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Multiple predators and conflicting refuge use in the wall lizard, *Podarcis muralis*

Luisa Amo, Pilar López & José Martín*

*Departamento de Ecología Evolutiva, Museo Nacional de Ciencias Naturales, CSIC, José Gutiérrez Abascal 2, 28006 Madrid, Spain (*corresponding author's e-mail: Jose.Martin@mncn.csic.es)*

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Multiple predators can have risk-enhancing effects due to conflicting predator-specific prey defenses. Wall lizards (*Podarcis muralis*) escape from searching predators by fleeing into refuges where they can also encounter ambush snakes (*Coronella austriaca*). We simulated attacks to lizards in the laboratory to compare their use of predator-scented refuges with that of control refuges, and examined whether lizards that suffered a second attack changed the refuge used in the first attack if they had been hidden before in an unsafe refuge. The presence of snake cues neither influenced time to enter the refuge nor refuge choice. However, appearance time was greater in the snake-scented refuge, probably due to time spent acquiring information to ensure the absence of the snake. This was supported because once lizards appeared, they resumed their activities in the same interval of time. Our results suggest a case of predator facilitation due to conflicting prey defenses.

Introduction

Understanding emergent multiple predators effects is a critical issue, given that many prey live in communities with multiple predators (Sih *et al*. 1998). Sometimes, multiple predators have risk-enhancing effects, causing higher predation rates than expected (Soluk & Collins 1988, Ferguson & Stiling 1996, Sih *et al*. 1998), but the behavioral response of prey to cope with multiple predators still remains to be explored. The mechanism that is usually thought to generate risk enhancement involves conflicting predator-specific prey defenses. Prey defenses against one predator may increase the risk of being killed by the other predator (Lima 1992, Matsuda *et al*. 1993). However, in some systems conflicting prey defenses did not produce risk enhancement (Rahel & Stein 1988, Kotler *et al*. 1992, Krupa & Sih 1998). This can be explained if flexibility in antipredatory behavior or compensatory prey defenses may enable prey to respond adequately to two types of predators (Krupa & Sih 1998, Turner *et al*. 1999, Hopper 2001).

Prey often respond to predator presence by increasing their use of refuges (Sih *et al*. 1992). However, refuges may have some costs that should be minimized, such as the loss of time available for other activities, reduced foraging efficiency, or physiological costs (e.g. Sih *et al*. 1990, Dill & Fraser 1997, Sih 1997, Martín & López 1999a). Also, some types of refuge may only be useful against some types of predators and expose prey to other types of predators (Sih *et al*. 1998). For example, the mortality of mayfly larvae prey in the presence of both fish and stoneflies larvae was greater than expected (Soluk 1993). This is because stoneflies caused mayflies to come out of hiding under rocks, resulting in greater exposure to fish (Soluk 1993). Also, many lizards may face saurophagous ambush snakes inside refuges when escaping from searching predators, such as birds and mammals (Downes & Shine 1998).

In this context, lizards as prey, sit-and-wait predator snakes, and humans, simulating searching predators, offer an excellent system to study whether prey show behavioral strategies to avoid multiple predators acting simultaneously. Wall lizards (*Podarcis muralis*) responded to simulated predatory attacks by hiding inside rock crevices, and when predation pressure increased, lizards increased time spent in refuges (Martín & López 1999b). However, by increasing refuge use, wall lizards may expose themselves to increased predation risk by ambushing smooth snakes (*Coronella austriaca*), which are often hidden in rock crevices waiting for lizards (Galán 1998).

Theoretical models of refuge use suggest that prey should adjust the time spent in a refuge so that the optimal emergence time is the time when the costs of staying exceed the costs of leaving (Sih *et al*. 1992, Martín & López 1999a). The decision of when to come out from a refuge should be optimized by considering the expected fitness effects of diminution of predation risk with time in the exterior, but also considering the cost of refuge use. When a refuge is potentially unsafe (e.g., because it contains predator chemical cues), the probability of being detected by a second predator hidden in that refuge increased with time spent in the refuge. Hence, a prey hidden in an unsafe refuge would have increased costs of refuge use and should emerge from the refuge sooner than a prey hidden in a predator-free refuge. Nevertheless, during ecological time the risk of being preyed upon may vary greatly (Lima & Dill 1990) and to allocate its antipredator behavior accordingly, the prey should be able to assess the current level of predation risk.

An important component of antipredator behavior is the ability to ascertain the presence of predators (Van Damme *et al*. 1995). Chemosensory cues may reliably reveal the presence of predators (or their presence in the immediate past) and they may also provide information on predator activity level and diet (Kats & Dill 1998). Snakes deposit chemical trails that can be detected by lizards with their highly developed vomeronasal system (e.g., Cooper 1990, Van Damme *et al*. 1995, Downes & Shine 1998). For example, *P. muralis* is able to detect and discriminate the chemical cues of *C. austriaca* snakes (Amo *et al*. 2004). Because snakes are not always visible, their chemical stimuli may be particularly important for lizards that share the same refuges (Downes & Shine 1998). For example, some geckos used their chemosensory ability to avoid entering rock crevices covered with snake scent (Downes & Shine 1998).

In this paper, we examined refuge use of wall lizards when they suffered repeated predatory attacks by a human, simulating a searching predator, which forced lizards to hide inside a refuge that could contain chemicals of a saurophagous snake. We carried out two laboratory studies to analyze (1) refuge use in successive attacks between predator-free refuges and refuges containing chemical signals of smooth snake, and (2) to examine whether wall lizards that had used unsafe refuges avoided using them again after suffering a second attack, and entered alternative but unknown refuges instead. We hypothesized that lizards may be able to modify their refuge use in relation to the potential risk of predation inside it (i.e., the presence/absence of smooth snake scent). Thus, lizards should emerge sooner from a refuge containing these signals than from a safe refuge. Furthermore, we hypothesized that lizards should change their refuge use in a second attack if they hid in an unsafe refuge in the first attack. Alternatively, lizards might consider that the current risk of being preyed upon by a predator in the exterior is much higher that the eventual risk of encountering a hidden snake, and then prey might not modify its expected refuge use against only one type of predator.

Materials and methods

Animals and their maintenance

We captured by noosing 29 *P. muralis* (Snout-vent length, SVL, mean ± SE = 66 ± 2 mm) at an artificial wall (120 m long × 5 m high) near Cercedilla (Madrid Province, Spain). The wall lizard, *P. muralis*, is a small lacertid lizard widespread in central Europe. In the Iberian Peninsula it is restricted to mountain areas of the northern half, where they occupy soil dwellings, talus and walls in shaded zones in forests (Martin-Vallejo *et al*. 1995). We chose this species because the microhabitats it selects are also inhabited by the smooth snake (*C. austriaca*), which is a saurophagous specialist that feeds mainly on these lizards (Galán 1998), and has geographic distribution and habitat preferences that overlap frequently with those of *P. muralis*. Thus, we also captured in the same wall an adult smooth snake to be used as a potential predator in the experiments. Smooth snakes seemed to be especially abundant on this wall. For example, during a parallel field study, we captured and marked seven snakes that were often seen during the day ambushing inside crevices or occasionally basking outside very close to the crevices (Amo, López & Martín unpubl. data). In addition, we often observed in the area searching predators known to capture this lizard, such as some birds (Martín & López 1990), and abundant feral cats that frequently chase and kill these lizards in this and other populations (Brown *et al*. 1995, Martín & López 2001).

Lizards were individually housed at "El Ventorrillo" Field Station 5 km from the capture site, in outdoor 60 × 40 cm PVC terraria containing sand substratum and rocks for cover. They were fed every day with mealworm larvae (*Tenebrio molitor*) dusted with multivitamin powder for reptiles and water was provided *ad libitum*. The photoperiod and ambient temperature was that of the surrounding region. Lizards were held in captivity at least one month before testing to allow acclimation to laboratory conditions. To prevent the lizards from contact with the odor stimuli before they were tested, the snake was housed separately in a glass terrarium (60 × 30 × 20 cm) with strips of absorbent paper fixed on the substrate to obtain its scent. All the animals were healthy during the trials and were returned to their exact capture sites at the end of experiments.

Refuge use as a function of the refuge's scent

We designed this experiment to compare the propensity to enter the refuge, time spent in it, and the variation in successive attacks between clean control refuges and potentially unsafe refuges, as indicated by the presence of snake's scent on the substrate of the refuge. We tested each individual ($n = 29$) in each of three trials in a counterbalanced sequence: (1) smooth snake's scent (predator treatment), (2) deionized water (odorless control), and (3) cologne (pungency control; i.e., a strong odor without biological significance). The experimental area was a terrarium (100 × 40 × 50 cm) with a sand substrate and one refuge situated in the middle of one end of the terrarium. We used aluminum boxes (23 × 7.5 × 9 cm) as refuges to avoid effects of size or shape in relation to refuge use. The only entry to the refuge box (7.5 × 9 cm) was initially closed with a door. Furthermore, aluminum, because of its good heat conduction properties, allowed us to control the temperature inside the refuge by placing two bulb lamps at different heights over the refuge. Air temperature inside the refuge during tests was maintained at 17.4 ± 0.1 °C to avoid the confounding effects of temperature differences on refuge use (Martín & López 1999a, 1999b). We used strips of absorbent paper fixed to the floor of the refuges to add the odor. In the predator treatment, we used a strip of absorbent paper that had been in the terrarium of the snake for at least three days, moistened with deionized water. We applied some deionized water or 50% diluted cologne to a similar clean strip of absorbent paper in the odorless or pungency control treatments, respectively. We used new papers and a new refuge in each trial to avoid the mixture of odors. After each trial, we cleaned thoroughly the refuges with water and an odorless detergent, and replaced the sand substrate to avoid lizards responses to chemical cues of conspecifics.

Lizards were gently transferred to the experimental terraria, where the refuge had the door initially closed, and given 5 min before trials for acclimatization to a new environment. Then, the experimenter opened the door of the refuge and simulated a predatory attack by tapping lizards close to the tail with a brush to stimulate them to run and hide in the refuge. Lizards usually ran for some time and frequently passed several times close to the refuge without entering. Thus, we recorded the time from the beginning of the attack until the lizard entered the refuge. When the lizard hid, we retreated to a hidden position and recorded the time that the lizard spent in the refuge until the head appeared from the refuge ('appearance time'), and the time from appearance until the lizard emerged entirely from the refuge ('waiting time'). Immediately after the lizard resumed normal activity, we simulated another predatory attack using the same procedure and measurements as in the first attack.

Successive refuge choices

We performed this experiment immediately after the previous one with 18 of the previous 29 individuals. We designed this experiment to examine whether lizards, after having been hidden in a potentially unsafe refuge (i.e., with chemical scents of a predatory snake), chose to hide in the previously known refuge or in an unknown refuge. We tested each individual in one of two trials in a random sequence. In each trial, a lizard was gently released in the terrarium in which there was a refuge (aluminum box, as above) with the door opened and with either snake's scent ('unsafe refuge') or odorless ('safe refuge') paper strip inside. In addition, there was also an identical but odorless refuge with the door initially closed ('unknown refuge'). The two refuges were placed at one end of the terrarium with 10 cm between them. Lizards were given 5 min before trials for acclimatization. Then, we simulated a predatory attack using the same procedure as in the previous experiment, until the lizard hid in the refuge. We measured the time until the lizard entered the refuge and time spent in the refuge ('appearance' and 'waiting times'). Immediately after the lizard emerged entirely from the refuge and resumed normal activity, we opened the door to the second refuge and simulated a second attack using the same procedure as above. We noted the refuge (known or unknown) chosen by the lizard, and recorded the same measurements as in the first attack. The air temperature inside the refuge was maintained at 17.4 ± 0.1 °C.

Data analyses

We used repeated measures two way ANOVAs to assess differences in time to enter the refuge, appearance and waiting times between treatments (water *vs.* predator *vs.* cologne) and between the two attacks of each individual (both within-factors). We included the interaction in the models to test whether responses to the different treatments changed between the first and the second attack (Sokal & Rohlf 1995).

To assess differences in refuge choice between treatments in the second experiment, we used a chi-square test. We further analyzed separately each treatment by using repeated measures two way ANOVAs to assess differences in time to enter the refuge, appearance and waiting times between lizards that entered always in the same refuge and those that hid in the unknown refuge in the second attack (between-subjects factor) and between the two attacks of each individual (within-subjects factors). We included the interaction in the model to analyze whether the responses changed from the first to the second attack as a function of the refuge used the first time being changed (Sokal & Rohlf 1995).

In both experiments the data were log-transformed to ensure normality. Tests of homogeneity of variances (Levene's test) showed that in all cases variances were not significantly heterogeneous after transformation (Sokal & Rohlf 1995). Pairwise comparisons were planned using Tukey's honestly significant difference (HSD) tests (Sokal & Rohlf 1995).

Results

Refuge use as a function of the refuge's scent

Time to enter the refuge since the beginning of the simulated attack did not differ significantly between the first and the second attack (Repeated measures two way ANOVA, $F_{1,28} = 0.19$, $p = 0.66$) or between treatments ($F_{2,56} = 1.05$, $p = 0.36$), and the interaction was not significant ($F_{2,56} = 0.25$, $p = 0.78$) (Fig. 1a).

Appearance from the refuge neither differed significantly between attacks (Repeated measures two way ANOVA, $F_{1,28} = 1.41$, $p = 0.24$), nor between treatments ($F_{2,56} = 1.41$, $p = 0.25$), but the interaction was significant ($F_{2,56} = 4.23$, $p = 0.02$) (Fig. 1b). In the first attack, lizards spent significantly more time until they appeared in the 'snake' than in the 'water' treatment (Tukey's test: $p < 0.009$), and tended to appear sooner in the 'snake' than in the 'cologne' treatment ($p = 0.057$), whereas appearance time did not differ significantly between the 'water' and 'cologne' treatments ($p = 0.98$). However, in the second attack there were no differences between treatments ($p > 0.97$ in all cases). This suggested that lizards might modify their refuge use as a function of the scent found in the refuge. In contrast, after appearing from the refuge, waiting time until resuming activity did not differ significantly between attacks (Repeated measures two way ANOVA: $F_{1,28} = 1.02$, $p = 0.32$), nor between treatments ($F_{2,56} = 0.45$, $p = 0.64$), and the interaction was not significant ($F_{2,56} = 1.37$, $p = 0.26$) (Fig. 1c).

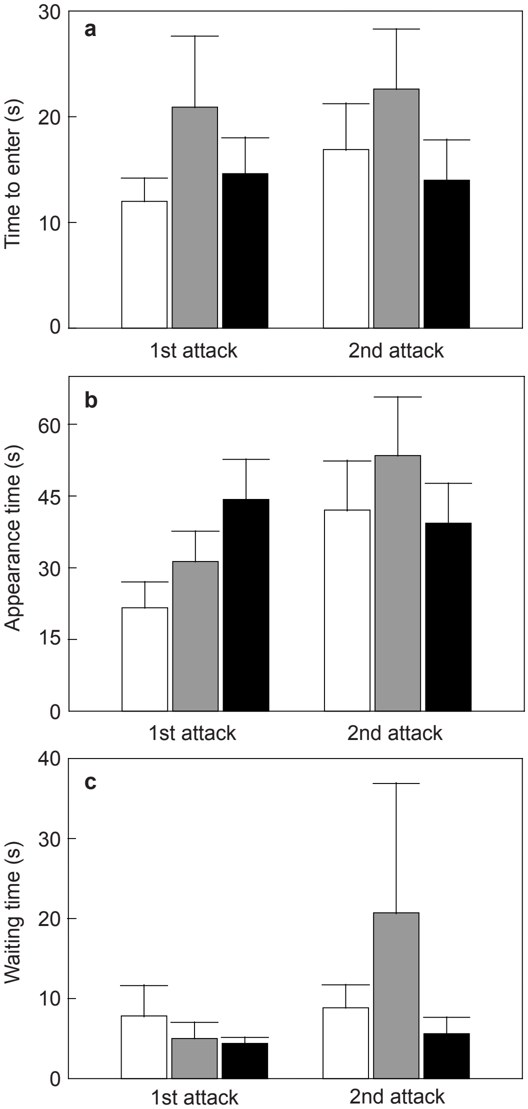

Fig. 1. Mean (+ SE) of (**a**) time to enter the refuge, (**b**) appearance time and (**c**) waiting time spent by wall lizards ($n = 29$) in refuges containing water (open bars), cologne (grey bars) or snake's scent (black bars) when suffered two simulated repeated attacks.

Successive refuge choices

In the second attack, refuge choice (known *vs.* unknown) did not differ significantly between treatments ($\chi^2 = 1.00$, df = 1, $p = 0.32$). Lizards did not show a significant preference for any of the two refuges in both treatments. Thus, when the refuge previously known (i.e., used in the first attack) had snake's scent, 10 from 18 lizards entered the unknown refuge in the second attack (Two-tailed binomial test: $p = 0.81$). When the known refuge was odorless, 7 from 18 lizards entered the unknown refuge in the second attack (Two-tailed binomial test: $p = 0.48$).

In the control treatment, there were marginal differences in time to enter the refuge between lizards that entered always the same refuge and those that hid in the unknown refuge in the second attack (Repeated measures two way ANOVA: $F_{1,16} = 3.43$, $p = 0.08$), the difference between attacks approached significance ($F_{1,16} = 3.93$, $p = 0.06$), and the interaction was not significant ($F_{1,16} = 1.59$, $p = 0.22$) (Fig. 2a). Although differences were not significant, after suffering a second attack, lizards tended to hide inside the refuge quicker than in the first attack, and tended to hide quicker if the refuge was the previously known one.

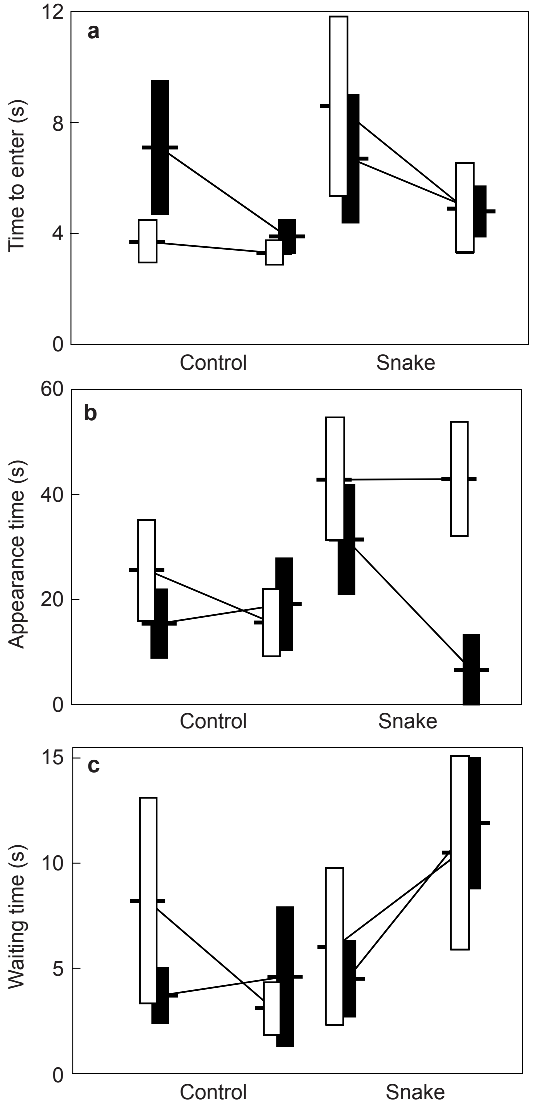

Fig. 2. Mean (+ SE) of (**a**) time to enter the refuge, (**b**) appearance time and (**c**) waiting time of wall lizards (*n* = 18) that entered always in the same refuge (open bars) and of those that hid in the unknown refuge (black bars) in the second attack, in treatments where the first refuge contained water (i.e. odorless) or snake's scent.

Also in the control treatment, the appearance time did not differ significantly as a function of refuge choice ($F_{1,16} = 0.01$, $p = 0.91$) or between attacks ($F_{1,16} = 0.14$, $p = 0.71$), and the interaction was not significant ($F_{1,16} = 0.75$, $p = 0.40$) (Fig. 2b). Similarly, waiting time did not differ significantly as a function of refuge choice ($F_{1,16} = 0.01$, $p = 0.99$) or between attacks ($F_{1,16} = 0.12$, $p = 0.74$), and the interaction was not significant ($F_{1,16} = 0.01$, $p = 0.92$) (Fig. 2c).

In the experimental treatment, time to enter the refuge did not differ significantly between lizards that entered always the same refuge and those that hid in the unknown refuge in the second attack (Repeated measures two way ANOVA: $F_{1,16} = 0.02$, $p = 0.88$), nor between attacks ($F_{1,16} = 0.34$, $p = 0.57$), and the interaction was not significant ($F_{1,16} = 0.01$, $p = 0.99$) (Fig. 2a). However, the appearance time differed significantly as a function of refuge choice ($F_{1,16} = 5.55$, $p = 0.03$), but not between attacks ($F_{1,16} = 1.69$, $p = 0.21$), and the interaction was significant ($F_{1,16} = 5.71$, $p = 0.03$) (Fig. 2b). Thus, lizards did not differ in appearance times in the first attack (Tukey's test: $p = 0.99$), but differed significantly in the second attack, with lizards that chose an unknown (i.e. odorless) refuge having shorter appearance times ($p = 0.02$) than lizards that used again the previously known refuge with snake's scent. In contrast, waiting time did not differ significantly as a function of refuge choice ($F_{1,16} = 0.45$, $p = 0.51$) or between attacks ($F_{1,16} = 0.01$, $p = 0.99$), and the interaction was not significant ($F_{1,16} = 1.95$, $p = 0.18$) (Fig. 2c).

Discussion

Our results show that time to enter a refuge by wall lizards was not influenced by the scent inside the refuge. Although it would be initially advantageous to assess the risk of encountering a snake inside a refuge before entering, this might not always be possible. In the conditions of our experiment, lizards had not been in the refuge before the attack, and thus had not previous information on its relative safety. Also, it could be virtually impossible, and very dangerous, for a lizard fleeing from a predator in the open to stop before hiding in order to explore the refuge by tongue-flicking. Moreover, even if lizards were able to discriminate the scent of a snake in a short time, the experimental refuge was the only one available in the terrarium. Thus, the lizards had no alternative ways to elude the attack but hiding in that refuge, even if it was considered not entirely safe. The need to elude the current attack of the predator in the open would probably be more important than the eventual risk of encountering a hidden ambush snake.

Nevertheless, the results of the second experiment, when lizards might have more experience with the experimental setup, also suggest that information on the refuge location and safety may be considered by lizards when escaping in successive events. Although differences only approached significance, lizards tended to hide quicker inside the refuge after suffering the second attack in the odorless treatment. Lizards also tended to hide quicker if the refuge was previously known. Other studies have shown that some lizards avoid using retreats that were soiled with snake's scent (Downes & Shine 1998, Stapley 2003). However, this capacity refers to when lizards chose to spend the night and not being forced to hide by a predator. Field observations of *P. muralis* suggest that they are able to gain information on the safety of some refuges and, after simulated attacks, avoid hiding in refuges that they have not previously explored with tongue-flicking before the attack (Amo *et al*. 2003).

Results of the first experiment suggested that the time spent in a refuge was related to the scent that was inside the refuge. This was probably a consequence of the ability of wall lizards to discriminate between snake's scent and other odors (Amo *et al*. 2004). This result is also supported by the lack of differences in times spent in odorless refuges and in those contained strong odors but without biological significance (i.e., cologne). However, in contrast to that expected, the time spent in the refuge was greater in the snake scent treatment. It might initially be predicted that lizards should decrease the time spent in refuges when these are potentially unsafe. However, this may not be the optimal strategy if the probability of being captured in the exterior is higher than the risk of the eventual presence of a snake in the refuge. Thus, an alternative strategy might be to gain more information on the scent of the snake (e.g., an old signal may suggest that the snake has been there a long time ago, and thus that the probability of its current presence is low). In doing this, lizards may need to increase their tongue-flicking rate and exploratory behavior, and may also try to get additional visual information on the actual presence of the snake, thus spending some extra time exploring the refuge. Also, when detecting the snake's scent lizards may reduce movements inside the refuge, or be more vigilant to avoid being located by the snake (e.g., Van Damme *et al*. 1995, Stapley 2004).

All of these changes of behavior may increase the time spent in the refuge until appearance, i.e. increase the costs of refuge use (Martín & López 1999a, 1999b). Thus, lizards might assume higher costs of refuge use to increase the acquisition of information on the probability of being preyed upon inside the refuge. This would be advantageous because if the predator in the open launched repeated new attacks, lizards would have to stay in the refuge for longer or hide several times in the same refuge, or decide whether to try alternative escape strategies such as running. Similarly, log skinks, *Pseudemoia entrecasteauxii*, decreased the use of snake-scented refuges as compared with that of predator-free refuges (Stapley 2004). However, when skinks were submitted not only to risk of predation by a snake inside the refuge but also by a bird in the open, skinks did not decrease the use of snake-scented refuges (Stapley 2004).

Subsequently, lizards may need to acquire information on the persistence of the searching predator in the exterior after they have partly appeared from the refuge (i.e. appearance time), and decide to resume their activities only if that predator is not detected outside (Martín & López 1999a). In a refuge with snake's scent, only when the lizard has ensured that the snake is not in the refuge, it may afford to stay there and look outside for the searching predator. This is supported because appearance time varied between treatments, but once lizards appeared, they resumed their activities in an interval of time that was independent of refuge's scent. Similarly, yellowhammers (*Emberiza citrinella*) that heard the alarm calls of conspecifics but could not locate visually a sparrowhawk predator model and, thus, had less complete information about the predation risk than those that actually saw the predator, exhibited alert perching more often immediately after the encounter than did birds that saw the sparrowhawk (Van der Veen 2002). Also, birds that saw the sparrowhawk resumed foraging earlier as compared with birds that only heard the alarm calls (Van der Veen 2002).

The same proportion of lizards entered the first (known) refuge as the alternative (unknown) one, regardless of whether the first refuge contained predator scent or not. This could be a consequence of the lack of time necessary to detect the scent inside the refuge before entering. Although the first refuge was considered unsafe, the closeness of both refuges may render the second one potentially unsafe too. Nevertheless, the time inside refuges also changed in the same direction as in the previous experiment. Lizards decreased appearance time when changed from a refuge that contained snake's scent to an odorless refuge. This indicates that, in each successive attack, lizards are adapting their refuge use to the current estimate of predation risk.

Our study suggests that predation pressure from searching predators in the open, such as birds or mammals, may force lizards to increase refuge use without being able to estimate potential risk of predation from sit-and-wait snakes before entering the refuge. Therefore, this may be a case of predator facilitation in which both types of predators will obtain benefits with their coexistence (Sih *et al.* 1998). This might result in a risk enhancement effect for the lizard prey. Similar cases have been observed in other animals. For example, when field voles were exposed to kestrels and weasels at the same time, voles continued using covered areas, thus subjecting themselves to be preyed upon by weasels while avoiding being captured by kestrels (Korpimäki *et al.* 1996). Similarly, mayflies came out of hiding under stones when stoneflies were present, thus exposing themselves to predatory fish (Soluk 1993). Furthermore, log skinks (*P. entrecasteauxii*) increased the use of snake-scented refuges when exposed to visual cues of a predatory bird (Stapley 2004). Nevertheless, our results indicate that refuge use behavior by wall lizards was sensitive to current predation risk levels both in the exterior and in the interior of the refuge. This flexibility in the antipredatory response may help wall lizards to avoid the risk enhancing effects of two types of predators requiring conflicting prey defenses.

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