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Repeated predatory attacks and multiple decisions to come out from a refuge in an alpine lizard

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Prey often respond to predator presence by increasing their use of refuges. However, because the use of refuges may entail several costs, the decision of when to come out from a refuge should be optimized. In some circumstances, if predators remain waiting outside the refuge and try new attacks or if predator density increases, the prey may suffer successive repeated attacks in a short time. Successive attacks may represent an increase in the risk of predation, but the costs of refuge use also may increase with time spent in the refuge. Thus, prey should make multiple related decisions on when to emerge from the refuge after each new attack. We simulated in the field repeated predatory attacks to the same individuals of the lizard *Lacerta monticola* and specifically examined the variation in successive times to emergence from a refuge under different thermal conditions (i.e., different costs of refuge use). The results showed that risk of predation but also thermal costs of refuge use affected the emergence decisions. Lizards increased progressively the duration of time spent in the refuge between successive emergence times when the costs of refuge use were lower, but tended to maintain or to decrease the duration of time spent in the refuge between successive emergence times when cost of refuge use increased. Additionally, lizards that entered the refuge with higher body temperatures had overall emergence times of longer duration. Optimization of refuge use and flexibility in the antipredator responses might help lizards to cope with increased predation risk without incurring excessive costs of refuge use. *Key words:* antipredator behavior, ectotherms, hiding behavior, lizards, predation risk, refuge use. *[Behav Ecol 12:386–389 (2001)]*

Prey often respond to predator presence by increasing their use of refuges (Cooper, 1998; Sih, 1986; Sih et al., 1992). However, refuge use may have some costs that should be minimised such as, for example, the loss of time available for foraging (Dill and Fraser, 1997; Koivula et al., 1995) or mate searching (Crowley et al., 1991; Sih et al., 1990), and physiological costs, such as hypoxia or hypothermia (Martín and López, 1999b; Wolf and Kramer, 1987). For this reason, animals should optimize the decision of when to come out from a refuge after a predator's unsuccessful attack by balancing antipredator demands with other requirements (Dill and Fraser, 1997; Sih, 1992, 1997; Sih et al., 1988). Risks and costs are balanced in determining when to flee to a refuge (Ydenberg and Dill, 1986) and when to emerge from this refuge as well (Martín and López, 1999a; Sih, 1992, 1997).

We have previously presented a special case of Ydenberg and Dill's (1986) model that predicted how emergence time from the refuge in lizards or other ectotherms should vary as a function of risk of predation and thermal conditions of the refuge (Martín and López, 1999a). In a field experiment, we showed that the variation in emergence time from a refuge of the lizard *Lacerta monticola* supported the predictions of the model (Martín and López, 1999a). Thus, time spent in the refuge decreased when thermal conditions of the refuge were unfavorable with respect to the thermal conditions outside (i.e., physiological costs of refuge use were higher). In this experiment lizards only had to decide once when to emerge, because we performed only one simulated attack on each lizard, thus suggesting that the predator had left the area searching for a new unaware prey after this particular one had disappeared into a refuge. However, many sit-and-wait predators may remain waiting for an individual prey outside the refuge and try a new attack. Alternatively, if predator density increases, the probability of an attack by a different individual predator also can increase. In these circumstances, a prey may consider that successive attacks represent an increase in the risk of predation. Each new attack may indicate that an individual predator persists in trying to capture that particular prey or that predator density has increased. Thus, the probability of a predator waiting for the prey outside the refuge or of a new predator appearing (i.e., probability of a new attack) will decrease more slowly with time after each successive attack. If predation risk was the only variable considered by the prey, an optimal response would require that the prey maximize time spent in the refuge to minimize the risk of suffering a new attack. Therefore, the successive emergence times should be longer than the previous one. Thus, when costs of refuge use are low, prey must tend to increase the time between attempts to emerge from the refuge with successive attacks.

On the other hand, in many situations the costs of refuge use may increase with time spent in the refuge. The total costs will be greater as the number of repeated attacks, and subsequent time spent in the refuge, increase. The prey should choose to be in the patch (refuge or exterior) with the higher expected future reproductive success (McNamara and Houston, 1986); this depends on prey survival of predation and on refuge conditions for prey physiological functions. Thus, prey should choose to get out of the refuge sooner when the costs of refuge use increase, although the risk to fitness of predation in the exterior might remain high (as indicated by the occurrence of previous repeated attacks). Thus, when costs of refuge use are high, prey should tend to maintain or decrease time spent in the refuge with successive attacks to minimize these costs.

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In this article we present the results of a field study to test these predictions in the Iberian rock lizard (*Lacerta monticola*), a small lizard inhabiting the high altitude mountains of the Iberian peninsula. We simulated repeated predatory attacks to the same individuals and specifically examined the variation in successive times to emergence from a refuge under different thermal conditions (i.e., different costs of refuge use).

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, together with meadows of *Festuca* and other grasses (Martín and Salvador, 1992). In this area, *L. monticola* (snout-to-vent length of adult individuals ranges between 65–90 mm) is active only from May to September due to limiting environmental temperatures, mating in May–June and producing a single clutch in July (Elvira and Vigal, 1985). Lizards of this species select microhabitats with abundant rocks, where they escape from predators by hiding under rocks or in rock crevices (Martín and Salvador, 1992). However, thermal conditions in the refuges are often unfavorable and well under the optimal temperature preferred by lizards (Bauwens et al., 1995; Martín and Salvador, 1993).

Procedure

We conducted the study in June 1998. We searched for lizards by walking the area between 0700 and 1200 h (G.M.T.). Only lizards with complete tails were included in the analysis because tailless individuals incur a higher predation risk and may show different antipredator behavior (Martín and Salvador, 1993). We approached individual lizards by simulating a predatory attack by walking directly at the lizard, which typically made a short flight and hid entirely in the nearest available rock crevice. To avoid confounding effects that may affect risk perception of lizards (Burger and Gochfeld, 1993; Cooper, 1997) the same person wearing the same clothing performed all approaches in a similar way, while another person recorded the lizard's behavior. 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 (time to emergence). Immediately after a lizard emerged from the refuge, we approached it, simulating another predatory attack with the same characteristics, until the lizard hid again. Then, we retreated to a hidden position to observe and record the second emergence time. We repeated this procedure with the same individual 10 successive times ($\bar{X}$ = 8.9 times, SE = 0.7) or until the lizard was lost, if it ran away from the refuge. During one trial, total time spent in the refuge by lizards was on average 145 ± 14 s (range: 58–332 s). At the end of the trial, we measured with a digital thermometer the temperature at the point where the lizard was before the attack (air and substrate temperature), and in the refuge (substrate).

Data analysis

To study the change in times to emergence, we used the difference between heating rate outside and in the refuge as a measure of thermal cost of refuge use (see Martín and López, 1999a). 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), as described in 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 through behavioral adjustments of basking postures (Martín et al., 1995), while this value was equal to zero 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 (temperature differential).

To study the change in response over a trial (i.e., changes in times to emergence), we used Pearson's product-moment correlation coefficient, *r,* to test the null hypothesis of $r > 0$ (times to emergence increase; i.e., lizards consider only the increase in predation risk) against the alternative hypothesis $r \leq 0$ (times to emergence decrease or maintain the same level; i.e., lizards consider the costs of refuge use) (Sun and Müller-Schwarze, 1998). The correlation coefficient, *r,* and the slope, *b,* of the estimated regression line measured the overall trend of response during each trial. Time to emergence data were log-transformed to ensure normality before calculating *r* and *b.* To analyze the relationships between changes in times to emergence and thermal costs of refuge use, we used Pearson linear regression between the measures of change within a trial (*r* or *b*) and the difference between external and refuge substrate temperatures (Sokal and Rohlf, 1995). We also calculated the average duration of all the successive emergence times along the trial, as a measure of the trade-off between costs of refuge use and predation risk. The average duration of times to emergence, the temperature differential and lizards' initial body temperature were log-transformed to ensure normality.

Given the large size of the area surveyed (more than 5 km^2), the high lizard density, and because we avoided walking routes taken previously, the probability of repeated sampling of the same individual was very low. We therefore treat all measurements as independent.

RESULTS

The coefficients of regression (*r*) of successive times to emergence in a trial (which measured the overall trend of response during each trial) decreased when the difference between external substrate temperature and refuge temperature increased ($r = -.68$, $F = 21.85$, df = 1,31, $p = .0001$) (Figure 1). Similarly, the slopes (*b*) of the regression lines, calculated for each trial, also decreased when the temperature differential increased ($r = -.49$, $F = 9.48$, df = 1,31, $p = .004$) (Figure 1). Thus, lizards increased progressively the duration of the successive times to emergence (*r* and $b > 0$) when the costs of refuge use were lower, but tended to maintain or to decrease (*r* and $b \leq 0$) the duration of successive times to emergence when cost of refuge use increased.

In contrast, the average duration of all times to emergence along a trial did not significantly change with the temperature differential ($r = -.13$, $F = 0.15$, df = 1,31, $p = .46$). However, the average duration of times to emergence was probably dependent on a lizard's initial body temperature, because it was significantly affected by the external temperature ($r = .50$, $F = 9.78$, df = 1,31, $p = .004$) (Figure 2). Thus, lizards that entered the refuge with higher body temperatures had overall times to emergence of longer duration.

DISCUSSION

The results of this experiment showed that risk of predation but also thermal costs of refuge use affected the duration of successive times to emergence from the refuge in *L. monticola.* Initially, an increase in the frequency of predatory attacks

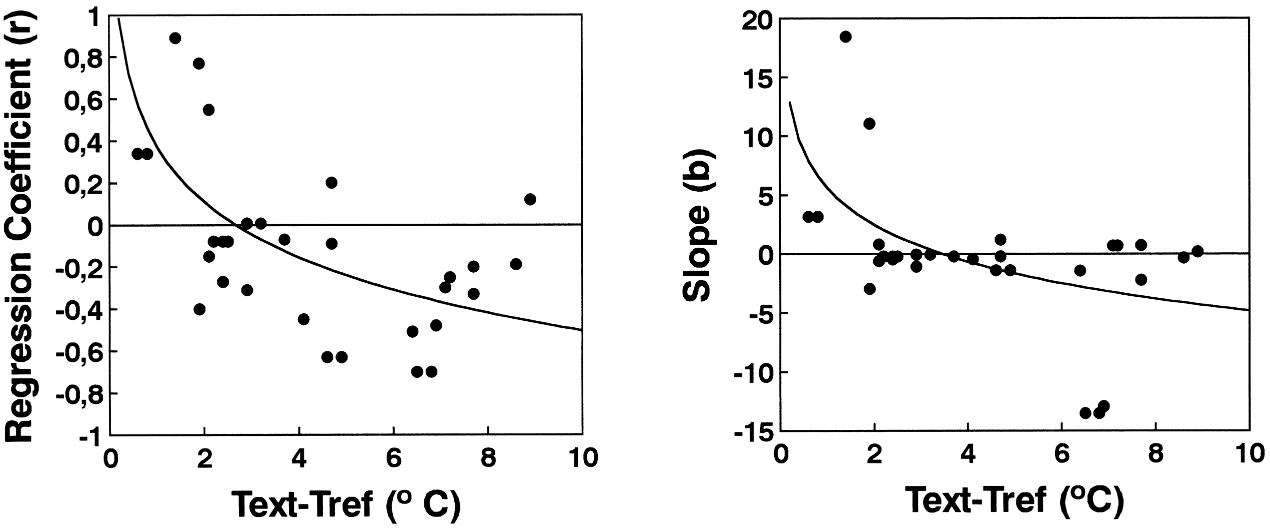

Figure 1
The relationship observed in the lizard *L. monticola* between the coefficients of regression or the slopes of the regression lines calculated for the duration of successive times to emergence after repeated predatory attacks (which measured the overall trend of response during each trial) and the difference between the external temperature (Text) and the refuge temperature (Tref). Costs of refuge use were higher when this difference was higher.

was probably interpreted as an increase in the probability of a new attack (i.e., diminution of predation risk with time is slower). Thus, when costs of refuge use are low, lizards tended to increase the duration of successive times to emergence to compensate for the increase in predation risk. This result agrees with the general tendency of many animals, including lizards, which modify their microhabitat or refuge use according to the estimated levels of predation risk (Lima and Dill, 1990; Martín and Salvador, 1992, 1993; Sih et al., 1992). In another experiment, the skink *Eumeces laticeps* also remained in refuges longer after the second of two successive similar approaches than after the first (Cooper, 1998). These data may indicate that lizards perceived a higher predation risk due to persistence by an individual predator, although individual recognition of the predator may not be needed if the assessment was just based on attack rate (Cooper, 1998).

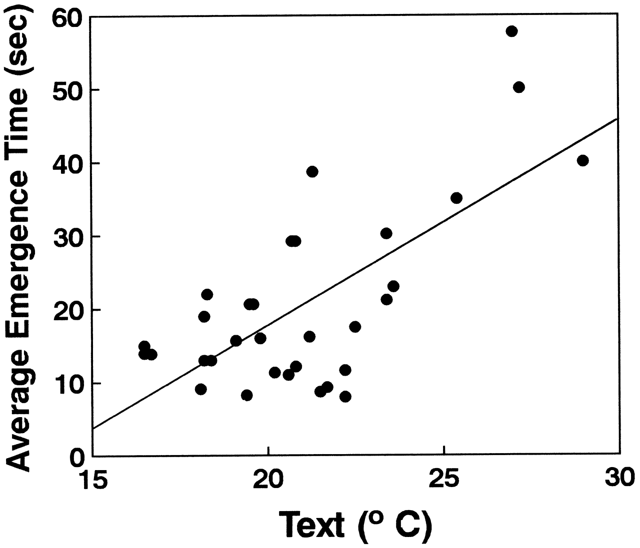

Figure 2
The relationship observed in the lizard *L. monticola* between the average duration of all emergence times along a trial after repeated predatory attacks and the external temperature (Text).

However, use of refuges by *L. monticola* may entail more costs than for lowland species because montane lizards are subjected to variable radiation levels and low environmental temperatures that constrain their activity times to a larger extent than at lower altitudes (Sinervo and Adolph, 1994). It is not surprising that *L. monticola* optimize their refuge use to minimize the time spent at unfavorable temperatures and the waste of time that could be devoted to other activities (Martín and López, 1999a). Thus, when the costs of refuge use increased, lizards tended to maintain or even to decrease the duration of successive times to emergence, in spite of the increase in predation risk. Alternatively, a decrease between successive emergence times might also be compatible with lizards habituating to the predator and ceasing to consider it a threat. However, this possibility could be dismissed because habituation is unlikely to be correlated with temperature differences.

Occasionally, when thermal costs were excessively high, we observed that some individuals that emerge from the refuge were reluctant to enter again with a short run after a successive attack. In contrast, these lizards performed an alternative escape tactic, running for longer to other refuges less safe or that were placed further (e.g., broom bushes) but where thermal costs were lower. Thus, lizards may assume a higher predation risk by being exposed for longer to a predator pursuit, but could decrease the costs resulting from refuge use. Similarly, expected long-term fitness costs of refuges also affected escape decisions of *L. monticola,* which had longer approach distances when the external heating rate and the refuge cooling rate were lower (i.e., when thermal costs were lower) (Martín and López, 2000).

The results also suggested that when lizards' initial body temperature was high, they could afford to increase time spent in the refuge. One of the costs of refuge use was probably the decrease of lizards' body temperature with time. Body temperature influences many aspects of lizard behavior including burst speed (Bauwens et al., 1995). Lizards with low body temperatures are more vulnerable to predation due to lower escape performance (Christian and Tracy, 1981). It is likely that, independently of other time costs, there could be a critical low value of body temperature when lizards should switch their antipredator strategy and emerge from the refuge to regain optimal body temperature. Because the probability of a new attack is high, lizards with excessively low body temperatures may be unable to run effectively to the refuge in case of a new attack. Thus, it would be advantageous to emerge when locomotor performance is still high because, although they might expose themselves to a new attack, the predator could be eluded easily with a short run to the refuge. In contrast, emerging with low body temperature and associated low performance would require some time spent in basking before regaining their optimal body temperature and sprint speed appropriate to escape. In accordance with this prediction, and similarly to the lizard *P. muralis* (Martín and López, 1999b), *L. monticola* that entered the refuge with higher initial body temperatures had overall times to emergence of longer duration. If this constraint exists, it might also explain why under unfavorable refuge thermal conditions the successive times to emergence tended to decrease. As body temperature decrease continuously in a cool refuge, the time to reach the critical temperature will be shorter after each successive attack, forcing the lizard to emerge sooner. Other studies have shown that recovering at a cool temperature severely retarded the ability of the lizard *Dipsosaurus dorsalis* to repeat both exhaustive and sprinting exercises (Wagner and Gleeson, 1997). Thus, it would be advantageous to emerge as soon as possible from a cool refuge.

The observed variation within successive emergence times might be also interpreted as a method to assess predation risk levels in the exterior more effectively. The decision to recover the normal activity will depend on the information on the presence of the predator, and many times this can only be known after emergence. Sampling for predator persistence at variable intervals of time may increase the quality of prey information, helping to decide the optimal antipredator strategy. Dynamic models have suggested that animals will show tolerance to imperfect information, but that the extent of this tolerance may change from one situation to the next, and that the rules of thumb should be flexible to local ecological conditions (Koops and Abrahams, 1998). In our experiment, the variation of successive times to emergence may be interpreted as a way to prevent the predator from being able to predict when the lizard would emerge again. This may represent a mixed evolutionarily stable strategy to a hiding-waiting game between prey and predators (Johansson and Englund, 1995).

We conclude that an increase in predation risk may force animals to use antipredator behaviors having increased associated costs (i.e., increasing time spent in the refuge). However, optimization of refuge use and flexibility in the antipredator responses (e.g., variability in the times to emergence) might help lizards to cope with changes in predation pressure without incurring excessive physiological costs.

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REFERENCES

Bauwens D, Garland Jr T, Castilla AM, Van Damme R, 1995. Evolution of sprint speed in lacertid lizards: morphological, physiological and behavioral covariation. Evolution 49:848–863.

Burger J, Gochfeld M, 1993. The importance of the human face in risk perception by black iguanas, *Ctenosaura similis.* J Herpet 27: 426–430.

Carrascal LM, López P, Martín J, Salvador A, 1992. Basking and antipredator behaviour in a high altitude lizard: implications of heat-exchange rate. Ethology 92:143–54.

Christian KA, Tracy CR, 1981. The effect of the thermal environment on the ability of Galapagos land iguanas to avoid predation during dispersal. Oecologia 49:218–223.

Cooper WE, 1997. Threat factors affecting antipredator behavior in the broad-headed skink (*Eumeces laticeps*): repeated approach, change in predator path, and predator's field of view. Copeia 1997: 613–619.

Cooper WE, 1998. Risk factors and emergence from refuge in the lizard *Eumeces laticeps.* Behaviour 135:1065–1076.

Crowley PH, Travers SE, Linton MC, Cohn SL, Sih A, Sargent RC, 1991. Mate density, predation risk, and the seasonal sequence of mate choices: a dynamic game. Am Nat 137:567–596.

Dill LM, Fraser AHG, 1997. The worm returns: hiding behavior of a tube-dwelling marine polychaete, *Serpula vermicularis.* Behav Ecol 8:186–193.

Elvira B, Vigal CR, 1985. Further data on the reproduction of *Lacerta monticola cyreni* (Sauria, Lacertidae) in Central Spain. Amphibia-Reptilia 6:173–179.

Johansson A, Englund G, 1995. A predator-prey game between bullheads and case-making caddis larvae. Anim Behav 50:785–792.

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

Koops MA, Abrahams MV, 1998. Life history and the fitness consequences of imperfect information. Evol Ecol 12:601–613.

Lima SL, Dill LM, 1990. Behavioral decisions made under the risk of predation: a review and prospectus. Can J Zool 68:619–640.

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.

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

Martín J, López P, Carrascal LM, Salvador A, 1995. Adjustments of basking postures in the high altitude Iberian rock lizard (*Lacerta monticola*). Can J Zool 73:1065–1068.

Martín J, Salvador A, 1992. Tail loss consequences on habitat use by the Iberian Rock lizard *Lacerta monticola.* Oikos 65:328–333.

Martín J, Salvador A, 1993. Thermoregulatory behaviour of rock-lizards in response to tail loss. Behaviour 124:123–36.

McNamara JM, Houston AI, 1986. The common currency for behavioral decisions. Am Nat 127:358–378.

Sih A, 1986. Antipredator responses and the perception of danger by mosquito larvae. Ecology 67:434–441.

Sih A, 1992. Prey uncertainty and the balancing of antipredator and feeding 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, Kats LB, Moore RD, 1992. Effects of predatory sunfish on the density, drift and refuge use of stream salamander larvae. Ecology 73:1418–1430.

Sih A, Krupa J, Travers S, 1990. An experimental study on the effects of predation risk and feeding regime on the mating behavior of the water strider, *Gerris remigis.* Am Nat 135:84–290.

Sih A, Petranka JW, Kats LB, 1988. The dynamics of prey refuge use: a model and tests with sunfish and salamander larvae. Am Nat 132: 463–483.

Sinervo B, Adolph SC, 1994. Growth plasticity and thermal opportunity in *Sceloporus* lizards. Ecology 75:776–790.

Sokal RR, Rohlf FJ, 1995. Biometry, 3rd ed. New York: Freeman.

Sun L, Müller-Schwarze D, 1998. Beaver response to recurrent alien scents: scent fence or scent match? Anim Behav 55:1529–1536.

Wagner EL, Gleeson TT, 1997. The influence of thermoregulation on behavioural recovery from exercise in a lizard. Funct Ecol 11:723–728.

Wolf NG, Kramer DL, 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 RC, Dill LM, 1986. The economics of fleeing from predators. Adv Study Behav 16:229–249.