

Diet Variability of Two Convergent Natricine Colubrids in an Invasive-Native Interaction

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Abstract. In cases of introductions where the exogenous species is morphologically and ecologically very convergent with one, or more, of the native species, the potential for resource (trophic, territory, sun, shelter, etc.) competition is high. In this regard we investigated in 2007 and 2008 the potential role of trophic resource competition in the invasive-native species system *Natrix maura*-*N. tessellata* on the shores of Lake Geneva in Switzerland, of which this paper is the follow-up. We confirmed, among other results, a strong similarity in the diet of both species and were able to calculate a large overlap of their trophic niches (METZGER et al. 2009). In addition to that work we report herein patterns of within-year variation of the diets of both snakes, and report on the observation of individual foraging behavior observed in an artificial environment.

Key words. Alien species, colubrids, diet, foraging behavior, Natricinae, seasonal variation

Introduction

Introduced species may play a key role in the ecosystem in which they have established themselves, even more so when they show patterns of invasiveness. After a period during which the newly introduced species is almost undetectable in the environment, called the lagging period, its population may grow sometimes dramatically (ELTON 1958, WILLIAMSON 1996). It is often then that the invasion is detected and characterized as such. Those invasive species may become very problematic when cohabiting with ecologically similar species. Direct (e.g. predation, territorial exclusion) or indirect (e.g. food, hibernaculas) competition may arise and start reshaping the local species populations (WILCOVE et al. 1998, BYERS 2000).

Natrix maura and *N. tessellata* are very similar species even though they have a mostly allopatric distribution (GUICKING et al. 2008). Both species cooccur naturally only in a few locations in northern Italy (SCALI 2011). Although not adelphotaxons (sister species), both species are ecologically and morphologically very convergent probably due to adaptation to similar ecological niches (GRUSCHWITZ et al. 1999, SCHÄTTI 1999), using the environment in seemingly similar fashion (METZGER et al. 2009, MAZZA et al. 2011), and having a similar diet in allopatric regions (BILCKE et al. 2006 for a review, SANTOS et al. 2006, LUISELLI et al. 2007) as well as in our region of sympatry in southwestern Switzerland (METZGER et al. 2009). Clear genetic segregation between both species has been shown by phylogeographic studies (GUICKING et al. 2006, GUICKING et al. 2008) and although some rare events of hybridization in captivity have been reported, none in the wild have ever been found (KABISCH 1999, SCHÄTTI 1999).

The dice snake was introduced into several lakes north of the Alps in Switzerland, where it is extralimital

of its natural distribution area (MEBERT 1993, LENZ et al. 2008). An initial introduction (first mention 1925: MORTON 1926) followed by subsequent introductions in the 1950s and 1960s (GARZONI & MONBARON pers. comm.) on the northern shore of Lake Geneva led to a large population of hundreds of individuals. After 10 years of monitoring of this invasive-native species system (1999 to present, KOLLER & URSENBACHER 1999, MONNEY 2004, URSENBACHER & MONNEY 2007, URSENBACHER & MONNEY 2008, MAZZA et al. 2011, URSENBACHER et al. submitted) the decline of the native colubrid population was estimated at -4.4% per year (URSENBACHER et al. submitted), indicating potential effect of the introduced species on the native one.

In order to evaluate if a competition for food occurs and to better understand the feeding behavior of both species coexisting in the the same region of Lake Geneva (also called Lake Lemman) in southwestern Switzerland, we studied *in situ* the invasive-native species system *N. maura*-*N. tessellata* along the shores of the lake, as well as *in vitro* in an aquarium setting for basic behavioral observations at the University of Lausanne. In this paper we report on our use of a comparative diet analysis to evaluate trophic regime variation from stomach contents of wild caught snakes and direct observation of feeding behaviors in aquaria to understand the ecological types of prey species found in the snakes' diets. The present report is an accompanying document to METZGER et al. (2009).

Material and Methods

Study Area

The area of introduction of *Natrix tessellata* is situated on the northern shore of Lake Geneva, in the region called the Lavaux (about 70 km east-north-east from Geneva, Switzerland). The species occurs in a nar-

row strip of riparian slope of about 3.5 km in length and 3 to 10 meters in width, which was used as a transect for sampling the snakes. This zone is appropriate for ecological and conservation studies, since it is narrow and severely hinders natural dispersion of the species due to its natural (deep and broad lake) and artificial barriers (abutting and uphill to the north of the habitat are: railroad tracks, a 5 to 10 m high concrete wall, a road; and on the eastern and western parts the area is flanked by urbanized regions such as towns or villages). These barriers also hinder the access for potential land-dwelling predators and humans resulting in a rather calm and safe area for snakes. It also limits the possible adaptation to other ecological niches. With its good geographical orientation (southerly exposed) this rather xeric slope terrain (between about 12° and 40° slope) receives optimal solar radiation and temperature conditions during most of the active field season. In addition the easy access to a large reservoir of trophic resources in the lake permits abundant feeding.

As a result of all these beneficial conditions, this region has one of Switzerland's highest density of reptiles (KOLLER & URSENBACHER 1999, METZGER et al. 2009). Unlike other regions inhabited by these snake species (BILCKE et al. 2006, SANTOS et al. 2006, LUISELLI et al. 2007), this area is entirely devoid of amphibians, thus leaving only fish as available trophic resource (MONNEY 2004). The area also has heterogeneous vegetation, with patches of naked stones, pioneer vegetation interspersed between larger sections of highly vegetated terrain (METZGER et al. 2009, MAZZA et al. 2011).

Data Sampling

Fieldwork consisted of manually capturing snakes of both species along the transect during the activity season in 2007 (July and August) and in 2008 (May through September). Sampling lasted between 5 and 7 hours, starting when the first solar radiations reached the ground in the area, which coincides with the earliest possible sightings of snakes (METZGER pers. obs.). Upon capture snakes were measured (snout vent length; to the nearest mm), weighted (to the nearest 0.1 g), their sex was determined by examining the sexual dimorphic shape of tail root (MEBERT 1993; juveniles were not sexed due to the potential risk of incorrect sex determination: FILIPPI 1995), their exact geographical location and time and date of capture were recorded. Regurgitation reflex was induced by gentle ventral palpation. Regurgitated prey items were measured (length and width, *sensu* DELLING 2003, see also METZGER et al. 2009 for a more detailed explanation), and determined in the field when possible, or otherwise preserved in 70% EtOH for further careful examination.

Artificial Environment Observations

Twenty snakes, ten of each species, were kept in hetero-specific pairs for 2 to 5 days in aqua-terraria with simulated lake bottom conditions (rocky bottom, with some larger rocks scattered around) and fed after 24 hours of acclimation with either one open-water free-swimming fish (either a roach, *Rutilus rutilus*, or a perch, *Perca fluviatilis*) or a small shoal of roach. The behavior and hunting strategies of the snakes in presence or absence of the prey were assessed by visual observation from the side or the top of the tank. To reduce the risk of distractions or disturbances by external, artificial incentives (e.g. humans passing by the tank), all sides of the aqua-terraria were blocked by card-board, leaving only a thin longitudinal opening to observe the inside of the tank. The top of the aqua-terraria was not blocked but nothing else than lights and the roof was visible over the aqua-terraria. The terrarium part of the installation consisted of a wooden box with an opening on its bottom to let the snakes access the aquarium part, again reducing visual distractions for the snakes (Fig. 1).

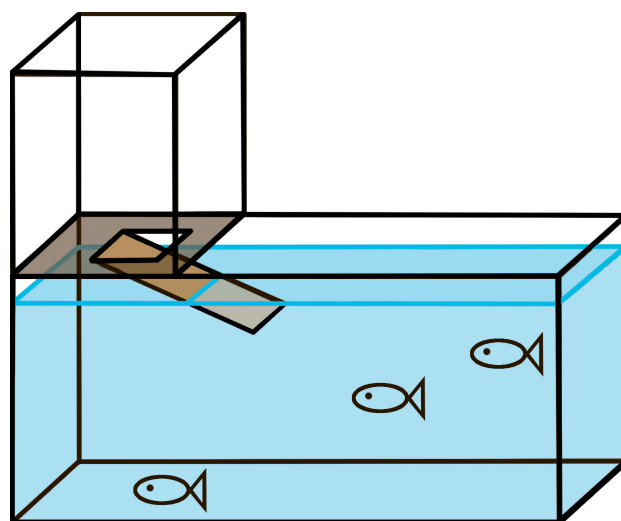


Fig. 1. *In vitro* observational set-up. Top-part shows the "dry area" or terrarium, lower part the "wet area" or aquaria. Passage from one to the other area was allowed by a large tree branch lying on an inclined slate, represented in the figure only by an inclined plane.

Statistical Procedure

We used a fairly new procedure to estimate the similarity of the seasonal variations in diet of both snake species. This procedure, called PerMANOVA, is a non-parametric method for multivariate analysis of variance based on a multivariate analogue to Fisher's F-Ratio and using subsequent permutations to calculate the *P*-value (ANDERSON 2001). It was analyzed using the software R (version 2.4.1, R Development Core Team 2006) with

the Vegan Package and its 'adonis' function (OKSANEN et al. 2007).

Results

We captured and measured 77 *Natrix maura* (58 females, 13 males and 6 juveniles) and 213 *N. tessellata* (158 females, 33 males and 22 juveniles). Only 22% of females and 15% of males regurgitated identifiable prey items, and thus were included in the analysis. Juvenile regurgitations (three of each natricine species) were not included in the analysis for obvious statistical reasons and sex determination problems. The prey species examination using both, external (color, shape) and internal characters (counting of fin rays), resulted in the identification of six distinct Actinopterygii species of which five were found in both predators' stomach contents and only one species (*Lota lota*, the burbot) was found twice in *N. tessellata* solely. The three most frequent prey species in both snakes' diets, occurring in the same order of predominance in both snake species, were: *Cottus gobio* (the European bullhead, 43.5% in *N. maura* and 61.4% in *N. tessellata*), *Perca fluviatilis* (the European perch, 26.1% in *N. maura* and 14.1% in *N. tessellata*), *Rutilus rutilus* (the common roach, 17.4% in *N. maura* and 10.5% in *N. tessellata*). Other, less frequent prey types in the diets of both snakes were the common bleak (*Alburnus alburnus*) with 4.3% in *N. maura* and 7.0% in *N. tessellata*

and the gudgeon (*Gobio gobio*) with a higher prevalence of 8.7% in *N. maura* as that in *N. tessellata* of only 3.5%. The burbot was found twice in *N. tessellata*, which represented 3.5% of its diet. No significant diet difference between the two snake species was found as detailed in METZGER et al. (2009).

Seasonal Variation in Diet Composition

Plotting the regurgitated prey against date of regurgitation showed a distinct pattern in prey capture per month. In Figures 2a and 2b, seasonal diet of the two natricines show a similar pattern of prey types captured per month. The frequency of *C. gobio*, the most frequently preyed fish, was higher in the early season and decreased until the mid-season. Snakes started to regurgitate *P. fluviatilis* in July and did so until the end of the season. *R. rutilus* was regurgitated throughout most of the season, with the exception of May where none of this species was recovered. *A. alburnus* was only occasionally regurgitated during the months of June and July. The data with *L. lota* is to be taken with caution since only two specimens were regurgitated in July and both by *N. tessellata*. Due to similarity between the diet patterns observed in both species (PerMANOVA, $F = 0.161$, $P = 0.96$) we pooled the datasets to obtain an overall view of the captured species per month throughout both years of fieldwork (Figs. 2c, d). With up to 46.15% of the to-

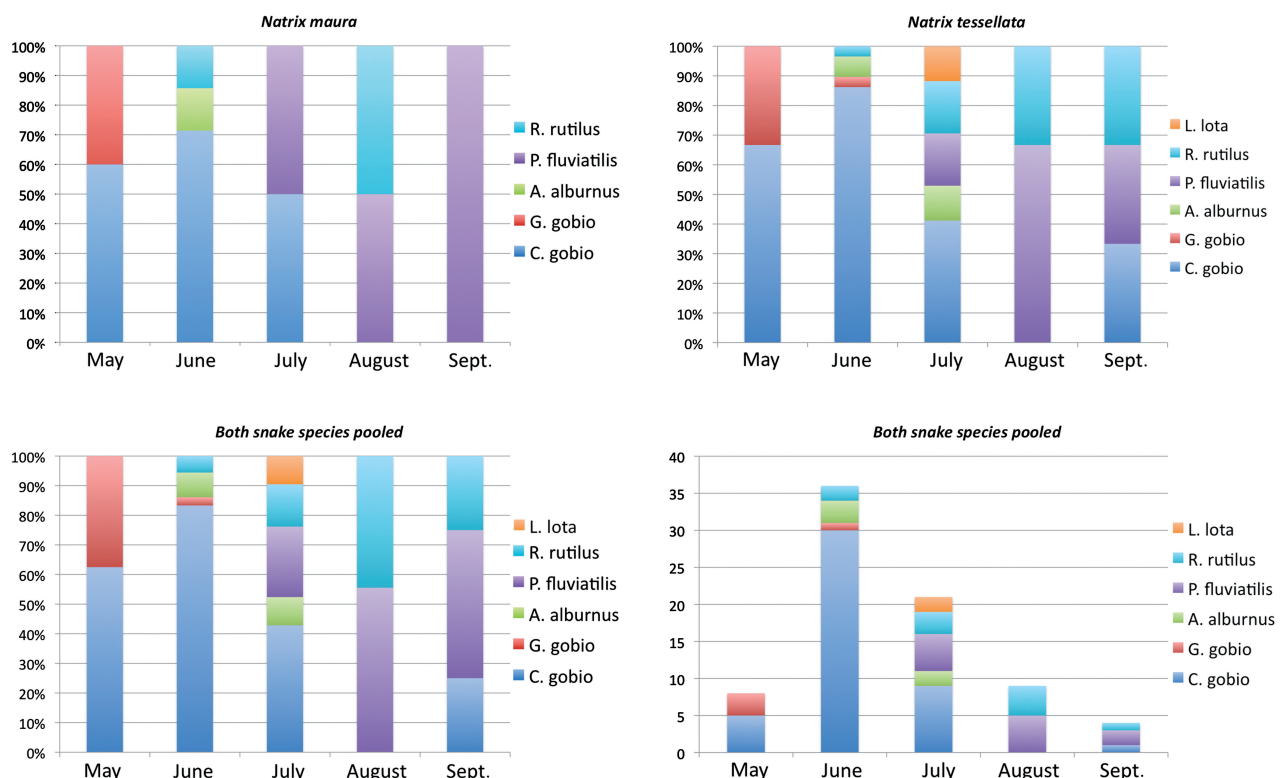


Fig. 2. Percentage of regurgitated prey species by month in (a) *Natrix maura*; (b) *Natrix tessellata*; and (c) both snake species pooled. (d) Number of regurgitated prey species by month, both snake species pooled.

tal amount of regurgitations, June was the month with the highest number of recovered prey items, followed by July with 26.92% of the regurgitations, August with 11.54%, and May with 10.26%, respectively. September, the last month of the active season showed also the least amount of recovered prey items with only 5.13%.

Diet Variation with Regard to Geographical Location

Plotting the prey species regurgitated against the position along the transect, where the predator was captured, showed some structuring along the shore (Fig. 3). Especially *C. gobio* and *P. fluviatilis* had an uneven distribution along the shore with the latter predominantly found between kilometers 10.2 and 11.4 and the former between kilometers 11.4 and 11.7 and again between 12.1 and 13.1. Although the boundaries were not clear and with some overlap, regions with a predominance of one of the two species of prey were observed. The other prey species were not regurgitated in large enough proportions to show regional partitioning tendencies along the transect.

Foraging Behaviors

The observation of 10 different snakes of each species in artificial conditions allowed us to identify five distinct hunting strategies to hunt three principal behavioral types of prey (Figs. 4, 5). Both species of snakes showed all five hunting strategies. Depending on the type of prey available in the tank the snakes would exhibit different hunting strategies. When the prey were bottom-dwelling fishes, or when there were no prey available to hunt, snakes would either actively search the gravel and rocks

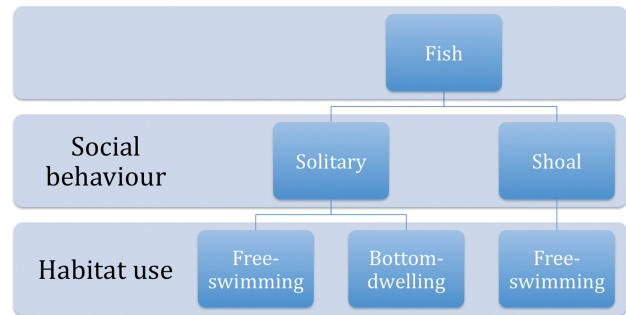


Fig. 4. Categories of fish behavior.

with their head, using their bodies and tails in a slow swimming motion and move forward (Strategy N°1) or hold themselves to a rock with their tail to avoid floating up to the surface, their body in a distinct ready-to-strike S-shape and sit and wait at the bottom of the tank (Strategy N°2). This behavior, which we named the “lurking behavior”, was also exhibited when the prey were pelagic fishes, solitary or in shoals. In addition to the lurking behavior, pelagic fishes were also hunted actively with snakes swimming through fish shoals (Strategy N°3), although this method did not appear to be very effective. Provided a branch or any other support was stretched over the water surface, snakes would spend time on this support looking at the surface of the water or even stretching their body to maintain the head just under the surface of the water and observing the movements in water (Strategy N°4). This passive strategy was rather an observation behavior than a hunting behavior per se, since no fish were ever captured directly from this position. But if a fish was spotted, the snake would immediately slide into the water and swim after the fish, another marginally effective hunting behavior (Strategy N°5).

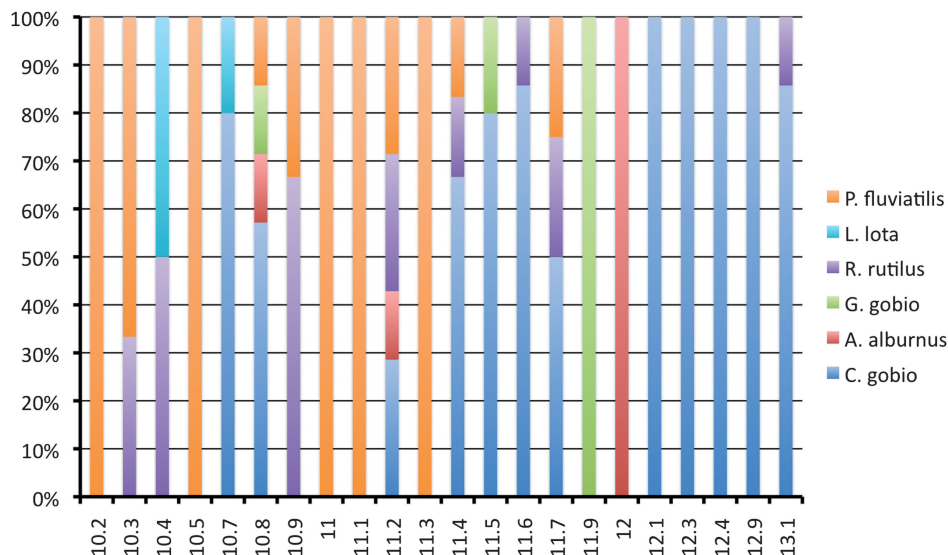


Fig. 3. Distribution of regurgitated prey species along the transect.

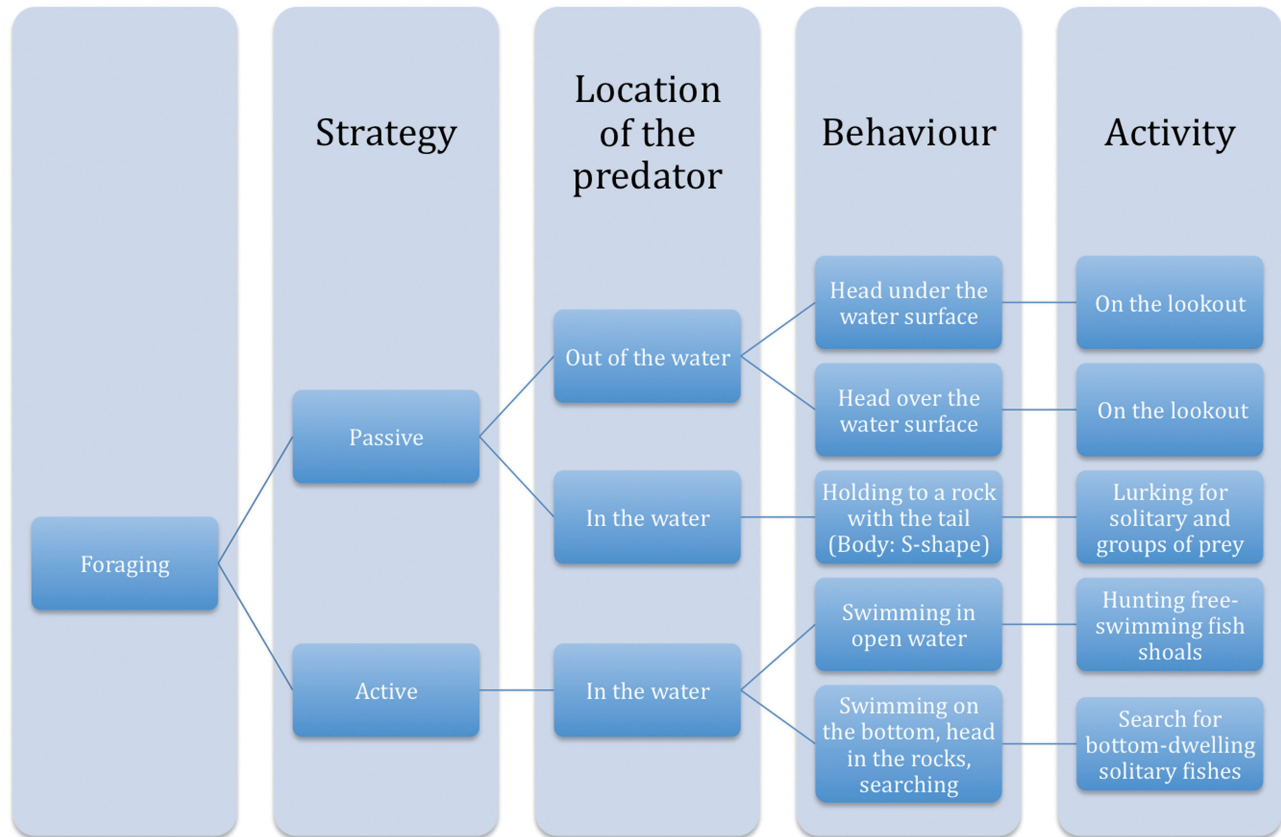


Fig. 5. Categories of snake hunting strategies and behaviors.

Prey Handling

In METZGER et al. (2009) we showed that 97.5% ($n = 80$) of collected prey were regurgitated tail first, which means that snakes ate their prey headfirst in almost every case. In our aqua-terraria observations snakes would catch fish by biting them at any random position on the fish body. The fish were in most cases dragged out of the water and then the snake would progressively move its upper and lower jaws alternately to position the prey headfirst in its mouth. Sometimes, when snakes did not manage to get out of the water quickly, the prey repositioning motion would be executed in the water.

Discussion

In a previous study we showed that the diet composition of the two natricine colubrids studied was significantly similar, with a strong overlap (between 75 and 95 %) of the trophic niches (METZGER et al. 2009). We show here that the composition of the diets of both snakes is not constant throughout the season but is subject to important variations. Both species showed similar patterns of variation in diet composition, indicating that this variation is not predator specific but rather due to some environmental or third party factors directly or indirectly acting on the availability of prey or even on the prey

populations in the lake. The early season as well as the late season (months of May and September) did not yield many regurgitated prey, as during these months not many snakes were captured due to the variably bad weather and colder temperatures. In addition, variance in the sensitivity of snakes to seasonal climatic changes can account for snakes becoming active at different time points in late April, in May, and even in early June, depending on the temperature and humidity. Variation in the hibernaculus' permeability to external temperature and humidity variations might also influence the emergence of each snake.

A similar reasoning can be applied to the end of the season, when snakes progressively return to their hibernaculus. The main season (end of May to end of August) had a good abundance of regurgitated prey. Variation in prey species abundance in the regurgitations during the main season may be accounted for by seasonal migrations of fish species. Fish have been shown to demonstrate patterns of diel migration as well as migration throughout the season in response to various incentives such as temperature changes at various depths in the water column, migration and abundance of plankton and search for spawning places among others (LUCAS & BARAS 2000, 2001). Although some of the species captured by *N. maura* and *N. tessellata* have more sedentary behaviors, such as the bullhead (*C. gobio*: MORRIS 1954, KNAEPKENS et al. 2005, SMYLY 1957), others are clearly

open-water free-swimming migratory fishes (perch, *P. fluviatilis*: ALLEN 1934, WANG & ECKMANN 1994, ECKMANN & IMBROCK 1996, roach, *R. rutilus*: VØLLESTAD & L'ABÉE-LUND 1987, L'ABÉE-LUND & VØLLESTAD 1987, HORPPILA et al. 1996, JÄRVALT et al. 2005). The major variation can also be explained by the birth and growth of cyprinids and perch during the season, reaching sizes big enough for the snakes to predate in July and August. At that time, big shoals of late juveniles (subadults) search for food along the shore and can consequently be eaten by the two *Natrix* species.

In addition to seasonal variation, a certain portion of the variation could be explained by capture success, some prey species being far easier to capture. The bullhead is a rather sedentary fish, sheltering under rocks during the day and being more active at night (TOMLINSON & PERROW 2003). It would make a perfect prey for the colubrids that are active during the day, searching the bottom of the lake for fish hidden between rocks. We were able to confirm this behavioral tendency by observing 10 snakes kept in tanks in the laboratory with no specific treatment other than a recreated facsimile of the natural environment and feeding them every 4–5 days with live fish.

Observational Study

In order to better understand the foraging behavior of *N. maura* and *N. tessellata* and better interpret the results obtained from the diet analysis, we set up 20 snakes, 10 from each species, in aqua-terraria and observed their foraging and feeding behaviors. Although we tried to control for potential biases, such as disturbances to snakes and their prey by visual cues of movements outside the aqua-terraria, artificial environment behavioral studies will always remain somewhat biased due to the very simple fact that they are done in artificial environments. Nonetheless in our case, the observation of the foraging and feeding behavior of the snakes in such conditions may still bring some realistic elements of response and contribute to our general understanding of their natural behavior.

Predators which are not very specialized on one type of prey need to be able to exhibit various hunting strategies in order to cope with the various behaviors exhibited by their prey. From the regurgitation data, we were able to identify species of prey that belong to very different behavioral types of fish including pelagic and benthic fish but also diurnal and nocturnal ones. *N. maura* and *N. tessellata*, being ectothermic and thus mostly diurnal organisms in the temperate climate of continental Europe, hunt predominantly during the day. Hunting requires the expenditure of large amounts of energy, even more when hunting in a large body of water such as Lake Geneva where constant swimming in variable water currents is required. Indeed swimming requires a lot of energy and the water is colder than the air during the summer, which decreases the body temperature

of the organism, lowering at the same time the available energy for motor activity. Catching nocturnal prey is possible for diurnal predators by actively searching between and under rocks for the day shelters of those prey. *C. gobio* is known to take shelter under rocks during the day and thus is an easy prey, which might contribute to their high prevalence in the snakes' diets. All other prey items regurgitated are diurnal pelagic fishes, mostly swimming in shoals. To catch these prey snakes developed mainly two strategies, the passive "sit-and-wait strategy", or lurking behavior (also termed ambush behavior), and the active "swimming through the shoal strategy". While the first strategy appeared to be more efficient by catching prey with a precise and fast strike, the low amount of prey swimming by close enough to be caught by such strikes lowered this strategy's comparative success. On the one hand swimming through a shoal is less efficient at catching the prey but there are a lot more prey available close by which in turn increases the success rate. The optimization of success rate probably explains why both strategies are being exhibited and neither one was selected against.

Due to obvious morphological constraints fish cannot be ingested in every way. They can either be eaten headfirst or tail first. But our observations confirmed the data from our previous study (METZGER et al. 2009), which showed prey being almost always eaten headfirst. We argue here that this behavior has evolved for two reasons. Fish have scales and fins that are strong solid structures, sometimes very sharp and long, but invariably growing outwards of the body in an aboral (away from the mouth) orientation. Thus eating a prey tail first might be hindered by the fins and scales protruding, and could eventually lead to the wounding of the predator. Secondly when the predator is hunting in the water, especially in larger bodies of water such as lakes, it might have to swallow its prey while still in the water. If the snake manages to place the prey headfirst in its mouth, the chances that the prey will escape by swimming are decreased since fish are highly efficient at swimming forward but only marginally so backwards. In addition to this, many fish species, when caught by a predator show sudden tail thrashes to liberate themselves from the predator. These thrashes were also observed in fishes caught headfirst by the snakes, but the ensuing result was that the fish pushes itself quicker into the mouth of the snake. This could be a case of counter adaptive fleeing behavior of fish, selected for by other predators' different hunting strategies (such as larger fish, or diving piscivorous birds that might not care about the orientation of the prey caught).

Implications for the Invasive-Native Species System

The herein shown similar pattern of seasonal variation in diet of both snake species, and taking into account the large diet overlap index calculated in METZGER et al. (2009), corroborating the aforementioned conclu-

sion, implies a seasonal variation in the composition of the fish community in this region. Potential effects of this variation on the invasive-native species system in question are unclear. We hypothesize that the early season, and the accessibility to prey during this period of higher energetic requirements (cool weather, reduced sunlight, mating activities, reproduction and preparation of the females for gestation are factors which happen early during the year in both species in this region, J.-C. MONNEY pers. comm.), may impact the reproductive success of the females and thus ultimately the overall fitness of the species. In the past 11 years of monitoring both species in this region, a clear tendency for earlier emergence from hibernation in *N. tessellata* than in *N. maura* was observed (pers. obs., and J.-C. MONNEY pers. comm.), which could give the former species a head start on feeding, especially considering that in the early season the availability of prey appeared to be reduced. We suggest that this longer feeding period of *N. tessellata* from emergence to oviposition can account for their tendency to produce more eggs (URSENBACHER et al. submitted) and it might even influence the quality of the eggs produced (more reserves in the eggs, leading to stronger juveniles at hatching) resulting in an increased fitness. Together with our observations and conclusions, the yearly *N. maura* population decline calculated by URSENBACHER et al. (submitted) indicates an indirect detrimental effect of the introduced *N. tessellata* on the native *N. maura*. Further investigations are needed, and are underway, to understand the exact nature of the (probably) indirect interaction leading to the slow replacement of the local species by its congeneric competitor.

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