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Structural Habitat Partitioning of *Natrix tessellata* and *Natrix maura* at Lake Geneva, Switzerland

Gaëtan Mazza, Jean-Claude Monney & Sylvain Ursenbacher

Abstract. In Switzerland all eight snake species are threatened and have been added to the Swiss Red List with different levels of concern. The most threatened is the viperine snake, *Natrix maura*, a semi-aquatic snake, which is considered as "Critically Endangered" (CR) in Switzerland. Only one population is presently living on the shores of Lake Geneva, mainly located between St-Saphorin and Treytorrens (Canton Vaud). But the population size estimation trends show a drastic reduction of this species. Alteration of the lake shore structure and the introduction of the ecologically very similar dice snake, *Natrix tessellata*, since the 1920s could be the causes of the observed decline of the viperine snake in the last 15 years. A higher fecundity and a larger body size render the alien species probably more competitive and possibly have a key role on the population decrease of the native species. In order to test the hypothesis of competition between both species, their habitats between St-Saphorin and Treytorrens were described in detail in order to detect differential interspecific use. In total 23 environmental variables were measured at the study area and data were subsequently analysed using tests of proportion. Results indicate that the dice snake prefers slopes with limited vegetation height (0.5–1 m), but inhabits also slopes with light vegetation cover and relatively narrow littoral zones. In contrast, the habitat use of the viperine snake relates to littoral zones with less steep slopes, but abundant vegetation. In addition, wide littoral zones seem to be preferred by the native species, such as the region near Treytorrens where the viperine snake was observed to be most numerous. Results obtained in this study were used to suggest particular shore management action, in particular to promote the native species.

Key words. Habitat partitioning, introduction, interspecific competition, *Natrix tessellata*, *Natrix maura*, Lake Geneva

Introduction

All snake species in Switzerland are present on the Swiss Red List for threatened species and the threat for most species is increasing (Monney & Meyer 2005). The main reason for this regression is the destruction and the fragmentation of their environment (Hofer et al. 2001). Indeed snakes require various environments in order to complete their life cycle, including a hunting area, open segments for thermoregulation, covered sites for daily shelters, oviposition and hibernacula sites, etc… Increasing urbanisation and draining of wetlands have drastically changed natural habitats and impacts on the species have sometimes become irreversible. Thus conservation plans for these species must be focused mainly on renaturalisation of the landscape as well as to preserve and manage the remnant habitats optimal for reptiles.

The viperine snake, *Natrix maura* (Linnaeus 1758) is a highly threatened semi-aquatic snake, considered as critically endangered (CR) on the last Red List of the Swiss Threatened Reptiles (Monney & Meyer 2005). Hofer et al. (2001) suggested that pollution, human disturbance and landscape modifications are the major reasons for the decline of this species. But locally, other threats may negatively impact population size of viperine snakes. Indeed, the dice snake (*Natrix tessellata* Laurenti 1768), which was voluntarily introduced on the shores of Lake Geneva near Le Lavaux between Vevey and Lausanne since the 1920s (Morton 1925), with specimens mostly from the lower Ticino, southern Switzerland (Mebert 1993, 1996), has a very similar ecological niche and possibly poses a competitive threat on *N. maura*. Since its first introduction and subsequent ones in the 1950s and 1960s (J. Garzoni and S. Monbaron pers. comm.), the population size of this alien species appears to have increased dramatically to become the dominant semi-aquatic snake species at the Le Lavaux region. Koller & Ursenbacher (1996) estimated the adult female population size of the viperine snake at 300 individuals compared to 500 adult females of local dice snakes. Later, a study summarizing observations from 1996 to 2006, clearly showed a major reduction of the viperine snake population and a simultaneous increase of the dice snake numbers (Ursenbacher et al. 2006). Recent studies deal with the dietary aspect of this local native-invasive system (Metzger et al. 2009, Metzger et al. 2011).

In order to preserve this remnant population of *N. maura*, additional knowledge about the role of the potential interspecific competition with the dice snake is needed. This study was consequently focused on the habitat occupancy by the two species. The aim was to analyse the habitat at Le Lavaux where the two snakes coexist between St-Saphorin and Epesses, in order to find potential differences in the utilization of the hab-

itats and consequently propose a management plan to improve the state of the native species.

Material and Method

The study consisted of three phases. First, the different habitats in the study area (Le Lavaux, Lake Geneva, Switzerland), which stretches along 4 km shoreline between St-Saphorin and Treytorrens, were defined. Second, the different habitats were described in details, and third, the frequency of each species in the different habitats was estimated. For each phase a specific protocol was conducted. The study area was split into three geographic sections (variable 3, Tab. 1): St-Saphorin, Rivaz and Treytorrens. The habitat evaluation was carried out only between the lake and the parallel running railway (a section between 1 and 10 m width), where most of the individuals have been observed.

Primary Habitat Variables (Linear Segmentation)

Two criteria were evaluated to define the primary nature of available habitat along the shoreline. First, the habitats were categorized as "slope" or "wall" (variable 1, Tab. 1). The former category represents a shore segment consisting of a more or less gentle slope between the lake and the railway (Fig. 1). The latter category was made of a vertical concrete wall that raises from the lake (Fig. 2), and whose horizontal top, interspersed with some vegetation, was frequently used by basking snakes, sometimes limiting drastically the snakes' access to the lake.

The second main criteria related to the vegetation cover. Both "wall" and "slope" habitats were categorized depending on the principal vegetation structure and the dominant stratum (variable 2: secondary structure). This first protocol allowed determining the main groups of habitat along the lake's shore.

Secondary Habitat Variables

An additional protocol was applied with a secondary set of variables that describes the various habitats in more details. The following characteristics were noted: general data (variables 3–7, 13–15: coordinates, surface, degree of the slope, orientation, access to the lake, granulometry of stones/blocks, i.e. measurement of their size distribution, proportions of concrete embankment and sections without vegetation), characteristics of the feet of the lakeside embankment (first ca. 0.5–1.0 m from the waterline; variable 8–12: mineral composition, presence/absence of vegetation, type of vegetation), surface char-

Table 1: List of variables used to describe the different habitats where *Natrix maura* and *N. tessellata* coexist.

Variables	Categories
1) Main structure	Slope or wall [1]
2) Secondary structure (principal vegetation cover)	9 types of slopes / 6 types of walls
3) Site	St-Saphorin / Rivaz / Treytorrens
4) Length of habitat (parallel shoreline)	Meters
5) Width of habitat	Meters
6) Angle of slope (degrees)	<30° / 30°–60° / >60°
7) Orientation	SW / S / SE
8) Lakeside embankment	Stone blocks / beach / other
9) Vegetation of the lakeshore	Yes / No
10) Ivy plants on the lakeshore	Yes / No
11) Bushes on the lakeshore	Yes / No
12) Trees on the lakeshore	Yes / No
13) non-obstructed access to the lake	Yes / No
14) Diameter of shore stones (centimetres)	<5 / 5–10 / 10–50 / 50–100 / >100
15) Percentage of concrete surfaces (percent)	No / <25 / 25–50 / 50–75 / >75
16) Surfaces without vegetation (percent)	No / <25 / 25–50 / 50–75 / >75
17) Presence of mowing waste	Yes / No
18) Presence of humus	Yes / No / Other
19) Length of the littoral zone (meters)	<5 / 5–10 / >10
20) Vegetation height (centimetres)	<10 / 10–50 / 50–100 / 100–300 / >300
21) Humidity, sensu Landolt (1977)	1 / 2 / 3 / 4 / 5
22) Luminosity, sensu Landolt (1977)	1 / 2 / 3 / 4 / 5
23) Temperature, sensu Landolt (1977)	1 / 2 / 3 / 4 / 5

[1] as described in Material and Method

acteristics of the slope or wall (variables 16–18: mean, percentage of surfaces without vegetation, presence/absence of mowing waste and humus), the aquatic habitat (variable 19: width of the first meters of the littoral zone, the area between the average waterline on the shore and the outer line where the prodominant rocks/stones still break trough the water surface), determination of the dominant plant species (not listed) its height (variable 20), and climatic factors (variables 21–23: humidity, temperature and amount of sunshine based on the vegetation and Landolt evaluation [cf. Landolt 1977]). The total of 23 variables and the selected categories are listed in Table 1 and examples of a slope and a wall habitat are depicted in Figures 1 and 2.

Natrix Observation Protocol

The number of observed individuals of both species was noted for all different habitats. The entire site (4 km) was searched 17 times between 16 July and 11 August 2007. The observations where conducted without catching the snakes. Although both species have different probability to be observed (variable "catchability"; *N. tessellata* have a higher catchability, SU unpubl. obs.), the variability in the percentages of *N. maura* observed is proportional to the variation of the percentage of occurrence of *N. maura*. Consequently, if the percentage of *N. maura* in one habitat is twice that in another habitat, the real proportion in the former segment is also twice as large. Additional information such as weather conditions and localisation (GPS coordinates) were also noted.

Statistical Analyses

We tested if a significant higher or lower proportion of viperine snakes were observed for some of the 23 retained variables using a test of proportion (also known as binomial distribution test). Statistical analyses were conducted with the program Minilab®, which produces exact *P*-values without particular conditions (Chavaz-Cirilli pers. comm.). However the statistical tests were conducted only when the total number of *Natrix* specimens was ≥ 15 individuals per habitat type.

Results

We determined 86 different habitats (all have at least one different value of the 23 variables) in the study area, which was estimated at about 14,000 m². One fourth was considered as "wall", the rest being categorized as "slope". We observed 387 *Natrix* specimens (307 *N. tes-*

Fig. 1: Study area considered as "Slope" (see Tab. 1)

Fig. 2: Study area considered as "Wall" (see Tab. 1)

sellata = 79%, and 80 *N. maura* = 21%). To simplify, we subsequently used a proportion of 80% of dice snakes and 20% of viperine snakes for subsequent analyses from this region.

Statistical Analyses

Dice snakes were significantly more frequent in the St-Saphorin area (binomial test, $P = 0.001$), as well as where the slope is more orientated to the south ($P = 0.036$) or the proportion of concrete is larger on the banks (≥75% of concrete; $P = 0.007$). In addition, the proportion of dice snake is also significantly higher when the bank is steeper ($P = 0.047$) or with a short vegetation height of 0.5–1.0 m ($P = 0.032$). On the other hand, the observed frequency of viperine snake is significantly higher at Rivaz ($P = 0.05$) or where most of the habitat structure consists of vertical "walls" with a grassy strip on the top ($P = 0.044$).

A marginally significant higher proportion of *N. maura* was also observed at Treytorrens ($P = 0.065$), as well as where the slope is orientated to southwest ($P = 0.052$), or where there was a higher mean humidity ($P = 0.051$).

The habitat characteristics at St. Saphorin, where only three viperine snakes of a total 80 *Natrix* specimens were observed, either seem to be more suited to the alien species or latter species competitively displaces the native species. Compared with Treytorrens and Rivaz, St. Saphorin is more exposed to the south (82%) and contains a higher proportion of concrete surface (14%, compared to only 4% in Treytorrens). The shore at St. Saphorin yields also a narrower littoral zone, as 45% of its littoral zone is less than 5 m wide. Its vegetation is also short and mainly (76%) ranges between 0.5 and 1.0 m.

In Treytorrens 138 dice snakes (74.6%) and 47 viperine snakes (25.4%) were observed. Even though the alien species is still more frequent, the proportion of the native species is considerably higher than in St. Saphorin. Here, 33% of the littoral surface is oriented to the southwest, and 30% consists of a "wall" with a vegetation strip on top. The vegetation at Treytorrens is slightly more humid compared to St-Saphorin.

Discussion

Distinct Results in the Different Geographic Sections

The study revealed important differences on interspecific use and possibly preferences of the available habitats between the two *Natrix* species. Indeed the environment at St-Saphorin is statistically more favourable to the dice snake, whereas those at Rivaz and Treytorrens seem to be slightly more preferred by the native viperine snake.

In 2007, a removal program of the alien dice snake was initiated by two of the authors (SU and JCM) that focused on Rivaz area. More than 100 dice snakes had already been removed during this study. This program consequently could have biased the results for the Rivaz region presented herein, and hence, the discussion will be focused on the two other areas, St-Saphorin and Treytorrens.

The results indicate that St-Saphorin is less favourable to the viperine snake as this section is more orientated to the south, the littoral zone is often very short and the vegetation is relatively high. On the opposite, the Treytorrens section seems more preferred by the native species due to a more southwestern orientation of the coast with more "wall" habitats characterized by a strip above of short vegetation. These different habitat parameters between St. Saphorin and Treytorrens could be associated to distinct habitat requirements by the two species and might explain the different proportions of each species observed. However, no such studies have been performed here or elsewhere that would confirm such interspecific differences. Only Scali et al. (2001) and Scali (2011) demonstrated the use of different microhabitats between both species, as well as different feeding behaviour. However, our location is clearly different, because the only available food is fish and the habitat size and variation is very limited. Consequently, both species are not able to select or evade to substantially different ecological niches in this particular location.

Biological Aspects

One important factor differentiating the two species' habitat is the orientation of the shores. It seems that the dice snake prefers southern orientation. We suggest that this species is comparatively more thermophilic and, hence, occupies habitat segments with a more direct solar radiation. Our observation is in contradiction to the conclusions of Hofer et al. (2001), who suggested that the dice snake prefers a south-western exposition. This conclusion was however based on the analyses of all locations of the dice snake in Switzerland, with most observations conducted in the Ticino region, southern Switzerland, where the species is native and more widespread. An explanation about this discrepancy could be the warmer climatic conditions in Ticino (compared to the shores of the Lake Geneva), where the dice snake is not required to seek the warmest locations. On the opposite, this species needs to find the warmest locations on the shore of Lake Geneva and consequently prefers southern exposition. This hypothesis could also explain why this species can be found in locations without any vegetation, thus experiencing warmer temperatures. On the opposite the viperine snake seems to be more related to habitats exposed to the south-west, which are more frequent in the Treytorrens and Rivaz sections. The solar radiation in these locations is perhaps limited and thus present less extreme conditions, that are perhaps more favourable to the native species. However, the viperine snake, which approaches its northern limit in Switzerland, obviously inhabits also these more thermophilic habitat, if the alien species would not be present, thus indicating a possible effect of competitive exclusion or displacement.

A narrow littoral zone seems to be favoured by the dice snake. Indeed 42 *N. tessellata* were observed in such habitat compared to only four *N. maura*. The larger body size of the introduced species enables them to consume larger prey than the native species. Thus the viperine snakes can find smaller prey species in a shallower littoral zone. The dice snake on the opposite can feed on larger prey that occurs in relatively deeper water in the lake (≥ 5m), confirming comparative observations by Scali (2011). Another scenario suggests that the competition between the two species implies that the dice snake is the physically stronger competitor and occupies the more favourable places such as slopes, displacing the weaker native competitor to the less suitable habitat of vertical walls, where it indeed was more common. The habitats with the slope allow an easy access to the lake, which is relevant as the only feeding ground. By being competitively excluded, the native species may have to regroup in the "wall" habitats. In Rivaz and Treytorrens "wall" habitats represent 30% of the area compared to 13% St-Saphorin. However, no such competitive scramble behaviour has been observed between the two species, in particular dice snakes physically forcing viperine snake out of the suitable habitat along the slopes. Mechanisms, by which such a direct competition should happen, are not known in snakes. But our additional observations may suggest that the viperine snake appears to be more agile than the dice snake, especially when the individuals contain any prey in their stomach. Therefore, *N. maura* is perhaps more adapted to climb walls and reach basking locations that are not easily accessible.

Humidity is another factor that likely influences the selection of habitats. During the 17 sampling days, a high concentration of snakes (58 dice snakes and 21 viperine snakes) were found in Treytorrens along a gentle slope of 15 m that yielded a large portion of the blackberry *Rubus fruticosus* between two shrubby areas. Although, this location structurally resembled other habitats, the mean humidity estimated by the Landolt coefficients was the highest observed in this study. This parameter can be an explanation of the high density observed there, but other factors may also have an impact, such as the several composts in gardens of a nearby village that offer suitable places for oviposition in June and July. Observations of matings in those gardens and regular findings of newborns by the villagers corroborate this presumption. In addition, we also observed juveniles during this study near this village (five out of the six observed newborns).

Management Suggestions

Our results suggest that the main management proposals could be the creation of new nesting sites in the study area. Such sites should be mounds (min 1 m high) constituted of rests of mowing and cut branches, as have been used elsewhere (Gruschwitz et al. 1999). Incorporating additional holes and crevices in the concrete zones would increase the amount of vegetation in those places that are currently dominated by the alien dice snake. Indeed, a higher density of vegetation would favour the native viperine snake. Finally the eradication measures of the alien species should be extended, because at St-Saphorin (where no removal program is conducted) the alien species strongly dominates.

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Authors

Gaëtan Mazza, Rue d'Or 12, CH-1700 Fribourg, Suisse, e-mail: gaetan.mazza@bluewin.ch; Jean-Claude Monney, karch, Centre de Coordination pour la Protection des Amphibiens et des Reptiles de Suisse, Passage Maximilien-de-Meuron 6, 2000 Neuchâtel, Switzerland; Sylvain Ursenbacher, Department of Environmental Sciences, Section of Conservation Biology, University of Basel, St. Johanns-Vorstadt 10, 4056 Basel, Switzerland, e-mail: s.ursenbacher@unibas.ch.