

Habitat use and body temperature differences between two Natricine species, a native, *Natrix maura*, and an introduced, *Natrix tessellata*, using radio telemetry

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1. Abstract

The introduction of a new species into a habitat has become a common and worldwide problem. Often competition between native and introduced species can arise due to the change in the community and can occur when species share similar ecological niches. In this study, two Natricine snake species were observed: the native viperine (*Natrix maura*) and the introduced dice snake (*Natrix tessellata*) on the shores of Lake Geneva, Switzerland. Since the viperine snake has been in decline, there is reason to believe that one contributing factor may be due to the morphologically similar dice snake. Natural habitat is limited within the study area and more often than not, dice and viperine snakes can be found within the same microhabitat. Therefore, to study differences in body temperature (T_b) and in habitat preferences, we placed radio transmitters inside of four female snakes: two viperine and two dice individuals. All individuals were repeatedly located and body temperatures and habitat parameters were taken following their subsequent location. Our analysis found dice snakes to have significantly higher mean body temperatures in comparison to viperine snakes. We also found dice snakes to achieve their highest body temperature in the late afternoon and the viperine snake achieved their highest temperature soon after in the early evening. Concerning habitat parameters, we found both species to be significantly different in every observed aspect (habitat, inclination, cover, etc.); therefore, there was evidence of possible habitat partitioning. In conclusion, dice snakes were found to have a higher mean body temperature and were using different habitat types than the viperine snake. Although, individual preference had a strong influence on our study, this study does indicate that it is possible that habitat partitioning may have already occurred.

Keywords

Natricinae, invasive species, competition, introduced, relocation

2. Introduction

Local species may be out competed by new, introduced species through subsequent changes and interactions that occur when the new species establish themselves in an existing species' community (Vorburger & Ribic, 1999; McIntosh et al. 2006). Introduced species that are able to manifest in a new habitat can negatively influence native species through competition, predation, habitat alteration, disease, and genetic effects (Manchester & Bullock, 2000; Dodd & Seigel, 1991). Through these different dynamics, introduced, or invasive species, can disturb the existing species' community. For example, the reactions of a new species to a disturbance of a predator, of which native predators may not be familiar with, can give the new species a competitive advantage (Polo-Cavia et al., 2008). Also, more introduced generalist species can have negative impacts on the native species (Romero-Nájera et al., 2006), which can then cause problems for the local species that may not be able to easily adapt. Therefore, if a species is able to better use different aspects of an environment and reach high abundances, then species that had originally occupied the ecological niche in that area could be pushed out. This leads to the main problem invasive species create for native species. The invasive species, if able to adapt and grow in numbers within a habitat, can add more pressure to the native species in the form of competition for required resources, e.g. food and habitat (McIntosh et al., 2006; Machetti, 1999).

Susceptibility of invasion begin to increase once resources within a population begin to increase, according to the fluctuating resource availability theory (Davis, 2003), which can therefore create instability for native populations. Competition for resources, such as habitat, could potentially lead to the exclusion of a species following "the competitive exclusion principle" by Hardin (1960). This principle describes that when two species, that are normally geographically isolated, share the same ecological resource requirements, they cannot coexist in the same habitat (Hardin, 1960). Generally, all species must compete for resources within a habitat. So, the addition of a new species can only increase the present competition. Some invasive species present potential threats to native species for required resources through both direct and indirect interactions (Sakai et al., 2001). For example, Garcia-Serrano et al. (2005), found in two alien plant species (*Senecio inaequidens* and *S. pterophorus*) to have higher relative growth rates compared to the native (*S. malacitanus* and *S. jacobaea*). This illustrates that some invasive species have clear advantages stemming from their ability to compete for required resources. Strong invasive competitors can also inhibit growth. For example, Vogel & Pechmann (2010) found *Anaxyrus fowleri*, a native species, to be negatively impacted

through competition during the tadpole stage with *Incilius nebulifer*, an invasive species. Tadpoles which competed with *I. nebulifer* had a smaller body size compared to the ones that did not compete (Vogel & Pechmann, 2010). This shows that the presence of an invasive species can affect the native community at any life stage. The additional pressure from an invasive introduction can be one out of many added pressures, therefore causing the ability to adapt to ever changing environments a selective trait.

Some species, invasives included, are better adapted to environments modified by humans. As habitat fragmentation, induced by humans, of natural habitats increases, it becomes important to understand habitat preferences of different potentially coexisting species. If one species is more adapted and can make use of fragmented habitats, an evolutionary advantage can be achieved. Hence, this can then effect competition between two similar species in a heavily fragmented landscape. Some species, for example, black rat snakes (*Elaphe obsoleta*), are indifferent to habitats created by humans, such as forest edges which they used for thermoregulation (Blouin-Demers & Weatherhead, 2001). *Bothrops asper* demonstrated a clear avoidance for developed areas and show preference for swamp areas where much of their activity cores were located. When individuals prefer natural habitat, with a decline in natural areas can cause a decline in population (Wasko, 2009). While *Morelia spilota* populations declined when agriculture landscapes were predominate and when no thick vegetated habitats could be found (Shine & Fitzgerald, 1996). Therefore, when an invasive species is able to use both favorable and unfavorable habitats, the species has an advantage to expand its distribution. For example, the invasive cane toad (*Chaunus [Bufo] marinus*), introduced to Australia, increased its distribution up to 1.2 million km² since its introduction in 1935 (Urban et al., 2007).

The occurrence of two morphologically very similar snake species has been observed on the shores of Lake Geneva; a landscape which has been highly developed under human influences with camping sites, towns, vineyards, etc. The viperine snake, *Natrix maura* (Linnaeus, 1758), can be found in five different countries across Europe: Portugal, Spain, France, Italy, and Switzerland (Naulleau et al., 2004). The only parts of Switzerland this species occurs include Lake Geneva and along the Rhône River (Naulleau et al., 2004). In contrast to the distribution of the viperine snake, the dice snake, *Natrix tessellata* (Laurenti, 1768), is found throughout Eastern Europe and Western Asia; this includes parts of Italy, Switzerland, Eastern Austria, Germany, Czech Republic, Dlovakia, Hungary, Balkan Peninsula, Moldavia, Southern Ukraine, Greece, Southwestern Russia, Turkey, Lebanon, and Israel (Nistri et al., 2004). Its distribution also goes up into Northwestern China and Western

and Southern Kazakhstan, as well as northern regions of Syria, Iran, Afghanistan, and Pakistan (Nistri et al., 2004). The regions in Switzerland include the canton Ticino (Nistri et al., 2004) and populations in Vierwaldstättersee, Zürichersee, and Alpnachsee, where this species is assumed to be introduced (Gautsch et al., 2002).

The natural distribution of the dice snake does not naturally include Lake Geneva (Guicking et al. 2006). The discovery of dice snakes in Lake Geneva was first documented by Morton (1925). Therefore, it can be theorized that the species was first introduced some time before 1925. However, subsequent introductions between 1950 and 1970 were also conducted (Gautschi et al., 2002, Jean Garzoni, pers. comm.).

In Switzerland, viperine snakes have been listed as “critically endangered” due to their limited distribution (Monney & Meyer, 2005). In addition, Ursenbacher et al. (pers. comm.) found an average decline of 4.4% per year in viperine snakes. The exact reason for this decline is unknown, but it is speculated to be related to the introduction of the competing dice snake. Reasons for this speculation are derived from similarities, between the viperine and dice snakes, in morphology and ecological niches, such as diet (Metzger et al., 2009) and habitat preference. Because of these similarities, many studies have been fueled with the objective of discovering the exact reason for the decline of the viperine snake.

Since the establishment of the dice snake population, the competition between these two morphologically, semi-aquatic similar species has been studied. Similar studies have shown that dice snakes have partially colonized some habitat areas that were unfavorable to viperine snakes (Mazza et al., in press). Metzger et al. (2009) found that these two species have similar diets and, therefore, have high trophic niche overlap. Metzger et al. (2009) also investigated, but not as a major focus, spatial distribution of both species and found no competitive exclusion. Mazza et al. (in press) focused on habitat preference of both species based on presence/absence data and found some differences in habitat use. However, Mazza et al. (in press) does not focus on a singular individual and its behavioral preferences. Our study has been designed to close the gap. We used a telemetry approach to locate the same individuals from each species in order to compare the thermoregulation, behavior, and habitat use.

2.1. Objectives

In this study, we investigated the differences between the viperine and dice snakes body temperatures and habitat preference through the use of radio telemetry. By studying these different aspects, we intended to examine whether there is any overlapping preference in habitat use. We hope, with the use of radio telemetry, to get more insight into the habitat preferences of both species. We used thermal regulation differences to determine whether or not activity patterns differed between both species. Consequently, our main questions were: (1) Do viperine and dice snakes have the same mean body temperatures and how would their body temperatures affect their daily lives in respect to competition for required resources? (2) Is habitat partitioning taking place between these two species? (3) In what way could we use these results to assist in the conservation of the native viperine snake?

Materials and Methods

3.1. Study Species

Morphologically, the dice and viperine snakes are very similar. Males of both species are smaller due to sexual size dimorphism (Kramer & Stemmler, 1992); therefore only females were implanted with transmitters. Other variations between the two species consist of different patterns and slightly different colors (Personal observations, Figure 1). The dice snakes grow to greater sizes in comparison to the viperine snakes. The female viperine snake grows to lengths of 60 – 80 cm (Kreiner, 2007), although, in our study population snakes were found to reach a maximum length of 90 cm (Personal observations). In contrast, the female dice snakes can grow to lengths of 65 – 90 cm (Kreiner, 2007) while they were also found to have a maximum length of 120 cm (Personal observations).



Figure 1. Viperine snake (left) and dice snake (right) are the two *Natricine* species studied. The viperine is an adult individual with a light and dark green pattern across its head and yellow coloring on the underside. This pattern is absent in the dice snake. Another difference between the two species is that the viperine snake (left) has three scales from the top of the head to the eye while the dice snake (right) has four scales between the top of the head to the eye.

3.2. Study site

The viperine snake species are native to the shores of Lake Geneva, while the dice snake was introduced in this area (Morton, 1925; Figure 2). Both species are found along the shoreline and it has also been documented that dice snakes have partially colonized some habitat areas that were unfavorable to the viperine (Mazza et al., in press). The viperine and dice snake populations studied were located between the towns of Cully and Treytorrens, in the canton of Vaud, Switzerland. This area has been highly influenced by humans through the development of villages, vineyards, roads, and railways. For instance, much of the shoreline has railroads constructed along side of it.

All snakes were caught in Treytorrens. The Treytorrens section of our study site consists of the riparian region of Lake Geneva: a rocky, partially vegetated slope terrain which typically has few visitors to the shore. The railroad tracks separate the lake from most of the vineyards with the exception of a few smaller vineyards. All vineyards are surrounded by concrete walls with shrubs and vines growing on and alongside the walls. Along the shoreline, the vast majority is surrounded by concrete walls and slopes with large rocks at the bottom. Some of these areas have bushes and vines growing on and along the concrete (Figure 3).

Due to the movement of one individual in our study, the Cully marina region was included as part of the study site when the individual took refuge there. The Cully marina is protected from the lake by large stones which act as wave breakers. Within the marina itself, there are storage rooms along the sides of the marina. Underneath the concrete walkway, connecting these storage rooms, are medium sized stones and holes with small stone substrate within the foundation which serve as another form of protection from weather elements. The marina itself is frequently used by the boat owners and local inhabitants of Cully. This area is more often visited during the summer. Outside the parameter of the marina lies a camp site and beach area where the banks are surrounded by large rocks. The land passed the rocks is grassy areas for swimmers.

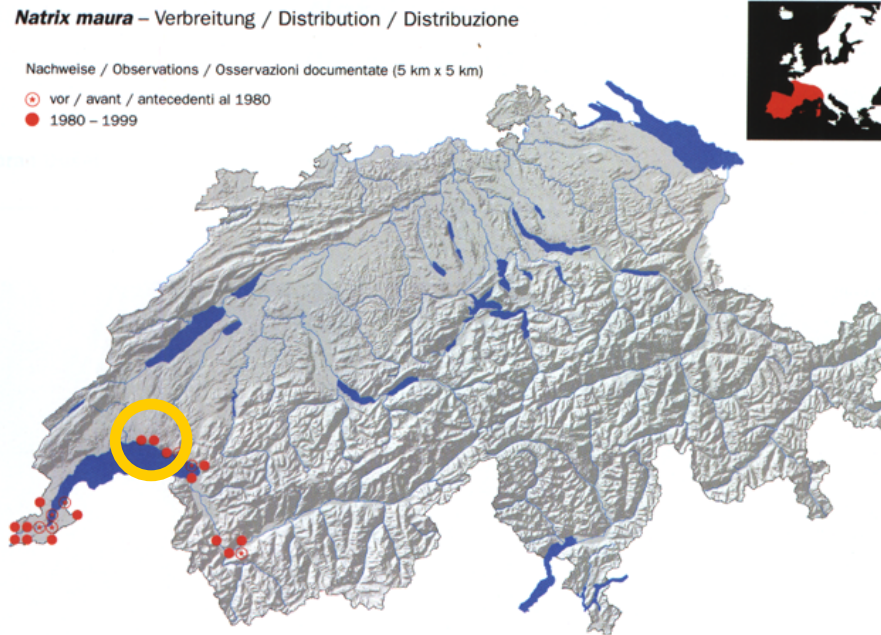


Figure 2. The above map of Switzerland shows the three different viperine populations. The population circled in yellow shows the location of the study site (Hofer et al., 2001).



Figure 3. The above picture is of a local vineyard in Treytorrens. Viperine 1 was often found in and along the stone wall. Sparse vines, bushes, and grape vines are located along this stone wall (picture from S. Ursenbacher).

3.3. Materials

Four R1680 transmitters (Advanced Telemetry Systems©, Isanti, Minnesota, USA) weighing 3.4 g (approximately the same weight as 1 or 2 eggs) were implanted into two viperine and two dice snakes. Each transmitter was thermosensitive, therefore, the frequency of signal emission was a function of the transmitter temperature. Since each transmitter varied in thermosensitivity, all transmitters had to be calibrated in order to calculate the temperature of each snake during the monitoring period. Ten pulses were timed for each transmitter at temperatures from 5 °C to 25°C, at ca. 5°C increments, in order to calibrate each transmitter individually at the University of Basel. The calibration procedure followed ATS® recommendations, except, instead of using ice, a climate chamber was used to regulate the water temperature. A thermometer was then placed in the water to give an accurate reading of the water temperature. For all calibrations, 30 to 45 minutes between each calibration was allowed to give the transmitters and water time to adjust to the new temperature.

When calibrating the transmitters, 10 pulses were timed in seconds. Following the calibration, the amount of time passed (seconds) was later put into separate equations, unique for each transmitter, to produce the body temperature (T_b). Equations were calculated following the example set by ATS©. This allowed for the determination of T_b of each snake throughout the field season. We were then able to calibrate snake temperatures to the nearest 0.1°C.

The detection of individuals was conducted using a portable scanning receiver Australis 26K (Titley Electronics, Ballina, Australia). One AY/C Yagi Directional antenna (Titley Electronics, Ballina, Australia) was used to locate animals at remote distances. This antenna was also used to evaluate the temperature of the snakes in different areas within the study area. An AW Wand antenna (Titley Electronics, Ballina, Australia), permits the user to locate the exact location of an individual using the homing technique (Mech & Barber, 2002) to identify an individual's location. This antenna was designed only for short range uses. All positions were marked using a Garmin map 60CSx with a precision of ± 3 to 10 m (Garmin Limited companies, Olathe, Kansas, USA). The environmental temperature was measured using a weather forecast station (Oregon Scientific©, Tualatin, Oregon, USA).

3.4. Surgery and Recovery

On July 22, 2010, two viperine and two dice snakes were each implanted with one transmitter. Surgeries were conducted by Prof. Dr. Jean-Michel Hatt at the Zurich Animal Hospital, University of Zurich. Each surgery took roughly one hour. During the days following the surgery, snakes were kept in two large boxes. Snakes were given water five days following the surgery and were kept at 18 □ 20°C as suggested by the veterinarian.

All four snakes were released in Treytorrens (Lavaux), Vaud, Switzerland, at the same location they were captured in. Snakes were weighed and measured upon release (Table 1). All snakes were observed and consistently located within the two months following their release.

Table 1. Each native viperine (*Natrix maura*) and invasive dice (*N. tessellata*) snake was weighed upon capture and before release. It should be taken into account that viperine 1 had some food in her stomach upon capture. The release weight does not include the transmitter weight of 3.4 g for any of the snakes.

Individual ID	Species	Sex	Weight Upon Capture (g)	Weight Upon Release (g)
Dice 1	<i>N. tessellata</i>	F	230	210.6
Dice 2	<i>N. tessellata</i>	F	104	98.6
Viperine 1	<i>N. maura</i>	F	100	72.6
Viperine 2	<i>N. maura</i>	F	114	100.6

In order to control the impact of the surgery, two of the four snakes, viperine 1 and dice 2, were recaptured. The viperine 1 was caught on September 13, 2010. Both scars could be seen with some remaining molted skin on viperine 1 (Appendix 1). In contrast to viperine 1, dice 2's transmitter incision healed well and showed no sign of difficulty during ecdysis with the exception of the small scar from the antenna, some molted skin was found (Appendix 2). The antenna within viperine 1 was quite prominent (Appendix 3). This was not the case in dice 2, where scarring was not so noticeable; this could possibly be due to their difference in weight and size. Based on their behavior, snakes exhibited no signs of discomfort. For instance, dice 1 was able to move roughly 2 km within the first 10 days of being released. Not one snake remained in the same point which they were first released. Snakes were located during the ten day period before data collection officially commenced.

3.5. Data Collection

Since the individuals were too far apart in location, it was not possible to locate or estimate the temperature of all from one location; field work was split and periods of one to one and a half hours was allotted for each site. Each site was visited two times per day and the order of site visits was alternated each day, therefore, rotations were established concerning which site was visited first each day in order to avoid gaps in the data. For example, if Cully was visited first on day 1, then Treytorrens was visited first on day 2. This allowed for recordings of 10 □ 15 body temperatures and 4 – 6 habitat recordings per day for each snake.

Table 2. The dates of observation varied for each individual because of the transmitter battery. For instance, viperine 2 had only T_b recordings until August 20th due to a faulty battery but we were still able to locate her until September 24th.

Individual ID	Dates of T_b Recordings	Number of T_b Days	Number of T_b Recordings	Dates of Habitat Locations	Number Days of habitat locations	Habitat Locations
Viperine 1	Aug. 9 □ Sept. 30	27	350	Aug. 9 □ Sept. 30	27	112
Viperine 2	Aug. 9 □ Aug. 20	9	118	Aug. 9 □ Sept. 24	23	94
Dice 1	Aug. 10 □ Sept. 30	25	292	Aug. 10 □ Sept. 30	25	126
Dice 2	Aug. 9 □ Sept. 30	27	350	Aug. 9 □ Sept. 30	27	113

Body and Weather Temperature Recordings

Body temperature (T_b) recordings were taken every 15 minutes following the last T_b recording. Ten pulses were counted each time equaling nine pulse intervals following the procedure used for the calibration. Time intervals were noticed on the field and evaluated temperatures were calculated later. They were then recorded along for each snake. All body temperatures of snakes within one area were taken within a five minute period, except when it was not possible to hear the pulses due to trains, helicopters, trucks, or waves from the lake.

Following T_b recordings, weather data was recorded. This allowed us to record the weather parameters following each T_b recording. Humidity and estimated cloud cover to the nearest 5%, temperature within shade, and temperature in sun was taken during each weather

recording. A period of at least five minutes was allowed for adjustment since the weather station was set out.

Relocations and Habitat Recordings

During the 15 minute intervals of T_b recordings, at least one snake was located. Roughly four to six locations were taken per day for each individual (two to three per site rotation). Once a snake was located, using the homing method (Mech & Barber, 2002), the type of habitat, substrate, cover, inclination, and exposure were recorded following the different categories described by Jäggi & Baur (1999; for an example refer to Appendix 4). All the categories are listed in Table 3. For each position, snake T_b and a GPS point were also recorded in addition to habitat variables.

Table 3. Variables used to characterize habitat following Jäggi & Baur (1999). For each location, all characteristics such as habitat, inclination, cover, substrate, and exposure were recorded.

Variables	Classes and categories	Method
Habitat	Concrete, rocky area, shrubby vegetation, sparse vegetation, water, woody debris	An evaluation of a 5 m radius was taken concerning the location of the snake.
Inclination	Five classes were used: 0°, 1 □ 35°, 36 □ 60°, 61 □ 89°, 90°	Estimates were taken of 1 m surrounding the point of location.
Cover	Concrete ⁱ , large stones (> 21 cm), medium stones (6 □ 20 cm), shrubby vegetation, sparse vegetation, water, no cover	A category was assigned to each location depending on the cover type within 1 m.
Substrate	Concrete ⁱ , large stones (> 21 cm), medium stones (6 □ 20 cm), small stones (< 5 cm), wire, dirt, shrubby vegetation, sparse vegetation, wood	Within a 1 m radius, one substrate category was categorized based on the surrounding variables.
Exposure	Degrees from north	A compass was used to find the exposure of the location.

(i) Concrete as a cover or substrate often refers to the stone walls and slopes as they were filled with concrete.

3.6. Statistical Analysis

Temperature analysis

In order to test if the T_b data was normally distributed, the Kolmogorov-Smirnov Test was implemented using PASW Statistics version 18.0 (IBM Corporation, Somers, New York, USA). The T_b of all four snakes was analyzed using R version 2.10.0 (R Development Core Team, Vienna, Austria) to better understand possible differences between the two species. First, to determine which parameters had a significant impact on T_b , a generalized additive model (GAM) was implemented because it allowed us to define both exploratory and categorical data. Therefore, T_b , time, date, and species were treated as exploratory data while species and individuals were treated as categorical data (Crawley, 2007). The same test was also conducted with species and individuals in separate models, for T_b differences throughout the day.

After running the GAM, an analysis of the variance (ANOVA) was conducted treating the data set in the same manner (e.g. time remained exploratory, etc.) as in the GAM. This ANOVA was used to see if there was any significance between species, T_b , time, or date. The advantage of using the ANOVA was that it allowed for a better understanding of the relationship between body temperature and possible effecting factors that the GAM could not.

Habitat analysis

Similar to the temperature analysis, to check the normality of the distribution, a one-sample Kolmogorov-Smirnov Test was conducted using PASW Statistics version 18.0 (IBM Corporation, Somers, New York, USA). Percentages of frequency for each category (habitat, inclination, cover, and substrate) were calculated for each category between species and individuals. These results were then plotted separately. In order to determine if the native viperine and invasive dice snakes use habitat in the same manor, a chi-square test was calculated for habitat and inclination using an interactive chi-square test (Preacher, 2001). Since there were differences in the distribution of the data, a Fisher's exact test was used on cover and substrate category using R 2.10.0 (R Development Core Team, Vienna, Austria) to also determine if there were any similarities in habitat use between species and all categories were analyzed between individuals to account for individual variance. To determine if there were any significant differences between the two species in concern of exposure, an ANOVA was conducted also using R 2.10.0 (R Development Core Team, Vienna, Austria).

4. Results

4.1. Body temperature analysis

Dice snakes were shown to have a higher mean body temperature (20.3° C) compared to the viperine snake (18.8° C; GAM, $p = < 0.001$; Table 4) when corrected for time and date. Results from the GAM were similar to the ANOVA using similar co-variables (Table 5). Species, time, and date were found to be a significant indicator in differences in T_b when the ANOVA was ran. Mean T_b variations by time through the course of a day and through August to September can be seen in the Figure 4. The viperine and dice snakes mean body temperature were plotted in the same graph to provide a better idea of the T_b differences between the two species (Figure 5) throughout a day's time. The viperine and dice snakes were also analyzed separately using both the GAM and ANOVA and all parameters (for example, differences in time, date, etc.) were still significant (Table 6, 7, 8, & 9). Mean T_b curves were also plotted for each individual (Appendix 5). The results of the more complicated models, which were incorporated with weather data, are included in Appendix 6. However, this study focuses on models without this data to allow for a more conservation managing oriented view. Through the body temperature analysis, a better understanding of the differences of the two species could be achieved. Knowledge pertaining to body temperatures (T_b) can help to better understand the activity patterns of snakes.

Table 4. Evaluation of the mean body temperature for both dice (*Natrix tessellata*) and viperine (*Natrix maura*) snakes ($n = 4$) based on a generalized linear model (GAM) including time, date, and species as variable affecting body temperature (T_b). Part A shows dice snakes have an overall higher T_b mean in comparison to viperine snakes. Part B shows the impact of time and date variables on the T_b variation.

(a)

	Estimate	Std. Error	t value	Pr(> t)
Dice	20.3	0.2	117.4	< 0.001***
Viperine	-1.5	0.3	-5.5	< 0.001***

(b)

	edf	Ref.df	F	p-value
Time	6.9	6.9	61.6	< 0.001***
Date	8.9	8.9	79.2	< 0.001***

Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

R-sq.(adj) = 0.493 Deviance explained = 50%

GCV score = 18.937 Scale est. = 18.632 n = 1110

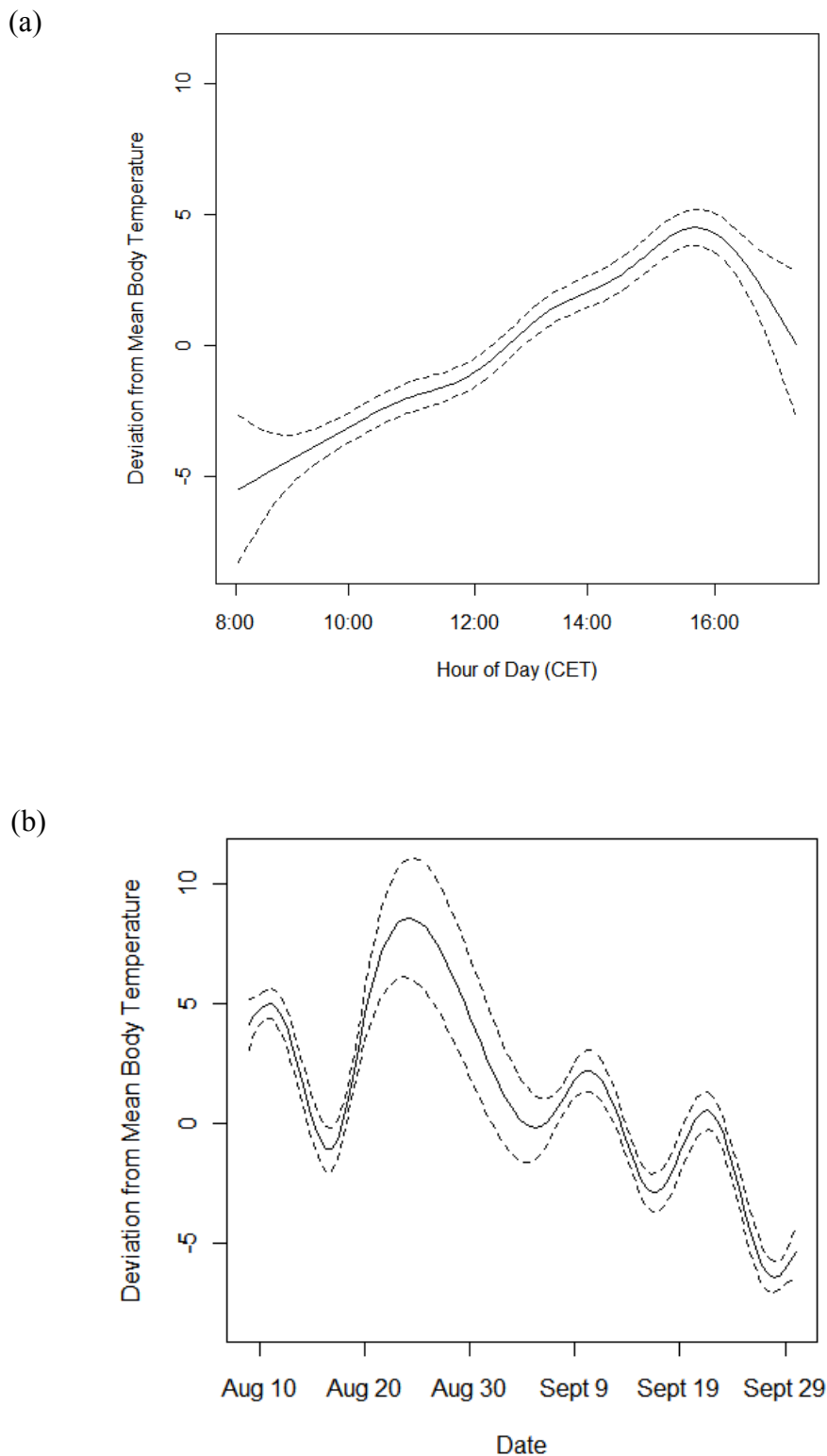


Figure 4. Above is the mean body temperature (T_b) variation within an average of all study days (a, 0 = 20.3) and of the August to September study period (b, 0 = 20.3) for both the viperine (*Natrix maura*) and dice (*Natrix tessellata*) snakes ($n = 4$). A gap in the data can be seen between August 22nd □ Sept 2nd because no surveys were conducted at that time.

Table 5. Analysis of the mean T_b variation between viperine (*Natrix maura*) and dice (*Natrix tessellata*) snakes, using an ANOVA, with day variation (time) and daily variation (date).

	df	F	p-value
Species	1	30	< 0.001***

	Edf	Ref.df	F	p-value
Time	6.9	6.9	61.6	< 0.001***
Date	8.9	8.9	79.2	< 0.001***

Table 6. Comparisons of the mean T_b of both ($n = 2$) viperine snake (*Natrix maura*) individuals using a GAM (calculations were conducted with the exclusion of dice snakes (*Natrix tessellata*)): (a) representation the variability between the viperine T_b and (b) time and date.

(a)

	Estimate	Std. Error	T-value	Pr(> t)
Viperine	19.4	0.2	104.9	< 0.001***

(b)

	edf	Ref.df	F	p-value
Time	7.1	8.1	31.6	< 0.001***
Date	8.9	9.0	44.4	< 0.001***

R-sq.(adj) = 0.559 Deviance explained = 57.4%

GCV score = 16.608 Scale est. = 16.007 n = 468

Table 7. Analysis of the mean T_b variation of the viperine (*Natrix maura*) snake individuals ($n = 2$), using an ANOVA, with day variation (time) and daily variation (date).

	edf	Ref.df	F	p-value
Time	7.1	8.1	31.6	< 0.001***
Date	8.9	9.0	44.4	< 0.001***

Table 8. Comparisons of the mean T_b of both dice snake (*Natrix tessellata*) individuals ($n = 2$) from the GAM model (calculations were conducted under the exclusion of the viperine snakes (*Natrix maura*)): dice body temperature (a) and time and date (b).

(a)

	Estimate	Std. Error	T-value	Pr(> t)
Dice	19.8	0.2	115.3	< 0.001***

(b)

	edf	Ref.df	F	p-value
Time	3.8	4.8	47.6	< 0.001***
Date	8.9	9.0	44.8	< 0.001***

R-sq.(adj) = 0.487 Deviance explained = 49.7%

GCV score = 19.414 Scale est. = 19.001 n = 642

Table 9. Analysis of the mean T_b variation of the dice (*Natrix tessellata*) snake individuals ($n = 2$), using an ANOVA, with day variation (time) and daily variation (date).

	edf	Ref.df	F	p-value
Time	3.82	4.77	47.15	< 0.001***
Date	8.86	9	44.81	< 0.001***

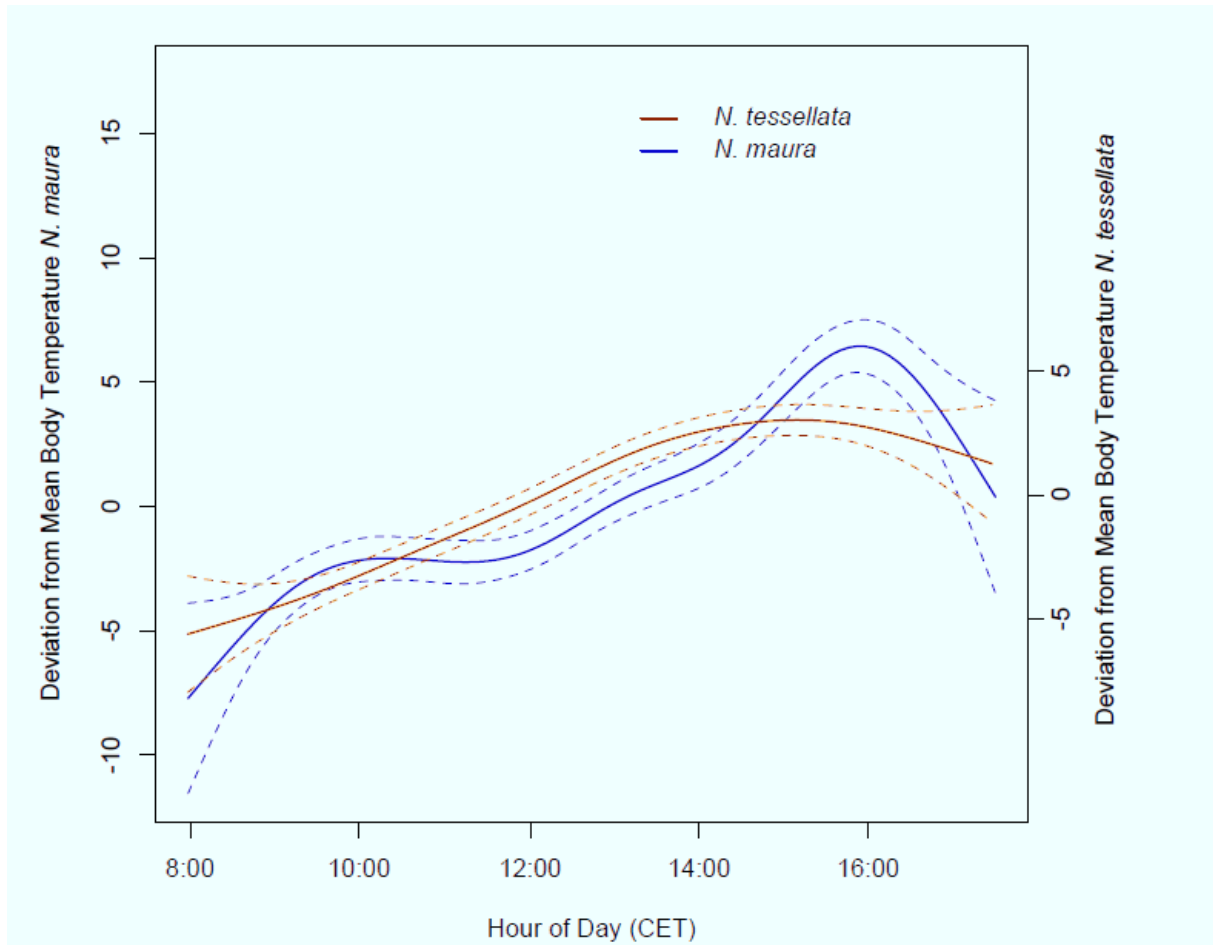


Figure 5. Mean body temperature variation throughout a day in the viperine (*Natrix maura*, $\theta = 19.4$, $n = 2$) in blue and dice (*Natrix tessellata*, $\theta = 19.8$, $n = 2$) in red snakes plotted from the GAM model.

4.2. Habitat Results

The utilization of sparsely vegetated areas within habitat preference was found to be more often the case in respect of the viperine snake individuals (48.3%, Table 10; Chi-square test: $p \leq 0.01$, Table 11). For the dice species, concrete habitat was more often used (44.3%, Table 10; Chi-square test: $p \leq 0.01$, Table 11). Viperine snakes frequented habitats with inclinations of 90° the most often (63.7%), than the dice snakes (36%, Table 12), indicating a preference for taking cover in stone walls. Although dice snakes spent time in stone walls, like the viperine snakes, the majority of their time, however, was spent at inclinations of $1 \square 35^\circ$ (44.9%, Table 12; Chi-square test: $p \leq 0.01$, Table 11). Concrete as a cover type was the most frequented by both species and rarely made use of other available cover types, such as shrubs, sparse vegetation, large stones, etc. (viperine = 87.3%, dice = 83.0%, Table 13; Fisher's test: $p = 0.04$, Table 14). Viperine and dice snakes were both significantly observed more often on

concrete as a substrate preference (viperine = 83.7%, dice = 34.2%, Table 15; Fisher's test: $p \leq 0.001$, Table 14). Dice snakes were also found using other substrates, such as small and medium sized stones, more often than viperine the individuals (Table 15). Exposure was also found to be significant between the two species (ANOVA, $p \leq 0.001$, Table 16). Since individuals were analyzed for differences in T_b , to check the variation between individuals in all habitat categories, a Fisher's exact test found all individuals to be significantly different ($p \leq 0.001$, Table 14).

Table 10. The frequency of habitat utilization for each species, viperine (*Natrix maura*, $n = 2$) and dice (*Natrix tessellata*, $n = 2$) snakes.

Habitat Categories	Habitat Utilization (%)	
	Viperine	Dice
Concrete	25.4	44.3
Rocky Area	0.0	5.1
Sparse Vegetation	48.3	20.7
Shrub	25.9	19.0
Water	0.5	5.5
Woody Debris	0.0	5.5

Table 11. Chi-square and Yates' chi-square test for the habitat and inclination categories. Differences between each species, viperine (*Natrix maura*) and dice (*Natrix tessellata*) snake, were found to be significantly different for both variables ($n = 4$).

Tests	Habitat	Inclination
Chi-Square	68.8	77.24
Degrees of freedom	5	4
p-value	< 0.01	< 0.01
Yates' Chi-Square	62.1	71.3
Yates' p-value	< 0.01	< 0.01

Table 12. The frequency of slope use by the viperine (*Natrix maura*, n = 2) and dice (*Natrix tessellata*, n = 2) snakes was devised to differentiate the differences in habitat use.

Inclination	Habitat Utilization (%)	
	Viperine	Dice
0°	5.4	14.2
1 □ 35°	5.9	44.9
36 □ 60°	8.8	4.0
61 □ 89°	16.2	0.4
90°	63.7	36.4

Table 13. The frequency of observed cover type use by the viperine (*Natrix maura*, n = 2) and dice (*Natrix tessellata*, n = 2) snakes.

Cover Categories	Habitat Utilization (%)	
	Viperine	Dice
Water	0.5	2.6
Concrete	87.3	83.0
Large Stones	1.0	3.0
Medium Stones	2.4	0.0
No Cover	3.0	3.8
Shrub	3.0	2.1
Sparse Vegetation	3.0	5.5

Table 14. Results of the Fisher's exact test for the different categories (Table 2) between both species, viperine (*Natrix maura*) and dice (*Natrix tessellata*) snakes, and individuals (Appendix 5) were produced. Only cover and substrate were analyzed using this test between species but all categories were analyzed between individuals (n = 4).

Categories	Species	Individuals
Habitat	□□□□	< 0.001***
Inclination	□□□□	< 0.001***
Cover	0.04*	< 0.001***
Substrate	< 0.001***	< 0.001***

Table 15. Observed substrate type for the viperine (*Natrix maura*, n = 2) and dice snakes (*Natrix tessellata*, n = 2).

Substrate Categories	Habitat Utilizations (%)	
	Viperine	Dice
Concrete	83.7	34.2
Dirt	3.4	2.2
Small Stones	1.9	11.7
Medium Stones	1.9	28.1
Large Stones	1.9	6.9
Shrub	3.4	1.3
Sparse Vegetation	1.9	0.9
Water	1.4	2.6
Wire	3.4	6.0
Wood	0.5	6.1

Table 16. An ANOVA was conducted to test the difference in exposure between the viperine (*Natrix maura*, n = 2) and dice snakes (*Natrix tessellata*, n = 2).

	Df	Sum of Squares	Mean Squares	F-value	Pr(>F)
Exposure	1	21.5	21.5	107.1	<0.001***
Residuals	432	86.6	0.2		

5. Discussion

Body Temperature

The invasive dice snakes were found to have a significantly higher mean T_b compared to the native viperine snakes (dice = 20.3°C). Considering the T_b of both species, modeled from the GAM, it was observed that both species experienced a steady increase in temperature during the day (Figure 4). Although, when referring to the observations of each species, the introduced dice snakes exhibit a much more steady increase in T_b (Figure 5). It is also important to note that the deviation from the mean is greater in comparison with the viperine species (Time deviation viperine = 7.1, Figure 5). The individuals of the viperine species also seem to reach their highest temperature later than the individuals of the dice species. Although the dice snake does show to have a higher mean T_b compared to the viperine it does not mean that the viperine cannot reach higher temperatures (Figure 5).

Concerning the separate species models, it should be noted that the results, from the different GAMs: analyzed separately (Table 4) and together (Table 6 & 8), differed from the first model. Although, this is due to the change in the intercept because when a model is altered, so is the intercept. With an altered intercept, results can slightly vary. Viperine snakes ($T_b = 19.40$, Table 6) still had lower T_b compared to the dice snakes ($T_b = 19.84$, Table 8) but, as they are estimated by separate models, it cannot be said if the results here were still significant between species.

Body temperature can give implications about the behavior in snake species. Hailey & Davies (1987) found viperine snakes, in the field, to bask longer than necessary to reach high T_b and that snakes basked at low temperatures and moved into shade during warmer parts of the day. Therefore, during lower temperatures, individuals found it necessary to move into warmer habitat areas and, in contrast, moved into cooler areas once the temperature rose. Much of our study session was conducted during the warm temperatures of August and September and also when activity was lower compared to activity during breeding and gestation periods (Personal observations). With the knowledge that dice snakes have a higher mean T_b , we assume that they make better competitors for essential resources. Also, with the ability to reach a higher T_b sooner and with more efficiency, dice snakes would not need to spend as much time in open areas where they would be exposed to predators. In addition, it would allow the dice snakes to seek prey sooner than the viperine if the required T_b to enter the water is met earlier.

It may also be possible that the viperine snakes choose not to take advantage of the favorable weather temperatures. Brown & Weatherhead (2000) found the water snake *Nerodia sipedon* to be moderate thermoregulators and, even when the opportunity presented itself, did not obtain the preferred body temperature compared to their captured counterparts. If this is the case, it may explain some of the differences in thermoregulation between the two species.

Differences in activity patterns were found by Scali (in press) between the viperine and dice snakes. Viperine snakes were found to be more nocturnal, while the dice snake exhibited a peak in activity in the afternoon (Scali, in press). Our findings parallel those of Scali (in press), the peak in late afternoon temperature, in the dice snakes, and the slightly later peaks concerning the viperine, hint to the possibility of more nocturnal movements by the viperine snakes. Although, our study differed from Scali (in press) both in location, north-western Italy, and in survey periods: from March to October.

High T_b obtained in the evening would explain the high frequency of unobserved movements. Snakes were often found to have moved after the survey was concluded for the day, and were found to have moved long distances by the next morning. For example, viperine 1 was found to have crossed the train tracks and moved into a stone wall within one of the vineyards; a distance of approximately 30 \square 40 m. Snakes would move gradually throughout the field site and then take a longer journey, across the train tracks for instance, in one movement. This was also the case for dice 1. Dice 1 began one long movement, at the end of September, back to the location where all snakes were originally captured, in the late afternoon (approximately 16:00 PM). We began tracking dice 1 at the marina in Cully while she moved through the water to the direction of Treytorrens. The next morning, she was found to be back in Treytorrens taking shelter near her original capture site, directly on the shore of the lake. Dice 2 showed a similar pattern but we cannot be sure since she crossed the train tracks during a period when no surveys took place. If these particular observations are representative of the biology of the species, and the dice snakes are able to obtain a higher temperature before the viperine, in addition, theoretically, the dice snakes would be able to move within the habitat sooner than the viperine and make them a better competitor. This suggests that it is possible for the introduced dice snakes to move earlier into a different location before the native viperine species can be active. This could allow for the invasive dice snake to have a better rate of dispersal.

Habitat Perimeters

All habitat analyses resulted in significant differences between both species and individuals. Our study found no overlap in habitat preference and, therefore, confirms Metzger et al. (2009)'s results. In this study, observations were conducted on the same population, where they did not find any trophic overlap in habitat use. Although, Metzger et al. (2009) did not focus on habitat preference, they also did not find any trophic overlap in habitat use.

Mazza et al. (in press) also conducted a habitat comparison between the viperine and the dice snakes which included part of our study site. Surveys were conducted between the railroad and lake; in Mazza et al. (in press)'s study, snakes were located and their habitat was categorized, therefore, all data was based on presence data. They found viperine snakes to use more "wall" type habitats (wall habitats were categorized in the same manor as our present study: concrete cover and substrate at a 90° inclination) with vegetation growing on it and dice snakes had a stronger preference for areas with less vegetation due to a possible requirement for warmer locations (Mazza et al., in press). Overall habitat was categorized depending on the outside vegetation or lack thereof. Our results confirmed the observed dice snake preference of open habitat. In our study, viperine snakes most often occurred in "wall" habitats with sparse vegetation while dice snakes were more often found in habitats with little to no vegetation of low graduations. Furthermore, our results found body temperatures of dice snakes to have a higher mean T_b ; therefore, it is possible to assume that the habitat locations have a great impact on their body temperatures supporting Mazza et al. (in press) and our findings. Since habitat preference may have a great effect on T_b , it is possible to assume that dice snake individuals choose these types of habitats in order to achieve their required T_b .

Through further research, it may be possible to determine whether or not dice and viperine snakes have already partitioned the current habitat. Meaning, the habitat currently occupied by the dice snake may be the more optimal habitat for both species. It is possible that niche differentiation has already taken place, hence the reason why we found significant differences in habitat. Although Scali (in press) also found significant differences, the study was conducted on populations were viperine and dice snakes naturally occur; resource partitioning occurred in microhabitat use between the viperine and dice snakes (Scali, in press). In addition, the differences between species can be partially explained by the high individual variability and the limited number of individuals studied, therefore this project

should be replicated with additional individuals to gain further insight in the observed patterns.

Further considerations

Even though the T_b and habitat analyses have produced significant results, it is more than likely that the small sample size has had an effect on the results due to the individual variance. The significant results are directly affected by the significant individual variance. To minimize this variance, it is recommended that this experiment should be conducted again with a larger sample size. However, we believe that our study will be a useful basis for an extended observation in the following year when the number of individuals is increased to 8 □ 10 individuals per species.

Another recommendation would be the use of data loggers. We propose that data loggers be useful to observe individual's T_b 24 hours a day during the active months. Habitat locations would still need to be conducted by hand but by including the data loggers for body temperatures, it would allow for a better understanding as to what time of day individuals are moving long distances.

Considering the prolongation of our study, further improvements could be made with changes in the surgery procedure. We believe that the scars at the end of the antenna entry could be minimized if the antenna is looped within the snake. This would not only shorten the length of the antenna but possibly help reduce scaring and help reduce the prominence of the antenna in the smaller sized snakes. Other than these recommendations to improve the quality of life following the surgery, we believe that the snakes showed to have little to no problems immediately following the surgery and release. All snakes seemed to be able to move about within their habitat with ease.

Conservation aspects

Our suggestions to help improve the conservation efforts of the viperine snakes include the continuation of those efforts already in place and one additional effort. One effort we believe to be important is the continuation of the removal of dice snakes. Another suggestion for conservation management of the viperine snake would be to establish more suitable basking areas within the vineyards. Until this time, the majority of studies and conservation efforts on

the Lake of Geneva focused along the shoreline, therefore, assisting the viperine during the latter half of the activity season could be just as beneficial.

Since viperine 1 moved into the vineyards in the middle August, two months before the active season concluded, it may be important to assist those viperine who have changed locations so early in the season. Often, viperine 1 was located between basalt slates which were propped near a shrubby habitat along a concrete wall. These slates would heat up during the day time hours; viperine 1, along with other viperine snakes, would take advantage of the slates. We propose that extra slates be placed near suitable habitat for the viperine snakes. Considering that viperine snakes are often considered shy, based on their frequency of capture, compared to the dice snakes (S. Ursenbacher, unpublished data), basking areas which provide more cover may increase the frequency of viperine within the vineyards. Although, this dice snakes may as well take advantage of this new basking area but since the viperine snakes are more reclusive, then it is more likely to be more suitable for the viperine.

Concluding Remarks

In conclusion, we believe that the introduced dice snake (*Natrix tessellata*) is a better, overall competitor when compared to the native viperine snake (*Natrix maura*). Due to their larger body size, higher mean T_b , and ability to move long distances, these competitors may be yet another factor contributing to the decline in the native viperine species.

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7. Appendix



Appendix 1. Scales of viperine 1 two months following surgery. On the left is the scar from the transmitter incision and, on the right, is the scar from the second incision from the antenna. Pieces of molted skin within the scar can be seen.



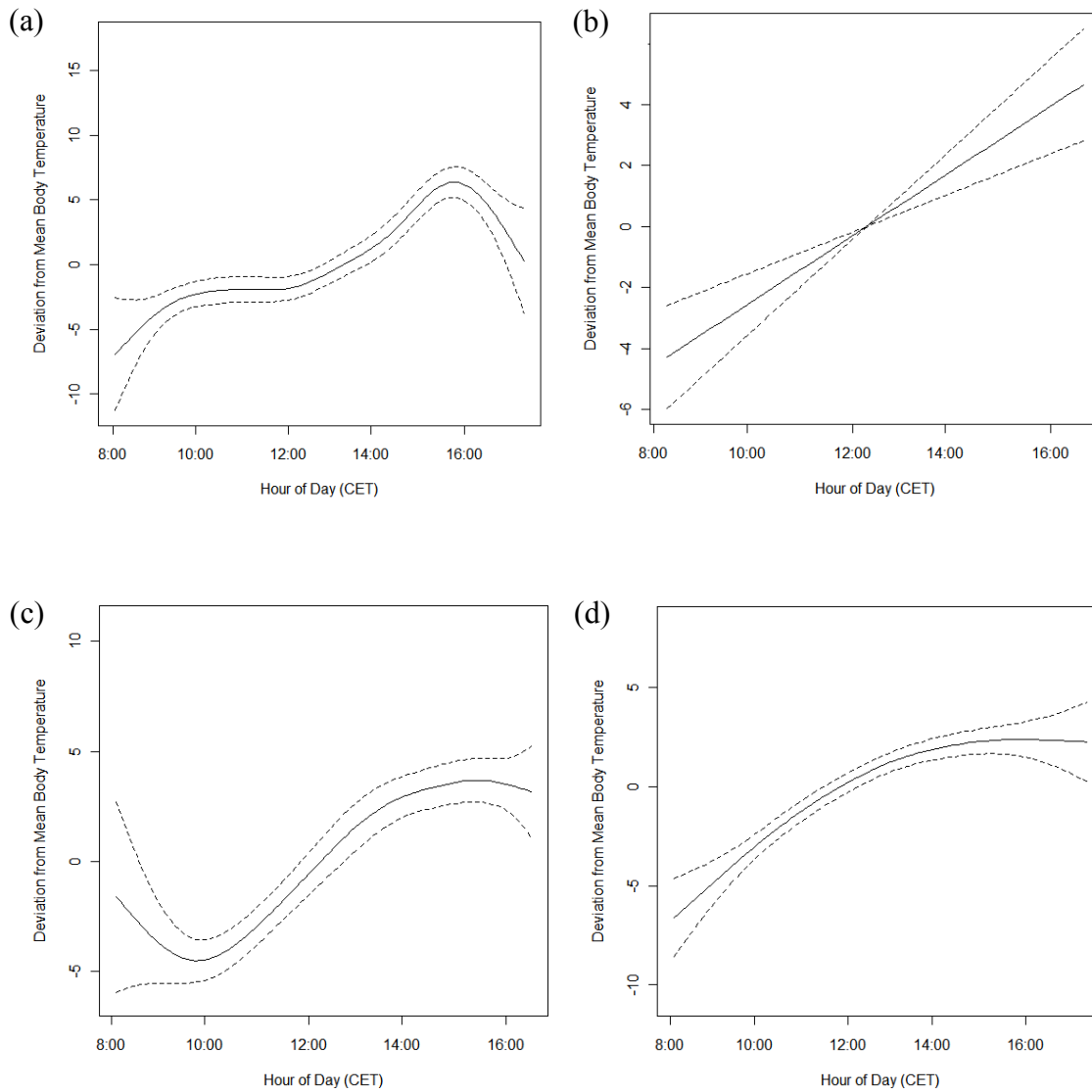
Appendix 2. Pictures of dice 2 caught on September 22, 2010, two months following the surgery. The scars from the implantation of the transmitter (left) and from the antenna (right) can be seen.



Appendix 3. The antenna wire can be seen throughout viperine snake viperine 1's body.



Appendix 4. Picture of dice 2 (back) with a second dice snake located within a tunnel in a house foundation which is used to access transport water. Snakes were often found in locations like these: overall concrete habitat, dirt substrate, concrete cover, and at an inclination of 0°.



Appendix 5. An average individual T_b throughout average of survey days is shown above: viperine 1 (a) and 2 (b) and dice 1 (c) and 2 (d).

Appendix 6. Below is the ANOVA from all models that were run with different weather data: sun (a), shade (b), humidity (c), and cloud cover (d). These ANOVAs were run in order to illustrate the effects of the weather on the two species.

(a)

	df	F	p-value
Species	1	32.1	< 0.001***

	edf	Ref.df	F	p-value
Time	6.9	8	16.6	< 0.001***
Date	8.9	9	22.4	< 0.001***
Sun	8	8.7	15.4	< 0.001***

(b)

	df	F	p-value
Species	1	30.6	< 0.001***

	edf	Ref.df	F	p-value
Time	7.1	8.2	23.3	< 0.001***
Date	8.9	9	29.6	< 0.001***
Shade	4	5	3.7	0.002

(c)

	df	F	p-value
Species	1	29.3	< 0.001***

	edf	Ref.df	F	p-value
Time	7.1	8.2	39	< 0.001***
Date	8.9	9	70.5	< 0.001***
Humidity	3.4	4.3	2.9	0.02

(d)

	df	F	p-value
Species	1	35.4	< 0.001***

	edf	Ref.df	F	p-value
Time	7.1	8.1	44.8	< 0.001***
Date	8.9	9	68	< 0.001***
Cloud Cover	6	7.1	13.7	< 0.001***