Journal of Thermal Biology 84 (2019) 146–153

Contents lists available at ScienceDirect

Journal of Thermal Biology

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

Waitin’ on a sunny day: Factors affecting lizard body temperature while hiding from predators

Marco Sannolo[a,b,*], Raquel Ponti[c], Miguel A. Carretero[a]

[a] CIBIO, Research Centre in Biodiversity and Genetic Resources, InBIO, Universidade do Porto, Campus de Vairão, Rua Padre Armando Quintas, Vairão, 4485-661, Vila do Conde, Portugal
[b] Departamento de Biologia, Faculdade de Ciências da Universidade do Porto, R. Campo Alegre, s/n, 4169-007, Porto, Portugal
[c] Departamento de Biogeografía y Cambio Global, Museo Nacional de Ciencias Naturales (CSIC), C/José Gutiérrez Abascal 2, Madrid, 28006, Spain

ARTICLE INFO

Keywords:
Thermal ecology
Refuge use
Thermoregulation
Antipredator behavior
Lacertidae
Timon lepidus

ABSTRACT

Most animals face predators in their daily life and have evolved antipredator strategies that promote survival while minimizing escaping costs. For example, many animals often hide into refuges when chased. Ectotherms rely on external sources of heat to raise their body temperature, and thermoregulate to keep their body temperature close to the optimal for performance. For many ectotherms living in temperate areas, it can be expected that they pay a cost in terms of heat loss while staying hidden. Indeed, refuges are often more thermally unsuitable than the external environment. Hence, the aim of this study was to assess if and to what extent hiding may result in a decrease of body temperature in a temperate lizard. We used infrared technology to measure the body temperature of a large-sized lizard (*Timon lepidus*) before individuals escaped from a simulated predation attempt to hide inside a refuge, and after they emerged back from the refuge. We quantified the change of body temperature that lizards experienced while hiding. Results show that while the decrease in body temperature covaried with the time spent hidden, it was also affected by the initial body temperature. Our key finding is that the time spent hidden depends mostly on the temperature inside the refuge. Indeed, lizards hiding in warmer refuges spent more time hidden, likely benefitting from a reduced cooling rate. This suggests that lizards perceive and evaluate the thermal quality of their refuges and integrate this information to react to predation attempts and minimize the potential thermal consequences of hiding.

1. Introduction

Many animals, both vertebrate and invertebrate, avoid predation by entering in temporary refuges small enough to prevent their pursuers to fit in (Frix et al., 1991; MacHutchon and Harestad, 1990). Several studies investigated hiding strategies, both theoretically (Hugie, 2003) and experimentally (Jennions et al., 2003), showing that many animal species use cues about their predators, like the angle or approach velocity to modulate their hiding behavior. Similarly, hiding time often depend on the predator pressure (Martín and López, 2001). Optimality models predict that antipredator behavior allows animals to increase their fitness through survival and future chances to reproduce (Cooper and Frederick, 2007a, 2007b). Various models predicting hiding time have been theorized and tested (Johansson and Englund, 1995; Polo et al., 2005), showing that, in general, preys wait hidden more than their predators, and are often able to modulate their hiding behavior by considering past predation experiences and information about their surroundings, including refuges characteristics.

Hiding in refuges usually entails costs as well as benefits. By hiding, animals often cannot feed, which entails a trade-off between short-term survival probability and energetics (Koivula et al., 1995). The loss of feeding opportunities depends on the relative balance of predation risk and food availability in the environment (Martín et al., 2003a). Likewise, while hiding an individual cannot engage in social activities like mating, thus losing opportunities to reproduce (Kålås et al., 1995). Other costs involve the risk of intrusion of competitors into the animal's territory (Díaz-Uriarte, 1999) or the exposure to a different predator while hiding (Soluk, 1993). Some of these costs may also vary depending on the sex or the season (Brown and Shine, 2004).

The physiological cost of hiding, especially regarding heat loss, may be particularly relevant for ectotherm species, since they rely on external sources of heat to raise their body temperature and keep it close

---

[*] Corresponding author. CIBIO, Research Centre in Biodiversity and Genetic Resources, InBIO, Universidade do Porto, Campus de Vairão, Rua Padre Armando Quintas, Vairão, 4485-661, Vila do Conde, Portugal.

E-mail address: marco.sannolo@gmail.com (M. Sannolo).

https://doi.org/10.1016/j.jtherbio.2019.07.001
Received 6 November 2018; Received in revised form 10 June 2019; Accepted 1 July 2019

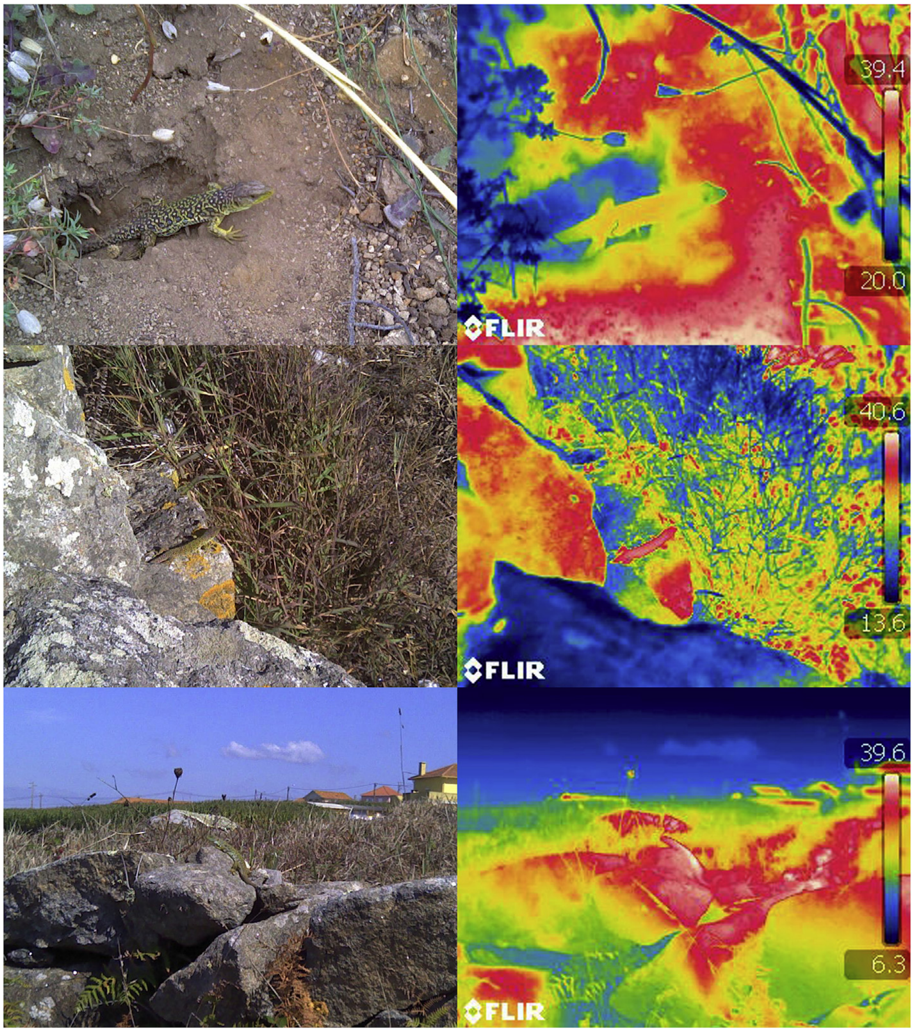

Fig. 1. Examples of the thermal and visible images of the lizard *Timon lepidus* taken during the study carried on at Castro S. Paio (Portugal) and used to extract body temperatures. The temperature scale on the right margin is expressed in Celsius degrees.

to a preferred and often narrow range (Angilletta, 2009; Hertz et al., 1993; Huey, 1982). Hiding lizards may experience suboptimal conditions inside their refuges (Wolf and Kramer, 1987) since air temperature is usually lower than the range of preferred body temperatures (Martín and López, 1999b). Hence, lizards often strive to maintain their body temperature within the range that maximize the individual performance, as suboptimal body temperatures —both too high or too low— may eventually lead to a decrease in performance, survival and, in general, in fitness (Angilletta, 2009). For example, temperate lizards often experience operative temperatures that are colder (as in spring) or warmer (as in summer) than their thermal preferences (Ortega and Martín-Vallejo, 2019). As a consequence, the body temperature of hiding lizards may drop below the range at which several physiological functions are optimized, like locomotion (Angilletta et al., 2002), digestion (Van Damme et al., 1991), and prey-handling (Avery and Mynott, 1990). Furthermore, when emerging from a refuge, lizards may be forced to spend time thermoregulating to recover their original body temperature. This implies an additional loss of feeding opportunities (Downes, 2001) and further exposition to predators (Martín and López, 2001). The reliance on external sources of heat, coupled with the suboptimal thermal conditions encountered inside refuges make lizards an excellent model to study the influence of hiding strategies in thermal ecology. Indeed, a vast wealth of knowledge is now available on optimal hiding time (Polo et al., 2005), on the effect of body size (Martín and López, 2010), on intrasexual competition (Díaz-Uriarte, 1999) and on the impact of multiple types of predators (Stapley, 2004). A recent compendium on antipredator behavior (Cooper and Blumstein, 2015) also summarized the hiding strategies of lizards (Martín and López, 2015), in which it is highlighted how lizards often take into account their body temperature as well as environmental and refuge temperature when it comes to decide how much time they spend hidden or how far they should run from a predator.

Unfortunately, to our knowledge, no study measured the decrease in body temperature that lizards may experience while hiding from a predator under natural conditions. Indeed, a recent review of antipredator behaviors stressed that methodological difficulties prevented so far to study the relationship between body temperature and escaping behavior (Cooper, 2015). Such challenges arise from the need to record the body temperature of an animal both before and after a predation attempt, in order to calculate the resulting difference due to hiding. A common practice in field research on lizards is to capture an individual only after a predation attempt, and measure its cloacal temperature with a thermocouple, thus getting a single measure of body temperature. Several studies recognized this methodological limit and inferred the thermal costs of hiding indirectly, for example using air or operative temperatures (Cooper and Wilson, 2008; Martín and López, 1999a, 1999b). Quantifying to what extent lizards' body temperature change while hiding is important to develop more accurate models of optimal hiding time and understand how behavior and physiology interplay in wild ranging ectotherms (Polo et al., 2005).

In the present study, we used infrared technology (IRT) to assess the change in body temperature that lizard experienced while hiding from a predator and which environmental and biological factors may influence heat loss and hiding time. We predicted that (1) lizard body temperatures will fall below ther range of their preferred body temperatures while hiding, due to the unsuitable thermal conditions inside the refuges; (2) lizards body temperature will decrease proportionally to the time spent inside refuges; that (3) bigger lizards will lose heat at a slower pace than smaller ones, due to their higher thermal inertia; and that (4) the thermal quality of the refuges will affect the duration of hiding, with warmer refuges inducing a prolonged retreat.

2. Material and methods

2.1. Species and study site

The ocellated lizard, *Timon lepidus* (Fig. 1) is the biggest European lizard, with a snout-vent length (SVL) that grow up to 240 mm in S Iberia, but only up to 195 mm in NW Iberia (Mateo and Castroviejo, 1991). It is a territorial and thermophilic species, usually associated with bushes and large rocky outcrops (Díaz et al., 2006). It is often preyed by large raptors (Martin and Lopez, 1996), snakes (Mateo, 2014) and occasionally, carnivorous mammals (Padial et al., 2002). In the study area, ocellated lizards live close to dry stone walls and rocky outcrops, inside which they seek refuge if pursued. The preferred body temperatures of the species have been estimated using both IRT and cloacal readings in a previous work, in which the body temperature of various body parts were measured with IRT while animals were free to move in a thermal gradient (Barroso et al., 2016). In a thermal gradient, the average of the preferred temperatures of adult males is ~32 °C, while the central 50% range of preferred temperatures measured at the head is 30.2–36.2 °C and 30.0–36.6 °C when the temperature is measured close to the cloaca. In the field the body temperature of this species in the southern part of its distribution range is comprised between 21.2 and 34.5 °C (Busack and Visnaw, 1989). We discarded juveniles (SVL $<$ 100 mm) due to the practical difficulties in measuring their body temperature accurately from a distance. Individuals between 100 and 125 mm were considered subadults.

The present study took place during 2016 at Castro São Paio (Labruge), a coastal area of approximately 5 ha in Northern Portugal (41° 16′ 54″ N; 08° 43′ 50″ W). The area is characterized by a mixture of small agricultural corn fields, grasslands, and bush patches (mainly *Ulex*, *Erica* and *Carpobrotus* species), while trees are almost absent. Low-height dry stone walls (50–150 cm) and rocky outcrops are abundant, delimiting walking paths and fields. Data collection occurred in September, a period during which ocellated lizards are not sexually active and dedicate most of their time to feed and thermoregulate (Mateo and Castanet, 1994). By focusing on the last part of the active season, we were able to exclude confounding factors like sexual competition, body condition, and egg-bearing-induced thermal shifts in female lizards (Carretero et al., 2005).

2.2. Data collection

Opportunistic sampling was carried on from approximately 9:00 to 19:00 h, covering the daily time span of activity of the ocellated lizard. Upon detecting a lizard with binoculars, one of us (MS) approached it slowly and took a thermal picture from ~3 m with a FLIR T335 thermal camera (Fig. 1: sensitivity: < 0.05 °C; accuracy: ± 2% of the reading; IR image resolution: 320 × 240 pixels, field of view 25° × 19°, lens 25°; Flir Systems Inc., Wilsonville, Oregon, USA). The same researcher then simulated a predation attempt by further approaching frontally the lizard at a constant speed to induce an escaping reaction. To avoid confounding effects that may affect risk perception of lizards (Cooper et al., 2003), the same person wearing the same cloths performed all approaches. Given its large body dimension, *Timon lepidus* seeks refuge into big crevices of the dry-stone wall or under large rocks (Díaz et al., 2006). As soon as the lizards hid, we started a stopwatch and moved away to observe from a distance (8–10 m) the entry of the refuge. Following the procedure of Martín and López (2010), we measured the time it took for the lizard to show the head first (appearance time) and the time for full-body emergence (recovery time, from the beginning of hiding).

As soon as the lizard fully emerged from the refuge it was approached again, a second thermal picture was taken, and then it was captured by noosing. We measured the SVL (snout-vent length; to the nearest mm with a digital caliper) and head length (to the nearest 0.1 mm). We also measured the air temperature and the relative humidity inside the refuge (Mini-Hygrometer Mod. GBC KTI-903; temperature precision ± 0.5 °C, humidity precision ± 2.5%), as well as the height from the ground of the refuge entrance (nearest cm). To avoid pseudoreplication, we took dorsal, ventral and lateral pictures of each individual and crossed photo-identification with biometric variables to ensure that each lizard was tested only once (Sacchi et al., 2016).

2.3. Thermal images analysis

We inspected each thermal image with the software FLIR Tools 2.1 and extracted temperatures using the *Spotmeter* tool (Copyright 2014 FLIR Systems, Inc; http://www.flir.com). For each picture, we extracted the head and trunk temperature, since in lacertid lizards these two body areas may be at a different temperature even in a controlled environment (Sannolo et al., 2014). A recent study demonstrated that the readings from both the head and trunk provide a good proxy for ocellated lizards' internal temperature, at least under laboratory conditions (Barroso et al., 2016). In the present study the cloacal and IRT trunk readings still correlate significantly, despite the lag in time between the shoot of the thermal picture and the following measurement of cloacal temperature ($R^2 = 0.50$, $P < 0.0001$, $y = 0.68x + 7.9$). We thus calculated the decrease of head and trunk temperature as the difference between the thermal picture shot before approaching the lizard and the one shot after the appearance of the head and the rest of the body, respectively.

2.4. Statistical analysis

We computed descriptive statistics for the change in temperature in the head and trunk, as well as for the time spent hidden until appearance and recovery time. So far, the only evidence for head-trunk temperature difference in lacertid lizards come from laboratory observations (Barroso et al., 2016; Sannolo et al., 2014). Hence, we used pairwise t-tests to compare head and trunk temperature both before the simulated attack and after the lizard emerged from the refuge. We compared the head and trunk temperature after hiding with published data on the preferred temperatures for the same population (Barroso et al., 2016), to estimate to what extent lizards are willing to let their body temperature drop below the range of thermal preferences. We used structural equation modeling (SEM) to assess the relationship between appearance and recovery time and several predictors (Lomax and Schumacker, 2004). In particular, we were interested in testing if lizards' body temperature decreased significantly while hiding, and if hiding time was significantly correlated with the characteristics of the refuges. Hence, the starting model for appearance time included as predictors the decrease in head temperature, the refuge temperature, the relative humidity inside the refuge, the initial head temperature, the head length and the height from the ground of the refuge. A second model was fitted for trunk temperature. The predictors were similar, but SVL replaced head length, initial trunk temperature replaced the initial head temperature, and the decrease in trunk temperature replaced the decrease in head temperature. Potential multicollinearity was checked both qualitatively through pairwise correlations plots and quantitatively through VIF analysis. VIF values $<$ 3 were considered as not correlated (Hair et al., 2006). Because SEM cannot deal with unordered factors, the potential contribution of sex and age on hiding behavior was assessed separately using ANOVA.

All statistics were performed in the R environment (R Development Core Team, 2018). SEM models were fitted using the package lavaan (Rosseel, 2012). Figures were produced with the package ggplot2 (Wickham, 2009). Unless otherwise specified, results are expressed as mean ± standard deviation (SD).

3. Results

3.1. Time spent hiding, cooling, and preferred temperatures

We collected full data for 56 lizards (20 males, mean SVL = 142 ± 17 mm; 19 females, mean SVL = 130 ± 10 mm; 17 subadults, mean SVL = 113 ± 6 mm). Appearance time ranged between 19 and 435 s (118 ± 96 s), while recovery time ranged between 29 and 613 s (156 ± 125 s). Head temperature before hiding was 30.97 ± 2.63 °C, while trunk temperature was 32.16 ± 3.11 °C. Such head-trunk temperature difference before hiding was statistically significant (Paired Student's t-test = −5.8474, $P < 0.0001$, d.f. = 55). After hiding, head temperature dropped to 29.82 ± 2.51 °C, while trunk temperature dropped to 30.46 ± 2.86 °C. The head-trunk temperature difference remained significant also after hiding (Paired t-test = −3.4422, P = 0.0005, d.f. = 55). The difference in temperature before and after hiding was significant for both the appearance and recovery time (Paired t-test = 8.6262, $P < 0.0001$, d.f. = 55; t-test = 10.414, $P < 0.0001$, d.f. = 55, respectively). After hiding, lizards lost 1.15 ± 1.04 °C in the head and 1.69 ± 1.27 °C in the trunk. The greatest decrease in head temperature was 3.6 °C, measured in an adult female after hiding for 370 s. Instead, the greatest decrease in trunk temperature was 5.3 °C, measured in a subadult that hid for 415 s. The mean rate of temperature decrease was 0.58 °C/min for the head and 0.65 °C/min for the trunk. Refuge temperature ranged between 18 and 27.6 °C (mean 23.3 ± 2.3 °C).

While both the head and trunk temperatures of lizards were, on average, close to mean temperature selected in the thermal gradients before escaping (Barroso et al., 2016), they dropped, on average, approximately 2 °C below this average value when emerging from the refuge. Furthermore, the mean head temperature after emergence (29.8 °C) was colder than 50% central range selected in the lab (30.2–36.2 °C).

3.2. Predictors for appearance and recovery time

The SEM model for the head accounted for 47.3% of the variance in appearance time, while the model for recovery time accounted for the 43.7% of the variation. The results of SEM analysis (Fig. 2 and Fig. 3) showed that hiding time and heat loss covaried (appearance time: z-value = 4.233, $P < 0.0001$; recovery time: z = 2.314, P = 0.021), but this relationship was modulated by refuge quality, with lizards hiding in warmer refuges waiting more before emerging (appearance time: z-value = 4.233, $P < 0.0001$; recovery time: z = 2.311, P = 0.021). The other predictors considered, like SVL, humidity, initial temperature and refuge height did not influence hiding time ($P > 0.05$ in all cases). Among the predictors, although all were only weakly correlated (S1 and S2 for all pairwise comparisons), the strongest relationships were between refuge humidity and temperature (−0.43) and between the heat loss and the initial head (0.30) or trunk temperature (0.37).

We found no statistical differences in hiding time among sexes ($F_{1,37} = 2.132$, P = 0.153). Similarly, adult lizards were not associated with refuges of higher thermal quality than subadults ($F_{1,54} = 0.265$, P = 0.609).

4. Discussion

We provide here the first field quantification of the decrease in body temperature that free-ranging lizards may experience as a consequence of hiding from a predator. Of the initial four hypotheses, we found statistical support for three of them. We showed that, after hiding, lizards' body temperature dropped below the preferred temperatures; that such a decrease was proportional to the time spent hidden and that the thermal quality of the refuge affected the recovery behavior. Instead, we found no support for the potential effect of body size, likely due to the reduced variability of body size of our sample, composed solely by adult lizards.

The most important result of this study is that both appearance and recovery times correlated with the thermal quality of the refuges, with lizards hiding in warmer refuges waiting more before showing the head and the rest of the body (Figs. 2 and 3). In the present case, lizards' body temperatures were close to the preferred ones before escaping. Conversely, when recovering from hiding, temperatures dropped approximately 2 °C below the average of preferred ones for this species. Also, the head temperature dropped below the set-point range. Such a result may have significant consequences for lizards. Indeed, lizards are able to use information on refuge quality in the context of antipredator behavior (Polo et al., 2005; Andersson et al., 2010), while in the field they show complex hiding strategies depending on the thermal quality of the refuge (Martín and López, 2000; Cooper and Wilson, 2008). Warmer refuges may slow the cooling rate of a lizard, thus directly reducing the thermal consequences of hiding from a predator. Hence, an ideal refuge would have a temperature close to the preferred by the lizard and entails no thermal cost (Huey and Slatkin, 1976). Therefore, if the temperature is viewed as a resource (Magnuson et al., 1979), it is likely that lizards compete for refuges of higher thermal quality, if they are limited. Competition may vary depending on population densities, predator pressure, external operative temperature, and refuges availability (Downes and Shine, 1998).

Cooling of both the head (Fig. 2) and the trunk (Fig. 3) covaried with hiding time. This result was the most expected since several studies already quantified the cooling rates over time for various lizard sizes under laboratory settings (Dzialowski and O'Connor, 2001; Kour and Hutchison, 1970). However, we present here novel quantifications for wild ranging lizards. In our sample, the duration of hiding, and hence the resulting decrease of body temperature were, on average, modest. Indeed, most lizards spent from a few seconds up to 7 min before showing the head, while lizards waited no more than 10 min before repositioning at their original position. Nonetheless, some lizards lost over 5 °C of their initial body temperature, indicating that in some cases hiding behavior may potentially entail high thermal costs. Such costs would be represented by the time needed to restore the original body temperature, which would depend on environmental conditions (radiation intensity, air temperature and wind speed), and by potential missed opportunity to feed, mating and defend a territory (Díaz-Uriarte, 1999; Downes, 2001; Kålås et al., 1995). The decrease in body temperature was mainly associated with the initial temperature either of the head or trunk, with warmer individuals losing more heat. However, warmer individuals did not spend more time hidden, nor were those individuals hiding in cooler refuges. The apparent contradiction may be explained when considering that cooling does not vary linearly with the difference of air temperature inside the refuge, but instead, it follows Newton's law on cooling (Maurone and Shiomos, 1983). It is hence possible that lizards tried to find a compromise to minimize the potential thermal costs of hiding, resulting in similar hiding times despite the initial differences in body temperatures.

We predicted that lizard's size would affect the cooling rate, but body length correlated neither with hiding time nor with the decrease in body temperature. It should be considered that having focused only adult lizards, we inevitably sampled only a small portion of the overall variability in body size for this species. Indeed, other animal groups

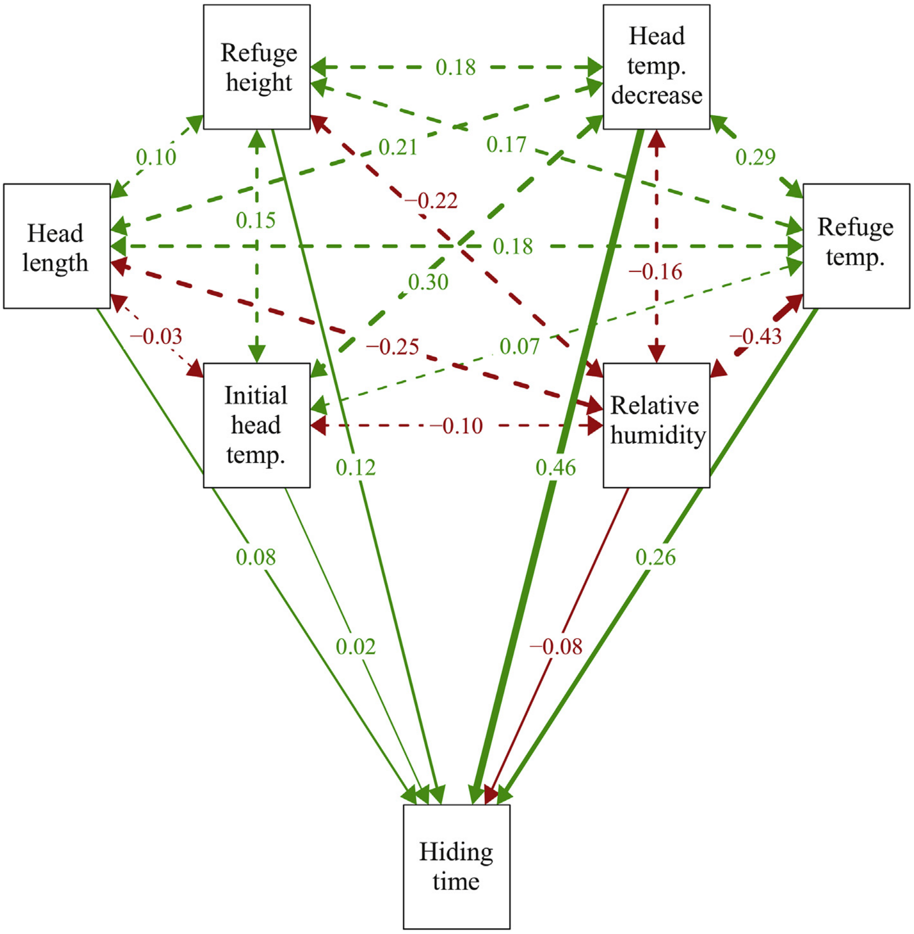

Fig. 2. Path analysis diagram showing the relationship among the outcome variable (emergence time, bottom) and predictors. Positive relationships are expressed in green, while negative relationships are in red. Arrows width is proportional to the strength of the correlation between the two variables. Note that the relationships among predictors are expressed as correlations coefficients (dotted lines), and the double-headed arrows do not imply causal relationship. Instead, the relationships between the outcome and predictors (full lines) are expressed by the path coefficients, which are standardized versions of linear regression weights. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

showed a size-related variation in antipredator behavior (Krause et al., 1998; Sih, 1992). Different behavioral, social, and thermal pressures on large and small individuals may explain our results as well. Larger individuals may choose refuges not only based on their thermal quality but also looking for protection against predators or as possible nesting sites (Kerr et al., 2003). However, it is unlikely to be the case here, because this study has been conducted outside the reproductive period. On the other hand, juvenile lizards may be more cautious due to their higher residual reproductive value (Clark, 1994), and refuge selection may be based mainly on their thermal properties. Similarly, due to their smaller dimensions, juveniles may choose a broader variety of refuges. However, juveniles were not measured in this study, thus reducing the range of variation in body size. Moreover, as already discussed, hiding time was generally short, possibly contributing to mask the effect of size. Finally, we simulated only a single predator attack. Multiple predation attempts may force lizards to hide for prolonged periods or force variation in activity pattern and antipredator behavior, potentially boosting heat loss (Martín et al., 2009).

Our results showed that sex did not influence hiding time, even though other lizard species have proved to vary in their hiding time depending on sex, at least during the reproductive season (Martín et al., 2003b). By choosing the post-reproductive season, we likely removed sex-related confounding factors, like egg and sperm development. Heliothermic lizards living in temperate areas like the ocellated lizards devote autumn mostly to optimising fat accumulation before winter for the subsequent breeding season, through eating and thermoregulating as accurately as possible (Carretero, 2006). Hence, intersexual differences that may otherwise play a role during the reproductive season were absent in our study. Furthermore, to estimate how the time in the refuge, throughout a season, would decrease fat accumulation, it would be needed a prolonged field study with observations over time to estimate how often lizards retreated in response to disturbance in a season. Such a research would be of interest, especially in conservation and management in areas with intense human, cat, and dog activity.

Relative humidity and the height from the ground of the refuge did not influence hiding time. Relative humidity was generally high in all refuges (range 50–88%, mean 65%) and likely the rate of heat loss inside the refuges was not affected by this variable. Instead, humidity may play a relevant role in nocturnal or wintering refuges (Galán, 1999). Height from the ground may influence the internal structure and thermal quality of refuges, as well as to affect the cooling rate and vary the exposure of lizards to predators and competitors (Bakken, 1989). Indeed, it can be hypothesised that increasing height may correlate with air flow, light intensity and inversely with humidity. Even though in this study ocellated lizards used refuges evenly from the ground to approximately 150 cm, it is challenging to ascertain the actual position of a lizard inside the wall. A more specific study on refuge quality and its physical characteristics (height, internal structure, light, temperature and humidity) may add meaningful data on the subject.

Finally, the results obtained in the present study with IRT would not be possible to obtain using an invasive method, like measuring the cloacal temperature. Indeed, by shooting thermal pictures both before and after a predation attempt, we were able to quantify heat loss without affecting lizards' behavior. However, our approach bears limitations as well. Indeed, a few lizards (4) showed negative values of heat loss for the head, suggesting that they gained some heat while hiding. Instead, this likely results from the observer being forced to wait for each lizard to fully emerge before shooting the second thermal picture, leading to underestimate heat loss from the head. Lizards that gained heat are those with longer vigilance time that lead their head to heat

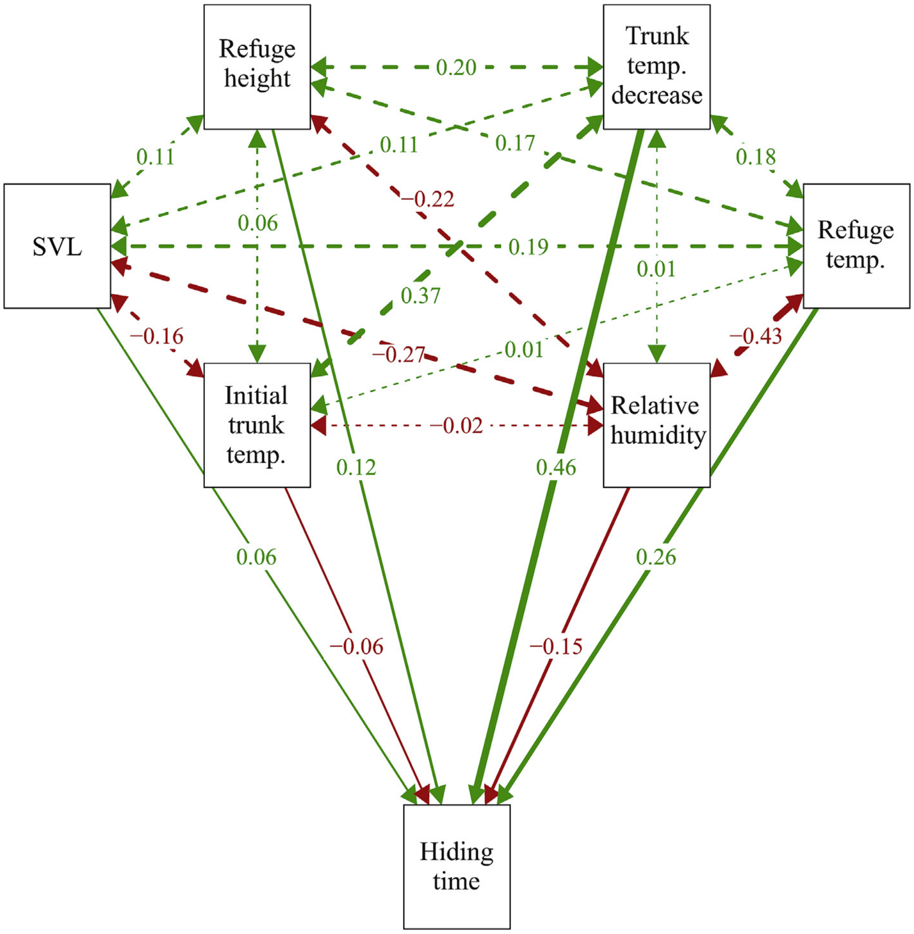

Fig. 3. Path analysis diagram showing the relationship among the outcome variable (recovery time, bottom) and predictors. Positive relationships are expressed in green, while negative relationships are in red. Arrows width is proportional to the strength of the correlation between the two variables. Note that the relationships among predictors are expressed as correlations coefficients (dotted lines), and the double-headed arrows do not imply causal relationship. Instead, the relationships between the outcome and predictors (full lines) are expressed by the path coefficients, which are standardized versions of linear regression weights. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

again before exiting with the rest of the body ("head basking", see for example Heath, 1964; Gregory, 1990). Hence, the trunk may represent a more accurate proxy than the head for measuring the thermal consequences of hiding behavior in those species that routinely patrol with the head before showing the rest of the body. Nonetheless, the lizards' head represents a fundamental component for thermoregulation, being the physiological thermostat (Cabanac et al., 1967). Hence, it is challenging to assess if lizards regulate more strictly the head or trunk temperature. Such a challenge is further confounded by the behavioral role (patrolling) that the emerging head often has in lizards. However, the observation that lizards emerged when head, but not trunk temperature, dropped below the set-point range may suggest that the head temperature is regulated more finely than trunk one.

5. Conclusions

By measuring lizards' body temperature both before and after a standardized predation attempt, we have been able to directly quantify the resulting decrease in body temperature, as a consequence of a predation attempt. Even though previous studies attempted to infer the thermal costs of hiding indirectly (Martín and López, 2010), as far as we know this is the first quantification of the thermal consequences of hiding behavior in lizards. Even though the average decrease in body temperature was modest regarding absolute values, it varied considerably among individuals and led to suboptimal body temperatures for this species (Barroso et al., 2016). The key finding of this study is that hiding time correlated with the decrease in body temperature and was modulated by the thermal quality of the refuges. Therefore, lizards hiding from a predator are likely forced to thermoregulate to regain the heat lost. However, basking may expose lizards to the old predator or a new one, or competitors (Huey and Slatkin, 1976). Hiding lizards are thus forced to balance potential thermal costs against predator pressure. It may be hypothesised that depending on predator and competitor pressure and refuge quality, lizards may show variable hiding times (Polo et al., 2005). Future works should focus on how the variability in the thermal quality of the refuges may affect antipredator behavior and how this is modified by other pressures such reproduction, predation intensity or competition (Frix et al., 1991; Hedrick and Kortet, 2006).

Conflicts of interest

There are no conflicts of interest to declare.

Author contributions

MS and RP conceived and designed the research; MS and RP collected the data; MS performed the analyses; MS, RP and MAC wrote the manuscript and gave final approval for submission.

Acknowledgements

We would like to thank José Martín for reviewing an early version of the manuscript and Sr. Fernando for the enjoying conversations on ocellated lizards. Memeo provided a valuable company during the study, and a Bruce Springsteen's song inspired the title. Marco Sannolo (MS) was supported by a doctoral grant (SFRH/BD/103549/2014) from Fundação para a Ciência e a Tecnologia (FCT, Portugal). Raquel Ponti (RP) was supported by CSIC (Spain) through the project (FPU13/03621) from the Ministerio de Educación, Cultura y Deporte (Spain). Miguel Angel Carretero (MAC) is supported by the project NORTE-01-

0145-FEDER-000007. The study is supported by the FCT project 28014 02/SAICT/2017 Projetos de Desenvolvimento e Implementação de Infraestruturas de Investigação, RNIE - Programa Operacional Regional do Norte - Portugal 2020. Permits for lizards capturing and handling were provided by Instituto da Conservação da Natureza e das Florestas (ICNF, Portugal no. 556/2016/CAPT). Experiments followed the ethical guidelines of the University of Porto.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jtherbio.2019.07.001.

References

Andersson, M., Krockenberger, A., Schwarzkopf, L., 2010. Experimental manipulation reveals the importance of refuge habitat temperature selected by lizards. Austral Ecol. 35, 294–299. https://doi.org/10.1111/j.1442-9993.2009.02035.x.

Angilletta, M.J., 2009. Thermal Adaptation: a Theoretical and Empirical Synthesis, Thermal Adaptation A Theoretical and Empirical Synthesis. Oxford University Press. https://doi.org/10.1093/acprof:oso/9780198570875.001.1.

Angilletta, M.J., Hill, T., Robson, M.A., 2002. Is physiological performance optimized by thermoregulatory behavior?: a case study of the eastern fence lizard, *Sceloporus undulatus*. J. Therm. Biol. 27, 199–204.

Avery, R.A., Mynott, A., 1990. The effects of temperature on prey handling time in the common lizard, *Lacerta vivipara*. Amphibia-Reptilia 11, 111–122.

Bakken, G.S., 1989. Arboreal perch properties and the operative temperature experienced by small animals. Ecology 70, 922–930.

Barroso, F.M., Carretero, M.A., Silva, F., Sannolo, M., 2016. Assessing the reliability of thermography to infer internal body temperatures of lizards. J. Therm. Biol. 62, 90–96. https://doi.org/10.1016/j.jtherbio.2016.10.004.

Brown, G.P., Shine, R., 2004. Effects of reproduction on the antipredator tactics of snakes (*Tropidonophis mairii*, Colubridae). Behav. Ecol. Sociobiol. 56, 257–262. https://doi.org/10.1007/s00265-004-0778-5.

Busack, S., Visnaw, J.A., 1989. Observations on the natural history of *Lacerta lepida* in Cádiz province, Spain. Amphibia-Reptilia 10 (3), 201–213. https://doi.org/10.1163/156853889X00386.

Cabanac, M., Hammel, T., Hardy, J.D., 1967. *Tiliqua scincoides*: temperature-sensitive units in lizard brain. Science 158, 1050–1051.

Carretero, M.A., Roig, J.M., Llorente, G.A., 2005. Variation in preferred body temperature in an oviparous population of *Lacerta* (*Zootoca*) *vivipara*. Herpetol. J. 15, 51–55.

Carretero, M.A., 2006. Reproductive cycles in Mediterranean lacertids: plasticity and constraints. In: Corti, C., Lo Cascio, P., Biaggini, M. (Eds.), Mainland and Insular Lizards. A Mediterranean Perspective. Firenze University Press, Florence, pp. 33–54.

Clark, C.W., 1994. Antipredator behavior and the asset-protection principle. Behav. Ecol. 5, 159–170. https://doi.org/10.1093/beheco/5.2.159.

Cooper, W.E., 2015. Reptiles. In: Cooper, W.E., Blumstein, D.T. (Eds.), Escaping from Predators: an Integrative View of Escape Decisions. Cambridge University Press, pp. 113–151.

Cooper, W.E., Blumstein, D.T., 2015. Escaping from Predators: an Integrative View of Escape Decisions. Cambridge University Press.

Cooper, W.E., Frederick, W.G., 2007a. Optimal flight initiation distance. J. Theor. Biol. 244, 59–67. https://doi.org/10.1016/j.jtbi.2006.07.011.

Cooper, W.E., Frederick, W.G., 2007b. Optimal time to emerge from refuge. Biol. J. Linn. Soc. 91, 375–382. https://doi.org/10.1111/j.1095-8312.2007.00802.x.

Cooper, W.E., Martín, J., López, P., 2003. Simultaneous risks and differences among individual predators affect refuge use by a lizard, *Lacerta monticola*. Behaviour 140, 27–41. https://doi.org/10.1163/156853903763999872.

Cooper, W.E., Wilson, D.S., 2008. Thermal cost of refuge use affects refuge entry and hiding time by striped plateau lizards *Sceloporus virgatus*. Herpetologica 64, 406–412. https://doi.org/10.1655/07-083r2.1.

Díaz-Uriarte, R., 1999. Anti-predator behaviour changes following an aggressive encounter in the lizard *Tropidurus hispidus*. Proc. R. Soc. B Biol. Sci. 266, 2457–2464. https://doi.org/10.1098/rspb.1999.0946.

Díaz, J.A., Monasterio, C., Salvador, A., 2006. Abundance, microhabitat selection and conservation of eyed lizards (*Lacerta lepida*): a radiotelemetric study. J. Zool. 268, 295–301. https://doi.org/10.1111/j.1469-7998.2005.00031.x.

Downes, S., Shine, R., 1998. Heat, safety or solitude? Using habitat selection experiments to identify a lizard's priorities. Anim. Behav. 55, 1387–1396. https://doi.org/10.1006/anbe.1997.0705.

Downes, S., 2001. Trading heat and food for safety: costs of predator avoidance in a lizard. Ecology 82, 2870–2881.

Dzialowski, E.M., O'Connor, D., 2001. Thermal time constant estimation in warming and cooling ectotherms. J. Therm. Biol. 26, 231–245.

Frix, M.S., Hostetler, M.E., Bildstein, K.L., 1991. Intra- and interspecific differences in responses of Atlantic sand (*Uca Pugilator*) and Atlantic marsh (*U. pugnax*) fiddler crabs to simulated avian predators. J. Crustac Biol. 11, 523–529.

Galán, P., 1999. Demography and population dynamics of the lacertid lizard *Podarcis bocagei* in north-west Spain. J. Zool. 249, 203–218. https://doi.org/10.1111/j.1469-7998.1999.tb00759.x.

Gregory, P.T., 1990. Temperature differences between head and body in garter snakes (*Thamnophis*) at a den in central British Columbia. J. Herpetol. 24, 241–245.

Hair, J.F., Black, W.C., Babin, B.J., Anderson, R.E., Tatham, R.L., 2006. Multivariate Data Analysis . Uppersaddle River.

Heath, J.E., 1964. Head-body temperature differences in horned lizards. Physiol. Zool. 37, 273–279.

Hertz, P.E., Huey, R.B., Stevenson, R.D., 1993. Evaluating temperature regulation by field-active ectotherms: the fallacy of the inappropriate question. Am. Nat. 142, 796–818.

Hedrick, A.V., Kortet, R., 2006. Hiding behaviour in two cricket populations that differ in predation pressure. Anim. Behav. 72, 1111–1118. https://doi.org/10.1016/j.anbehav.2006.03.018.

Huey, R.B., 1982. Temperature, physiology, and the ecology of reptiles. In: Biology of Retilia. Academic Press, Cambridge, UK, pp. 25–91.

Huey, R.B., Slatkin, M., 1976. Cost and benefits of lizard thermoregulation. Q. Rev. Biol. 51, 363–384.

Hugie, D.M., 2003. The waiting game: a “battle of waits” between predator and prey. Behav. Ecol. 14, 807–817. https://doi.org/10.1093/beheco/arg054.

Jennions, M.D., Backwell, P.R.Y., Murai, M., Christy, J.H., 2003. Hiding behaviour in fiddler crabs: how long should prey hide in response to a potential predator? Anim. Behav. 66, 251–257. https://doi.org/10.1006/anbe.2003.2190.

Johansson, A., Englund, G., 1995. A predator-prey game between bullheads and case-making caddis larvae. Anim. Behav. 50, 785–792. https://doi.org/10.1016/0003-3472(95)80138-3.

Kålås, J.A., Fiske, P., Saether, S.A., 1995. The effect of mating probability on risk taking: an experimental study in lekking great snipe. Am. Nat. 146, 59–71. https://doi.org/10.2307/2678832.

Kerr, G.D., Bull, C.M., Burzacott, D., 2003. Refuge sites used by the scincid lizard *Tiliqua rugosa*. Austral Ecol. 28, 152–160. https://doi.org/10.1046/j.1442-9993.2003.01268.x.

Koivula, K., Rytkonen, S., Orell, M., 1995. Hunger-dependency of hiding behaviour after a predator attack in dominant and subordinate willow tits. Ardea 83, 397–404.

Kour, E., Hutchison, V., 1970. Critical thermal tolerances and heating and cooling rates of lizards from diverse habitats. Copeia 219–229. 1970. https://doi.org/10.2307/1441644.

Krause, J., Loader, S.P., McDermott, J., Ruxton, G.D., 1998. Refuge use by fish as a function of body length-related metabolic expenditure and predation risks. Proc. R. Soc. B Biol. Sci. 265, 2373–2379. https://doi.org/10.1098/rspb.1998.0586.

Lomax, R.G., Schumacker, R.E., 2004. A Beginner's Guide to Structural Equation Modeling. Psychology Press.

MacHutchon, A.G., Harestad, A.S., 1990. Vigilance behavior and use of rocks by columbian ground-squirrels. Can. J. Zool. 68, 1428–1433. https://doi.org/10.1139/z90-213.

Magnuson, J.J., Crowder, L.B., Medvick, P.A., 1979. Temperature as an ecological resource. Am. Zool. 19, 331–343.

Martin, J., Lopez, P., 1996. Avian predation on a large lizard (*Lacerta lepida*) found at low population densities in Mediterranean habitats: an analysis of bird diets. Copeia 722–726. 1996. https://doi.org/10.2307/1447538.

Martín, J., López, P., 1999a. When to come out from a refuge: risk-sensitive and state-dependent decisions in an alpine lizard. Behav. Ecol. 10, 487–492. https://doi.org/10.1093/beheco/10.5.487.

Martín, J., López, P., 1999b. An experimental test of the costs of antipredatory use in refuge the wall lizard, *Podarcis muralis*. Oikos 84, 499–505. https://doi.org/10.2307/3546428.

Martín, J., López, P., 2000. Costs of refuge use affect escape decisions of Iberian rock lizards *Lacerta monticola*. Ethology 106, 483–492.

Martín, J., López, P., 2001. Repeated predatory attacks and multiple decisions to come out from a refuge in an alpine lizard. Behav. Ecol. 12, 386–389.

Martín, J., López, P., 2010. Thermal constraints of refuge use by Schreiber's green lizards. *Lacerta schreiberi*. Behaviour 147, 275–284.

Martín, J., López, P., 2015. Hiding time in refuge. In: Cooper, W.E., Blumstein, D.T. (Eds.), Escaping from Predators: an Integrative View of Escape Decisions. Cambridge University Press, pp. 227–261.

Martín, J., López, P., Cooper, W.E., 2003a. When to come out from a refuge: balancing predation risk and foraging opportunities in an alpine lizard. Ethology 109, 77–87. https://doi.org/10.1046/j.1439-0310.2003.00855.x.

Martín, J., López, P., Cooper, W.E., 2003b. Loss of mating opportunities influences refuge use in the Iberian rock lizard, *Lacerta monticola*. Behav. Ecol. Sociobiol. 54, 505–510. https://doi.org/10.1007/s00265-003-0659-3.

Martín, J., López, P., Polo, V., 2009. Temporal patterns of predation risk affect antipredator behaviour allocation by Iberian rock lizards. Anim. Behav. 77, 1261–1266. https://doi.org/10.1016/j.anbehav.2009.02.004.

Mateo, J.A., 2014. *Timon lepidus* (daudin, 1802). In: Fauna Iberica. Reptiles, 2a Edición Revisada Y Aumentada. Museo Nacional de Ciencias Naturales. CSIC., Madrid, pp. 623–639.

Mateo, J.A., Castanet, J., 1994. Reproductive strategies in 3 Spanish populations of the ocellated lizard, *Lacerta-lepida* (Sauria, Lacertidae). Acta Oecologica-International J. Ecol. 15, 215–229.

Mateo, J.A., Castroviejo, J., 1991. Variation morphologique et révision taxonomique de l'espèce *Lacerta lepida* Daudin, 1802 (Sauria,Lacertidae). Bull. du Muséum Natl. d'histoire Nat. 12, 691–704.

Maurone, P.A., Shiomos, C., 1983. Newton's Law of Cooling with finite reservoirs. Am. J. Phys. 51, 857–859. https://doi.org/10.1119/1.13505.

Ortega, Z., Martín-Vallejo, F.J., 2019. Main factors affecting lacertid lizard thermal ecology. Integr. Zool. 14, 293–305.

Padial, J.M., Ávila, E., Gil-Sánchez, 2002. Feeding habits and overlap among red fox (*Vulpes vulpes*) and stone marten (*Martes foina*) in two Mediterranean mountain

habitats. Mamm. Biol. 67, 137–146.
Polo, V., López, P., Martín, J., 2005. Balancing the thermal costs and benefits of refuge use to cope with persistent attacks from predators: a model and an experiment with an alpine lizard. Evol. Ecol. Res. 7, 23–35.
R Development Core Team, 2018. R: a Language and environment for statistical computing, Vienna, Austria. Available at: https://www.R-project.org/. RFoundationforStatisticalComputing. https://doi.org/10.1007/978-3-540-74686-7.
Rosseel, Y., 2012. Lavaan: an R package for structural equation modeling. J. Stat. Softw. 48, 1–36. http://www.jstatsoft.org/v48/i02/.
Sacchi, R., Scali, S., Mangiacotti, M., Sannolo, M., Zuffi, M.A.L., 2016. Digital identification and analysis. In: Dodd, C.K.,J. (Ed.), Reptile Ecology and Conservation. A Handbook of Techniques. Oxford University Press, New York, pp. 59–72.
Sannolo, M., Mangiacotti, M., Sacchi, R., Scali, S., 2014. Keeping a cool mind: head–body temperature differences in the common wall lizard. J. Zool. 293, 71–79.
Sih, A., 1992. Prey uncertainty and the balancing of antidepredaton and feeding need. Am. Nat. 139, 1052–1069. https://doi.org/10.1086/285372.
Soluk, D.A., 1993. Multiple predator effects predicting combined functional response of stream fish. Ecology 74, 219–225.
Stapley, J., 2004. Do mountain log skinks (*Pseudemoia entrecasteauxii*) modify their behaviour in the presence of two predators? Behav. Ecol. Sociobiol. 56, 185–189. https://doi.org/10.1007/s00265-004-0771-z.
Van Damme, R., Bauwens, D., Verheyen, R.F., 1991. The thermal dependence of feeding behaviour, food consumption and gut-passage time in the lizard *Lacerta vivipara* Jacquin. Funct. Ecol. 5, 507–517.
Wickham, H., 2009. ggplot2: Elegant Graphics for Data Analysis. Springer-Verlag, New York.
Wolf, N.G., Kramer, D.L., 1987. Use of cover and the need to breathe: the effects of hypoxia on vulnerability of dwarf gouramis to predatory snakeheads. Oecologia 73, 127–132.

Marco Sannolo, He is a Post-Doc researcher at CIBIO-InBio. He is particularly interested in studying ectotherms thermal ecology. He also studies the possible interactions and trade-off between the thermal and water balance in ectotherms, with a special focus on the possible physiological responses at the individual and population level to the current global trend of climate change.

Raquel Ponti, She is a Post-Doc researcher at the National Museum of Natural Sciences in Madrid, Spain. The main goal in her research is finding out the engine of bird migration and evaluate the shifts in migratory distances through time, under global climatic changes in an evolutionary context. She is also interested in studying the behavior of other groups, especially reptiles; as well as biogeography and ecology of both birds and herpetofauna.

Miguel A. Carretero, He is PhD for the University of Barcelona and currently principal researcher at CIBIO-InBio, where he leads a group on Functional Biodiversity, as well as assistant professor at the University of Porto. He considers himself an integrative biologist using reptiles as main model organisms. His interests embrace ecology, physiology, behavior, morphology, life history, biogeography, interspecific relationships and conservation focusing on functional aspects, using experimental procedures and working under an evolutionary framework.