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Thermal benefits of artificial shelters in snakes: A radiotelemetric study of two sympatric colubrids

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ABSTRACT

1. In temperate climates, reptiles face constraining thermal conditions, and thus tradeoff predator avoidance against thermoregulatory requirements.
2. Selection of high thermal quality shelters can entail substantial fitness gains by enabling the selection of optimal body temperatures for physiological performance (e.g., high body temperature for digestion), whilst minimizing predation risk.
3. We studied two species of sympatric colubrid snakes (*Hierophis viridiflavus* and *Zamenis longissimus*) with contrasted thermal preferences in a forested area, offering a diversity of natural and anthropogenic shelters. Individuals were monitored using radiotelemetry. Physical models were used to assess operative environmental temperature.
4. The exploitation of particular artificial shelters, both during diurnal and nocturnal phases, entailed important thermal benefits to the snakes.
5. As predicted, the most thermophilic species, *H. viridiflavus*, used hot shelters more often than the less thermophilic species *Z. longissimus*.

1. Introduction

Predation is a major selective pressure acting on behaviour (Lima and Dill, 1990). Predation risk can be reduced by selecting refuges that offer an effective protection (Bauwens et al., 1999; Cooper et al., 1999; Goldsbrough et al., 2004; Cooper and Wilson, 2008). In reptiles, microhabitat selection is driven mainly by thermal requirements because of the tight link between variations in body temperature and performance in ectotherms (Stevenson et al., 1985; Huey and Kingsolver, 1989; Hertz et al., 1993; Grover, 1996; Blouin-Demers and Weatherhead, 2002; Row and Blouin-Demers, 2006a). Optimal use of shelters by reptiles thus implies maximizing predator avoidance, whilst minimizing thermal costs (Cooper, 1998; Martin and Lopez, 1999; Downes, 2001). The ability of individuals to select shelters that are both safe and thermally suitable entails clear fitness gains (Milne and Bull, 2000; Sabo, 2003; Webb and Whiting, 2005; Goldsbrough et al., 2006). Under hot desert climates, refuges must confer significant protection against high temperatures (Melville and Schulte, 2001; Kerr et al., 2003) and evaporative water loss (DeNardo et al., 2004; Davis et al., 2008). In temperate climates, however, since an ambient temperature is generally limiting, natural shelters are usually too cool, and thus provide lower thermal conditions than are optimal for performance (Martin, 2001).

Anthropogenic structures have been shown to provide high quality shelters for reptiles, and such structures can be used successfully for conservation (Webb and Shine, 2000; Arida and Bull, 2008; Grillet et al., 2010). Artificial refuge use may be particularly beneficial in altered and urbanized environments, where human activities have direct negative impacts on reptile populations (Rosen and Lowe, 1994; Bonnet et al., 1999; Whitaker and Shine, 2000; Row et al., 2007) and indirect impacts through habitat fragmentation and degradation (Shine et al., 1998; Blouin-Demers and Weatherhead, 2001; Driscoll, 2004; Butler et al., 2005). In cool climates, artificial shelters should provide both efficient protection against predators and optimal thermal conditions by offering warm and stable temperatures within thermally fluctuating environments. Thus, structures with high thermal inertia that accumulate solar radiation during the day and give out heat during the night may be most favourable (Huey et al., 1989).

A radiotelemetric survey conducted on two sympatric colubrid species of snakes, in a natural landscape, (Lelièvre et al., 2010) revealed that snakes exploit artificial refuges regularly. Here we

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used thermal data obtained from free ranging snakes to address the following questions:

(1) Do artificial structures with significant thermal inertia provide better thermoregulatory opportunities than natural retreat-sites?
(2) To what extent do *Hierophis viridiflavus* and *Zamenis longissimus* use artificial shelters?
(3) What are the physiological benefits associated with artificial refuge exploitation?

We expected that exploitation of high thermal quality shelters should be particularly common in the thermophilic species (*H. viridiflavus*), because it would gain higher performance benefits. To assess this expectation, we quantified artificial refuge use by both species and measured temperature in snakes and in various shelters. Then, we estimated the performance gain accrued through use of natural *versus* artificial refuges by converting the body temperatures experienced in the two types of refuges to food transit time, a proxy of energy acquisition (Lelièvre et al., 2010).

2. Materials and methods

2.1. Study site and study animals

We conducted field surveys at the Centre d'Études Biologiques de Chizé in western France (46°07′ N; 00°25′ O), between 2006 and 2008, during the snake activity season (from May to September). Climatic conditions are temperate oceanic with annual precipitation between 800 and 1000 mm, annual mean temperature of 12 °C, and an average of 2000 h of sunshine per year. The study site was a 2600-ha integral biological reserve (RBI) managed by the Office National des Forêts and dominated by deciduous trees (*Fagus*, *Quercus*, *Carpinus*, *Acer*), regeneration areas characterized by scrubby species (*Rubus*, *Clematis*), and grasslands. We emphasize that natural refuges are very common in our study site because heterogeneous scrublands represent almost 60% of total surface area, and we observed numerous burrows associated with small mammal abundance in such habitats. In turn, anthropogenic infrastructures that could constitute shelters for snakes are relatively scarce in the study area and consist mainly of 55 km of narrow asphalt roads (roads may provide shelters, where snakes can gain access underneath; noted as under road in this paper), 3 barns, 3 small concrete buildings, 750 concrete boards used to attract snakes (Bonnet et al., 1999), and 3 artificial egg-laying sites built by stacking stones around peat and covering the pile with plastic tarpaulin (Shine and Bonnet, 2009). Physical characteristics of artificial shelters available to snakes are summarized in Table 1. Vehicle access and speed are limited in the reserve and collision risk is therefore not significant for snakes (Shine and Bonnet, 2009).

European whip snakes *Hierophis viridiflavus* and Aesculapian snakes *Zamenis longissimus* are medio-European oviparous colubrids. Both species are mainly diurnal during the active season at our study site (Naulleau, 1984). *H. viridiflavus* is a typical racer according to its morphological (slender body, long tail, large eyes), behavioural (fast moving, diurnal, terrestrial), and ecological characteristics (high levels of activity and exposure), whereas *Z. longissimus* shows strong morphological and behavioural similarities (constricting abilities, semi-arboreal, highly secretive) with rat snakes. These two species differ markedly in their range of preferred body temperature (T_{set}): *H. viridiflavus* is a thermophilic snake (T_{set} 27.5 – 31 °C), whereas *Z. longissimus* prefers cooler temperature (T_{set} 21.5 – 25.5 °C; Lelièvre et al., 2010).

2.2. Field surveys

Snakes were captured under concrete boards placed throughout the study area. Surveys were conducted between May and September in 2007 and 2008 on 59 individuals (30 *Z. longissimus*, 29 *H. viridiflavus*) that were monitored via radio-telemetry for 20–116 days. A temperature data logger (miniaturized 8 kb *iButton thermochron DS1922, Dallas Semiconductor, Dallas, USA*; see Robert and Thompson (2003) for details on miniaturization) and a radio-transmitter (*R1650, Advanced Telemetry Systems, Isanti, USA*) sterilized in diluted benzalkonium chloride were surgically implanted in the abdominal cavity of the snakes under isoflurane anaesthesia (see Reinert and Cundall (1982); Whitaker and Shine (2002); Whitaker and Shine (2003) for details). Total mass of logger and transmitter represented at most 2.2% of snake body mass. We kept snakes under observation for six days and then released them at their exact point of capture.

Snakes were located every 48 h during the day from May until September. We systematically changed relocation order to avoid sampling the same individual at the same time of day every day. Upon locating a snake, we recorded its precise position using GPS (*eTrex, Garmin, Olathe, USA*), its posture, and its behaviour (concealed, underground, under concrete board, basking, moving). We only kept locations, where snakes were concealed for analysis.

2.3. Artificial refuge availability

To estimate the extent of artificial refuge use in relation to their availability, we quantified the availability of the different types of artificial refuges used by snakes within the home range of each individual. Home ranges were calculated with 95% Minimum Convex Polygons (Hayne, 1949; Powell, 2000; Row and Blouin-Demers, 2006b) using the Hawth extension in ArcGIS 9.2 (ESRI, Redlands, CA). Then, we calculated the number of artificial refuges in the home range when refuges were quantifiable

Table 1
Broad characteristics of the potential artificial refuges used by the snakes in the forest of Chizé. Concrete boards and artificial laying sites were setup specifically for snakes; by contrast, the other items were not. Radio-tracking showed that all of them are regularly used by snakes.

Type of refuge	Description	Dimension	Thickness	Surface colour	Thermal inertia	Proportion of total surface area (%)
Under road	Cavity or burrow under asphalt roads	Width 5 m total 55 km	25 cm	Black	High	1.05
Concrete board	Undulated board used for roof construction	L120cm × w90 cm	4 mm	Ligth grey	Low	0.003
Artificial egg-laying site	Rock walls filled with soil and compost, covered with plastic tarpaulin	4 m × 4 m	1.2 m	Dark grey	High	< 0.0001
Covered wood stack	Stacking wood covered with plastic tarpaulin	L6 m × w0.5 m	2.5 m	Dark grey	Medium	< 0.0001
Barn	Metallic barns	L15 m × w8 m	4 m	Grey	High	< 0.0001

(concrete boards, laying sites, barns, wood stacks) or the percent of total home range area refuges represented if count was not possible (under roads).

2.4. Thermal quality of refuges and thermoregulation

We simultaneously measured body temperature of the snakes (T_b) and, using 20 physical models, operative environmental temperatures (T_e) in the various natural and artificial microhabitats available to the snakes (Bakken, 1992). We measured T_b in 30 *H. viridiflavus* (21 males, 9 females SVL=89.5 ± 7.3 cm; BM=234.1 ± 64.9 g) and 27 *Z. longissimus* (18 males, 9 females; SVL=95.4 ± 8.4; BM=249.3 ± 62.1 g) every 30 min for 4–103 days (mean=42 d). We ensured the realism of our physical models by calibrating them against two fresh snake carcasses (correlation coefficients=0.95 and 0.97). We placed the models in each of five habitats: on the ground in forest (N=4), on the ground under scrubs (N=3), in an underground natural retreat (N=3), on the ground in the open (N=4), inside artificial egg-laying sites (N=1), and under concrete boards (N=5). We were not able to measure T_e in all the artificial microhabitats selected by snakes (under roads, barns, wood stacks) during the radio-telemetry study. We sampled these microhabitats subsequently using the same methodology.

Each day was divided in daytime (8:00–18:00 h) and nighttime (18:00–8:00 h). We measured thermal quality of each habitat by the mean deviation of T_e from T_{set} (Hertz et al., 1993), the daily duration when T_e was above the lower bound of T_{set} ($T_{set\ low}$), and the daily duration when T_e was within the T_{set} of each species in each habitat. Because snakes were only located every two days, telemetry was probably insufficient to quantify the actual exploitation of artificial shelters. Therefore, we used T_b profiles to estimate the proportion of snakes using artificial shelters offering hotter conditions than the natural shelters, in which we measured T_e. This method was appropriate for artificial refuges with thermal conditions that clearly differ from those of surrounding habitats (see Section 3), enabling us to identify habitat use by the snakes (Davis et al., 2008). Daytime and nighttime snake thermal profiles were classified according to the duration for which T_b was above the maximal T_e measured with physical models ($T_{e\ max}$): $T_b > T_{e\ max}$ for less than 1 h, $T_b > T_{e\ max}$ between 1 and 5 h, and $T_b > T_{e\ max}$ for more than 5 h.

2.5. Digestion speed estimates

Thermal reaction norms for transit time have been measured in both species (Lelièvre et al., 2010). We used equations predicting digestion speed based on body temperature. Snakes consistently regurgitate their meals at 10 °C (Naulleau, 1983; Stevenson et al., 1985; Hailey and Davies, 1987; Tsai et al., 2008). We fixed the lower thermal limit at 15 °C for both species, as it corresponds to the lowest experimental temperature that enables complete digestion (Lelièvre et al., 2010). Then, we randomly sampled 10,000 T_b from individuals of each species exploiting artificial refuges *versus* other individuals observed in natural refuges. Random samples were bootstrapped 100 times and mean sample sizes (± SD) were calculated for 1 °C intervals. Applying the thermal performance equations to those temperatures, we obtained distributions of performance that would be achieved by snakes in artificial and in natural refuges.

2.6. Statistical analyses

All statistical tests were performed in R software (R Development Core Team, 2007). We used generalized linear models (GLM) to test for the effects of species and shelter type on snake T_b. We used χ^2 tests to compare distributions and estimate the performance gain accrued through thermoregulation. Means are provided ± 1SE. We accepted significance at an alpha level of 0.05.

3. Results

3.1. Artificial shelter use

All potential artificial shelters were not always available within the home ranges of the monitored snakes. Concrete boards were available within the home range of all individuals (from 1 to 71 boards; accounting for 0.15 ± 0.03% of the home range by area). The home ranges of 85% of individuals (N=50) contained roads, which accounted for 7.40 ± 1.48% of the total home range area in those cases. Barns were available for 22% of individuals (N=13; accounting for 4.26 ± 2.04% of the home range), and artificial egg-laying sites were available for 20% of individuals (N=12; 0.06 ± 0.02% of the home range). A covered wood stack was available for only one individual. On an average, the area represented by potential artificial refuges relative to natural habitats was small (Table 1).

During our telemetry survey, we located 15 *Z. longissimus* and 17 *H. viridiflavus* in artificial refuges for a total of 151 times (Table 2). We estimated that individuals exhibited T_b within or close to the range of T_e available in natural shelters for at least 75% of thermal profiles both at night and during daytime (Fig. 1). In both species, T_b exceeded $T_{e\ max}$ more frequently during the night. Thermal profiles with T_b exceeding $T_{e\,max}$ occurred more frequently in *H. viridiflavus* than in *Z. longissimus* both at night and during the day (18.1 *vs.* 6.3% of daytime profiles; 25.9 *vs.* 14.8% of nighttime profiles; Fig. 1).

3.2. Thermal quality of natural and artificial shelters

During the day, shelters were always thermally constraining for snakes and time available above the lower boundary of T_{set}

Table 2
Observations of snakes exploiting artificial refuges during a radio-telemetry survey in 2007–2008 and associated deviation of body temperature (calculated as T_b of snakes exploiting artificial refuges minus T_b of snakes exploiting natural refuges for simultaneous thermal measurements). Deviations are given ± SE.

Refuge type	Number of locations (%)	Number of individuals (%)	T_b deviation from mean (°C)	
			Night	Day
Under road	26 (2.0)	9 (15.3)	4.43 ± 0.18	−0.77 ± 0.26
Concrete board	88 (6.9)	32 (54.2)	−0.03 ± 0.08	−0.09 ± 0.11
Artificial egg-laying site	23 (1.8)	10 (16.9)	1.39 ± 0.14	1.35 ± 0.17
Covered wood stack	1 (0.1)	1 (1.7)	4.86 ± 0.49	3.34 ± 0.22
Barn	13 (1.0)	3 (5.1)	−0.72 ± 0.13	−0.76 ± 0.19
Total artificial refuges	N=151	N=32		
Total observations	N=1283	N=59		

($T_{set\ low}$) was much shorter in shelters compared to direct exposure (Table 3). Importantly, deviation between thermal conditions in refuge and T_{set} was much higher for *H. viridiflavus* than for *Z. longissimus*. During hot days when $T_{e\ max}$ in the open exceeded 40 °C, retreats under roads had the best thermal quality for both species, while artificial egg-laying sites were also close to $T_{set\ low}$ for *Z. longissimus* (Table 3). Concrete boards exhibited high thermal quality and weakly reduced time above $T_{set\ low}$ compared to direct exposure (30% for *H. viridiflavus* and 18% for *Z. longissimus*; Table 3, Fig. 2). At night, retreats under roads had the highest thermal quality for both species based on d_e, time above $T_{set\ low}$, and time within T_{set}.

3.3. Thermoregulation in artificial shelters

Thermal profiles exhibited by snakes exploiting artificial refuges differed from those of other individuals. Deviation of snake T_b located in artificial refuges from T_b of other individuals did not differ significantly between species (GLM, $F_{1,3440}=0.11$, $P=0.74$), but strongly differed between shelter types (GLM, $F_{4,3494}=90.562$, $P=0.0001$) and period of the day (GLM, $F_{1,3494}=45.218$, $P<0.0001$) with a significant interaction between period of the day and shelter type (GLM, $F_{4,3494}=105.69$, $P<0.0001$). Snakes sheltering under roads were able to maintain high and stable T_b, irrespective of ambient temperatures (Fig. 3). At night, retreats under roads and wood stacks provided the greatest thermal benefits to the snakes, while concrete boards and barns were less thermally beneficial (Fig. 4). During the day, only wood stacks and artificial egg-laying sites offered thermal gain to snakes (Fig. 4).

3.4. Digestion speed improvement

Distributions of randomly sampled T_b of snakes exploiting artificial refuges were significantly different from the distributions generated from the T_b of other snakes (χ^2 tests, $P<0.0001$; Table 4, Fig. 5). Converting T_b to transit time with the equations of the thermal reaction norm indicated that using artificial shelters improved transit time in all cases, but particularly at night in *H. viridiflavus* (Table 4). In *H. viridiflavus*, transit time decreased from 11.33 ± 0.38 days to 8.49 ± 0.34 days when selecting artificial refuges (improvement of 25.1%) at night, but only from 11.45 ± 0.36 days to 10.96 ± 0.34 days in *Z. longissimus* (improvement of 4.4%).

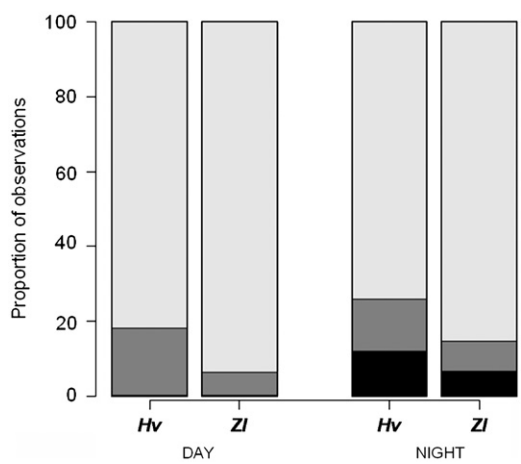

Fig. 1. Proportion of individual thermal profiles with body temperature (T_b) above the maximum operative temperature ($T_{e\ max}$) measured with physical models in *Z. longissimus* (*Zl*) and *H. viridiflavus* (*Hv*) during daytime and nighttime. T_b and T_e are simultaneously measured every 30 min. Light grey boxes represent periods when snake body temperature (T_b) is above $T_{e\ max}$ for less than 1 h. Dark grey boxes represent periods when T_b is above $T_{e\ max}$ from 1 to 5 h. Black boxes represent periods when T_b is above $T_{e\ max}$ for more than 5 h.

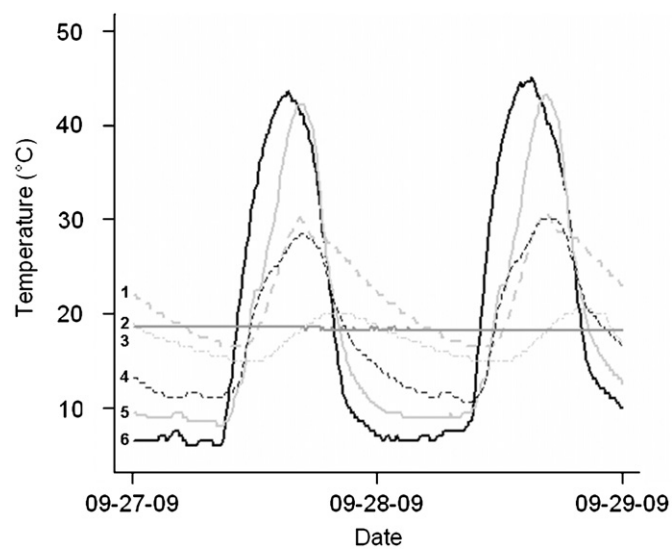

Fig. 2. Mean operative environmental temperatures (T_e) in various shelter types during two hot days. Temperatures were measured with physical models placed in retreats under roads (1; $N=4$), inside artificial egg-laying sites (2; $N=2$), underground (3; $N=2$), inside a barn (4; $N=2$), under concrete boards (5; $N=3$), and in open fields (6; $N=3$). Note that retreats under roads here monitored showed more thermal variations than those used by snakes (see Fig. 2).

Table 3
Thermal quality of natural and artificial refuges exploited by *H. viridiflavus* and *Z. longissimus* compared to outside temperature (open field) during daytime (8:00–18:00) and nighttime (18:00–8:00). Thermal measurements were taken during four hot days (maximal temperature in open field > 40 °C) between 09–26–2009 and 10–06–2009. d_e: mean of thermal deviation from the range of preferred temperatures (T_{set}). $T_{set\ low}$: lower bound of T_{set}.

Habitat	*H. viridiflavus*						*Z. longissimus*					
	d_e (°C)		Time above $T_{set\ low}$ (h)		Time within T_{set} (h)		d_e (°C)		Time above $T_{set\ low}$ (h)		Time within T_{set} (h)	
	Day	Night	Day	Night	Day	Night	Day	Night	Day	Night	Day	Night
Open field	8.68	17.32	6.31	0.44	0.76	0.28	9.87	11.78	6.89	1.11	0.42	0.50
Burrow	11.28	9.46	0.00	0.00	0.00	0.00	5.28	3.46	0.00	0.00	0.00	0.00
Under road	6.89	7.27	1.29	0.55	1.29	0.55	2.96	2.35	4.38	5.04	2.40	3.75
Concrete board	8.54	13.89	4.50	0.57	0.79	0.47	7.80	8.50	5.69	1.58	1.00	0.76
AES	9.65	9.61	0.00	0.00	0.00	0.00	3.65	3.61	0.00	0.00	0.00	0.00
Barn	8.12	12.25	1.77	0.25	1.77	0.25	4.40	6.65	3.96	1.79	1.73	1.40

AES: artificial egg-laying site.

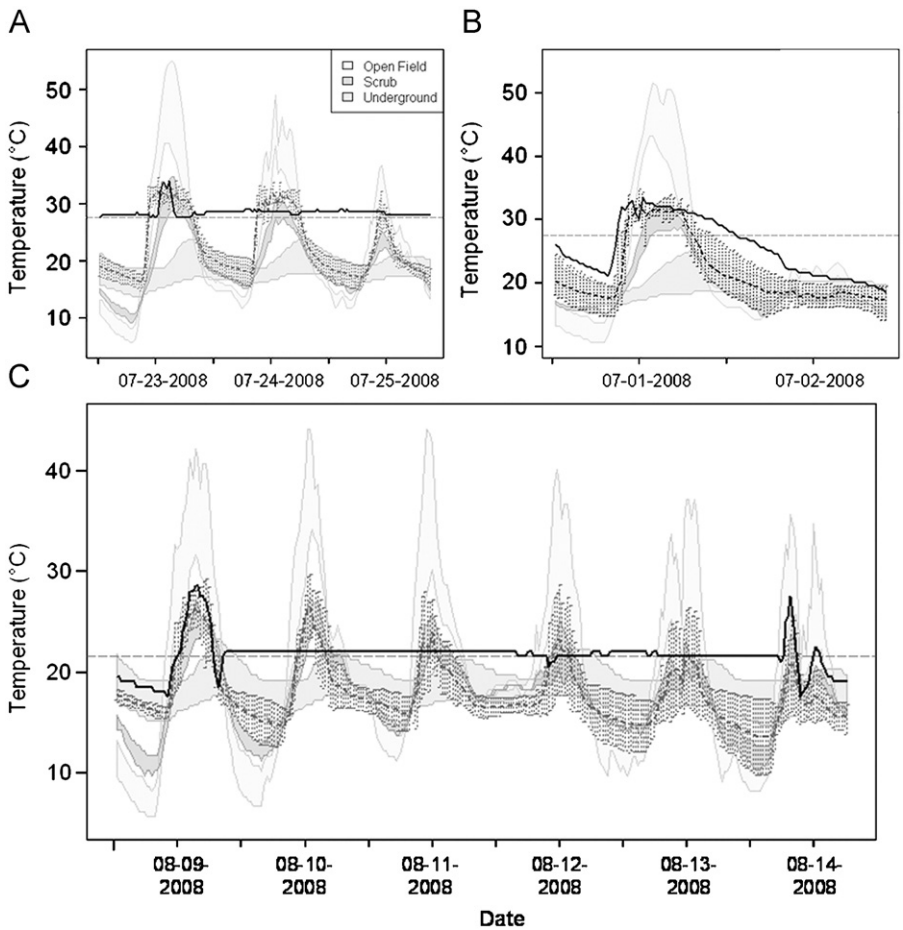

Fig. 3. Body temperature (T_b) of snakes using artificial shelters *versus* natural habitats (open field, scrub, and underground). Dark bold line represents snake T_b and bold dashed line represents mean T_b with standard error of other radiotracked individuals. Thin dashed line represents the lower bound of the range of preferred body temperature ($T_{set\ low}$). (A) *H. viridiflavus* under road; (B) *H. viridiflavus* under a covered wood stack; (C) *Z. longissimus* under road.

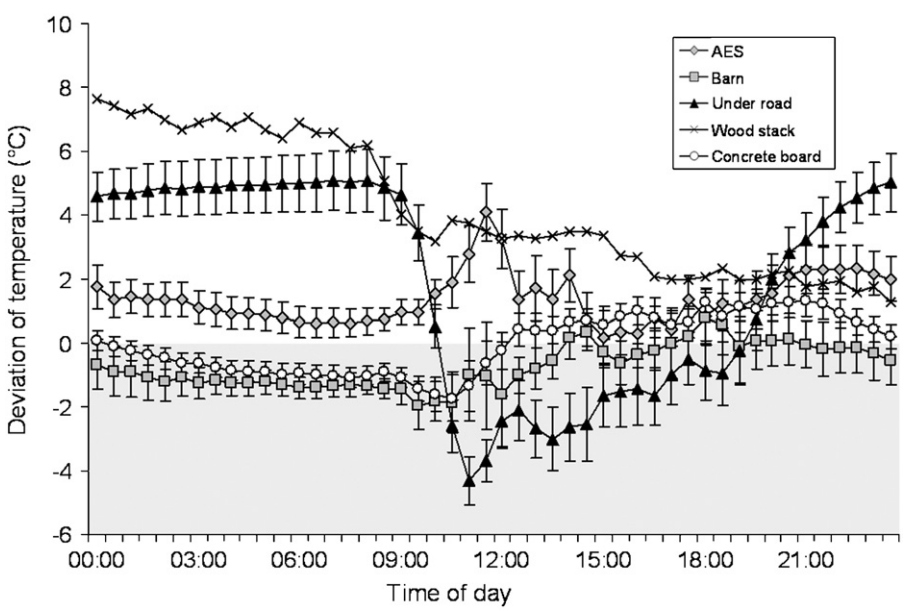

Fig. 4. Mean body temperature deviation (d_b) between snakes using artificial shelters and other individuals (calculated as T_b of snakes exploiting artificial refuges minus T_b of snakes exploiting natural refuges for simultaneous thermal measurements). Shelter use is thermally beneficial when $d_b > 0$, but detrimental when $d_b < 0$ (indicated by the grey box). Both species are pooled. AES: artificial egg-laying site (see description in Table 1).

4. Discussion

Snakes are generally highly secretive animals that spend a lot of time in shelters (Huey et al., 1989; Whitaker and Shine, 2003; Webb et al. 2004). Surprisingly, however, only a few studies have focused on refuge use in snakes (Huey et al., 1989; Webb and Shine, 1998; Whitaker and Shine, 2003; Webb et al., 2004; Webb and Whiting, 2005; Bonnet and Brischoux, 2008; Bonnet et al., 2009). We found that both *H. viridiflavus* and *Z. longissimus* used all the anthropogenic structures present in the integral biological reserve as refuges (roads, barns, concrete boards, etc. see Table 2). Despite the low availability of artificial shelters at the study site, at least in terms of area compared to natural habitats ($<1\%$; Table 1), nearly 12% of relocations were in such refuges and estimates from the body temperature profiles indicated a higher exploitation of these microhabitats particularly at night ($\sim$20% in *Z. longissimus* and $\sim$28% in *H. viridiflavus*; Fig. 1). In natural conditions, snakes avoid critically low temperatures during the night by selecting underground retreats, such as burrows, rocks, or natural cavities (Huey et al., 1989). Our study site lacks large rocks that could provide thermally suitable retreats, and we showed that some artificial refuges had better nocturnal thermal conditions than available natural shelters. Roads and covered wood stacks notably allowed snakes to maintain higher body temperatures at night than in natural shelters (Figs. 3 and 4). This is likely due to significant heat accumulation during the day in those refuges, which possess important thermal inertia; road surface at night is used by snakes and other ectotherms precisely for such thermal inertia (Klauber, 1939; Rosen and Lowe, 1994). During the day, most shelters offered thermal conditions that were too cool compared to what would be achieved via basking, except under concrete boards deployed in the field to catch snakes (Shine and Bonnet, 2009). Thermal profiles of physical models placed under boards were very similar to those of models directly exposed to solar radiation (Fig. 2). Thus, concrete boards allow body temperatures to be reached that are normally achieved through basking, while still being protected from avian predators. Artificial egg-laying sites showed stable, but relatively cool conditions, especially at the bottom. Snakes exploiting artificial nesting sites during daytime, however, exhibited higher T_b than other snakes (Fig. 4), probably because of a marked thermal gradient available from the surface to the bottom, enabling the snakes to select their preferred body temperature (Shine and Bonnet, 2009).

Overall, our results showed that exploitation of anthropogenic refuges may provide substantial benefits to snakes. Fitness benefits should be particularly noticeable in species with a strong dependence on high body temperature for optimal performance.

Table 4
Results of statistical tests (χ^2) for difference in distribution of body temperature (T_b) of snakes exploiting artificial refuges *versus* other snakes using natural refuges and associated improvement in transit time. *Hv* for *H. viridiflavus*; *Zl* for *Z. longissimus*.

		Distributions comparison			Transit time improvement (%)
		χ^2	*df*	*P*	
Hv	Night	12,285.08	26	<0.0001	25.1
	Day	7305.82	26	<0.0001	8.6
Zl	Night	4817.31	26	<0.0001	4.4
	Day	4304.69	26	<0.0001	1.9

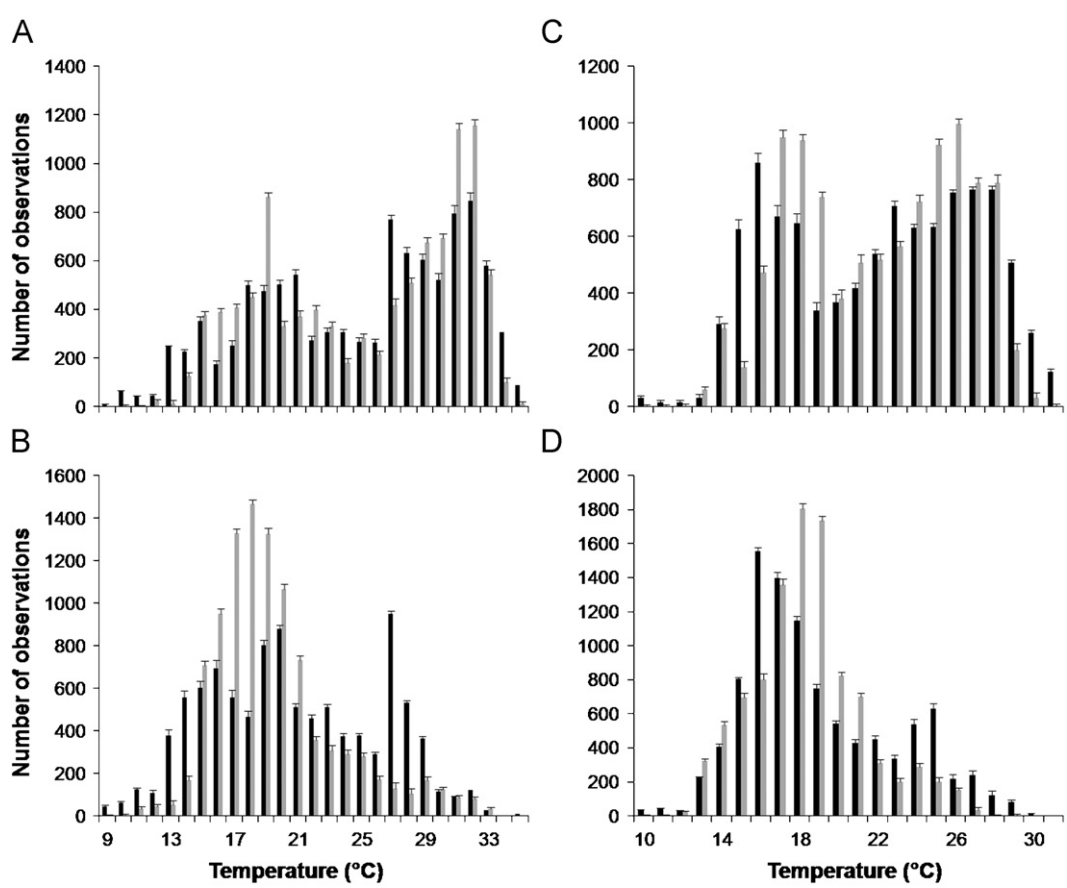

Fig. 5. Frequency distributions of body temperature (T_b) for 10,000 observations randomly sampled in individuals using artificial shelters (black bars) and individuals using natural shelters (grey bars). Observations for *H. viridiflavus* for daytime (A) and nighttime (B). Observations for *Z. longissimus* for daytime (C) and nighttime (D).

Here, we observed that the most thermophilic species, *H. viridiflavus* exploited artificial refuges to a greater extent than *Z. longissimus*. In *H. viridiflavus*, shifting from heliothermic basking to a thigmothermic strategy when concrete boards are available appears beneficial, because it reduces predation risk significantly without substantial thermal costs. Artificial structures also allow snakes to improve nocturnal thermoregulation, thus significantly decreasing transit time. Use of hot refuges during the night can be energetically costly, however. Standard metabolic rate (SMR) measurements conducted in these species (Lelièvre et al., 2010) showed that energy expenditure was more than twice as high at 25 °C ($\sim$0.050 mL h^{-1} g^{-1}) than at 15 °C ($\sim$0.020 mL h^{-1} g^{-1}). Therefore, in addition to species differences, use of refuges is likely dependent on specific physiological needs associated with heat demanding processes, such as skin shedding, digestion, or reproduction. Unfortunately, individual physiological states were not assessed during our study, because it required snakes to be caught regularly which is likely to disturb normal behaviour. Further studies are thus required to explore the links between physiological requirements and refuge use.

Among artificial shelters used by *Z. longissimus* and *H. viridiflavus*, retreats under roads constitute the "nearly perfect refuge" as they display very stable and warm temperatures by accumulating sun radiation during the day, and then radiating conductive heat at night. In addition, during dry periods, humidity under roads is probably higher than at the surface, and this could therefore facilitate skin shedding or egg incubation. The use of asphalt roads as laying sites by the two snake species monitored has been observed in the forest of Chizé (X. Bonnet, Pers. Obs.), and elsewhere (Guiller, 2009). Nevertheless, net benefit of exploiting roads as shelter or laying sites depends on vehicular traffic because collision risks may outweigh thermal benefits in other situations (Bonnet et al., 1999; Row et al., 2007). We also noted that some snakes exploited anthropogenic structures characterized by low thermal quality such as barns (Table 2; Figs. 3 and 4). Artificial refuges may offer other benefits, however, such as providing foraging opportunities and/or favourable hygrometric conditions for skin shedding (Blouin-Demers and Weatherhead, 2001).

In conclusion, our results have important implications for snake management. Anthropogenic development is usually detrimental to snake populations because it induces habitat fragmentation and direct mortality (Bonnet et al., 1999; Row et al., 2007). Some snakes, however, are able to exploit much altered environments (Butler et al., 2005). Here, we showed that even in a well-protected area, snakes used all the anthropogenic refuges available regularly, despite the small area they occupy; probably because snakes obtained important thermal benefits combined with predation avoidance. Therefore, management of snake populations should consider refuge availability (Webb and Shine, 2000; Arida and Bull, 2008) and entail tests of the efficacy of artificial structures as refuges depending on their microclimatic properties (Croak et al., 2010). In this context, a better understanding of refuge use remains a key aspect of snake ecology and management. Further studies are required to explore how snakes use their shelters in relation to individual parameters (physiological status, home-range familiarity, individual strategies, etc.). In a practical conservation context, our empirical results suggest that it can be beneficial to retain artificial refuges within the landscape. Indeed, in the common perception of pristine habitats, sealed roads, concrete boards, or buildings in ruin are usually viewed as unnatural eyesores. Therefore, habitat restoration often includes removing such infrastructure from nature reserves even though they can act as refuges for a variety of animals, including many reptiles (Croak et al., 2010). More generally, many habitats suitable for snakes are considered "rubbish tips" by managers, but allocating efforts to clean habitats might not always be wise for conservation. Instead, examining their potential as refuges is important for conservation, especially in the light of recent evidence on the general decline of snakes (Mullin and Seigel, 2009; Reading et al., 2010).

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