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ORIGINAL PAPER

Thermal strategies and energetics in two sympatric colubrid snakes with contrasted exposure

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Abstract The thermoregulatory strategy of reptiles should be optimal if ecological costs (predation risk and time devoted to thermoregulation) are minimized while physiological benefits (performance efficiency and energy gain) are maximized. However, depending on the exact shape of the cost and benefit curves, different thermoregulatory optima may exist, even between sympatric species. We studied thermoregulation in two coexisting colubrid snakes, the European whipsnake (*Hierophis viridiflavus*, Lacépède 1789) and the Aesculapian snake (*Zamenis longissimus*, Laurenti 1768) that diverge markedly in their exposure, but otherwise share major ecological and morphological traits. The exposed species (*H. viridiflavus*) selected higher body temperatures (~30°C) than the secretive species (*Z. longissimus*, ~25°C) both in a laboratory thermal gradient and in the field. Moreover, this difference in body temperature was maintained under thermophilic physiological states such as digestion and molting. Physiological and locomotory performances were optimized at higher temperatures in *H. viridiflavus* compared to *Z. longissimus*, as predicted by the thermal coadaptation hypothesis. Metabolic and energetic measurements indicated that energy requirements are at least twice higher in *H. viridiflavus* than in *Z. longissimus*. The contrasted sets of coadapted traits between *H. viridiflavus* and *Z. longissimus* appear to be adaptive correlates of their exposure strategies.

Keywords Ectotherm · Thermal preference · Coadaptation · Metabolic reaction norm · Energy budget · Thermoregulatory strategy

Introduction

The body temperature of ectotherms affects most traits, from physiological performance (Angilletta et al. 2002; Blouin-Demers et al. 2003; Stevenson et al. 1985) to growth rates (Goldsbrough et al. 2004), and reproductive success (Shine et al. 1997). Ultimately, therefore, temperature has a significant impact on fitness in ectotherms (Huey and Kingsolver 1989). Terrestrial reptiles can buffer to some extent the ubiquitous impacts of body temperature on performance by thermoregulation. Thermoregulation is achieved mainly via habitat selection (Blouin-Demers and Weatherhead 2001a, 2002; Huey 1991; Reinert 1984). The optimal investment in thermoregulation depends on the ratio between associated costs and benefits (Huey and Slatkin 1976). Costs are mainly ecological because thermoregulatory behavior can increase predation risk (Hertz et al. 1982; Pianka and Pianka 1970) and reduce the time available for other activities (Gregory et al. 1999; Huey and Slatkin 1976). Benefits are mainly physiological because locomotory performance and digestive efficiency are temperature-dependant (Angilletta et al. 2002; Blouin-Demers et al. 2003; Stevenson et al. 1985). The different cost–benefit ratios result in a gradient of optimal

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behavioral strategies from thermal conformity to precise thermoregulation (Huey and Hertz 1984; Kearney and Predavec 2000).

The thermal coadaptation hypothesis predicts that the range of body temperatures experienced by ectotherms in the wild should match the optimal temperature for performance (Angilletta et al. 2002, 2006; Huey and Bennett 1987). The cost of thermoregulation might be the primary driver of coadaptation in variable thermal environments (Angilletta et al. 2006). Environments in which the cost of thermoregulation is low (high thermal quality or low predation risk) are expected to favor precise thermoregulation. Thermoregulatory costs may be minimized in two ways: by shifting thermal reaction norms toward cooler temperatures or by selecting habitats of high thermal quality (Fitzgerald et al. 2003; Kearney 2002). In temperate or cold climates, thermal conditions are limiting, and the cost–benefit model predicts that ectotherms should invest less in thermoregulation because costs outweigh benefits (Huey and Slatkin 1976). Nevertheless, many reptiles in temperate climates exhibit active thermoregulation with pronounced basking behavior (Blouin-Demers and Nadeau 2005; Downes 2001; Dubois et al. 2009; Gvoždík 2002; Martin and Lopez 1999). In addition, a single thermoregulatory strategy does not necessarily dominate in a given area; several strategies can coexist if they entail similar fitness gains. Within a heterogeneous thermal environment, different species may exploit temperature in contrasted ways with distinct associated costs and benefits due to coadaptation between traits (Belliure et al. 1996; Du et al. 2006; Grover 1996; Sartorius et al. 2002; Scheers and Van Damme 2002; Singh et al. 2002). For instance, a thermophilic strategy is beneficial in terms of food processing because it accelerates transit time, but is energetically costly in terms of maintenance.

Sympatric species with contrasted thermoregulatory strategies are useful to improve our understanding of the evolution of optimal behavioral thermoregulation, since they allow standardized comparisons of thermal adaptations in species that respond differently to similar ambient conditions (Blouin-Demers et al. 2003; Luiselli et al. 2007; Reinert 1984; Secor and Nagy 1994). These comparative studies that are based on a priori predictions suffer less from limitations inherent to two-species comparisons (Garland and Adolph 1994), and have proven useful to our understanding of behavioral thermoregulation. For instance, strong links of covariation between thermoregulatory strategy and major ecological traits such as reproductive mode (Du et al. 2006) and foraging mode (Belliure et al. 1996; Secor and Nagy 1994) have been uncovered. A comparison of thermoregulatory strategies is particularly valuable in coexisting species that are very similar in their other major ecological traits (habitat, food, phenology, and morphology).

We took advantage of such a situation by studying two sympatric colubrid species from Western Europe, the Aesculapian snake *Zamenis longissimus* and the European whipsnake *Hierophis viridiflavus* which largely codominate the snake community at our study site (>40% of all snake captures for both species) and elsewhere (Filippi and Luiselli 2006). Available data on these species indicate strong morphological and ecological similarities (body size, diet, habitat use, reproductive mode, phenology for wintering and egg-laying) and sympatry at large and fine spatial scales (Luiselli and Capizzi 1997; Naulleau 1997). They are both active foragers, but they strongly differ in exposure strategy: *Hierophis viridiflavus* is very exposed and highly observable whereas *Zamenis longissimus* is more cryptic and secretive (Naulleau 1997). These two species living in the same environment (same predation pressure and habitat thermal quality), but exhibiting contrasted exposures and thermal strategies provide an opportunity to describe patterns of coadaptation between traits. Our approach is descriptive, and we do not attempt to reconstruct an evolutionary scenario, which is impossible with two-species comparative studies (Garland and Adolph 1994).

We specifically addressed three complementary predictions:

Lifestyle contrast (exposed vs. secretive) should be linked to differences in active selected body temperature in the field *Zamenis longissimus* displays a risk-adverse strategy and adopts a secretive lifestyle, which involves the use of undercover or underground microhabitats characterized by low temperatures. We thus expected that this species should select lower body temperatures than *Hierophis viridiflavus* in the field. We also tested the effect of physiological status on selected body temperature in a laboratory thermal gradient to verify whether the interspecies differences were maintained under thermophilic conditions.

Preferred body temperatures are coadapted with the optimal temperature for performance We tested whether coadaptation between optimal temperature for performance and preferred body temperature occurs in these species. Various physiological or locomotory activities may affect fitness differently in different species. For instance, temperature may affect more or less one kind of activity in one species (e.g., crawling speed in a terrestrial species) than in another (e.g., crawling speed in an arboreal species). Because we compare two species with phylogenetic and ecological divergences, we used several measures of performance, including tongue flicking frequency, crawling speed, and digestion rate.

Thermoregulatory strategies should have strong energetic implications and translate into contrasted energy *balance* We assessed the energetic consequences of the contrasted thermoregulation strategies by measuring standard metabolic rate. To confirm the direct influence of thermoregulatory strategy on the energy budget, we measured changes in body mass for snakes held over a long period in a thermal gradient.

Methods

Study site and study animals

We studied Aesculapian snakes (*Zamenis longissimus*) and European whipsnakes (*Hierophis viridiflavus*) at the Centre d'Études Biologiques de Chizé in western France (46°07′N; 00°25′O) between April and September of 2006–2007. The CÉBC is composed of 2,600 ha of forest, scrubland, and prairie. Climatic conditions are temperate oceanic with annual precipitations between 800 and 1,000 mm, annual mean temperature of 12°C, and annual sunlight of 2,000 h. We used concrete tiles disposed throughout the study area to catch snakes.

Hierophis viridiflavus and *Zamenis longissimus* are medio-European oviparous colubrids. Both species are medium sized (140–160 cm for *Z. longissimus* and 120–150 cm for *H. viridiflavus*; Naulleau 1984) and occur in the same micro and macro habitats (syntopy). Moreover, reproductive cycles are synchronous (Bonnet et al. 1999; Rugiero et al. 2002) and diets largely overlap: both species forage actively and feed mostly on small mammals (*Microtus* sp., *Clethrionomys glareolus*, *Apodemus sylvaticus*; Capizzi et al. 1995; Capizzi and Luiselli 1996; Naulleau 1984; Rugiero et al. 2002). Both species are locally common and have broadly overlapping geographical ranges. These two snakes are often the dominant species in western European snake communities (Filippi and Luiselli 2006; Luiselli and Capizzi 1997). For instance, in our study area whipsnakes account for 44% of all snake captures, while Aesculapian snakes account for 41% (more than 600 marked individuals from each species over 8 years). The other two species present (*Natrix natrix* and *Vipera aspis*) are scarce.

Thermoregulation in the field

We measured body temperature in eight *H. viridiflavus* (SVL = 90.8 ± 9.1 cm; BM = 241.0 ± 66.4 g) and nine *Z. longissimus* (SVL = 102.4 ± 6.4 cm; BM = 302.2 ± 47.7 g) every 30 min for 30 days between July and September 2007. We implanted a temperature data logger (miniaturized iButton thermochron, Dallas Semiconductor, Dallas, USA; see Robert and Thompson 2003 for details on miniaturization) and a radio-transmitter (PD2, Holohil Systems Ltd, Carp, Canada) in the abdominal cavity of the snakes (see Reinert and Cundall 1982; Whitaker and Shine 2002, 2003 for details). Total mass of logger and transmitter represented at most 2.2% of snake body mass. We kept snakes under observation for 6 days and then released them at their exact point of capture.

Simultaneously, we measured operative environmental temperatures (T_e) in the various microhabitats available to the snakes (Bakken 1992). We used 15 physical models reproducing the thermal characteristics of the study species. We ensured the realism of our models by calibrating them against two fresh snake carcasses (correlation coefficients = 0.95 and 0.97, respectively). We placed the models in each of four habitats: on the ground in forest ($N = 3$), on the ground under scrubs ($N = 4$), on the ground in the open ($N = 4$), and in an underground retreat ($N = 4$). We selected three hot days (max T_e in the open >40°C) at least 10 days after surgery when snakes could thermoregulate to calculate mean active T_b.

Thermal preference in captivity

Preferred body temperature (T_{set}) should be measured in an environment devoid of thermoregulatory costs (Hertz et al. 1993; Huey and Slatkin 1976). Hence, we measured T_{set} in a laboratory thermal gradient. The gradient was a 3-m^2 concrete box. A heat source at one end and cooled air at the other produced a smooth temperature gradient ranging from 22 to 45°C. Light and temperature cycles reproduced the natural photo and thermo periods. Refuges were provided by a plastic cover stretched over the whole gradient. We recorded the body temperatures (T_b) selected by eight *H. viridiflavus* (SVL = 92.1 ± 9.9 cm; BM = 204.9 ± 66.9 g) and ten *Z. longissimus* (SVL = 96.8 ± 6.5 cm; BM = 213.5 ± 48.2 g) in the gradient every 30 min for at least 4 days via data loggers (iButton thermochron, Dallas Semiconductor, Dallas, USA) surgically implanted in the body cavity. Because laboratory measurements were conducted after field measurements, it allowed for at least 30 days between surgery and testing in the gradient. We ensured snakes were post-absorptive, were not preparing to shed, and were not reproductive. We used the bounds of the central 50% of selected T_b for each individual when temperature under the heat source was not limiting as our measure of T_{set} (Christian and Weavers 1996; Hertz et al. 1993).

To test for the presence of a potential body temperature increase in response to particular physiological requirements, we also measured thermal preference under other physiological states associated with high metabolic activity: digestion and molting. To assess the influence of digestion on T_{set}, we fed snakes mice (about 10% of their body mass) and then placed them again in the thermal gradient. One or two postprandial responses were recorded for each snake (total of 17 in *H. viridiflavus* and 14 in *Z. longissimus*). We also measured T_{set} in molting snakes. Imminent molting event is characterized by blue milky eyes and white bellies. We measured T_{set} in four molting *H. viridiflavus* and five molting *Z. longissimus*.

Thermal sensitivity of locomotory performance

We examined the influence of body temperature on performance (crawling speed and tongue-flicking) on 23 *H. viridiflavus* (SVL = 83.3 ± 9.6 cm; BM = 179.8 ± 86.4 g) and 17 *Z. longissimus* (SVL = 92.2 ± 10.4 cm; BM = 219.4 ± 72.3 g). We tested each snake at T_b of 10, 15, 20, 25, 30, and 33°C. We randomized the order of temperature trials for each individual and ensured at least 12 h of rest between trials. Prior to each test, snakes were placed in a climatic chamber (Pharmaclim, Vötsch Industrietechnik, Balingen, Germany) for approximately 6 h to equilibrate their T_b to the appropriate test temperature. We measured T_b from skin surface temperature immediately before and after each test with an infrared laser thermometer (Raytek Corporation, Santa Cruz, USA). We conducted all trials in an environmental chamber set at the test temperature.

We conducted crawling trials in a plywood raceway (2.2 m long, 0.3 m high, and 0.16 m wide). We encouraged snakes to crawl at their maximum speed by gently tapping their tails throughout the trial. We recorded the time for the head to traverse the raceway with a stopwatch. If a snake stopped or turned around during the trial, we immediately restarted the trial. Three successive trials were conducted, and we used only the fastest trial for analysis.

We measured tongue-flicking frequency by positioning the snake in front of a video camera and recording tongue-flicking bouts. Using frame-by-frame playback, we determined the duration of each tongue-flicking bout (each frame is 1/25 s) and the number of vertical direction changes. Tongue-flicking frequency was calculated as the number of vertical direction changes divided by the duration of the tongue-flicking bout. Six to eight bouts were recorded per individual, and maximal frequency was then used for analysis.

Thermal sensitivity of metabolism and energy gain

We used closed system respirometry to measure standard metabolic rate (SMR) on 7 *H. viridiflavus* (SVL = 89.2 ± 10.5 cm; BM = 246.2 ± 84.0 g) and 11 *Z. longissimus* (SVL = 96.4 ± 9.3 cm; BM = 234.7 ± 70.5 g). Measurements were performed on post-absorptive snakes shortly after spring emergence, and were restricted to males to avoid metabolic contribution from follicular development in females. We measured rates of oxygen consumption (analyzed in ml h^{-1} with body mass as cofactor, but presented in ml h^{-1} g^{-1} in figures and tables for better understanding) at T_b of 15, 20, 25, 30, and 33°C. We randomized the order of trials, and ensured at least 12 h of rest between each trial. Trials were conducted in opaque test chambers (internal volume 3,170 ml) covered with a glass lid made air-tight using closed cell foam. The individual was placed into the test chamber and maintained in a temperature-controlled environmental chamber (stability ±1°C) 3 h prior to testing for stabilization of the test temperature. Outside air was drawn into each chamber using a Bioblock Scientific 5 l air pump for 5 min assuring 99 + % air turn over (Lasiewski et al. 1966). Baseline samples of outside air were collected at the onset of each trial. The test chambers were carefully sealed, and the time of closure was recorded. Snakes could be observed during the trial through a small viewing port. Snakes showed limited exploratory movements, rapidly coiled, and stayed motionless during the entire trial. Trial duration was predetermined in a pilot study and adjusted for each test temperature (40–180 min) to ensure sufficient O_2 suppression 0.5–1%). At the end of each trial, an end air sample was collected using two 140-ml syringes connected to the chamber via a three-way stopcock. O_2 concentration was then determined using an oxygen analyzer (FC10A, Sable Systems, Las Vegas, USA). Each air sample was striped through drierite to absorb moisture and sent at a controlled rate to the analyzer using an infusion pump (KDS 210, KD Scientific Inc, Holliston, USA). Oxygen suppression was derived by subtracting final from baseline values. Analyzers were calibrated at the infusion pump flow rate prior to each session. We converted measurements of O_2 consumption to joules (J) of energy expended per day using the relationship of 19.64 J per milliliter of O_2 (fat metabolism; Nagy 1983). We used metabolic reaction norms obtained in captivity to derive an estimate of field resting energy expenditure in natural conditions. We only considered hot days when thermoregulation opportunities were not limited for snakes.

Digestion speed and efficiency

Eight fasted *H. viridiflavus* (SVL = 93.8 ± 4.9 cm; BM = 268.8 ± 47.8 g) and five fasted *Z. longissimus* (SVL = 104.8 ± 9.9 cm; BM = 293.4 ± 67.7 g) were fed mice (9.4–15.2 g, ca. 12% of snake body mass). A plastic tag was affixed to the tail of the mice to ensure that the prey was entirely digested when the tag was retrieved in the feces. Just after feeding, snakes were placed in an environmental chamber set at 18, 25, or 30°C. Digestion duration (time to first feces, time to tag passage) and digestion efficiency were then measured. To calculate digestion efficiency, we used the ratio between dry weight of prey and dry weight of feces. Dry weight of prey was estimated from a calibration equation obtained with seven freshly killed mice dried in a steam room. The equation was: Dry weight = 0.0098 + 0.3072 fresh weight (linear regression; $R^2 = 0.999$; $P < 0.001$).

We kept 19 male *H. viridiflavus* (SVL = 94.1 ± 8.4 cm; BM = 203.1 ± 64.5 g) and 16 male *Z. longissimus* (SVL = 100.6 ± 7.9 cm; BM = 217.3 ± 53.3 g) in the thermal gradient for extended periods (17–67 days, mean 38 days) and fed them mice regularly. For each individual, we calculated the daily mass change and the total mass of ingested prey, expressed in % of snake body mass.

Statistical analyses

We analyzed performance curves by fitting the mean of the maximum performance at each temperature to three functions, and used Akaike's information criterion (AIC) to select the best model for each species and performance (Table 1). All three functions used were left-skewed and provided good estimation of performance in ectotherms (Ben Ezra et al. 2008; Bulté and Blouin-Demers 2006; Ratkowsky et al. 1983; Stevenson et al. 1985). The function with the lowest AIC value for each combination was subsequently used to fit the data for each individual and determine two parameters: the optimal temperature for performance (T_o) and the 80% performance breadth (B_{80} the range of temperatures at which the individual can perform ≥80% of its maximum; Huey and Stevenson 1979). Crawling speed and tongue-flicking frequency were normalized per individual (i.e., expressed as a percentage of individual maximum) prior to curve fitting to control for factors systematically affecting absolute performance (e.g., sex, body size, musculature; Bulté and Blouin-Demers 2006; Huey and Stevenson 1979).

All statistical comparisons were performed in R software (R Development Core Team 2007) using linear models (stats package) and mixed models (nlme package) with individual as random effects when it was required. Because *Z. longissimus* attains a slightly larger body size than *H. viridiflavus*, it was difficult to obtain samples of individuals of the same size for both species. Hence, we tested morphological differences between species for each measured trait with independent *t* tests. SVL was significantly smaller in *H. viridiflavus* for thermal sensitivity (10.9%), field thermoregulation (11.3%), and digestion (10.5%) measurements but not for thermal preference in captivity and metabolic measurements. All study animals, however, were adults, and this precluded a potential bias linked to a possible ontogenetic shift in thermal ecology. Means are provided ± 1 SD. We accepted significance at an alpha level of 0.05.

Table 1 A comparison of functions used to describe the thermal performance curves of *H. viridiflavus* (EWS) and *Z. longissimus* (AS) using Akaike's information criterion (AIC)

Species	Performance (*N*)	Function	AIC	*K*	w_i
AS	Crawling (16)	**Log-exponential**[a]	−6,635.58	7	0.79
		Quartic	−6,632.97	6	0.21
		Ratkowsky[b]	−6,613.30	3	0.00
	Tongue-flicking (16)	**Log-exponential**[a]	−6,788.27	7	1.00
		Quartic	−6,669.79	6	0.00
		Ratkowsky[b]	−6,536.31	3	0.00
EWS	Crawling (23)	**Quartic**	−13,853.73	6	1.00
		Ratkowsky[b]	−13,831.20	3	0.00
		Log-exponential[a]	−13,824.22	7	0.00
	Tongue-flicking (23)	**Quartic**	−14,027.33	6	1.00
		Log-exponential[a]	−13,944.32	7	0.00
		Ratkowsky[b]	−13,788.18	3	0.00

The function with the lowest AIC is the one that best describes the data

Models in boldface were selected for analyses

K number of parameters in the function; w_i Akaike weight

[a] Stevenson et al. (1985)

[b] Ratkowsky et al. (1983)

Results

Thermoregulation in the field

At night (between 00:00 and 07:00), T_b of the two species did not differ significantly ($T_b = 18.53 \pm 1.50$°C in *H. viridiflavus* and 18.38 ± 1.03°C *Z. longissimus*; linear mixed effects model, $t_{1,19} = 0.10$, $P = 0.92$). Nocturnal T_b was not significantly different from T_e in burrows ($T_e = 17.18 \pm 2.06$°C; linear mixed effects model, $t_{1,19} = -0.58$, $P = 0.57$) and was significantly higher than surface T_e ($T_e = 7.70 \pm 2.06$°C; linear mixed effects model, $t_{1,19} = -5.19$, $P = 0.0001$). During the day, when active thermoregulation was possible (T_e for open field >40°C), mean T_b was significantly higher in *H. viridiflavus* ($T_b = 31.23 \pm 0.59$°C) than in *Z. longissimus* ($T_b = 26.11 \pm 0.41$°C; linear mixed effects model, $t_{1,15} = 8.67$, $P < 0.0001$; Fig. 1).

Thermal preference

Hierophis viridiflavus had higher T_{set} (27.5–31.0°C) than *Z. longissimus* (21.5–25.5°C, linear mixed effects model,

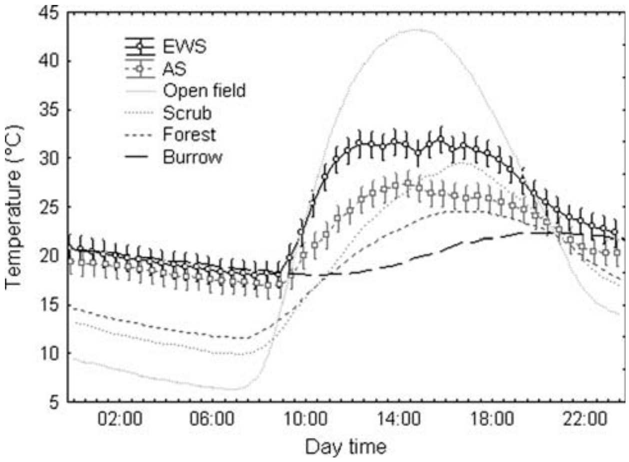

Fig. 1 Field thermoregulation during hot summer days in male *H. viridiflavus* (EWS) and *Z. longissimus* (AS). Snake selected body temperature and operative temperature in various habitat types are represented. *Bars* of 95% confidence intervals are represented for snakes. Habitat operative temperature confidence intervals are not indicated to facilitate reading

$t_{1,16} = 9.14$, $P < 0.0001$; Fig. 2). Mean T_b calculated during thermoregulation periods showed a post-prandial elevation with a peak in days 1 and 2 post-feeding (linear mixed effects model, $t_{1,50} = -2.50$, $P = 0.0156$; Fig. 2). Fed snakes selected significantly higher T_b that fasted snakes in *Z. longissimus* (24.07 ± 1.21 vs. 22.21 ± 1.56°C; paired *t* test, $t_{1,9} = 4.01$, $P = 0.003$; Fig. 2), but the T_b elevation was only marginally significant in *H. viridiflavus* (28.71 ± 0.87 vs. 27.96 ± 1.00°C; paired *t* test, $t_{1,7} = 2.35$, $P = 0.051$; Fig. 2). Molting status had no effect on thermal preferences (linear mixed effects model, $t_{1,36} = 1.45$, $P = 0.156$; Fig. 2).

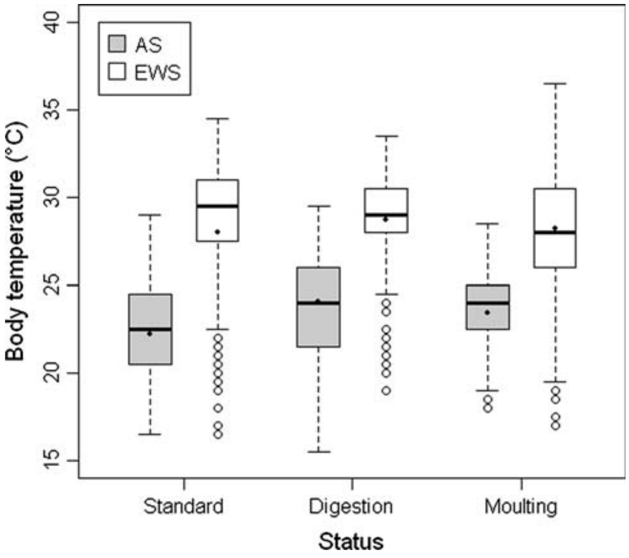

Fig. 2 Thermal preferences in *Z. longissimus* (AS) and *H. viridiflavus* (EWS) with various physiological statuses in a laboratory gradient. The median is represented by the *middle horizontal line* in the *box-plot* and the mean by the *black circle*. Interval between 25 and 75% quartiles is represented by *boxes*, and range is represented by *whiskers*. *Open circles* are outliers

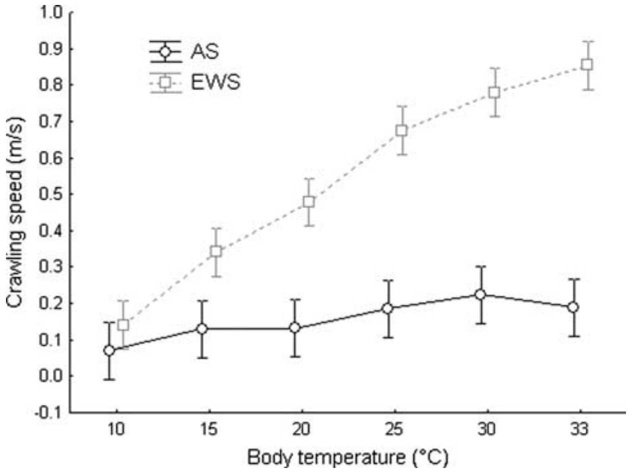

Fig. 3 Thermal influence on absolute crawling speed in *H. viridiflavus* (EWS) and *Z. longissimus* (AS). *Bars* represent 95% confidence intervals

Thermal sensitivity of locomotory performance

Hierophis viridiflavus was faster than *Z. longissimus* at all test temperatures (linear mixed effects model, $t_{1,37} = -2.91$, $P = 0.006$; Fig. 3), but the difference was greatest at high temperatures (*H. viridiflavus* 4 times faster at 33°C; Fig. 3). We found no difference between species in absolute performance for tongue-flicking frequency (linear mixed effects model, $t_{1,37} = -0.92$, $P = 0.364$). According to AIC, the quartic function was the best model to describe both crawling speed and tongue-flicking frequency for *H. viridiflavus*, whereas the logistic-exponential function was the best model for *Z. longissimus* (Table 1).

T_o fell within T_{set} for crawling speed in *H. viridiflavus* and for tongue-flicking frequency in *Z. longissimus* and T_o was less than 2.5°C from upper or lower bounds for the other cases (Fig. 4). T_o was higher for crawling speed than for tongue-flicking frequency in *H. viridiflavus* (30.6 ± 1.0 vs. 26.6 ± 2.4°C; linear model, $F_{1,44} = 54.67$, $P < 0.0001$; Table 2) and in *Z. longissimus* (27.6 ± 4.0 vs. 24.9 ± 3.3°C; linear model, $F_{1,30} = 4.37$, $P = 0.04$; Table 2). *H. viridiflavus* exhibited higher T_o than *Z. longissimus* for crawling speed (30.6 ± 1.0 vs. 27.6 ± 4.0°C; linear model, $F_{1,37} = 11.87$, $P = 0.001$; Table 2), and the difference was marginally significant for tongue-flicking frequency (26.6 ± 2.4 vs. 24.9 ± 3.3°C; linear model, $F_{1,37} = 3.18$, $P = 0.08$; Table 2).

B_{80} were wider for crawling speed than for tongue-flicking frequency in *H. viridiflavus* (10.5 ± 1.4 vs. 15.7 ± 1.5°C; linear model, $F_{1,44} = 155.20$, $P < 0.0001$;

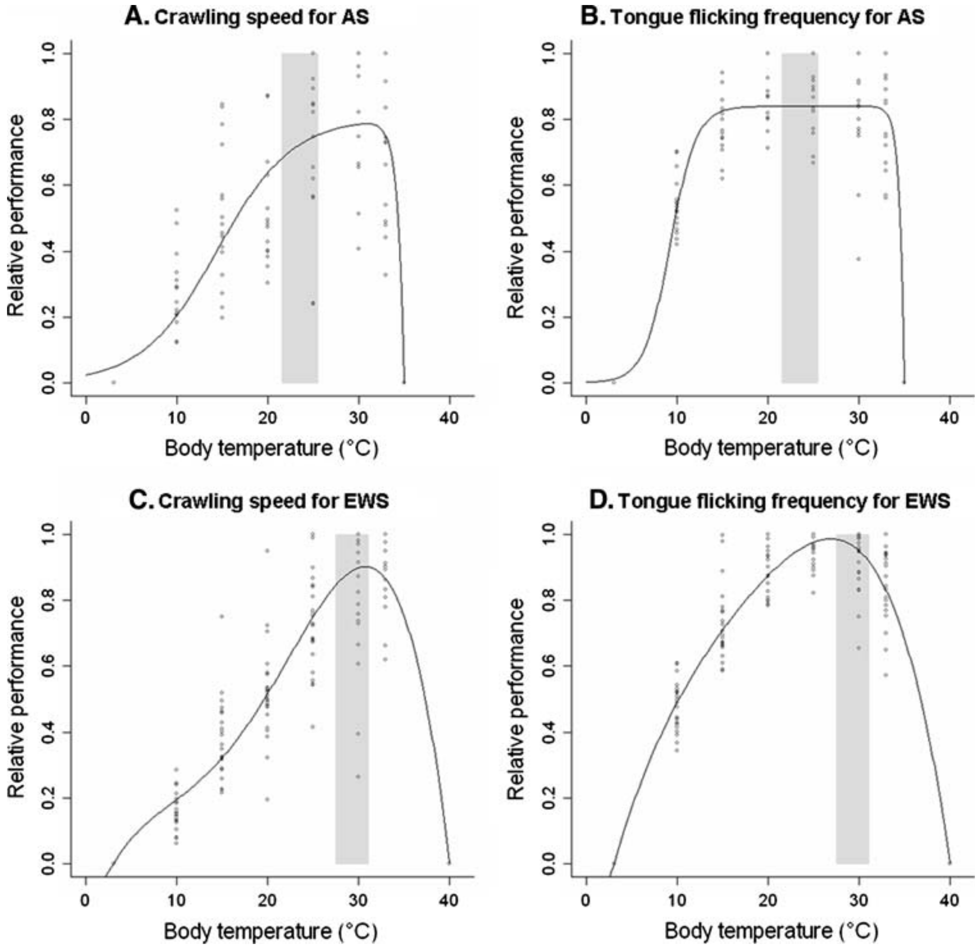

Fig. 4 Mean fitted thermal performance curves (*lines*) and individual responses (*circles*) of *H. viridiflavus* (EWS) and *Z. longissimus* (AS). The *gray boxes* indicate the mean preferred temperature range in the thermal gradient

Table 2 Mean (°C ± SD) T_o and B_{80} for crawling speed and tongue-flicking frequency performances for *H. viridiflavus* (EWS) and *Z. longissimus* (AS)

Species	Performance	T_o (°C)	B_{80} (°C)	N	Curve
AS	Crawling	27.6 ± 4.0	12.2 ± 5.1	16	Log-exponential[a]
	Tongue-flicking	24.9 ± 3.3	21.1 ± 2.4	16	Log-exponential[a]
EWS	Crawling	30.6 ± 1.0	10.6 ± 1.4	23	Quartic[b]
	Tongue-flicking	26.6 ± 2.4	15.7 ± 1.5	23	Quartic[b]

[a] Performance $= S\left\{1/\left[1+k_1 e^{-k_2(T_b-CT_{min})}\right]\right\}\left[1-e^{k_3(T_b-CT_{max})}\right]$

[b] Performance $= aT^4 + bT^3 + cT^2 + xT + z$

Table 2) and in *Z. longissimus* (12.2 ± 5.1 vs. 21.1 ± 2.4°C; linear model, $F_{1,30} = 39.03$, $P < 0.0001$; Table 2). B_{80} were not statistically different between the two species for crawling speed (10.6 ± 1.4°C in *H. viridiflavus* vs. 12.2 ± 5.1°C in *Z. longissimus*; linear model, $F_{1,37} = 2.15$, $P = 0.15$; Table 2), but differed for tongue-flicking frequency (15.7 ± 1.5°C in *H. viridiflavus* vs. 21.1 ± 2.4°C in *Z. longissimus*; linear model, $F_{1,37} = 73.06$, $P < 0.0001$; Table 2).

Thermal sensitivity of metabolism and energy gain

Oxygen consumption was positively influenced by temperature (linear model; $F_{3,86} = 115.3$; $P < 0.0001$; Fig. 5). Male *H. viridiflavus* and *Z. longissimus* exhibited similar metabolic reaction norms (no interaction between species and temperature; linear model, $t_{3,86} = 0.59$, $P = 0.56$). *H. viridiflavus* had higher SMR (linear model, $t_{3,86} = 2.29$, $P = 0.02$), especially at high T_b, but this difference was only significant at 30°C (linear model, $t_{2,15} = 3.14$, $P = 0.007$). For the two species, the best fit was a quadratic regression (O_2 consumption $= 0.04687 - 0.005203\ T_b + 0.0002283\ T_b^2$ in *Z. longissimus*, adjusted $R^2 = 0.988$ and O_2 consumption $= 0.04425 - 0.004726\ T_b + 0.0002264\ T_b^2$ in *H. viridiflavus*, adjusted $R^2 = 0.985$). Using metabolic reaction norms, we calculated the predicted oxygen consumption within T_{set}, and we estimated the energy expenditure at T_b selected in the field during hot days (Table 3). Energy expenditure was significantly higher in *H. viridiflavus* (33.86 ± 1.66 J g^{-1} day^{-1}) than in *Z. longissimus* (21.77 ± 1.13 J g^{-1} day^{-1}; linear mixed effects model, $t_{1,15} = 7.29$, $P < 0.0001$). The difference was more pronounced during

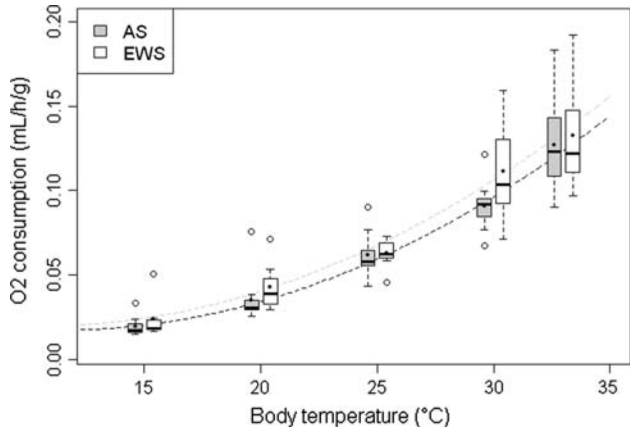

Fig. 5 Metabolic reaction norms in male *H. viridiflavus* (EWS) and *Z. longissimus* (AS). The median is represented by the *middle horizontal line* in the *box-plot* and the mean by the *black circle*. Interval between 25 and 75% quartiles is represented by *boxes*, and range is represented by *whiskers*. *Open circles* are outliers. *Dashed lines* are regression curves for *H. viridiflavus* (*gray line*) and *Z. longissimus* (*black line*; see text for equations)

the activity period (10:00–18:00 h) when thermoregulation was possible (51.95 ± 1.54 J g^{-1} day^{-1} in *H. viridiflavus* vs. 29.85 ± 1.04 J g^{-1} day^{-1} in *Z. longissimus*; linear mixed effects model, $t_{1,15} = 14.39$, $P < 0.0001$; Table 3).

We found a positive effect of temperature on prey assimilation in *Z. longissimus* (59.99 ± 6.52% at 18°C vs. 72.11 ± 5.43% at 25°C; generalized linear model, $F_{1,5} = 7.25$, $P = 0.04$) but not in *H. viridiflavus* (66.14 ± 10.45%, 70.32 ± 7.48% and 72.28 ± 2.24% for 18, 25, and 30°C, respectively; generalized linear model, $F_{2,19} = 1.14$, $P = 0.34$). We detected no difference between species at their preferred temperature (72.11 ± 5.43% at 25°C in *Z. longissimus* vs. 72.28 ± 2.24% at 30°C in *H. viridiflavus*; generalized linear model, LSD post-hoc test, $P = 0.97$). Transit duration was strongly influenced by temperature in *H. viridiflavus* for time until first defecation (generalized linear model, $F_{2,19} = 26.27$, $P < 0.0001$; Fig. 6) and until last defecation (generalized linear model, $F_{2,9} = 13.98$, $P = 0.002$), but only until first defecation in *Z. longissimus* (generalized linear model, $F_{1,5} = 24.28$, $P = 0.004$; Fig. 6). No difference of transit time for first defecation was detected between species at their preferred temperature (2.75 ± 1.26 days at 25°C in *Z. longissimus* vs. 1.50 ± 0.55 days at 30°C in *H. viridiflavus*; generalized linear model, LSD post-hoc test, $P = 0.06$). At 30°C, we noted that digestion was compromised in *Z. longissimus*, and prey were systematically regurgitated within the first 24 h. In the laboratory thermal gradient, *H. viridiflavus* showed higher weight loss (0.64 ± 0.18 g day^{-1}) than *Z. longissimus* (0.17 ± 0.13 g day^{-1}; linear mixed effects model, $F_{1,23} = 7.23$, $P = 0.01$) despite a greater amount of food provided (34.29 ± 16.65% of snake mass vs. 23.54 ± 8.97%; *t* test, $t_{1,34} = -2.37$, $P = 0.02$).

Table 3 Standard metabolic rate within T_{set} and field resting energy expenditure in *H. viridiflavus* (EWS) and *Z. longissimus* (AS)

Species	Oxygen consumption (ml h^{-1} g^{-1})		Energy expenditure (J g^{-1} day^{-1})
	Lower T_{set} bound	Upper T_{set} bound	Field active T_b
AS	0.041	0.063	29.85
EWS	0.086	0.115	51.95

Oxygen consumption is calculated after the regression equations fitted from SMR data of each species (see text and Fig. 5)

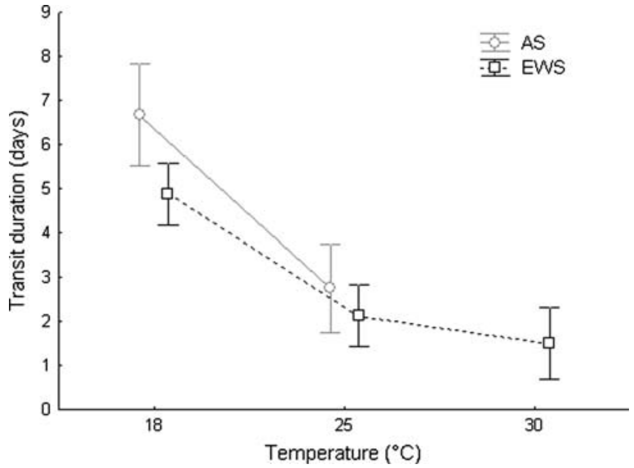

Fig. 6 Thermal influence on transit duration in *H. viridiflavus* (EWS) and *Z. longissimus* (AS). At 30°C, all prey were regurgitated in *Z. longissimus*. *Bars* represent 95% confidence intervals

Discussion

In temperate climates, terrestrial ectotherms face a major challenge for the regulation of body temperature (Huey and Slatkin 1976). Because thermal conditions are constraining, thermoregulatory behaviors generally involve direct exposure to solar radiation which is associated with an increased predation risk (Blouin-Demers and Weatherhead 2001a; Row and Blouin-Demers 2007, Sperry and Weatherhead 2009). Use of cover or underground refuges provides protection against predators, but is thermally costly as temperature in those microhabitats rarely reaches the preferred body temperature of temperate reptiles (Cooper 1998; Downes 2001; Martin 2001). Snakes are usually very secretive with extremely low detectability (Kery 2002). Nevertheless, they display a large array of thermoregulatory strategies ranging from reclusive thermoconformers (Fitzgerald et al. 2003; Pearson et al. 2003) to active heliotherms (Blouin-Demers and Weatherhead

2001b; Brown and Weatherhead 2000). These strategies are tightly related to their degree of exposure.

Hierophis viridiflavus and *Z. longissimus* are broadly sympatric snakes that represent contrasted ecological strategies in colubrids. *H. viridiflavus* and other similar species called racers or whipsnakes (e.g., genera *Masticophis*, *Coluber*, *Psammophis*, and *Demansia*) share morphology (slender bodies, long tails, and large eyes) and ecological lifestyle (alertness, diurnality, and high degree of exposure; Luiselli 2006; Secor and Nagy 1994; Shine 1980). *Z. longissimus* and other similar species called ratsnakes (e.g., genera *Elaphe, Pantherophis,* or *Ptyas*; Lenk et al. 2001) are stouter, more secretive, often potentially nocturnal, and partially arboreal (Carfagno and Weatherhead 2008; Pierce et al. 2008). Accordingly, we found a major contrast in thermal preferences between these two sympatric colubrids. Both in a thermal gradient and in the field, *H. viridiflavus* maintained higher T_b than *Z. longissimus*. Preferred T_b differences were maintained even under specific physiological states generally associated with thermophilic responses (Gibson et al. 1989; Sievert et al. 2005; Tattersall et al. 2004; Tsai and Tu 2005). While *H. viridiflavus* voluntarily selects T_b above 30°C, digestion was compromised at this temperature in *Z. longissimus* and prey were systematically regurgitated. Thermal coadaptation between thermal preference and physiological performance (Angilletta et al. 2006) was observed. *H. viridiflavus* showed higher T_o and narrower B_{80} for performance, especially for crawling speed and digestion rate, than *Z. longissimus*. We also found a strong difference in crawling speed at T_{set} between the two species. *H. viridiflavus* was much faster. Better performance in thermophilic species predicted by the “hotter is better” hypothesis (Huey and Kingsolver 1989) has been shown in other ectotherms (Huey and Hertz 1984; Knies et al. 2009). Fast locomotion by *H. viridiflavus* is probably associated with a very active foraging mode consisting of chasing prey, whereas *Z. longissimus* is more likely to use an ambush strategy based on camouflage. Comparative data on foraging tactics and movement rates at fine scales are lacking for these two species, but correlates with thermoregulatory and energetic strategies are likely to exist (Secor and Nagy 1994; Carfagno and Weatherhead 2008). Metabolic rate was highly temperature-dependant, but we did not detect strong metabolic differences under imposed body temperature regimes excepted for 30°C: SMR reaction norms were very similar in the two species. It is essential, however, to consider metabolic rate with reference to thermal preference. We found that within its range of preferred body temperatures, resting *H. viridiflavus* expends twice as much energy as *Z. longissimus*. Our data on food intake supported this difference in energy consumption as captive *H. viridiflavus* lost weight significantly faster than *Z. longissimus* in a thermal gradient with controlled food input. Interestingly, however, we did not detect any difference in digestion efficiency between the two species. Undoubtedly, digestion was strongly affected by temperature in both species, but within their T_{set} they performed equally well regarding percentage of prey assimilation and transit duration. This demonstrates the striking thermal adaptation for digestion at high temperatures in *Z. longissimus*. Overall, our findings revealed contrasted thermal specialization. *H. viridiflavus* is a highly thermophilic snake that performs optimally at elevated temperature, whereas *Z. longissimus* is specialized to perform well at cooler conditions.

The cost–benefit model of thermoregulation (Huey and Slatkin 1976) predicts that costs increase with an increasing difference between thermal preference and available environmental temperature. Undoubtedly, *H. viridiflavus* and *Z. longissimus* living in the same habitat have found different optima where costs and benefits are balanced. *H. viridiflavus* is a mobile species that actively and precisely thermoregulates. This requires extended periods of exposure to maximize physiological performance. Because a proximal link is likely to exist between high T_{set}, aerobic capacity, and activity (Bennett et al. 2000), *H. viridiflavus* may benefit from better flight and foraging capacities. The high T_b strategy may appear energetically costly, but the increased activity capacity must confer significant advantages, for example by allowing faster growth and earlier sexual maturity. On the other hand, *Z. longissimus* selects cooler body temperatures that are compatible with a secretive lifestyle in more closed microhabitats. The low T_b strategy represents a “low energy approach” associated with limited exposure and low activity levels that limit energy expenditures.

In conclusion, we are fully cognizant of the limitations inherent to our two-species comparison: because we had a single high T_b species and a single low T_b species, we are unable to separate species effects from thermal strategy effects (Garland and Adolph 1994). Nevertheless, it seems highly improbable that the differences we observed in thermal strategies are due to developmental plasticity. The high degree of ecological specialization and the coadaptation between traits revealed at different scales underlie profound differences. Although the different thermal strategies employed by these two species may illustrate evolutionary adaptive responses resulting from past or present competition, an alternative hypothesis is that these different strategies may reflect distinct and independent evolutionary histories without involving competition. Further comparative studies between racers and ratsnakes (Carfagno and Weatherhead 2006, 2008) are required to establish to what extent *H. viridiflavus* and *Z. longissimus* illustrate two contrasted adaptive syndromes (Nevo et al. 1998).

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