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TESTING THE COMPETITIVE EXCLUSION PRINCIPLE USING VARIOUS NICHE PARAMETERS IN A NATIVE (*NATRIX MAURA*) AND AN INTRODUCED (*N. TESSELLATA*) COLUBRID.

Master of Sciences in Behaviour Evolution and Conservation

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Testing the Competitive Exclusion Principle using various niche parameters in a native (*Natrix maura*) and an introduced (*N. tessellata*) colubrid.

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Abstract

English abstract

Despite the increase of animal and plant introductions worldwide and the strong augmentation of the reptile trade, few invasive snake populations have been studied. Dice snakes (*Natrix tessellata*) were introduced to the shores of Lake Geneva (Switzerland) in the early 1920s, and are now well established. This region of introduction was previously inhabited by Viperine snakes (*N. maura*). Ever since these two species have been under monitoring (which began in 1996) the Viperine snake population has shown drastic decline. We examine here the possibility of trophic competition by analysing diet composition, prey size and trophic niche overlap. Spatial distribution is also assessed in order to address the question of spatial competitive exclusion. We found very similar diets, and thus a high trophic niche overlap, indicating no partitioning of the trophic resource. No arguments in favour of spatial competitive exclusion were found. Our study suggests that trophic competition may occur between the two natricines and that it may give an explanation for the drastic decline of the Viperine snake in this area. Other pathways potentially playing a role in the exclusion of the Viperine snake are discussed.

Résumé français

Malgré l'augmentation des introductions d'espèces animales et végétales dans le monde et la progression du commerce de reptiles peu d'espèces invasives de serpents ont été étudiées. Les couleuvres tessellées (*Natrix tessellata*) furent introduites sur les rives du Lac de Genève (Suisse) au début des années 1920 et y sont maintenant bien établies. Cette région d'introduction était précédemment habitée par des couleuvres vipérines (*N. maura*). Le monitoring de ces deux espèces, qui débutât en 1996, montre un fort déclin de la population de couleuvres vipérines. Nous adressons par la présente étude la possibilité d'une compétition trophique entre ces deux espèces par l'analyse de leur régime alimentaire, la taille des proies et le recouvrement de niche trophique. Leur distribution spatiale est également évaluée dans le but d'apporter une réponse à la question de l'exclusion spatiale induite par compétition. Notre étude montre que ces deux espèces ont des régimes alimentaires similaires et voient un fort recouvrement de leurs niches trophiques n'indiquant pas de partitionnement de leur ressource alimentaire. Aucun argument en faveur d'une compétition spatiale ne fut observé. Notre étude suggère donc que la compétition pourrait avoir lieu entre les deux espèces de natricines et qu'elle pourrait apporter une explication au déclin drastique de la population de vipérines dans cette zone. D'autres paramètres pouvant potentiellement jouer un rôle dans l'exclusion de la couleuvre vipérine sont également discutés.

Keywords

Natricinae, competition, alien species, diet, foraging, colubrids

Introduction

Long term coexistence of species sharing same resources, niches or other limiting factors has been described as impossible by many authors (Volterra, 1928; MacArthur and Levins, 1964; Levins, 1968; Rescigno and Richardson, 1965; Levin, 1970) and was qualified as the “competitive exclusion principle” by Hardin (1960). This principle states that in the case of coexisting organisms sharing the same resource(s), competition will eventually take place once the densities of the coexisting species and/or the availability of their resource(s) will have reached their respective carrying capacities.

Ecological niche competition is one of the possible competitive mechanisms that may arise between coexisting species (Begon, Harper and Townsend, 1986). Such competition may either be exploitative (i.e. indirect competition in which “populations or individuals reduce one another’s growth or reproductive rate through utilization of common resources”, Schoener, 1977) or interference (i.e. direct interaction between competitors, such as territoriality). Outcomes of ecological niche competition have been described as being either the exclusion of one of the competitors (Gause’s Principle: Gause, 1932; Lack, 1945; MacArthur 1958; Holt, Grover, and Tilman, 1994; Byers, 2000) or the specialization of the competitors on different resources (Connell, 1980; Losos, 1992). In the case of trophic competition, the exclusion of one competitor can either lead to its local extinction (Moulton and Pimm, 1986) or to its displacement to another part of the habitat (i.e. habitat shift, MacArthur, 1972; May, 1974; Schoener, 1974; Inoue et al., 2008), whereas specialization would result in a shift in the competitors’ diets, either emphasizing on another trophic resource (Arlettaz et al., 1997) or on different sizes of the same resource as was shown, for example, in Darwin's Finches (Grant & Grant, 2006).

Trophic competition for prey items may be induced by colonization or introductions. Many cases of disturbance of a native species by an alien one on a trophic level have been reported in a wide range of taxa (e.g. Williamson, 1996) including in squamates (Klawinski et al., 1994; Petren and Case, 1996). The difficulty of controlling invasive species and their potential harmful effects on the biodiveristy (Elton, 1958; Wilcove et al., 1998) is a serious threat especially in the light of the increase of species introductions (see Byers, 2000 and references therein, Sala et al., 2000; Jenkins, 2003; Olden et al., 2004). Thus understanding the mechanisms by which alien species impact local ones is essential for conservation efforts.

Introduction in the 1920s (Morton, 1925) and subsequent decades (J. Garzoni, pers. comm.) of the Dice snake (*Natrix tessellata*), stemming from Italian populations, to the riparian land of Lake Geneva was pointed out as the probable reason for the strong decline of the native Viperine snake (*Natrix maura*) (Koller & Ursenbacher, 1999; Monney, 2004; Ursenbacher and Monney, 2007, 2008; Ursenbacher et al., submitted). The natural distributions of these species do not normally overlap due to physical barriers such as the Mediterranean Sea and the Alps (Guicking et al., 2006), with the exception of the region of Lombardia in northern Italy where they share some areas of sympatry (Bernini et al., 2004).

In this study we assess the potential of trophic competition, through diet analysis and trophic niche overlap estimation, as one of the possible mechanisms leading a native population of colubrids into decline. Furthermore, we examine intra-specific trophic resource partitioning due to sexual size dimorphism. Finally, we discuss possible research avenues with the potential to help clarify the interactions between native and introduced colubrids.

Material & Methods

Study site

Our study was carried out on the shore of Lake Geneva in the region of the Lavaux (altitude 372m, about 70km East-North-East from Geneva, Switzerland). This riparian region has been monitored by the KARCH (Center for the coordination of amphibian and reptilian conservation of Switzerland, Neuchâtel) for the past 14 years because of its particular situation (Koller and Ursenbacher, 1999; Monney, 2004; Ursenbacher and Monney, 2007, 2008; Ursenbacher et al., submitted). Bordered by xeric vineyards – unfavourable for semi-aquatic natricines – to the north and by the lake to the south, the habitat of both natricine species is a 3 to 10 metres wide and 3500 metres long stretch of rocky partially vegetated slope-terrain (for a more specific description see Hofer et al., 2001). Patches of well-suited habitat as well as areas of unfavourable terrain are scattered all along the shore. The herpetofauna of this riparian area is mainly composed of the Common wall lizard (*Podarcis muralis*), the Viperine snake (*N. maura*) and the Dice snake (*N. tessellata*), although occasional sightings of terrestrial colubrids were reported (*Coronella austriaca* and *Zamenis longissimus*, Hofer, Monney and Dusej, 2001; *Hierophis viridiflavus*, J-C. Monney, pers. comm., 2007) and documented by ourselves (*Coronella austriaca*).

Model Species

Natrix maura Linnaeus, 1758 and *Natrix tessellata* Laurenti, 1768 are semi-aquatic macrostomate (i.e. eating large prey: Greene, 1997) natricine colubrids (Colubroidea: Colubridae: Natricinae) that feed on amphibians and fish in most of their natural range (see Bilcke, Herrel and Van Damme, 2006 for a review; Santos et al. 2006; Luiselli et al., 2007). Both snakes have convergent phenotypes most probably due to ecological niche adaptation (freshwater and marshy habitats, see Gruschwitz et al. 1999; Schätti, 1999) rather than hybridization. Although some events of hybridization have been reported in captivity, there are no indications of hybridization in natural conditions probably due to pheromonal or behavioural mechanisms preventing it (Kabish, 1999; Schätti, 1999). In addition, phylogeographic studies indicate clear genetic segregation between both species (Guicking et al., 2006; Guicking, Joger and Wink, 2008).

Data collection

Data were collected during the summer of 2007 (July and August) and subsequently during the whole natricine feeding-season in 2008 (May through September) for a total of 42 successful collection days. Collection usually lasted 5 to 7 hours starting when the sun would hit the ground in the region, summoning the snakes to come out of their shelters. Fieldwork was not conducted during rainy or cold days, since these were known from previous monitoring efforts to exhibit no snakes (Ursenbacher & Monney, pers. comm.). Although very hot summer days did not exhibit many snakes either, some specimens were found by searching through closed gutters and by turning rocks over. Snakes caught by hand were scanned for and identified by microchips (RF-Tags, DataMars SA, Lugano, Switzerland; implanted during previous monitoring projects by the KARCH), standard morphometrical measures such as snout-to-vent length (SVL; to the nearest mm) and weight (to the nearest 0.1 g) were taken, their sex was determined when possible (juveniles were not sexed due to the possibility of incorrect sex determination, Filippi, 1995), their exact location was recorded and regurgitation reflex was gently induced by palpation. If easily identifiable, prey items were measured (length and depth, *sensu* Delling, 2003, see *Laboratory prey identification* hereafter for a description) and determined, otherwise they would be stored in 70% EtOH and brought back to the laboratory for minute examination. Some SVL data were missing due to field difficulties. After handling, untagged *N. maura* were implanted with a microchip and released at their capture location. As part of a conservation effort aiming at favouring the native *N. maura* population, captured specimen of the introduced species were not released into the wild (Conservation de la Faune de l'Etat de Vaud - Autorisation spéciale N°974).

Laboratory prey identification

N. maura and *N. tessellata* almost always ate their prey headfirst (78 preys out of 80 were eaten head first), thus digesting the anterior part of the fish-body first. Consequently, traditional identification keys (such as Pedroli, Zaugg, and Kirchhofer, 1991) were unusable to identify partially digested preys missing their heads, since many of the standard determination criteria used in these keys are situated around and in the cranium of fish. Thus we constructed our own identification key (based on Fatio, 1882; Masson, 1989; Pedroli, Zaugg and Kirchhofer, 1991) to name lake Geneva fishes using mostly posterior criteria such as length and shape of the dorsal, anal, and caudal fins. Identified preys were also measured for depth (*sensu* Delling, 2003), the dorso-ventral measure taken at the dorsal fin origin. This measure correlates well with body length in whole fishes (all regurgitated prey items were used for this statistic, $R^2 = 0.72$, Pearson's correlation test: $t_{51} = 11.58$, $P < 0.001$). In addition this measurement is the most relevant for gape-limited predators such as colubrids since it defines the maximum prey size acceptable for intra-oral transport (Vincent et al., 2006).

Statistical Analysis

Statistical analyses were conducted using the open-source software R 2.4.1 GUI 1.18 (4038) (R Development Core Team, 2006).

Trophic niche overlap was estimated using the Freeman-Tukey statistic (Matusita, 1955; also see Arlettaz et al., 1997),

$$FT_{ab} = \sum_{s=1}^{S} \sqrt{(p_{sa} \cdot p_{sb})}$$

where p_{sa} and p_{sb} are the proportions of prey species s out of a total of S prey species consumed by snake category (species or gender) a and b respectively. FT_{ab} values vary between 0, for absence of niche overlap, and 1 for complete overlap. A second, less precise but more robust, mathematical method was also used as comparison. The niche overlap percentage method or Renkonnen index (also known as Overlap Percentage or Schoener index, Schoener, 1970; Krebs, 1989),

$$P_{ab} = 100 \cdot \sum \left[\min(p_{sa}, p_{sb}) \right]$$

uses the same prey consumption parameters as the Freeman-Tukey Statistic and similarly varies between 0 and 1 for absence of and complete overlap respectively. Levels of significance for both methods were obtained by testing estimated niche overlap values against niche values calculated by random permutations procedures (10'000 random permutations between rows and columns, Manly, 1991). The

Freeman-Tukey statistic with randomization procedures was also used to examine intra-species sexual partitioning of trophic niches.

Differences of consumed prey sizes between species and between sexes within each species were analyzed using one-way ANOVAs. A two-way ANOVA with separation of effects by a Tukey's Honest Significance Differences test (Miller, 1981) was performed to test for sexual dimorphism and inter-species size variation. Covariance between snake SVL and prey depth was tested with an ANCOVA with snake species and sex as factors. Non-significant interactions were removed from the analysis. Means ± Standard Deviations are reported.

Results

Dietary data overview

Seventy-seven *N. maura* (58 females, 13 males, and 6 juveniles) and two hundred and thirteen *N. tessellata* (158 females, 33 males, and 22 juveniles) were captured and measured. Approximately 22% of females (18 for *N. maura* and 37 for *N. tessellata*) and 15% of males (2 for *N. maura* and 5 for *N. tessellata*) regurgitated recognizable prey items. Only 6 juveniles regurgitated prey items (3 for each snake species), and thus were not included in the statistical analysis. A total of five fish species were found in both snake species, and one additional fish species (the Burbot, *Lota lota*) was solely found in *N. tessellata* (table 1). Both snakes ate principally European Bullheads (*Cottus gobio*), and used European Perches (*Perca fluviatilis*) and Common Roaches (*Rutilus rutilus*) as secondary prey. All other fishes were consumed occasionally (table 1).

Trophic niche overlap

Both the Freeman-Tukey Statistic and the Renkonnen index showed a significant overlap of the trophic niches between snake species ($FT_{maura\text{-}tessellata}$ = 0.95, randomization tests $P < 0.01$; $P_{maura\text{-}tessellata}$ = 0.76, randomization tests $P < 0.05$). No significative intra-species trophic niche overlap was found between sexes in either species (*N. maura*: $FT_{male\text{-}female}$ = 0.58, randomization tests $P = 0.89$, *N. tessellata*: $FT_{male\text{-}female}$ = 0.74, randomization tests $P = 0.35$)

Prey size variation between snake species

A strong positive relationship between the size of the predator and the size of the prey was found ($F_{1,63} = 9.66$, $P < 0.01$). Comparison between species showed a slightly significant difference in prey depth (*N. maura*: 1.75 ± 0.79 cm, *N. tessellata*: 1.72 ± 0.67 cm, $F_{1,63} = 4.48$, $P < 0.05$) and interaction between snake size and snake species was also significant ($F_{1,63} = 6.62$, $P < 0.05$, figure 1). Although a significant sexual dimorphism in size was shown in both species (see below) there was no difference between sexes for prey size (*N. maura*: $F_{1,21} = 1.41$, $P = 0.25$, *N. tessellata*: $F_{1,55} = 1.91$, $P = 0.17$).

Size variation in snake species

Comparison of body lengths (SVL) between species showed that *N. maura* were significantly smaller than *N. tessellata* ($F_{1,230} = 41.21$, $P < 0.001$) and between sexes that males were significantly smaller than females ($F_{1,230} = 92.22$, $P < 0.001$).

Using pairwise comparisons for multiple testing (Tukey's HSD) we show that, at the interspecies level, female *N. tessellata* (n = 150) were significantly longer than female

N. maura (n = 48; $P < 0.001$) but males did not differ in length (*N. maura* n = 9, *N. tessellata* n = 27; $P = 0.75$). At the intraspecies level, we detected a sexual dimorphism for both *N. maura* (Female n = 48, SVL: 57.9 ± 8.7 cm, Male n = 9, SVL: 44.8 ± 3.7 cm; $P < 0.01$) and *N. tessellata* (Female n = 150, SVL: 69.5 ± 12.0 cm, Male n = 27, SVL: 48.9 ± 7.5 cm; $P < 0.001$).

Spatial distribution

Both species of snakes were found living sympatrically along the first almost two-thirds of the study area (1.9 km out of a total of 3 km, mean number of specimen per hundred meters: *N. maura*: 4.0 ± 2.9, *N. tessellata*: 7.4 ± 5.0). The last kilometre, constituted of less vegetated pioneer habitat and with a steeper mean slope, was only partially inhabited by *N. tessellata* (mean number of individuals per hundred meters: 3.75 ± 5.8; figure 2).

Temporal hourly distribution

Recorded between 09:30 and 13:30 hours on 19 (out of 42) randomly chosen days of capture, no temporal exclusion could be shown (figure 3).

Discussion

Our study shows that *N. maura* and *N. tessellata*, two species with allopatric distributions, have very similar trophic niches both in terms of prey composition and prey sizes in the region of the riparian land of Lake Geneva, the only region of sympatry of both species where *N. tessellata* have been introduced. In their native ranges both species seem to occupy similar trophic niches (reviewed in Bilcke, Herrel and Van Damme, 2005; Santos et al., 2005, 2006; Luiselli et al., 2007). Furthermore we find that their trophic niches are more specialized than in their respective natural distributions, where they have access to fish but also to amphibians, the latter resource being absent from our study area (C.M. and S.U. pers. obs., and J.-C. Monney, pers. comm.). Even though obligate specialization on fish is observed, both snake species were rather generalists since they fed on ecologically different fishes. Their primary prey (European Bullhead) is a rather solitary nocturnal fish hiding under rocks during the day and hunting at sundown or at night in the benthic zone (bottom-feeder, Tomlinson and Perrow, 2003), whereas both secondary preys (European Perch and Common Roach) are diurnal and mainly swim in shoals in the pelagic zone of the water body. This dichotomy in ecological types of prey could be explained by hunting strategies. We were able to observe in a laboratory pilot study of predation effectiveness (*N. maura* and *N. tessellata* had similar success when two individuals, one of each species, were offered fish to prey upon), that *N. maura* and *N. tessellata* have at least two hunting strategies. They can either forage between rocks on the waterbed or lay still, holding on to a rock with the posterior part of their body and their tail, and strike at schools of fish swimming by.

Most cases of feeding regime studied in snakes show partitioning of the trophic niches (by prey type or by prey size) or, in a lower amount of cases, a separation in spatial distribution, yet in other rarer cases, partitioning of the thermal or the temporal resources (reviewed in Luiselli, 2006). Our data do not indicate any partitioning of the trophic resource, nor any competitive exclusion for the spatial, the thermal (mixed groups of up to 15 individuals of *N. maura* and *N. tessellata* were sometimes found basking together), nor the temporal resource. Both snake species were randomly distributed along the linear study area in all suitable habitats. Some more pioneer habitats, uninhabited by *N. maura*, were mildly colonized by *N. tessellata*, thus showing a higher tolerance for unsuitable habitats by the latter species.

In addition, even though sexual size dimorphism was found in both species, no significant trophic niche overlap between sexes could be shown and there was no difference in sizes of prey consumed between sexes in either species. Thus the strong decline in the population of the native natricine shown by monitoring efforts in our study region (Koller and Ursenbacher, 1999; Monney, 2004; Ursenbacher and Monney, 2007, 2008; Ursenbacher et al., submitted) could be an indication of exploitative competition leading to the local extinction of one of the competitors (Moulton and Pimms, 1986). However, many levels of interaction between both colubrids have yet to be explored. One of these, resource conversion effectiveness, is a mechanism that could account for less energetic waste and a higher fitness for the introduced species, through increased fecundity but also prolonged longevity or faster growth rate (both of which may in turn increase fecundity; Byers, 2000). Higher fecundity, potentially due to larger adults (this study; Kramer and Stemler, 1982), of *N. tessellata* could also influence its success over *N. maura* (Kramer and Stemler, 1982; Ursenbacher et al., submitted).

Introduced alien species are sometimes vectors of new parasites such as helminths, acari, bacteria or even viruses which can all bear consequences on local fauna (Hudson and Greenman, 1998). Although we did not quantify parasite load and effect on fitness, we witnessed variable amounts of undetermined mites on individuals of both natricines. Co-evolutionary past of the vector and the parasite could explain lesser fitness impact than that on newly exposed species (Hudson and Greenman, 1998; Prenter et al., 2004). *N. tessellata* might have been responsible for the introduction of new diseases in the Lavaux with detrimental effects on the fitness of *N. maura*.

Although this study has focused on studying adults, neonates might yield under exploitative competition too. Due to their smaller sizes, neonates exploit a different trophic niche than adults. Competition for trophic resources in neonates as well as other types of competition may also influence the population dynamics. Competition could even take place before parturition, when the gravid females search for laying sites. Although we did not detect spatial partitioning between adults during the active season, egg-laying sites or over-wintering caches (Carpenter, 1953) may be limiting resources. Competition for them could favour snakes laying eggs earlier in the season, or going into hibernation at higher temperatures.

The history of our study area shows that the *N. maura* population might have been more or less isolated from other conspecific populations for hundreds of years, whereas the introduced *N. tessellata* most probably stemmed from larger less isolated populations in Italy. Fragmented populations such as the *N. maura* population of the Lavaux often have severely reduced gene flow (Guicking, Joger, and Wink, 2008) and high levels of inbreeding leading to reduced fitness or higher susceptibility to infectious agents, parasites and other environmental stresses (reviewed in Keller and Waller, 2002).

In conclusion our study is, to the best of our knowledge, the first ecological study of inter-specific competition between a snake species and its introduced congeneric species. As such it is the first account of ongoing disappearance of a snake species by its introduced ecological counterpart and it points out the risk incurred by local snake fauna in similar cases of introductions, an increasing hazard given the augmentation of the live snake trade (Reed, 2005).

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Tables & Figures

Table 1.

	Natrix maura (n = 23)				*Natrix tessellata* (n = 57)			
Prey	♂	♀	Juv.	(% of diet)	♂	♀	Juv.	(% of diet)
Cottidae								
European Bullhead (*Cottus gobio*)	2	6	2	(43.5)	5	27	3	(61.4)
Cyprinidae								
Common Bleak (*Alburnus alburnus*)	0	1	0	(4.3)	0	4	0	(7.0)
Gudgeon (*Gobio gobio*)	0	2	0	(8.7)	1	1	0	(3.5)
Common Roach (*Rutilus rutilus*)	0	4	0	(17.4)	0	6	0	(10.5)
Gadidae								
Burbot (*Lota lota*)	0	0	0	(0.0)	0	2	0	(3.5)
Percidae								
European Perch (*Perca fluviatilis*)	0	5	1	(26.1)	0	8	0	(14.1)
Total	2	18	3	(100.00)	6	48	3	(100.00)

Figure 1.

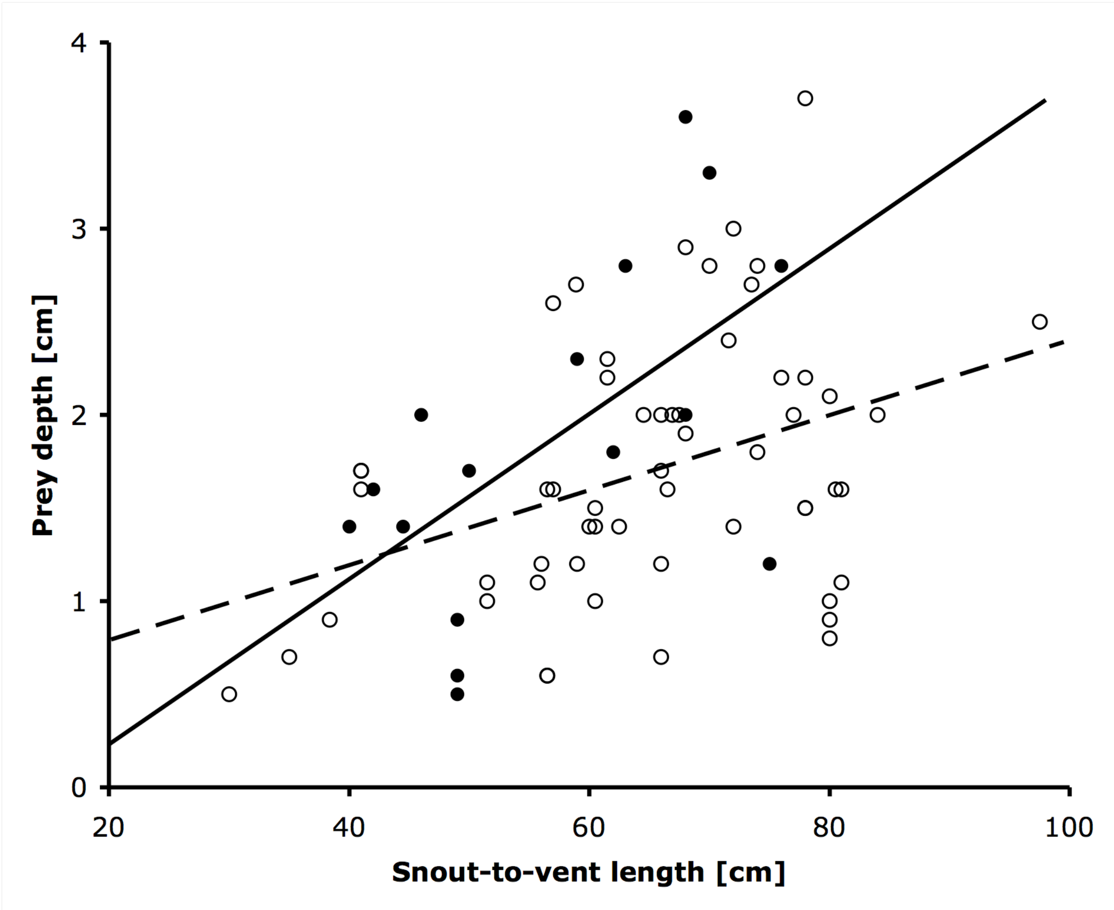

Figure 2.

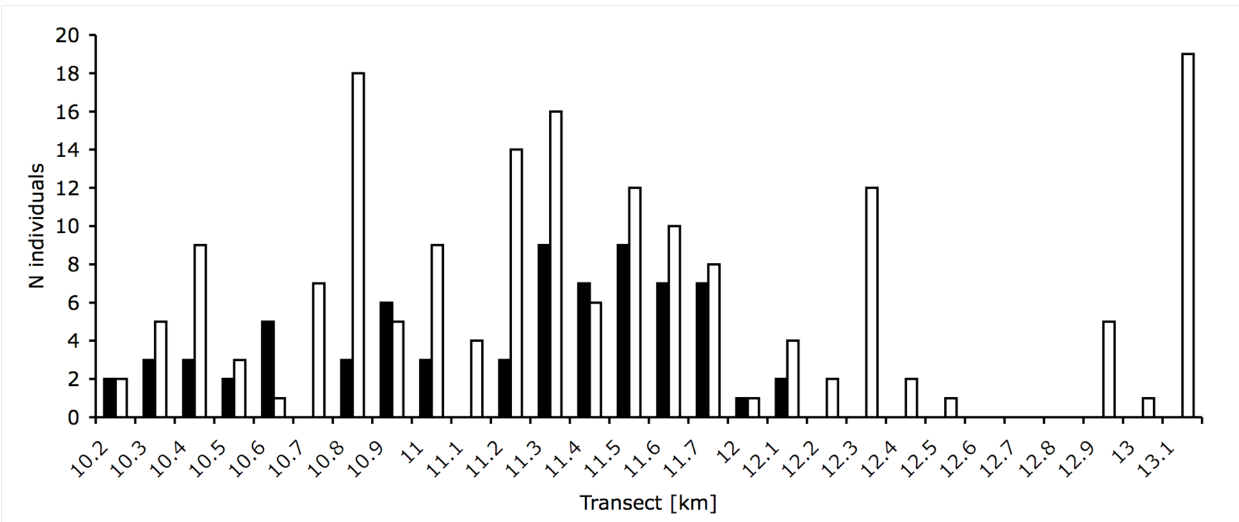

Figure 3.

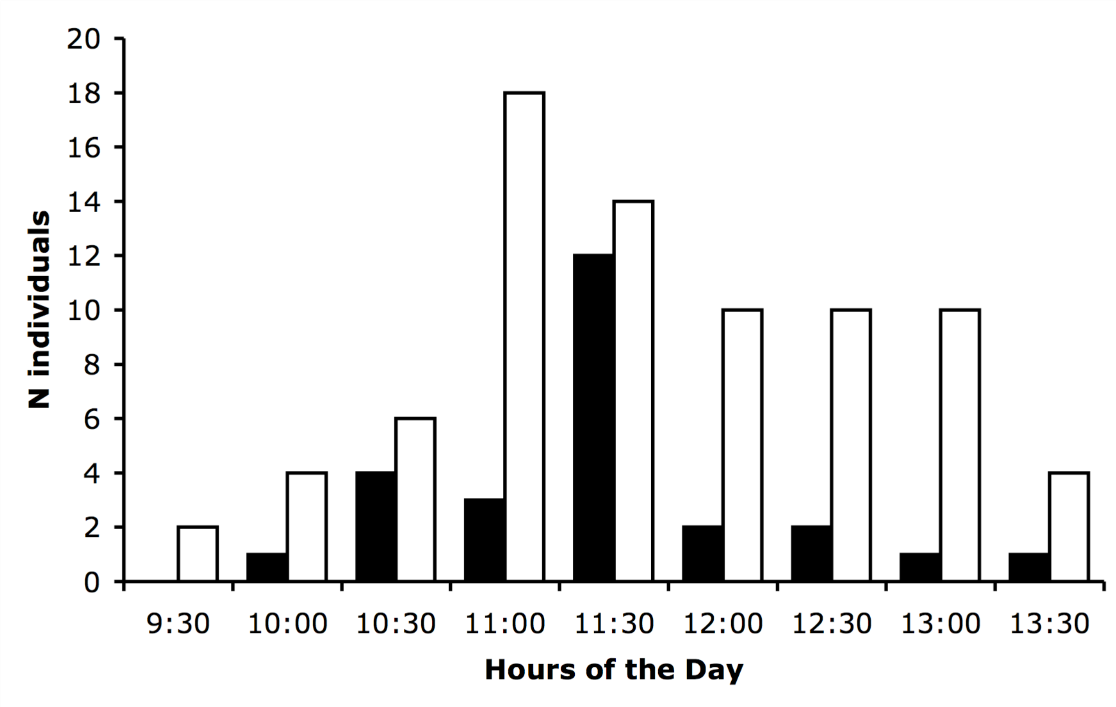
N individuals
0
2
4
6
8
10
12
14
16
18
20
9:30
10:00
10:30
11:00
11:30
12:00
12:30
13:00
13:30
Hours of the Day

Figure Legends

Table 1. List and number of prey items regurgitated from *Natrix maura* and *Natrix tessellata* from the riparian land of Lake Geneva, Switzerland. Symbols: ♂ = Males, ♀ = Females, Juv. = Juveniles (Sex undetermined), (% of diet) = Total percentage of the prey in the overall diet of the snake species

Figure 1. Sizes of prey ingested by *N. maura* and *N. tessellata*. Filled circles and full line: *N. maura*, Empty circles and dotted line: *N. tessellata*.

Figure 2. Distribution of *N. maura* and *N. tessellata* along the linear study area. White bars: *N. tessellata*, Black bars: *N. maura*.

Figure 3. Sample of snakes captured by half-hours of the day between 09:30 and 13:30. Filled bars: *N. maura*, Empty bars: *N. tessellata*.