Journal of Thermal Biology 52 (2015) 90–96

Contents lists available at ScienceDirect

Journal of Thermal Biology

journal homepage: www.elsevier.com/locate/jtherbio

Thermal dependence of sprint performance in the lizard *Psammodromus algirus* along a 2200-meter elevational gradient: Cold-habitat lizards do not perform better at low temperatures

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ARTICLE INFO

Article history:
Received 17 March 2015
Received in revised form
1 June 2015
Accepted 8 June 2015
Available online 16 June 2015

Keywords:
Body temperature
Elevation
Psammodromus algirus
Reproductive condition
Sprint speed.

ABSTRACT

Sprint speed has a capital relevance in most animals' fitness, mainly for fleeing from predators. Sprint performance is maximal within a certain range of body temperatures in ectotherms, whose thermal upkeep relies on exogenous thermal sources. Ectotherms can respond to diverse thermal environments either by shifting their thermal preferences or maintaining them through different adaptive mechanisms. Here, we tested whether maximum sprint speed of a lizard that shows conservative thermal ecology along a 2200-meter elevational gradient differs with body temperature in lizards from different elevations. Lizards ran faster at optimum than at suboptimum body temperature. Notably, high-elevation lizards were not faster than mid- and low-elevation lizards at suboptimum body temperature, despite their low-quality thermal environment. This result suggests that both preferred body temperature and thermal dependence of speed performance are co-adapted along the elevational gradient. High-elevation lizards display a number of thermoregulatory strategies that allow them to achieve high optimum body temperatures in a low thermal-quality habitat and thus maximize speed performance. As for reproductive condition, we did not find any effect of it on sprint speed, or any significant interaction with elevation or body temperature. However, strikingly, gravid females were significantly slower than males and non-gravid females at suboptimum temperature, but performed similarly well at optimal temperature.

1. Introduction

Sprint speed is a trait of paramount importance for many animals' fitness, as it is involved in a number of life-history traits. In fact, many species avoid predation by quickly fleeing (Calsbeek and Cox, 2010; Lima and Dill, 1990), and sprint speed is related to survival (Husak, 2006a; Irschick and Meyers, 2007; Strobbe et al., 2009). In turn, many predator strategies to capture preys are based on speed (Lima, 2002). However, speed does not affect animal fitness exclusively through predator–prey interactions: faster individuals also show social dominance (Garland et al., 1990) or improved mating success (Byers et al., 2010; Husak et al., 2006).

Performance of most metabolic and physiologic processes strongly relies on body temperature, due to thermal kinetics (Angilletta, 2009; Angilletta et al., 2010). Speed performance also depends on body temperature, since it is closely linked to muscular activity (Taylor et al., 1980). For example, the sprint speed of lizards of the genus *Takydromus* peaks at 30–32 °C of body temperature, diminishing gradually towards warmer or cooler temperatures (Chen et al., 2003; Xiang et al., 1996). Similar results have been found in ants (Hurlbert et al., 2008), fish (Wilson, 2005), a number of other ectotherms (Bennett, 1990), and even endotherms (Carr and Lima, 2013; Rojas et al., 2012).

Speed performance, thus, depends on body temperature in both endotherms and ectotherms. However, body temperature is rather constant in most endotherms (Bennett and Ruben, 1979), whereas in ectotherms, it depends strongly upon environmental temperature (Hertz et al., 1993). Therefore, geographic shifts in environmental temperature can affect ectotherm thermal biology (Andrews, 1998; Sunday et al., 2010; Van Damme et al., 1989). Some ectotherms face different thermal environments by shifting their thermal preferences accordingly (Hertz et al., 1993), as described by the "labile hypothesis" of ectotherm thermal-environment adaptation (Hertz et al., 1983; Rodríguez-Serrano et al., 2009). Contrarily, according to the "static hypothesis" of ectotherm

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http://dx.doi.org/10.1016/j.jtherbio.2015.06.003
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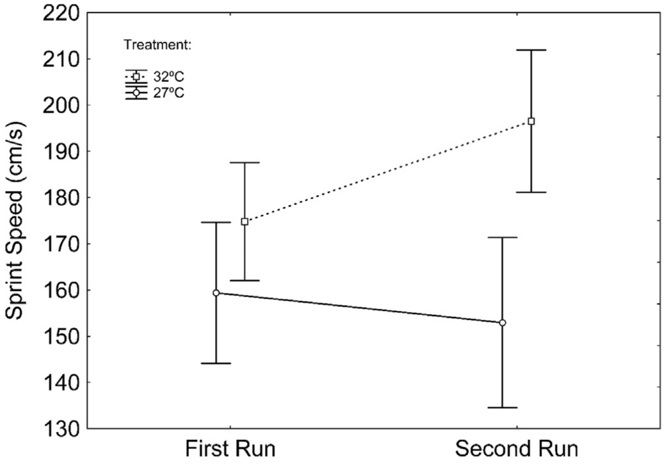

Fig. 1. First run was performed at 27 °C of body temperature for all lizards. Differences in first run sprint speed were not significant regarding treatment. In the second run, the lizards at 27 °C did not change their speed, while lizards at 32 °C ran significantly faster than them, and also than themselves in their first run. Vertical bars represent 95% Confidence Intervals. Sample sizes are indicated in Table 2.

thermal-environment adaptation, other ectotherms may not be able to shift thermal physiology despite environment thermal limitations, due to evolutionary constraints (Crowley, 1985; Hertz et al., 1983). Consequently, in many cases animals do not show local variation in thermal physiology, so thermal biology is often evolutionarily conserved throughout wide regions, even across continents (Youssef et al., 2008). In these cases, several behavioral and physiological mechanisms allow ectotherms to fulfill their thermal preferences in different thermal environments (Stevenson, 1985): variation in frequency and duration of basking periods (Carrascal et al., 1992; Gvoždík, 2002; Hertz, 1992), in skin color (in order to absorb a wider or narrower spectrum of solar radiation; Clusella-Trullas et al., 2007), or even in metabolic-heat generation (Dickson, 1995).

The static hypothesis of ectotherm thermal-environment adaptation (Crowley, 1985; Hertz et al., 1983) is applicable to the lizard *Psammodromus algirus* in a 2200-meter elevational gradient in Sierra Nevada (SE Spain). In this study system, environmental temperature when lizards are active diminishes 8 °C in elevation on average, while lizard field body temperature decreases less than 2 °C from the lowest to the highest elevation, with no elevational trend (Zamora-Camacho et al., 2013). Similarly, operative temperature decreases drastically in elevation (Fig. 2 in Zamora-Camacho et al., 2013), although radiation seems to play an important role in high-elevation lizard heating (Zamora-Camacho et al., 2013). In fact, lizards from this system selected similar body temperatures in a laboratory thermal gradient, regardless of their elevational provenance (Zamora-Camacho et al., submitted). Therefore, lizards in the highest elevations seem to have adaptations such as darker dorsal color (Reguera et al., 2014) and larger body size (Zamora-Camacho et al., 2014b) that may allow them to cope with low environment temperature. Consequently, given that lizards from different elevations show similar body temperature, it is not surprising that they also show similar maximal sprint speed in experiments under controlled body temperature (32 °C; Zamora-Camacho et al., 2014a). However, lizards from high elevations face lower environmental temperatures when active (Zamora-Camacho et al., 2013) and, therefore, are more likely to undergo lower field body temperatures. Moreover, although high-elevation lizards have adaptations to heating and maintaining body temperature in such a climate, they probably spend more time basking, as other high-elevation lizards (Hertz and Huey, 1981; Carrascal et al., 1992; Gvoždík, 2002), and are thus presumably at higher risk of predation (Webb and Whiting, 2005), mainly at the first hours in the morning, while their body temperature is rising up. Consequently, we predict that this increased predation risk should select high-elevation lizards to be faster than low-elevation lizards at lower body temperatures.

In this study, we test the aforementioned hypothesis by comparing sprint speed at optimal and suboptimal temperature in lizards from different elevations. Moreover, we analyze sexual differences in sprint speed according to temperature. Males in this system run faster than females at body temperatures similar to those they attain in the field (32 °C; Zamora-Camacho et al., 2014a), so we expect them to be faster also at a lower body temperature, as in other species (Lailvaux et al., 2003). Similarly, we analyzed the effect of female gravidity on run speed. In the system we study, in contrast with others (Goodman, 2006), gravid females do not run more slowly than non-gravid females at 32 °C (Zamora-Camacho et al., 2014a), but it is unknown whether this tendency persists at lower body temperatures.

2. Materials and methods

2.1. Study species and study area

Psammodromus algirus is a medium-sized (53–95 mm of snout-vent length [SVL] in our study area), generalist Lacertid lizard that occupies Mediterranean areas of southwestern Europe and northwestern Africa. It can be found from the sea level to around 2600 m asl (Salvador, 2011). Lizards inhabit shrubby zones, where they crawl around bushes that they use as refuges (Díaz and Carrascal, 1991). They feed on a variety of invertebrates, and their foraging strategy is flexible: they can either use a sit-and-wait strategy, or search actively for prey (Verwaijen and Van Damme, 2008). These lizards select different body temperature seasonally: 30.9–34.7 °C in spring and 32.8–36.9 °C in summer (Díaz and Cabezas-Díaz 2004).

We caught 118 lizards by hand during their reproductive season (April–June) in 2013, on the southern face of Sierra Nevada (SE Spain). Sampling was performed in six plots located at 300, 700, 1200, 1700, 2200, and 2500 m asl (see Appendix A in Zamora-Camacho et al., 2013). For accurate detection of geographical trends, we grouped those sampling plots into three elevation belts: low elevations (plots at 300 and 700 m asl), mid elevations (plots at 1200 and 1700 m asl), and high elevations (plots at 2200 and 2500 m asl). Grouping in elevation belts was justified on the basis of similarities in population traits within belts, such as phenology, demography, morphology, and even genetic structure (Reguera et al., 2014; Zamora-Camacho et al., 2013, 2014a, b; unpublished data). Since habitat landscape can affect the flight strategy of this species (Iraeta et al., 2010; Martín and López, 1995), we chose locations as similar as possible regarding vegetation structure (see Appendix A in Zamora-Camacho et al., 2013). We recorded time of capture of each lizard, and classified it into hourly time intervals (0900–1000–1700–1800), according to the European Standard Time (EST). Also, from 2010 to 2012, we measured field body temperature (T_b) of 245 lizards, by putting a thermocouple (1 mm diameter) assembled to a thermometer (Hibok 14, accuracy 0.1 °C) 8 mm into each lizard's cloaca, within 30 s after capture.

2.2. Laboratory procedures

Captured lizards were transported to the laboratory, where they were sexed. Also, we considered three reproductive conditions: males, gravid females, and non-gravid females. Males were identified by their proportionally larger heads, orange patches in the corners of their mouths, and more numerous and conspicuous femoral pores in their hind limbs. We recognized gravid females by manual abdomen palpation of the developing eggs. Also, we measured biometrical variables involved in sprint speed: hind-limb length (HLL), since it has been found that lizards with longer hind-limbs run faster, both inter- (Bauwens et al., 1995), and intraspecifically (also in the case of *P. algirus* in this system; Zamora-Camacho et al., 2014a), and occiput-vent length (OVL), with a millimeter-marked ruler. We used OVL instead of SVL in order to control for distance between fore and hind limbs, because males had significantly longer heads than females ($F_{1,\ 116}=13.18$, $P=0.0004$). Tailless lizards were not used in this study, since tail loss negatively affects sprint speed in this species (Martín and Avery, 1998). We marked lizards by toe-clipping, as a part of a long-term ongoing project. Toe-clipping has been found not to alter Lacertid motility (Dodd, 1993; Huey et al., 1990; Husak, 2006b) and in no case did we clip the longest (fourth) toe. During their captivity, lizards were kept in individual plastic terrariums ($20 \times 13 \times 9\ \mathrm{cm}^3$), with pine cork substrate, a heat cable underneath to allow thermoregulation, a window as a source of natural light for circadian rhythms, and water (in the form of nutritious aqueous gel) and food (mealworm, *Tenebrio molitor* larvae) were provided *ad libitum*.

Two days after capturing the lizards, we performed sprint-speed trials in a wooden, straight raceway (320 × 20 × 40 cm), lined with artificial cork to provide an appropriate traction (Bauwens et al., 1995), to measure sprint speed. The raceway was divided into twelve 25- cm stretches, delimited with contrasting-color transversal strips, since lizards in the wild run short distances to their shelters (Martín and López, 2000). We put a dark background at one end of the raceway, to simulate a refuge and thereby encourage the lizards to run forward. In each trial, a lizard was released at the opposite end of the raceway, and a researcher chased it to make it run. Lizards ran individually. Each lizard ran three consecutive times in each trial, as they exhibited no sign of fatigue. All lizards performed the first trial at 27 °C of body temperature, as a baseline running speed, which provided a control of each lizard itself. Four hours afterwards, they performed the second trial similarly, but randomly assigned to one of two treatments of body temperatures: 27 °C (suboptimum) or 32 °C (optimum). Values of optimal and suboptimal temperature were established according to temperatures preferred by this lizard in a free-ranging thermogradient (e.g., Díaz and Cabezas-Díaz, 2004). Furthermore, field body temperature that lizards attain in this system is around 32 °C (31–33 °C; Zamora-Camacho et al., 2013). In all cases, the target temperature was achieved by putting lizards into an incubator at the selected temperature for the adequate amount of time (c. 10 min). Body temperature was ascertained by inserting a thermocouple (1 mm diameter) assembled to a thermometer (Hybok 18, accuracy 0.1 °C) 8 mm inside each lizard's cloaca.

All trials were videotaped with a photo and video camera Canon EOS 550D, at 25 frames per second. Then, videos were analyzed using the software Movavi v.11, with which we could measure millisecond intervals (Chen et al., 2003). Thus, we recorded the time interval for each stretch, considering a stretch as passed when the snout of the lizard reached the strip that delimited it (Martín and López, 2001). Afterwards, we calculated the difference in speed as the second run speed value minus the first. Since our aim was to know how body temperature affected lizard sprint speed to escape predators, we performed our analyses with the fastest stretch of each lizard. Furthermore, lizards often stopped during the trials, so that the average speed of all stretches would be an inaccurate measurement of lizard actual speed. In our study system, gravidity stage, clutch size, or egg burden have no effect on gravid female *P. algirus* sprint speed (Zamora-Camacho et al., 2014a).

2.3. Statistical analyses

We performed parametric statistics, provided that data accomplished the criteria of residual normality and homoscedasticity (Quinn and Keough, 2002). We conducted Ordinary Least Squares Linear Models. Firstly, we analyzed the effect of elevation, time interval, and their interaction on T_b. Secondly, we performed a three-way factorial ANOVAs, to test for the effects of treatment, elevation, reproductive condition, and their interactions on OVL, HLL, first run speed, second run speed, and difference in speed. In order to detect relative differences in HLL, we controlled for OVL, introduced into the model as a covariate. Then,

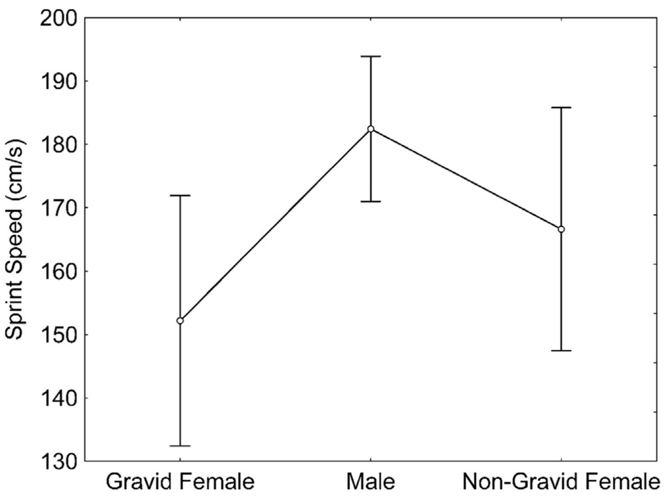

Fig. 2. In the first run, at suboptimum body temperature, gravid females were significantly slower. Vertical bars represent 95% Confidence Intervals. Sample sizes are indicated in Table 2.

Table 1
ANOVAs testing the effects of treatment, elevation, reproductive condition, and their interactions on occiput-vent length (OVL), hind limb length (HLL), first run speed, second run speed, and difference in speed of lizards. *F* statistics are shown. Symbols indicate: * for $P < 0.05$, ** for $P < 0.01$, and *** for $P < 0.001$. In bold, significant results. Note that analyses for HLL were conducted controlling for OVL, so error *d.f.* are 99.

	d.f.	OVL	HLL	First Run Speed	Second Run Speed	Difference in speed
Treatment	1	0.43	1.65	2.36	**13.00*****	**7.26****
Elevation	2	**21.33*****	0.07	0.00	0.69	0.90
Reproductive Condition	2	**11.34*****	**18.06*****	**3.74***	0.55	2.32
Reproductive Condition*Elevation	4	0.23	0.75	1.40	1.24	1.21
Reproductive Condition*Treatment	2	1.55	0.02	1.49	2.15	0.97
Elevation*Treatment	2	0.60	0.22	0.94	0.04	1.32
Reproductive Condition*Elevation*Treatment	4	0.24	1.18	2.38	0.16	1.71
Error	100					

we performed a similar analysis, including gender in the place of reproductive condition. Statistical analyses were performed with the software Statistica 7.1 (StatSoft Inc, Tulsa, OK, USA).

3. Results

3.1. Elevation

We confirmed that, although lizard T_b was significantly higher in the lowest elevations ($F_{2,\ 218}=4.110$; $P=0.02$), differences hardly reached 2 °C (T_b [average ± SE] in: low-elevation lizards = 33.11 ± 0.57 °C, $N=81$; mid-elevation lizards = 30.90 ± 0.78 °C, $N=52$; high-elevation lizards = 31.31 ± 0.38, $N=112$). Time interval ($F_{8,\ 218}=0.508$; $P=0.85$), and elevation*time interval interaction ($F_{16,\ 218}=0.881$; $P=0.59$) had no significant effect on T_b. As for morphological traits, high-elevation lizards showed the largest OVL, but HLL did not vary with elevation (Tables 1 and 2). Elevation and its interactions had no effect on either the first or second run speed, or on difference in speed (Tables 1 and 2). This result suggests that body temperature had a similar effect on lizards from different elevations, despite environmental temperature differences that the lizards had to face in their habitats.

3.2. Treatment

Since lizards were assigned randomly to the treatments, there were no significant differences between groups in OVL, HLL, or first run speed (Tables 1 and 2; Fig. 1). In the second run, lizards at 32 °C (within selected temperature range for this species; Díaz and Cabezas-Díaz, 2004) ran faster than those at 27 °C (Tables 1 and 2, Fig. 1), as expected. As expected, speed differences between trials were significantly higher in lizards running at 32 °C in the second run. Actually, their speed increased significantly, and lizards that ran at 32 °C in the second run were 21.75 cm/s faster than those that ran at 27 °C, with 95% confidence intervals excluding zero (8.42 and 35.07 cm/s; Nakagawa and Cuthill, 2007), while lizards running at 27 °C in the second run did not shift their speed in the second trial, as the difference in speed was −6.45 cm/s, but 95% confidence intervals did include zero (−22.38 and 9.48 cm/s).

3.3. Gender and reproductive condition

Gravid females showed larger OVL, but males had relatively longer hind limbs (Tables 1 and 2). Despite morphological differences, neither reproductive condition nor its interactions had any effect on second run speed or difference in speed (Tables 1 and 2). Nevertheless, gravid females were significantly slower than males in the first run, at suboptimum temperature (Tables 1 and 2; Fig. 2). In another model replacing reproductive condition with gender, results were qualitatively similar. However, males ran significantly faster than females in the first run at 27 °C ($F_{1,\ 106}=6.973$; $P=0.01$), as they do at 32 °C (Zamora-Camacho et al., 2014a). Moreover, triple interactions were significant for first run ($F_{2,\ 106}=3.718$; $P=0.03$) and difference in speed ($F_{2,\ 106}=3.874$; $P=0.02$), but with no recognizable trend (data not shown).

4. Discussion

Sprint speed has a great impact on animal fitness in general (Johnson et al., 2008; Strobbe et al., 2009), and in lizards in particular (Irschick and Garland, 2001; Irschick and Meyers, 2007; Le Galliard et al., 2004). As other life-history traits, lizard sprint speed is optimal within a certain range of body temperatures (Artacho and Jouanneau 2013; Pinch and Claussen, 2003; Waldschmidt and Tracy, 1983), which in turn depends on environmental temperature (Alford and Lutterschmidt, 2012; Hertz et al., 1993). Accordingly, our results show that lizards run faster at optimum than at suboptimum body temperature. This result is not surprising, since it is well established that body temperature strongly influences ectotherm overall activity (Grant and Dunham, 1988) and performance (Huey and Kingsolver, 1989), also in the case of sprint speed (e.g., Bonino et al., 2011; Gaby et al., 2011; Herrel and Bonneaud, 2012). Notably, high-elevation lizards did not perform better than mid and low-elevation lizards at suboptimum body temperatures, despite inhabiting a low-quality thermal environment (Zamora-Camacho et al., 2013).

Psammodromus algirus follows the static thermoregulation strategy (Hertz et al., 1983) along this elevational gradient: although environmental temperatures strongly decline with elevation, body temperature of active lizards remains similar along the elevation gradient (Zamora-Camacho et al., 2013). Moreover, field body temperature was not correlated with capture hour ($r^2 < 0.001$; $P=0.720$). As sprint speed is faster at the body temperature that lizards seek to attain throughout the entire elevational gradient than at a lower body temperature, thermal preferences and thermal dependence of sprint performance seem coadapted in this system (Gilchrist, 1995). Coadaptation between thermal preferences and thermal dependence of sprint performance appears in a number of lizards (Bonino et al., 2011; Hertz et al., 1983; Kubisch et al., 2011), even when it involves variation in thermal environment, both in elevational (Crowley, 1985) and latitudinal thermal gradients (van Berkum, 1988). Sprint speed of several *Anolis* and *Liolaemus* lizard species that differ in body temperature peaked at each species' field body temperature (Bonino et al., 2011; van Berkum, 1986). In this study system, thermal preferences do not vary in elevation despite diminishing

Table 2
Average ± standard error values of occiput-vent length (OVL), hind-limb length (HLL), first race speed, second race speed, and difference in speed regarding treatment, elevation, and reproductive condition of lizards. Sample sizes (n) are indicated for each group.

		N	OVL (mm)	HLL (mm)	First Race Speed (cm/s)	Second Race Speed (cm/s)	Difference in Speed (cm/s)
Treatment (°C)	**27**	56	52.19 ± 0.85	35.58 ± 0.41	159.38 ± 7.69	152.93 ± 9.27	−6.45 ± 8.03
	32	62	51.87 ± 0.81	34.90 ± 0.39	174.78 ± 6.43	196.52 ± 7.76	21.75 ± 6.71
Elevation	**Low Elevation**	33	46.90 ± 0.85	34.64 ± 0.61	167.11 ± 10.30	185.64 ± 12.42	18.53 ± 10.5
	Mid Elevation	43	51.09 ± 0.74	34.98 ± 0.47	166.72 ± 7.35	168.70 ± 8.86	1.97 ± 7.67
	High Elevation	42	57.00 ± 0.75	35.92 ± 0.56	167.40 ± 8.12	169.84 ± 9.80	2.44 ± 8.48
Reproductive Condition	**Male**	58	49.91 ± 0.71	37.18 ± 0.34	182.45 ± 5.78	181.07 ± 6.97	−1.38 ± 6.03
	Non-Gravid Female	24	49.52 ± 1.10	34.08 ± 0.52	166.61 ± 9.66	166.91 ± 11.66	0.30 ± 10.09
	Gravid Female	36	57.10 ± 0.90	32.81 ± 0.47	152.18 ± 9.97	176.21 ± 12.02	24.03 ± 10.41

environmental temperatures (Zamora-Camacho et al., 2013; submitted), so co-adaptation implies a similar impact of body temperature on lizards' speed regardless of different thermal environments. On the other hand, Díaz et al., (2006) found that, in another population, this lizard does not shift thermal preferences in a 700 m elevational gradient, as in our system, but increases them by about 2 °C from spring to summer, thus showing seasonal plasticity.

Hence, sprint performance is at least one of the reasons why lizards thermoregulate, when the body temperature that optimizes sprint speed performance matches the body temperature that ectotherms seek (Bennett, 1990; Huey and Kingsolver, 1989). Therefore, the fact that thermal ecology and optimum speed-performance temperature are invariant along the elevational gradient in *P. algirus* has an important consequence: high-elevation *P. algirus* need to be as warm as mid- and low-elevation lizards in a lower thermal-quality habitat in order to maximize speed performance. Several thermoregulatory strategies can allow lizards to exploit efficiently a low-quality thermal environment. High-elevation lizards in our study system are larger, and exhibit lower cooling rates, enabling them to retain heat for longer (Zamora-Camacho et al., 2014b). Furthermore, they are darker (Reguera et al., 2014), this presumably helping them to warm up faster (Clusella-Trullas et al., 2007). Moreover, high-elevation *P. algirus* probably bask for longer periods, as reported for other alpine lizards (Carrascal et al., 1992; Gvoždík, 2002; Hertz, 1992).

By contrast, other studies on elevational gradients report that lizards from colder habitats (high elevations) usually show lower body temperatures in the field, but similar (or even slower) sprint speed for a given temperature than do lizards from warmer environments (Crowley, 1985; Gabirot et al., 2013; Van Damme et al., 1989). As a result, these lizards, when below their optimum body temperature, may not defend themselves from predators by fleeing, but by aggressive counterattacks, which do not involve sprint speed (Hertz et al., 1982). Also, many lizards flee from predators over greater distances when they are below their optimum temperature, increasing their possibilities to escape successfully in a situation of impaired sprint speed (Braun et al., 2010; Rocha and Bergallo, 1990).

However, ectotherm thermal physiology seems to be evolutionarily constrained to some extent (Angilletta et al., 2002; Angilletta and Werner, 1998; Gaby et al., 2011), so thermal physiology could not be an easily evolvable trait (Angilletta et al., 2002; Gaston et al., 2009; Van Damme et al., 1990). In this situation, different degrees of evolvability of thermal physiology among taxa could be the basis of divergence of thermal dependence of sprint-speed performance in different thermal environments (Clusella-Trullas and Chown, 2014). Consequently, lizards show three different evolutionary strategies in order to enhance speed performance in environments with different thermal qualities. (1) Some lizards seem to evolve physiological changes that allow them to achieve appropriate speed in colder environments even at lower body temperatures (e.g., McElroy, 2014). (2) Others, such as the lizard in our study, show adaptations in order to achieve similar body temperature regardless of environmental temperature along climatic gradients, and in this way, maintain the optimal body temperature for its sprint speed. (3) Finally, still others do not seem to raise their body temperature or sprint speed when in colder habitats. In this case, they develop behavioral adaptations, showing alternative strategies against predators (Hertz et al., 1982).

Lastly, at all elevations, males and gravid as well as non-gravid females showed impaired sprint speed at suboptimum body temperatures. Thus, lizards in all reproductive conditions must achieve optimum body temperatures in order to maximize sprint speed. The finding that individuals in all reproductive conditions performed better at optimum than at suboptimum body temperatures is not surprising (Lailvaux, 2007). As in our study, no sexual differences in sprint speed are frequently found in lizards (Ling-Jun and Wei-Guo, 2007; Tang et al., 2013). In turn, the fact that gravid females presented longer OVL than non-gravid females could be a consequence of males preferring to mate with larger females, since larger females can produce more offspring (Olsson, 1993). However, this finding is worth further research.

Nevertheless, it bears mentioning that gravid females were significantly slower than non-gravid females in the first run, performed at suboptimum body temperature. This result is surprising, since a previous work in this system showed that gravid females at optimum body temperature (32 °C) did not differ from males or non-gravid females in sprint speed (Zamora-Camacho et al., 2014a). Therefore, reduced sprint performance at suboptimum body temperature could be a cost of reproduction. First, gravid females below optimum body temperatures may suffer increased predation risk (Miles et al., 2000; Sinervo et al., 1991). Furthermore, gravid females could need longer basking periods in order to attain a body temperature that enhances escape speed, during which they would be particularly susceptible to be preyed on (Shine, 1980). On the other hand, this result suggests that the physiologic mechanism that prevents gravid females from impaired sprint speed is temperature-dependent, so they must be at optimum temperatures in order to reduce susceptibility to predators. Similarly, Iraeta et al. (2010) found that females of *P. algirus* from two populations in central Spain ran slower, and performed shorter runs, when gravid than after oviposition. Other studies show that gravid females whose sprint speed is impaired can shift their strategy towards crypsis in order to avoid predators (Schwarzkopf and Shine, 1992), but that is not supported in the study system studied here, where gravid females are even less criptic than non-gravid females (González G-Granda, 2014).

In conclusion, lizards ran faster at optimum than at suboptimum body temperature. Strikingly, high-elevation lizards at suboptimum temperature were not faster than middle or low-elevation conspecifics, despite the low-quality thermal environment. So, we failed to find evidence of local adaptation in lizard sprint speed in the study system studied here. Taking into account that these lizards kept a quite constant field body temperature along this elevational gradient, we found that coadaptation between thermoregulatory preferences and thermal dependence of speed performance exists at all elevations, at the same time as lizard thermal ecology and optimum speed-performance temperature are conservative over the entire elevational gradient. High-elevation *P. algirus* display a number of thermoregulatory strategies that allow them to achieve warm optimum body temperatures in a habitat of low thermal quality and thus maximize speed performance. At suboptimum body temperatures, gravid females were slower than males and non-gravid females, while at optimum temperatures they were not, suggesting that the physiological mechanisms that allow gravid females to offset their egg burden are temperature-dependent. Also, gravid females particularly need to thermoregulate accurately in order to flee effectively from predators.

Acknowledgments

The authors thank the personnel from the *Espacio Natural de Sierra Nevada* for their constant support. This work was economically supported by the Ministerio de Ciencia e Innovación (project CGL2009-13185). FJZC and SR were supported by two pre-doctoral grants from the Ministerio de Ciencia e Innovación (FPU program). Research and animal capture were conducted in accordance with both Junta de Andalucía and National Park of Sierra Nevada research permits (references GMN/GyB/JMIF and ENSN/JSG/JEGT/MCF) issued to the authors. MariCruz Tuset Arcas, Miguel Leandro López Gracia, Laureano González González-Granda, Elena Melero Martínez, and Susana Silva González helped us during field work. Comments by Juan Manuel Pleguezuelos and three anonymous referees improved the manuscript. David Nesbitt improved the English.

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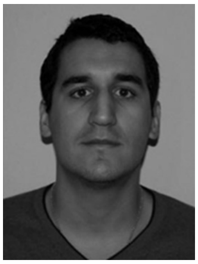

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