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When to come out from a refuge: risk-sensitive and state-dependent decisions in an alpine lizard

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Prey often respond to predator presence by increasing their use of refuges. However, unfavorable thermal conditions in refuges might entail physiological costs for an ectothermic prey. Thus, the decision of when to come out from a refuge should be optimized by considering the expected fitness effects of diminution of predation risk with time, but also by considering the cost of the loss of time spent at optimal body temperature maximizing physiological functions. The model of Ydenberg and Dill describes the trade-off between risk and cost for a prey fleeing to a refuge. We present a special case of this model to predict how emergence time from the refuge in lizards or other ectotherms should vary as a function of risk of predation and thermal costs of refuge use. The analyses of the variation in emergence time from a refuge of *Lacerta monticola* lizards in the field under two different predation risk levels supported the predictions of the model. As predicted, time spent in the refuge was longer when the threat of the initial attack had been higher, and therefore the subsequent diminution of risk was slower, but only when lizards emerged at the same place where they hid. When initial body temperature was high, some lizards decreased emergence time by emerging from a different place. In addition, the effects of thermal costs were more relevant in the high-risk situation. Time spent in the refuge under high risk increased when thermal conditions of the refuge were more similar to thermal conditions outside (i.e., physiological costs of refuge use were lower). We conclude that optimization of refuge-use strategies might help lizards cope with changes in predation risk without incurring excessive physiological costs. *Key words:* antipredator behavior, decision rules, ectotherms, hiding behavior, *Lacerta monticola,* lizards, predation risk, refuge use. *[Behav Ecol 10:487–492 (1999)]*

Animals should optimize their antipredatory responses by balancing antipredator demands with other requirements (Lima and Dill, 1990; Pitcher et al., 1988; Sih, 1980). Thus, many prey are able to optimize their foraging behavior according to levels of predation risk (Lima and Dill, 1990). Moreover, even when predatory attack is imminent, some prey adjust their escape response to minimize the costs of flight (Ydenberg and Dill, 1986). Numerous studies have shown that prey often respond to the presence of a predator by increasing their use of refuges (Kotler, 1984; Sih, 1986; Sih et al., 1992; Werner et al., 1983), but relatively few studies have analyzed how prey decide when to resume their behavior after a predator's unsuccessful attack (Dill and Fraser, 1997; Pitcher et al., 1988; Sih et al., 1988; Sih, 1992, 1997). This is important because refuge use may have some costs that should be minimized, such as the loss of time available for foraging (Dill and Fraser, 1997; Godin and Sproul, 1988; Koivula et al., 1995) or mate searching (Crowley et al., 1991; Sih et al., 1990). In addition, unfavorable conditions in refuges (e.g., suboptimal temperatures or oxygen levels) might entail physiological costs such as hypothermia or hypoxia (Weatherhead and Robertson, 1992; Wolf and Kramer, 1987).

In ectothermic reptiles, the attainment and maintenance of an optimal body temperature is essential to maximize numerous physiological processes (Huey, 1982; Stevenson et al., 1985) and behaviors with important future fitness consequences (e.g., sprint speed and foraging efficiency; Avery et al., 1982; Bennett, 1980). Careful behavioral thermoregulation increases the time that lizards spend at physiologically favorable body temperatures (Bauwens et al., 1996; Grant and Dunham, 1988). However, effective thermoregulation requires appropriate sources of heat from solar radiation and/or warm substrates (Huey, 1982). Limitations of the thermal environment may frequently prevent reptiles from achieving optimal body temperatures (Huey, 1982; Huey et al., 1989; Peterson, 1987). Thus, lizards are constrained to occupy specific thermal microclimates within their home range when they are active (Grant and Dunham, 1988).

Many lizards escape from predators by fleeing into the nearest refuge (Greene, 1988). However, this simple and safe strategy may have some costs because available or safer refuges may be in microhabitats with shadier and colder conditions, such as rock crevices. The body temperature of a lizard that has retreated into a cool refuge will decrease below optimal levels after a period of time. This is especially important for small lizards with low thermal inertia because it could result in temperature impairment in only a few minutes. Lizards should minimize time spent in a refuge, especially when refuge thermal conditions are unfavorable relative to external ones. Costs will be higher when differences between external and internal thermal conditions are greater. Therefore, after an unsuccessful attack of a predator, an ectothermic prey should optimize the decision of when to come out from a refuge by balancing the fitness effects of the diminution of predation risk with time against the costs of loss of time available for other activities and loss of time spent at optimal body temperature.

The optimality model of Ydenberg and Dill (1986) describes the trade-off between risk and cost for a prey fleeing to a refuge, such that the distance at which an animal starts to flee (approach distance) would be the point where the

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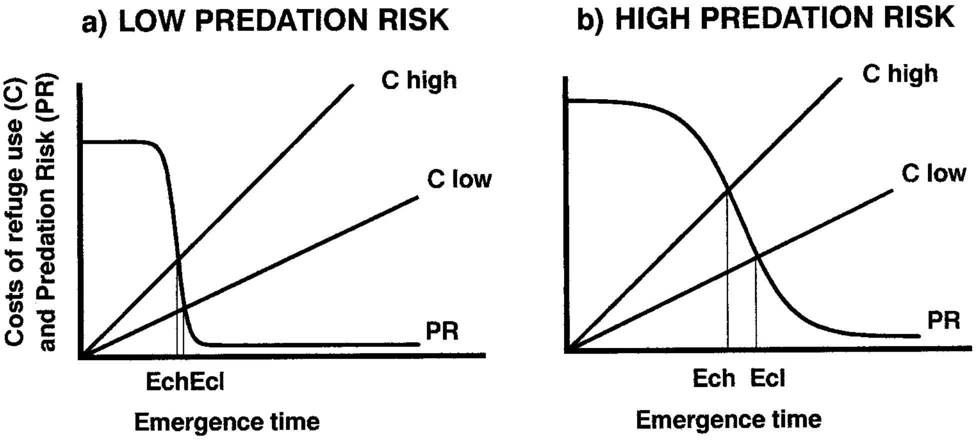

Figure 1
A simple economic model to predict emergence time of lizards from a refuge after a predatory attack as a function of the expected fitness effects of the diminution of the risk of predation in the exterior with time (PR) and two levels of costs (C) of refuge use. Two situations with different levels of risk of predation are considered. The optimal emergence times for each situation (Ech, high cost; Ecl, low cost) are shown.

costs of staying (i.e., predation risk) exceed the cost of fleeing (i.e., mainly lost opportunities). Risks and costs must clearly be balanced in determining emergence from refuge as well. We present a special case of Ydenberg and Dill's (1986) model to predict how emergence time from the refuge in lizards or other ectotherms should vary as a function of two factors: risk of predation and thermal conditions of the refuge.

Consider that the decision variable for the prey is the time spent in the refuge (Figure 1). The risk of predation in the exterior will be maximal at the moment of the attack, but thereafter it will decrease gradually as time spent in the refuge increases. This is because, at least when prey are abundant, most predators will probably leave the area and divert their attack to other exposed and unaware prey after this particular prey has disappeared into a refuge. Thus, the probability of the predator waiting for the prey outside the refuge (i.e., probability of a new attack) will decrease with time.

In contrast, the costs of refuge use will increase with time spent in the refuge. The prey should choose to be in the patch (refuge or exterior) with the higher expected future reproductive success (McNamara and Houston, 1986), which depends on prey survival of predation and on refuge conditions for prey physiological functions. Thus, prey should choose to get out of the refuge when the cost of refuge use is higher than the risk to fitness of predation in the exterior. The crossover of both curves defines an optimal emergence time from the refuge (Figure 1). This optimal emergence time could be modified in two ways: by decreasing the rate of diminution of predation risk (then the time spent in the refuge should increase) or by increasing the cost of refuge use (then the time spent in the refuge should decrease).

Diminution of predation risk might be, or be estimated by the prey to be, different in relation to the threat of the previous attack. Particularly, the diminution of predation risk might be fast when the prey has retreated into the refuge as a preventive strategy to elude a predator that is too close but has not actually attacked directly (low predation risk; Figure 1a). In these circumstances, the model predicts that costs of refuge use may be relatively unimportant because the optimal emergence time for different levels of costs coincides with the moment that predation risk drops. This moment might be estimated by the prey according to information acquired from the refuge or based on previous experiences. Prey should emerge from the refuge at this moment, although favorable thermal conditions would allow staying longer without excessive additional costs. In contrast, in a high predation risk situation (i.e., a direct attack by the predator; Figure 1b), the initial level of predation risk is higher, and in addition the risk diminishes more slowly. If there are no thermal costs of refuge use, prey might maximize time spent in the refuge to minimize the risk of suffering a new attack. However, when there are thermal costs of refuge use, an optimal response should require that when thermal costs are greater, emergence time should decrease.

The model makes three predictions. (1) Time spent in the refuge should be longer when the threat of the initial attack has been higher, and therefore the subsequent diminution of risk is slower (i.e., the probability of a new attack is higher). (2) Time spent in the refuge should be longer when thermal conditions of the refuge are more similar to thermal conditions outside (i.e., physiological costs of refuge use are lower). (3) The effects of thermal costs should be more relevant in the high-risk situation. In the low-risk situation prey should emerge after a certain short period of time (when predation risk level drops), regardless of thermal conditions.

In this paper we present the results of a field study to test the predictions of this model in the Iberian rock lizard (*Lacerta monticola*), a small lizard inhabiting high-altitude mountains of the Iberian peninsula. We specifically examined the variation in emergence time from a refuge of these lizards under two different predation risk levels and under different thermal conditions.

METHODS

Species and study site

We performed the study in the Guadarrama Mountains (Madrid Province, Central Spain) at an elevation of 1900 m. Granite rock boulders and screes interspersed with shrubs (*Cytisus oromediterraneus* and *Juniperus communis*) predominated at the study site, along with meadows of *Festuca* and other grasses (Martín and Salvador, 1992). In this area, *L. monticola* lizards (snout-to-vent length of adult individuals ranges between 65 mm and 90 mm) are active only from May to September due to limiting environmental temperatures; they mate in May–June and produce a single clutch in July (Elvira and Vigal, 1985; Salvador, 1984). We chose this species because, at high altitude, unfavorable thermal conditions are limiting for lizards (Carrascal et al., 1992; Van Damme et al., 1989). The optimal body temperatures for performance for this species (Bauwens et al., 1995) are often not achieved by lizards in the field (Martín and Salvador, 1993). Lizards of this species select microhabitats with abundant rocks, which they use to escape from predators by hiding under rock boulders and rock screes or in rock crevices (Martín and Salvador, 1992). In addition, during their daily activities, these lizards are able to modulate the risk of predation by modifying the distances to the nearest refuge as a function of their ability to run, which is dependent on their body temperature (Carrascal et al., 1992; Martín and Salvador, 1993).

Procedure

We conducted the study from May to June 1996. We searched for lizards by walking the area between 0700 h and 1200 h (Greenwich mean time). Only lizards with complete tails were included in the analysis because tailless individuals incur a higher predation risk and may show different antipredator behavior (e.g., they selected shorter distances to available refuges during basking periods; Martín and Salvador, 1993). Lizards and other animals may react differentially to the approach of a predator as a function of the threat of the attack (Burger and Gochfeld, 1981, 1990; Cooper, 1997). We approached individual lizards in one of two ways: by walking slowly near but tangentially to the lizard, looking straight ahead and without paying attention to the lizard (low predation risk situation), or by simulating a predatory attack by walking directly toward the lizard (high predation risk). To avoid confounding effects that may affect risk perception of lizards (Burger and Gochfeld, 1993) the same person wearing the same clothing performed all approaches in a similar way, while another person recorded the lizard's behavior. 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 more than half of the lizard's body emerged from the refuge (emergence time). Because thermal conditions of the refuge did not affect the lizard once most of its body was outside of the refuge, thermal costs of refuge use were considered to be relevant only until this emergence time. Therefore, we used this time in our analysis of thermal costs. We also recorded the time until the lizard resumed normal activity after emerging. On some occasions, lizards emerged from a different place from where they had entered (e.g., by walking under a rock scree). We considered that this behavior might increase the rate of diminution of predation risk because predators might expect the prey to appear from the same place where it hid initially, and therefore the lizard may elude the predator more easily.

Immediately after a lizard emerged from the refuge and resumed its activity, we measured with a digital thermometer the temperature at the point where the lizard was before the attack (air and substrate temperature) and the temperature in the refuge (substrate). Because the study design did not allow us to capture lizards to measure their body temperature immediately before they hid, potential body temperatures were estimated from air temperatures according to the relationship described by Martín and Salvador (1993).

Data analysis

We used the difference between heating rate outside and in the refuge as a measure of thermal cost of refuge use. Potential heating rates of *L. monticola* lizards are a function of lizard body mass, angle of incidence of sun rays on the lizard's body (heliothermic contribution), and substrate temperature (thigmothermic contribution) (Carrascal et al., 1992). We assumed that the angle of incidence of sun rays was a constant outside the refuge because it may always be maximized by behavioral adjustments of basking postures (Martín et al., 1995), whereas this value was equal to 0 in the shaded refuge. Body mass was also constant for a given individual. Thus, in our study the only variable for a given individual was the difference between external and refuge substrate temperatures.

Given the large size of the area surveyed (> 5 km^2), the high lizard density, and because we avoided walking routes taken previously, the probability of repeated sampling on the same individual was low. We therefore treated all measurements as independent. To assess differences in emergence time with risk, we used a two-way ANOVA with the level of predation risk (low versus high) and the place of emergence (same versus different) as factors. Data were log transformed to ensure normality. Tests of homogeneity of variances (Hartley's F_{max} test) showed that in all cases variances were not significantly heterogeneous. Relationships between costs of refuge use (temperature difference) and emergence time were estimated with Pearson linear regression (Sokal and Rohlf, 1995).

RESULTS

Predation risk and place of emergence significantly affected emergence time of lizards (two-way ANOVA; risk effect: F = 9.61, df = 1,125, p =.002; place effect: F = 12.48, df = 1,125, p =.0006; interaction: F = 6.67, df = 1,125, p =.01; Figure 2a). The significant interaction shows that the effect of place of emergence on emergence time varied with predation risk. Lizards waited longer in the refuge when the risk of predation was higher only if they emerged at the same place where they hid. In high-risk situations, emerging from another place allowed emergence times similar to those shown in the low-risk situations.

In low-risk situations lizards that emerged from the same place (28.9° ± 0.1°C, n = 34) or at another place (28.8° ± 0.1°C, n = 43) had similar estimated initial body temperatures, whereas in high-risk situations lizards that emerged at another place had estimated initial body temperatures (29.1° ± 0.2°C, n = 20) higher than lizards that emerged from the same place (28.5° ± 0.1°C, n = 32) (two-way ANOVA; risk effect: F = 1.82, df = 1,125, p = .18; place effect: F = 9.99, df = 1,125, p = .002; interaction: F = 10.66, df = 1,125, p = .001). This result suggests that only lizards with higher internal thermal state might be able to walk under the refuge to emerge some other place, instead of remaining, waiting immobile in the refuge.

One piece of evidence suggests that lizards acquired information on the presence of the predator when they emerged from the refuge. The time until the lizard resumed normal activity after emerging was not significantly different among treatments (two-way ANOVA; risk effect: F = 1.20, df = 1,122, p = .27; place effect: F = 0.42, df = 1,122, p = .53; interaction: F = 0.86, df = 1,122, p = .37; Figure 2b). The same analysis removing the interaction term also produced nonsignificant results (risk effect: F = 1.35, df = 1,123, p = .25; place effect: F = 0.78, df = 1,123, p = .39). In addition, emergence time and time to resume normal activity after emerging were not significantly correlated in the low-risk situation (r = −.18, F = 1.93, df = 1,76, p = .17) or in the high-risk situation (r = −.24, F = 2.58, df = 1,51, p = .12). These results suggest that, because the predator was not detected when the lizards emerged from the refuge, lizards resumed their activities after an interval of time independent of initial level of predation risk.

The effect of thermal conditions of the refuge on emergence time was greater in the high-risk situation, consistent with the model prediction for the effect of difference in temperatures between the refuge and the outside environment. Thus, in the low-risk situations emergence time (log transformed) was not correlated with the difference between external substrate temperature and refuge temperature (r =

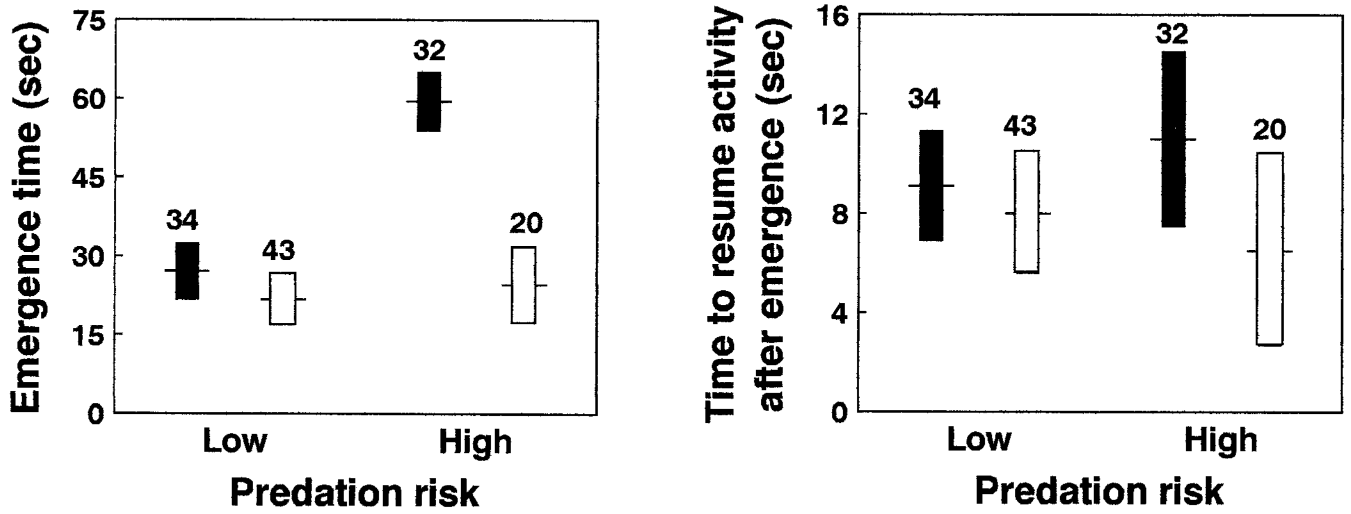

Figure 2
The observed emergence time from a refuge (x̄ ± SE) and time to resume activity after emerging of *L. monticola* lizards after a predatory attack under two levels of risk of predation. Solid bars indicate situations when lizards emerged from the same place that they hid; open bars indicate situations when lizards emerged from a different place from where they hid. Samples sizes are shown above each bar.

$-.04$, $F = 0.14$, df = 1,76, $p = .70$; Figure 3a), whereas in the high-risk situation they were negatively and significantly correlated ($r = -.56$, $F = 22.42$, df = 1,51, $p = .00002$; Figure 3b). These two correlation coefficients were significantly different ($t_s = 2.83$, $p < .005$). Thus, emergence time under high risk increased when thermal costs of refuge use were lower. Place of emergence modified these relationships only in the high-risk situation; emergence time was significantly correlated with temperature differential if lizards emerged from the same place ($r = -.71$, $F = 25.65$, df = 1,31, $p = .00003$), but not when lizards emerged from a different place ($r = -.25$, $F = 1.45$, df = 1,19, $p = .24$). These correlation coefficients were significantly different ($t_s = 3.11$, $p < .05$). In the low-risk situation the place of emergence had no significant effect (same place: $r = -.13$, $F = 0.53$, df = 1,33, $p = .53$; different place: $r = -.03$, $F = 0.05$, df = 1,42, $p = .82$; $t_s = 0.42$, $p > .60$). In contrast, emergence times of lizards were not significantly correlated with their estimated initial body temperature either in the low-risk situation ($r = .08$, $F = 0.48$, df = 1,76, $p = .49$) or in the high-risk situation ($r = -.26$, $F = 1.75$, df = 1,51, $p = .20$).

DISCUSSION

Risk of predation and thermal costs of refuge use affected emergence times from the refuge in *L. monticola,* but thermal costs were more relevant in the high predation risk situations as predicted by the model. The results also showed that when initial body temperature was high, lizards decreased recovery time by emerging from a different place, probably because with this escape strategy lizards estimated that predation risk diminished faster.

The results of our study indicate that *L. monticola* lizards were able to compensate for higher predation risk by increasing the time spent in refuge. Many animals (Gilliam and Fraser, 1987; Lima and Dill, 1990; Sih et al., 1992), including some lizards, modify their microhabitat or refuge use (Carrascal et al., 1992; Martín and Salvador, 1992, 1993) or their escape behavior (Burger and Gochfeld, 1990, 1993; Cooper, 1997; Martín and López, 1995) according to the estimated levels of predation risk. Animals require information to make such decisions (Bouskila and Blumstein, 1992). A simple rule of thumb for this lizard might be to always hide at a critical distance before getting complete information on the actual threat of the approaching predator. This could be considered as an overestimation of predation risk that might be optimal and lead to lower mortality (Bouskila and Blumstein, 1992). Acquiring completely accurate information before deciding to retreat might be expensive in terms of being captured, whereas acquiring more information later from the safety of the refuge entails generally low costs, provided that the time need-

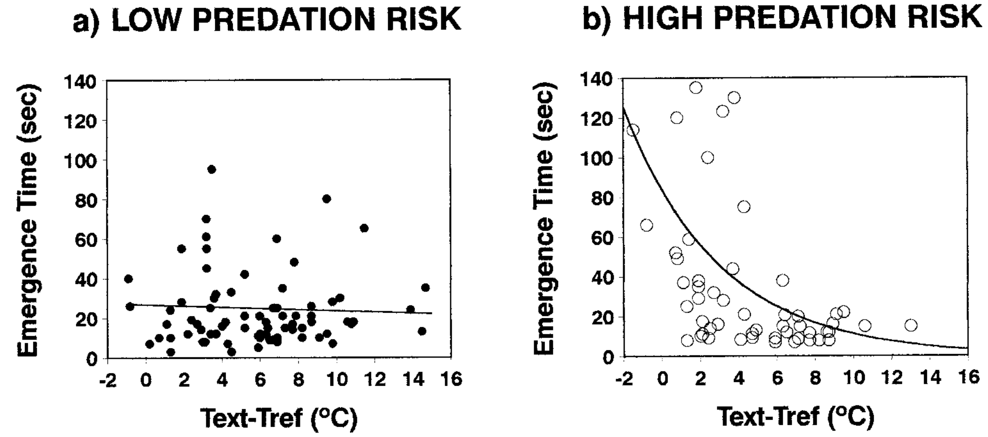

Figure 3
The relationship observed in *L. monticola* lizards between emergence time from a refuge after a predatory attack and the difference between the external temperature (Text) and the refuge temperature (Tref) (costs of refuge use are higher when this difference is higher) under two levels of risk of predation.

ed to evaluate actual risk and resume activity is short. Emergence time varied in this study with the level of initial threat, but once lizards emerged, they resumed their activities in an interval of time that was independent of initial level of predation risk. Lizards probably acquired information on the presence of predator when they partly emerged from the refuge, and they decided to resume their activities if the predator was not detected. With this strategy lizards may have quite good information about the current level of predation risk, and this may help them to behave optimally without incurring higher costs of refuge use.

Montane lizards are subjected to variable radiation levels and low environmental temperatures that constrain their activity times to a larger extent than lizards at lower altitudes (Sinervo and Adolph, 1994). Use of refuges by *L. monticola* lizards may thus entail more costs than for lowland species. The main costs might be related to a loss of the time available for foraging, social interactions, searching for mates, and so on. Because lizards' body temperatures decrease in the refuge, they subsequently have to either spend more time basking to regain their optimal body temperature or start to forage at suboptimal temperatures with a lower sprint speed and predatory efficiency (Avery et al., 1982; Bennett, 1980). In addition, when reptiles are prevented from attaining their selected body temperatures, the time available for voluntary food intake and the excess of energy stored as fat decreases, and they should display reduced growth rates (Avery, 1984; Martín and López, 1999; Sinervo and Adolph, 1994). This is important because the amount of stored fat affects the survival and future reproductive success of lizards (Pond, 1981).

Taking into account all of these costs of refuge use, it is reasonable that *L. monticola* lizards optimize their refuge use to minimize the time spent at unfavorable temperatures and the waste of time that could be devoted to other activities. The model predicted and the results showed that, in a low predation risk situation, time spent in the refuge was short. In the high risk situation, hiding time was influenced by thermal costs of refuge use.

An unexpected result was the effect on emergence times of the behavioral strategy of walking under the rocks to reappear at a different place. Lizards may minimize time in the refuge while also minimizing predation risk by leaving the predator waiting for the prey to appear at the wrong place. Only individuals with initial high body temperatures adopt this strategy. Walking under the low ambient temperatures of the refuge might be too costly for lizards with initial low body temperatures. A similar variation in the optimal antipredator strategy has been described in another lizard species, which shifted from an "escape by fleeing" at high temperatures to a "fight with the predator" strategy at low body temperatures (Hertz et al., 1982).

Refuge use and retreat site selection by ectotherms might have a profound effect not only on current energy budgets and growth, but also on the evolution of thermal sensitivity of physiological performance and development (Huey et al., 1989; Huey and Kingsolver, 1989). Foraging animals may shift habitats in the presence of predators at the cost of obtaining a lower foraging rate (e.g., Gilliam and Fraser, 1987). Similarly, when predation risk increases, lizards may shift their microhabitat use to safer but "cooler" places with a lower potential heating rate (Martín and Salvador, 1992, 1993). This habitat shift may affect the time spent at optimal body temperatures and limit the time available for other activities (Martín and Salvador, 1997). In these circumstances, lizards and other ectotherms might respond to an increase in predation pressure through evolutionary adjustments of their thermal physiology and a shift of the optimal values for physiological performance (Huey et al., 1991). Predation on lizards thus might constitute a selection pressure not only on the thermal sensitivity of maximum sprinting performance needed to escape efficiently (Bauwens et al., 1995), but also on the thermal sensitivity of other physiological functions (e.g., those that promote growth) that need to be maximized when lizards have retreated into refuges with unfavorable thermal conditions. Optimization of behavioral antipredator strategies such as those described in this paper might help lizards overcome the limitations of their thermal physiology, allowing them to cope with changes in predation pressure without incurring excessive physiological costs.

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