

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

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ABSTRACT

When prey take refuge to reduce predation risk, they forfeit time for other activities. They may also pay a physiological cost. In particular, optimal regulation of body temperature is essential for ectotherms. Qualitative models predict that lizards have to balance anti-predatory decisions in relation to thermal conditions of the refuge and predation risk when deciding when to resume activity. However, these models are not general and empirical tests of their assumptions are scarce. We modified previous models to include the case of a high and maintained level of predation risk. The predictions of the model were further investigated in a laboratory experiment using male Iberian rock lizards. The same level of predation risk was displayed in two treatments in which temperature inside the refuge was high or low, and in the mating or the post-reproductive season. As predicted, lizards increased successive emergence times – an increase that was not linear but accelerating – and they had shorter emergence times when thermal costs of refuge use were higher. Nevertheless, body size of lizards and the season of the experiment had no effect on these decision rules. Our results are in line with an economical balance between costs and benefits in the decision rules controlling active versus inactive periods.

Keywords: costs of refuge use, *Lacerta monticola*, lizards, predation risk.

INTRODUCTION

Prey often seek refuge when confronted by predators (Sih *et al.*, 1992; Cooper, 1998). However, refuge use may be costly in terms of the reduced time available for other activities (Koivula *et al.*, 1995; Dill and Fraser, 1997), or because of physiological costs (Wolf and Kramer, 1987; Martín and López, 1999a,b). For this reason, animals should optimize their decision of when to leave a refuge by balancing anti-predator demands with other requirements (Sih *et al.*, 1988; Sih, 1992, 1997; Dill and Fraser, 1997; Martín and López, 1999a, 2001).

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In ectotherms such as reptiles, the attainment and regulation of an optimal body temperature is essential to maximize physiological and ecological processes, which may conflict with predation risk costs (Christian and Tracy, 1981; Huey, 1982). Many lizards escape from predators by fleeing to the nearest refuge (Greene, 1988). However, when a lizard hides in a cold refuge (e.g. a rock crevice), its body temperature will quickly fall below optimal values (Martín and López, 1999a). This may affect general physiological performance, such as somatic growth (Martín and López, 1999b), and may increase susceptibility to predators after emergence (Christian and Tracy, 1981).

Previous field studies have shown that lizards' escape decisions and refuge use may be influenced by level of predation risk and the thermal conditions of the refuge (Martín and López, 1999a, 2000a, 2001). However, in the field many confounding variables may affect refuge use, such as perceived predation risk (Martín and López, 2000b), other conflicting demands (Cooper, 1998, 1999), or the 'thermal history' (i.e. the opportunities for thermoregulation in the immediate past). Ontogenetic changes in body size affect thermal exchange rates (Stevenson, 1985; Carrascal *et al.*, 1992) and thus the extent of the thermal costs of refuge. Also, microclimate conditions are difficult to measure (Huey *et al.*, 1989) and nearly impossible to control in the field. Thus, the effects of thermal costs on the refuge use of lizards remain to be examined experimentally under manipulated and controlled conditions.

In this paper, we present a theoretical model to determine how lizards, or other ectotherms, decide on the optimal time spent in a refuge during continuous attacks, taking into account thermal costs. We then analyse in a laboratory experiment whether Iberian rock lizards (*Lacerta monticola*) can deal with sustained high levels of predation risk by modifying refuge use according to the predictions of the model. This lizard is found in rocky habitats of high mountains of the Iberian Peninsula, where unfavourable thermal conditions are limiting (Carrascal *et al.*, 1992), and often uses refuges that are thermally disadvantageous (Martín and López, 1999a,b). Lizards are active from May to October, but the amount of time each day with thermal conditions suitable for activity is often restricted by severe climatology. Mating occurs during a 2 week period in May–June and females produce a single clutch (Elvira and Vigal, 1985). Males are polygynous and gain access to several females by increasing their movements (Aragón *et al.*, 2001). Thus time spent in the refuge may also reduce their opportunities for reproduction (Martín *et al.*, 2003).

Our experimental study addresses four questions: (1) How do lizards decide on successive emergence times from a refuge when subjected to persistent attacks? (2) Can the temporal pattern of refuge use be modified when the thermal conditions inside the refuge (i.e. thermal costs) change? (3) Do smaller lizards show differences in refuge use compared with large lizards? (4) If males forfeit opportunities for reproduction by using refuges, are the refuges used less often during the mating period?

A MODEL OF REFUGE USE WITH THERMAL COSTS AND PERSISTENT ATTACKS

We present a qualitative model to predict the effects of the persistent presence of predators – or of an increase in the density of different individual predators – and of the thermal cost of refuge use on a prey's decision rules about the time spent in a refuge. Our model is based on a previous economic graphical model proposed by Martín and López (1999a) as an extension of the optimal escape model of Ydenberg and Dill (1986). That model predicted when prey should emerge from a refuge after a single attack, taking into account that predation risk (PR) decreases gradually after the attack and that the cost of refuge use (C)

increases linearly with time spent in the refuge. In this paper, we extend these previous models to predict consecutive emergence times from a refuge under persistent attacks and modify some previous assumptions in a more realistic way.

We consider a prey living in a simple habitat with two patches: an open area, sometimes visited by predators, and a refuge. When the prey chooses the open area, it can thermo-regulate and attain an optimal body temperature but is exposed to predators. When a predator is present, the prey can evade it by retreating into the refuge, where it is safe but loses heat. The decision variable for the prey is when to leave the refuge. The probability of the predator waiting for the prey outside the refuge will decrease with time. Therefore, the function that defines predation risk level (PR) may be at its maximum at the moment of the attack, decreasing gradually as time in the refuge increases (Fig. 1). The function PR may be written by a sigmoidal function as:

$$PR(x) = \frac{2}{e^{x/a} + e^{-x/a}}$$

where a is a parameter with units of time that determines how fast the function decreases with time (i.e. the higher a , the slower the diminution of perceived risk of predation). We choose this function because it fits very well with the probability that predators are still present with time, since a predator was detected in the model of Sih (1992) (see figure 1 in Sih's model). Thus, the maximum point of the function represents the moment of the attack, when the probability that the predator is present is equal to 1.

On the other hand, when a prey is in a refuge, its body temperature gradually decreases. Its body temperature will be closer to the temperature of the refuge as time spent in the refuge increases. Therefore, we choose a Bertalanffy function (Bertalanffy, 1960; Kaufman, 1981) to define the cost (C) of refuge use (Fig. 1):

$$C(x) = b(1 - e^{-x/c})$$

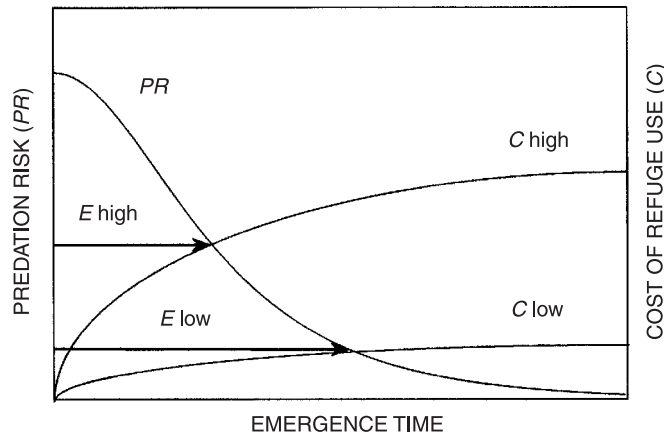


Fig. 1. An economic model to predict the emergence time of lizards from a refuge after a predatory attack as a function of the expected fitness effects of the diminution of the risk of predation in the exterior with time (PR), and two levels of costs (C) of refuge use. The optimal emergence times (E) for each particular level of costs are shown.

where b represents the maximum cost (i.e. when the body temperature of the prey has reached the temperature of the refuge, and thermal costs are independent of time spent in the refuge). In contrast to previous models, we consider that the function C tends to a maximum that is always lower than the maximal value of PR . This is justified because predation is a more severe event than losing body heat. On the other hand, c is a parameter (the time constant) that determines how fast the function increases with time (i.e. the higher c , the slower the decrease in body temperature).

The prey should balance costs and benefits of both functions related to the time spent in the refuge. Therefore, the optimal emergence time (E) from the refuge is obtained at the point where the two curves intersect. This optimal emergence time should increase when thermal costs decrease (Fig. 1).

In our model, we consider that a prey that retreats into a refuge has some information on the environment regarding the presence of the predator after the attack, and can also use its previous experience to assess the threat of this potential predator in subsequent encounters with it. Our aim is to consider how optimal emergence time is affected when the attacks from predators are persistent. Imagine that at the precise moment that the prey emerges from the refuge, it is subjected to a second attack that forces it to retreat back into the refuge. In this case, two main factors can be highlighted.

First, the prey may use its previous experience to determine whether emerging is more risky now than was considered previously (PR_2 curve in Fig. 2). Each new attack may increase the prey's perception of risk (i.e. because an individual predator persists in capturing that particular prey or because the density of different individual predators in the area has increased) (Cooper, 1998). Thus, this second curve starts from the same maximal value (i.e. the probability that the predator is present during each attack is always equal to 1), but the prey may perceive that the probability of a new attack will decrease more slowly with time after each successive attack (i.e. the parameter a is greater).

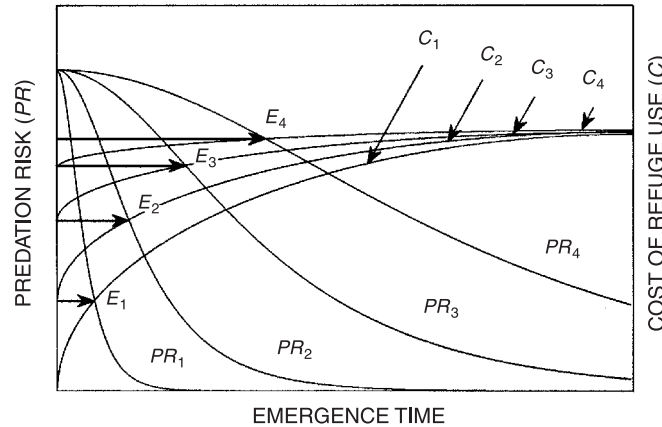


Fig. 2. An economic model to predict the emergence time of lizards from a refuge after successive continuous attacks as a function of the expected fitness effects of the diminution of the risk of predation in the exterior with time (PR) after each attack (successive PR curves), and variations with time in costs (C) of refuge use after each attack (successive C curves). The optimal emergence times (E) after each successive attack are shown.

Second, at the beginning of this second period in the refuge, the prey has lost heat due to the time previously spent in the refuge (C_2 curve in Fig. 2). Thus, the second curve is similar to the first (diminution of body temperature follows a similar Bertalanffy function) but it does not start from 0, but from the maximum point reached in the previous emergence time (i.e. it starts from the current body temperature, which is lower than the initial one). Then C_2 may be written as:

$$C(x) = b + (d - b)e^{x/c}$$

where b and c have the same values as in the first curve, and d represents the new initial point of the function (determined from the value of C after the first emergence time). The reasoning is similar for subsequent attacks (in subsequent PR curves, a will tend to be greater, and in subsequent C curves, d will tend to be higher). In these circumstances, the model predicts that the optimal time spent in the refuge should increase following subsequent attacks (see E_2 and the successive emergence times in Fig. 2) and that this increase should not be linear but accelerating.

MATERIALS AND METHODS

Experimental procedure

The experiment was conducted with captive male *L. monticola* lizards from July to August 1999 (post-reproductive season, 14 individuals) and June 2000 (mating season, 15 individuals) at 'El Ventorrillo' field station (1500 m above sea level, 40°45'N 04°01'W, Sierra de Guadarrama, Madrid province, Central Spain). Lizards were captured by noosing at different locations over a large area ('Puerto de Navacerrada', Guadarrama Mountains), 5 km from the field station. They were individually housed in outdoor plastic cages (80 × 50 cm) containing rocks for cover. Food (mealworms and crickets) dusted with a multivitamin powder and water were provided *ad libitum*. We measured the size of lizards (snout-to-vent length, SVL) to the nearest millimetre and their body mass to the nearest gram. Only individuals with complete tails were used because tail-less individuals incur a higher predation risk and may show differences in their anti-predatory behaviour (e.g. Martín and Salvador, 1993). Lizards were held in their home cages for at least a week before testing. The animals were healthy during the trials and at the end of the experiments were released at their capture site, by which time they had all maintained or increased their original body mass.

To analyse the pattern and duration of successive emergence times of lizards under different thermal costs of refuge use, we designed a laboratory experiment. The experiment was divided into four trials where the treatments were alternated between 'low' and 'high' thermal costs. We used a repeated-measures design whereby each individual participated twice in each treatment in a counterbalanced order. Each lizard was tested just once every 3 days. Each set of four trials was repeated in a similar way but with different individuals during the mating season (June) and during the post-reproductive season (July–August). All experimental variables were the same in both treatments, except for the temperature inside the refuge, which was set at a mean ($\pm$ standard deviation) of $26.6 \pm 1.5^\circ\text{C}$ in the 'low' cost treatment and $18.0 \pm 1.0^\circ\text{C}$ in the 'high' cost treatment.

The experimental cage was a 50 × 50 × 100 cm (width × height × length) terrarium placed in a dark room. The cage had a sand substrate, with only a refuge placed in the middle of

one end of the terrarium. Three light bulbs were positioned over the terrarium: over the refuge (60 W), over the middle of the cage (100 W) and at the opposite end of the cage (250 W). The heights of the bulbs over the terrarium were modified during the trials to stabilize the temperature outside and inside the refuge. Two digital thermometers were positioned inside the refuge and in the ground 50 cm from the refuge (i.e. the opposite side of the cage), respectively, to control the temperature. To simulate a refuge, we attached two aluminium cages of a rectangular cross-section ($4 \times 5 \times 25$ cm, width $\times$ height $\times$ length). The cages were only opened at one of their ends. Therefore, lizards only could enter and leave the refuge by the same opening. Aluminium is a good heat conductor; this made control of the temperature in the refuge much easier. Before the experiment, we performed a pilot study to determine the dynamics of the temperature inside the refuge. Ten heating and cooling trajectories were fitted to a Bertalanffy model ($y = a - be^{-x/\tau}$; variance explained by the model = 99.7%, $P < 0.0001$). The time constant in the model, τ , represents the time inside the metallic cage required to cover 63.2% of the range in temperature (i.e. the difference between the temperature of the refuge at the beginning and the final temperature after stabilization). This gave a time slow enough ($\tau = 10.05$ min) to ensure that the temperature was stable in the aluminium cages throughout the experiment.

Trials were performed between 09.30 h and 16.00 h (GMT) when the lizards were fully active. At the beginning of each trial, lizards were gently transferred to the experimental terraria. The lizards were left undisturbed for 10 min before trials, for acclimatization to a novel environment and to allow them to bask and attain an optimal body temperature. In previous experiments, we allowed the lizards to bask in their outdoor home cages for at least 2 h. We measured the body temperature of lizards previously in similar thermal gradients and showed that they were both able to attain and maintain a body temperature within the activity and preferred temperature range of the species (i.e. range of mean selected body temperatures: 29.8–33.9°C) (see Martín and Salvador, 1993; Bauwens *et al.*, 1995). Thus, in this experiment, lizards typically started to bask for a short time under the bulbs and then moved normally through the terraria. Then, the experimenter simulated a predatory attack by tapping lizards close to the tail with a brush to stimulate them to run and hide in the refuge. With this procedure we simulated an attack from an avian predator attacking from above the lizard. The same person performed all ‘predatory attacks’, while another person recorded the lizard’s behaviour. Observations of emergences from the refuge were made from a nearby hide in the darkness.

The perceived risk of predation was manipulated by simulating successive ‘predatory attacks’. Each time that at least the entire head of the lizard emerged from the refuge, we noted the time spent inside the refuge (emergence time) with a digital stopwatch, and we simulated another predatory attack until the lizard returned inside the refuge. Lizards may acquire information on the presence of predators when they have partly emerged from a refuge (Martín and López, 1999a). Therefore, we also recorded the time that the lizards stayed near the entrance to the refuge (i.e. with its snout closer than 1 cm to the exit of the refuge) until they emerged fully (waiting time). To avoid stress to the lizards, the duration of each trial was less than 90 min. Thus we were able to simulate between four and eight consecutive attacks, depending on emergence time durations.

Sometimes lizards did not emerge from the refuge even after a long period. We considered that these long periods spent in the refuge might decrease the perceived risk of predation. Therefore, we simulated the persistence of the predator waiting for the prey or an increase in the density of different individual predators. Each time that a lizard did not emerge from the

refuge after 20 min, we noted whether it was waiting near the entrance to the refuge or was deep inside the refuge. Then, we touched the open end of the refuge with a paintbrush to simulate another predatory attack, where the predator was trying to flush the lizard out from the refuge, and we assigned an emergence time of 20 min.

To evaluate the thermal costs of refuge use, the lizard was captured at the end of each trial and its body temperature and the temperature inside the refuge were measured with a digital thermometer (to the nearest 0.1°C). No lizard suffered a physical injury or showed physical stress due to the experimental conditions or captivity.

Data analyses

Only lizards with data for at least six successive emergences in both treatments were included in the study. Thus, 23 lizards were used in the analyses (10 individuals at the beginning of the mating period in 2000 and 13 individuals when the mating period had finished in 1999). For lizards with an equal number of emergences in the two trials within each treatment, mean values of emergence times (and waiting times) by order of emergence were used. In all other cases, only data from the trial with the higher number of emergences were included. For analyses of the effect of differences in body size between individuals, lizards with a body mass of less than 6.5 g (average SVL = 70 mm) were included in the small individuals group, while lizards with a body mass of more than 7 g (average SVL = 75 mm) were included in the large individuals group. These size categories also corresponded, approximately, with two age categories of adult males (unpublished data).

We used two-way repeated-measures analyses of variance to assess differences in emergence and waiting times. We used cost of the refuge (low *vs* high cost) as the fixed factor and the sequence of successive emergences from a refuge (the means of the two trials of each lizard in each of the six first emergences) as the repeated factor within each individual. To assess differences in emergence time with body size (small *vs* large) and season (mating *vs* post-reproductive), we used a repeated-measures analysis of variance (ANOVA) with treatment, size and date as fixed factors and the sequence of successive emergences as the repeated factor. The effect of thermal condition of the refuge and the time spent in the experimental terrarium (i.e. the addition of all emergence times) on body temperature was evaluated with an analysis of covariance, with treatment as the fixed factor and the total time of the trial as the covariate. Emergence and waiting times were Box-Cox transformed, and total time of a trial was log-transformed before the analyses.

RESULTS

The body temperature of lizards at the end of the trials (high- *vs* low-cost treatment: 21.8 *vs* 27.3°C) was significantly affected by thermal condition of the refuge and by the total duration of the trial (treatment effect: $F_{1,39} = 134.48$, $P < 0.001$; total duration effect: $\beta = -0.66$, $R^2 = 42.9\%$, $P < 0.001$). Thus lizards lost less heat when they emerged earlier from the refuge or when the thermal cost of the refuge was lower. In addition, the relationship between body temperature and thermal cost of the refuge was only significant in the high-cost treatment (parallelism effect: $F_{1,38} = 9.49$, $P < 0.004$; Fig. 3). The time constant for the Bertalanffy function adjusted to the data for the high-cost treatment was 7.5 min (see Fig. 3). The initial body temperature adjusted to the curve (i.e. the point at which the curve intersected the y axis) was 31°C.

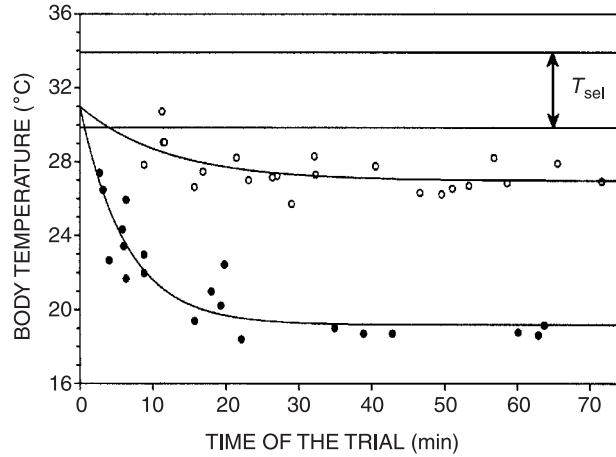


Fig. 3. Body temperature of *L. monticola* lizards at the end of the trials as a function of total duration of the trial in the low- (○) and high-cost (●) treatments. Body temperatures are corrected for slight differences in refuge temperatures. The Bertalanffy functions adjusted to the data of diminution of temperature with time, and the range of mean selected body temperatures by this lizard in a thermal gradient (T_{sel} , horizontal continuous lines), are shown.

Emergence times were significantly shorter in the high-cost treatment (i.e. decreased with the thermal cost of the refuge) (high- vs low-cost treatment: 2.48 ± 0.41 vs 4.79 ± 0.47 min; two-way ANOVA: $F_{1,22} = 30.92$, $P < 0.001$). Thus, lizards spent significantly more time inside the refuge when the physiological costs of refuge use were lower. Also, lizards spent longer inside the refuge in response to successive encounters (effect of the repeated factor in the ANOVA: $F_{5,110} = 7.02$, $P < 0.001$; Fig. 4a). The increase of emergence time with successive emergences was not different between treatments (interaction effect: $F_{5,110} = 0.72$, $P = 0.61$). These results suggest that lizards may change their perceived risk of predation with successive emergences. Thus, lizards may consider that the reduction in predation risk becomes less after successive attacks (see Fig. 2).

In the low-cost treatment, lizards waited inside but close to the entrance of the refuge for longer before emerging than in the high-cost treatment (high- vs low-cost treatment: 0.66 ± 0.26 vs 2.12 ± 0.39 min; two-way ANOVA: $F_{1,22} = 15.51$, $P < 0.001$). Lizards waited for longer after successive attacks (effect of the repeated factor in the ANOVA: $F_{5,110} = 2.97$, $P = 0.015$; Fig. 4b), but the increase in successive waiting times was not different between treatments (interaction effect: $F_{5,110} = 0.40$, $P = 0.85$). These results suggest that lizards acquired information on the presence of predators before they emerged from the refuge.

In 34 of 464 cases (the first four emergence times of all lizards), the lizard did not emerge after 20 min but stayed immobile and apparently inactive deep inside the refuge. This behaviour was more often observed in the low-cost treatment (low- vs high-cost treatment: 27 vs 7 cases; Yates corrected chi-squared test: $\chi^2_1 = 10.44$, $P = 0.001$). In addition, the frequency of this behaviour increased with the emergence order in both treatments (low-cost treatment: $\chi^2_3 = 9.89$, $P = 0.019$; high-cost treatment: $\chi^2_3 = 9.57$, $P = 0.023$). However, when considering only the trials in which lizards were the victims of eight attacks (low- vs high-cost treatment: 232 vs 208 emergences), the frequency of this behaviour was significantly greater in the high-cost treatment (low- vs high-cost treatment: 1 vs 8 cases;

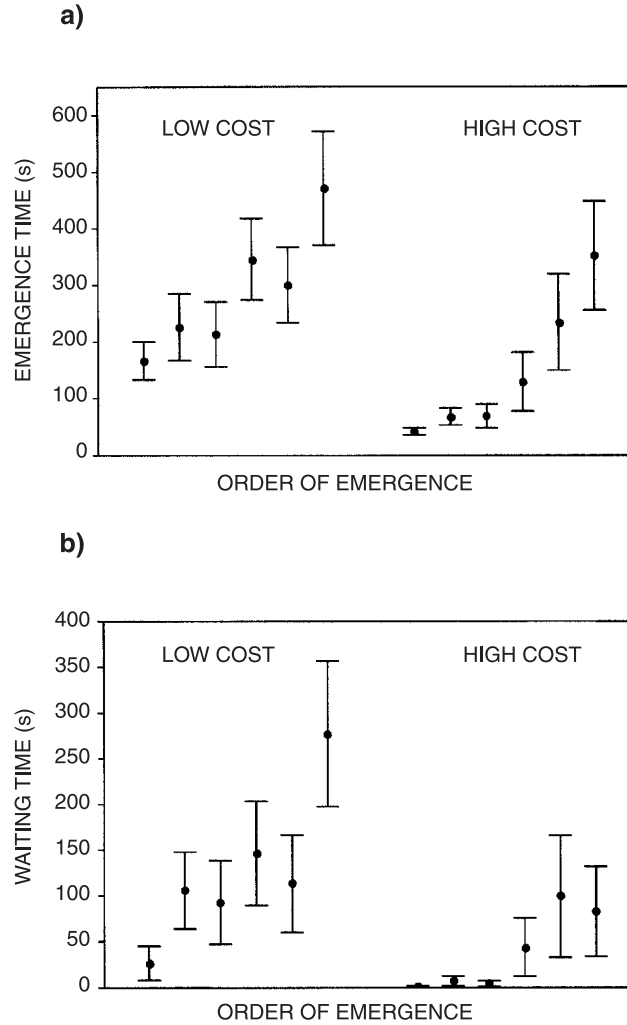


Fig. 4. The observed successive (a) emergence and (b) waiting times from a refuge (mean $\pm$ standard error) of *L. monticola* lizards after continuous predatory attacks in the low- and high-cost treatments.

$\chi^2_1 = 4.57$, $P = 0.033$). Additionally, the observations in the high-cost treatment were more often found in the last of the successive attacks ($\chi^2_7 = 22.00$, $P = 0.0025$). The average accumulated time spent before this behaviour was observed was 20.63 min; this is quite long enough to ensure that the lizard's body temperature was very similar to the temperature of the refuge (see Fig. 3).

Season and body size of lizards did not significantly affect either emergence time (mating *vs* post-reproductive period: 3.27 ± 0.42 *vs* 3.92 ± 0.45 min, $F_{1,38} = 0.88$, $P = 0.35$; small *vs* large individuals: 3.83 ± 0.61 *vs* 3.55 ± 0.38 min, $F_{1,38} = 0.03$, $P = 0.84$) or waiting time (mating *vs* post-reproductive period: 1.50 ± 0.35 *vs* 1.52 ± 0.30 min, $F_{1,38} = 0.78$, $P = 0.39$; small *vs* large individuals: 1.30 ± 0.40 *vs* 1.61 ± 0.30 min, $F_{1,38} = 2.15$, $P = 0.15$).

DISCUSSION

Refuge use in the field may be costly for lizards because they may lose heat (Martín and López, 2000a). The thermal conditions in the refuges simulated in the present study also inferred an important cost to the lizards' body temperature. At the beginning of each experiment, lizards could attain an optimal body temperature of around 31°C by basking (fitted value at time 0 in Fig. 3) (see also Martín and Salvador, 1993; Bauwens *et al.*, 1995), but in the refuge their body temperature decreased on average by 5 and 10°C for the low- and high-cost treatment, respectively. Lizards in the high-cost treatment emerged at the end of the repeated attacks with a suboptimal body temperature. Lizards with a low body temperature are more vulnerable to predation (Christian and Tracy, 1981) because of decreased escape performance (Bauwens *et al.*, 1995), and may incur physiological costs (Huey, 1982; Martín and López, 1999b). Thus, it is reasonable that *L. monticola* lizards may optimize refuge use to minimize the time spent at unfavourable body temperatures and away from other activities.

The results of the present study confirm the predictions of the model. Time spent in the refuge increased during subsequent attacks, but lizards spent more time inside the refuge when the thermal costs were lower. This is similar to previous field observations (Martín and López, 1999a, 2001). However, in the laboratory, potential confounding variables were maintained constant, and changes from the low- to the high-cost treatment were observed consistently in the same individual lizards (i.e. repeated-measures design). Therefore, our results clearly suggest that *L. monticola* lizards change their refuge use as a function of thermal costs, and independently of the possible effect of other variables.

Lizards increased the duration of successive emergence times, probably to compensate for the increase in risk of repeated attacks, which may indicate that the probability of a new attack in the immediate future is high. Lizards should increase the duration of successive emergence times so as to wait until the predator leaves the area (Cooper, 1998; Martín and López, 1999a, 2001). Lizards may perceive a higher risk when a given individual predator is persistent, although individual recognition of the predator may not be needed if the assessment was just based on attack rate, and lizards might respond equally to an increase in the density of different individual predators (Cooper, 1998). Our results indicate that the increase in successive emergence times is not linear, but accelerating (i.e. the rate of increase in time spent in the refuge increased over successive emergence times). This was expected because thermal costs do not increase linearly, but follow a Bertalanffy function (see Fig. 1). Also, after some time in a refuge, a lizard's body temperature is close to the temperature of the refuge, when the cost of losing body heat is independent of additional time spent in the refuge. Emergence times should increase due to the effect of increased predation risk of successive attacks (see successive *PR* curves in Fig. 2).

Lizards may appear partly from the refuge to acquire information on the persistence of the predator outside, and decide to emerge only if the predator is not detected (Martín and López, 1999a). In our study, lizards increased waiting time spent near the entrance to the refuge after successive attacks. Because the probability that a predator is outside is higher after successive attacks, lizards should increase time being vigilant. The greater the time spent without detecting the predator, the higher the probability that the predator has left the vicinity (Sih, 1992). However, this strategy was affected by thermal costs, and thus lizards waited for longer in the low-cost treatment than in the high-cost one.

Emergence times in the laboratory were often much longer than those in the field (Martín and López, 1999a, 2001). This may be because lizards perceived the risk under laboratory

conditions to be extremely high because the predator pursued them closely and persistently (i.e. tapping the tail with the brush), whereas in the field most lizards hid when the predator was still approaching. In addition, in the field microhabitats are more complex; refuges (i.e. rock crevices) have multiple possible exits, lizards often walk under the rocks to reappear at a different location, and may run to different alternative refuges (Martín and López, 1999a, 2001). In contrast, only one refuge (and exit) was available in the laboratory. The lack of alternatives may also contribute to increase perceived predation risk.

When predation risk appears too high, animals may adopt a conservative strategy and decide to remain inactive. The decision of remaining inactive is not rare in lizards as an alternative strategy (Huey, 1982). Thus, not all individual lizards in a population are simultaneously active even when thermal conditions are suitable (Simon and Middendorf, 1976; Rose, 1981). Inactivity could be important because it may decrease predation risk, conserve energy or reduce intraspecific competition (Simon and Middendorf, 1976; Rose, 1981; Adolph and Porter, 1993; Martín and Salvador, 1995; Martín and López, 2000c). Our results suggest that some lizards decided to remain inactive in the refuge for long periods. This behaviour was more frequent after suffering repeated attacks, but it was dependent on temperature inside the refuge. When the temperature of a refuge is low, the lizard should emerge as soon as possible to avoid the loss of heat. However, after suffering repeated attacks, it might be more favourable to remain inactive until the risk decreases, because emerging with a low body temperature, and thus poor locomotor performance, may be more dangerous. In contrast, in a refuge with a high temperature, a lizard will never attain a low body temperature, and thus it may recover normal activity immediately after emerging.

We did not observe differences in emergence times of lizards with different body sizes. Smaller lizards have faster cooling rates (Stevenson, 1985; Carrascal *et al.*, 1992), and thus they lose heat more quickly in a cool refuge (i.e. the costs of refuge use are higher). However, this may be important only for short emergence times. The diminution in body temperature will be quicker in the first seconds, but the rate of diminution will later decrease and body temperature will slowly approach the temperature of the refuge. Thus, when emergence times are long enough, the effect of different cooling rates may be unimportant or remain undetected. Nevertheless, if differences between thermal exchange rates were greater (e.g. juveniles *vs* large adults), their effect may be more important and affect refuge use.

In the field, during the mating season male lizards had greater general activity levels and shorter emergence times than in the non-mating season, which cannot be explained by thermal constraints (Aragón *et al.*, 2001; Martín *et al.*, 2003). These seem to reflect different balances between the cost of losing mating opportunities and the benefit of avoiding predation. However, we did not observe differences between seasons in the laboratory. In the field, when a receptive female was nearby, male lizards allowed predators to approach them more closely before escaping (Cooper, 1999; Martín and López, 1999c) and had shorter emergence times (Martín *et al.*, 2003) than males found alone. Because there are increased costs for a male who must leave his mate to escape, an optimal decision will require that the approach distance and emergence time decrease even if predation risk increases (Ydenberg and Dill, 1986; Cooper, 1999; Martín *et al.*, 2003). Nevertheless, an increase in risk may force lizards to increase emergence times. Under laboratory conditions, the level of risk was higher and the current opportunities to mate were low even in the mating season, because females were not available. Therefore, the optimal response in these circumstances may be little affected by the season *per se*.

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REFERENCES

- Adolph, S.C. and Porter, W.P. 1993. Temperature, activity and lizard life histories. *Am. Nat.*, **142**: 273–295.
- Aragón, P., López, P. and Martín, J. 2001. Seasonal changes in activity and spatial and social relationships of the Iberian rock-lizard *Lacerta monticola*. *Can. J. Zool.*, **79**: 1965–1971.
- Bauwens, D., Garland, T., Jr., Castilla, A.M. and Van Damme, R. 1995. Evolution of sprint speed in lacertid lizards: morphological, physiological and behavioral covariation. *Evolution*, **49**: 848–863.
- Bertalanffy, L., von. 1960. Principles and theory of growth. In *Fundamental Aspects of Normal and Malignant Growth* (W.W. Nowinski, ed.), pp. 137–259. Princeton, NJ: Elsevier.
- Carrascal, L.M., López, P., Martín, J. and Salvador, A. 1992. Basking and antipredator behaviour in a high altitude lizard: implications of heat-exchange rate. *Ethology*, **92**: 143–154.
- Christian, K.A. and Tracy, C.R. 1981. The effect of the thermal environment on the ability of Galapagos land iguanas to avoid predation during dispersal. *Oecologia*, **49**: 218–223.
- Cooper, W.E., Jr. 1998. Risk factors and emergence from refuge in the lizard *Eumeces laticeps*. *Behaviour*, **135**: 1065–1076.
- Cooper, W.E., Jr. 1999. Tradeoffs between courtship, fighting, and antipredatory behavior by a lizard, *Eumeces laticeps*. *Behav. Ecol. Sociobiol.*, **47**: 54–59.
- Dill, L.M. and Fraser, A.H.G. 1997. The worm re-turns: hiding behaviour of a tube-dwelling marine polychaete, *Serpula vermicularis*. *Behav. Ecol.*, **8**: 186–193.
- Elvira, B. and Vigal, C.R. 1985. Further data on the reproduction of *Lacerta monticola cyreni* (Sauria, Lacertidae) in Central Spain. *Amphib.-Rept.*, **6**: 173–179.
- Greene, H.W. 1988. Antipredator mechanisms in reptiles. In *Biology of the Reptilia*, Vol. 16 (C. Gans and R.B. Huey, eds.), pp. 1–152. New York: Wiley.
- Huey, R.B. 1982. Temperature, physiology and the ecology of reptiles. In *Biology of the Reptilia*, Vol. 12 (C. Gans and F.H. Pough, eds.), pp. 25–91. New York: Academic Press.
- Huey, R.B., Peterson, C.R., Arnold, S.J. and Porter, W.P. 1989. Hot rocks and not-so-hot rocks: retreat site selection by garter snakes and its thermal consequences. *Ecology*, **70**: 931–944.
- Kaufman, K.W. 1981. Fitting and using growth curves. *Oecologia*, **49**: 293–299.
- Koivula, K., Rytönen, S. and Orell, M. 1995. Hunger-dependency of hiding behaviour after a predator attack in dominant and subordinate willow tits. *Ardea*, **83**: 397–404.
- Martín, J. and 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.
- Martín, J. and López, P. 1999b. An experimental test of the costs of antipredatory refuge use in the wall lizard, *Podarcis muralis*. *Oikos*, **84**: 499–505.
- Martín, J. and López, P. 1999c. Nuptial coloration and mate-guarding affect escape decisions of male lizards, *Psammodromus algirus*. *Ethology*, **105**: 439–447.
- Martín, J. and López, P. 2000a. Costs of refuge use affect escape decisions of iberian-rock lizards, *Lacerta monticola*. *Ethology*, **106**: 483–492.
- Martín, J. and López, P. 2000b. Fleeing to unsafe refuges: effects of conspicuousness and refuge safety on the escape decisions of the lizard *Psammodromus algirus*. *Can. J. Zool.*, **78**: 265–270.
- Martín, J. and López, P. 2000c. Social status of male Iberian rock-lizards (*Lacerta monticola*) influences their activity patterns during the mating season. *Can. J. Zool.*, **78**: 1105–1109.
- Martín, J. and 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. and Salvador, A. 1993. Thermoregulatory behaviour of rock lizards in response to tail loss. *Behaviour*, **124**: 123–135.
- Martín, J. and Salvador, A. 1995. Effects of tail loss on activity patterns of rock-lizards, *Lacerta monticola*. *Copeia*, **1995**: 984–988.
- Martín, J., López, P. and Cooper, W.E., Jr. 2003. Loss of mating opportunities influences refuge use in the Iberian rock lizard, *Lacerta monticola*. *Behav. Ecol. Sociobiol.*, **54**: 505–510.
- Rose, B. 1981. Factors affecting activity in *Sceloporus virgatus*. *Ecology*, **62**: 706–716.
- Sih, A. 1992. Prey uncertainty and the balancing of antipredator and foraging needs. *Am. Nat.*, **139**: 1052–1069.
- Sih, A. 1997. To hide or not to hide? Refuge use in a fluctuating environment. *Trends Ecol. Evol.*, **12**: 375–376.
- Sih, A., Petranka, J.W. and Kats, L.B. 1988. The dynamics of prey refuge use: a model and tests with sunfish and salamander larvae. *Am. Nat.*, **132**: 463–483.
- Sih, A., Kats, L.B. and Moore, R.D. 1992. Effects of predatory sunfish on the density, drift and refuge use of the stream salamander larvae. *Ecology*, **73**: 1418–1430.
- Simon, C.A. and Middendorf, G.A. 1976. Resource partitioning by an iguanid lizard: temporal and microhabitat aspects. *Ecology*, **57**: 1317–1320.
- Stevenson, R.D. 1985. Body size and limits to the daily range of body temperature in terrestrial ectotherms. *Am. Nat.*, **125**: 102–117.
- Wolf, N.G. and 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.
- Ydenberg, R.C. and Dill, L.M. 1986. The economics of fleeing from predators. *Adv. Stud. Behav.*, **16**: 229–249.

