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## Loss of mating opportunities influences refuge use in the Iberian rock lizard, *Lacerta monticola*

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**Abstract** Because time spent in refuge may be costly if prey lose opportunities to forage, fight, or mate, prey allow predators to approach closer before beginning to flee when opportunity costs are high. Because the same opportunity costs may apply to refuge use as to escape, prey should make similar trade-offs between risk of emerging and cost of remaining in refuge. In the Iberian rock lizard, *Lacerta monticola*, we studied the effects of sex, reproductive season, speed of predator approach, and potential loss of mating opportunities on time spent in refuge following simulated predatory attacks. Lizards of both sexes adjusted refuge use to the level of risk by spending more time in refuge when approached rapidly than slowly. Females remained in refuge for equal times in the mating and postreproductive seasons, but males emerged sooner during the mating season, suggesting adjustment to a cost of lost opportunity to search for mates during the mating season. When a tethered female was nearby, males emerged from refuge earlier than if no female was present, indicating a trade-off between risk and mating opportunity. Approach speed affected emergence time when females were absent, but not when a female was present. Approach speed did not affect the probability that, after emerging, a male would return to court the female. For males that courted females intensely (bit them) before entering refuge, approach speed did not affect latency to emerge, but males that courted less intensely emerged sooner if approached slowly than rapidly. These findings show that males adjust the length

of time spent in refuge to both risk of predation and reproductive cost of refuge use.

**Keywords** Refuge use · Lizards · Costs of reproduction · Antipredatory behavior · Mating opportunities

### Introduction

An increasing number of studies are reporting that predation risk is a major cost of reproduction (see review in Magnhagen 1991). Reproductive activities per se may expose both sexes to increased risk of predation, and thus many animals compensate by decreasing mating activities (Candolin 1997; Koga et al. 1998; Krupa and Sih 1998) or by modifying some aspects of behavior (e.g. Cooper et al. 1990; Lima and Dill 1990). However, limited mating opportunities may force animals to increase risk-taking behaviors (Hazlett and Rittschof 2000). For instance, animals may delay escape decisions (i.e. increasing exposure to predation) when the costs of losing opportunities for mating or defending a reproductive territory increase (Cooper 1999; Díaz-Uriarte 1999; Martín and López 1999a). The optimal antipredatory behavioral decision may depend on the individual's current reproductive prospects (asset-protection principle, Clark 1994). Thus, animals may be less responsive to predation risk during the reproductive season than during the non-reproductive season. For example, some prey fish species may largely ignore predators during the reproductive period (Helfman 1986).

Prey often increase refuge use to cope with predatory attacks (Sih 1986; Sih et al. 1992; Cooper 1998). However, refuge use may be costly in terms of the loss of time available for foraging (Koivula et al. 1995; Dill and Fraser 1997) or mate searching (Sih et al. 1990; Crowley et al. 1991), or because of physiological costs (Wolf and Kramer 1987; Martín and López 1999b). For this reason, animals should optimize the decision of when to emerge from a refuge after a predator's unsuccessful attack by balancing antipredator demands with other

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requirements (Sih et al. 1988; Sih 1992, 1997; Dill and Fraser 1997). Flexibility in the antipredatory responses might help animals to cope with predation risk without incurring excessive costs of refuge use (Sih 1992, 1997; Martín and López 1999c, 2001). Several costs (e.g., loss of mating or feeding opportunities) and benefits (i.e., diminution of predation-risk levels) should be balanced when deciding optimal emergence times from refuges. These multiple factors may naturally vary together and, thus, animals should be able to assess the variations in one or both of these factors simultaneously. Many animals are able to modify their antipredatory behavior according to the estimated levels of predation risk (Lima and Dill 1990; Sih et al. 1992), which prey may assess sometimes from the predator's behavior (Burger and Gochfeld 1990, 1993; Martín and López 1996; Cooper 1997a, 1997b). Emergence times from a refuge may depend on the characteristics (i.e., risk level) of the previous attack of the predator (Cooper 1998; Martín and López 1999c). Different levels of risk and different benefits to be gained after emerging may, thus, lead to different optimal solutions of refuge use.

Polygyny is widespread in lizards, although the range of number of females per male is substantial (Stamps 1983). For copulation, a male must find a female within her home range and court her there (Stamps 1983). Thus, to access more than one female, males should increase movements during the mating season. Repeated searches of the home range increase the encounter rate of males with prospective mates (McCloskey et al. 1987). However, there may be a trade-off between mating and antipredator requirements if increased movements attract predators (Magnhagen 1991). Also, time spent in the refuge by males after an unsuccessful predatory attack may reduce the time available for searching for females, and thus decrease their opportunities for reproduction. Thus, we hypothesized that male lizards should risk more (i.e., have shorter emergence times) in the mating season and when a receptive female is actually present. However, the antipredatory responses under different expected opportunities of mating should also depend on the level of predation risk. Because the reproductive success of females does not depend on number of matings, cost of refuge use is not expected to vary as greatly for females as for males between the mating and postreproductive seasons. Thus, statistical interaction is expected between sex and season.

In this paper, we present the results of a field study to test these predictions in the Iberian rock lizard (*Lacerta monticola*), a small lizard inhabiting high-altitude mountains of the Iberian peninsula. At high altitude, cool temperatures limit activity of lizards (Carrascal et al. 1992), making use of refuges costly (Martín and López 2000). Lizards are active from May to October, but the daily period with thermal conditions suitable for activity is often restricted by severe climatology. Mating occurs during a limited period of about 2 weeks in May/June, and females produce a single clutch in July (Elvira and Vigal 1985). Males are polygynous: the number of females is

approximately double that of males (Pérez-Mellado et al. 1987). Males gain access to several females by increasing their movements and home-range size (Martín and Salvador 1997; Aragón et al. 2001). With respect to their antipredator behavior, approach distances and emergence times from refuges may vary as a function of predation-risk level and costs of refuge use (Martín and López 1999c, 2000, 2001).

We conducted two experiments to test whether potential mating opportunities influenced the time lizards spent in refuges. The first experiment examines whether there are differences between the sexes in the responses to different levels of predation risk, and whether these responses change from the mating to the postreproductive season. In a second experiment, conducted during the mating season, we introduced tethered females to males, and then simulated a predatory attack by approaching lizards directly at one of two different approach speeds. We compared emergence times of these males to control males that were not exposed to females.

## Methods

### Study area and general methods

We performed the study in the Guadarrama Mountains (Madrid Prov., central Spain) at an elevation of 1,900 m. Granite rock boulders and scree 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). We searched for lizards by walking the area between 0700 and 1200 hours G.M.T.). Only adult lizards (approx. snout-to-vent length, SVL > 75 mm) with complete tails were used in the experiments. Before the trials, we noted their sex, which was easily identifiable at a distance by dorsal coloration (green males vs brown females) and morphological features (i.e., large head-size proportions of males). To ensure that each lizard was tested only once, we moved through a given portion of the study site once on 1 day and then moved to a new location for further observations on another day. Also, observations from the two seasons were made in sectors within the same area having identical characteristics, but separated by 1.5 km. Given the large size of the area surveyed (more than 5 km<sup>2</sup>) and the high lizard density, the probability of repeated sampling of the same individual was very low. We therefore treated all measurements as independent.

### Effects of sex, predator speed, and season on emergence times

We conducted this experiment during May (mating season) and July (postreproductive season). When we detected a lizard, we approached it directly at one of two different approach speeds: slow (ca. 45 m/min) or fast (ca. 140 m/min). We predicted that rapid approach should be considered by lizards as a higher risk of predation (Cooper 1998). To avoid confounding effects that may affect risk perception of lizards (Burger and Gochfeld 1993; Cooper 1997b), the same person wearing the same clothing performed all approaches.

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 a 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). We tested a total of 80 lizards, 10 males and 10 females in each treatment (slow vs fast) during the mating

season, and another 10 males and 10 females in each treatment during the postreproductive season.

#### Effects of female presence and predator approach speed on emergence times

We conducted this experiment during May/June 2001, which coincided with the mating season of lizards in this population (Aragón et al. 2001). Each day we captured by noosing two to three adult females (SVL ranged between 75 and 82 mm). We selected females that had not mated yet, as indicated by characteristic mating scars on the belly (personal observation), because after mating females may be unreceptive to males. Each female participated in a maximum of five trials, and was kept in a small terrarium between trials. We released females at the same capture sites at the end of the trials after a maximum of 4 h.

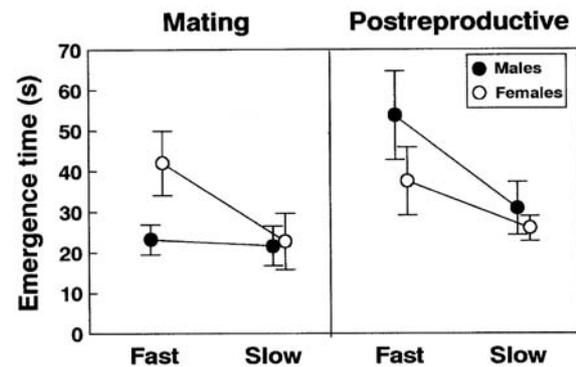
When we detected an adult male lizard, one experimenter slowly approached it and stopped at a distance of 2 m. Usually, lizards permitted such close approach at slow speed without attempting to escape. We slowly moved either a tethered female or a small piece of wood having the approximate size and shape of a female to a position 0.5 m from the male. The wood served as a control for the effects of the experimental disturbance. The female or wood was tied to a 1-m rod by a 0.3-m string. Males typically approached the female and started to court her, or remained close to the introduced wood. During courtship displays, the male approached the female slowly and began to tongue-flick the body or tail or the surrounding substrate. He next gripped and shook the female's tail with a gentle bite, and then attempted mounting. The experimenter waited immobile after courtship began or a similar period of time (about 20 s) in the control treatment. Thereafter, another experimenter chased the lizard as above, simulating a predatory attack directly at one of two different approach speeds (slow vs fast, see above), forcing the lizard to hide in a rock crevice, and then retreated. The order of presentation of the different treatments was counterbalanced. We tested 20 different males in each treatment.

Trials were aborted if lizards showed signs of disturbance and escaped before being chased due to the observer's presence. Lizards typically made a short flight to the nearest available refuge and hid entirely from the observer. When the lizard hid, we started a stopwatch, and the experimenter that remained immobile close to the refuge slowly moved either the tethered female or the wood within 15 cm of the refuge. We recorded the time until more than half of the male's body emerged from the refuge (emergence time) (Martín and López 1999c). In the female treatments, we also recorded whether the male returned to court the introduced female again, and the time elapsed since emergence to the start of the new courtship. We also noted whether the male had bitten the female during the first courtship approach.

#### Data analyses

Because temperature can affect emergence times of lizards (Martín and López 1999c), immediately after a lizard emerged from the refuge and resumed its activity, we used a digital thermometer to measure the substrate temperatures at the point where the lizard was before the attack and in the refuge. Thermal costs of refuge use were estimated from the difference between substrate temperature outside and in the refuge (see Martín and López 1999c). Also, potential body temperatures can be estimated from substrate temperatures according to the relationship described by Martín and Salvador (1993). These thermal costs and potential body temperatures did not differ significantly among treatments in any of the experiments (ANOVAs,  $P > 0.45$  in all cases), and thus could not have influenced the results of these experiments.

In the first experiment, we used three-way ANOVA to analyze differences in emergence times between approach speed, sex, and seasons. We included the interactions in the model to analyze how the responses of males and females may vary with the season, and whether the responses to different approach speeds vary between



**Fig. 1** Emergence times ( $\bar{X} \pm 1$  SE) from a refuge of male (filled circles) and female (unfilled circles) *Lacerta monticola* lizards after being approached directly by an experimenter at one of two different approach speeds (slow vs fast) in the mating or the postreproductive seasons

sexes or seasons. In the second experiment, we used two-way ANOVAs to assess differences in emergence time among treatments. We included the interaction between female presence and speed of approach to examine how different levels of predation risk might influence the males' response to the female presence. Data were log-transformed to achieve normality. Tests of homogeneity of variances (Levene's test) showed that, in all cases, variances were not significantly heterogeneous after transformation (Sokal and Rohlf 1995). Differences between pairs of treatments were assessed a posteriori using Tukey's honestly significant difference (HSD) tests.

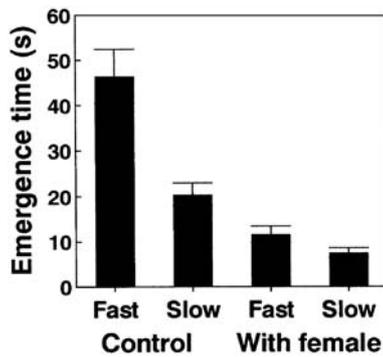
## Results

### Effects of sex, predator speed, and season on emergence times

After a predatory attack, lizards emerged significantly earlier when the approach was made at slow speed than when it was made at fast speed (three-way ANOVA, speed effect:  $F_{1,72}=7.87$ ,  $P=0.006$ ), but the sexes did not differ significantly (sex effect:  $F_{1,72}=0.04$ ,  $P=0.95$ ), and the difference between the mating and the postreproductive seasons was also not significant (season effect:  $F_{1,72}=3.78$ ,  $P=0.056$ ) (Fig. 1). However, the interaction between sex and season was significant (sex $\times$ season effect:  $F_{1,72}=4.31$ ,  $P=0.04$ ), with males having shorter emergence times in the mating than in the postreproductive season (Tukey's HSD tests,  $P=0.029$ ), whereas females did not differ in emergence times between seasons ( $P=0.99$ ). All other interactions were non-significant (season $\times$ speed:  $F_{1,72}=0.47$ ,  $P=0.49$ ; sex $\times$ speed:  $F_{1,72}=0.10$ ,  $P=0.75$ ; speed $\times$ sex $\times$ season:  $F_{1,72}=2.15$ ,  $P=0.15$ ).

### Effects of female presence and predator approach speed on emergence times

After a predatory attack, males emerged significantly earlier from the refuge when a female was present than in the control situation (two-way ANOVA, female effect:  $F_{1,76}=85.55$ ,  $P < 0.0001$ ) (Fig. 2), and emerged significant-



**Fig. 2** Emergence times ( $\bar{X} \pm 1$  SE) from a refuge of male *Lacerta monticola* lizards in presence or absence (control) of a tethered female after being approached directly by an experimenter at one of two different approach speeds (slow vs fast) in the mating season

ly earlier when the approach was made at slow speed than when it was at fast speed (speed effect:  $F_{1,76}=19.67$ ,  $P<0.0001$ ). The interaction between female presence and predator speed was not significant ( $F_{1,76}=2.71$ ,  $P=0.10$ ). However, post-hoc tests indicated that, in the control situation, males emerged significantly earlier when the speed was slow (Tukey's HSD test,  $P=0.0004$ ), but that emergence times did not differ significantly between approach speeds when a female was present ( $P=0.21$ ).

The approach speed did not significantly affect the propensity of the male to return and court the female after the predatory attack (16 vs 10 males returned to court after being approached rapidly or slowly, respectively; 2-tailed binomial test  $P=0.33$ ). Emergence times did not differ significantly between males that returned to court ( $\bar{X} \pm \text{SE}=10.0 \pm 1.4$  s,  $n=26$ ) and males that did not return ( $8.7 \pm 1.6$  s,  $n=14$ ) (ANOVA:  $F_{1,38}=0.16$ ,  $P=0.69$ ). When males returned to court the female, latency to resume courtship after emerging from the refuge did not differ significantly between predator approach speeds (fast:  $\bar{X} \pm \text{SE}=4.7 \pm 0.8$  s; slow:  $3.6 \pm 1.0$  s; ANOVA:  $F_{1,24}=0.21$ ,  $P=0.65$ ).

When a male bit a female during courtship, it might be considered that the interest of this male in the female was greater than when a male licked the female, but did not attempt to mount her. All males that had bitten the female returned to court her after the attack. However, emergence times did not differ significantly between males that bit and those that did not bite the female (two-way ANOVA, bite effect:  $F_{1,36}=0.26$ ,  $P=0.31$ ) or between approach speeds (speed effect:  $F_{1,36}=1.09$ ,  $P=0.30$ ), and the interaction was not significant ( $F_{1,36}=1.03$ ,  $P=0.30$ ). Nevertheless, in a separate analysis, emergence times did not differ significantly between approach speeds for males that bit the female (fast:  $\bar{X} \pm \text{SE}=7.8 \pm 1.7$  s; slow:  $7.5 \pm 1.4$  s; ANOVA:  $F_{1,7}=0.001$ ,  $P=0.98$ ), but for males that did not bite females, emergence times were significantly longer for fast than slow approaches (fast:  $\bar{X} \pm \text{SE}=12.9 \pm 2.2$  s; slow:  $7.5 \pm 1.4$  s; ANOVA:  $F_{1,29}=4.22$ ,  $P<0.05$ ).

## Discussion

The different levels of predation risk posed by a predator approaching at different speeds strongly affected latency to emerge from refuge. Rapid approach by a predator is an important indicator of immediate threat of predation to which prey in many species respond by increasing both the flight-initiation distance (e.g., Dill 1974; Martín and López 1996; Cooper 1997a; but see Bonenfant and Kramer 1996) and latency to emerge from refuge (Cooper 1998; Martín and López 1999c).

Many animals, such as some fishes (Endler 1987; Candolin 1997), frogs (Ryan et al. 1982), crabs (Koga et al. 1998), or aquatic insects (Sih et al. 1990), may reduce mating activity under predation risk. However, when there is a trade-off between mating opportunities and predator avoidance, the degree of risk taking should be related to the probability of future mating opportunities (Magnhagen 1991; Clark 1994). Thus, for example, young *Gobius niger* fishes stopped spawning under predation risk, whereas older individuals readily spawned in a similar situation (Magnhagen 1990). Similarly, in *L. monticola*, where the mating period is very short, sex and season also affected decisions about refuge use, as indicated by the significant interaction term. During the mating season, males had shorter emergence times than in the postreproductive season. Male *L. monticola* also have greater general activity levels during the mating season and these seasonal differences cannot be explained by thermal constraints or changes in microhabitat use (Aragón et al. 2001). Thus, when mating opportunities are high, males seem to be less sensitive to predation risk, at least in a situation where the predator has disappeared after an unsuccessful attack. Nevertheless, it may be expected that an increase in risk may force prey to increase emergence times. Thus, in the second experiment during the mating season, when we increased risk by remaining close to the refuge, emergence times were longer and were affected by approach speed in the control treatment, but not in the female treatment. Therefore, variations in emergence times seem to reflect different balances between the costs of losing mating opportunities and the benefit of a diminution of predation risk with time.

The absence of any effect of season on refuge use of females may be explained in part by the greater reproductive investment of females (Clark 1994) and by the lack of a relationship between reproductive success and number of matings. Whereas males can increase the number of eggs fertilized by mating with multiple females, females may fertilize all their eggs by mating once. Thus, females should risk less than males. Also, during the mating season, female *L. monticola* remain relatively stationary, but males must search for females (Martín and Salvador 1997; Aragón et al. 2001). Thus, females do not lose reproductive opportunities by increasing refuge use. Nevertheless, it might be expected that gravid females later in the year have greater latency to emerge than males or nongravid females because their

risk of predation is greater in many species due to decreased sprint speed, which impairs their ability to escape (Shine 1980; Cooper et al. 1990; Magnhagen 1991). Gravid lizards are known to modify other aspects of antipredatory behavior and may be predicted to spend more time in refuge unless the increased risk is outweighed by decreases in body temperature while in refuge (Martín and López 1999b, 1999c) at a time when basking may be important for development of offspring. Thus, the concurrence of different ecological pressures may lead females to have similar optimal emergence times in the different phases of their reproductive cycle.

When a tethered female was presented, males had even shorter emergence times, and these did not differ between approach speeds. When a female is nearby, staying in the refuge may result in losing opportunities to mate. A similar situation was observed in mate-guarding males of the skink *Eumeces laticeps* (Cooper 1997a, 1999) and the lacertid lizard *Psammotromus algirus* (Martín and López 1999a), which allowed closer approach than males found alone, before escaping from potential predators. Because costs of fleeing and refuge use increase for a male that must leave his mate to escape, an optimal decision requires that the approach distance and emergence time decrease even if predation risk increases (Ydenberg and Dill 1986; Martín and López 1999a). A male leaving a female not only loses mating opportunities, but also risks sneaked copulations by subordinate males if they are not able to relocate their mates immediately after the predatory attack. Risk of loss of copulations to rivals may be high in dense populations such as the one we studied (Martín and Salvador 1997; Aragón et al. 2001). Risk of losing mating opportunities due to inability to relocate the female may be especially great for transient females and unfamiliar females (Cooper 1985), in which case our results may indicate maximum effects of female presence.

Return by males to court tethered females despite the proximity of the predator indicates the willingness of males to take risks to obtain mating opportunities. The predator's approach speed influenced neither a male's decision to return to court, nor the latency to resume courtship after emergence. Furthermore, in males that had already attempted mounting (i.e., those that had bitten the female), the value of the female was probably assessed as greater, and emergence times decreased regardless of approach speed.

Taken together, the results of both experiments suggest that males adjust emergence times simultaneously to the degree of predation risk and the cost of lost mating opportunities. Therefore, refuge use in the lizard *L. monticola* reflects a trade-off between survival and reproduction.

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