Patterns of seasonal activity in a Mediterranean lizard along a 2200 m altitudinal gradient

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ABSTRACT

Ectothermy in reptiles involves strong environmental temperature dependence to maintain body temperature. High mountains are extreme habitats which, because of their marked temperature decrease with altitude, impose difficulties for reptile thermoregulation, as the number of optimum-temperature days diminish in altitude. We studied the activity patterns of the lizard *Psammodromus algirus*, which has a wide altitudinal distribution, at six sampling stations that spanned an altitudinal range from 300 to 2500 m asl in Sierra Nevada (SE Iberian Peninsula). We performed censuses of the species during the seasonal and daily activity period, and measured lizard body temperature and environmental temperature in the six sampling plots along the altitude gradient. The body temperature of the lizards remained closely the same even though environmental temperature decreased around 9 °C along that gradient. Seasonal activity peaked at the beginning of the activity period in highlands, but in the middle of the season in middle and lowland regions. However, newborns appeared in the field almost at the same time along the altitude gradient. We suggest that the thermoregulatory strategies of the lizards must vary along this altitudinal gradient, permitting lizards to keep their body temperature close to a very similar optimum and thus, develop very similar circa-annual activity patterns.

1. Introduction

The activity patterns of animals depend on both biotic (ecological interrelationships, vegetation structure, etc) and abiotic factors (altitude, environmental temperature, moisture, etc) in the environment they inhabit. Reptiles, as ectotherms, are strongly dependent on environmental temperature for maintaining their physiology (Bennet, 1980). They display a set of mainly ethological mechanisms to keep their body temperature as close as possible to their metabolic optimum (Hutchinson and Maness, 1979). Preferred temperature range (PTR; Hertz et al., 1993) is defined as the body temperature range ectotherms select. At PTR, locomotion, digestion and metabolism are supposed to be the most effective for the highest maintenance and production rates (Adolph and Porter, 1993). Thus, reptile dependence on environmental temperature may constrain their life-history patterns, and limit their ability to live in cold habitats, where heat sources are less available (Hertz et al., 1993).

Due to environmental constraints, the PTR of terrestrial reptiles varies with latitude both inter and intraspecifically, diminishing the lower thermal limits as latitude increases (Sunday et al., 2010). As environmental temperature follows a similar pattern with latitude

and altitude (Graae et al., 2012), we can also expect a PTR variation with altitude. High mountains encompass extreme low temperature habitats (McCain, 2010), and overall, gradients of environmental parameters such as temperature, solar radiation, and atmospheric pressure occur from low to highlands (Körner, 2007). Days and hours with suitable temperature during the reptile activity season diminish as altitude increases, which seriously limits reptile thermoregulation capabilities in high elevations. This variation in the thermal environment is likely to involve differences in the thermoregulatory needs of lizards, behaviors and phenology along altitudinal gradients (Adolph and Porter, 1993; Chettri et al., 2010; Gutiérrez et al., 2010). Nevertheless, there are opposing effects of the adiabatic temperature decrease and the increase in solar radiation in altitude (Angilletta, 2009). As altitude increases, the narrower depth of atmosphere results in a higher transmission of radiation (Gates, 1980). This could have buffering consequences in the operative temperatures of lizards at high altitude.

Phenology is a key aspect in an organism's life history: cardinal phenomena, such as hibernation, gametogenesis, mating, egg-laying and hatching or parturition, may cause a reproductive failure or death if they do not take place in the appropriate time (Mathies and Andrews, 1995; Sinervo and Adolph, 1989). This is especially relevant in short-lived animals such as many lizards, since they may lose one of their scarce, or even their only, opportunity to reproduce. Because of their ectothermy, reptile phenology is closely constrained by the thermal cycle in their

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habitat (Moreno-Rueda et al., 2009; Smith, 1998), so it is expected to vary with altitudinal gradients (Mathies and Andrews, 1995; Navas, 2002). Reptiles must synchronize their activity patterns with the daily and annual thermal cycles, in order to optimize their productivity (Ibargüengoytía, 2005). Therefore, lowland and highland reptiles are expected to have different phenology due to the different climatic conditions they experience (Castilla et al., 1999). Moreover, the lower thermal availability with altitude might cause differences in field body temperature and phenology. Otherwise, reptiles could be locally adapted, in which case phenology and body temperature could not be as different as expected considering the contrasting climatic conditions along the altitudinal gradient.

In this work, we analyzed circadian and circa-annual activity patterns of the Large Psammodromus lizard (Psammodromus algirus) along an altitudinal gradient, in Sierra Nevada (SE Spain). In the region, the species can be found from sea level to more than 2500 m asl (Salvador, 2011), being one of the widest altitudinal ranges for a single lizard species in Europe. Therefore, this species is an ideal model for the study of the effects of altitude on reptiles. In lowlands, high environmental temperature might limit lizard activity during summer, whilst in highlands, low environmental temperature might constrain activity in spring and autumn. In this altitude gradient, we predict that the circadian activity patterns within the same season and circa-annual activity cycles will be wider in lowlands. On the other hand, if some degree of local adaptation exists, highland lizards will be active at lower temperatures than lowland lizards.

2. Materials and methods

Psammodromus algirus is a medium-sized lacertid distributed in South West Europe and North West Africa, strongly linked to warm Mediterranean areas with shrub formations (Salvador, 2011). It behaves as an eurioic and generalist species for most of its ecological traits. This lizard is diurnal and avoids the coldest time of the year by hibernating for a variable period, from October–November until March–April, depending on the environmental temperature. The taxonomy of this species is controversial (Verdú-Ricoy et al., 2010), but all the populations studied here belong to the same clade.

The field work was performed in 2010, in the southern slope of Sierra Nevada (SE Spain), which shows a pronounced altitudinal range (200–3481 m asl). We established six sampling stations in the study area, separated by about 500 m in altitude from each other, from 300 to 2500 m asl (Appendix A), within the altitudinal range of the species in the study area (200–2600 m asl). All sampling stations met the ecological requirements of P. algirus, i.e.: shrubs and bushes 40–100 cm high and rather high vegetation cover (Díaz and Carrascal, 1991; Appendix A). Mean vegetation cover ranged between 53% and 67%, except for 2200 m asl, where it reached 82%. For the six sampling stations, neither vegetation cover nor mean shrub height followed any clear altitudinal pattern (Appendix A).

To quantify lizard activity, we performed 500 m transects every 2 weeks in each sampling station during the annual activity season of the lizard in the study area (ca. April–October), although we began in May in the highest sampling station, because the access was closed by snow. Censuses were replicated every 2 h during daytime, from sunrise to sunset, and we recorded the number of active adult and newborn individuals seen in each transect. We assumed the detectability of lizards to be the same in all sampling stations. Air temperature was measured 1 m above the ground, under a shadow, using a thermometer Hibok 14 (accuracy 0.1 °C). This census method allowed us to quantify the relative circadian and circa-annual activity of lizards with altitude

for comparative purposes in relation to temperature (Blomberg and Shine, 1996). Number of active individuals obtained by this procedure are assumed to be positively related to the real population density (Díaz et al., 2006b).

We captured adult individuals from the study area, but far away (> 100 m) from the transect zone. We measured the body temperature of lizards within 30 s of capture, with a 1-mm diameter thermocouple, 8 mm inside the cloaca (TP (K) INCONEL 600), assembled to the thermometer (Hibok 14). At the same time, air temperature was also measured as during transects (above). This allowed us to compare body temperature of active individuals with environmental temperature. We used 5×1 cm hollow copper models in order to obtain which temperature lizards would show if they did not actively thermoregulate (null hypothesis). Copper models heat up like a lizard, and have been largely used for similar purposes in this and other species (Bauwens et al., 1996; Díaz, 1997). Models were almost totally sealed in their both ends with synthetic corks, except for a small hole in one of them to insert the thermocouple. In every sampling plot, we placed 31 hollow copper models separated 1 m one from another, with a "ventral" part in contact with the substrate. We measured the temperature of every model five times, once an hour, during the morning, in every sampling plot, recording the environmental temperature in each case as described above. We recorded whether each model were fully exposed to sun (F), partially exposed (P), or under a shadow (S).

All data were analyzed with parametric tests when the residuals accomplished the assumptions of homoscedasticity and normality (Quinn and Keough, 2002), otherwise we applied non-parametric tests (Siegel and Castellan, 1988). We tested whether the mean appearance date of newborns varied with altitude by ANOVA. For analyzing the circa-annual variation in adult activity, we used the average of the adult observations made in all transects of every sampling day by altitude sampling plot. We considered three seasons: Spring (April, May, June), with months of increasing average environmental temperature; Summer (July, August), with months of asymptotical high temperature; and Autumn (September, October), with months of decreasing average environmental temperature. We considered two independent variables: season and altitude (categorical), and conducted a General Linear Model (GLM) of Ordinal Least Squares (OLS). In order to analyze the circadian activity patterns of adults, we tested for seasonal and altitudinal differences among three defined hourly intervals: H1 from sunrise to 11:59, H2 from 12:00 to 15:59, H3 from 16:00 to sunset. We performed a three-ways ANOVA, and analyzed the interactions among hour, season and altitude. To know how the operative temperature of lizards varied with altitude, we analyzed the temperature of the copper models by an ANOVA, including the altitude, the exposure to sun, and the interaction between them. We repeated the analysis controlling for the environmental temperature at the time of the measurement, to obtain information about the effects of heat sources other than air temperature, i.e., solar radiation.

3. Results

3.1. Temperature and activity

Environmental temperature measured in transects (T_t) diminished significantly as altitude increased ($F_{5, 63} = 6.10$; $p = 0.0001$), and varied with the activity season, with a maximum in mid season (Kruskal–Wallis $H_{6, 69} = 22.40$, $p = 0.001$; Fig. 1). When we found active lizards in transects, T_t was higher than when we did not (20.77°C $\pm$ SE $= 0.34$ vs. 19.25°C ± 0.48, respectively; $F_{1,351} = 6.64$; $p = 0.01$), suggesting that lizards were active when temperature was higher. Lizards were active at lower T_t as altitude increased ($F_{5,216} = 14.48$; $p < 0.001$). The temperature of
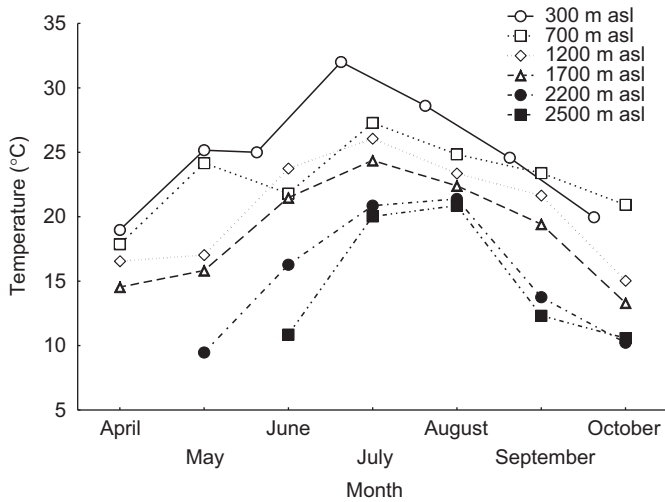
Fig. 1. Altitudinal variation of average monthly air temperature (°C) (measured 1 m above the ground) along the activity period of *Psammodromus algirus* in the southern slope of Sierra Nevada (SE Spain).
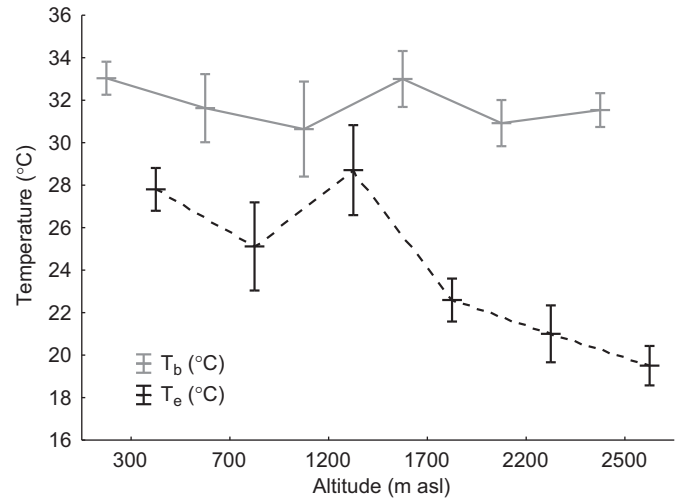

Fig. 3. Body temperature (T_b) of *Psammodromus algirus* and environmental temperature (T_e) in the six sampling plots ranked according altitude in Sierra Nevada (SE Spain). Bars indicate 95% Confidence Intervals.
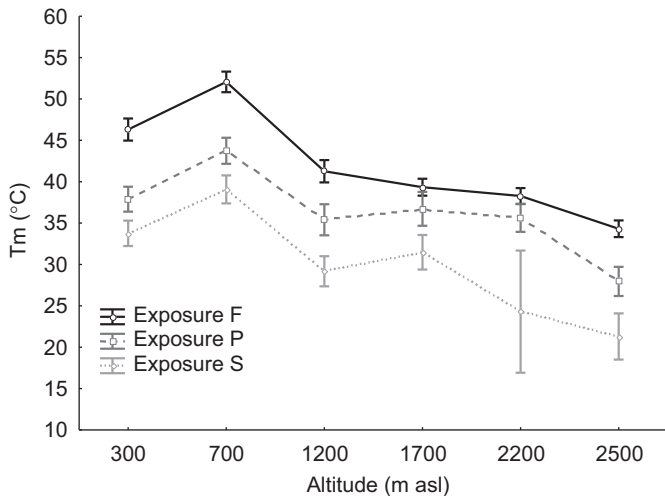

Fig. 2. Copper models temperature (T_m) diminished as altitude increased, following similar patterns in fully sun-exposed (Exposure F, continuous line), partially exposed (Exposure P, discontinuous line) and shadowy (Exposure S, spotted line) models. Bars indicate 95% Confidence Intervals.
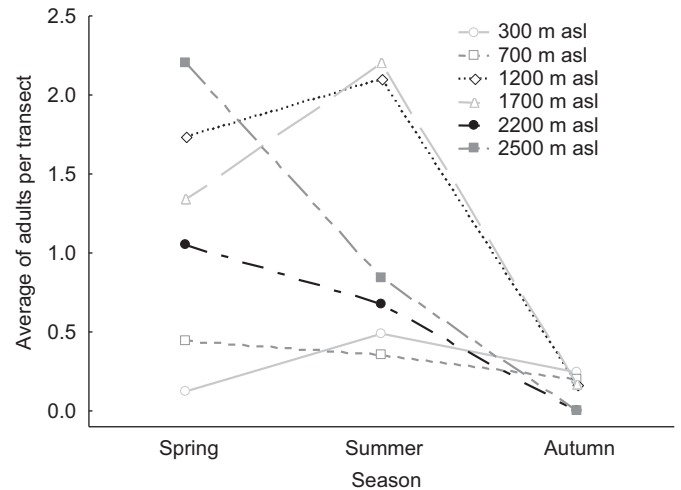

Fig. 4. Altitudinal variation in the number of *Psammodromus algirus* individuals censed along the three seasons of the activity period in Sierra Nevada (SE Spain).

the copper models (T_m) showed a general tendency to fall as altitude increased ($F_{5,\,882}=122.15$; $p < 0.0001$; Fig. 2). Copper model temperature depended on the degree of exposure to sun of the model ($F_{2,\,882}=176.28$; $p < 0.0001$), being highest in totally exposed models, intermediate in partially exposed models, and minimum in totally shadowed models. When controlling for environmental temperature at the time of the measurement, T_m tended to increase with altitude ($F_{5,\,881}=24.758$; $p < 0.0001$), suggesting that thermal sources other than air temperature contributed to warm copper models.

We found slight differences between sampling stations in body temperature (T_b) of active lizards ($H_{5,\,207}=13.25$, $p=0.02$), but with no clear pattern with altitude (Fig. 3). Environmental temperature when active lizards were caught (T_e) diminished significantly with altitude ($F_{5,\,206}=35.31$; $p < 0.001$; Fig. 3), suggesting that as altitude increases, lizards may be active at lower environmental temperatures. We also found that the relationship between T_e and T_b differed with altitude (significant interaction, $F_{5,195}=5.34$; $p < 0.001$). Body temperature of active lizards was

not correlated with T_e in 300, 700 and 1700 m asl ($p > 0.50$ in all cases), but it was positively correlated with T_e in 2500 m asl ($r=0.39$; $p=0.006$) and 2200 m asl ($r=0.27$; $p=0.06$). We also found a significant negative correlation between T_b and T_e in 1200 m asl ($r=-0.62$; $p=0.004$).

3.2. Circa-annual and circadian activity patterns

The number of adults observed in transects showed a significant variation with altitude ($F_{5,\,54}=5.45$; $p=0.0004$), being maximum in mid altitudinal ranges, intermediate in highlands and minimum in lowlands (Fig. 4). The interaction between altitude and season was significant ($F_{10,\,54}=2.17$; $p=0.034$): relative density had a peak in the middle of the activity period, except in the highest altitudes, where it peaked at the beginning of the activity season (Fig. 4). This implies that the seasonal activity patterns varied with altitude. The appearance mean date of newborns did not show statistical differences with altitude ($F_{5,\,26} < 0.01$; $p=0.89$). The variance of newborn appearance did not vary with altitude, either (Levene's test, $p=0.53$). The number of active individuals detected did not vary with the hourly interval ($F_{2,\,326}=1.94$; $p=0.14$). The statistical interaction

between season and hour ($F_{4, 326}=1.48$; $p=0.21$), between hour and altitude ($F_{10, 326}=1.62$; $p=0.10$), and the triple interaction between hour, altitude and season, were not significant ($F_{20, 326}=0.96$, $p=0.51$). Thus, we detected no clear variation in circadian activity pattern.

4. Discussion

4.1. Activity patterns

Reptile activity patterns show close connection with many factors (Díaz et al., 2005a), such as population density, habitat availability, prey abundance, predation pressure, and mainly environmental temperature (Moreno-Rueda et al., 2009; Nelson and Gregory, 2000; Vidal et al., 2010). As some of these factors vary with altitude, particularly thermal environment, we could expect lizard activity patterns to be dissimilar along an altitudinal gradient (Grant and Dunham, 1990). We found that environmental temperature fell with altitude, but kept a very similar seasonal pattern across all the gradient: rising temperature during spring, a peak in July–August, and falling temperature from August onward. The activity patterns of lizards were related to these seasonal temperature-changes in mid and low altitudes, reaching a maximum of activity in the middle of the activity period, which coincided with the highest temperatures. The higher heat availability at mid season could increase their thermoregulation accuracy, augmenting their chance to reach their optimum body temperature faster (Huang et al., 2006). But in the two highest altitudes, the activity peaks occurred at the beginning of the season, when the environmental temperature is not the highest (compare Fig. 1 vs. Fig. 4). The activity period of lizards (both, seasonal and daily) should be narrower as altitude increases, as the availability of optimum-temperature days in year, and hours in day, falls. Therefore, high altitude lizards would have less time to forage and reproduce. However, they could counter this thermal constraint by an early activity peak; waiting for higher activity at the thermally more favorable summer period would cause a delay in mating that could lead to a reproductive failure in the year. Highland lizards were active at lower environmental temperatures, which enabled these lizards to be more active at the beginning of the seasonal activity period.

Differences in reproductive phenology are also expected to arise in this thermal gradient (Díaz et al., 2005b; Doughty and Shine, 1998). However, newborns appeared at the end of the activity season, in near synchrony along the gradient. This reproductive synchrony, altogether with similar adult field body temperature along the gradient, may point to altitudinal differences in thermoregulation which are necessary to develop similar reproductive cycles in quite a different set of habitat conditions (Du et al., 2005).

Although environmental temperature changed within daytime, circadian activity showed no clear pattern with altitude, and active lizards were found at any sunny hour in day. This supports the idea that lizards possess capabilities to counter thermal constrains (Bauwens et al., 1996).

4.2. Thermal gradient

The difference of the average environmental temperature (T_e) between the highest and the lowest altitudes was about 9 °C. Despite this thermal gradient, the difference in the average body temperature (T_b) of active lizards among sampling stations was quite small, with no clear altitudinal pattern. Thus, P. algirus was a thermally conservative lizard in the altitudinal gradient of Sierra Nevada. In fact, we found no significant correlation between T_b

and T_e in the medial and lowest altitudes (except at 1200 m asl). However, T_b was positively correlated with T_e at the highest altitudes. This result suggests that thermoregulation in this lizard is not limited by T_e in low and midlands. Nevertheless, thermoregulation seems to be limited in highlands, where T_e is positively correlated with lizard T_b, probably because an increase in T_e in highlands allows lizards to reach a T_b closer to optimum. The fact that P. algirus reaches similar T_b in spite of strong differences in T_e with altitude suggests that this lizard possess different thermoregulatory capabilities along the gradient. Díaz et al. (2006a) studied P. algirus thermal preferences in two 700-altitude-meters separated sampling plots in central Spain, and they also failed to find differences in thermal preference, which supports our findings. The altitudinal pattern found in this lizard is similar to other thermally conservative species, as the wide-distributed lizard Microlophus atacamensis which shows no latitudinal differences in field body temperature (Sepúlveda et al., 2008). Similarly, lizards of the genus Sceloporus have no significant variation in body temperature in altitudinal gradients, from 45 to 4400 m asl (Andrews, 1998).

Temperature measured in copper models (T_m) decreased with altitude in a similar way as T_e. However, when we controlled statistically for environmental temperature of the air, T_m increased with altitude, suggesting that solar radiation contributed to increase the temperature of the copper models. Nevertheless, the effect of increased solar radiation with altitude was not enough to counteract the adiabatic cooling with altitude. Considering all models (totally exposed to sun, partially exposed, and totally shadowy), T_m differed 12 °C between the lowest and the highest altitudes. Therefore, copper models reflect that, if lizards were not capable of active thermoregulation their T_b would decrease as altitude increases, and altitudinal differences would be similar (12 °C) to T_e altitudinal differences (9 °C). The small differences in T_b between sampling stations we found had no altitudinal pattern, which suggested the presence of an active thermoregulation strategy (Díaz and Cabezas-Díaz, 2004).

4.3. Thermoregulation mechanisms

All previous results suggest differences in thermoregulation with altitude that may permit animals under very different thermal conditions to reach a similar optimum temperature and, thus, develop similar circa-annual activity and reproductive patterns (Bauwens et al., 1996). Many factors, such as solar radiation, convective heat flow, longwave radiation, conductive heat flow, metabolic heat gain and respiratory energy loss, are involved in lizard thermoregulation, as can be seen in recent physical models (Fei et al., 2012). The relative importance of some of those factors may vary seasonally (Díaz and Cabezas-Díaz, 2004), so their seasonal availability with altitude may constrain P. algirus thermoregulation capabilities.

Several physiological or ethological traits could permit high altitude lizards in our study to reach body temperatures as high as low altitude lizards, despite the lower environmental temperature. A trait implicated in the thermoregulation of an animal is coloration, since darker animals heat faster than pale ones (Clusella-Trullas et al., 2007, 2008). In our study, lizard dorsal coloration is significantly darker at high altitude (Reguera et al., submitted for publication). Dark coloration could protect highland lizards against the harmful effects of ultraviolet radiation (Porter and Norris, 1969), help them benefit from the altitudinal increase in radiation to warm up faster (Vences et al., 2002), or both.

The basking behavior may be a key ethological thermoregulatory mechanism in these diurnal lizards (Belliure and Carrascal, 1998). The time a lizard spends basking has been proved to depend on environmental factors such as light composition, increasing basking time when wavelengths < 540 nm are removed (Tosini

and Avery, 1996a), and physiological factors such as dermal light sensibility, which determines its ability to position under a heat source (Tosini and Avery, 1996b). For example, the high altitude lizard *Iberolacerta monticola* spends more time basking when environmental temperature is lower, but basks more frequently and for shorter periods when environmental temperature is higher (Carrascal et al., 1992). Small lizards have shorter basking periods, as they heat up faster, and there could be an inverse relationship between body size and heat gain (Carrascal et al., 1992). In our study, lizards are larger at high altitude (unpublished data), so they could reach high temperatures by spending more time basking. Furthermore, larger body mass with altitude slows down cooling rates, helping lizards to maintain high temperature once reached (unpublished data). Differences in thermoregulation according to altitude could be defined as phenotypic plasticity or local adaptation mechanisms. Phenotypic plasticity could mean a higher individual possibility to move among different habitats (Lorenzon et al., 2001), as the same genotype can result in different phenotypes depending on the environmental pressures during the organism development. Then, plastic individuals could survive under different environmental conditions, and some degree of gene flow can be possible between disparate habitats. Otherwise, local adaptation implies a scenario that limits gene flow among populations because of a negative selection on the individuals allocated outside from the habitats they are adapted to (North et al., 2011). Therefore, population differentiation may occur in the second case (Palo et al., 2003). Thereby, local selection has been pointed as a determinant factor in coloration differentiation in Aegean lizard (*Podarcis gaigeae*) populations between the continent and some islets they inhabit (Runemark et al., 2010).

4.4. Implications under the global change scenario

Mediterranean animals have evolved in a rather unpredictable climate, they are adapted to survive to short-term environmental variations, so they may be able successfully to face the present Global Warming (Chamaillé-Jammes et al., 2006; Moreno-Rueda and Pleguezuelos, 2007; Zamora-Camacho et al., 2010). In mountains, the Global Warming is expected to allow animals to increase their altitudinal upper limit for their thermal optimum; otherwise, some of them could come extinct (Wilson et al., 2005). In the case of *P. algirus*, our results suggest few thermal limitations arise to prevent populations to extent their altitudinal range in response to climatic change. Limitations for this species can be related to availability of shrub formations, which in the southern slope of Sierra Nevada now arrive to 2600 m asl. However, if bushes also respond to Climate Change by extending their altitudinal range (Randin et al., 2009; Benito et al., 2011), then lizards should be able to follow them. If this ability is similar in other species, we expect Mediterranean reptiles from low and mid altitudes to have little trouble in colonizing higher altitudes, mainly if their capability to face different environmental conditions is due to phenotypic plasticity mechanisms. But Eurosiberian species which are now isolated in high altitudinal ranges, like the smooth snake, *Coronella austriaca*, in Sierra Nevada (Santos et al., 2009; Caro et al., 2012), may then suffer from the new Mediterranean incomers, some of them acting either as predators or competitors. In that forecasted scenario, Eurosiberian species in Mediterranean mountains could be the losers.

4.5. Conclusions

Psammodromus algirus showed to be a thermoconservative lizard in Sierra Nevada. Field body temperature were rather similar along a 2200-m altitudinal gradient, whilst the average environmental temperature decreased more than 9 °C within the same

altitude range when lizards were active. Circa-annual activity peak occurred at the beginning of the season at high altitude, despite the warmest period being later, probably because the constraint in reproductive time requires full activity immediately after emergence from hibernation. In mid and lowlands, when time for reproduction is wider, the activity peak occurred in mid-season, when the temperature is highest, as expected. Nevertheless, newborns appeared in synchrony all along the gradient and almost at the same time of the year, meaning altitudinal similitude in reproductive cycles in spite of strong environmental shift. These findings point to differences in thermoregulatory mechanisms with altitude that permit lizards to exploit dissimilar environmental heat conditions and reach similar body temperature and synchronized reproductive cycles.

Appendix A. Supplementary information

Supplementary data associated with this article can be found in the online version at http://dx.doi.org/10.1016/j.jtherbio.2012. 11.002.

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