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Effect of prey- and predator size on the capture success of an aquatic snake

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ABSTRACT. Large aquatic snakes typically do not include small prey into their diet. This is hypothesized to be so because small preys are difficult to catch in an aquatic environment. Also an effect of snake size on capture success is plausible, with large snakes having a lower capture success then small snakes for similarly sized prey. We tested the effect of snake- and prey-size on the capture success of the specialized aquatic snake *Natrix tesselata*. No effect of snake size on capture success was found for the size range that was tested. Possibly size becomes only important from a minimum absolute size (larger than the maximal size tested in our study) onwards. Unexpectedly, *Natrix tesselata* needs fewer attempts to capture small fish. In contrast, *N. maura*, a congeneric more generalist species, needs fewer attempts to capture larger fish. A possible explanation for this conundrum lies in difference in the degree of specialization between these two species. An in-depth study of the hydrodynamics of this snake-prey system could provide ways to evaluate the importance of size effects.

KEY WORDS : capture, *Natrix tesselata*, prey size, specialisation

INTRODUCTION

Whereas the diet of most large terrestrial snakes contains both large and small prey (ontogenetic telescope in lower prey size limit), the amount of small prey in the diet of aquatic snakes typically decreases when they grow larger (ontogenetic shift in lower prey size limit, see ARNOLD, 1993; Table 1). Thus, large aquatic snakes appear to no longer include small prey in their diet. Previous authors have posited two non-mutually exclusive hypotheses to explain this phenomenon.

First, absolute snake size in itself might affect capture success. Due to the density and viscosity of water, large snakes are predicted to push more water away in front of their heads compared to small snakes (proportional to the surface area exposed to the flow; see VOGEL, 1994). With respect to feeding, this means that a large snake could potentially push the prey away from, or to the side of its own head, or alarm the prey earlier by triggering its lateral line system through the displaced water column. Both these effects could then result in a decreased capture success of large snakes (for more background on the dynamics of prey capture under water in vertebrates see e.g. MULLER & OSSE, 1984; VAN LEEUWEN, 1984; LAUDER, 1985; YOUNG, 1991; VOGEL, 1994). Thus, due to the physical properties of the aquatic environment large snakes are predicted to have lower capture success then small snakes.

Second, small prey might simply be difficult to capture in aquatic environments, independent of snake size. As large fish have larger surface areas, they will resist potential bow wave effects more and might not be pushed away from the strike trajectory of the snake and might therefore be captured more easily. Preliminary experimental support for this hypothesis was provided in a study by HAILEY & DAVIES (1986) who found a significant effect of prey size on the capture success of *Natrix maura*, with large fish indeed being captured more easily than small fish. Unfortunately, no quantitative models predicting how snake size or shape should affect the dynamics of prey capture have been proposed which would allow us to test these predictions.

Thus, we decided to empirically test the effect of snake and fish size on capture success (capture attempts and capture time) in *Natrix tesselata* (Laurenti 1768), a specialised aquatic snake that captures its prey under water using frontally directed strikes (LUISELLI & RUGIERO, 1991; FILIPPI et al., 1996; GRUSCHWITZ et al., 1999). Unlike the closely related *N. maura*, which includes both fish and frogs in its diet (GALAN, 1988; PLEGUEZELOS & MORENO, 1989; SANTOS & LLORENTE, 1998; SCHÄTTI, 1999; SANTOS et al., 2000), *N. tesselata* is a dietary specialist preying almost exclusively on fish (LUISELLI & RUGIERO, 1991; FILIPPI et al., 1996; GRUSCHWITZ et al., 1999).

MATERIALS AND METHODS

We used 9 *N. tesselata* (5 males, 4 females) in the experiments and classified 4 of them as being 'small' (mean±se: 34±2cm snout-vent length (SVL)), and 5 as being 'large' (mean±se: 51±2cm SVL). We measured SVL as the length from the tip of the snout to the posterior edge of the anal scute (POUGH & GROVES, 1983). Animals were housed in glass terraria (50x30x25cm) containing a sandy substrate, shelters, vegetation and a tub filled with water. Two 58-W fluorescent lamps suspended above the substrate provided heat and light for 9h per day. We fed the snakes goldfish, *Carassius auratus*, once weekly (Linnaeus 1758). Snakes were always eager to feed when placed in the experimental arena and did not show any signs of disturbance or stress.

TABLE 1

Prey size – snake size relationships for various snake species. All species shown have increasing average upper prey size limit with increasing snake size.

species	prey size-snake size relationship	diet	references
Alsophis cantherigerus	T	T	Henderson et al., 1988
Antillophis parvifrons	T	T	Henderson et al., 1988
Austrelaps labialis	T	T	Shine, 1987
Austrelaps ramsayi	T	T	Shine, 1987
Austrelaps superbus	T	T	Shine, 1987
Darlingtonia haetiana	T	T	Henderson et al., 1988
Drymobius chloroticus	T	T	Seib, 1984
Elaphe obsoleta	T	T	Weatherhead et al., 2003
Hypsirhynchus ferox	T	T	Henderson et al.,1988
Masticodryas melanolomus	T	T	Seib, 1984
Morelia spilota	T	T	Shine, 1991
Notechis scutatus	T	T	Shine, 1977
Pseudechis porphyriacus	T	T	Shine, 1991
Uromacer catesbyi	T	T	Henderson et al., 1988
Uromacer frenatus	T	T	Henderson et al., 1988
Uromacer oxyrhynchus	T	T	Henderson et al., 1988
Acrochordus arafurae	T	P	Shine, 1986
Regina grahamii	T	P	Godley et al., 1984
Regina septemvittata	T	P	Godley et al., 1984
Drymobius margaritiferus	S	T	Seib, 1984
Gloydius shedaoensis	S	T	Shine & Sun, 2003
Vipera latastei	S	T	Brito, 2004
Agkistrodon piscivorus	S	P	Vincent et al., 2004
Cerberus rynchops	S	P	Jayne et al., 1988
Enhydrina schistosa	S	P	Voris & Moffett, 1981
Laticauda colubrina	S	P	Shine et al., 2002
Laticauda frontalis	S	P	Shine et al., 2002
Natrix maura	S	P	Santos & Llorente, 1998
Nerodia fasciata	S	P	Miller & Mushinsky, 1990
Nerodia harteri	S	P	Greene et al., 1994
Nerodia rhombifer	S	P	Kofron, 1978; Plummer & Goy, 1984
Nerodia sipedon	S	P	King, 1993
Thamnophis atratus	S	P	Lind & Welsh, 1994

With regard to lower prey size limit, species that delete small prey from their diet when they grow are characterized by an ontogenetic shift (S); species that feed on large as well as small prey when getting larger, are categorized by an ontogenetic telescope (T). We distinguished piscivorous species (P) from species feeding on terrestrial prey (T).

In the experiments we used *C. auratus* as prey, ranging from 1 to 13g (i.e. 2 to 32%RPM (relative prey mass, i.e. prey mass divided by snake mass)) for both size classes of snakes. Although goldfish are not part of the natural diet of these snakes, other cypriniform fish are part of the natural diet of these snakes (Luiselli & Rugiero, 1991; Filippi et al., 1996; Gruschwitz et al., 1999). Fish were weighed with an electronic balance (Fx-3200, A&D, Johns Scientific Inc., Japan). Our prey range seemed sufficiently large, as the heaviest fish presented to the snakes were at times too large to ingest. We randomly retrieved fish from a large holding tank and presented each snake different sizes of fish spanning the entire range tested during the experiments. At the beginning of the experiments we placed a single *C. auratus* in a plexiglass aquarium (45x22x20cm) filled with water and a terrestrial section of 11cm wide. The water was kept at 25°C using a water heater. Subsequently, we introduced a snake into the aquarium and filmed it using a JVC digital video camera (Victor Company, Japan). We analysed the video-sequences to record the number of capture attempts and capture time for *N. tesselata* feeding on goldfish.

Capture attempts

We counted the number of strikes needed to capture a fish. When the snake released the fish after more than one second, the attempt was regarded as successful and subsequent capture attempts after releasing were not considered. Sometimes snakes performed multiple undirected strikes with jaws opened widely after an unsuccessful strike (see Bilcke et al., 2006). We did not include these strikes in the overall count.

Capture time

We defined capture time as the time elapsed between the first orientation of a snake towards a fish and the time when a snake grasped the fish with its jaws. Although this measure of capture performance includes a significant behavioural component on the part of both prey and predator, we do believe this is an ecologically relevant indicator of capture performance as both the approach to the prey and the actual strike determine the success and cost of a foraging attempt.

Statistics

We used Shapiro-Wilks tests to check the continuous data for normality before and after transformation. We $\log_{10}(x+1)$ transformed the number of capture attempts and capture time to obtain normal distributions (SOKAL & ROHLF, 1995). We identified five outliers using box plots and subsequently removed them from the dataset [i.e. extremely high values of capture attempts (49 and 32 attempts) and capture time (4669, 4033 and 3285sec)].

To test for the effect of snake and fish size on capture attempts and capture time, we used a mixed-model ANCOVA with snake size (small / large) as a fixed effect and fish mass as co-variable. We modelled individual (snake 1 to snake 9) nested within snake size as random effect to account for inter-individual variation in capture attempts and capture time. We performed the analyses using the proc MIXED procedure in SAS (LITTELL et al., 1996). Degrees of freedom of the fixed effects F-tests were adjusted for statistical dependence using Kenward Roger formulae. Residuals and estimates of the random effect of the final models were normal distributed (Shapiro-Wilks tests).

RESULTS

Since the relationship between fish mass, capture attempts and capture time did not differ between small and large snakes (i.e. no interaction effect: capture attempts: $F_{1,138}$=2.63, p=0.11; capture time: $F_{1,137}$=0.78, p=0.38), we omitted the interaction terms from the final models. We found significant inter-individual variation in the number of capture attempts and the capture time of the snakes (LR-test statistic, capture attempts: χ^2_1=49.8-45.7=4.1, p=0.04; Fig.1a; capture time: χ^2_1=319.5-311.2=8.3, p=0.004; Fig. 1b).

Large snakes needed more strikes to catch a fish (6±1 and 5±1 attempts, respectively) and spent more time capturing a fish than small snakes (685±118s and 292±42s, respectively). However, neither of these trends are significant (capture attempts: $F_{1,7.43}$=0.85, p=0.38; capture time: $F_{1,7.31}$=1.88, p=0.21). Snakes, however needed more strikes to catch larger fish ($F_{1,136}$=3.77, p=0.05; Fig. 1a). No relationship was found between fish size and capture time ($F_{1,135}$=0.00, p=0.97; Fig. 1b).

DISCUSSION

We tested the effect of snake and fish size on the capture success of the specialist aquatic snake *Natrix tesselata* to investigate hypotheses suggesting that 1) small snakes are better at catching fish than large snakes and 2) that larger fish are easier to catch than smaller fish. Unexpectedly, our study could not demonstrate significant effects of snake size on capture ability. Yet, despite significant inter-individual variation, we did find that small fish were significantly easier to capture than larger fish (in terms of the number of capture attempts needed, not in terms of capture time).

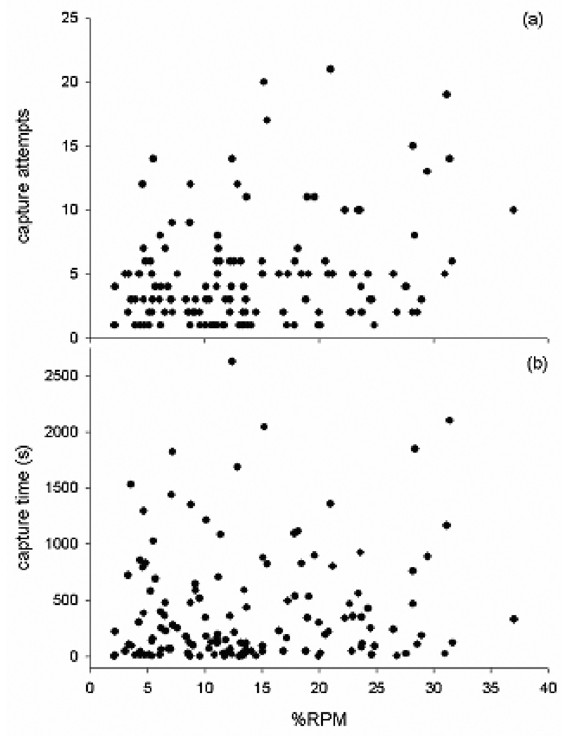

Fig. 1. – Relationship between the relative mass of goldfish (%RPM) with (a) the number of capture attempts and (b) capture time, for *Natrix tesselata*.

We found no significant effects of snake size on capture performance. Similar results were obtained by HAILEY & DAVIES (1986), suggesting that within the size range tested, snake size does not seem to have a big impact on capture performance. Maybe size effects become important only from a minimum size; i.e. there exists a minimum absolute size that will start to create disadvantages to prey capture in an aquatic environment. In support of this hypothesis, some generalist semi-aquatic snakes shift from aquatic prey to terrestrial prey (e.g. frogs) when they reach a specific size. For instance, *Nerodia erythrogaster* and *N. fasciata* shift from fish to frogs when they exceed 50cm SVL (MUSHINSKY et al., 1982). Also in *Rhabdophis tigrinus* and *Natrix maura* a shift from fish to frogs with increasing SVL was shown (MORIGUCHI & NAITO, 1982; SANTOS & LLORENTE, 1998). However, some species such as *Thamnophis validus* show the reverse trend: it shifts from frogs to fish when it exceeds 50-70cm SVL, suggesting that size effects might have complex interactions with prey capture behaviour or prey capture habitat (DE QUIEROZ et al., 2001). However, until we have a better understanding of the hydrodynamics and kinematics of aquatic prey capture in snakes it will be difficult to resolve these issues.

Our data also indicated no significant effects of fish size on capture time, but demonstrated large inter-individual variation. This observation may the consequence of our definition of capture time which includes an important behavioural component. For instance, capture time will depend on which foraging strategy is used: sit and wait or active foraging (BILCKE et al., 2006). Thus snakes may use behavioural shifts when confronted with prey of different size to keep capture time constant. However, a significant effect of prey size was found on the number of capture attempts needed. Unexpectedly, and in contrast with data for *N. maura*, *N. tesselata* needs fewer attempts to catch small fish compared to large fish. Although these results appear contradictory at first, differences in the degree of aquatic specialization between the two snake species might lie at the basis for this observation. For example, a previous study showed that, despite similar foraging behaviours, *N. tesselata* has a higher capture success then *N. maura* (35% compared to 20%; Bilcke et al., 2006). Possibly, *N. tesselata* is morphologically better adapted to catch prey in the aquatic environment than *N. maura*. Indeed, compared to its more terrestrial congener *N. maura*, *N. tesselata* possesses a very narrow and streamlined head. Such a head shape is thought to reduce the hydrodynamic drag encountered during prey capture (Young, 1991; Hibbits & Fitzgerald, 2005). However, this needs to be assessed quantitatively. Why *N. tesselata* captures small fish more easily remains unclear at this point but may be in part due to differences in the escape response of large and small fish when confronted with a specialized aquatic predator such as *N. tesselata*. Clearly, further data on the kinematics and hydrodynamics of this prey-predator system are needed to better understand our results.

In conclusion, snake size does not affect the capture performance of *N. tesselata* within the size range tested. Possibly size becomes only important from a minimum absolute size, which is larger than the ones covered in our study. Moreover, *N. tesselata* needs fewer attempts to capture small fish, whereas *N. maura* needs less to capture big fish. Possible explanation lies in difference in morphology/kinematics between these species. An in-depth study of the hydrodynamics of this predator-prey system could provide ways to evaluate the importance of size effects.

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