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Climate warming and activity period extension in the Mediterranean snake *Malpolon monspessulanus*

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Abstract Plants and animals are responding to climate warming with predictable changes in distribution and physiology. Ectothermic animals are dependent upon environmental temperature, and their seasonal activity patterns are constrained by temperature. Ectotherms (such as snakes) may alter their activity patterns in concordance with climatic change, and we tested this hypothesis in a Mediterranean region (SE Spain) with the Montpellier snake (*Malpolon monspessulanus*). Temperature showed an increasing trend of 0.07°C per year in the study area between 1983 and 2004, and activity period in this species increased in concert with annual mean temperature. These snakes had a wider dispersion in activity dates and the annual last record was delayed as years progressed, suggesting that the activity period for this snake has increased over time in response to climatic change. These results were not influenced by the elevation at which samples were taken, and annual variation in the number of snakes recorded, sex-ratio, or precipitation. Therefore, this study reports a definite phenological shift for a reptile in response to climatic change.

1 Introduction

Earth is undergoing general climate warming (IPCC 1994; Schneider and Root 1998; Huang et al. 2000; Jones et al. 2001) and, because traits defining biology and ecology in organisms are often temperature dependent, changes in distribution and activity patterns attributable to global warming may be expected (Hughes 2000; Walther

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et al. 2002; Parmesan and Yohe 2003). Ectothermic animals, dependent upon external temperatures, are sensitive to climatic change (Walther et al. 2002). In temperate regions thermal environment constrains seasonal activity because ectotherms are active when external temperatures are suitable, and fall into lethargy (or die if they have an annual cycle) when external temperatures fall below critical minimum temperatures (Pough et al. 2004). Annual activity periods could increase in response to rising average temperatures, due to an earlier beginning or a later ending. While there is some evidence for this phenomenon in insects (Roy and Sparks 2000; Stefanescu et al. 2003; Gordo and Sanz 2005), data supporting this phenomenon for ectothermic vertebrates are scarce and most of them confined to amphibians (Beebee 1995; Forchhammer et al. 1998; Blaustein et al. 2001; Gibbs and Breisch 2001; Tryjanowski et al. 2003), probably because of the lack of long term-data for reptiles. In fact, we only know of two studies showing an advance of breeding in reptiles related to climatic change (for the lizard *Tiliqua rugosa* and the seaturtle *Caretta caretta*; Bull and Burzacott 2002 and Pike et al. 2006, respectively).

In free-living organisms long-term data can document temporal variation in population size and phenology attributable to natural causes (Cody 1996). The clandestine nature of many snakes, combined with patchy distributions, low population densities and rareness of congregational behavior, makes long-sampling program in this group very difficult (Gibbons et al. 2000). We examined records for snakes from the south-eastern Iberian Peninsula gathered during the last 22 years to determine whether activity period in the Montpellier snake (*Malpolon monspessulanus*) has increased. Because environmental temperature has increased during this period, we predicted that the within-year activity period in this snake has also increased.

Malpolon monspessulanus, widely distributed around the Mediterranean Basin, is the largest and most common snake in our study area. It is a typical generalist in habitat and diet, occupying most natural and man-made habitats from sea level to 2,200 m, and preys upon over 30 invertebrate and vertebrate species (Valverde 1967; Pleguezuelos 1998). In the warmest areas of the southern Iberian Peninsula (i.e. close to the seashore), the species is active during winter warm spells (Fig. 3 of Busack and Jaksić 1982; Pleguezuelos 1998), from which we can deduce that *M. monspessulanus*, unlike some snake species, is not endogenously inactive during the winter months (Gibbons and Semlitsch 1987). Thus, the species is suitable for the study of the response of ectotherms to climatic warming in Mediterranean ecosystems. In general, snakes are good study animals for investigating general questions of thermal ecology (Peterson et al. 1987).

2 Material and methods

Analyses of field data resulting from searches performed in the south-eastern Iberian Peninsula (38°30′–37°15′ N, 5°30′–2°30′ W) were restricted to records from 500–1,300 m, an area of climatic regimes corresponding to the Meso-Mediterranean thermoclimate (Rivas-Martínez 1981) and occupying approximately 17,500 km^2. We assumed that activity patterns varied little within this elevationally constrained area where climate is typically Mediterranean [temperatures ($\overline{X}$±SD) in winter (January) = 7.2 ± 1.96°C, in summer (July) = 25.3 ± 2.36°C, and annual = 16.4 ± 1.72°C; yearly rainfall = 412.1 ± 226.72 mm.; data from 98 meteorological stations for the 1980–2004 period; Junta de Andalucía (2001), and other information provided by the regional administration]. Mean annual temperatures between 1983 and 2004 were used to determine whether warming had occurred in our study area.

Field sampling was conducted from 1983 to 2004 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 two to four field days per month (approximately 4–6 h each) throughout all months of the year. A total of 334 specimens were collected, considering only active live specimens (basking, moving, foraging) or traffic casualties within an estimated 24-h period (from our experience and according to carcass condition). Road-killed snakes were active prior to death, and we consider these data informative about when individuals are active and therefore allow inference regarding extent of seasonal activity.

For each year, we considered the following variables: (1) date first individual collected or observed; (2) date last individual collected or observed; (3) difference (in days) between first and last record of activity (length of activity period); (4) elevation of the records (m asl); and (5) standard deviation of record dates (a measure of dispersion of activity dates within each year). The first three variables were scored using the Julian calendar. Both, length of activity period and standard deviation of records are estimates of the activity period, and they are well correlated (see Section 3). Although length of activity period is a more natural estimate, it only uses two data per year. However, standard deviation of dates, which use all data available per year, is probably a more reliable measurement, less dependent of extreme data.

Years with the most records would be expected to best elucidate the shift in seasonal activity period during the study period. Because the Montpellier snake is an elusive super-predator (Valverde 1967) for which encounters represent stochastic events (as general in snakes; Fitch 1987), distribution of activity dates may increase measurement error in activity season length. This error, however, should diminish the statistical power of our analysis (Yezerinac et al. 1992), causing results to be conservative. To minimize this type of error, we considered only years with a minimum of 10 records, although this reduced inter-year sample size to 16 years (number of records in parentheses): 1983 (10), 1986 (12), 1987 (25), 1988 (41), 1989 (38), 1990 (35), 1991 (14), 1993 (10), 1994 (11), 1997 (13), 1998 (11), 1999 (12), 2001 (16), 2002 (28), 2003 (32), 2004 (26).

Moreover, results could be skewed for some confounding factors like elevation of the records, sex-ratio or sample size per year. Elevation within the study area (500–1,300 m a.s.l.) could affect timing of seasonal activity, extended in populations at lower, warmer areas, with respect to populations at higher, colder ones. Adult males emerged from dens approximately 2 weeks earlier than adult females and juveniles (Feriche 1998), thus, interannual variation in sex-ratio could also be responsible of some variation. At the last, interannual variation in activity period could be a consequence of interannual difference in sample size. We used partial correlation analyses to control for these confounding factors (elevation mean, elevation range, sex-ratio, and sample size of the records per year), which were introduced as covariates. This analysis allows consider the correlation of temperature and year with activity period variables, setting the confounding variables statistically constant (Sokal and Rohlf 1995). Moreover, we tested the effect of precipitation (only information for 12 years was available) on activity period, controlling statistically for the effect of temperature by mean of a multiple regression. The goal of this analysis was to examine whether the effect of temperature on activity was independent of precipitation.

All variables were normally distributed (Lillierfors test) and we used parametric statistics. The correction of Bonferroni was not applied because variables measuring activity are not independent (Rice 1989). In most analyses the predictions were strongly directional, and one-tailed tests were performed (Bart et al. 1998).

3 Results

Between 1983 and 2004 mean annual temperature in the study area increased, in average (±SE), 1.54 ± 0.66°C ($F_{1,378} = 4.28$; $p < 0.05$; $\beta = 0.07 \pm 0.03$; meteorological station introduced as random factor: $F_{97,378} = 13.83$; $p < 0.001$; sum of squares type III). Controlling statistically for mean elevation, range of elevation, sex-ratio and

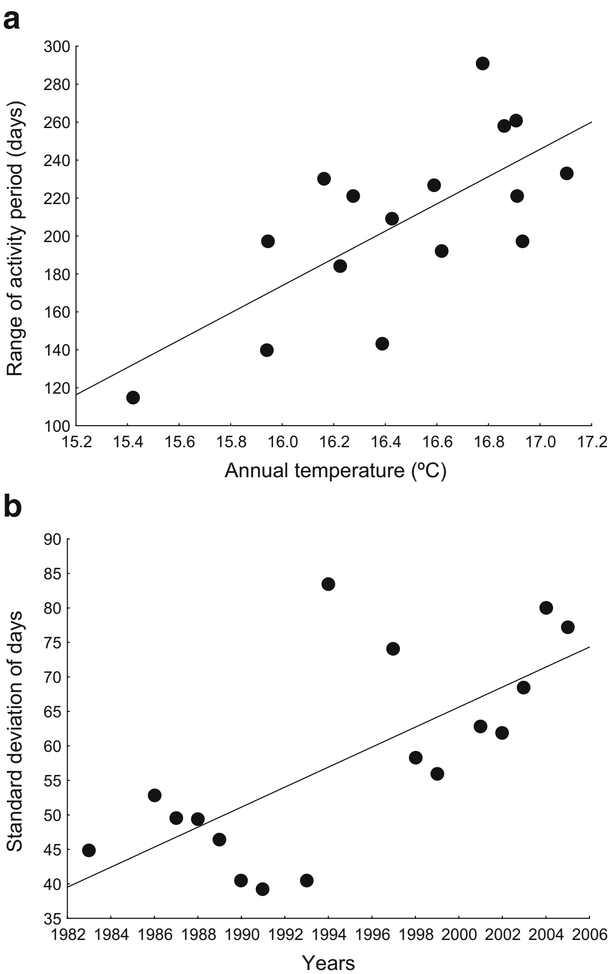

Fig. 1 **a** Relationship between average annual temperature and length of activity period (see Moreno-Rueda and Pleguezuelos 2007). **b** Relationship between years and standard deviation of dates

Table 1 Partial correlations of temperature and year with activity variables in the Montpellier snake, *Malpolon monspessulanus*, in southeastern Iberian Peninsula, controlled for confounding factors (mean elevation, range of elevation, sex-ratio and sample size; details in Section 2)

	Temperature	Years
Range of activity	$r_{\text{partial}} = 0.62$ $p = 0.02$	$r_{\text{partial}} = 0.30$ $p = 0.19$
Standard deviation of dates	$r_{\text{partial}} = 0.38$ $p = 0.14$	$r_{\text{partial}} = 0.53$ $p < 0.05$
Date of first record	$r_{\text{partial}} = -0.46$ $p = 0.08$	$r_{\text{partial}} = 0.34$ $p = 0.31$
Date of last record	$r_{\text{partial}} = 0.30$ $p = 0.19$	$r_{\text{partial}} = 0.60$ $p < 0.05$

All tests were one-tailed; 1983–2004 period; $n = 16$ years

sample size (see Section 2), the range of activity was positively and significantly correlated with temperature (Fig. 1a and Table 1; also see Moreno-Rueda and Pleguezuelos 2007). Standard deviation of dates, date of first, and date of the last record were not correlated with temperature after controlling for the confounding factors (Table 1). As the annual activity period of the Montpellier snake varied with temperature, and temperature increased in the study area during the period considered, the extension of the activity period should increase with years. When controlling statistically for mean elevation, range of elevation, sex-ratio and sample size, the correlation between range of activity and years was not significant, but the standard deviation of dates was (Fig. 1b and Table 1). Both standard deviation of dates and range of activity were positively correlated ($r = 0.71$; $p = 0.002$). The date of last record, but not the date of the first record, was also significantly correlated with years (Table 1).

We failed to find significant inter-year trends in elevational distribution of records ($r = -0.39$; $p = 0.13$), elevational range ($r = 0.18$; $p = 0.52$), male/female ratio ($r = 0.42$; $p = 0.12$), and snake sample size ($r = -0.003$; $p = 0.99$; all tests two-tailed), and no interannual trend in average date of records was identified ($r = 0.35$; $p = 0.18$; two-tailed test). Lastly, precipitation did not have significant effect on standard deviation of dates, the date of the first record or the date of the last record (always $p > 0.15$), but it had a significant positive effect on the length of activity period, which was independent of the effect of temperature ($F_{2,9} = 12.87$; $p = 0.002$; $n = 12$ years; effect of precipitation: $r_{\text{partial}} = 0.65$; $p = 0.03$; effect of temperature: $r_{\text{partial}} = 0.68$; $p = 0.02$). Annual precipitation and temperature, jointed, account for 74% of variance in the length of activity period.

4 Discussion

Annual dispersion of records for *Malpolon monspessulanus* in the south-eastern Iberian Peninsula increased over time, suggesting that the annual activity period for this snake has become longer over the last 22 years. A similar trend was found for date of last seasonal record. These results may be due to climate warming. Temperature is the environmental factor most closely tied to extension of seasonal activity period for ectotherms in Temperate regions (Gibbons and Semlitsch 1987), having increased in the same period of time at global (Jones et al. 2001), regional (Jones et al. 1999) and local (this study) scales. Other reptiles with temperate distribution become active when environmental temperatures enable them to warm up and carry out temperature-dependent functions of their life cycles (Peterson et al. 1987). Autumn temperatures in temperate regions, being too low for reptiles to maintain active metabolism, cause lethargy (hibernation) which lasts until adequate warming the next spring (Gibbons and Semlitsch 1987). The temporal range of activity in *M. monspessulanus* increased significantly, along with mean annual temperature, in our study area, and the standard deviation in dates tends to increase with temperature, although not significantly. Therefore, if mean annual temperatures rise we can expect snakes to be active earlier in spring and enter lethargy later in autumn, as these results for *M. monspessulanus* suggest. Similarly, in the North American Rocky Mountains, the yellow-bellied marmot (*Marmota flaviventris*) has reduced its hibernation period as a consequence of climatic change (Inouye et al. 2000). These phenological shifts may be the consequence of phenotypic plasticity in phenology (Przybylo et al. 2000), although phenological shifts may also result from evolutionary responses (genetic) to climatic change (Bradshaw and Holzapfel 2001).

Because this was a correlational study, we cannot establish causal relationships without discarding other alternative hypotheses, but such is the rule for most studies on ecological effects of climatic change (Parmesan and Yohe 2003). The most plausible alternative hypotheses are that our findings result from an increase in sample size through the years, implying a wider range for dates of records; a sequential sampling in lower (warmer) elevation areas, implying extension for annual timing of records; or a change in the population's sex ratio, with more males appearing in later years. Throughout the study period, however, neither sample size, mean elevation, range of elevation, nor male/female ratio changed significantly. Moreover, after controlling for these variables, our results continued to demonstrate an increase in length of activity period with temperature, and an increase of date dispersion with years. The effect of precipitation, moreover, was independent of the effect of temperature. Alternative explanations may, therefore, be rejected.

Global climate change is one of six factors known or suspected to be associated with reptile decline worldwide (Gibbons et al. 2000). Our results suggest, however, that climate warming might favor thermophilous snakes in temperate regions throughout the extension of their activity periods. As nearly all aspects of snake ecology are potentially affected by body temperature, and body temperature is determined primarily by heat obtained directly from the physical environment (Peterson et al. 1987), the selective advantage delivered to a large snake in a Mediterranean climate by a longer seasonal activity period could be more opportunity to feed, grow, reproduce, and, probably, increase population size. In our study area, in fact, the annual temperature has positive long-term effects on population size of this snake in the field (Moreno-Rueda and Pleguezuelos 2007), and the relative importance of this species in the snake community has increased during the study period from 27% to 52% of snakes recorded (C. Segura, unpublished data). However, while climatic warming seems to favor some reptiles (Frazer et al. 1993; Chamaillé-Jammes et al. 2006), Cheylan and Grillet (2005) found that another Mediterranean reptile, the ocellated lizard (*Lacerta lepida*), did not profit from rising temperatures in southern France during the past 150 years, as other environmental changes overrode possible climatic benefit for this thermophilous lizard.

Other studies have reported evidence of climatic change affecting phenology of plants and animals (reviews in Hughes 2000; Walther et al. 2002; Parmesan and Yohe 2003; Root et al. 2003; Parmesan 2006), but data supporting changes in phenology of ectothermic vertebrates are limited to the timing (usually advance) of the reproductive period in amphibians (Beebee 1995; Forchhammer et al. 1998; Blaustein et al. 2001; Gibbs and Breisch 2001; Tryjanowski et al. 2003) and, to our knowledge, two reptiles (Bull and Burzacott 2002; Pike et al. 2006). This study provides evidence of a snake's annual activity period having increased in sequential years in concert with climate warming.

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