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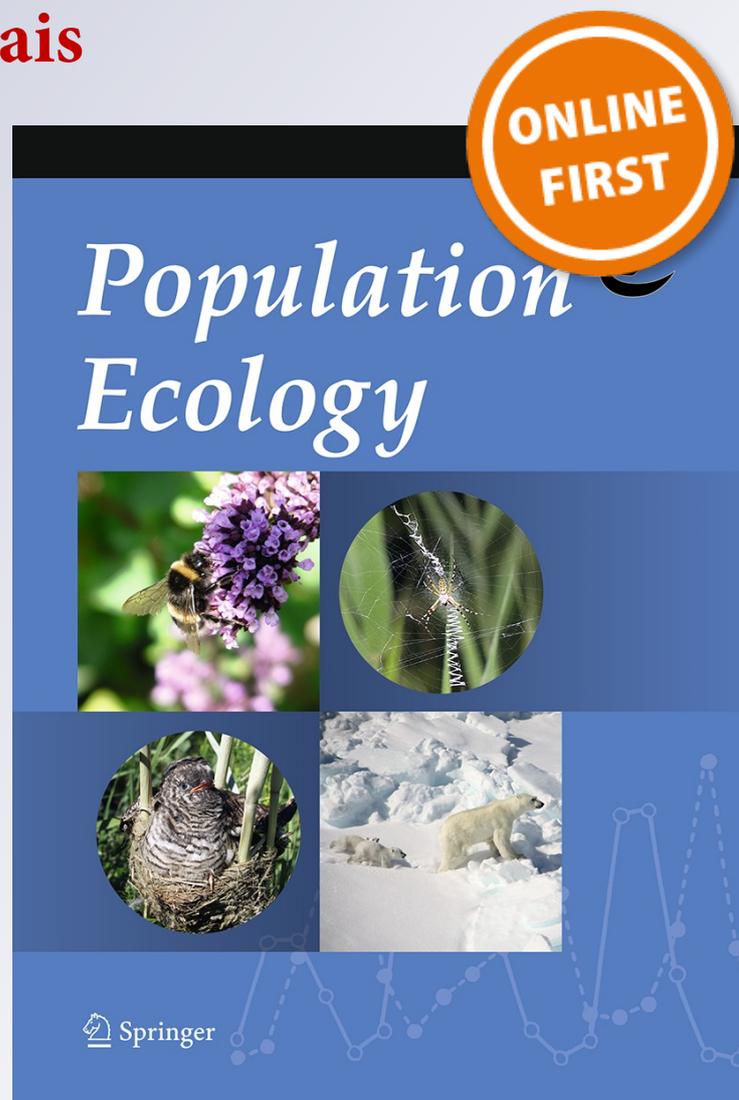
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The thermoregulatory strategy of two sympatric colubrid snakes affects their demography

Hervé Lelièvre · Philippe Rivalan · Virginie Delmas ·
Jean-Marie Ballouard · Xavier Bonnet ·
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Abstract Population dynamics of terrestrial vertebrates are affected by climatic fluctuations, notably in ectotherms. An understanding of the interaction between physiology and demographic processes is necessary to predict the impacts of climate change. Reptiles are particularly sensitive to temperature, but only a few studies have explored the relationship between thermoregulatory strategy and demography in these animals. Using 12 years of mark-recapture data on two sympatric colubrid snakes (*Hierophis viridiflavus* and *Zamenis longissimus*), we tested whether demographic parameters are influenced by contrasted thermoregulatory strategies. The thermophilic and conspicuous species (*H. viridiflavus*) grew faster than the thermoconforming and secretive species (*Z. longissimus*), and this difference was most pronounced in open habitats, suggesting that the metabolic benefits associated with high thermal preferences depend on environmental factors at small spatial scales. Survival varied annually in both species, but was not lower in *H. viridiflavus* despite a higher degree of exposure. In *Z. longissimus*, survival was negatively affected by low temperatures during the active season, possibly underlying an exposure trade-off.

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Introduction

Climatic conditions affect population dynamics by influencing a variety of ecological processes (Stenseth et al. 2002). The effects of seasonality, El Niño–Southern Oscillation (ENSO), and global warming on demography are well documented in a broad range of species (Jaksic et al. 1997; Sæther et al. 2000; Lima et al. 2003; McDonald et al. 2004). Over the past decades, most studies of demographic responses to climate have focused on endothermic mammals and birds. This is surprising, however, because ectotherms are particularly sensitive to climatic variations (Madsen and Shine 2000; Lourdais et al. 2004; Chamaillé-Jammes et al. 2006; Marquis et al. 2008; Le Galliard et al. 2010; Sinervo et al. 2010). Indeed, in ectotherms body temperature depends on environmental temperature and influences physiological performance (Huey and Stevenson 1979), metabolism (Secor and Nagy 1994; Dubois et al. 2008), locomotion (Bennett 1980; Stevenson et al. 1985; Ojanguren and Braña 2000), immune function (Mondal and Rai 2001), foraging ability (Ayers and Shine 1997; Carrière and Boivin 1997), and growth (Kingsolver and Woods 1997). Therefore, we should expect a particularly strong effect of climate on demography in ectotherms (Kearney and Porter 2004; Helmuth et al. 2005; Deutsch et al. 2008; Le Galliard et al. 2012; Weatherhead et al. 2012).

In terrestrial reptiles, species subjected to similar environmental constraints nonetheless can diverge in thermoregulatory strategy (Belliure et al. 1996; Scheers and Van Damme 2002; Du et al. 2006). Under cool climates,

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thermoregulation primarily involves direct exposure to solar radiation (Huey and Slatkin 1976; Blouin-Demers and Nadeau 2005). Because basking behaviour is associated with increased exposure in open habitats, it may entail significant survival costs (Webb and Whiting 2005). On the other hand, a thermophilic species should show enhanced performance and obtain fitness benefits through faster growth and earlier sexual maturity. Because of coadaptation between traits (Angilletta et al. 2006), species with distinct thermoregulatory strategies can exhibit divergent energy budgets (Secor and Nagy 1994), foraging modes (Belliure et al. 1996), habitat use (Du et al. 2006; Carfagno and Weatherhead 2008), and degrees of exposure (Daly et al. 2008). Therefore, we should expect divergent thermoregulatory strategies to be associated with different demographic characteristics (growth, survival) and sensitivity to climatic conditions. Yet, this issue has heretofore not been investigated.

Detailed information on the effect of thermal ecology on demography is not currently available for snakes; yet lizard studies (*Sceloporus* sp.*)* revealed complex links between thermal environment, population dynamics, and many life history traits (Angilletta et al. 2002). Although conducting long-term demographic studies on a suite of sympatric and syntopic species differing in their thermal ecologies would afford the most inferential power, this may not prove logistically feasible. Therefore, species pair comparisons provide an initial step. To be meaningful, a comparison of two species must rely on the analysis of a set of life history traits that allow a priori predictions on the direction of the trait considered (Garland and Adolph 1994). For instance, two species comparisons have been used successfully in sympatric snakes with contrasted foraging modes (a sit-and-wait and an active forager) to compare activity, growth, maturity, survival, and energy budgets (Secor and Nagy 1994; Webb et al. 2003).

We studied two sympatric colubrid snakes, the European whip snake *Hierophis viridiflavus* (Lacépède, 1789; HV) and the Aesculapian snake *Zamenis longissimus* (Laurenti, 1768; ZL) to examine the consequences of thermoregulatory strategy on demography while minimizing the limitations inherent to two-species comparisons (Garland and Adolph 1994). Both species are morphologically and ecologically similar for several major traits (body size, diet, habitat, reproductive mode, and activity periods; Naulleau 1984; Lelièvre et al. 2012), and are also largely sympatric and syntopic (Luiselli and Capizzi 1997; Naulleau 1997a, b). However, they exhibit contrasted exposure strategies, thermal specialization and energy requirements (Lelièvre et al. 2010, 2011). HV is fast, active, and performs optimally at high temperatures whereas ZL is elusive and prefers cooler temperatures. The two species are so similar in aspects other than their thermal ecologies (see

"Methods") that we can confidently rule out many factors (e.g., food availability) as the source of variation in demography. We used mark-recapture data gathered over 12 years on syntopic populations of HV and ZL in Western France. We tested the hypothesis that the demography of ectotherms depends on their thermoregulatory and exposure strategies. More specifically, that species preferring high body temperatures should be characterized by fast life histories. We tested the following set of predictions:

1. Since physiological performances depend on body temperature, the thermophilic HV should grow faster than the thermoconforming ZL, particularly as juveniles because adults invest energy in reproduction;
2. Growth should be more dependent on environmental conditions (e.g., basking site availability) in HV because of higher energy requirements;
3. Because high thermal requirements imply basking, and thus higher risks of predation, HV should exhibit lower survival.

Methods

Study species and study site

Hierophis viridiflavus and *Zamenis longissimus* are medio-European sympatric colubrid snakes that frequently occur in syntopy (Naulleau 1997a, b; Rugiero et al. 2002). Both species have approximately equal body size ($\sim$130–150 cm) and are active foragers showing important overlap in their diets (mostly composed of small mammals; Naulleau 1984; Capizzi et al. 1995; Lelièvre et al. 2012). On the other hand, they diverge in thermoregulatory and exposure strategies. HV is a typical racer (Luiselli 2006) characterized by fast moving ability, high levels of activity and exposure, and elevated preferred body temperatures (T_{set} 27.5–31.0 °C; Lelièvre et al. 2010). Conversely, ZL is an elusive ratsnake (similar to *Elaphe*, *Pantherophis*, or *Ptyas* genera; Lenk et al. 2001), using closed microhabitats (Lelièvre et al. 2011), and selecting cooler temperatures (T_{set} 21.5–25.5 °C; Lelièvre et al. 2010). We have previously shown that both species differ in optimal temperatures for physiological performance and in the shape of their performance curves (Lelièvre et al. 2010). Energy requirements reflect contrasted thermal preference and are higher in the racer (Lelièvre et al. 2010).

Population monitoring was conducted at the Centre d'Études Biologiques de Chizé in Western France (46°07′N; 00°25′W; Fig. 1). The study site is a 2600-ha biological reserve managed by the Office National des Forêts. The forest is dominated by deciduous trees (*Fagus*, *Quercus*, *Carpinus*, *Acer*), regeneration areas characterized
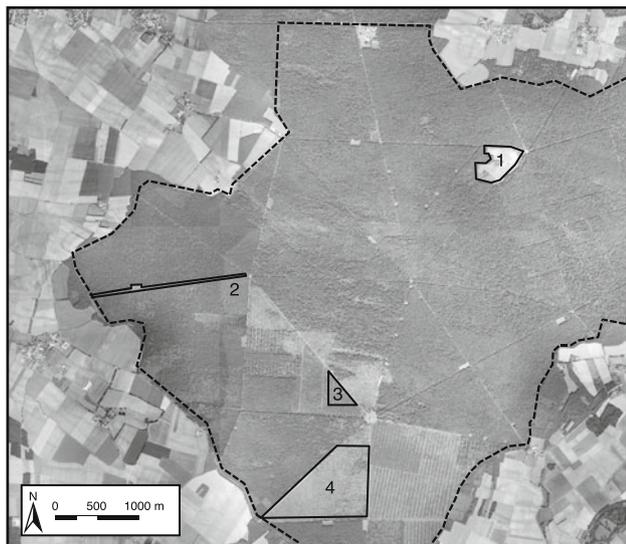
Fig. 1 Location of the four study sites at the Centre d'Études Biologiques de Chizé (Western France). *Area 1* is grassland. *Areas 2, 3*, and *4* are forest. *Dashed line* indicates the border of the biological reserve

by scrub species (*Rubus*, *Clematis*), and grasslands. Climatic conditions are temperate oceanic with annual precipitations between 800 and 1,000 mm, annual mean temperature of 12 °C, and an average of 2,000 h of sunshine per year.

Capture-mark-recapture

Snakes were captured during the active season (April–September) under undulated concrete boards (120 × 80 cm) disposed in four areas of the study site for this purpose (Bonnet et al. 1999; Shine and Bonnet 2009; Fig. 1). Importantly, these four areas are distant enough that individuals almost never move between them. Data were gathered on 1,608 snakes between 1997 and 2009 (844 ZL; 764 HV; Table 1). We recorded snout–vent length (SVL: from the tip of the snout to the cloacal scale) to the nearest 0.5 cm, body mass to the nearest 1 g in adults and to the nearest 0.1 g in small snakes (less than 100 g), and sex by eversion of the hemipenes and from tail shape. Each snake was individually and permanently identified by

burning ventral scales in unique combinations. Snakes were then released at their capture site as soon as possible.

Climatic data

Data were gathered from Météo-France station in Niort situated 20 km from the study site. Available variables were daily minimum and maximum temperatures, and daily precipitation between 1997 and 2009.

Growth

Growth in snakes is the increase in SVL over time. To limit the influence of measurement error, which can be substantial in snakes (Luiselli 2005), we restricted our analyses to long time intervals (>60 days) between captures. Negative values of growth were not removed because we assumed that positive measurement errors should be equally prevalent, but not identifiable (Blouin-Demers et al. 2002; Bonnet et al. 2002). As juvenile snakes show much lower capture rates than adults (Pike et al. 2008), we were unable to build robust Von Bertalanffy growth models. Instead, growth rate was expressed as the difference in body size (SVL in cm) between captures divided by the time elapsed in days. Overwintering (150 days per year) was deducted from growth intervals for captures not in the same active season because snakes are inactive and do not grow during this period. We used time between captures as a covariate in the model because it may influence error in growth rate if significant measurement error occurred. We also used SVL at first capture as a covariate because snake growth decreases with increasing body size (Blouin-Demers et al. 2002). In our study site, both species become sexually mature at a similar size (∼70 cm SVL, X. Bonnet, personal observation). We used the same criterion for males and females to separate juveniles from adults. We compared juvenile growth rates in two habitats: grassland (Area 1 in Fig. 1) and forest (Areas 2, 3, and 4 in Fig. 1).

Survival

We estimated local annual survival and recapture probabilities from 1997 to 2009 using the Cormack–Jolly–Seber

Table 1 Annual numbers of captures and recaptures of *Z. longissimus* (ZL) and *H. viridiflavus* (HV) at the Centre d'Études Biologiques de Chizé (Western France)

Species	State	1997	1998	1999	2000	2001	2002	2003	2004	2005	2006	2007	2008	2009
ZL	Capture	37	61	62	74	42	53	49	38	74	50	107	135	62
	Recapture	15	23	18	36	14	27	31	30	12	29	38	102	49
HV	Capture	39	38	54	38	19	50	57	50	102	76	77	105	59
	Recapture	11	20	15	20	6	23	29	34	43	67	93	145	74

Data were gathered before 1997, but only data from 1997 to 2009 were used for analyses

Fig. 2 Climatic data for the study area in Western France used as covariates in survival models for *Z. longissimus* and *H. viridiflavus* from 1997 to 2009. *Lines* show mean daily maximum temperatures during snake activity season (April–September) and the *histogram* shows cumulated rainfall during the same period. Data were obtained from Niort meteorological station (Météo France) situated approximately 20 km from the study area
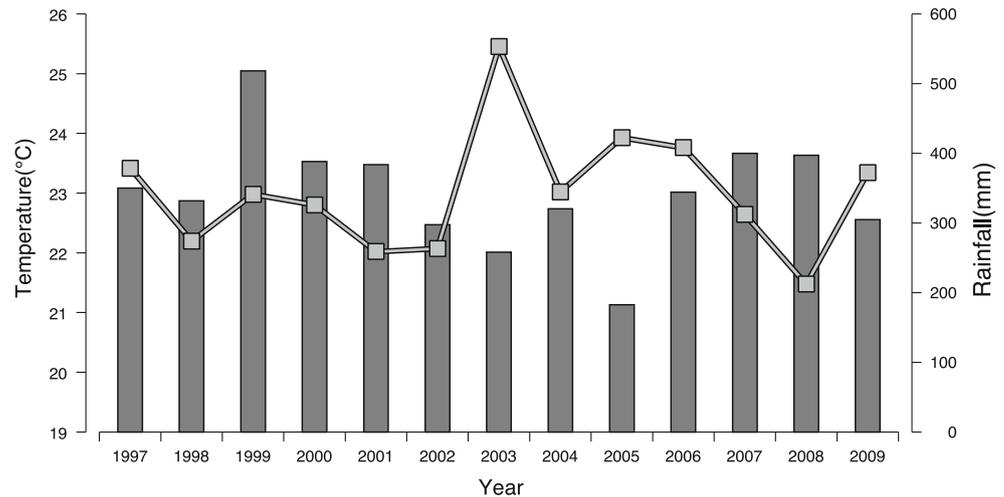
(CJS) model in program MARK 4.1 (White and Burnham 1999). Assumptions of capture-recapture modeling were tested by a χ^2 goodness-of-fit test (Pollock et al. 1990) using program U_CARE 2.2 (Choquet et al. 2009). The model adequately fitted the data ($\chi^2 = 68.73$; $df = 125$; $P = 0.99$) as we found evidence for neither trap dependence (Test2.CT: $P = 0.97$) nor transience (Test3.SR: $\chi^2 = 1.62$, $P = 0.10$).

A set of candidate models with various parameterizations for survival rate (φ) and capture probabilities (p) (i.e., time-dependent (t), constant over time (.), group dependent (g), group being sex or species) were then developed and we used Akaike's Information Criteria (AIC$_c$) to rank and select models (QAIC; Burnham and Anderson 2002). If models could not be classified from AIC$_c$ (Δ AIC$_c$ < 2), we performed model averaging (Buckland et al. 1997) using the AIC weight to recalculate an intermediate estimate (Burnham and Anderson 2002).

Model selection based on AIC$_c$ showed that capture probability was time-dependant and differed slightly between the sexes in HV (average $p = 47.1$ %, 95 % CI: 24.6–68.8, in males vs. 33.1 %, 95 % CI: 15.0–56.7, in females) and ZL (average $p = 48.3$ %, 95 % CI: 28.8–76.6, in males vs. 25.8 %, 95 % CI: 16.3–59.8, in females). Because we captured snakes under shelter, capture probability cannot be used to estimate level of exposure.

We tested for the influence of climatic covariates (temperature, rainfall) on survival rates. For temperature, we used the mean of daily maxima during the snake activity season (April–September) and for rainfall we used the total precipitation during the same period (Fig. 2). We used the procedure ANODEV in MARK 4.1 to test whether the variance explained by these covariates was statistically significant (Harris et al. 2005). We assessed the fraction of temporal variation in survival explained by covariates using the following formula:
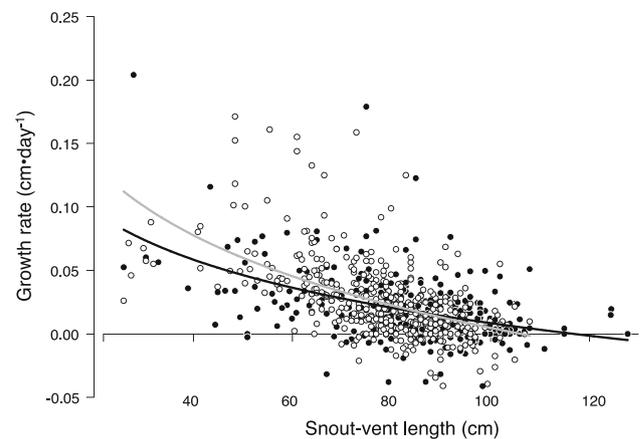

Fig. 3 Individual growth rates obtained through mark recapture of *H. viridiflavus* (HV) and *Z. longissimus* (ZL) in the Centre d'Études Biologiques de Chizé, Western France, from 1997 to 2009 (*white circles* for HV and *black circles* for ZL). *Curves* (*grey* for HV and *black* for ZL) represent logistic regression fits

$$R_{\text{Dev}}^2 = \frac{\left(\text{Dev}_{\text{model}\varphi(.)} - \text{Dev}_{\text{model}\varphi(\text{cov})}\right)}{\left(\text{Dev}_{\text{model}\varphi(t)} - \text{Dev}_{\text{model}\varphi(\text{cov})}\right)}$$

where $\varphi(.)$ is the constant model, $\varphi(t)$ is the time dependent model, and $\varphi(\text{cov})$ is the model with covariate.

All values are reported as mean $\pm$ SE.

Results

Growth

In both species, growth rates decreased with body size (regressions initial SVL-growth rate in HV: $df = 1,402$; $R^2 = 0.33$; $P < 0.0001$; in ZL: $df = 1,284$; $R^2 = 0.19$; $P < 0.0001$; Fig. 3). Growth rates of juvenile HV ($N = 95$) were significantly higher than those of ZL [$N = 51$;
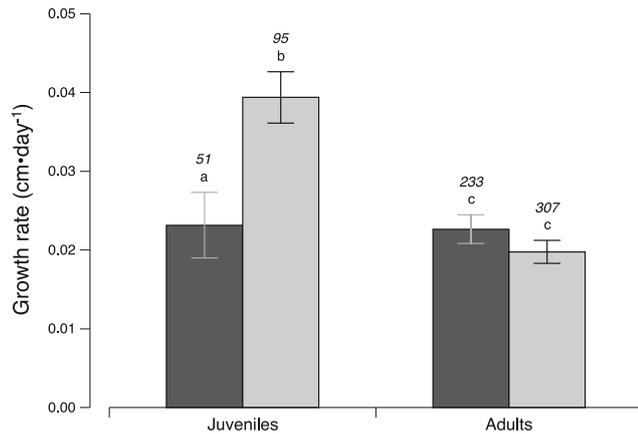
Fig. 4 Comparison between growth rates of juvenile and adult snakes in *H. viridiflavus* (HV) and *Z. longissimus* (ZL) obtained through mark recapture in the Centre d'Études Biologiques de Chizé, Western France, from 1997 to 2009 (*light grey bars* for HV and *dark grey bars* for ZL). *Bars* represent SE and *same letters* indicate no significant difference. Sample sizes are in *italic*

general linear model (GLM) with change in body size as the dependent variable, species and sex as factors, and initial SVL and time between recaptures as covariates; $F_{1,140} = 5.79$; $P = 0.02$; with no significant interaction between species and sex $F_{1,140} = 0.47$; $P = 0.49$; Fig. 4]. No interspecific difference in growth rate was detected in adults ($N = 308$ and 234; GLM; $F_{1,536} = 0.05$; $P = 0.83$; interaction between species and sex $F_{1,536} = 0.78$; $P = 0.38$; Fig. 4).

Importantly, juveniles grew faster in grassland than in forest ($N = 41$ and 70; GLM; $F_{1,105} = 7.81$; $P = 0.002$; Fig. 5) with an interaction between species and area (GLM; $F_{1,105} = 9.59$; $P = 0.003$). The effect of habitat on growth was pronounced in juvenile HV [least significant difference (LSD) Fisher post hoc test; $P < 0.0001$), but absent in ZL (LSD Fisher post hoc test; $P = 0.56$).

Survival

For HV, the most parsimonious survival model identified by AIC was $\varphi(t)\ p(g + t)$ (Table 2). Survival was time-dependant and did not differ between the sexes (average $\varphi = 54.7\ \%$, 95 % CI: 36.8–82.7; Fig. 6). The model failed to estimate survival in 2000, 2004, and 2008 because of low captures. For ZL, three models were equally parsimonious, and we thus performed model averaging on survival parameters (Table 2). Averaged survival was time-dependant and did not differ between the sexes (average $\varphi = 50.6\ \%$, 95 % CI: 22.8–76.6). Survival rates did not differ between species. The best-supported two-species model (with species as group factor and pooled sexes) was $\varphi(t)\ p(g + t)$, where survival was time-dependant and capture probability varied with time and species.
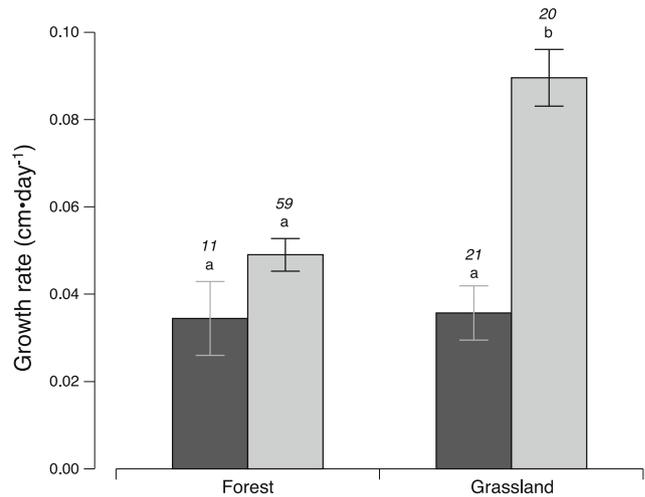

Fig. 5 Comparison between growth rates in juvenile *H. viridiflavus* (HV) and *Z. longissimus* (ZL) captured in different habitats obtained through mark recapture in the Centre d'Études Biologiques de Chizé, Western France, from 1997 to 2009 (*light grey bars* for HV and *dark grey bars* for ZL). *Bars* represent SE and *same letters* indicate no significant difference. Sample sizes are in *italic*

Influence of climate on demography

Maximum temperature and precipitation during the snake activity season were strongly negatively correlated ($R^2 = 0.99$, $P < 0.0001$). Each parameter significantly affected adult survival in ZL when taken independently. Maximum temperatures explained 43.3 % of interannual variation in survival (ANODEV; $F_{1,8} = 6.10$; $P = 0.04$) and precipitation explained 62.2 % (ANODEV; $F_{1,8} = 13.19$; $P = 0.007$). Nevertheless, precipitation had no effect when added to temperature (ANODEV; $F_{1,7} = 1.35$; $P = 0.28$), which is unsurprising given their very high correlation. Survival was highest in ZL when climatic conditions were hot and dry during the activity season (Figs. 2, 6). Conversely, none of the climatic variables tested explained variation in adult survival for HV (maximal temperature: ANODEV; $F_{1,7} = 0.39$; $P = 0.55$; precipitation: ANODEV; $F_{1,7} = 2.06$; $P = 0.19$).

Discussion

This long-term study allowed us to examine the hypothesis that the demography of snakes depends on their thermo-regulatory strategy. As predicted, the thermophilic species exhibited faster juvenile growth. By selecting higher body temperatures, HV can enhance foraging performance and digestion speed (Lelièvre et al. 2010, 2011), and potentially better exploit prey populations. As both species mature at a similar length, the faster growth of HV should result in a lower age at maturity compared to ZL and, if prey are

Table 2 Summary of the Cormack–Jolly–Seber mark-recapture models used to compare the survival rates of *Z. longissimus* and *H. viridiflavus* from 1997 to 2009 in Western France

Model	AIC$_c$	Δ AIC$_c$	AIC$_c$ weights	Model likelihood	k	Deviance
Z. longissimus						
$\varphi(t)\,p(g+t)$	939.54	0.00	0.36	1.00	23	202.09
$\varphi(g+t)\,p(g+t)$	939.70	0.16	0.33	0.92	24	200.08
$\varphi(.)\,p(g+t)$	941.39	1.85	0.14	0.40	14	223.14
$\varphi(g)\,p(g+t)$	941.87	2.33	0.11	0.31	15	221.53
$\varphi(g+t)\,p(t)$	944.19	4.65	0.03	0.10	23	206.73
$\varphi(g)\,p(t)$	944.90	5.35	0.02	0.07	14	226.65
$\varphi(.)\,p(.)$	979.90	40.36	0.00	0.00	2	286.36
H. viridiflavus						
$\varphi(t)\,p(g+t)$	1,013.14	0.00	0.45	1.00	22	203.99
$\varphi(g+t)\,p(g+t)$	1,015.26	2.12	0.16	0.35	23	203.93
$\varphi(t)\,p(g)$	1,015.51	2.38	0.14	0.30	14	223.50
$\varphi(.)\,p(g+t)$	1,017.06	3.92	0.06	0.14	14	225.04
$\varphi(g+t)\,p(g)$	1,017.63	4.49	0.05	0.11	15	223.50
$\varphi(g+t)\,p(t)$	1,017.88	4.74	0.04	0.09	22	208.74
$\varphi(t)\,p(t)$	1,018.50	5.36	0.03	0.07	21	211.52
$\varphi(g)\,p(g+t)$	1,019.05	5.91	0.02	0.05	15	224.92
$\varphi(g)\,p(t)$	1,020.51	7.37	0.01	0.03	14	228.49
$\varphi(.)\,p(t)$	1,020.66	7.52	0.01	0.02	13	230.75
$\varphi(.)\,p(.)$	1,031.97	18.83	0.00	0.00	2	264.71

Only the best models (AIC weight >0.01), with the constant model (.) as a reference, are presented. Candidate models describe local survival (φ) and capture probabilities (p) of snakes with t as time effect, g as sex effect, and k as the number of model parameters at yearly intervals

Fig. 6 Annual variations in mean temperature (*thick grey line*) and adult survival of *Z. longissimus* (ZL) and *H. viridiflavus* (HV) obtained through mark recapture in the Centre d'Études Biologiques de Chizé, Western France, from 1997 to 2009 (*light grey triangles* for HV and *dark grey squares* for ZL). Both sexes are pooled (see text for model selection). *Bars* represent SE
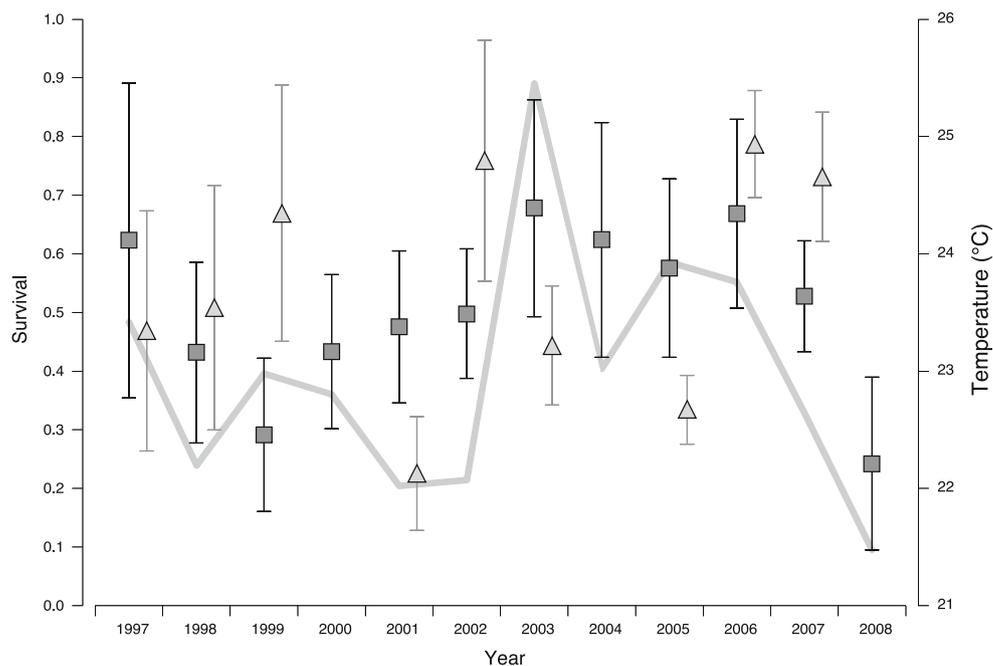
readily available, this could result in a higher population growth rate in HV compared to ZL.

Growth rates were also affected by habitat type in HV: HV exhibited faster growth in grasslands than in forest.

This habitat difference in growth was possibly driven by divergent food availability since rodents, and notably common voles (Naulleau 1984), are more abundant in open fields compared to forest (Gauffre et al. 2008). Food

availability is probably a key parameter affecting growth rate and reproductive output in these active predators. The difference in growth across habitats could also be related to enhanced physiological performances associated with open habitat use since open habitats allow to maintain higher body temperatures (Lelièvre et al. 2011, but see also Michel and Bonnet 2010). Because snakes were monitored in a single grassland site, however, we cannot tease apart site from habitat effects and further study is thus required.

The thermophilic HV did not exhibit lower survival, contrary to our prediction. Survival estimates were not available every year for HV, thereby reducing our ability to detect a difference. Alternatively, our initial hypothesis on survival might have been too simplistic. For instance, a high exposure thermal strategy may be associated with compensatory responses that minimize predation risk. Selection of high body temperatures enhances locomotor performance and fleeing ability (Arnold and Bennett 1984; Bauwens et al. 1995; Brodie and Russel 1999), notably in HV (Lelièvre et al. 2010). In addition, disruptive colouration in HV may help evade predators (Stevens et al. 2008). A comparative study conducted on two Australian nocturnal elapid snakes showed the same pattern: the two species exhibited similar adult survival rates despite contrasted foraging modes (active vs. sit-and-wait) and exposure strategies (Webb et al. 2003).

Climatic conditions during the activity season do not affect survival in HV, while ZL was sensitive to fluctuations in rainfall and temperature. The relatively low thermal requirements of ZL are related to a more secretive lifestyle (Lelièvre et al. 2011). When thermal conditions are hot, closed habitats such as scrub and forest provide favourable temperatures for ZL (Lelièvre et al. 2011). Conversely, closed habitats are usually too cool for HV, even in hot conditions. Therefore, colder conditions should be more detrimental to ZL because these conditions would impose the need for individuals to bask and thus potentially increase their risk of predation. Predation pressure is high in our study site because of the presence of raptors foraging on snakes: *Circaetus gallicus* and *Buteo buteo* (Bonnet et al. 1999; Gil and Pleguezuelos 2001; Selas 2001). Moreover, both ZL and HV exhibit extensive movements during the reproductive period (Bonnet et al. 1999). Given the poor crawling performance of ZL (Lelièvre et al. 2010), a higher sensitivity to avian predation is expected.

Overall, our empirical data allow a better understanding of the consequences of different thermal strategies on demography in ectotherms. Our results also underline the importance of considering thermal specialization as well as exposure strategies to elaborate realistic predictions on the potential effects of climate change on reptiles (Huey et al. 2009; Weatherhead et al. 2012). The impact of global warming on European reptiles attracted significant interest

(Araujo et al. 2006; Le Galliard et al. 2012). In our study system, survival should be positively influenced by a mild warming in the elusive species while growth should be more affected in the exposed species because of increased thermoregulatory opportunities. The exact response will depend on the extent of warming, however, notably in the thermoconformer that displays lower thermal preferences and depends on the coolest habitats. In this species, deviant (high) temperature experienced during the day should have negative impacts such as elevated maintenance costs, altered digestive efficiency and a reduction in the active time window. However, these potential costs can be alleviated by a behavioural shift from diurnal to nocturnal activity (Sinervo et al. 2010; Weatherhead et al. 2012) as observed in southern populations (L. Luiselli, personal communication).

Thermoregulatory and exposure strategies should also influence the biogeographical response to climate change. Mobile species characterized by high activity and "risk prone" behavioural tactics should respond more dynamically and be better able to colonize newly favourable habitats. The distribution of HV has shown a clear progression at the northern margin of its range over the past 60 years (Naulleau 2003). Such observations provide evidence for a rapid response to global change (climate and habitat) in this species. Further studies conducted on sympatric reptiles that differ on their physiological and ecological traits would help evaluate the generality of these differences in the ability to respond to perturbations (Huey et al. 2009).

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