that frogs are commonly, but not exclusively, consumed by *N. tessellata* in southwestern Syria, in the same general area of large-headed population at Lake Tiberiade (Fig. 5). The slender head morphology suggesting a fish diet in specimens from Lake Garda in Figure 5 is supported by MEBERT (1993, 1996), who captured nearly 100 *N. tessellata* from this lake for a morphological study and retrieved several dozens of fish, but not a single amphibian from the snake stomachs. On the other hand, we did not find populations in which individuals have a mixed diet, although this occurs to a low proportion also in predominantly fish-eating populations (e.g. LUISELLI et al. 2007, and refs. in MEBERT 2011). The question remains if the individuals or populations which have an average overall frontal surface will prey upon both frogs and fish in equal numbers. It would therefore be interesting to look at the habitat and behavior of the 'large headed' *N. tessellata*'s. It can be predicted that, as the main preferred prey of *N. tessellata* is fish (GRUSCHWITZ et al. 1999, SCHÄTTI 1999), the habitat of large headed frog eating *N. tessellata*'s is completely different from the normal situation. Perhaps the environment is drier, with streams and puddles only periodically maintaining water, resulting that

fish do not exist in the habitat, or frogs are simply more numerous (e.g. ESTERBAUER 1985, 1994).

Interpopulational differences in head morphology have been documented in many snakes (e.g. FORSMAN 1991, AUBRET et al. 2004). Also in *Natrix tessellata* MEBERT (1993, 1996) found significant microgeographic variations in the posterior head length (distance between eye and mouth corner) and width of frontal shield between populations of approximately 30 km distance in mountainous terrain. However, no diet analysis has accompanied that study. Future studies testing whether the observed differences in head shape observed between individuals and/or populations have a genetic basis or are the result of phenotypic plasticity are warranted as plasticity has been suggested as an important mechanism driving the initial divergence of populations in the face of changing ecological conditions in squamates (LOSOS 2000, AUBRET et al. 2004).

Acknowledgements

We would like to thank the curators of the museums that allowed us to visit the collections and for their assistance during our stay at the different museums. We are especially grateful to the Field Museum of Natural History and the Californian Academy of Sciences who made a visit possible by means of a grant of the Scholarship Committee (FM) and a Charles Stearns Memorial Grant in Aid in Herpetology (CAS). JB is funded by a Ph.D. grant of the Instituut voor de Aanmoediging van Innovatie door Wetenschap en Technologie in Vlaanderen (Institute for the Promotion of Innovation by Science and Technology in Flanders).

References

- ALFARO, M.E. (2002): Forward attack modes of aquatic feeding garter snakes. – *Functional Ecology* **16**: 204–215.
- AUBRET, F., SHINE, R. & X. BONNET (2004): Adaptive developmental plasticity in snakes. – *Nature* **31**: 261–262.
- BILCKE, J., HERREL, A. & P. AERTS (2007): Effect of prey- and predator size on the capture success of an aquatic snake. – *Belgian Journal of Zoology* **137**: 191–195.
- BILCKE, J., HERREL, A. & R. VAN DAMME (2006): Correlated evolution of aquatic prey capture strategies in European and American Natricine snakes. – *Biological Journal of the Linnean Society* **88**: 73–83.
- CAPULA, M., FILIPPI, E., RUGIERO, L. & L. LUISELLI (2011): Dietary, thermal and reproductive ecology of *Natrix tessellata* in central Italy: A Synthesis. – *Mertensiella* **18**: 147–153.
- CUNDALL, D. & H.W. GREENE (2000): Feeding in snakes. – In: SCHWENK, K. (Ed.): *Feeding: Form, Function and Evolution in Tetrapod Vertebrates*. – Academic Press, London: 293–333.
- DRUMMOND, H. (1983): Aquatic foraging in garter snakes: a comparison of specialists and generalists. – *Behaviour* **86**: 1–30.
- ESTERBAUER, H. (1985): Zur Herpetofauna Südwestsyrrens. – *Herpetofauna* **7**: 23–34.
- ESTERBAUER, H. (1994): Lebensweise und Verhalten der Würfelnatter im Masil al Fawwar (Syrien). – *DATZ* **47**: 308–311.
- FILIPPI, E., CAPULA, M., LUISELLI, L. & U. AGRIMI (1996): The prey spectrum of *Natrix natrix* (Linnaeus, 1758) and *Natrix tessellata* (Laurenti, 1768) in sympatric populations (Squamata: Serpentes: Colubridae). – *Herpetozoa* **8**: 155–164.
- FORSMAN, A. (1991): Adaptive variation in head size in *Vipera berus* L. populations. – *Biological Journal of the Linnean Society* **43**: 281–296.
- FORSMAN, A. & L.E. LINDELL (1993): The advantage of a big head: swallowing performance in adders, *Vipera berus*. – *Functional Ecology* **7**: 183–189.
- GHIRA, I., BUTĂNESCU, D. & B. MAROSI (2009): Feeding behavior of the dice snake (*Natrix tessellata*). – *Herpetologica Romanica* **3**: 1–7.
- GÖÇMEN, B., ÇIÇEK, K., YILDIZ, M.Z., ATATÜR, M.K., DİNÇASLAN Y.E. & K. MEBERT (2011): A preliminary study on the feeding biology of the dice snake, *Natrix tessellata*, in Turkey. – *Mertensiella* **18**: 365–369.
- GRUSCHWITZ, M., LENZ, S., MEBERT, K. & V. LAŇKA (1999): *Natrix tessellata* (Laurenti, 1768) – Würfelnatter. – In: BÖHME, W. (Ed.): *Handbuch der Reptilien und Amphibien Europas*, Vol. 3/Schlangen II. – AULA-Verlag, Wiesbaden, Germany: 581–644.
- HAILEY, A. & P.M.C. DAVIES (1986): Diet and foraging behavior of *Natrix maura*. – *Herpetological Journal* **1**: 53–61.
- HERREL, A., MEYERS, J.J. & B. VANHOODYONCK (2001): Correlations between habitat use and body shape in a phrynosomatid lizard (*Urosaurus ornatus*): a population-level analysis. – *Biological Journal of the Linnean Society* **74**: 305–314.
- HERREL, A., VINCENT, S.E., ALFARO, M.E., VAN WASSENBERGH, S., VANHOODYONCK, B. & D.J. IRSCHICK (2008): Morphological convergence as a consequence of extreme functional demands: examples from the feeding system of natricine snakes. – *Journal of Evolutionary Biology* **21**: 1438–1448.
- HIBBITS, T.J. & L.A. FITZGERALD (2005): Morphological and ecological convergence in two natricine snakes. – *Biological Journal of the Linnean Society* **85**: 363–371.
- JAYNE, B., VORIS, H.K. & P.K.L. NG (2002): Herpetology: Snake circumvents constraints on prey size. – *Nature* **418**: 143–143.
- LOSOS, J.B. (2000): Evolutionary implications of phenotypic plasticity in the hindlimb of the lizard *Anolis sagrei*. – *Evolution* **54**: 301–305.
- LOSOS, J.B. & D.J. IRSCHICK (1994): Adaptation and constraint in the evolution of specialization of Bahamian *Anolis* lizards. – *Evolution* **48**: 1786–1798.
- LUISELLI, L., CAPIZZI, D., FILIPPI, E., ANIBALDI, C., RUGIERO, L. & M. CAPULA (2007): Comparative diets of three populations of an aquatic snake (*Natrix tessellata*, Colubridae) from Mediterranean streams with different hydric regimes. – *Copeia* **2007**: 426–435.
- LUISELLI, L. & L. RUGIERO (1991): Food niche partitioning by water snakes (genus *Natrix*) at a freshwater environment in Central Italy. – *Journal of Freshwater Ecology* **6**: 439–444.
- McDOWELL, S.B. (1972): The evolution of the tongue of snakes and its bearing on snake origins. – In: DOBZHANSKY, T., HECHT, M.K. & W.C. STEERE (Eds.): *Evolutionary Biology*, Vol. 6. Appleton-Century-Crofts, New York: 191–273.

- MEBERT, K. (1993): Untersuchung zur Morphologie und Taxonomie der *Würfelnatter Natrix tessellata* (Laurenti 1768) in der Schweiz und im südlichen Alpenraum. – M.S. thesis, Zoological Museum, University of Zürich, Switzerland.
- MEBERT, K. (1996): Comparaison morphologique entre des populations introduites et indigènes de *Natrix tessellata* de l'Arc Alpin. – Bull. Soc. Herp. Fr. **80**: 15–25.
- MEBERT, K. (Ed.) (2011): The Dice Snake, *Natrix tessellata*: Biology, Distribution and Conservation of a Palaearctic Species. – Mertensiella **18**, DGHT, Rheinbach, Germany.
- PLEGUEZUELOS, J.M. & M. MORENO (1989): Alimentación primaria de *Natrix maura* (Linnaeus, 1758) (Ophidia, Colubridae) en el S.E. de la Península Ibérica. – Revista Española De Herpetología **3**: 221–236.
- POUGH, F.H. & J.D. GROVES (1983): Specializations of the body form and food habits of snakes. – American Zoologist **23**: 443–454.
- RODRIGUEZ-ROBLES, J.A., BELL, C.J. & H.W. GREENE (1999): Gape size and evolution of diet in snakes: feeding ecology of erycine boas. – Journal of Zoology **248**: 49–58.
- SANTOS, X. & G.A. LLORENTE (1998): Sexual and size-related differences in the diet of the snake *Natrix maura* from the Ebro Delta, Spain. – Herpetological Journal **8**: 161–165.
- SANTOS, X., GONZALEZ-SOLIS, J. & G.A. LLORENTE (2000): Variation in the diet of the viperine snake *Natrix maura* in relation to prey availability. – Ecography **23**: 185–192.
- SAVITZKY, B.A.C. (1992): Laboratory studies on piscivory in an opportunistic predator, the cottonmouth, *Agkistrodon piscivorus*. – In: CAMPBELL, J.A. & E.D. BRODIE, Jr. (Eds.): Biology of the Pitvipers. – The University of Texas at Arlington Press, USA: 347–368.
- SCHÄTTI, B. (1999): *Natrix maura* (Linnaeus 1758) - Vipernatter. – In: BÖHME, W. (Ed.): Handbuch der Reptilien und Amphibien Europas, Vol. 3/Schlangen II. – AULA-Verlag, Wiesbaden, Germany: 483–503.
- SCHAEFFEL, F. & U. MATHIS (1991): Underwater vision in semi-aquatic European snakes. – Naturwissenschaften **78**: 373–375.
- SCHWENK, K. (1994): Why do snakes have forked tongues? – Science **263**: 1573–1577.
- SNELL, H.L., JENNINGS, R.D., SNELL, H.M. & S. HARCOURT (1988): Intrapopulation variation in predator-avoidance performance of Galápagos lava lizards: the interaction of sexual and natural selection. – Evolutionary Ecology **2**: 353–369.
- VAN DAMME, R., VANHOODYDONCK, B., AERTS, P. & F. DE VREE (2002): Evolution of lizard locomotion: context and constraint. – In: BELS, V., GASC, J.P. & A. CASINOS (Eds.): Vertebrate Biomechanics and Evolution. – BIOS Scientific Publishers, Oxford: 267–282.
- VINCENT, S.E. & A. MORI (2008): Determinants of feeding performance in free-ranging pit-vipers (Viperidae: *Oviphis okinavensis*): key roles for head size and body temperature. – Biological Journal of the Linnean Society **93**: 53–62.
- VINCENT, S.E., BRANDLEY, M.C., HERREL, A. & M.E. ALFARO (2009): Convergence in trophic morphology and feeding performance among piscivorous natricine snakes. – Journal of Evolutionary Biology **22**: 1203–1211.
- VINCENT, S.E., DANG, P.D., HERREL, A. & N.J. KLEY (2006a): Morphological integration and adaptation in the snake feeding system: a comparative phylogenetic study. – Journal of Evolutionary Biology **19**(5): 1545–1554.
- VINCENT, S.E., HERREL, A. & D.J. IRSCHICK (2004a): Sexual dimorphism in head shape and diet in the cottonmouth snake (*Agkistrodon piscivorus*). – Journal of Zoology **264**: 53–59.
- VINCENT, S.E., HERREL, A. & D.J. IRSCHICK (2004b): Ontogeny of intersexual head shape and prey selection in the pitviper *Agkistrodon piscivorus*. – Biological Journal of the Linnean Society, **81**: 151–159.
- VINCENT, S.E., HERREL, A. & D.J. IRSCHICK (2005): Aquatic versus terrestrial strike performance and kinematics in the pitviper, *Agkistrodon piscivorus*. – Journal of Experimental Zoology **303**: 476–488.
- VINCENT, S.E., MOON, B.R., SHINE, R. & A. HERREL (2006b): Functional meaning of “prey size” in water snakes (*Nerodia fasciata*, Colubridae). – Oecologia **147**: 204–211.
- YOUNG, B.A. (1991): The influences of the aquatic medium on the prey capture system of snakes. – Journal of Natural History **25**: 519–531.
- VOGEL, S. (1981): Life in Moving Fluids. – Willard Grant Press, Boston, USA.

Authors

JONATHAN BRECKO, BART VERVUST, KONRAD MEBERT, RAOUL VAN DAMME, Dept. Biology, University of Antwerp, Universiteitsplein 1, B-2610 Antwerp, Belgium, e-mail: jonathan.brecko@ua.ac.be; ANTHONY HERREL, UMR 7179 C.N.R.S/M.N.H.N., Département d'Ecologie et de Gestion de la Biodiversité, 57 rue Cuvier, Case postale 55, 75231, Paris Cedex 5, France.

Appendix I

MNHN Paris		ZFMK Bonn	
Catalog No.		Catalog No.	
**25*44	Yamouné, Syria	21012-7	Lake Homs, Syria
**25*51-3	Ataïbe, Syria	23287-9	Bad Kreuznach, Germany
**25*54 (A-Q)	Ataïbe, Syria	23295-9	Peloponnese, Greece
**35*350-2	Hama, Syria	24681-3	Trient, Italy
**8501	Batoum, Russia	25712-3	Lake Homs, Syria
*84*155	Serpilor, Ukraine	27537	Nahr-el-Kabir, Syria
1925.47	Ataïbe, Syria	31611-13	Shiraz, Iran
1925.49-50	Ataïbe, Syria	31750-1	Bad Kreuznach, Germany
1926.32-6	Smyrne, Turkey	34668	LHbN, Germany
1935.347	Iraq	38508	Bireçik, Turkey
1935.349	Hama, Syria	41225	S-Tirol, Italy
1961.381	Bologna, Italy	41550	RPL, Germany
1963.1008	Peloponnese, Greece	41986-8	Lake Prespa, Greece
1990.4602	Bologna, Italy	42803-4	North Syria
1991.1622-4	Lake Tiberiade, Syria	44057	North Syria
1991.1626	Lake Tiberiade, Syria	46977	Sile, Turkey
1991.1646-7	Ataïbe, Syria	49130-2	LHbN, Germany
1991-1658	Lake Gotscha, Armenia	49134-7	LHbN, Germany
3177 (A-B)	Dalmatia, Croatia	49139-41	LHbN, Germany
5639	Caspian Sea	51888	Sivas, Turkey
5645	Caspian Sea	53037-8	Terracina, Italy
6181	Lake Gotscha, Armenia	54789	Castiglione del Lago, Italy
6185 (A-B)	Lake Gotscha, Armenia	56869	Hatay, Turkey
641-2	Serpilor, Ukraine	62501-2	Peloponnese, Greece
6469-70	Lake Tiberiade, Syria	64942-4	Djebel Druz, Syria
		71561	Mazanderan, Iran
		71563-5	Mazanderan, Iran
		71682-3	Peloponnese, Greece
		76326-8	Peloponnese, Greece
	Po Delta, Italy	82106	Peloponnese, Greece
	Beysehir, Turkey	82108	Peloponnese, Greece
	Antalya, Turkey	82114-5	Peloponnese, Greece
	Antalya, Turkey	83031-4	Peloponnese, Greece
	Sweti Thoma, Bulgaria	84048-50	Peloponnese, Greece
	Sweti Thoma, Bulgaria	84053	Messenien, Greece
	Bireçik, Turkey	MKHTG	Turkey
	Shiraz, Iran		
	Pescasseroli, Italy		

The Field Museum

Catalog No.

141607	Mazanderan, Iran
141618	Iran
141653	Iran
141655	Iran
141657	Khorassan, Iran
141660	Fars, Iran
141662-3	Fars, Iran
141668-9	Fars, Iran
141671	Fars, Iran
161112	Afghanistan
161180	Afghanistan
161204	Afghanistan
171217-8	Iran
171220-26	Iran
171228-9	Kurdistan
171232	Iran
171234-6	Iran
171238-9	Iran
171241	Iran
171243	Iran
171245	Iran
171247-8	Iran
200215-25	Kant Co, Kirgisia
234281-2	Former USSR

CAS San Francisco

Catalog No.

17086	Styria, Austria
55190	Austria
87424	Tantura, Israël
105192-202	Antalya, Turkey
105607	Hopa, Turkey
105755-6	Igdir, Turkey
105795-6	Dogubayazit, Turkey
105825	Pülümür, Turkey
111687-92	Ardesen, Turkey
115972	Pagman, Afghanistan
119972	Ardi, Turkey

CAS San Francisco

Catalog No.

147589	Asraq, Jordania
157112-3	Alkut, Iraq
167859-60	Konqi River, China
167863-77	Konqi River, China
168038-45	Konqi River, China
170295	Gorna Brezica, Bulgaria
CAS 180050	Ashgabad, Turkmenistan
CAS 182698-700	Tersko-Kumskaya, Russia
CAS 182854	Kumtorkala, Dagestan
CAS 182971-74	Chambaylyk, Russia
CAS 183087-94	Stansstad, Swiss
CAS 183095-102	Brienzersee, Swiss
CAS 183103-112	Genfersee, Swiss
CAS 183113-117	Albogassio, Swiss
CAS 183118-122	Lake Garda, Italy
CAS 185158	Ashgabad, Turkmenistan
CAS 185292-316	Astrakhan, Russia
CAS 192900-1	Tersko-Kumskaya, Russia
CAS 197118-21	Korla, China
CAS 197139	Yining, China
CAS 210871-2	Kresna-Hancheto, Bulgaria
CAS 215245	Primorsko, Bulgaria
CAS 217585-99	Gelinkaya, Turkey
CAS 217742	Kortukeli, Turkey
CAS 218068	Haran, Turkey
CAS 218242-4	Kilis, Turkey
CAS 219929	Ropotamo river, Bulgaria

NHMS Frankfurt

Catalog No.

52771	Serpilor, Ukraine
-------	-------------------