Flexibility in antipredatory behavior allows wall lizards to cope with multiple types of predators

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Animals in natural environments usually face different types of predators, and conflicting prey defenses can increase risk of predation if prey responses to one predator result in a greater risk from another predator. Wall lizards (*Podarcis muralis*) respond to predators in the open, such as birds or mammals, by hiding inside rock crevices, where they may be exposed to predation by ambushing saurophagous smooth snakes (*Coronella austriaca*). This offers an excellent system to study how prey behave to avoid multiple predators acting simultaneously. We first performed a field study to examine the escape behavior and refuge use of wall lizards. Lizards mainly responded to the simulated attack by fleeing to hide in the nearest refuge. However, lizards that were far from known refuges sometimes used an alternative escape behavior; lizards fled for longer while passing potential refuges without hiding, thus, presumably avoiding hiding when their reliance in refuge safety was low. This was supported by a further analysis of movement patterns of wall lizards. Spontaneous locomotor patterns could be described as an amount of bursts of locomotion separated by short and long pauses. Lizards stopped near refuges more often, but previously they spent more time in short pauses when moving in or close to refuges exploring them by tongue flicking, than in open rocks. This agreed with a laboratory experiment where we analyzed responses of lizards to substrate scent deposits of smooth snakes. Lizards detected the snake's scent, and responded by increasing their movement rate in an effort to leave the risky area. However, in the field, after a simulated attack in the open, lizards emerged from the refuge and left the area quickly, decreasing the frequency of short pauses, probably to avoid a new attack in the open. Flexibility in antipredatory behavior may help wall lizards to avoid the risk enhancing effect of two types of predators requiring conflicting prey defenses.

Introduction

Predation is a major selective force in the evolution of several morphological and behavioral characteristics of animals (Lima & Dill 1990).

However, although almost all prey live in communities with many predator species, most experimental studies of predation have, until recently, examined only the effects of one predator species or have considered different predators

only at a time (Sih *et al.* 1998). Conflicting prey defenses against different types of predators can increase risk of predation if prey responses to one predator result in a greater risk from another predator (Soluk & Collins 1988, Losey & Denno 1998). These conflicting prey defenses can be due to variations in how predators forage. For example, widely foraging predators can force prey to increase its movement rate to escape, but this may increase risk of encountering a sit-and-wait predator (Sih *et al.* 1998). Flexibility in antipredatory behavior might, however, enable prey to respond adequately to both types of predators (Krupa & Sih 1998, Hopper 2001).

Prey often respond to some predators by increasing refuge use (Sih *et al.* 1992, Martín & López 1999a, 1999b). However, intensive use of refuges may have some costs that should be minimized, such as the loss of time available for other activities or physiological costs (Dill & Fraser 1997, Sih 1997, Martín & López 1999a, 1999b). Also, some types of refuges may be useful only against some particular type of predators, but may expose prey to other types of predators. For example, the mortality of a mayfly prey in the presence of both fish and stoneflies was greater than expected, because stoneflies under rocks caused mayflies to come out of hiding under rocks, thus resulting in greater exposure to fish (Soluk 1993). Similarly, lizards responded to predatory attacks of birds in the open by hiding inside rock crevices (Martín & López 1999b, Amo *et al.* 2003), where lizards may expose themselves to predation risk by saurophagous snakes (Rugiero *et al.* 1995, Galán 1998, Amo *et al.* 2004a, 2004b). In this context, lizards as prey, sit-and-wait snakes, and active foraging predators, such as birds or mammals, offer an excellent system to study the antipredatory adaptations of prey to avoid multiple predators acting simultaneously.

The first antipredatory mechanism used by lizards to avoid snake predators is the ability to detect chemical cues released by these (e.g., Van Damme *et al.* 1995, Downes & Shine 1998a, Amo *et al.* 2004a). Because snakes, especially those that are hiding in refuges, are not always visible to their prey, their chemical stimuli may provide important cues to ascertain their presence (Van Damme *et al.* 1995, Kats & Dill 1998). Especially the scent of a sedentary ambush predator provides a strong and reliable indication of danger (Downes & Shine 1998a, 1998b). Site familiarity provides an advantage in predator avoidance through specific knowledge of escape routes and refuges (Clarke *et al.* 1993, López *et al.* 2000). While walking through their home ranges, lizards may pause near potential refuges and use their chemosensory abilities to assess their safety. Thus, in case of a predatory attack in the open, lizards may avoid hiding in hazardous refuges potentially occupied by snakes, and employ alternative strategies such as fleeing without hiding in close refuges. Thus, although theoretical models suggest that the optimal approach distance (i.e., the distance between the approaching predator and the prey when it starts to flee) should increase with the distance to the nearest refuge (Ydenberg & Dill 1986), the extent of reliance on refuges when escaping and the degree of safety that the refuges provide may strongly affect this relationship (Martín & López 2000).

Another important cost of refuge use is the time spent at low temperatures (Martín & López 1999a, 1999b). Because available or safer refuges may be in microhabitats with shadier and colder conditions, such as rock crevices, the body temperature of a lizard that has retreated into a refuge will decrease below optimal levels after a short time. This is especially important for small lizards with a low thermal inertia because it could result in temperature impairment in only a few minutes. Since in ectothermic reptiles the maintenance of an optimal body temperature is essential to maximize numerous physiological processes (Huey 1982, Stevenson *et al.* 1985) and behaviors with important future fitness consequences such as spring speed (Avery *et al.* 1982), theoretical models of refuge use (Martín & López 1999b) predict that a lizard should emerge from the refuge when costs of refuge use (temperature impairment) exceed the costs of leaving (predation risk). However, after emerging from a cold refuge, a lizard should also consider that it may be more susceptible to predation due to lower sprint speed caused by suboptimal body temperatures. Thus, lizards might be able

to modify their behavior after leaving a cold refuge to avoid being preyed.

In this paper, we report the results of three experiments to examine whether the variation in antipredatory strategies of common wall lizards (*Podarcis muralis*) are aimed to avoid simultaneously being preyed by two types of predators requiring conflicting prey defenses. Firstly, we analyzed in the field the escape strategies of wall lizards after suffering a predatory attack in the open, examining whether wall lizards employed different escape responses, and the factors that determined which tactic was used. We also examined whether approach distance and emergence time from refuges depended on the type of escape response used. We hypothesized that lizards that were observed standing close to a refuge before being attacked should hide inside this presumably known refuge, whereas lizards that were walking far from a refuge may employ alternative escape strategies to avoid hiding in unknown refuges. Furthermore, we expected that lizards that hid in potentially unsafe unknown refuges should emerge sooner than lizards that hid in a nearest refuge previously known.

Second, we performed focal observations in the field to analyze the movement rate and movement patterns of wall lizards in a control undisturbed situation and after emerging from refuges where they had hidden in response to simulated predatory attacks in the open. We hypothesized that, during their normal displacements through their home ranges, lizards might pause near refuges to examine them by chemoreception. This would allow them to assess their safety respect to snakes' presence, and then decide whether to use these refuges for hiding in case of being attacked in the open. Furthermore, when resuming activity after being hidden in a refuge, we expected lizards to modify their locomotor patterns to minimize their vulnerability due to time spent at low temperatures inside refuges. Finally, we report the results of a laboratory study to investigate whether wall lizards were able to discriminate substrate scent deposits of smooth snakes. We expected that lizards perceived a high risk of predation when detecting chemical cues of snakes and that they respond by trying to escape from the risky area.

Material and methods

Study area and species

We performed the study in the Guadarrama Mountains, in a pine forest of Cercedilla (Madrid Prov., central Spain) at an elevation of 1500 m. The dominant vegetation at this altitude consists of *Pinus sylvestris* forest, with shrubs such as *Juniperus communis* and *Cytisus scoparius*. We conducted the experiment at an old granite rock wall (120 m long × 5 m high). Active lizards were found basking or walking on the wall and using the numerous crevices between rocks as refuges. The common wall lizard is a small lacertid lizard (60–76 mm adult snout-to-vent length) widespread in central Europe, although in the Iberian Peninsula it is restricted to mountain areas of the northern half, where they occupy soil dwellings, rocks and walls in shaded zones in forests (Martin-Vallejo *et al*. 1995). We chose this study area because smooth snakes (*C. austriaca*) are often found hidden inside rock crevices during the day in the microhabitats selected by wall lizards (Rugiero *et al*. 1995, Galán 1998). In addition, in the area we often observed active foraging predators known to eat this lizard (Martín & López 1990), such as jays (*Garrulus glandarius*), magpies (*Pica pica*), great gray shrikes (*Lanius excubitor*), buzzards (*Buteo buteo*), short-toed eagles (*Circaetus gallicus*), or kestrels (*Falco tinnunculus*), as well as abundant feral cats that frequently chased and killed these lizards in this and other populations (Boag 1973, Brown *et al*. 1995).

Escape strategies

We searched for lizards from April to June, between 1000 and 1600 hrs when lizards were fully active, by walking a track close to the study wall until an adult lizard (*n* = 135) was sighted with binoculars. Then, we approached the lizard by simulating a predatory attack by walking directly towards it at high speed (ca. 140 m/min) until the lizard fled. With this procedure we simulated a direct attack from a predator coming from the ground, such as a feral cat or a bird attacking

from low height bush perches placed in front of the wall. To avoid confounding effects that may affect risk perception of lizards (Burger & Gochfeld 1993, Cooper 1997), the same person wearing the same clothing performed all approaches in a similar way, and recorded the lizard's behavior. We noted the type of escape response used: 'hiding' in the nearest refuge after a short run *vs.* 'fleeing' for a longer while passing potential refuges without hiding or occasionally hiding after a long run (> 3 m) (Amo *et al.* 2003). We also measured the 'approach distance' (i.e., distance between the lizard and the observer when the lizard first moved), distance to the nearest available refuge, and the height on the wall at the lizard's initial location. If the lizard hid in a refuge, we started a stopwatch and retreated to a distance of 5–7 m to observe from a hidden position with binoculars. We measured the time that the lizard spent in the refuge until it emerged entirely from the refuge ('emergence time').

Escape behavior and emergence times of lizards may depend on their body temperature and thermal conditions inside the refuge (e.g., Hertz *et al.* 1982, Smith 1997, Martín & López 1999a, 1999b). The study design did not allow us to capture lizards immediately before they hid to measure their initial body temperature, but we still wanted to control for the effect of environmental temperature on escape responses and refuge use. Thus, immediately after a lizard emerged from the refuge, we measured the air temperature with a digital thermometer to the nearest 0.1 °C at the point the lizard occupied before the attack (shaded bulb, 2 cm above the point), and the substrate temperature inside the refuge. We assumed that these measures were a good approximation of lizards' body temperatures, given the strong dependence of these on the ambient thermal conditions (Braña 1991, Martín-Vallejo *et al.* 1995).

As the lizard density was high, and because we avoided sampling the same wall section twice, the probability of repeated measurements on the same individual was low. We therefore treated all measurements as independent. We used logistic regression to test for independence of the binomial variable "escape strategy" (hiding *vs.* fleeing) in relation to the distance to the nearest refuge, initial height on the wall, and

air temperature (Hosmer & Lemeshow 1989). Since results of a previous study indicated that sex of lizards did not influence their escape strategy (Amo *et al.* 2003), we did not consider this variable in this paper. Data analyses were performed using Windows-SPSS package (SPSS, Inc; Statistical Package for the Social Sciences 1993, McGraw-Hill). This analysis provides a likelihood ratio statistic as a goodness-of-fit estimator for the model, and maximum likelihood estimators and standard errors of the independent parameters. To assess the significance of the independent variables, we calculated the difference in deviance for a model with and without the variable of interest. The resulting difference in deviance between the two models followed a χ^2 distribution with one degree of freedom (Hosmer & Lemeshow 1989).

Relationships between approach distance or emergence times and temperatures and other environmental variables were estimated with Pearson's correlations. Because emergence times may depend on temperature (Martín & López 1999a, 1999b; *see* Results), we used analysis of covariance (ANCOVA) with air and refuge temperatures as covariates, to examine differences in emergence times between lizards with different escape responses (Sokal & Rohlf 1995). 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.

Spontaneous locomotion and effects of predatory attacks in the open on locomotor patterns

We performed this study in the same wall as above in May. We searched for adult lizards between 1000 and 1600 hrs, when lizards were fully active, by walking a track close to the wall until an adult lizard (*n* = 84) was sighted with binoculars. We then initiated focal observations under two conditions. In the 'control' treatment, we noted the spontaneous lizard activity during 10 min without disturbing it. In the 'predation risk' treatment, we approached lizards by simulating a predatory attack by walking directly towards it (*see* above), forcing it to hide entirely

in a refuge (rock crevices). We only considered lizards that hid in the nearest refuge. Then we retreated to a hidden position, and immediately after the lizard emerged from the refuge, we noted its behavior during the next 10 min. We observed the lizard's behavior with binoculars at a distance of 7–10 m to avoid disturbing it.

Lizards typically moved in a discontinuous way, alternating short periods of locomotor activity with 'short pauses' with duration shorter than 5 s (Avery *et al.* 1987a, 1987b, Braña 2003). Therefore, a movement sequence can be considered as several bursts of locomotion separated by short pauses. Lizards also performed 'long pauses' with duration of more than 5 s between movement sequences. Short pauses were typically associated with tongue-flick explorations of the substrate or visual scans (Avery *et al.* 1987a, 1987b), whereas long pauses were often associated with basking events. We noted the time spent in movement, and, for each type of pause, the number, duration and location. We distinguished two locations, in refuges (inside the refuge or within 5 cm of it) or in open rocks (more than 5 cm from a refuge).

We treated all measurements as independent (*see* above). Not all focal observations had the same duration, because we could not always follow the lizards during 10 min, as lizards were sometimes lost or unintentionally disturbed before the end. Therefore, we calculated all measurements in relation to the total duration of the trial. We calculated the percentage of time spent in movement as the duration of all movement sequences, including time spent in short pauses within them, divided by the total duration of the trial. We calculated the percentage of time spent in short pauses as the total duration of short pauses divided by the total duration of all movement sequences, and the percentage of time spent in long pauses as the duration of long pauses divided by the total duration of the trial. We also calculated the frequency of short pauses by dividing the number of short pauses by the total duration of movement sequences, and the frequency of long pauses by dividing the number of long pauses by the total duration of the trial. One-way analysis of variance (ANOVA) was used to assess differences in percentage of time in movement between treatments. We used repeated measures two-way ANOVA to assess differences in frequency and duration of short and long pauses between treatments (before *vs.* after the attack, between factor) and between locations (in refuges *vs.* in open rocks, within factor) (Sokal & Rohlf 1995). We included the interaction in the models to test whether responses to the different treatments (before *vs.* after the attack) changed between locations (in refuges *vs.* in open rocks) (Sokal and Rohlf 1995). Previous analyses showed that sex of lizards did not influence the movement patterns, neither in the interactions between sex and treatment, nor between sex and type of location. Thus, we did not consider sex in further analyses. Data were arcsin-transformed to ensure normality. Tests of homogeneity of variances (Levene's test) showed that in all cases variances were not significantly heterogeneous after transformation. Pairwise comparisons of means were planned using the Tukey's honestly significant difference (HSD) test.

Effects of substrate scent deposits of snakes on locomotor patterns of lizards

We captured 29 adult wall lizards (snout-vent length: mean ± SE = 66 ± 2 mm) near the study area (*see* above) in April. We also captured in a nearby wall two adult smooth snakes to be used as source of chemical scents of a potential predator. 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 mealworm larvae (*Tenebrio molitor*) every day and water was provided *ad libitum*. The photoperiod and ambient temperature were those of the surrounding region. Lizards were held in captivity at least one month before testing to allow acclimation to laboratory conditions and human presence. To prevent lizards from having contact with the scent stimuli before they were tested, snakes were housed separately in two outdoor glass terraria (60 × 30 × 20 cm) with rocks for cover, and with absorbent paper on the substrate in order to obtain their scent.

To examine the lizards' responses to snake chemical cues, two trials in a randomized block design were carried out with each individual

lizard. Each trial was conducted in a terrarium (75 × 50 × 50 cm), which was virtually divided into two halves. In the 'predator' treatment, on the floor of one half absorbent paper soiled with deionized water, and on the floor of the other half absorbent paper soiled with snake scent were placed. In the 'control' treatment on the floor of both halves absorbent paper soiled with deionized water was placed. We used this design to compare the behavior of lizards under simulated predation risk with that in an unfamiliar but predator-free situation. One trial per day was conducted for each animal. Lizards were allowed to bask in their terraria for at least two hours before trials. Trials were carried out in outdoor conditions in May between 1100–1700 hrs when lizards were fully active. After each trial the terraria were cleaned thoroughly with water for 20 min and dried at the outdoor temperature.

Experiments were recorded on the videotape (Hi-8 format, 25 frames s⁻¹) using a Sony CCD-V800E video-camera aligned perpendicularly over the terrarium. Lizards were filmed as they moved spontaneously along the terrarium during 15 min. To avoid disturbing the lizards, the experimenter was not present during filming. Later, we analyzed tapes and noted lizard behavior in the experimental half of the terrarium (i.e., the half that contained the snake-scented paper in the 'predator' treatment, or one of the odorless papers in the 'control' treatment). We noted the total time spent in the experimental area, the time spent moving, and time spent standing up (i.e., the lizard stands in an upright position against

Table 1. Results from logistic regression analysis of escape strategy (hiding *vs.* running without hiding) on several environmental variables in wall lizards, *Podarcis muralis.*

Source	*b*	SE	*p*
Distance to nearest refuge	0.04	0.01	0.001
Initial height	0.01	0.01	0.12
Air temperature	−0.05	0.13	0.67
Constant	−1.22	2.29	0.59

The maximum likelihood partial regression estimates (*b*), the standard errors (SE) of the estimates and the level of significance (*p*) of each independent variable are shown.

the wall of the terrarium and performs scratching movements with the forelegs). We also recorded the tongue-flick (TF) rates (number of TFs per minute). Since chemical cues could remain long after the predator has gone (Kats & Dill 1998), the response of lizards to the scent of the snake could change with time spent in an area. Thus, to determine possible changes in rate of response for each variable with time, we divided the 15 min period into three consecutive periods of 5 min each.

We used two-way repeated measures analysis of variance (ANOVA) to test for differences between treatments (control *vs.* experimental) and between the three time sequences for each individual (both within-subjects factors). Data of total time spent in the experimental half of the terrarium were log-transformed to ensure normality. We used the duration of movement and duration of standing-up acts in relation to the total time spent in the respective area. The TF rate was calculated as the number of tongue extrusions in relation to the total time spent in the respective area. The TF rate of lizards increases while they are moving (Van Damme & Castilla 1996), as TF is associated with short pauses within bursts of locomotion (Avery *et al.* 1987a, 1987b). We controlled this effect by using the time spent moving as a covariate in a repeated measures two way analysis of covariance (ANCOVA) examining differences in TF rates between treatments and between sequences. Angular transformations of all percentages were made to ensure normality. Tests of homogeneity of variances (Levene's test) showed that in all cases variances were not significantly heterogeneous after transformation. Pairwise comparisons of means were planned using Tukey's HSD tests (Sokal & Rohlf 1995).

Results

Escape strategies

The logistic regression of escape strategy (hiding *vs.* fleeing) showed that the distance to the nearest refuge significantly affected this strategy (χ^2 = 20.44, df = 3, *p* = 0.0001) (Table 1). In 81.3% of the cases, the lizards that hid in the nearest

refuge were initially closer to the refuge than the lizards that fled without hiding. Neither height on the wall nor air temperature significantly influenced the escape strategy.

Approach distances of the lizards were not significantly correlated with air temperature (r = 0.01, $F_{1,133}$ = 0.03, p = 0.87) or with the initial height at which they were on the wall (r = 0.02, $F_{1,131}$ = 0.07, p = 0.79). The correlation between the approach distance of the lizards and their distance to the nearest refuge only approached significance (r = 0.16, $F_{1,120}$ = 3.22, p = 0.07). However, when we analyzed separately the two types of escape responses, we found that when lizards actually hid in the nearest refuge, the approach distance was weakly but significantly correlated with distance to that refuge (r = 0.21, $F_{1,94}$ = 4.24, p = 0.04), whereas there was no significant relationship between the approach distance and the distance to the nearest refuge when the lizards hid, after a long run, in a refuge that was not the nearest one (r = 0.01, $F_{1,24}$ = 0.003, p = 0.96). Approach distances did not differ significantly between the two escape strategies, even after removing the potential effect of differences in the distance to the nearest refuges (hiding: 90 ± 10 cm, fleeing: 125 ± 19 cm, ANCOVA: $F_{1,119}$ = 0.01, p = 0.94).

In general, lizards emerged from the refuge later when air temperature in the exterior and refuge temperature were higher (r = 0.51, $F_{1,25}$ = 8.70, p = 0.007, and r = 0.46, $F_{1,33}$ = 8.77, p = 0.006, respectively). When the effects of covariation with the air and refuge temperatures were removed, there were no significant differences in the emergence time between the lizards with different escape responses (nearest refuge: 68 ± 10 s, other refuge after fleeing: 62 ± 31 s, ANCOVA: $F_{1,22}$ = 0.77, p = 0.39).

Spontaneous locomotion and effects of predatory attacks in the open on locomotor patterns of lizards

The lizards did not modify significantly the percentage of time spent in movement when emerging from refuges after a predatory attack (control: 14% ± 3%, after attack: 14% ± 2%;

one-way ANOVA: $F_{1,82}$ = 0.01, p = 0.96). The percentage of time spent in long pauses did not differ significantly between treatments (repeated measures two-way ANOVA: $F_{1,82}$ = 0.01, p = 0.97), but the lizards spent significantly more time in long pauses in or close to refuges than in open rocks ($F_{1,82}$ = 30.44, p < 0.0001). The interaction was not significant ($F_{1,82}$ = 0.15, p = 0.69) (Table 2). Similarly, the frequency of long pauses did not differ significantly between treatments ($F_{1,82}$ = 0.70, p = 0.40), but the lizards paused significantly more often in or close to refuges than far from them ($F_{1,82}$ = 18.52, p < 0.0001). The interaction was not significant ($F_{1,82}$ = 0.01, p = 0.99) (Table 2).

The percentage of time spent in short pauses did not differ between treatments ($F_{1,82}$ = 2.06, p = 0.15), but the lizards spent a significantly higher percentage of time in short pauses performed within bursts of locomotion while moving in or close to refuges than when moving through open rocks ($F_{1,82}$ = 18.55, p < 0.0001). The interaction was not significant ($F_{1,82}$ = 0.01, p = 0.99) (Table 2). However, the lizards significantly decreased the frequency of short pauses after a predatory attack ($F_{1,82}$ = 4.91, p = 0.03), and paused more often in refuges than far from them ($F_{1,82}$ = 16.83, p = 0.0001). The interaction was not significant ($F_{1,82}$ = 0.01, p = 0.95) (Table 2).

Table 2. Mean ± SE of variables describing pausing behavior between movement sequences (long pauses) and within movement sequences (short pauses) of wall lizards, *Podarcis muralis*, in each of the two microhabitats (open rocks or refuges), in a control situation (i.e., without disturbing them) and after emerging from refuges where they had hidden in response to simulated predatory attacks in the open.

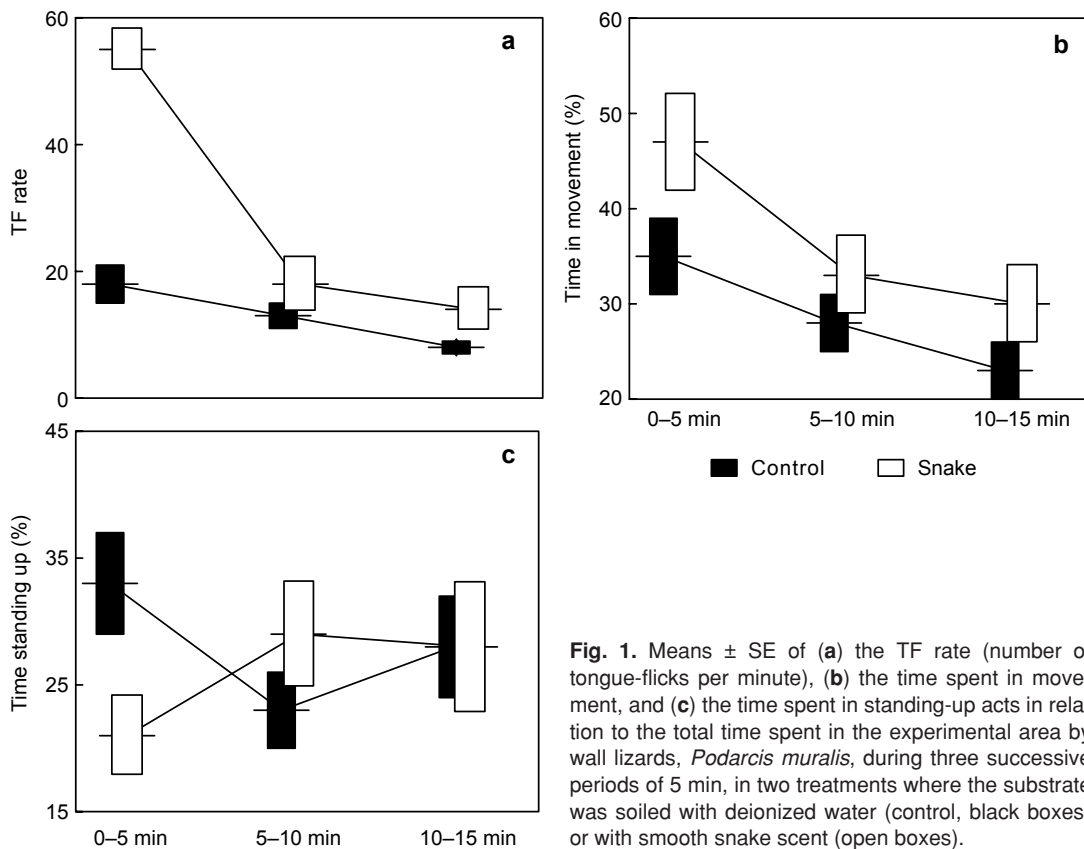|	Control undisturbed (n = 44)		After an attack (n = 40)	
	Open rocks	Refuges	Open rocks	Refuges
Long pauses				
Time (%)	21±3	52±4	22±4	50±5
Frequency	0.8±0.1	1.4±0.1	0.8±0.1	1.0±0.1
Short pauses				
Time (%)	15±2	30±2	17±3	32±4
Frequency	7.0±0.7	11.0±1.0	6.0±0.7	9.0±1.0

Fig. 1. Means ± SE of (**a**) the TF rate (number of tongue-flicks per minute), (**b**) the time spent in movement, and (**c**) the time spent in standing-up acts in relation to the total time spent in the experimental area by wall lizards, *Podarcis muralis*, during three successive periods of 5 min, in two treatments where the substrate was soiled with deionized water (control, black boxes) or with smooth snake scent (open boxes).

Effects of substrate scent deposits of snakes on locomotor patterns of lizards

When the experimental area was soiled with snake scent, the TF rate of the lizards was significantly greater than when the area was odorless, after controlling for time spent moving (repeated measures two way ANCOVA: $F_{1,28} = 6.18$, $p = 0.02$), and differed significantly among sequences (S), i.e., periods of time ($F_{2,56} = 11.31$, $p = 0.0001$). The interaction was not significant ($F_{2,56} = 1.23$, $p = 0.30$) (Fig. 1a). Thus, the lizards decreased their TF rate after the first five minutes (Tukey's test, S1-S2: $p = 0.008$, S1-S3: $p = 0.0002$, S2-S3: $p = 0.31$).

The total time that the lizards spent in the experimental area differed neither between treatments (repeated measures two way ANOVA: $F_{1,28} = 2.13$, $p = 0.16$) nor among sequences ($F_{2,56} = 0.87$, $p = 0.42$), and the interaction was not sig-nificant ($F_{2,56} = 0.87$, $p = 0.42$). However, when the experimental area was soiled with snake scent, the lizards spent significantly more time in movement ($F_{1,28} = 7.84$, $p < 0.01$). The lizards decreased their movement rate after the first five minutes ($F_{2,56} = 14.65$, $p < 0.0001$) (Tukey's test, S1-S2: $p = 0.001$, S1-S3: $p = 0.0001$, S2-S3, $p = 0.37$). The interaction was not significant ($F_{2,56} = 2.21$, $p = 0.12$) (Fig. 1b).

Duration of standing-up acts differed neither between treatments (repeated measures two way ANOVA: $F_{1,28} = 0.28$, $p = 0.60$) nor among sequences ($F_{2,56} = 0.51$, $p = 0.60$) (Fig. 1c). However, the interaction was significant ($F_{2,56} = 3.73$, $p = 0.03$). The lizards tended to stand up longer in the control than in the predator treatment during the first 5 min (Tukey's test, $p = 0.10$), but there were no significant differences between treatments in the other sequences ($p > 0.84$ in all cases).

Discussion

Escape strategies

Wall lizards mainly responded to the simulated predatory attacks in the open by running to hide in the nearest rock crevice, but they sometimes used alternative escape responses. They seemed to avoid hiding in refuges when they were far from them, even if they subsequently passed by close to them while fleeing. Lizards might avoid entering presumably unknown refuges because they may find there the other type of predator (i.e., a saurophagous snake). Similar differences in the choice of escape response depending on the degree of knowledge and reliance on refuges have been observed in other animals (Clarke *et al*. 1993, López *et al*. 2000, Martín & López 2000). Alternatively, different escape responses might be related to lizards having different body temperatures (e.g., Hertz *et al*. 1982, Smith 1997). However, our results indicated a lack of effect of ambient temperatures — and thus presumably also the body temperatures — on escape responses. Also, lizards might avoid entering unknown refuges to avoid aggression from a conspecific that could be retreated there (Boag 1973, Edsman 1986, Downes & Shine 1988b).

In general, approach distances were not dependent on distances to available refuges. This result is contrary to that of Ydenberg and Dill (1986) regarding an optimization of escape decisions. Since the risk of capture is higher for prey that are farther from a refuge, the approach distance should have increased with the distance to the refuge (Dill & Houtman 1989, Bonenfant & Kramer 1996). However, those lizards that hid in presumably known close refuges did begin to escape earlier even when they were farther from that refuge. This means that these lizards had information about the safety and location of that refuge, and that they adjusted their escape decisions considering the time needed to reach it. In contrast, approach distances of lizards that escaped without intending to use the nearest refuge should not be correlated with distances to that particular nearest but unused refuge.

There were no differences in approach distances between lizards that hid and those that fled. This apparently contradictory result may be explained if lizards escape decisions were not only based on the risk of being captured while fleeing. Thus, when lizards use a close refuge, they may escape sooner to decrease the probability of the predator remembering the exact location of the refuge and capturing them after they have resumed activity (Martín & López 2000). Therefore, although for different reasons, the point where the costs of fleeing exceed the costs of remaining may be similar for both, lizards fleeing and lizards using close refuges.

The results indicated that thermal costs of refuge use affected emergence times from the refuge in wall lizards, which agrees with theoretical models of refuge use (Martín & López 1999a) and with previous results (Martín & López 1999b, Amo *et al*. 2003). On the other hand, predation risk inside the refuge might also have influenced emergence times (Amo *et al*. 2004a, 2004b). Our results, however, did not show differences in emergence times between lizards that hid in the nearest refuge and lizards that fled to another refuge. This could be explained if lizards only hid in known safe refuges. Thus, lizards that hid after a long flee also might have ran to hide in a known, although far, refuge.

Spontaneous locomotion and effects of predatory attacks in the open on locomotor patterns

In a low risk situation, spontaneous locomotory patterns of lizards can be described as an amount of bursts of locomotion separated by short and long pauses. Lizards stopped near refuges more often, and spent more time in short pauses in refuges, exploring them by tongue flicking, than in open rocks. Many lizard species move in such a characteristically discontinuous way (Avery *et al*. 1987a, 1987b, Avery & Bond 1989, Martín & Avery 1998, Braña 2003). Pausing provides some benefits such as an increase of probability of prey capture (Avery 1993), or an increase of endurance (Weinstein & Full 1999), but also a reduction of predation risk. On one hand, pausing seems to decrease the attack rate of some

predators, such as birds, that are more likely to attack moving prey, which may be more easily detected or recognized (Martel & Dill 1995). On the other hand, pausing improves detection of predators by the prey (Martín & Avery 1998, McAdam & Kramer 1998, Scannell *et al.* 2001). While moving, lizards stopped near each rock crevice that they found and explored it by tongue flicking, probably to avoid entering refuges containing smooth snakes, or even aggressive conspecifics (Boag 1973, Edsman 1986, Downes & Shine 1988b). Although less often, lizards also stopped in open rocks far from refuges, which may improve their visual detection of predators such as birds. Lizards also spent more time in long pauses, often basking, close to refuges that they previously had explored. Thus, lizards could respond to the attack of a predator by quickly hiding inside this previously known snake-free refuge.

Focal observations suggest that wall lizards modified slightly their patterns of locomotion when resuming activity after an unsuccessful predatory attack. Although lizards did not modify the percentage of time in movement or the duration of pauses, they decreased the frequency of short pauses, which may decrease the time of exposure to visually guided predators when moving in the open. This suggests that lizards perceived an increase in risk due to the recent presence of a predator (Martín & López 2001), and/or a decrease in their sprint speed after emerging from cold refuges with low body temperatures (Bennett 1980). However, contrary to expectations, lizards did not increase the time spent motionless in basking (i.e., in long pauses) to regain an optimal body temperature after being hidden in a cold refuge, but left the refuge area quickly. This may be an antipredatory strategy to avoid a persistent predator that could attempt a new attack in the same area where a potential prey has already been located.

Effects of substrate scent deposits of snakes on locomotor patterns of lizards

The results of the laboratory experiment showed that lizards detected the chemical cues of smooth snakes and changed their locomotor patterns

accordingly. A greater number of tongue flicks were observed when lizards were in the area soiled with snake scent. This result agrees with the ability of wall lizards to detect and discriminate the chemical cues of smooth snakes presented on cotton swabs (Amo *et al.* 2004a, 2004c). Lizards did not reduce the use of the risky area, probably because once they detected the snake scent the entire terrarium was considered equally risky, and because they could not escape from the terrarium. However, lizards spent more time moving while they were in the area soiled with snake scent. Remaining in the vicinity of snake scent may increase the risk of being preyed upon, because the probability that a predator still continues to be in that area increases (Gurney *et al.* 1999), especially in the case of ambush predators (Kats & Dill 1998). Thus, lizards may increase their movement rate to escape from the risky area, trying to reach a safe refuge.

Tongue flick rate is greater when lizards are moving because it is associated with short pauses within bursts of locomotion (Cooper *et al.* 1994, Van Damme & Castilla 1996). Thus, an alternative, but not excluding, explanation could be that lizards increase their movement in the area soiled with snake scent to improve their possibilities to recognize the source of chemical cues. However, after the effect of movement on tongue flick rate was evaluated statistically, the results still suggested that lizards responded to the snake scent by increasing the number of tongue extrusions. Thus, lizards could investigate the risky area better to obtain information about the predator activity (Kats & Dill 1998). However, since chemical cues of predators could remain after the predator has gone (Kats & Dill 1998), response of lizards to these cues might change with time. The decrease in TF and movement rates with time could indicate that lizards were able to assess the decrease in the probability that a snake was actually presented in the area. Furthermore, since lizards could easily oversee the entire terrarium, they might soon have realized that the snake was not there.

In contrast to our results, previous studies have shown that other rock-dwelling lizards decrease their activity in the presence of chemical cues from a predator snake (Van Damme &

Castilla 1996). These differences could be attributed to the snake species tested. We used chemicals from a specialized saurophagous ambush snake (*C. austriaca*), whereas other studies used chemicals from a not so saurophagous specialized viper (*Vipera latastei*). Prey should respond differently to chemical signals of predators that pose different risk (Stapley 2003, Amo *et al.* 2004c). The optimal antipredatory strategy of lizards that find chemical signals of a saurophagous snake should be to leave the area quickly. This was confirmed by our results and has also been observed in the velvet gecko (*Oedura lesueurii*), which avoid entering crevices containing scents of ambush snakes (Downes & Shine 1998a). However, when the predator is not so risky an avoidance response may be an overestimation of risk, and therefore, the optimal antipredatory strategy might be to reduce movements trying to locate the viper visually.

We conclude that wall lizards were able to detect the chemical cues of a smooth snake on the substrate, and to respond to the presence of such cues by increasing their movement rate in an effort to leave the risky area. This ability would be very important for lizards to ascertain the presence of snakes inside refuges. Thus, during spontaneous movements, lizards stopped more often in or close to rock crevices and explored them by tongue flicking. When lizards were attacked in the open by a simulated predator, they mainly responded by hiding inside the nearest refuge but, sometimes they employed an alternative escape strategy, fleeing without hiding. This could be reflecting the lack of knowledge on the safety of the nearest refuge. After emerging from the refuge, lizards left the area quickly, decreasing the frequency of short pauses, probably to avoid a new attack if the predator remained in the area and launched a new attack. This flexibility in antipredatory behavior of wall lizards may help them to avoid the risk enhancing effect of two types of predators requiring conflicting prey defenses.

Acknowledgements

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