Long-term and short-term effects of temperature on snake detectability in the wild: a case study with *Malpolon monspessulanus*

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The relationship between temperature and rates of detection of the Mediterranean snake *Malpolon monspessulanus* (Montpellier snake) in the wild was analysed over a 26-year period. We used records of live and freshly road-killed snakes in south-eastern Spain. A short-term effect of temperature on rates of snake detection was found: the higher the yearly temperature, the higher the snake detectability was that year. Moreover, a long-term effect of temperature on snake detectability was found, as snake abundance in year x was also strongly affected by temperature during year x–1 and x–2. A multiple-regression model demonstrated that these effects were independent. These long-term effects are probably due to an effect of temperature on snake population dynamics.

Key words: abundance, climate, Montpellier snake, population dynamics, Spain

INTRODUCTION

In contrast to endotherms, ectotherms do not regulate their temperature by means of metabolism, but as a function of external temperature (Pough et al., 2004). This makes them very sensitive to environmental temperature, and in fact, many traits of ectotherm biology are temperature-dependent (e.g. Shine, 2005). As global temperatures are currently increasing (Houghton et al., 2001), it is predictable that many aspects of ectotherms' natural history will be affected (Hughes, 2000; Walther et al., 2002). Indeed, some studies have shown variation in the phenology of ectotherms in response to climate change (e.g. Forchhammer et al., 1998), as well as variation in body size (Tryjanowski et al., 2006), or even variation in fitness (Chamaillé-Jammes et al., 2006).

Because of their limited dispersal abilities, amphibians and reptiles are probably more vulnerable than endotherms to a rapid climatic change (Gibbons et al., 2000). As a result of their sensitivity to water availability, it is predictable that climatic warming will harm amphibians (Alford & Richards, 1999). However, for reptiles, the effect of climate warming is unclear (Araújo et al., 2006). Rising temperatures may provide more opportunities for feeding, growth and breeding in temperate reptiles (Frazer et al., 1993; Chamaillé-Jammes et al., 2006), which may provoke a population increase, although it may be negative for equatorial or montane reptiles. In this study, we analyse the short- and long-term effects of environmental temperature on the detection of the Montpellier snake (*Malpolon monspessulanus*) in the wild. The annual activity period of this snake increases with temperature ($r=0.62$, $P=0.02$, $n=16$ years; Fig. 1; unpublished data), and therefore, the within-year number of individuals detected should increase as a short-term response to temperature increase. Moreover, growth in the population size of the Montpellier snake would be expected as a long-term effect of environmental temperature.

MATERIALS AND METHODS

Field searches for the Montpellier snake were performed in the south-eastern Iberian Peninsula (38º30'–37º15'N; 5º30'–2º30'W), a region with altitudes ranging from sea level to 3482 m a.s.l. Analyses, however, were restricted to records from 500–1300 m, an area demonstrating similar climatic regimes corresponding to the Meso-Mediterranean thermoclimatic stage (Rivas-Martínez, 1981) and occupying approximately 17,500 km². We assumed that population dynamics in this species varied little within the elevation-constrained area considered. The climate in this area is typically Mediterranean; mean ± standard deviation of temperature was 7.2±1.96 ºC in winter (January) and 25.3±2.36 ºC in summer (July); average yearly rainfall was 412.1±226.72 mm (climatic data for the 1980–2005 period; Junta de Andalucía, 2001; and data on the web).
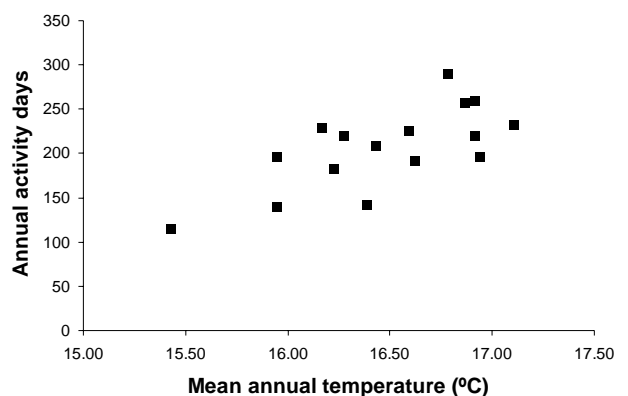

Fig. 1. Relationship between Montpellier snake annual activity period and temperature during the study (1983–2004).
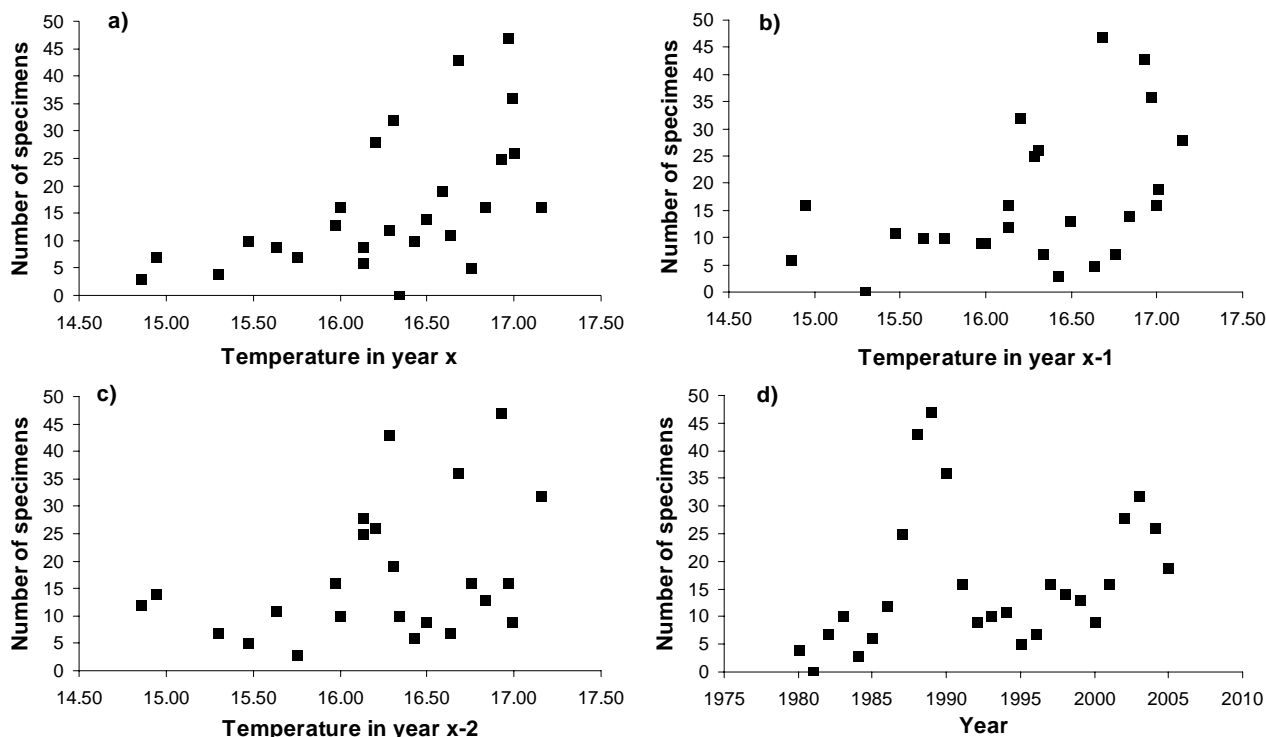

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Fig. 2. Relationship between Montpellier snake detectability and temperature in a) year x, b) year x–1, c) year x–2, and d) with year during the study period.

Field sampling was conducted from 1980 to 2005, within the framework of a larger study on the snake fauna of the region (details in Feriche, 1998). Searches were scheduled on the basis of a rather constant effort, both within and among years, of about three field days per month (approximately 5 h each), throughout all months of the year. We recorded data from live and road-killed individuals, mainly on unpaved roads. As road-killed snakes were active prior to death, we consider these data informative regarding behavioural and population dynamics of this snake. Moreover, the number of road-killed snakes was positively correlated with the number of live snakes recorded ($r=0.77$, $P<0.001$, $n=18$ years; only years with data for both sampling methods were used), suggesting that both means of sampling gave similar patterns. With these data, we considered the number of individuals detected per year as an indicator of snake abundance and snake activity in the field. Nevertheless, we are dealing with a model organism, the Montpellier snake, which is a predator (Valverde, 1967; Pleguezuelos, 1998), relatively scarce, very elusive, and for which encounters are scarce, as in most snake species (Fitch, 1987). This probably increased the measurement error for snake abundance, but this error should diminish the statistical power of our analysis (Yezerinac et al., 1992), causing our results to be conservative.

To analyse the effect of climate on snake detectability, we used a multiple linear regression with number of specimens detected per year as the dependent variable. We analysed the effect of the mean annual temperature of year x, as well as mean annual temperature of year x–1 and the year x–2. We also tested the effect of annual precipitation. Climatic data were compiled from 98 meteorological stations homogeneously distributed within the study area, and which did not show spatial autocorrelation (Junta de Andalucía, 2001; and additional data on the web). We used mean annual temperature because it was the thermal measure available for most meteorological stations, and is strongly correlated with minimum and maximum temperature in the study area ($r>0.80$). All variables had a normal distribution (Lillierfors test), justifying the use of parametric statistics (Sokal & Rohlf, 1995).

RESULTS

Throughout the study period, we detected 424 (249 road-killed) snakes in the field (16.3 snakes per year $\pm$ 2.43 S.E., range 0–47, $n=26$ years). The annual number of observations of males and females were highly correlated ($r=0.81$, $P<0.001$, $n=26$ years), and the two sexes were grouped for a more reliable measure of annual snake detectability. Snakes detected in year x were positively correlated with the average temperature that year ($r=0.56$, $P=0.003$, $n=26$ years; Fig. 2a), but also significantly correlated with the temperature of year x–1 ($r=0.47$, $P=0.02$, $n=25$; Fig. 2b) and almost significantly correlated with the mean temperature during year x–2 ($r=0.37$, $P=0.077$, $n=24$; Fig. 2c). Temperature for year x did not correlate with temperature for year x–1 ($r=0.003$, $P=0.99$, $n=25$) or year x–2 ($r=-0.01$, $P=0.96$, $n=24$), suggesting that the effect of each year was independent and that there was no temporal autocorrelation, justifying the use of multiple-regression methods (Stewart-Oaten et al., 1986). A multiple-regression model with temperature for years x, x–1 and x–2 as predictors revealed an independent and significant effect of temperature in each of those years on snake detectability

Table 1. Multiple-regression model statistics for the relationship between the effects of temperature in the year x, x–1 and x–2 on snake detectability in the year x. $R^2=0.64$, $F_{3, 20}=11.61$, $P<0.001$.

	Beta ($\pm$ SE)	t_{20}	P
Year x	0.57±0.14	4.19	<0.001
Year x-1	0.42±0.14	3.12	=0.005
Year x-2	0.38±0.14	2.84	=0.01

in the wild (Table 1). The mean temperature for year x–3 had no significant effects on snake detectability (multiple regression, $t_{18}=0.66$, $P=0.52$). There was no correlation between total precipitation and snake detectability ($r=-0.02$, $P=0.93$, $n=20$ years). No correlation was found, either, between mean altitude of records each year and snake detectability ($r=-0.23$, $P=0.27$, $n=26$ years), suggesting that the results were not confounded by altitude. Lastly, snake detectability did not vary significantly with years ($r=0.28$, $P=0.17$; Fig. 2d).

DISCUSSION

This study shows that detectability of the Montpellier snake in the wild in year x was affected by environmental temperature that year. This result is to be expected, because activity is regulated by temperature in ectotherms (Pough et al., 2004), and the extension of the activity period of the Montpellier snake is affected by environmental temperature (unpublished data). The higher the temperature for a given year, the more time the snakes were active, and the more snakes were detected. However, notably, the average temperature for years x–1 and x–2 also affected snake detectability during year x. It is improbable that climate in the previous years affected the activity of snakes during year x, but it is more conceivable that temperature in the previous years affected snake population size by increasing individual survival and/or breeding success (Lourdais et al., 2002). However, only 2.8% of individuals found were immature, suggesting that temperature affected mainly adult survival.

Chamaillé-Jammes et al. (2006), for example, showed that higher temperatures favoured breeding success and juvenile growth in the common lizard (*Lacerta vivipara*), and Altwegg et al. (2005) showed that higher winter temperature favours the survival of juvenile asp vipers (*Vipera aspis*). Similarly, temperature may favour breeding and juvenile survival in the Montpellier snake. However, we have no data on breeding success and juvenile abundance in the field according to year, although the low frequency of immature individuals recorded in this study suggests that the effect on breeding success was small. The effect of temperature on snake survival and breeding success may be mediated by many factors (Peterson et al., 1993), the most crucial being improved mobility of snakes, which increases with temperature (Stevenson et al., 1985), affecting their foraging performance (more time to forage, improved strike speed; Greenwald, 1974) and probably also their capacity to escape from predators (Peterson, 1987; Goode & Duvall,

1989). Moreover, the availability of prey for snakes may also be positively affected by climate (e.g. Morrison & Bolger, 2002), especially considering that the Montpellier snake is mainly lizard-eating (Pleguezuelos, 1998). However, because of the secretive nature of most snakes, data to test these hypotheses are difficult to gather, at least under natural conditions, and thus we did not test these mechanisms.

The environment is currently changing, and temperature is increasing (Houghton et al., 2001; Jones et al., 1999, 2001; unpublished data for the study area). Climate warming may increase the extinction risk of many species (Thomas et al., 2004), and it has been related to the global decline of amphibians (e.g. Alford & Richards, 1999) and reptiles (Gibbons et al., 2000). However, climate warming may also favour some species or populations (see Chamaillé-Jammes et al., 2006). For example, butterfly species richness in the United Kingdom has increased in response to climate warming (Menéndez et al., 2006). Findings in this study suggest that the Montpellier snake may benefit from climatic warming, as its detectability in the wild (and presumably its population size) increases with temperature. In fact, it is a thermophilous snake (Blázquez, 1995) and its relative importance in the snake community in the study area has increased during the study period from 27.1% to 52.0% of the snakes recorded (C. Segura, unpublished data). In conclusion, this study suggests that the climate affects the population size of the Montpellier snake, and therefore, that climate warming may favour this ectothermic and thermophilous vertebrate, increasing its population size.

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