Thermal constraints of refuge use by Schreiber's green lizards, *Lacerta schreiberi*

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Summary

Prey should balance cost and benefits when deciding optimal refuge use. In ectotherms, such as lizards, body temperature can decrease in cold refuges, which has negative effects on physiological and locomotor performance. Thus, refuge use of ectotherms should be influenced by the thermal environment as well as by the body size-dependent thermal inertia of each individual. We simulated predator attacks to Schreiber's Green lizards (*Lacerta schreiberi*) and analyzed their refuge use. Results indicated that temperatures outside and inside a refuge had opposite effects on refuge use decisions. Thus, when initial external temperatures were higher and lizards had higher thermal inertia, lizards could spend longer times inside refuges before reaching a 'critical' low body temperature. However, when refuge temperature was low lizards did not decrease refuge use. If low refuge temperatures increased risk upon emerging because lizards had lower escape performance, lizards would need to compensate by remaining in a refuge for longer to scan the surroundings before emerging to ensure that the risk of a new attack decreased. Therefore, when deciding refuge use, *L. schreiberi* lizards seem to consider physiological costs of being at low temperatures and also the risk of emerging with low escape performance.

Keywords: predation risk, refuge use, thermal costs, ectotherms, lizards.

Introduction

Prey often respond to predator presence by retreating to refuges (Sih, 1997). By increasing time spent hidden in a refuge prey can minimize the risk of

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suffering a new attack after emergence (Sih, 1992; Cooper, 1998; Martín & López, 1999a, 2004, 2005; Hugie, 2003; Polo et al., 2005). However, prey animals should optimize their anti-predatory responses by balancing anti-predator demands with other ecological requirements (Lima & Dill, 1990; Sih, 1992). Refuges may have costs that should be minimized, such as the loss of time available for foraging (Dill & Fraser, 1997; Krause et al., 1998; Martín et al., 2003a; Blumstein & Pelletier, 2005) or mate searching (Sih et al., 1990; Martín et al., 2003b). Unfavorable conditions in refuges (e.g., sub-optimal temperatures or oxygen levels) might also entail thermoregulatory and physiological costs, such as hypothermia or hypoxia (Wolf & Kramer, 1987; Huey et al., 1989; Weatherhead & Robertson, 1992; Polo et al., 2005), which may affect body condition and the health state of prey (Martín & López, 1999b; Amo et al., 2007a,b). Therefore, prey should balance cost and benefits when deciding optimal emergence times from refuges (Sih, 1992, 1997; Martín & López, 1999a; Hugie, 2003; Cooper & Frederick, 2007; Cooper, 2009).

Ectotherms regulate their body temperatures through heat exchange with the environment, and effective thermoregulation requires that appropriate sources of heat from solar radiation and/or warm substrates are available (Huey, 1982). The maintenance of an optimal body temperature is essential to maximize numerous physiological processes and important behaviours, such as sprint speed, escape performance and foraging efficiency (Huey & Kingsolver, 1989; Bauwens et al., 1995). Many ectotherms, such as lizards, escape from predators by fleeing into the nearest refuge (Cooper, 1998; Martín & López, 1999a,b). This may be costly when refuges are located in microhabitats with shady and cold thermal conditions, such as rock crevices, because body temperature of ectothermic prey will decrease below preferred levels in short amount of time (Polo et al., 2005), which may negatively affect physiological and locomotor performance (Bauwens et al., 1995; Martín & López, 1999b; Amo et al., 2007a,b). Thus, we hypothesized that refuge use of lizards and other ectotherms should be influenced by the thermal conditions within the refuge and the external thermal conditions (Martín & López, 1999; Cooper & Dawns, 2008). Also, differences in body size may have consequences for thermoregulation. Smaller individuals, with high surface-to-volume ratios, are subjected to faster heating and cooling rates, and can reach an equilibrium body temperature in a shorter time than larger ones (Stevenson, 1985; Carrascal et al., 1992; Martín & López, 2003). Thus, we

hypothesized that individuals that differ in body size will modify their refuge use in relation to their thermal-exchange properties, thus compensating for differences in the thermal costs of refuge use.

We present results of a field study to test these predictions in Schreiber's Green lizards (*Lacerta schreiberi*), a large (130 mm maximum snout-to-vent length, SVL) diurnal lacertid lizard found in the northwest, west and central areas of the Iberian Peninsula (Pérez-Mellado, 1998). We simulated predator attacks and analyzed refuge use of lizards in relation to the thermal environment inside and outside of refuges and the body-size of the lizards. We predicted that variation in thermal environment and cooling rates of lizards may entail different levels of costs, which should affect refuge use.

Methods

The study was performed during spring 2007 at a large pine forest area ('Valle de La Fuenfría') in the Guadarrama mountains (40°44′N, 4°02′W; Madrid Province, Spain). The dominant vegetation consists of *Pinus sylvestris* forest, with shrubs such as *Juniperus communis* and *Cytisus scoparius*. In this area, Schreiber's green lizards (*L. schreiberi*) are active from March to September, mate in April–May, and produce a single clutch during June (Marco & Pérez-Mellado, 1990). Lizards occupy relatively moist well vegetated areas often close to streams (Pérez-Mellado, 1998). During spring most lizards are located close to rock cliffs or artificial walls, very often remaining for long periods in close proximity to rock crevices used as refuges.

We walked through the area between 0700 and 1200 h GMT until a lizard was sighted with binoculars. In many studies of anti-predatory behaviour, humans are usually used as standardized stimuli to induce escape and refuge entry because prey respond to humans as if they were potential predators (Frid & Dill, 2002; Stankowich & Blumstein, 2005). Thus, we simulated a predatory attack by walking directly towards the lizard at the same training speed. To maintain risk level constant in all approaches and to avoid confounding effects that may affect risk perception of lizards (Cooper et al., 2003), the same person wearing the same clothing performed all approaches in a similar way, while another person recorded the lizard's behaviour. Lizards typically made a short flight to the nearest available refuge (under a rock or into a rock crevice) and hid entirely from the observer. When the lizard hid

we started a stopwatch and retreated to a distance of 5–7 m to observe from a hidden position with binoculars. We recorded the time that the lizard spent in the refuge until at least the head appeared from the refuge ('appearance time'), and the total time spent hidden until the lizard emerged entirely from the refuge and resumed its normal activity ('recovery time'). Because lizards typically appeared partially from the refuge and then waited before emerging entirely from the refuge, we also calculated the time interval between appearance and recovery ('waiting time').

Immediately after a lizard emerged from the refuge and resumed its activity, we noosed it to record SVL (to the nearest mm; mean $\pm$ SE $= 107 \pm 1$ mm, range 100–115 mm; $N = 27$, 18 males and 9 females), tail condition (only adult lizards with complete tails were used in the study), and body mass (measured to the nearest 0.1 g with a Pesola spring scale; mean $\pm$ SE $= 26.7 \pm 0.8$ g, range 20.5–30.3 g). We also measured, to the nearest 0.1°C, with a digital thermometer the substrate temperature at the point where the lizard was before the attack (shaded bulb) (external temperature, T_{ext}: mean $\pm$ SE $= 22.4 \pm 0.7$°C, range 16.9–27.2°C) and the substrate temperature inside the refuge (interior temperature, T_{int}: mean $\pm$ SE $= 15.9 \pm 0.8$°C, range 11.0–24.2°C). We considered that thermal conditions in any given micro-site actually influenced body temperature of lizards because these lizards are rather sedentary and remain stationary in optimal microhabitats for long periods (Marco & Pérez-Mellado, 1999). Body temperature (T_b) of lizards before hiding or immediately after emergence could not be measured with reliability given the experimental design. Field studies show that average T_b of *L. schreiberi* is 31°C, which is about 10°C above air temperature (Salvador & Argüello, 1987). In a thermal gradient in the laboratory this lizard has a selected T_b of 36.5°C (Bauwens et al., 1995).

Given the large size of the area surveyed (more than 5 km^2), the high lizard density, and our avoidance of walking routes taken previously, the probability of repeated sampling of the same individuals was very low. We, therefore, treated all measurements as independent. We used forward step-wise general multiple regression models (GMRs) in Statistica Software (StatSoft, Tulsa, OK, USA) to determine how T_{int}, T_{ext} and body mass of lizards (independent variables) influenced appearance, recovery or waiting times (dependent variables). Previous analyses showed that the sex of the lizard did not influence significantly refuge use in any case (i.e., it was not included in any

final model) and, thus, sex was not considered in final analyses. To ensure normality, data were logarithmically transformed (Sokal & Rohlf, 1995).

Results

The time since the lizards hid until they appeared partially for the first time from the refuge (appearance time) ranged between 12 and 180 s (mean $\pm$ SE $= 79 \pm 12$ s). Appearance times were significantly longer when T_{ext} was higher, T_{int} was lower and body mass was greater (stepwise GRM, model: $R^2 = 0.70$, $F_{3,23} = 18.31$, $p < 0.0001$; T_{ext}: $\beta = 1.19$, $t = 6.99$, $p < 0.0001$; T_{int}: $\beta = -0.58$, $t = -3.48$, $p = 0.002$; body mass: $\beta = 0.27$, $t = 2.14$, $p = 0.04$).

The total time spent hidden in the refuge before emerging entirely and returning to 'normal' activity (recovery time) ranged between 12 and 196 s (mean $\pm$ SE $= 113 \pm 11$ s). Recovery times were significantly longer when T_{ext} was higher and T_{int} was lower (stepwise GMR model: $R^2 = 0.62$, $F_{2,24} = 19.84$, $p < 0.0001$; T_{ext}: $\beta = 1.06$, $t = 6.17$, $p < 0.0001$; T_{int}: $\beta = -0.88$, $t = -5.12$, $p < 0.0001$) (Figure 1), whereas body mass was not included in the final model.

When a lizard appeared partially from a refuge, they typically spent a waiting time with part of the body exposed scanning the surroundings before emerging fully. These waiting times ranged between 0 and 117 s (mean $\pm$
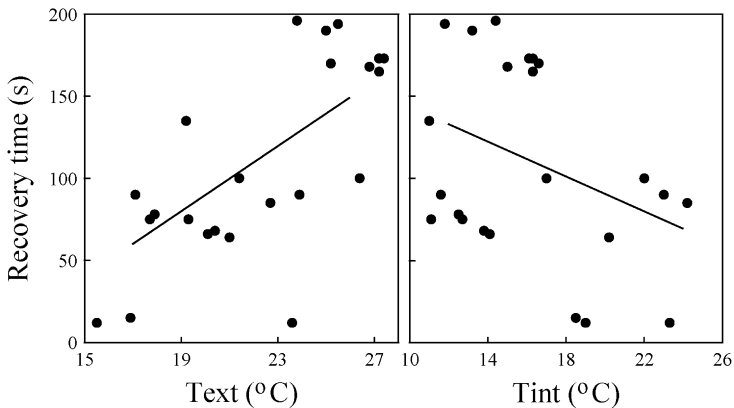
Figure 1. Relationships between the temperatures in the exterior (T_{ext}) or in the interior of the refuge (T_{int}) and the total time that lizards spent hidden in the refuge before emerging entirely and returning to 'normal' activity (recovery time).
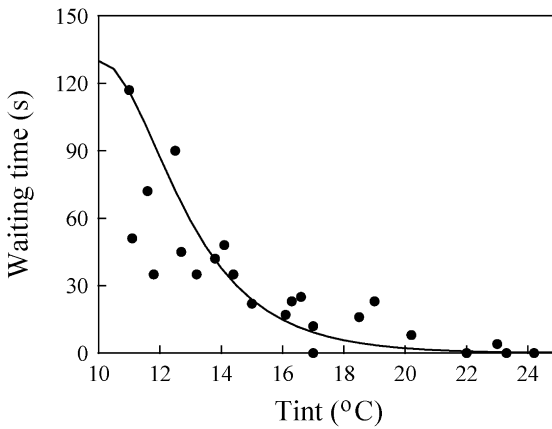
Figure 2. Relationship between the temperature in the interior of the refuge (T_{int}) and the time that lizards spent waiting and scanning the surroundings since they appear partially from the refuge until total emergence (waiting time). The line represents a visual adjustment of the data to a sigmoidal-type function.

SE $= 37 \pm 7$ s). Waiting times were significantly longer when T_{int} was lower (stepwise GMR model: $R^2 = 0.62$, $F_{1,25} = 41.10$, $p < 0.0001$; T_{int}: $\beta = -0.79$, $t = -6.41$, $p < 0.0001$) (Figure 2), whereas T_{ext} and body mass were not included in the final model. Lizards that had longer appearance times subsequently had significantly shorter waiting times ($r = -0.46$, $F_{1,25} = 6.68$, $p = 0.016$).

Discussion

Our results indicated that the thermal environment at the point where the lizard was before the attack (T_{ext}), the thermal conditions inside the refuge (T_{int}) and the body mass of the lizard affected its refuge use decisions. On the one hand, lizards with presumably higher initial body temperatures (T_b) (i.e., higher T_{ext}; see Salvador & Argüello, 1987) and with a greater body mass (i.e., slower cooling rates) could hide for longer in the refuge. This is explained because these lizards could spend a longer time at low refuge temperatures before reaching a 'critical' low body temperature.

On the other hand, refuge temperature (T_{int}) had an opposite, and apparently contradictory, effect on refuge decisions. We initially expected that when T_{int} was lower lizards cooled faster and the costs of refuge use would

be higher and, thus, lizards should decrease time spent hidden. However, we found that when T_{int} was lower lizards increased time spent in the refuge. This could be explained because lower T_{int} resulted in lower T_b, which may negatively affect sprint speed and escape performance of lizards and other ectotherms (Huey & Kingsolver, 1989; Bauwens et al., 1995). When T_{int} and T_b were lower, lizards could be at greater risk upon emerging because they would have a lower escape performance in case of subsequent predatory attacks. Thus, when T_{int} is lower lizards should increase refuge use to ensure that the risk of a new attack after emerging decreased (Martín & López, 1999a; Hugie, 2003; Cooper & Frederick, 2007). Therefore, the final decision of how long to remain in a refuge seems to be the result of considering both the physiological costs of being at low temperature and the risk of emerging with low T_b and low escape performance before the predator has left.

Once a lizard appeared from the refuge, it typically spent time scanning the surroundings before fully emerging. Waiting times were longer when T_{int} was lower. This result also suggested that the risk of emerging with low T_b and lower escape performance forced lizards to increase time waiting and scanning the surroundings before emerging entirely from the refuge, thus ensuring that the predator had left the area and a new attack would not occur (Martín & López, 1999a; Hugie, 2003; Cooper & Frederick, 2007). Moreover, the decrease in waiting time with increased refuge temperature might be visually adjusted to a sigmoidal-type function (see Figure 2). Interestingly, theoretical models have proposed that the probability that a predator is still present with time, since a predator was detected, should follow a decreased sigmoidal-type function (Sih, 1992; Polo et al., 2005). In addition, because lizards sometimes could spend this waiting time with half of the body outside of the refuge and exposed to the sun, they may also be trying to increase T_b to optimal levels to enhance escape performance before leaving the refuge. However, this 'basking while in the refuge' behaviour is not always possible given the particular conditions of each refuge (which are often in shade). This limitation was also reflected in our analyses because T_{ext} and body mass, which would affect the time needed to recover T_b, did not significantly affect waiting times.

Our results also show that lizards that had longer appearance times subsequently had shorter waiting times. This suggests that lizards might try to

compensate the costs of a greater proportion of time hidden entirely by reducing the posterior waiting time. Also, the risk of suffering a new attack decrease with time and should decrease faster after the prey has disappeared entirely inside a refuge (Martín & López, 1999a; Hugie, 2003; Cooper & Frederick, 2007). Thus, lizards that had longer appearance times would require shorter scanning times than lizards that had shorter appearance times.

Acknowledgements

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