

## When to run from an ambush predator: balancing crypsis benefits with costs of fleeing in lizards

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Many studies show that prey should not flee immediately from approaching predators, but should adjust their fleeing distance to minimize flight costs. We explored a new scenario where an ambush predator appears close to a relatively cryptic prey, that the predator has not yet detected. Then, instead of approaching further, the predator stops and starts looking for prey from a vantage point, while maintaining a constant distance with the still undetected prey. Probability of detection of prey will increase with time of searching. We predicted that prey should wait before escaping until the time ('fleeing time') when the risk of being detected, which depends on prey conspicuousness, equals fleeing costs. We tested this prediction in the field by simulating an ambush predator and examining escape decisions of rock lizards, *Iberolacerta cyreni*, considering two risk levels (i.e. the predator has or does not have information on the prey location) and relative conspicuousness of lizards (i.e. differences in coloration and body size). Lizards fled after some time, even if the distance between predator and prey remained constant and an attack had not been launched, probably because risk of being detected increases with time. However, to minimize fleeing costs, lizards modulated their fleeing times depending on probability of being detected (related to colour conspicuousness differences) and on size-dependent escape performance. Nevertheless, conspicuousness seemed unimportant after the predator had acquired information on the location of a prey, and/or the predator was considered as more dangerous because it had previously attacked the prey.

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Theoretical models and empirical evidence suggest that prey should not flee immediately upon detecting an approaching predator, but instead should adjust their escape response to minimize the costs of flight (Ydenberg & Dill 1986; Lima & Dill 1990; Cooper & Frederick 2007). Predators do not always pose an immediate threat, and environmental variables may also affect risk perception (Stankowich & Blumstein 2005). Consequently, the distance at which an animal starts to flee should be the point where the costs of staying (i.e. predation risk) exceed the costs of fleeing (Ydenberg & Dill 1986), or the point where the balance between expected fitness consequences of fleeing versus not fleeing is optimized (Cooper & Frederick 2007). Predictions from escape theory have been successfully tested in many animals (reviewed in Lima & Dill 1990; Stankowich & Blumstein 2005). However, most of these studies usually consider a situation where a predator has already detected

a prey and is approaching it at different speeds or with different trajectories. The prey has detected the predator too and has to decide on which approach distance (or flight initiation distance) between the predator and the prey is optimal to initiate flight considering both risks and costs of fleeing. Factors such as availability of food or mates, group size, microhabitat characteristics, distance to refuges, predator density and risk posed by the predator, assessed from predator behaviour, often influence flight decisions of many prey (Lima & Dill 1990; Stankowich & Blumstein 2005).

A recent theoretical model considered a different scenario where a cryptic prey is approached by a predator that has not yet discovered the prey, but that has an increasing likelihood of doing so as it gets closer to the prey (Broom & Ruxton 2005). The cryptic prey may face a conflict in deciding whether and when to flee because the act of fleeing might alert the predator and consequently trigger an attack that might not have occurred otherwise. This model suggests that the optimal strategy for prey is either to run as soon as they detect a predator approaching or only to flee in response to having been detected by the predator (Broom & Ruxton 2005). The optimal decision will depend on a variety of factors such as predator search speed, cost of fleeing, probability of reaching a refuge and conspicuousness of the prey and the predator.

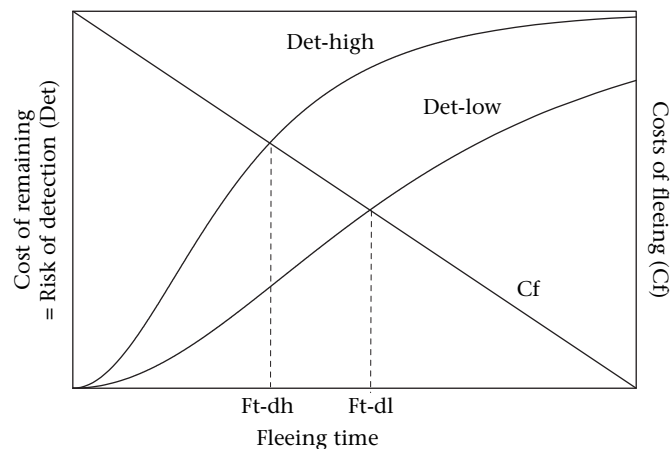
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We explored here a variation of this model. In this new scenario an ambush predator appears close to, and in sight of, a relatively cryptic prey, but the predator has not yet detected the prey. Then, instead of approaching further, the predator stops and remains at a vantage point from where it starts looking for any prey, while maintaining a constant distance with the still undetected prey. For example, many raptors and shrikes often perch exposed on the top of trees, rocks or electric pylons from where they search visually for small prey on the ground, and eventually launch attacks from there. Potential prey may often clearly detect and see this predator, and have the advantage of monitoring predator behaviour (Cooper 2008), but prey should decide whether to remain exposed and maintain their normal activity or whether and when to flee to a refuge.

Both remaining without fleeing and fleeing have costs. Costs of fleeing include loss of time and opportunities, energetic costs of the fleeing sequence, and subsequent costs of refuge use (Ydenberg & Dill 1986; Cooper & Frederick 2007), and in this situation also the risk of attracting an otherwise unaware predator by the action of fleeing (Broom & Ruxton 2005). The cost of remaining (i.e. risk of capture) is the product of the probability that the predator detects the prey, the probability that the predator successfully catches the prey if it initiates the attack after detection, and the prey's future reproductive fitness. With an ambush predator, the probability of successful capture can be regarded as constant because the distance between the predator and the prey does not change over time. As a result, the probability of detection becomes the major determinant of the cost of remaining. Even if the prey remains static and cryptic, the probability that a predator detects the prey will increase with time of searching by the predator (Fig. 1). Therefore, risk of predation (i.e. cost of remaining) will increase with time even if the distance between predator and prey remains constant. Similarly to previous models of escape decisions (Ydenberg & Dill 1986; Cooper & Frederick 2007), we could predict that prey should wait before escaping until the time ('fleeing time'; Ft) when the costs of remaining equal the costs of fleeing.

The rate of increase in the function of risk of detection by the predator will first depend on the degree of crypsis or conspicuousness of prey in relation to the background environment (see Det-high versus Det-low in Fig. 1), where both body size and



**Figure 1.** A simple economic model to predict fleeing time of lizards once a predator has stopped at a vantage point, from where it looks for prey while maintaining a constant distance with the still undetected prey, as a function of the cost of remaining (=probability of detection of the prey by the predator with time; Det), and costs of fleeing. Two situations with different rates of increase in the function of probability of detection (high versus low) are considered. The optimal fleeing times (Ft) for each particular situation are shown: Ft-dh when the probability of detection is high and Ft-dl when it is low.

pattern or coloration of the prey may be important (Cooper 1998a; Forsman & Appelqvist 1998; Cuadrado et al. 2001; Merilaita et al. 2001). Consequently, more conspicuous prey should delay their fleeing decisions for shorter times (see Ft-dh versus Ft-dl in Fig. 1). Costs of fleeing may decrease with time (e.g. loss of opportunities) or be constant (e.g. energetic costs of fleeing) but this will not affect the prediction that more conspicuous prey should initiate fleeing early.

The distance between predator and prey, and the distance of prey to available refuges, may also influence the risk of detection and the probability of a successful escape if the fleeing prey triggers a predator attack (Dill & Houtman 1989; Martín & López 1995a; Cooper 1997a). Thus, prey positioned away from the predator or closer to safe microhabitats should allow longer times before escaping, because the probability of detection is lower and the probability of a successful escape should be greater, even if the predator detects the prey and launches an attack.

Prey may also consider its immediate previous experience with a given individual predator in deciding risk level (Martín & López 2004). If, in the recent past, there has already been a failed attack and/or the prey has revealed its spatial location to the predator by fleeing, then the predator may concentrate its new search in a small area with the additional benefit of having a search image of that particular prey (Gendron 1986). Thus, the probability of locating the prey again (i.e. the slope of the risk of the detection curve in Fig. 1) will increase with time more quickly, as a result of search image formation and area-restricted search, than if the predator had no previous indication of where a potential prey could be, which would require searching over a larger area. Therefore, after a failed attack, prey facing the same individual predator again should decide to escape earlier because that predator has information on the prey's location and characteristics, or because the prey could consider that this individual predator is actually foraging for prey (i.e. the predator has already launched an attack) rather than just passing by. In this study, we examined experimentally in the field these predictions of escape behaviour decisions (based on time elapsed since the predator appears) with a simulated ambush predator and a relatively cryptic lizard prey.

Lizards have been extensively used as models for many studies of antipredator behaviour testing many of the predictions of escape theories (e.g. Martín & López 1995a, b, 2000a, b; Cooper 1997a, b, 1998a, b, 1999, 2003, 2008; Cooper et al. 2003a, b). We used as a model species the Carpetane rock lizard, *Iberolacerta cyreni* (formerly *Lacerta monticola cyreni*), a medium-sized and robust lacertid lizard found in high-altitude mountains in central Spain. Rock lizards select microhabitats with extensive rock cover, and typically escape from predators by hiding under rocks in scree or in rock crevices (Martín & Salvador 1997; Martín & López 1999a). Previous studies have shown that these lizards are able to modulate their antipredator behaviour by balancing several costs and benefits, which results in subtle modifications of their escape behaviour (Carrascal et al. 1992; Martín & López 2000a, 2003) and patterns of refuge use as a function of risk level, thermal conditions, and foraging or mating expectations (Martín & López 1999a, 2001; Cooper et al. 2003a; Martín et al. 2003a, b; Amo et al. 2007). Rock lizards can track changes in risk level through successive attacks and modify their refuge use with flexibility when required (Martín & López 2001, 2004; Polo et al. 2005; Martín et al. 2009). In the present field study, an experimenter simulated an ambush predator searching for motionless prey from a vantage point, and examined escape decisions (fleeing time) of lizards. We considered two different levels of risk (i.e. the predator has or does not have information on the approximate location of the prey), the relative conspicuousness of the lizard prey (based on age and sex variation in body size and coloration) and the probability of a successful

escape (distance between the predator and the prey and distance to refuges). We also analysed the time spent hidden in refuges after fleeing (emergence times; Martín & López 1999a) to test whether the previous fleeing decisions affected subsequent hiding decisions once the lizard is safe in a refuge and may reassess predation risk to adjust its responses (Martín & López 2004).

## METHODS

### *Study Site and Species*

We performed the study from July to August in the Guadarrama Mountains, Madrid Province, central Spain, at an average elevation of 1900 m. Granite rock boulders and screes interspersed with shrubs (*Cytisus oromediterraneus* and *Juniperus communis*) predominate in the study site, together with meadows of *Festuca* and other grasses, although lizards select rocky areas (Martín & Salvador 1997). Visually guided ambush predators of lizards in this area include several raptors, such as booted eagles, *Hieraetus pennatus*, buzzards, *Buteo buteo*, and kestrels, *Falco tinnunculus*, as well as shrikes, *Lanius meridionalis*, crows, *Corvus corax*, and rock thrushes, *Monticola saxatilis* (Martín & López 1990; Salvador & Veiga 2003). All of these birds usually look for prey from vantage points by perching on trees or pylons, or by hovering in the sky for relatively long periods, while searching visually for terrestrial prey.

In this mountainous area, *I. cyreni* is active only from May to September owing to limiting environmental temperatures, mating in May–June and producing a single clutch in July (Aragón et al. 2004; Salvador et al. 2008). We performed the study only on days with favourable weather and after the mating season had finished, reducing differences between sexes caused by reproductive constraints (e.g. Martín et al. 2003a).

Rock lizards show ontogenetic and sexual dimorphism in coloration (Aragón et al. 2004). While adult females have dorsal coloration with a dull brown background and a pattern of blackish dark spots, and whitish or pale yellow ventrolateral sides, adult males have a bright blue–green dorsal coloration background with black spots, blue ventrolateral coloration, and a conspicuous row of small but distinctive blue spots that runs along their body side on ventrolateral scales of the outer margin of the belly (Aragón et al. 2004; López et al. 2004). These blue spots reflect ultraviolet (UV) light in lizards (Arribas 2001; Thorpe & Richard 2001). Both male and female subadults have dorsal brown coloration similar to that of adult females, although some subadult males may show a few lateral blue spots. Juveniles have dorsal light brown coloration but the tail is greenish or blue, which reflects UV light. The tail turns brown when juveniles become subadults and remains brown thereafter.

Because the conspicuousness of lizard coloration may affect their escape responses, we considered that the dull brown colour of subadult males and females, and adult females, should allow them to be relatively cryptic against the environment background, whereas the bright green coloration of adult males would make them more conspicuous. Furthermore, as many birds can perceive the reflectance of UV light (Cuthill et al. 2000) and even use UV marks to detect their prey (Honkavaara et al. 2002), we expected that UV-blue spots of male lizards increased conspicuousness to avian predators (Cabido et al. 2009). Similarly, the blue tail of juveniles should make them more conspicuous to avian predators. In fact, blue tails in lizards are thought to deflect the attacks of predators to the tail, which can be autotomized and later regenerated, allowing the lizard to escape and avoid attacks to the more vulnerable body (Cooper & Vitt 1985). According to these criteria of conspicuousness, we classified lizards as: ‘juveniles’ (with blue tails), ‘subadults’ (brown; we pooled males and females as they

have similar coloration and sex is not easily determined without capturing them), ‘adult females’ (brown) and ‘adult males’ (green with blue spots).

Body size may also affect conspicuousness, smaller lizards being more difficult to locate by the predator from long distances. Body size may also affect vulnerability to predators because larger lizards have higher escape performance ability than smaller ones (Martín & López 1995b, 1996, 2003). Because body size increases with age in lizards we considered three size classes of lizards according to their snout–vent length (SVL): ‘small’ (SVL < 50 mm approximately; included all juveniles and some small subadults), ‘medium’ (50 mm < SVL < 70 mm; most subadults), and ‘large’ (SVL > 70 mm; included adult males and females). Categories of body size were estimated by sight according to our previous field experience with this lizard.

The experiments were done under licence from the Environmental Council of the Madrid Regional Government (Consería de Medio Ambiente de la comunidad de Madrid).

### *Experimental Procedure*

We used a human experimenter as a simulated predator. In most studies of escape decisions, humans have been used as model predators, since human disturbance causes antipredator responses similar to those elicited by natural predators (Frid & Dill 2002). Between 0900 and 1700 hours (GMT), an experimenter walked slowly through the area until a lizard was sighted at a long distance with binoculars. Then, the experimenter attempted to approach the focal lizard in one of two randomly selected different procedures (‘low’ versus ‘high’ predation risk). In the ‘low predation risk’ situation, the observer approached slowly without paying direct attention to the lizard. Then, the observer stopped quietly and stood motionless at a distance from the focal lizard (‘stopping distance’:  $\bar{X} \pm 1 \text{ SE} = 183 \pm 8 \text{ cm}$ ; range 85–290 cm). This stopping distance was long enough to avoid the lizard escaping but short enough to pose a potential threat for the lizard (the observer made his body clearly visible and looked from above at the area surrounding the lizard’s location, although neither directly nor continuously at the lizard). Preliminary trials indicated that stopping distances that fulfil these requirements should be approximately between 1 and 3 m. In the experiments, the exact stopping distance in each case depended on microhabitat characteristics, topography and the lizard’s location, and was accurately measured at the end of the trial to be included in analyses. We discarded observations when the lizard fled earlier than the observer had stopped motionless (i.e. stopping distance was too short). We verified that the lizard could clearly see the experimenter, by corroborating characteristic alert behaviours (e.g. head often turned or raised towards the observer). Then, the experimenter remained motionless and recorded with a stopwatch the time since he stopped until the lizard fled at relatively high speed and hid in a refuge (‘fleeing time’), usually a rock crevice, indicating that it was escaping from the simulated predator. We discarded a few observations where lizards walked to another location, but did not hide, apparently unaffected by the experimenter’s presence. With this procedure we simulated a nearby ambush predator that had not noticed the presence of that particular lizard.

In the ‘high predation risk’ situation, once a lizard was detected from a long distance with binoculars, the experimenter approached slowly and stopped for about 2 s close to the lizard as above, but then immediately simulated a direct predator attack by running fast (approximately 140 m/min) and directly towards the lizard, looking directly at it, until the lizard hid in a refuge as a direct consequence of the attack. We discarded observations when the lizard fled before the observer had launched the attack.

Immediately after the attack, the experimenter retreated to a far position (about 4–5 m), but remained standing still and visible until the lizard emerged from the refuge. After a short time (30 s), the experimenter followed the same protocol as in a 'low predation risk' situation, approaching slowly and waiting motionless close to the individual lizard that had flushed immediately before ('stopping distance':  $\bar{X} \pm 1 \text{ SE} = 176 \pm 11 \text{ cm}$ ; range 80–250 cm), and recorded the time until the lizard fled to a refuge again (fleeing time). With this procedure, we simulated a predator having information about the presence of a particular individual lizard in a small restricted area, but not knowing the exact location of that lizard (lizards often emerged from a different place from where they had entered the refuge; e.g. by walking under a rock scree) and was waiting and looking at a smaller area than in the low-risk situation, trying to locate that individual lizard again. This procedure also simulated a predator that could concentrate its search on a particular type of prey, after having formed a 'search image' of the previously attacked prey (Gendron 1986). Also, this high-risk predator should be considered more dangerous by the individual lizard because this predator had already launched an attack on it, in comparison with a low-risk situation where it was uncertain whether the predator was actually trying to capture prey or was simply passing by.

In all cases, when the lizard hid, we retreated to a distance of 5–7 m to observe from a hidden position with binoculars and recorded the time that the lizard spent in the refuge until all the lizard's body emerged from the refuge ('emergence time'). We also noted the 'distance to the refuge' from the initial position of the lizard ( $\bar{X} \pm 1 \text{ SE} = 17 \pm 1 \text{ cm}$ ; range 1–55 cm), and the age/sex (juvenile, subadult, adult male or adult female) and size class (small, medium or large) of the lizard.

To avoid confounding effects that may affect risk perception of lizards (Cooper et al. 2003a) the same person wearing the same clothing performed all approaches in a standardized way. To avoid differences in thermal costs (Martín & López 1999a) and thermal-dependent escape performance of lizards, we did experiments on summer days with favourable sunny weather and similar thermal conditions, and at times of day when lizards would have been able to obtain body temperatures that maximized sprint speed and escape performance (Carrascal et al. 1992). To avoid differences in relative conspicuousness or safety of lizards between microhabitats caused by differences in background or cover characteristics, we did all simulated attacks on lizards occupying sunny exposed granite rocks or rock gravels without bush cover above. This coincides with the preferred microhabitat of these lizards (Martín & Salvador 1997) and, thus, it was the situation where most lizards were found.

#### Data Analyses

Given the large size of the area surveyed (more than 10 km<sup>2</sup>), the high lizard density and the avoidance of previously sampled sites, the probability of repeated sampling of the same individuals was very low. We used two-way analyses of variance (ANOVAs) to examine variation in fleeing time or emergence time depending on the risk level (low versus high) and age/sex class of lizards with different coloration (juvenile versus subadult versus adult female versus adult male) or between body size classes (small versus medium versus large), and including the interaction in the model to examine whether different classes of lizards respond differentially to the different risk levels. We also included in the ANOVA models for fleeing time both the stopping distance and the distance to the nearest refuge as covariates. Data were log transformed to ensure normality. Pairwise comparisons used Tukey's honestly significant difference (HSD) tests (Sokal & Rohlf 1995).

Although these two classifications of lizards (coloration and size) were not entirely independent, they did differ in some aspects and we wanted to know whether both coloration and/or age/size affect waiting times. Thus, we decided to analyse data considering both types of classifications. An alternative analysis considering both size and coloration in the same ANOVA test was not possible because there were missing cells and the design of the ANOVA was incomplete (e.g. the smallest lizards were always juveniles with blue tails). Also, because the classifications were not independent, if we restricted our analyses to just one of the classifications, we would lose information on whether the second classification was what really explained the observed differences.

## RESULTS

### Fleeing Times

Time elapsed until fleeing (fleeing time) was on average  $\pm \text{SE}$   $93 \pm 9 \text{ s}$  (range 2–507 s). However, there was a substantial variation between individuals and situations. Fleeing time depended significantly on the risk level (two-way ANOVA:  $F_{1,128} = 48.26$ ,  $P < 0.0001$ ) and did not vary significantly between lizard age/sex classes ( $F_{3,128} = 1.77$ ,  $P = 0.15$ ), but the interaction was significant ( $F_{3,128} = 2.78$ ,  $P = 0.044$ ; Fig. 2a). There were no significant effects of the stopping distance between the simulated predator and the lizard ( $F_{1,128} = 0.09$ ,  $P = 0.76$ ) or the distance to the refuge ( $F_{1,128} = 0.85$ ,  $P = 0.36$ ). Thus, in the high-risk situation, there were no significant differences between lizard age/sex classes (Tukey's HSD tests:  $P > 0.70$  in all cases). However, in the low-risk situation adult females had significantly longer fleeing times than juveniles ( $P < 0.01$ ) and adult males ( $P < 0.05$ ), but females did not differ from subadults ( $P = 0.20$ ). In the low-risk situation, adult males had fleeing times that did not differ significantly from those of juveniles ( $P = 0.73$ ) and that were only marginally shorter than those of subadults ( $P = 0.08$ ). The comparison of fleeing times between the low- and high-risk situations within each lizard class showed that subadults ( $P < 0.0001$ ) and adult females ( $P < 0.001$ ) had significantly shorter fleeing times in the high-risk situation. In contrast, fleeing times did not differ significantly between the low- and high-risk situations in juveniles ( $P = 0.68$ ) and adult males ( $P = 0.19$ ).

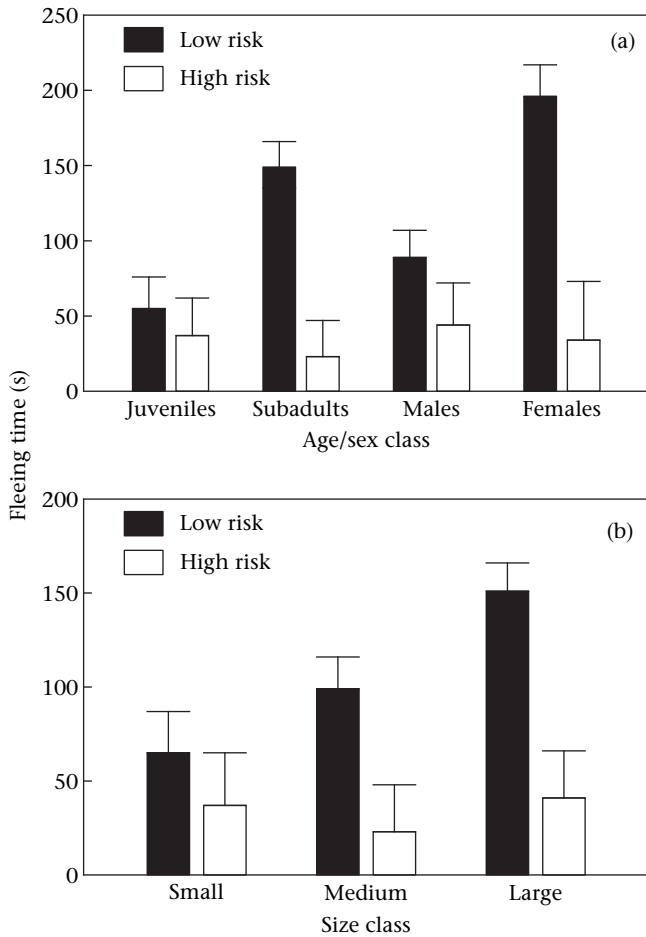
A similar analysis classifying lizards according to their body size (small versus medium versus large) showed that fleeing times varied significantly with risk level (two-way ANOVA:  $F_{1,130} = 46.01$ ,  $P < 0.0001$ ), and variation in fleeing time between lizard size classes was significant ( $F_{2,130} = 6.91$ ,  $P < 0.01$ ), but the interaction was significant ( $F_{2,130} = 3.62$ ,  $P = 0.03$ ; Fig. 2b). There were no significant effects of the stopping distance ( $F_{1,130} = 0.22$ ,  $P = 0.64$ ) or the distance to the refuge ( $F_{1,130} = 1.51$ ,  $P = 0.22$ ). Thus, when risk was high, lizards did not show significant differences in fleeing time between size classes (Tukey's HSD test:  $P > 0.50$  in all cases), but, when risk was low, large lizards had significantly longer fleeing times than medium lizards ( $P = 0.04$ ) and than small lizards ( $P = 0.0005$ ), whereas fleeing times of small and medium lizards were not significantly different ( $P = 0.65$ ).

### Emergence Times

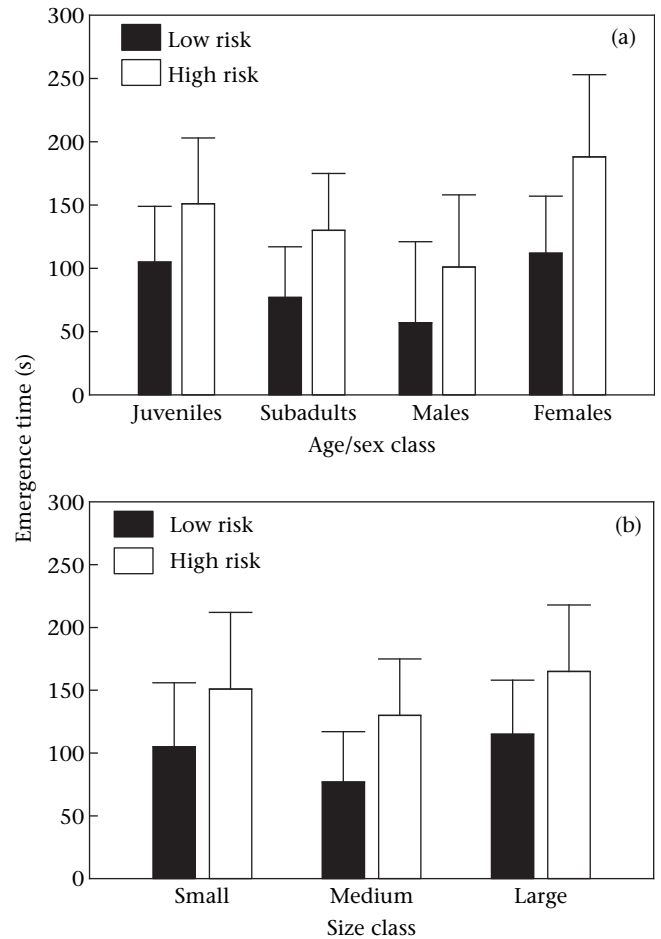
Emergence times from the refuge of lizards were significantly longer in the high-risk situation ( $168 \pm 29 \text{ s}$ ) than in the low-risk situation ( $88 \pm 25 \text{ s}$ ; two-way ANOVA:  $F_{1,130} = 4.44$ ,  $P = 0.037$ ), but did not vary significantly between lizard age/sex classes ( $F_{3,130} = 1.45$ ,  $P = 0.23$ ) and the interaction was not significant ( $F_{3,130} = 0.45$ ,  $P = 0.72$ ; Fig. 3a).

Emergence times of lizards classified according to body size classes also varied significantly between risk levels (two-way





**Figure 2.** Fleeing time ( $\bar{X} \pm SE$ ) of *I. cyreni* lizards since a simulated predator had stopped at a vantage point maintaining a constant distance with the prey. Solid bars indicate low-risk situations when lizards fled for the first time from a predator that had not launched an attack. Open bars indicate high-risk situations when lizards fled for the second time from a predator that had launched an unsuccessful attack in the recent past. Lizards were classified according to differences in conspicuousness based on (a) age/sex variation in coloration and (b) differences in body size.



**Figure 3.** Emergence times ( $\bar{X} \pm SE$ ) from a refuge of *I. cyreni* lizards after fleeing from a simulated predator that stopped at a vantage point maintaining a constant distance with the prey. Solid bars indicate low-risk situations when lizards fled for the first time from a predator that had not launched an attack. Open bars indicate high-risk situations when lizards fled for the second time from a predator that had launched an unsuccessful attack in the recent past. Lizards were classified according to differences in conspicuousness based on (a) age/sex variation in coloration and (b) differences in body size.

ANOVA:  $F_{1,132} = 4.44$ ,  $P = 0.037$ ), but did not vary significantly between lizard size classes ( $F_{2,132} = 0.68$ ,  $P = 0.51$ ) and the interaction was not significant ( $F_{2,132} = 1.03$ ,  $P = 0.36$ ; Fig. 3b).

Emergence times were not significantly related to the previous fleeing times when considering all lizards together (low risk:  $F_{1,137} = 0.01$ ,  $R^2 = 0.001$ ,  $P = 0.93$ ; high risk:  $F_{1,42} = 0.02$ ,  $R^2 = 0.004$ ,  $P = 0.89$ ). However, separate analyses for each lizard age/sex class showed that there were no significant relationships between fleeing and emergence times for females, subadults or juveniles ( $P > 0.34$  in all cases), but, only in the low-risk situation, adult males that had longer fleeing times thereafter had significantly longer emergence times ( $F_{1,31} = 10.76$ ,  $R^2 = 0.40$ ,  $P = 0.003$ ).

**DISCUSSION**

Our results are consistent with the hypothesis that lizards assessed that risk of predation increases with time since the potential predator stopped close to the prey and started searching. When we simulated a static ambush predator looking for prey, lizards that were performing normal activities stopped and, after some time of waiting, ran to hide in a refuge before an actual attack had been launched. This is probably because the risk of being detected by the predator, and consequently of being attacked,

increased with time even though the distance between the predator and the prey remained constant. This result reveals a new predator–prey situation that allows us to examine predictions of optimal escape behaviour in different contexts not considered previously (Ydenberg & Dill 1986; Cooper & Frederick 2007; but see Broom & Ruxton 2005).

The model of Broom & Ruxton (2005) for cryptic prey approached by a predator that has not yet discovered the prey suggests that the optimal strategy for prey is either to run as soon as they detect an approaching predator, or to flee only in response to having been detected by the predator. Prey that escape before the predator has detected them may have a higher probability of escaping, and they might even remain undetected by the predator, avoiding further attacks. However, our experimental study showed that lizards did not flee immediately after detecting the predator. This is probably because although an early fleeing strategy would decrease risk of capture, it would also increase costs of fleeing too much. The optimal strategy for a prey is to flee when risk of capture equals the costs of fleeing (Ydenberg & Dill 1986; Cooper & Frederick 2007). Thus, lizards delayed fleeing for some time after the predator had stopped, increasing risk but decreasing costs of fleeing. However, lizards did not delay fleeing until the predator

detected the prey and attacked, probably because risk of capture would suddenly increase too much after detection. Similarly, other experiments have shown that if an approaching predator suddenly turns towards prey, makes eye contact, or accelerates towards the prey, suggesting that it has detected the prey, the prey's assessment of risk may be altered dramatically and nearly instantaneously, and prey should initiate fleeing immediately (Cooper 1998b; Cooper & Frederick 2007).

Lizards in our experimental situation would do best if they fled just before they were detected because this minimizes the cost of fleeing (Fig. 1), particularly if the predator then gives up and leaves the area. However, the exact detection time might be impossible to determine or assess by lizards. Although lizards could estimate the rate of increase in the function of cumulative probability of being detected by the predator in each situation (see Fig. 1), the instantaneous probability of detection is stochastic (i.e. the predator could detect the prey at any moment, even within the first second of starting the search). Nevertheless, our study showed that lizards did not have random fleeing times but that they modified their fleeing times depending on factors that may affect probability of detection (detection time). Thus, lizards might be using some unknown proximate mechanisms to estimate when they should flee. For example, the ability to monitor predator behaviour (Cooper 2008) before deciding when to escape might help lizards to decide when detection is more likely to occur (e.g. by monitoring where the predator is looking or when the predator performs movements indicating an imminent attack). Also, lizards might use past experience with predators, considering the previous times elapsed since a predator appeared and an attack was launched, to assess when an attack is likely to occur. Also, the presence of a predator might act like a stimulus that affects the motivational state of lizards, with a threshold effect different for each situation or individual. Further experiments might examine whether different individuals show consistent fleeing times in repeated encounters with predators, which may be explained by different shy–bold personalities related to different conspicuousness or escape performance abilities (López et al. 2005; Cabido et al. 2009).

In support of the idea that risk assessment by lizards is based on probability of being detected by the predator, our results further showed that fleeing time depended on lizard coloration and presumably conspicuousness to predators. Thus, lizards with less conspicuous coloration (brown adult females and subadults) delayed the fleeing decision for longer than more conspicuous ones (green adult males and juveniles with blue tails). Similar effects of relative conspicuousness on escape decisions, but for distance between prey and an approaching predator, have been found in other lizards and other animals (Heatwole 1968; Eterovick et al. 1997; Cooper 1998a; Martín & López 1999b; Cuadrado et al. 2001; Carretero et al. 2006). Also, interindividual differences in anti-predator behaviour (time exposed or hidden from potential predators) of males of a related species of rock lizard are dependent on the relative conspicuousness (number of blue shoulder ocelli) of each individual (Cabido et al. 2009).

However, in our experiment, the effect of different conspicuousness on fleeing times was only noted when the predator had not detected the lizard in the recent past (low-risk situation), but not after the predator had already attempted an attack (high-risk situation). After an attack had occurred in the recent past, the predator presumably had information on the approximate location and a concrete search image of the lizard prey (Gendron 1986). Also, the predator might be considered more dangerous simply because it had already attacked. In this situation, probability of being relocated and attacked by the predator should be equally high for all classes of lizards. This is because the predator could restrict its searching to a small area where an already identified

lizard was expected to be rather than randomly looking at a large area and for undetermined prey. Consequently, fleeing times of all classes of lizards were shorter in the high-risk than in the low-risk situation, and we did not find differences between lizard classes. Benefits of relatively cryptic coloration might not be so great as to affect fleeing times significantly when risk of being detected increases or the predator is considered as more dangerous. Nevertheless, more cryptic types of prey might require much greater increments of risk before leaving their cryptic strategy. Further experiments should examine how increasing risk affects the magnitude of differences in fleeing times of prey with different conspicuousness.

Comparisons of fleeing times of lizards according to their body size, however, have led to apparently contradictory results. Larger lizards should apparently be more easily detected, but they delayed fleeing for longer than smaller lizards. It is likely that, considering the long distance between the predator and the lizard, differences in body size between lizards were too small (a maximum difference of 5–6 cm length) to affect conspicuousness significantly. Alternatively, differences between size classes could rather be attributed to the different escape performance abilities of lizards of different body sizes (Martín & López 1995b, 2003). By waiting for longer, larger lizards might take the risk of the predator detecting them because they are faster (i.e. higher absolute running speed) and had a higher probability of escaping than smaller lizards. Alternatively, larger lizards might have longer fleeing times because when they initiate fleeing the probability of alerting the predator and triggering an attack (a cost of fleeing) is higher than for smaller fleeing lizards. Small lizards might have shorter fleeing times if they were trying to escape or move to safer areas and still remain undetected by the predator. However, again, the effect of body size differences was only noted in the low-risk situation, and not when lizards assessed that the predator was presumably trying to capture that particular lizard (high-risk situation). Therefore, differences in escape performance or in probability of alerting the predator by fleeing may be unimportant when a lizard expects the predator to be already aware of it and will launch an attack immediately after relocating it.

Neither the stopping distance nor the distance to refuge had significant effects on fleeing time decisions of lizards in our experiment. Stopping distance between the predator and the prey might affect prey conspicuousness, and distance to refuges might affect prey safety. However, in our experimental situation there was only a small variation between trials and both distances were relatively short, so any effect might have been too weak to notice. It is likely that in a natural situation lizards respond to predators that stop at much longer distances with much longer fleeing times. Even lizards may ignore predators when the stopping distance is long enough (Blumstein 2003) or when microhabitat cover is high and, thus, the probability of being detected is very low. Also, it could be predicted that lizards at long distances from refuges should have much shorter fleeing times, an effect noted in other studies for fleeing decisions based on distance between predator and prey (Dill & Houtman 1989; Martín & López 1995a; Cooper 1997a).

Hiding decisions of lizards after fleeing might be affected by the previous escape decision. This is because once in the refuge a prey should be able to reassess the predation risk and adjust its response (Martín & López 2004). A prey may reassess risk by considering whether the predator has detected it after fleeing, remains unaware of its presence or has left the area. We did not find an overall effect of fleeing time decisions on emergence times from the refuge. However, and only in the low-risk situation, more conspicuous adult males (larger and with green coloration) that waited for longer before fleeing subsequently had longer emergence times. This suggests that conspicuous lizards that delay fleeing for longer

might try to compensate for a higher risk of having been detected before or after fleeing by spending longer hidden in refuges. Longer emergence times might increase the probability that the predator has left the area even if it had detected the prey (Martín & López 1999a; Hugie 2003). Other classes of lizards are less conspicuous and might consider that if they had fled before the predator had detected them, the fleeing sequence should not alert the predator. These results also support the hypothesis that conspicuousness of lizards affects their antipredator decisions, at least when risk is not too high.

Our results are consistent with the idea that an increase with time in the probability of detection by an unaware stationary predator represents an increase in predation risk, which requires that the prey flees after some time, even if the distance between predator and prey remains constant. Lizards might try to delay fleeing until the moment just before being detected by the predator because this delay will minimize costs of fleeing without increasing risk. However, detection time might be impossible to determine by lizards. Relative colour-dependent conspicuousness and size-dependent escape performance affect fleeing time decisions when risk is low. However, when risk increases, the effect of differences in conspicuousness seems unimportant (i.e. after the predator has presumably acquired additional information on the location and characteristics of a given prey, or when the predator is considered more dangerous after a previous attack). Finally, at least more conspicuous lizards may try to compensate for the higher risk of being detected with subsequent hiding decisions inside refuges.

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## References

- Amo, L., López, P. & Martín, J. 2007. Refuge use: a conflict between avoiding predation and losing mass in lizards. *Physiology & Behavior*, **90**, 334–343.
- Aragón, P., López, P. & Martín, J. 2004. The ontogeny of spatio-temporal tactics and social relationships of adult male Iberian rock lizards, *Lacerta monticola*. *Ethology*, **110**, 1001–1019.
- Arribas, O. J. 2001. Diseños en la banda del ultravioleta en algunos lacértidos europeos: datos preliminares. *Boletín de la Asociación Herpetológica Española*, **13**, 35–38.
- Blumstein, D. T. 2003. Flight-initiation distance in birds is dependent on intruder starting distance. *Journal of Wildlife Management*, **67**, 852–857.
- Broom, M. & Ruxton, G. D. 2005. You can run or you can hide: optimal strategies for cryptic prey against pursuit predators. *Behavioral Ecology*, **16**, 534–540.
- Cabido, C., Galán, P., López, P. & Martín, J. 2009. Conspicuousness-dependent antipredatory behavior may counteract coloration differences in Iberian rock lizards. *Behavioral Ecology*, **20**, 362–370.
- Carrascal, L. M., López, P., Martín, J. & Salvador, A. 1992. Basking and antipredator behaviour in a high altitude lizard: implications of heat-exchange rate. *Ethology*, **92**, 143–154.
- Carretero, M. A., Vasconcelos, R., Fonseca, M., Kaliontzopoulou, A., Brito, J. C., Harris, D. J. & Perera, A. 2006. Escape tactics of two syntopic forms of the *Lacerta perspicillata* complex with different colour patterns. *Canadian Journal of Zoology*, **84**, 1594–1603.
- Cooper, W. E., Jr. 1997a. Escape by a refuging prey, the broad-headed skink (*Eumeces laticeps*). *Canadian Journal of Zoology*, **75**, 943–947.
- Cooper, W. E., Jr. 1997b. 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, W. E., Jr. 1998a. Effects of refuge and conspicuousness on escape behavior by the broadheaded skink (*Eumeces laticeps*). *Amphibia-Reptilia*, **19**, 103–108.
- Cooper, W. E., Jr. 1998b. Direction of predator turning, a neglected cue to predation risk. *Behaviour*, **135**, 55–64.
- Cooper, W. E., Jr. 1999. Tradeoffs between courtship, fighting, and antipredatory behavior by a lizard, *Eumeces laticeps*. *Behavioral Ecology and Sociobiology*, **47**, 54–59.
- Cooper, W. E., Jr. 2003. Effect of risk on aspects of escape behavior by a lizard, *Holbrookia propinqua*, in relation to optimal escape theory. *Ethology*, **109**, 617–626.
- Cooper, W. E., Jr. 2008. Visual monitoring of predators: occurrence, cost and benefit for escape. *Animal Behaviour*, **76**, 1365–1372.
- Cooper, W. E., Jr. & Frederick, W. G. 2007. Optimal flight initiation distance. *Journal of Theoretical Biology*, **244**, 59–67.
- Cooper, W. E., Jr. & Vitt, L. J. 1985. Blue tails and autotomy: enhancement of predation avoidance in juvenile skinks. *Zeitschrift für Tierpsychologie*, **70**, 265–276.
- Cooper, W. E., Jr., Martín, J. & López, P. 2003a. Simultaneous risks and differences among individual predators affect refuge use by a lizard, *Lacerta monticola*. *Behaviour*, **140**, 27–41.
- Cooper, W. E., Jr., Perez-Mellado, V., Baird, T. A., Baird, T. A., Caldwell, J. P. & Vitt, L. J. 2003b. Effects of risk, cost, and their interaction on optimal escape by nonrefuging Bonaire whiptail lizards, *Cnemidophorus murinus*. *Behavioral Ecology*, **14**, 288–293.
- Cuadrado, M., Martín, J. & López, P. 2001. Camouflage and escape decisions in the common chameleon *Chamaeleo chamaeleon*. *Biological Journal of the Linnean Society*, **72**, 547–554.
- Cuthill, I. C., Partridge, J. C., Bennett, A. T. D., Church, S. C., Hart, N. S. & Hunt, S. 2000. Ultraviolet vision in birds. *Advances in the Study of Behavior*, **29**, 159–214.
- Dill, L. M. & Houtman, R. 1989. The influence of distance to refuge on flight initiation distance in the gray squirrel (*Sciurus carolinensis*). *Canadian Journal of Zoology*, **67**, 233–235.
- Eterovick, P. C., Figueira, J. E. C. & Vasconcelos-Neto, J. 1997. Cryptic coloration and choice of escape microhabitats by grasshoppers (Orthoptera: Acrididae). *Biological Journal of the Linnean Society*, **61**, 485–499.
- Forsman, A. & Appelqvist, S. 1998. Visual predators impose correlated selection on prey color pattern and behavior. *Behavioral Ecology*, **9**, 409–413.
- Frid, A. & Dill, L. M. 2002. Human-caused disturbance stimuli as a form of predation risk. *Conservation Ecology*, **6**, 11.
- Gendron, R. P. 1986. Searching for cryptic prey: evidence for optimal search rates and the formation of search images in quail. *Animal Behaviour*, **34**, 898–912.
- Heatwole, H. 1968. Relationship of escape behavior and camouflage in Anoline lizards. *Copeia*, **1968**, 109–113.
- Honkavaara, J., Koivula, M., Korpimäki, E., Siitari, H. & Viitala, J. 2002. Ultraviolet vision and foraging in terrestrial vertebrates. *Oikos*, **98**, 505–511.
- Hugie, D. M. 2003. The waiting game: a 'battle of waits' between predator and prey. *Behavioral Ecology*, **14**, 807–817.
- Lima, S. L. & Dill, L. M. 1990. Behavioral decisions made under the risk of predation: a review and prospectus. *Canadian Journal of Zoology*, **68**, 619–640.
- López, P., Martín, J. & Cuadrado, M. 2004. The role of lateral blue spots in intra-sexual relationships between male Iberian rock-lizards, *Lacerta monticola*. *Ethology*, **110**, 543–561.
- López, P., Hawlena, D., Polo, V., Amo, L. & Martín, J. 2005. Sources of individual shy-bold variations in antipredator behaviour of male Iberian rock-lizards. *Animal Behaviour*, **69**, 1–9.
- Martín, J. & López, P. 1990. Amphibians and reptiles as preys of birds in South-western Europe. *Smithsonian Herpetological Information Service*, **82**, 1–43.
- Martín, J. & López, P. 1995a. Influence of habitat structure on escape tactics of the lizard *Psammotromus algirus*. *Canadian Journal of Zoology*, **73**, 129–132.
- Martín, J. & López, P. 1995b. Escape behaviour of juvenile *Psammotromus algirus* lizards: constraint of or compensation for limitations in body size? *Behaviour*, **132**, 181–192.
- Martín, J. & López, P. 1996. The escape response of juvenile *Psammotromus algirus* lizards. *Journal of Comparative Psychology*, **110**, 187–192.
- Martín, J. & López, P. 1999a. When to come out from a refuge: risk-sensitive and state-dependent decisions in an alpine lizard. *Behavioral Ecology*, **10**, 487–492.
- Martín, J. & López, P. 1999b. Nuptial coloration and mate guarding affect escape decisions of male lizards, *Psammotromus algirus*. *Ethology*, **105**, 439–447.
- Martín, J. & López, P. 2000a. Costs of refuge use affect escape decisions of Iberian rock lizards, *Lacerta monticola*. *Ethology*, **106**, 483–492.
- Martín, J. & López, P. 2000b. Fleeing to unsafe refuges: effects of conspicuousness and refuge safety on the escape decisions of the lizard *Psammotromus algirus*. *Canadian Journal of Zoology*, **78**, 265–270.
- Martín, J. & López, P. 2001. Repeated predatory attacks and multiple decisions to come out from a refuge in an alpine lizard. *Behavioral Ecology*, **12**, 386–389.
- Martín, J. & López, P. 2003. Ontogenetic variation in antipredatory behavior of Iberian-rock lizards (*Lacerta monticola*): effects of body size dependent thermal exchange rates and costs of refuge use. *Canadian Journal of Zoology*, **81**, 1131–1137.
- Martín, J. & López, P. 2004. Iberian rock lizards (*Lacerta monticola*) assess short-term changes in predation risk level when deciding refuge use. *Journal of Comparative Psychology*, **118**, 280–286.
- Martín, J. & Salvador, A. 1997. Microhabitat selection by the Iberian rock-lizard *Lacerta monticola*: effects on density and spatial distribution of individuals. *Biological Conservation*, **79**, 303–307.
- Martín, J., López, P. & Cooper, W. E., Jr. 2003a. Loss of mating opportunities influences refuge use in the Iberian rock lizard, *Lacerta monticola*. *Behavioral Ecology and Sociobiology*, **54**, 505–510.
- Martín, J., López, P. & Cooper, W. E., Jr. 2003b. When to come out from a refuge: balancing predation risk and foraging opportunities in an alpine lizard. *Ethology*, **109**, 77–87.

- Martín, J., López, P. & Polo, V.** 2009. Temporal patterns of predation risk affect antipredator behaviour allocation by Iberian rock-lizards. *Animal Behaviour*, **77**, 1261–1266.
- Merilaita, S., Lyytinen, A. & Mappes, J.** 2001. Selection for cryptic coloration in a visually heterogeneous habitat. *Proceedings of the Royal Society B*, **268**, 1925–1929.
- Polo, V., López, P. & Martín, J.** 2005. 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. *Evolutionary Ecology Research*, **7**, 23–25.
- Salvador, A. & Veiga, P.** 2003. Lagartija serrana (*Lacerta monticola*) depredada por Aguillilla Calzada (*Hieraaetus pennatus*) en la Sierra de Guadarrama. *Boletín de la Asociación Herpetológica Española*, **14**, 44–45.
- Salvador, A., Díaz, J. A., Veiga, J. P., Bloor, P. & Brown, R. P.** 2008. Correlates of reproductive success in male lizards of the alpine species *Iberolacerta cyreni*. *Behavioral Ecology*, **19**, 169–176.
- Sokal, R. R. & Rohlf, F. J.** 1995. *Biometry*, 3rd edn. New York: W.H. Freeman.
- Stankowich, T. & Blumstein, D. T.** 2005. Fear in animals: a meta-analysis and review of risk assessment. *Proceedings of the Royal Society B*, **272**, 1433–1442.
- Thorpe, R. S. & Richard, M.** 2001. Evidence that ultraviolet markings are associated with patterns of molecular gene flow. *Proceedings of the National Academy of Sciences, U.S.A.*, **98**, 3929–3934.
- Ydenberg, R. C. & Dill, L. M.** 1986. The economics of fleeing from predators. *Advances in the Study of Behavior*, **16**, 229–249.