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Thermobiology and Microclimate of the Dice Snake at its Northern Range Limit in Russia

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Abstract. Microclimatic characteristics of habitats and thermobiology of the dice snake, *Natrix tessellata*, were investigated along its northern range limit in the "Samarskaya Luka" National Park, Samara Oblast in Russia. All 123 snakes examined from 2001–2008 were melanistic. Snakes were active at surface air temperatures ≥ 14.0 °C and substrate temperature ≥ 13.2 °C. Females selected more open areas than males. Females' body temperatures (measured in the esophagus) were just slightly higher than those of males, whereas males exhibited a higher surface (skin) temperature at the ventral and dorsal area of the tail. At an internal body temperature of 28 °C, a dice snake prevents further rising of temperature by moving to a cooler site (behavioral thermoregulation). An experiment was conducted to measure the speed of temperature decrease and increase of snakes switching between a sunlit spot (> 30 °C) and a cool water bath. The body temperature decrease was 2.2 °C/min and the increase followed by 0.3–0.4 °C/min untill a preferred body temperature of about 28 °C was reached.

Key words. *Natrix tessellata*, body temperatures, environmental impact, heating and cooling rate, Samara province.

Introduction

In Russia, the dice snake, *Natrix tessellata*, reaches the 54° Northern Latitude along the Volga River as far north as Samara oblast (province) , where they have been documented as early as 1636 (Olearius 1906). Putative findings of dice snakes at localities farther north in Ulyanovsk province (Osipova 1993) and the Republic of Tatarstan (Popov 1949) could not be confirmed after many years of personal field prospecting in these regions.

There are a few literature data from far Eastern Europe and central Asia on the thermobiology of dice snakes. For example, Bogdanov (1962) reports that in the Murgab Valley, Turkmenia, dice snakes emerge in spring at air temperatures ≥ 15.5 °C and surface temperature ≥ 16.0 °C. Shcherbak (1966) points out, that in the Crimea, Ukraine, dice snakes were observed on 15 April during cloudy weather at an air temperature of 10.0 °C. He measured a minimum cloacal temperature of 12 °C, and a maximum temperature of 31 °C, with the highest frequency of snakes found at air temperatures from 18.0–26.0 °C. For the Ukrainian Carpathians, Shcherbak & Shcherban (1980) observed dice snakes on sunny days on 24 April at an air temperature of 19 °C, and on 1 July at 32 °C with a soil temperature of 36 °C, whereas the cloacal temperatures of the snakes ranged from 29.0–32.3 °C.

Chikin (1981) points out that dice snakes from a mountainous part of the Augren flood-plain in Uzbekistan emerged from hibernation on 8 April at an air temperature of 18.5 °C, soil temperature in the sun of 19.5 °C and in the shadow of 15.5 °C, respectively. Emergence in the last ten days of April started when ambient temperature was equal to the temperature inside a hibernation shelter (16.8–17.3 °C). Most dice snakes were visibly active on the surface in late May at 11.30 am at air temperatures from 25.8–27.2 °C and relative humidity of 55–70%, probably due to mating activities. Beginning in June, these Uzbek dice snakes exhibited two activity peaks daily (morning and afternoon) due to a mid-day decrease in surface presence when air temperature rose above 28.0 °C. Snakes reached cloacal temperature from 13.0–13.5 °C to 26.5–27.4 °C after 20–25 minutes of basking and maintained it on this level by thermotactic behavior.

In Western Europe, Luiselli & Zimmermann (1997) studied some aspects of thermal ecology and reproductive cyclicity in two populations of the dice snake, one in central Italy and one in southern Austria. The climate was significant colder at the Austrian site. But snakes of both populations were similar in various traits, including average body temperature, higher body temperature of gravid than non-gravid individuals, significantly higher substratum temperatures selected by gravid than by non-gravid individuals, trends of relationships between body, air and substratum temperatures, average length of reproductive females, and average preparturition mass of reproductive females. However, Austrian snakes were found in water significantly less often than their Italian conspecifics (19.23% and 77.27% of snakes were found in water respectively), and exhibited a lower frequency of reproduction (biannual rather than annual) than Italian ones. Another Italian study by Scali (2011) found similar results in regards to dice snakes, except that body temperatures were lower probably due to a substantial portion of nocturnal captures in cooler water in his data set.

Despite all these information from previous studies, the data are mostly snippets and not standardized. No comparative data are available from the northern range limit of the dice snake, where a restraint climate with cool temperatures exerts relevant restrictions on the

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survival of regional populations. We thus try to provide more detailed information of the thermobiology and microclimatic characteristics of habitats occupied by dice snake from its northern range limit.

Material, Methods and Terminology

Snakes were sampled at the Samara Bend, National Park "Samarskaya Luka", Volzhskiy district, Samara province, Russia, from late April to early May in 2001–2008 (see Figs. 1a, b for habitats in this region). For each individual, various temperature data in the field were measured before the snakes were brought into a laboratory to record temperatures in an experimental set up. Additional observations were made in July 2008. The sex of 107 from a total of 123 snakes was determined by examining sexualdimorphic tailroot thickness or in the case of doubt by applying a rectal sonde.

A thermistor sensor connected to a digital micromultimeter was used to measure surface air temperature 3–5 cm above the ground and the temperature of the substrate where the snake was collected. The sensor is calibrated using electric thermometer "Checktemp" ("Hanna instruments", Portugal) with a digital display and a resolution of 0.1 °C. The same sensor was used to record body temperatures (internal and external). External body temperature of dice snakes was measured by holding the temperature-sensitive element of the thermistor on the skin for several seconds. Temperatures were taken at six points: midbody dorsal, midbody ventral, top of the head (parietal), throat, dorsal and ventral side of the tail. In the field we measured the snake's internal body temperature in the esophagus and in the cloaca, but during laboratory experiments we measured the internal body temperature in the stomach and in the cloaca of the snake. Even though, cloaca temperature does not reflect actual internal body temperature, we measured it to acquire a comparative value to the multitude of studies on snake thermobiology that applied cloaca temperature to approach internal body temperature. Esophagus and stomach temperatures are practically always higher than cloaca temperature.

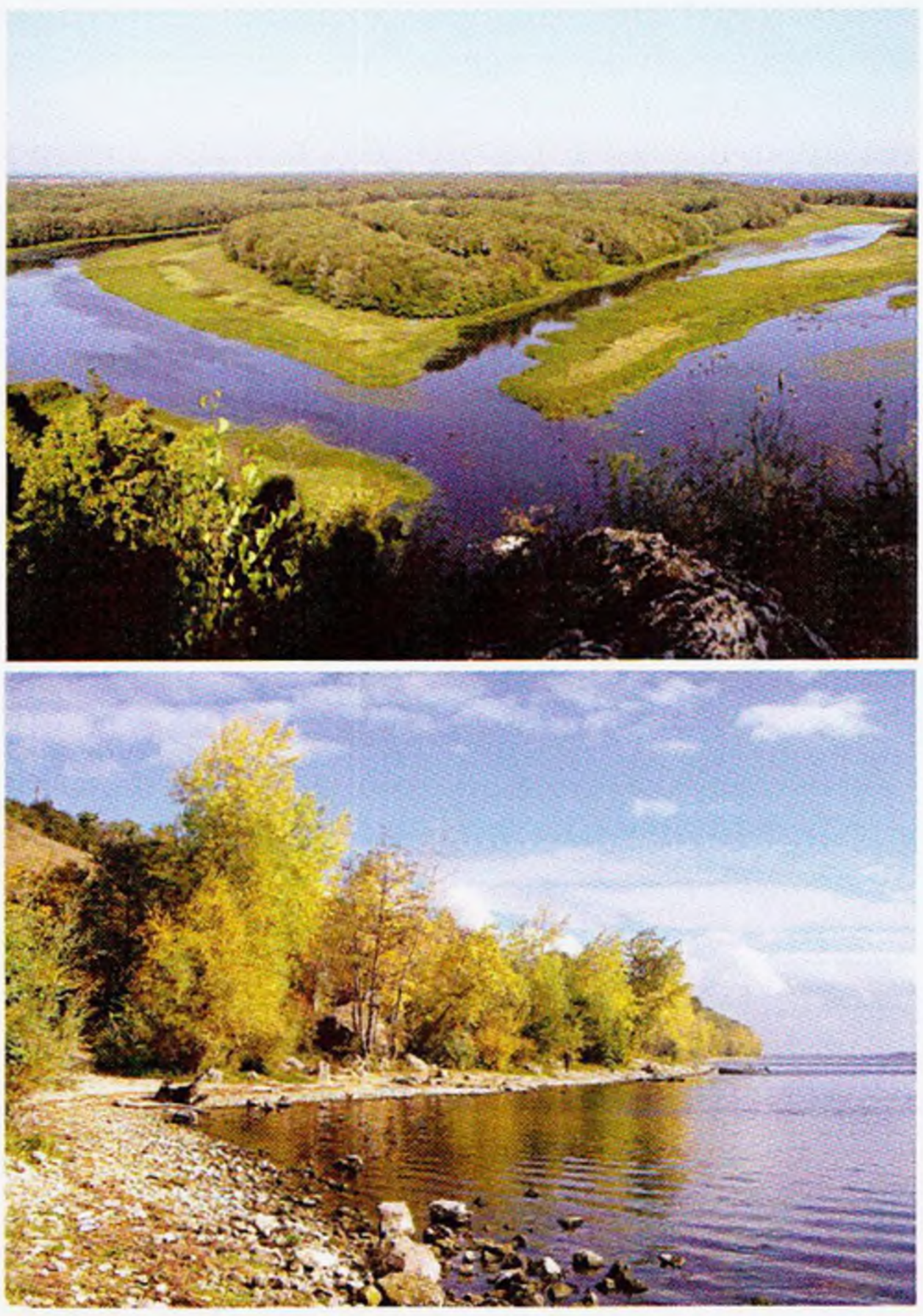


Fig. 1. Habitat of *N. tessellata* near its northern limit along the Volga River: (a) Snake Creek from up on the hill, Samara Bend, National Park "Samarskaya Luka", Volzhskiy district, Samara province, Russia, (b) shore area inhabited by *N. tessellata* at Perevoloki, approximately 30 km west of the Snake Creek, Syzranskiy district, Samara province, Russia. Photos: (a) Irinia Gerasimova, (b) Nastja Poklonzewa

A temperature registrator – iBDL "logger-tablet" ("Dallas Semiconductor", USA) was introduced into the snake's stomach to acquire internal body temperatures. Long-term temperature and humidity from the habitat was measured with iBDL-HS data-loggers, and instant relative humidity was taken with a portable device "Hydrocheck" ("Hygrocheck", USA). Specific capacity of the heat absorption and emission by a substratum was measured by a portable heat-flux density register IPP-2 ("Eksis", Russia). Strength and capacity (watts/m²) of light flux and ultraviolet radiation reaching the spot, where a dice snake was captured, was measured with a combined device "TKA-PKM" ("TKA", Russia).

We estimated the influence of ambient temperature on internal body temperature with the help of the Plokhinskiy method (Lakin 1990). Ambient temperature is a combination of substrate surface temperature where the snake was located and a surface air temperature from the same spot. To investigate a snake's optimal temperature, the one it deliberately prefers, we exposed individuals experimentally to slowly rising temperatures. We consider individual body temperature at the snake's desired optimum, when the rising internal body temperature reaches an ambient temperature, above which it begins to actively thermoregulate by seeking a cooler place. This optimal temperature is calculated, not measured, by the two temperature curves (internal body and ambient) on the diagram, representing the experimentally rising temperartures. The intersection of the two curves corresponds to the optimal internal body temperature.

Results and Discussion

Field Data

Dice snakes in the Samara Bend emerge from hibernation between late April and early May and subsequently

begin with mating. The hibernacula and place of mass maiting are located along sections of southerly exposed rocky banks of the Volga River. All snakes sampled and obeserved in this region were melanistic (Fig. 2).

The dynamic of surface air temperatures and relative humidity was recorded in a habitat near the Snake Creek over approximately 36 hours between the evening of 30 April and morning 2 May, 2008 (Fig. 3). On 1 May, the surface air temperature rose from 4.6 °C at 7:20 h up to 25.2 °C at 16:30 h. The relative air humidity varied from 20.5% at 16:50 h on 1 May to 82.5% at 5:30 h on 2 May. All microclimatic results and body temperatures of dice snakes from the Samara Bend are presented in Table 1.

Statistically significant differences between males and females and their place of capture (during thermoregulation) were revealed for the following traits: specific capacity for heat emission of substratum ($t = 8.14$, $P < 0.001$), illumination (the intensity of light the snake is receiving) ($t = 13.74$, $P < 0.001$), specific capacities for light flux ($t = 9.24$, $P < 0.001$) and ultraviolet radiation ($t = 3.91$, $P < 0.001$), dorsal tail temperature ($t = 4.14$, $P < 0.001$), and ventral-tail temperature ($t = 5.24$, $P < 0.001$). No significant differences were found between sexes for the other traits measured ($P > 0.05$).

Fig. 2. Melanistic *N. tessellata* feigning death, Perevoloki, Volga River. Photo: Nastja Poklonzewa

In summary, females prefer more illuminated (= open) places that receive intense ultraviolet radiation and light flux, consequently, their thermoregulatory spots yielded a higher heat emission. However, their body temperature is only slightly higher than that of males, which may be due to the mixture of gravid with non-gravid females in our sample. Luiselli & Zimmermann (1997) found that gravid female dice snakes in Italy and Austria exhibited higher body (cloacal) temperatures than non-gravid females due to selecting spots for thermoregulation with higher air and substrate temperatures. We suggest that non-gravid females resemble males in thermoregulatory needs and activities, as both groups would not be urged to achieve higher body temperatures to develop embryos like gravid females do. But the abbreviated sampling period in this study up into early May likely had the larger impact in generating our small sexual difference in body temperatures. Our sampling scheme covered the mating period though, but unlike in Luiselli & Zimmermann (1997), it missed the relevant period of embryogenesis, and hence, the most relevant period of thermoregulatory active gravid females, i.e. when they are expected to seek higher temperatures.

Males exhibited a higher temperature on the surface of their tails, ventrally and dorsally. Probably, this sexual difference is related to the smaller sizes of males, producing also a larger surface/volume ratio at the tail, and hence, a more rapidly heatable body segment.

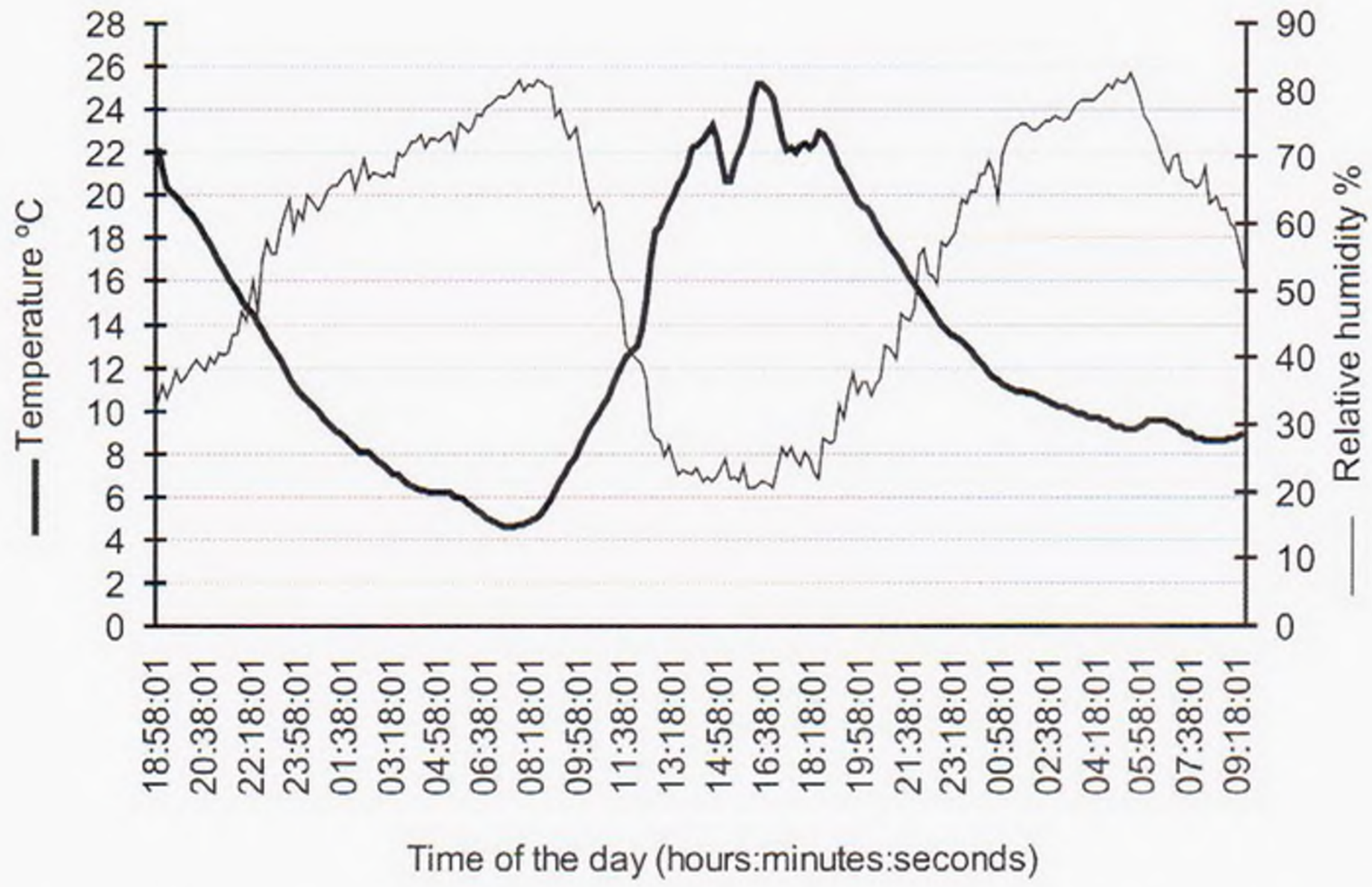


Fig. 3. Spring surface air temperature and humidity in a habitat near Snake Creek in the Samara Bend, Russia (evening 30 April – 2 May 2008).

Tab. 1. Microclimatic results and various body temperatures in dice snakes from the Samara Bend, Russia: Sexes combi. (= Sexes combined), *M* = mean, *m* = standard error.

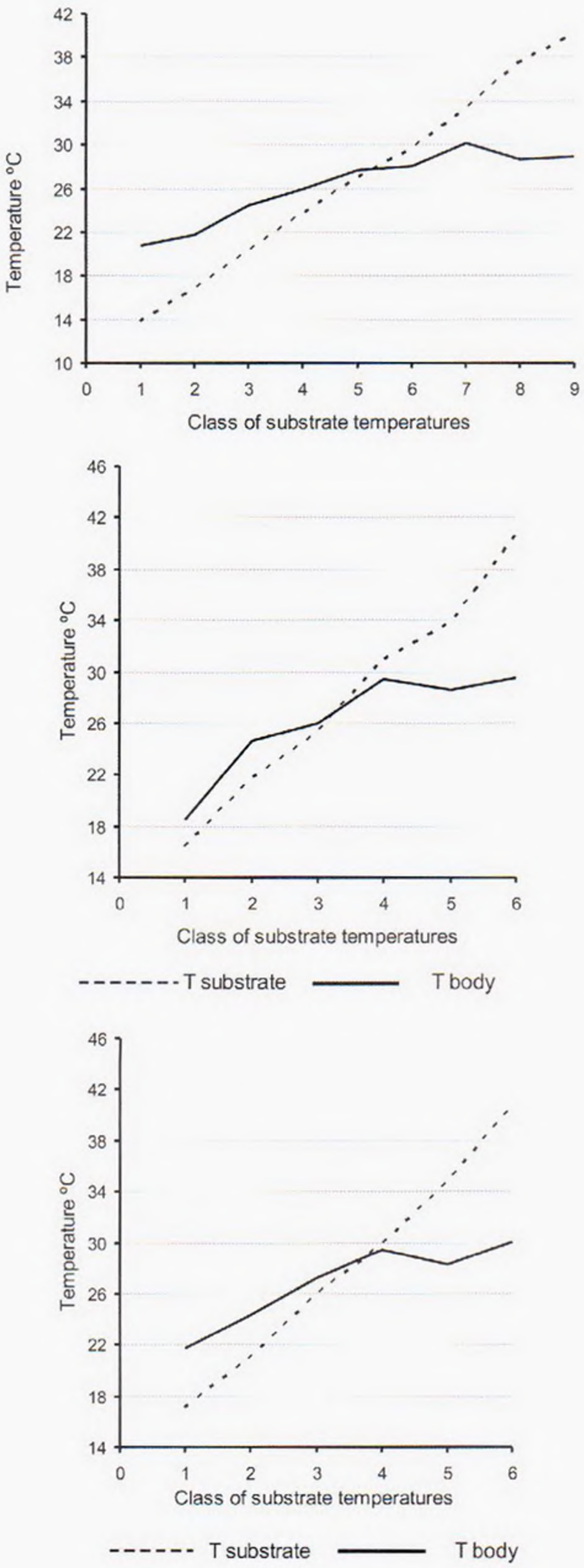
Field variable	Sexes combi. (*n* = 123)	Males (*n* = 60)	Females (*n* = 47)
	M ± *m* / *min–max*		
Surface air temperature (°C)	23.8 ± 0.41 14.0–38.6	24.4 ± 0.61 14.0-38.6	23.5 ± 0.66 15.7-38.6
Substrate temperature (°C)	25.4 ± 0.56 13.2–40.7	25.7 ± 0.71 16.1-40.7	26.4 ± 0.96 15.8-40.7
Specific capacity of incident heat (W/m²)	206.6 ± 60.4 188.9–280.0	204.6 ± 2.30 191.9–280.0	207.3 ± 2.23 188.9–240.6
Specific capacity for heat emission of substrate (W/m²)	78.3 ± 22.7 35.0–170.0	73.0 ± 20.70 35.0–170.0	82.8 ± 16.80 38.6–165.0
Illumination (intensity of light receiving, in klx)	82.7 ± 7.66 55.1–122.7	78.9 ± 8.30 55.1–102.2	101.0 ± 7.00 94.0–122.7
Specific capacity for light flux (W/m²)	328.2 ± 30.4 218.8–487.2	313.4 ± 11.48 218.8–471.4	342.5 ± 13.70 233.9–487.2
Specific capacity of ultraviolet radiation (W/m²)	4.8 ± 0.74 0.6–9.8	4.1 ± 0.53 0.6–5.0	5.2 ± 0.63 2.9–9.8
Relative humidity (%)	51.3 ± 4.91 27.0–68.0	47.3 ± 3.91 27.0–68.0	52.7 ± 4.17 36.0–66.0
Internal body temperature (°C) esophagus	26.4 ± 0.31 14.8–33.2	25.9 ± 0.44 14.8–33.2	26.5 ± 0.50 17.9–31.5
Cloacal temperature (°C)	24.3 ± 0.33 14.6–32.3	24.2 ± 0.48 14.6–32.2	24.3 ± 0.56 15.4–32.3
Mid-dorsal temperature (°C)	23.4 ± 0.28 14.8–33.0	22.9 ± 0.44 14.8–33.0	23.8 ± 0.42 18.0–29.8
Ventral temperature (°C)	23.4 ± 0.26 15.1–32.2	23.1 ± 0.40 15.1–32.2	23.7 ± 0.41 18.5–30.0
Parietal temperature (°C)	23.1 ± 0.29 16.0–30.8	22.9 ± 0.38 16.0–30.0	23.2 ± 0.42 16.0–30.8
Throat temperature (°C)	23.5 ± 0.28 16.2–31.4	23.2 ± 0.37 16.2–30.0	23.6 ± 0.41 16.9–31.4
Tail temperature, dorsal (°C)	24.0 ± 0.36 19.5–29.6	24.5 ± 0.37 21.7–29.6	22.8 ± 0.64 19.5–26.5
Tail temperature, ventral (°C)	24.1 ± 0.38 18.2–29.6	24.7 ± 0.36 22.0–29.6	22.5 ± 0.76 18.2–26.7

The intensity strength index shows the influence of air and substrate surface temperatures on body temperature of dice snakes (Tab. 2). Ambient temperature significantly influences body temperatures of all snakes analysed ($P < 0.01$), thus corroborating results by Luiselli & Zimmermann (1997) and Scali (2011). When substrate and air temperatures increase, the internal body temperature of a thermoregulating dice snake also increases correspondingly. At our study site, the associated basking behavior usually took place in the morning after snakes left their shelter. The internal body temperature was raised up to an optimum level, at which point the snakes switched to other activities, such as mating and foraging (termed r thermoregulation). Alternatively, at reaching a desired temperature level, thermoregulating snakes exhibited a behavior to maintain that temperature to promote relevant physiological processes (e.g. embryogenesis, digestion, ecdysis) and avoid dan-

Tab. 2. Strength index values of ambient temperature impact on body temperature of dice snakes.

Ambient temperature	Sexes combined (*n* = 123)	Males (*n* = 60)	Females (*n* = 47)
Air temperature (%)	59.38	55.68	59.88
Substrate temperature (%)	65.01	64.32	67.03

gerous overheating, a strategy termed "K thermoregulation" according to Hailey & Davies (1987). We found, that if the ambient temperature continues rising for a only few degrees (< 3 °C) beyond an optimum level, the snake's body temperature increased with an appreciable backlog slower and remained below the ambient temperature. If ambient temperatures continued rising, a snake retreated to a shelter with lower temperatures than on the surfcace. Finally, the point, where the curves of internal body temperature and ambient temperature intersect, is viewed as the absolute temperature optimum fot the snake. At this point, the substratum temperature is equal to the preferred ambient temperature. In dice snakes, the point of an absolute temperature optimum was measured and identified for both sexes combined at 28.0 °C (Fig. 4a). This temperature confirms similar results about preferred body temperatures in dice snakes from other areas in Europe, e.g. Luiselli & Zimmermann (1997) and Velenský et al. (2011). There is a sexual difference, as the male's absolute optimum temperature was determined at 27.0 °C (Fig. 4b), whereas the female's preferred temperatures two degrees higher at 29.0 °C (Fig. 4c). This result corroborates the 0.6 °C higher body temperatures found in females than in males ($t = 2.02$; $P < 0.05$), and reflects the observation by Luiselli & Zimmermann (1997) for dice snakes and by Brown & Weatherhead (2000) for a related North American natricine, as in both species females prefered places with relatively higher temperature.



Experimental Data

Dice snakes exhibit a natural behavior of fleeing into the water, when a large potential predator such as a human approaches. But unlike in the summer, the water temperature in the spring is relatively cold at around 15 °C. Under such circumstances, the snakes do not stay long in the water and return to the shore after a few minutes to reach temperatures more suitable for their physiological needs. We have performed controlled experiments to elucidate the dynamics of internal body temperature of dice snakes when they are immersed in cold water in natural basins. Prior to the experimental immersion of a large female dice snake (SVL 870 mm, tail length 170 mm), she was confined for half an hour on a sunny warm substrate with a high temperature range between 40.0–54.4 °C. The body temperature of the snake was recorded by the register-tablet iBDL placed in the stom-

Fig. 4. Relationship of substrate temperature / body temperature of *Natrix tessellata*: a) sexes combined, b) a male, c) a female. X-axis: Classes of substrate temperatures; whereby a class represents a mean of several measurements of substrate temperature. The mean of simultaneously measured body temperatures of snakes is also shown for each class. Classes contain different numbers of temperature measurement.
The range of class intervals was defined by using Brooks-Karruzers formula.

$i = \frac{x_{max} - x_{min}}{5 \cdot \lg n}$, i – range of class intervals; x_{max}, x_{min} = max. and min. of substrate temperatures; n = number of substrate temperature measurements

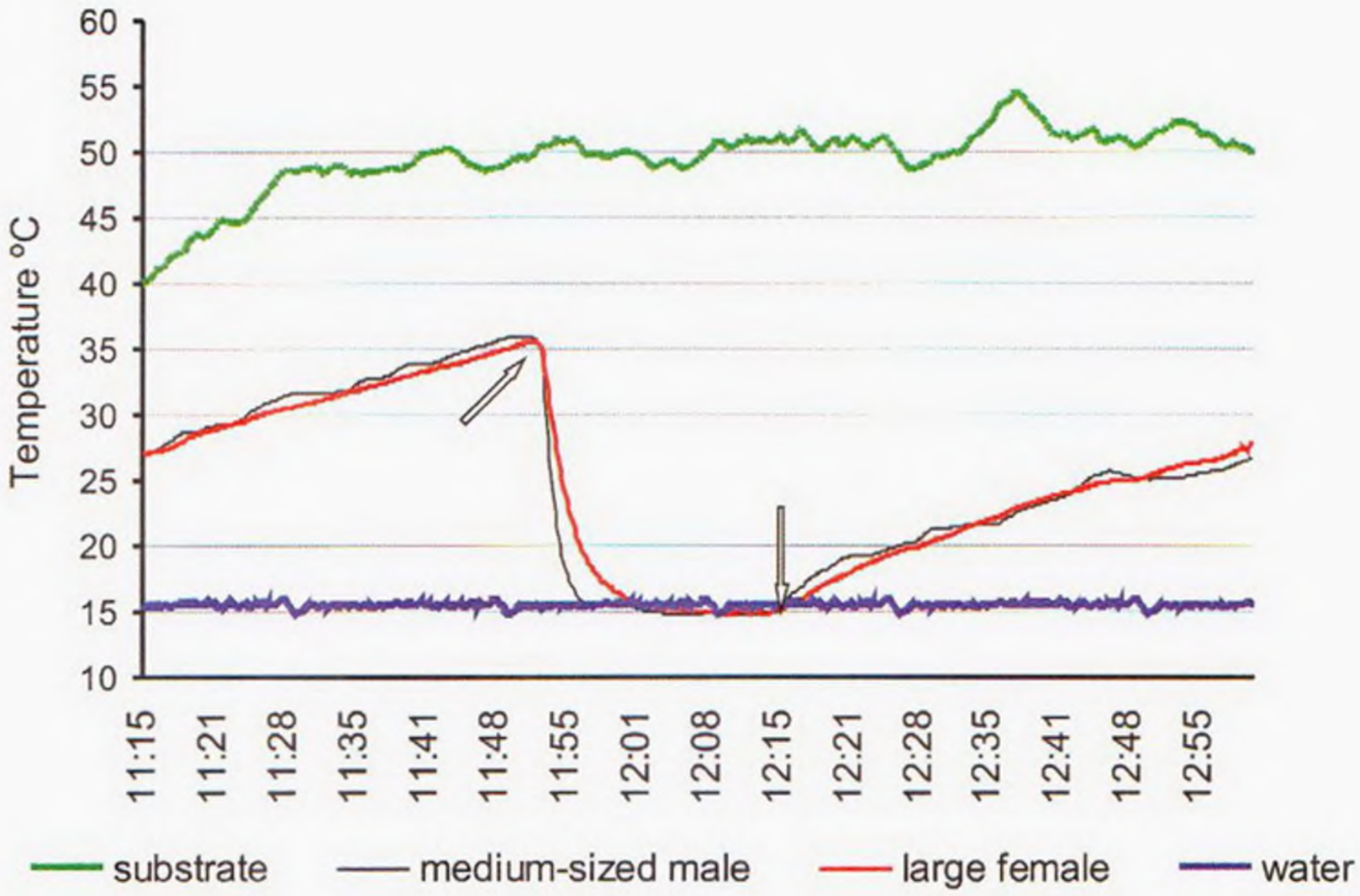


Fig. 5. Dynamics of internal body (stomach) temperature in a dice snakes immersed into cold water. Arrows indicate moments of imnmersion into and removal from water.

ach. During this heating period the snake's body temperature reached its maximum at 35.6 °C. The temperature of the cooling bath ranged from 14.8–16.0 °C, Subsequent to the immersion of the snake, its body cooled rapidly. Within nine minutes the body temperature dropped to 19.7 °C by an average of 2.2 deg/min until it stabilized at the level of the water temperature. After removing the snake from the water, its body temperature slowly began to rise at an average of 0.3 deg/min, until it leveled at 27.9 °C. The speed of temperature rise was nearly seven times less than its decrease. An even faster cooling rate of 4.0 deg/min was obtained by immersing a male dice snake (Fig. 5). Presumably its smaller size (SVL 570 mm, tail length 150 mm) was responsible for the rapid cooling

In summer, the water temperature at the Samara Bend ranges from 22.5–26.4 °C (mean 23.9 ± 0.57 °C), and the body temperature of dice snakes removed from the water produced similar values from 20.7–28.3 °C (mean 23.6 ± 1.08 °C), i.e. it approximately corresponded to the water temperature, similar to results found for dice snakes in Luiselli & Zimmermann (1997), Scali (2011), and Velenský et al. (2011) Under such temperature conditions, dice snakes can stay for a long period in the water and still maintain a fair amount of relevant physiological processes.

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