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ORIGINAL ARTICLE

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Long-term, climate-change-related shifts in feeding frequencies of a Mediterranean snake population

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Abstract In a context of climate change, ecological and physiological adaptations of organisms are of central importance for determining the outcome of niche challenges (e.g., with potential competitors) and species persistence. Typically, long-term data on free-ranging populations are needed to investigate such phenomena. Here, long-term data on a free-ranging population of western whip snakes (*Hierophis viridiflavus*: Colubridae) from central Italy were used in order to test the hypothesis that snake feeding frequencies should increase in relation to climate warming, thus positively affecting individual performance because of longer annual activity period, increased daily activity and larger prey base. Data from 231 'female snake-years' of records (including inter-annual recaptures) were collected were collected between 1990 and 2014. The frequency of fed snakes varied remarkably across the study period with a significant increase over the years. There was a significant positive effect of the mean annual temperature on the percentage of fed animals, whereas there was a non-significant relationship between yearly rainfall and percentage of fed animals. There was a positive relationship between mean annual temperature and yearly diversity-of-prey index. No other climatic variables were significantly correlated with yearly diversity-of-prey index. This study supported the hypothesis that global warming may be favorable for thermophilic species (such as *H. viridiflavus*), as it enhances their foraging performances and hence their feeding frequencies. The same may not be necessarily true for other species which have colder preferenda (e.g., *Zamenis longissimus*).

Keywords Diversity-of-prey index · Percent of fed animals · Global warming · Mediterranean · Serpentes

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Introduction

In the current climate change context, ecological and physiological adaptations of organisms are of central importance for determining the outcome of niche challenges (e.g., with potential competitors) and the species persistence (e.g., Smit and Wandel 2006; Ujvari et al. 2011) and these are likely to be altered by climate change. Long-term data on free-ranging populations are needed to investigate these adaptations and the outcomes of such processes.

Reptiles, being mostly ectothermic, depend directly on the external thermal conditions for their activities and performances (e.g., Avery 1978; Huey and Stevenson 1979; Lourdais et al. 2004; Angilletta 2006), and therefore are theoretically directly affected by global warming (Janzen 1994; Walther et al. 2002; Araujo et al. 2006). Recently, some long-term studies on single reptilian populations have been published with emphasis on the ecological consequences of the global warming (e.g., Ujvari et al. 2011); some of these studies have focused on Mediterranean snake species (Rugiero et al. 2012a, 2013a; Capula et al. 2014). Although the effects of global warming seem to be potentially detrimental to many animal species worldwide (e.g., Thomas et al. 2004), it has been argued that Mediterranean populations of snakes might benefit from the ongoing climate changes (Rugiero et al. 2013a; Capula et al. 2014). Indeed, global warming can produce shifts in the phenology patterns of snakes and might increase the annual activity time spent above-ground by these animals (Rugiero et al. 2013a). This increased time spent above-ground could in turn, for example, translate into having more time to feed and therefore would imply faster growth, increased reproductive output, and even greater population growth (Rugiero et al. 2013a). At the same time, increased time spent above-ground may also be associated with greater metabolic costs, thus implying that the species may be limited by access to warm habitats.

Whether, however, the feeding frequency of Mediterranean snakes does increase under a climate change (= warming) scenario, has not been directly tested by field investigations, although being obviously a major issue of ecological investigations. In this paper, we used a long-term monitored population of western whip snakes (*Hierophis viridiflavus*: Colubridae) from central Italy (Filippi et al. 2007; Luiselli et al. 2011; Rugiero et al. 2012b, 2013b) to test the hypothesis that snake feeding frequencies should increase in relation to climate warming, thus positively affecting individual performance and speeding their growth.

Materials and methods

Study area

The field study was conducted at Oriolo Romano (province of Viterbo, about 400 m a.s.l.), 60 km north of Rome. The site is characterized by a partially dilapidated building (a cuboid stone building, measuring 5.0 m × 3.5 m, height 5 m) bordered by rich thorny vegetation (mainly *Rubus* spp.) and surrounded by cultivated fields and small oak (*Quercus cerris*) woodland patches. The climate of the study area is Mediterranean (Tomaselli et al. 1973).

Study population

The snake population was monitored around a communal nesting site (CNS), that was used every year by snakes at least since 1990 (Filippi et al. 2007). The CNS was visited only by gravid females and by a small number of males (Filippi et al. 2007), whereas newborn snakes were observed frequently after hatching (Rugiero et al. 2012b). Each gravid female visited the CNS for a mean of 2.2 years (Filippi et al. 2007), although some females oviposited at the site in six different years (Luiselli et al. 2011). The period of egg-laying was, with some yearly variation, at the end of June to mid July. In the last years, most egg-laying events occurred in late June. Population size at CNS, using the Jolly-Seber model, fluctuated between fewer than 10 (2003) and about 40 (1994 and 2004) (Luiselli et al. 2011). Hatchlings were usually hatched by mid-August (Rugiero et al. 2012b).

Field protocol

The field study was conducted in 1990–1997 and 2001–2014 (methodological details are presented in Filippi et al. 2007; Luiselli et al. 2011; Rugiero et al. 2012b, 2013b). The whole area surveyed was 3.0 ha in 1990–1997 and in 2001, and 9.3 ha in 2002–2014 (Luiselli et al. 2011). In each field day, three people independently searched for snakes. The overall field effort was approximately 360 person hours per year in 1990–1997 and in 2001, and 720–840 person hours per year in 2002–2009.

Snakes were captured, by hand, when basking and under cover objects specifically distributed throughout the study area. Snakes were individually marked by ventral scale clipping for future identification, and their sex was determined by examination of the cloacal region structure. We used only gravid females for this study to minimize the detectability issues that can bias the results if individuals of different gender/reproductive status are considered. Indeed, gravid females may spend considerably more time in the open than males (outside the mating period) or non-gravid females, thus making inter-annual and inter-gender comparisons problematic if these divergent categories of individuals are pooled in the analyses. Reproductive condition of captured females was assessed by abdominal palpation. Because we used only gravid females for this paper, we confined our analyses to data collected only in May and June.

Gravid females were processed for any ingested food by gentle collection of feces or forced regurgitation. Snakes were re-fed with their prey items after identification. If a food item was obtained, the snake was attributed to the category 'fed animal', otherwise to the 'non-fed animal' category. When a given gravid female was recaptured multiple times in a single year (that is, for this study, in May–June), it was enough that she was containing food in just one of such capture events for being assigned to the category 'fed' in our analyses. Moreover, all females typically feed soon after oviposition, thus our attribution of fed/unfed status to a given female in a given year is relative to only the period in which she was gravid and nearby the CNS for ovipositing.

Statistical analyses

Data on the local climate throughout the whole study period was obtained from the Meteorological Station of Viterbo (available at http://www.ilmeteo.it). Feeding patterns were correlated with one thermal variable (annual mean temperature) and one rainfall variable (annual number of rainy days). Annual mean temperature was selected among the various available in the climatic database because all the available variables were collinear (Table S1).

For this study, we considered each female in each year as an independent data-point ('female snake-years' of records, as in Capizzi et al. 1996). That is: if the same female was recaptured in three different years, she counted as three distinct data points in the analyses (for raw data of individual patterns of captures and recaptures across years, see Luiselli et al. 2011; Rugiero et al. 2012b, 2013b). In this case, pseudo-replication should not be an issue because the feeding frequency of a given gravid female in the (year + 1) cannot be influenced by that of the (year + 0) neither can influence that of (year + 2).

Correlations between percent of fed snakes and (1) year, (2) mean annual temperature (°C), (3) rainfall (expressed as the number of rainy days per year), and (4) number of favorable days for snakes in active season, were performed by Pearson's correlation coefficient. We used the Curve Estimation procedure in SPSS to assess which model type (linear, quadratic, cubic, inverse, logarithm) best fitted to the data.

The predation diversity trend along the investigated period was estimated yearly by using the Shannon entropy Index, calculated each year.

$$H' = -\sum_{i=1}^{R} p_i ln p_l$$

where, in this case, p_i is the proportion of individuals preyed on belonging to the ith species in a yearly pooled sample of snake. The Shannon entropy quantifies the uncertainty in predicting the species identity of an individual that is taken at random from the dataset.

Because, as mentioned above, a strong increase of prospection effort (time spent looking for snakes and study area surface prospected) occurred across the survey, we cannot exclude that results are partially influenced by this methodological change (for instance, if new prospected area in the second part of the survey differs from the previous one in prey availability). In addition, it remains possible that prey items were more systematically collected in the second part of the study. Therefore, we repeated all analyses also to the dataset collected only in 2002–2014, when prospection effort was identical.

From 1990 to 2001, the number of snakes containing identifiable prey items was too small to get quantitative information about food diversity. Since 2002, the increased sampling area (from 3 to 9.3 ha) resulted in a sharp increase of the number of captured snakes with identifiable prey items. For this reason, we used only the 2002–2014 dataset for evaluating the food-habits related issues of the present study. In only one case, in 2003, the same prey species was found in the three captured fed snakes.

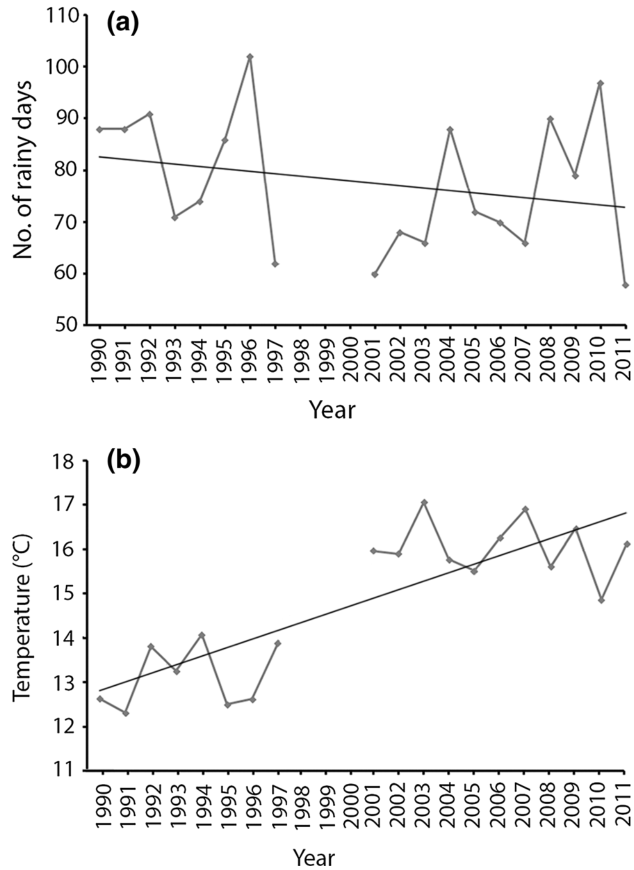

Fig. 1 Yearly variations of the climatic variables (mean annual temperature and yearly number of rainy days) across the years of study at Oriolo Romano. Trend lines are also indicated. Data from 1998 to 2000 are not available

Yearly H' indices and their relation with the various climatic variables (Fig. 1) were investigated by means of linear models. All analyses were performed with STATISTICA and SPSS (version 16.0) software, with all tests being two-tailed and alpha set at 5 %.

Results

Overall, we examined 231 'female snake-years' of records (including inter-annual recaptures). 75 'snake-years' of records were 'fed' at the time of capture. The summarized dataset on the yearly variation of the percent frequencies of fed snakes is presented in Table 1. Grouping the study years into 3-year-blocks, there were statistically significant differences among the various blocks in terms of yearly percentage of fed snakes (Kruskal–Wallis ANOVA: H (X^2) = 16.97, P < 0.01).

Table 1 Frequency and relative yearly percentage of fed snakes (only gravid females being considered in this table) across the years at the study area

Year	No. captured	No. with food	% fed
1990	5	0	0
1991	6	0	0
1992	6	1	16.7
1993	7	1	14.3
1994	5	1	20
1995	7	2	28.6
1996	6	1	16.7
1997	6	1	16.7
2001	4	1	25
2002	11	4	36.4
2003	9	3	33.3
2004	12	4	33.3
2005	15	5	33.3
2006	16	5	31.3
2007	15	6	40
2008	17	6	35.3
2009	16	7	43.8
2010	13	5	38.5
2011	14	6	42.9
2012	11	4	36.4
2013	14	6	42.8
2014	16	6	37.5
Total	231	75	32.5

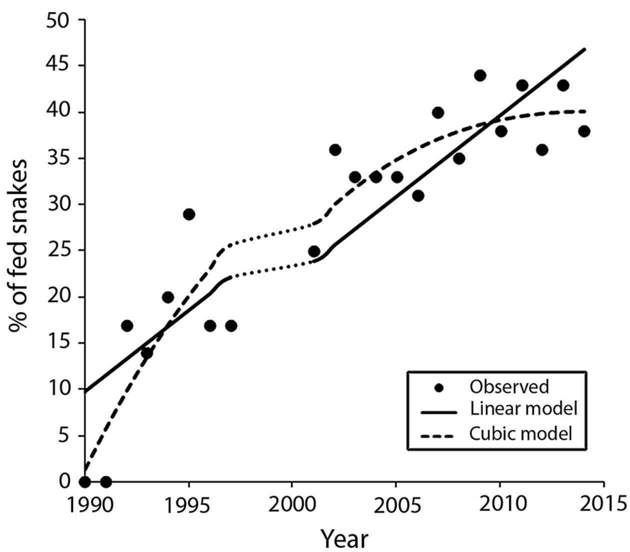

Fig. 2 Relationship between year and percent of fed snakes at the study area. The regression lines of linear and cubic models were added to the graphs, with the latter better fitting to the data. *Dotted lines* indicate a gap in the data (from 1998 to 2000)

The percentage of fed snakes increased significantly over the years ($R = 0.899$, $R^2 = 0.808$, $N = 22$, $P < 0.00001$; Fig. 2). However, the relationship was better explained by non-linear models (see Table 2), with percentage of fed snakes first increasing and then leveling out in a plateau (Fig. 2). Percentage of fed snakes also increased significantly over the years when the 2002–2014 dataset was analyzed ($R = 0.591$, $R^2 = 0.350$, $N = 13$, $P < 0.05$). There was a significantly positive effect of the mean annual temperature on the percent of fed animals both on the overall dataset ($R = 0.819$, $R^2 = 0.670$, $N = 22$, $P < 0.00001$) and the 2002–2014 dataset ($R = 0.735$, $R^2 = 0.541$, $N = 13$, $P < 0.005$). On the other hand, no relationship was detected between yearly rainfall and percentage of fed animals both on the overall dataset ($R = -0.291$, $R^2 = 0.085$, $N = 22$, $P = 0.227$) and the 2002–2014 dataset ($R = -0.102$, $R^2 = 0.010$, $N = 13$, $P = 0.739$). Number of favorable (sunny) days for snakes in active season did not influence the percentage of fed snakes both on the overall dataset ($R = -0.147$, $R^2 = 0.022$, $N = 22$, $P = 0.548$) and the 2002–2014 dataset ($R = -0.187$, $R^2 = 0.035$, $N = 13$, $P = 0.541$).

Summarized food data obtained from the overall female sample are reported in Table 3, and the food type dataset divided by year is given in Table 4. Since 2002, a considerably higher number of prey items was recorded annually (Table 4). This fact depended on that we expanded our surveyed area, thus collecting more snake specimens (for details, see Luiselli et al. 2011). Lizards represented the main bulk of the diet both overall and yearly (Tables 3, 4).

Yearly prey diversity was positively significantly related with the number of fed snakes ($R^2 = 0.336$, $N = 22$, $P < 0.05$), which was in turn proportional to the overall number of captured snakes ($R^2 = 0.628$, $N = 22$, $P < 0.01$). There was a significantly positive relationship between annual temperature and yearly number of examined snakes ($R = 0.471$, $R^2 = 0.687$, $N = 22$, $P < 0.005$). Another significant relationship was found between mean annual temperature and yearly evenness H' ($R^2 = 0.436$, $N = 22$, $P < 0.05$), but only excluding the data regarding to the year 2003 (a statistical outlier). No other climatic variables, already selected for the study of this snake population, were significantly correlated with H index (data available from authors, not shown for brevity).

Table 2 Statistics of the curve estimation procedure performed to assess which model type best fitted to the collected data

Model	R^2	d.f.	F	P	b0	b1	b2	b3
Linear	0.78	20	70.96	< 0.001	8.0032	1.7647		
Logarithm	0.872	20	136.06	< 0.001	−4.1663	14.7345		
Inverse	0.655	20	37.98	< 0.001	36.4465	−48.575		
Quadratic	0.875	19	66.41	< 0.001	−1.9973	4.2648	−0.1087	
Cubic	0.876	18	42.34	< 0.001	−3.4217	4.9347	−0.1799	0.0021

Comparison of R^2 values showed that data were best explained by non-linear models (cubic and quadratic)

Table 3 Food data obtained from the overall female sample of snakes at the study area

Species	No. of items	% of total diet
Podarcis muralis	47	55.3
Lacerta bilineata	8	9.4
Chalcides chalcides	3	3.5
Hierophis viridiflavus	2	2.4
Passerine birds	9	10.6
Undetermined rodents	5	5.9
Rattus rattus (juv)	8	9.4
Crocidura suaveolens	3	3.5

Discussion

Overall, we observed a dramatic yearly range of variation in terms of the proportion of fed snakes (0–43.8 %) during the May–June period. Certainly, this annual range of variation was deeply influenced by the very specific atmospheric conditions of the May–June period of each year, and probably also by prey availability. Atmospheric conditions are important because this species' activity is heavily dependent on external atmospheric conditions and specifically positively affected by high temperatures for its physiological performances (e.g., Lelièvre et al. 2010, 2012). Thus, for instance, the percentage of fed snakes tended to decrease in weeks with heavy rainfall accomplished to comparatively lower ambient temperatures (our unpublished observations). However, such yearly short-term effects were partly mitigated in our dataset given that heavy rainfall/low temperature conditions did not last for 7–8 weeks during late spring in Mediterranean central Italy, and snakes can start to forage quickly when such external conditions finish. In addition, our study was performed for such a long timespan (22 years) that short-term stochastic effects on percentage of fed snakes could be minimized.

The positive correlation at our study area between annual frequency of fed snakes and annual temperatures was consistent with the a priori hypothesis that warmer climate positively affected the feeding activity of Mediterranean snakes. It seems logical that the positive effect of warmer climate (= higher annual temperature) on Mediterranean snake feeding frequency is due to a prolonged time that these animals can spend in above-ground foraging activity (especially in spring and fall). Indeed, by examining monthly patterns of dead-on-road (DOR) specimens, it was demonstrated for the same population of western whip snakes that increasing ambient temperatures over the years caused an earlier onset of above-ground activity of snakes and delayed hibernation, albeit reducing the intensity of snake above-ground activity during the hottest and driest period of the year (Capula et al. 2014). Conversely, rainfall variables had no impact on long-term snake above-ground activity (Capula et al. 2014), and the same was true also on snake feeding frequencies (this study). It is noteworthy that the above-mentioned pattern was not linear, thus suggesting that a plateau is reached (type II functional response). In other words, this fact would mean that the response of snake populations to future increases in temperature may be different from those so far exhibited. Anyway, there are no data to explore whether any of the prey species are limited by predators. It is also to be pointed out that, winter temperature has

Table 4 Food data obtained from the female sample of snakes, divided by year and by individual, at the study area

Year	Prey items
1992	1 *Podarcis muralis*
1993	1 *Podarcis muralis*
1994	1 Passerine bird
1995	4 Newborn mice; 1 *Podarcis muralis*
1996	2 *Podarcis muralis*
1997	1 *Rattus rattus*
2001	1 Passerine bird
2002	1 Passerine bird; 1 *Podarcis muralis*; 2 *Podarcis muralis*; 1 *Rattus rattus*
2003	1 *Podarcis muralis*; 1 *Podarcis muralis*; 1 *Podarcis muralis*
2004	1 *Podarcis muralis*; *2 Podarcis muralis*; *1 Podarcis muralis*; *1 Rattus rattus*
2005	1 Passerine bird; 1 *Podarcis muralis*; 1 *Podarcis muralis*; 1 *Lacerta bilineata*; 1 *Lacerta bilineata*
2006	1 *Podarcis muralis*; *1 Podarcis muralis*; *1 Podarcis muralis*; *1 Rattus rattus*; *1 Chalcides chalcides*
2007	1 Passerine bird; 1 *Podarcis muralis*; *2 Podarcis muralis*; *1 Lacerta bilineata*; *1 Crocidura suaveolens*; 1 undet. Mouse
2008	1 *Podarcis muralis*; *1 Podarcis muralis*; *1 Podarcis muralis*; *1 Podarcis muralis*; *2 Podarcis muralis*; *1 Crocidura suaveolens*
2009	1 *Rattus rattus*; *1 Rattus rattus*; 1 Passerine bird; 1 Passerine bird; 1 *Podarcis muralis*; *1 Lacerta bilineata*; *1 Lacerta bilineata*
2010	1 *Podarcis muralis*; *1 Podarcis muralis*; *1 Podarcis muralis*; *1 Podarcis muralis*; *1 Lacerta bilineata*
2011	1 *Podarcis muralis*; *1 Podarcis muralis*; *1 Podarcis muralis*; *1 Podarcis muralis*; *2 Chalcides chalcides*; *1 Crocidura suaveolens*
2012	2 *Podarcis muralis*; *1 Lacerta bilineata*; *1 Rattus rattus*; *1 Hierophis viridiflavus* newborn
2013	1 *Podarcis muralis*; *1 Podarcis muralis*; *1 Passerine bird*; *1 Passerine bird*; *1 Lacerta bilineata*; *1 Rattus rattus*
2014	1 *Podarcis muralis*; 1 *Podarcis muralis*; 1 *Podarcis muralis*; 1 *Podarcis muralis*; 1 *Podarcis muralis*; 1 *Hierophis viridiflavus* (newborn)

The symbol ';' denotes a prey content coming from a distinct snake individual from the previous individual in a given year not the same influence on snakes compared to temperature during activity period. For instance, increase of temperature during winter could negatively influence snake survival, by increasing metabolic rate and energy expenditure during hibernation. On the other hand, an elevation of temperature during activity period may increase predation risk, because of increased time spent above ground. In this cost/benefit context of thermoregulation, ultimate fitness gain of climate warming is not necessarily associated with better fitness. For instance, climate warming may be positive for thermophilic species such as our study species but not necessarily for other species which have colder preferenda (e.g., *Zamenis longissimus*, as for sympatric species is concerned). In addition, the adaptive advantage of temperature elevation depends directly on prey availability, as high temperature associated with low food availability should be certainly detrimental for the study species.

As expected, prey diversity increased linearly with sample size, but we also found that there was a significant relationship between annual temperature and prey diversity. Specifically, the more the annual temperature increased, the more diverse the snake diet became. We acknowledge that this noteworthy pattern may be linked to the collinearity between annual temperature increases and yearly number of examined snakes. However, it is also possible that the climate-warming-derived increased time available to snakes for their foraging activities may enhance their probability of meeting with a more variable spectrum of potential prey types, thus influencing their overall diet composition. Our observations may also reflect a positive effect of growing season length on the lizards and other prey populations. Indeed, since some of the prey are also ectothermic, they may be responding to climate change in similar ways. Unfortunately, we do not have demographic data on lizards to explore any interannual variations in their population sizes.

In conclusion, our study, although mostly correlational and based only on a single snake population monitored over long-time, supports the notion that global warming may be favorable for Mediterranean snake populations, as it enhances their foraging performances and in turn their feeding frequencies (see Rugiero et al. 2012a, 2013a). However, although the fitness component investigated responded positively to the increase in temperature, our analysis suggested that a maximum has been reached: therefore, it is likely that the response to further, future increases in temperature will not be the same as recorded so far. It should also be taken into account that gravid females may be consistently more anorexic than non-gravid females or males (e.g., Gregory et al. 1999), thus the feeding frequencies reported in this study may be lower than those relative to conspecific non-gravid females and males at the same study area. The transitory anorexia of gravid females is due to the presence of eggs which obstruct digestive tract. Thus, it cannot be excluded that the observed increase in proportion of fed individuals only exists in gravid females because other snakes usually feed more often and have already often the maxima in time spent foraging (the ‘‘plateau’’ in present study). Maybe only individuals which usually do not feed during this period (especially gravid females) will shift in foraging strategy if thermal conditions are warmer.

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References

Angilletta MJ Jr (2006) Estimating and comparing thermal performance curves. J Thermal Biol 31:541–545

Araujo MB, Thuiller W, Pearson RG (2006) Climate warming and the decline of amphibians and reptiles in Europe. J Biogeogr 33:1712–1728

Avery RA (1978) Activity patterns, thermoregulation and food consumption in two sympatric lizard species (*Podarcis muralis* and *P. sicula*) from central Italy. J Anim Ecol 47:143–158

Capizzi D, Capula M, Evangelisti F, Filippi E, Luiselli L, Trujillo Jesus V (1996) Breeding frequency, clutch size, reproductive status and correlated behaviours in sympatric females *Elaphe quatuorlineata* and *Elaphe longissima* (Reptilia, Colubridae). Rev Ecol (Terre et Vie) 51:297–311

Capula M, Rugiero L, Capizzi D, Milana G, Vignoli L, Franco D, Petrozzi F, Luiselli L (2014) Long-term, climate-change-related shifts in monthly patterns of roadkilled Mediterranean snakes (*Hierophis viridiflavus*). Herp J 24:97–102

Filippi E, Anibaldi C, Capizzi D, Ceccarelli A, Capula M, Luiselli L (2007) Long-term fidelity to communal oviposition sites in *Hierophis viridiflavus*. Herp J 17:7–13

Gregory PT, Crampton LH, Skebo KM (1999) Conflicts and interactions among reproduction, thermoregulation and feeding in viviparous reptiles: are gravid snakes anorexic? J Zool (Lond) 248:231–241

Huey RB, Stevenson RD (1979) Integrating thermal physiology and ecology of ectotherms: discussion of approaches. Am Zool 19:357–366

Janzen FJ (1994) Climate change and temperature dependent sex determination in reptiles. Proc Natl Acad Sci USA 91:7487–7490

Lelièvre H, Le Hénanff M, Blouin-Demers G, Naulleau G, Lourdais O (2010) Thermal strategies and energetics in two sympatric colubrid snakes with contrasted exposure. J Comp Physiol B 180:415–425

Lelièvre H, Legagneux P, Blouin-Demers G, Bonnet X, Lourdais O (2012) Trophic niche overlap in two syntopic colubrid snakes (*Hierophis viridiflavus* and *Zamenis longissimus*) with contrasted lifestyles. Amph-Rept 33:37–44

Lourdais O, Shine R, Bonnet X, Guillon M, Naulleau G (2004) Climate affects embryonic development in a viviparous snake, *Vipera aspis*. Oikos 104:551–560

Luiselli L, Rugiero L, Capula M (2011) Are communal nesting counts as useful as mark-recapture data for estimating population size in snakes? Herp J 21:73–81

Rugiero L, Milana G, Capula M, Amori G, Luiselli L (2012a) Long term variations in small mammal composition of a snake diet do not mirror climate change trends. Acta Oecol 43:158–164

Rugiero L, Capula M, Vignoli L, Luiselli L (2012b) Offspring condition determines dispersal patterns in Western whip snakes, *Hierophis viridiflavus*. Herp J 22:259–261

Rugiero L, Milana G, Petrozzi F, Capula M, Luiselli L (2013a) Climate-change-related shifts in annual phenology of a temperate snake during the last 20 years. Acta Oecol 51:42–48

Rugiero L, Capula M, Vignoli L, Luiselli L (2013b) Interpreting dispersal patterns of reproductive female *Hierophis viridiflavus* (Lacépède, 1789), around a communal nesting site. Herpetozoa 25:143–150

Smit B, Wandel J (2006) Adaptation, adaptive capacity and vulnerability. Global Environ Change 16:282–292

Thomas CD, Cameron A, Green RE, Bakkenes M, Beaumont LJ, Collingham YC, Erasmus BFN, de Siqueira MF, Grainger HL, Hughes L, Huntley B, van Jaarsveld AS, Midgley GF, Miles L, Ortega-Huerta MA, Townsend Peterson A, Phillips OL, Williams SE (2004) Extinction risk from climate change. Nature 427:145–148

Tomaselli R, Balduzzi A, Filipello S (1973) Carta bioclimatica d'Italia. Roma (Ministero dell'agricoltura e delle foreste, Collana Verde no. 33)

Ujvari B, Shine R, Luiselli L, Madsen T (2011) Climate induced reaction norms for life-history traits in pythons. Ecology 92:1858–1864

Walther GR, Post E, Convey P, Menzel A, Parmesan C, Beebee TJ, Fromentin GM, Hoegh-Guldberg O, Bairlein F (2002) Ecological responses to recent climate change. Nature 416:389–395