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Seasonality provokes a shift of thermal preferences in a temperate lizard, but altitude does not

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Abstract

1. We compared the mean, limits and breadth of the preferred thermal range (PTR) of two Iberian populations of the lizard *Psammodromus algirus* separated by 700 m altitude in May and July.

2. Seasonality had a pronounced effect on the mean and limits of PTR, but altitude and sex did not. The breadth of PTR remained constant between seasons.

3. The observed seasonal shift in PTR facilitated thermoregulation in May but not in July.

4. The location, breadth, and seasonal shift of PTR may be a result of the neurohormonal effects of the photoperiod and the functional implications of body temperature for muscle-contraction speed.

Keywords: Altitudinal variation; *Psammodromus*; Seasonality; Selected temperature range; Thermoregulation

1. Introduction

Thermoregulation may be defined as the maintenance of body temperature (T_b) within a specified range, the preferred temperature range (PTR), when operative temperatures (T_e's) extend above and below that range. It is an active process that can be demonstrated by comparing the deviations from PTR of the T_b's of animals with the deviations from PTR of the environmental temperatures available (Hertz et al., 1993). If such deviations are smaller for T_b's than for T_e's, it can be concluded that animals are actively regulating their T_b (Hertz et al., 1993; Bauwens et al., 1996; Díaz, 1997; Gvoždik, 2002). Because lizards thermoregulate between lower and upper threshold temperatures (Barber and Crawford, 1977), an adequate knowledge of the set-points that enclose PTR is essential for evaluating the extent and mechanisms of thermoregulation (Hertz et al., 1993; Bauwens et al., 1996; Díaz and Cabezas-Díaz, 2004). These set-points can best be measured in a laboratory thermal gradient where environmental constraints can be controlled, thus allowing to estimate the T_b's that ectotherms would attempt to attain in the field in the absence of physical or biotic restrictions (Huey, 1974; Christian and Tracy, 1981; Van Marken Lichtenbelt et al., 1997; Brown and Griffin, 2005).

However, PTR should not be considered as a fixed trait. Instead, several studies have demonstrated that the thermal preferences of lizards vary among age classes, sexes, and seasons (Patterson and Davies, 1978; Huey, 1982; Van Damme et al., 1986). Sexual and seasonal differences have been attributed to changes in the physiological requirements of reproduction (Joly and Saint Girons, 1975; Rock et al., 2000; Rock and Cree, 2003). For instance, pregnant females of several species of (ovo)viviparous lizards select lower temperatures than non-pregnant ones (Mathies and Andrews, 1997; Le Galliard et al., 2003), presumably to avoid decrements in offspring fitness. Seasonal changes in PTR are seemingly triggered by the neuroendocrine coupling between photoperiod and temperature selection (Underwood, 1992). In laboratory simulations, longer photoperiods lead to an activation of the rhythm of T_b selection, whereas fall photoperiods lead to an overall decline in T_b until rhythmicity disappears (Rismiller and

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Heldmaier, 1988). Of course, reproductive activity undergoes seasonal cycles in most species (Nelson et al., 1990; Díaz et al., 1994), so that both types of explanations (functional and causal) are complementary rather than mutually exclusive.

However, the functional significance, or even the very existence of geographical variations in PTR, is much less clear. Variations in selected temperatures between low- and high-altitude populations were negligible in *Anolis cristatellus* (Huey and Webster, 1976), *Tarentola boettgeri* (Brown, 1996), *Lacerta vivipara* (Van Damme et al., 1990; Gvoždik and Castilla, 2001), and *Podarcis tiliguerta* (Van Damme et al., 1989). This lack of altitudinal variation is surprising because in some cases the T_b's of field-active montane lizards fell several °C below PTR, severely impairing locomotion (Van Damme et al., 1989, 1990). Although some studies have indicated a possible differentiation of thermal preferences between various European populations of *L. vivipara* (Van Damme et al., 1986; Gvoždik and Castilla, 2001), unequivocal evidence for such differentiation is not available, since it is difficult to prove that the reported variations are not an artifact due to differences in experimental procedures or equipment (Van Damme et al., 1986).

In this study, we compare the selected temperatures measured under identical laboratory conditions of two populations of the temperate lizard *P. algirus* separated by 700 m altitude in central Spain. We also explore the effects of seasonality on T_b selection by comparing the thermal preferences of lizards from both sexes in spring (May: breeding season) and summer (July: post-breeding season), and we consider the extent to which field thermoregulation is facilitated by seasonal shifts in PTR. For each individual, we calculate the lower and upper limit and the breadth of the preferred temperature range. Our objectives are: (1) to estimate PTR for each individual lizard considering not only its central tendency (mean) but also its breadth and limits; (2) to compare the extent to which PTR characteristics vary among individuals, sexes, populations or seasons; and (3) if such differences exist, to discuss their possible functional significance and the mechanisms that may be responsible for the observed patterns of geographical or seasonal variation.

2. Materials and methods

2.1. Study species and study areas

P. algirus is a medium-sized (adult snout–vent length 60–85 mm; mass 6–15 g), terrestrial, oviparous lacertid inhabiting shrub and woodland habitats of the western Mediterranean region (Arnold, 1987; Díaz and Carrascal, 1991). It has a wide altitudinal distribution, ranging from the sea level up to 2340 m in the Spanish Betic Mountains (Pleguezuelos and Villafranca, 1997). It is therefore an appropriate model for studying the altitudinal variation of thermal preferences.

Lizards were caught in two locations situated near Madrid (central Spain). In both locations *P. algirus* was the most abundant lizard species (Díaz, 1997). The low elevation site was located at El Pardo (40°31′N, 03°47′W; 650 m; monthly average of mean daily temperatures = 15.0 and 23.4 °C in May and July, respectively; mean precipitation = 54.0 and 14.8 mm), a perennial holm oak (*Quercus ilex*) forest with a shrub layer dominated by *Q. ilex* and *Cistus ladanifer*. The high elevation site was located at Morcuera (40°54′N, 03°53′W; 1300–1400 m; mean temperature = 11.9 and 18.8 °C in May and July, respectively; mean precipitation = 78.7 and 21.7 mm), a deciduous *Quercus pyrenaica* forest with a shrub layer of *Q. pyrenaica* and *Cistus laurifolius*. These two populations have been studied by Díaz (1997), who reported a higher abundance of *P. algirus* at the montane site despite its lower T_e's and lower thermal quality.

2.2. Husbandry of lizards and measurement of preferred temperature ranges

In each location and season (May and July) we captured 6 lizards (3 males and 3 females) that were transported to the laboratory (Department of Zoology, Universidad Complutense de Madrid) on the same day of capture. Lizards were housed in glass terraria (120 × 30 cm and 40 cm high). The lab had natural daylight (setting the photoperiod to which animals were exposed during acclimation and testing) and ventilation. Terraria were filled with moistened earth and covered with a leaf litter layer. Some rocks and thin fallen wood increased the structural complexity and provided lizards with additional shade and refuge. A thermogradient was created in the terraria by a 150 W bulb suspended above one end at a height of ca. 20 cm. This gradient offered a wide range of available temperatures (between 20.1 ± 0.7 °C [mean ± s.d.] and 50.6 ± 1.1 °C in May, and between 23.9 ± 0.5 °C and 52.0 ± 1.4 °C in July); T_e's were measured three times per season, always on different days and at different times, using copper models as the ones employed by Díaz (1997) and Díaz and Cabezas-Díaz (2004). Lizards were kept in terraria in groups of three; we observed no social interactions that could have limited the accessibility of some individuals to the heat source. Food (crickets and mealworms) and water were provided ad libitum. After 3 days of acclimation, the T_b's of lizards were measured with a Miller–Weber quick-reading thermometer using standard precautions (Avery, 1982). For each individual, temperatures were registered four times between 0800 and 1100 h (Mean European Time), three times between 1100 and 1400 h, and three times between 1400 and 1700 h. No more than three measurements per day were obtained from any individual.

The PTR of each individual lizard (lower and upper limits and breadth) was estimated by measuring both the central 50% (Huey, 1982; Hertz et al., 1993) and the central 80% (Bauwens et al., 1995; Gvoždik, 2002) of the ten T_b's selected in the laboratory by that particular lizard. Differences in mean selected temperatures were tested by means of nested ANOVAs, with the random factor 'individual' nested within the three-way (season × locality × sex) design, and with T_b measurements as the within-individual replicates. Differences in upper and lower limits, and in the breadth of the preferred range, i.e. those data for which there was a single replicate per individual, were analyzed using three-way ANOVAs with season, locality, and sex as factors.

2.3. *Implications of seasonal variation in PTR for field thermoregulation*

We examined the extent to which seasonal changes in preferred temperatures could facilitate lizard thermoregulation in the field. For this purpose, we employed the data on T_e's collected by Díaz and Cabezas-Díaz (2004), and we followed a modification of the protocol proposed by Hertz et al. (1993) to evaluate thermoregulation by small, field-active ectotherms. Data were collected at the low-altitude site (see Díaz and Cabezas-Díaz, 2004 for details) during the 1997 activity season both in May (six sampling days between 9 and 31 May) and in July (six sampling days between 17 and 31 July), covering the whole daily activity period of the species (07.00–20.00 h Mean European Time). To analyze whether the temperatures selected in May helped to facilitate thermoregulation in that season, we calculated the mean of the absolute values of deviations of May T_e's from the 80% PTR measured in May (d_{May}), and we compared it with the mean of the absolute values of deviations of May T_e's from the 80% PTR measured in July (d_{July}). If d_{May} is significantly smaller than d_{July} (i.e., if T_e's measured in May are closer to the temperature range selected by lizards in May than they are to the range selected in July), it can be concluded that the contribution of the observed shift in PTR to temperature regulation in May is significant, and such a contribution can be quantified by the difference $d_{\mathrm{July}} - d_{\mathrm{May}}$ (Bauwens et al., 1996; Díaz and Cabezas-Díaz, 2004). We used the same procedure to analyze whether the temperatures selected in July helped to facilitate thermoregulation in that season.

3. Results

Preferred body temperatures differed among individuals of the same population, season and sex (nested ANOVA: $F_{16,216} = 1.98$, $P = 0.015$). On average, the temperatures selected by lizards (Table 1) were lower in May than in July. Thus, the mean selected temperatures differed significantly between seasons (nested ANOVA: $F_{1,16} = 32.8$, $P < 0.001$), but not between sexes ($F_{1,16} = 0.7$, $P = 0.428$) or populations ($F_{1,16} = 0.5$, $P = 0.487$). Similarly, none of the interactions between season, sex or population was significant (all P's > 0.2).

The upper and lower limits of the preferred range (Table 2) were also lower in May than in July (Table 3). The grand means for the limits of the 80% PTR were 31.2–35.0 °C in May, and 32.7–36.9 °C in July. For the 50% PTR, these values were 32.4–34.2 °C in May, and 33.9–36.1 °C in July. Of the remaining main effects and interactions, only two were significant (Table 3), both concerning the upper limit of the 80% PTR, that was slightly higher for males than for females due to a sexual difference found at the high-elevation site (Table 2; effect of sex: $P = 0.026$; interaction between population and sex: $P = 0.007$). However, these effects should be regarded with caution; since their size is small, they are not based on

Table 1
Mean (±SE) temperatures selected by lizards (in °C; $n = 10$ measurements per individual) according to season, site of capture, and sex

	El Pardo (650 m)		Morcuera (1200 m)	
	Males	Females	Males	Females
May (breeding season)	33.0 ± 0.14	32.8 ± 0.39	33.8 ± 0.35	33.2 ± 0.47
July (post-breeding season)	35.2 ± 0.25	34.9 ± 0.53	35.3 ± 0.37	34.4 ± 0.31

The sample size is three lizards for all categories.

Table 2
Mean (±SE) lower and upper limits, and breadth of the preferred temperature range, according to season, site of capture, and sex

	El Pardo (650 m)		Morcuera (1200 m)	
	Males	Females	Males	Females
PTR 50				
Lower PTR 50				
May	32.1 ± 0.07	32.1 ± 0.28	33.1 ± 0.62	32.2 ± 0.32
July	34.3 ± 0.23	34.1 ± 0.85	34.2 ± 0.64	33.2 ± 0.37
Upper PTR 50				
May	33.9 ± 0.06	33.9 ± 0.35	34.6 ± 0.44	34.2 ± 0.70
July	36.4 ± 0.20	35.8 ± 0.15	36.4 ± 0.50	35.7 ± 0.23
Breadth PTR 50				
May	1.8 ± 0.09	1.8 ± 0.09	1.5 ± 0.26	2.0 ± 0.42
July	2.0 ± 0.37	1.7 ± 0.75	2.3 ± 0.15	2.5 ± 0.32
PTR 80				
Lower PTR 80				
May	31.1 ± 0.53	30.7 ± 0.86	31.6 ± 0.33	31.3 ± 0.20
July	32.6 ± 0.26	32.9 ± 0.83	32.7 ± 0.51	32.5 ± 0.13
Upper PTR 80				
May	34.6 ± 0.05	34.8 ± 0.10	35.7 ± 0.35	34.9 ± 0.39
July	36.9 ± 0.38	37.0 ± 0.09	37.5 ± 0.41	36.1 ± 0.20
Breadth PTR 80				
May	3.6 ± 0.50	4.1 ± 0.81	4.0 ± 0.22	3.5 ± 0.22
July	4.3 ± 0.19	4.1 ± 0.75	4.8 ± 0.90	3.6 ± 0.23

The data (all in °C) are for the central 50% (PTR 50) and 80% (PTR 80) of the temperatures recorded for each individual lizard. The sample size is three lizards for all categories.

Table 3
Three-way ANOVA tables for the effects of season, locality and sex on the lower limit, upper limit, and breadth of the preferred temperature range, calculated using both the central 50% (PTR 50) and central 80% (PTR 80) of all temperatures measured in the laboratory

Source of variation	Lower limit PTR 50		Upper limit PTR 50		Breadth PTR 50		Lower limit PTR 80		Upper limit PTR 80		Breadth PTR 80	
	$F_{1,16}$	P	$F_{1,16}$	P	$F_{1,16}$	P	$F_{1,16}$	P	$F_{1,16}$	P	$F_{1,16}$	P
Season	20.56	<0.001*	50.09	<0.001*	1.89	0.189	16.83	<0.001*	90.15	<0.001*	1.00	0.333
Locality	0.00	0.981	0.74	0.402	0.74	0.401	0.41	0.531	1.20	0.289	0.01	0.967
Sex	2.64	0.124	2.56	0.129	0.23	0.638	0.15	0.699	6.06	0.026	0.80	0.386
Season × locality	2.64	0.124	0.97	0.339	1.25	0.280	1.05	0.322	3.24	0.091	0.01	0.967
Season × sex	0.03	0.867	0.74	0.402	0.45	0.512	0.26	0.620	0.79	0.387	0.87	0.364
Locality × sex	1.41	0.252	0.31	0.587	0.98	0.337	0.07	0.799	9.50	0.007	1.79	0.200
Season × locality × sex	0.01	0.943	0.03	0.856	0.01	0.925	0.12	0.732	0.59	0.455	0.01	0.950

Significant differences after applying the sequential Bonferroni correction are marked with asterisks.

planned comparisons or specific hypotheses, and, unlike those concerning seasonal differences, they would not be considered significant after applying the sequential Bonferroni correction to obtain adequate table-wide significance levels in Table 3. All locality effects were non-significant (all P's>0.25). The breadth of the preferred range did not vary between seasons, localities or sexes (all P's>0.18).

The seasonal shift in PTR contributed towards facilitation of field thermoregulation in May but not in July. Thus, the T_e's measured in May (mean $T_e \pm$ s.d. $= 25.8 \pm 9.5\,^{\circ}\mathrm{C}$) were closer to the 80% PTR of that month (May mean $d_{\mathrm{May}} \pm$ s.d. $= 8.28 \pm 5.98\,^{\circ}\mathrm{C}$; Díaz and Cabezas-Díaz, 2004) than to the 80% PTR obtained in July (May mean $d_{\mathrm{July}} = 9.48 \pm 6.27\,^{\circ}\mathrm{C}$; $t_{2338} = 4.75$, $P<0.001$); the contribution of the observed shift in 80% PTR to field thermoregulation in May was therefore of 1.2 °C ($d_{\mathrm{July}} - d_{\mathrm{May}}$). However, the T_e's measured in July (mean $T_e \pm$s.d. $= 31.5 \pm 13.3\,^{\circ}\mathrm{C}$) were not closer to the 80% PTR of that month (July mean $d_{\mathrm{July}} = 8.32 \pm 8.29\,^{\circ}\mathrm{C}$) than to the 80% PTR obtained in May (July mean $d_{\mathrm{May}} = 8.33 \pm 8.81\,^{\circ}\mathrm{C}$; $t_{2338} = 0.043$, $P = 0.96$).

4. Discussion

Our results raise several interesting points. The preferred temperature range varied markedly between seasons but not between sexes or altitudes, and this variation concerned not only the central tendency (mean) but also the lower and upper limits of the preferred range. However, the breadth of the range remained constant between seasons.

Seasonality had a pronounced effect on PTR, since both the mean and the limits of the preferred range were approximately 2 °C lower in May than in July. Similar variations have been found in many other lizard species (Patterson and Davies, 1978; Van Damme et al., 1986; Sievert and Hutchinson, 1989; Christian and Bedford, 1995). Studies by Rismiller and Heldmaier (1982, 1987, 1988) have shown that rhythms of T_b selection respond to light–dark cycles that simulate natural variations of photoperiod, and that the T_b's selected during the photophase tend to increase with laboratory simulations of spring photoperiods. This seasonal timing is coupled with reproduction, an energy-demanding activity that has evolved to coincide with environmental conditions that promote survival (Nelson et al., 1990). In addition, the thermal requirements of eggs or embryos may also select for lower T_b's in gravid or pregnant females (Beuchat and Ellner, 1987; Mathies and Andrews, 1997; Le Galliard et al., 2003). We have preliminary data showing that the T_b's of gravid *P. algirus* females are lower than those selected by the same females after laying their eggs. From this viewpoint, the seasonality of PTR may be of functional significance. However, we did not find any major difference between the sexes (see Braña (1993), Lailvaux et al. (2003) for similar results).

The utility of the seasonal shift in PTR for facilitating thermoregulation is more questionable, as suggested by two different lines of evidence. First, the thermoregulatory contribution of the observed change in PTR at the low-elevation site was significant only in May, when T_e's were on average lower than the preferred temperatures (Díaz and Cabezas-Díaz, 2004), and the decreased PTR helped to shorten the difference between them. The thermoregulatory contribution of this lowered PTR, although relatively small (1.2 °C; see Section 3), was comparable to that of the daily activity times in different populations of lacertid lizards (Bauwens et al., 1996; Díaz and Cabezas-Díaz, 2004). However, this small contribution disappeared in July, when deviations from PTR of T_e's were unaffected by the relatively minor shift in the selected thermal range.

Second and more important, thermal preferences did not vary significantly with altitude (Huey and Webster, 1976; Van Damme et al., 1989, 1990; Brown, 1996; Gvoždik and Castilla, 2001), consistent with the viewpoint that thermal physiology is evolutionarily conservative (Crowley, 1985; Van Damme et al., 1990). This lack of variation cannot be attributed to similar selective pressures in both populations, because lizard body temperatures and the accuracy of thermoregulation (sensu Hertz et al., 1993) were somewhat lower, and lizard selectivity for basking sites was more pronounced, at the thermally inferior montane site (Díaz, 1997). Thus, a lower PTR should be advantageous for the high-altitude population. This lack of response to altitudinal variation is intriguing because there was substantial interindividual variation in preferred temperatures after controlling for the effects of season, population and sex (Gvoždik and Castilla, 2001). If such a variation is heritable, thermal preferences should be able to evolve. Perhaps the tight link between PTR and photoperiod not only provokes the clear-cut seasonal shift observed in both populations but it also prevents the evolution of altitudinal differences between populations living at the same latitude.

Interestingly, the breadth of PTR was the only trait that remained invariable between seasons. Moreover, the PTR of *P. algirus* is quite narrow ($\approx$4.0 °C) when compared with other species of Lacertidae (Bauwens et al., 1995). This raises the question of why lizards do not combine the observed spring lower limit and summer upper limit to produce a wider selected range ($\approx$6.0 °C) that would increase the percentage of T_e's within PTR, thus facilitating thermoregulation (Hertz et al., 1993). We suggest that the location, breadth, and seasonal shift of PTR can be explained by considering not only the causal effects of photoperiod but also the functional implications of T_b for sprint speed in lizards, and perhaps more generally for muscle-contraction speed (Huey and Stevenson, 1979; Huey, 1982; Hertz et al., 1983; Van Damme et al., 1989; Bauwens et al., 1995). Because sprint performance is likely related to fitness (Christian and Tracy, 1981), we should expect PTR to closely match the thermal dependence curves of sprint speed (although the narrowness of PTR may also be driven by the thermal sensitivity of other physiological processes such as digestion; Angilletta et al., 2002a, b). This is actually what our results suggest (Fig. 1). In fact, the spring and summer PTRs mirrored each other around the T_b (34.3 °C) which is optimal for sprint speed in *P. algirus* (Bauwens et al., 1995). Moreover, none of the 240 T_b values registered in the thermogradient was beyond the limits of the 80% thermal performance breadth or TPB (28.3–40.3 °C; Bauwens et al., 1995), i.e. the range of body temperatures over which lizards can run at 80% or more of their maximum capacity (see Range of T_b's in Fig. 1). The average lower limit of May's 80% PTR fell 2.9 °C above the lower limit of the 80% TPB, whereas the upper limit of July's 80% PTR fell 3.4 °C below the upper limit of the 80% TPB (Fig. 1). Thus, the narrowness of the preferred thermal range, which remained constant between seasons, might have evolved as a safety mechanism to prevent the negative effects of variable preferred T_b's, and hence relaxed thermoregulation, near the limits of the 80% TPB. This interpretation, while allowing for neurohormonally induced seasonal differences, would be consistent with the finding that species that have evolved to reach high sprint speeds, as it seems to be the case of *P. algirus*, combine the ability to run at near-maximum levels over a wide thermal range, with the maintenance of T_b's within a narrow selected range near the optimal temperature for sprinting (Bauwens et al., 1995).

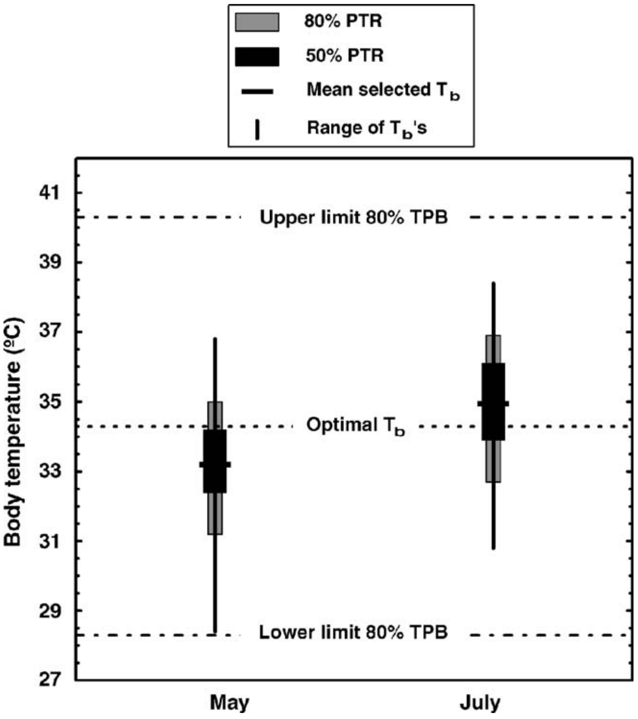

Fig. 1. Thermal preferences of *Psammodromus algirus* in May and July: mean selected body temperatures, preferred thermal ranges defined by mean lower and upper limits of the central 80% (80% PTR) and 50% (50% PTR) of all temperatures selected in a thermogradient, and overall ranges of body temperature measurements. The horizontal lines use data by Bauwens et al. (1995) to show the body temperature at which the sprint speed is maximal (optimal T_b) and the upper and lower limits of the 80% thermal performance breadth (80% TPB, or range of temperatures over which lizards can run at 80% or more of their maximum capacity).

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