Wall lizards combine chemical and visual cues of ambush snake predators to avoid overestimating risk inside refuges

LUISA AMO, PILAR LÓPEZ & JOSÉ MARTÍN

Departamento de Ecología Evolutiva, Museo Nacional de Ciencias Naturales, Madrid

The threat sensitivity hypothesis assumes that multiple cues from a predator should contribute in an additive way to determine the degree of risk-sensitive behaviour. The ability to use multiple cues in assessing the current level of predation risk should be especially important to prey exposed to multiple predators. Wall lizards, *Podarcis muralis*, respond to predatory attacks from birds or mammals by hiding inside rock crevices, where they may encounter another predator, the smooth snake, *Coronella austriaca*. We investigated in the laboratory whether chemical cues may be important to wall lizards for detection of snakes. The greater tongue-flick rate and shorter latency to first tongue-flick in response to predator scents indicated that lizards were able to detect the snakes' chemical cues. We also investigated the use of different predatory cues by lizards when detecting the presence of snakes within refuges. We simulated successive predator attacks and compared the propensity of lizards to enter the refuge and time spent within it for predator-free refuges, refuges containing either only visual or chemical cues of a snake, or a combination of these. The antipredatory response of lizards was greater when they were exposed to both visual and chemical cues than when only one cue was presented, supporting the threat sensitivity hypothesis. This ability may improve the accuracy of assessments of the current level of predation risk inside the refuge. It could be especially important in allowing lizards to cope with threats posed by two types of predators requiring conflicting prey defences.

© 2004 The Association for the Study of Animal Behaviour. Published by Elsevier Ltd. All rights reserved.

The ability to detect the presence of predators is an important component of antipredatory behaviour (Van Damme et al. 1995). Prey should use multiple cues of predators to assess accurately the level of predation risk (McCarthy & Fisher 2000). The importance of chemical cues for predator recognition has being documented for a number of taxa (review in Kats & Dill 1998). Chemosensory cues may reliably reveal the presence of predators (Kats & Dill 1998), even in the absence of other cues (Chivers & Smith 1998; Kats & Dill 1998; Chivers et al. 2001). However, visual cues, such as predator size and activity, may provide information more temporally specific to a predator's current motivation and threat (Smith & Belk 2001).

Only a few studies have compared the relative importance of the two types of stimuli. These suggest that prey can combine information from both chemical and visual cues to make a better assessment of the level of risk under conflicting situations (Vanderstighelen 1987; Hartman & Abrahams 2000; Mathis & Vincent 2000; Chivers et al.

2001). The threat sensitivity hypothesis proposes that animals should accurately assess the risk of predation, and respond in a graded manner in accordance with the threat posed by the predator (Helfman 1989). Animals that give antipredator responses to inappropriate stimuli expend time and energy that could be used in other activities, but animals that fail to respond to a dangerous stimulus have a lower probability of survival. Thus, the threat sensitivity hypothesis assumes that multiple predator cues should contribute in an additive way to determine the degree of risk-sensitive behaviour (Helfman 1989; Smith & Belk 2001). For example, detection of chemical cues of an ambush predator may cause prey to increase vigilance to detect the predator itself. Studies have provided support for the threat sensitivity hypothesis (Mathis & Vincent 2000; Chivers et al. 2001). For example, the western mosquitofish, *Gambusia affinis*, responded more when confronted with visual and chemical cues of predatory fish, *Lepomis cyanellus*, than when only one cue was presented (Smith & Belk 2001).

Prey often respond to predator presence by increasing refuge use (Sih et al. 1992; Dill & Fraser 1997). However, some types of refuges may expose prey to other types of predators (Sih et al. 1998). Thus, conflicting prey defences

Correspondence: J. Martín. Departamento de Ecología Evolutiva, Museo Nacional de Ciencias Naturales, C.S.I.C. José Gutiérrez Abascal 2, 28006 Madrid, Spain (email: jose.martin@mncn.csic.es).

can cause higher predation rates than expected. For example, the mortality of a mayfly, *Ephemerella subvaria*, prey in the presence of both fish, *Cottus bairdi*, and stoneflies, *Agnetina capitata*, was greater than expected, because stoneflies under rocks caused mayflies to come out of hiding from under rocks, thus resulting in greater exposure to fish (Soluk 1993). However, flexibility in antipredator responses may help prey to avoid the risk-enhancement effects. For example, when exposed to predators that occupy different microhabitats, male water striders, *Aquarius remigis*, reduced predation risk by decreasing not only general activity but also mating activities that attracted the attention of predators (Krupa & Sih 1998).

Theoretical models of refuge use suggest that prey should adjust the time spent in a refuge according to predation risk and cost of staying in the refuge. The optimal emergence time is the time when the costs of staying (i.e. costs of refuge use) exceed the costs of leaving (i.e. predation risk in the exterior; Sih et al. 1992; Martín & López 1999a). When a refuge contains chemical cues from an ambush predator it is likely that the predator is there or close by and, if the prey remains in the refuge, the probability that that predator detects the prey increases over time. Hence, prey hidden in an unsafe refuge should emerge sooner than from a predator-free refuge. However, this response may expose prey to another type of predator. This example may be a case of predator facilitation caused by conflicting prey defences to avoid the different types of predators acting simultaneously (Sih et al. 1998). Furthermore, although there are significant advantages for prey able to detect predators via chemical cues, particularly when other cues are unavailable, chemical assessment might lead to excessively conservative estimates of risk, because chemical cues may persist long after the predator has departed, giving an inflated indication of current risk (Kats & Dill 1998). Thus, prey could overestimate the risk of predation inside a refuge, exposing itself to the risk of predation in the exterior. Minimizing the negative effects of the trade-off between emerging too soon and remaining inside the refuge would require prey to discriminate between different predator cues inside the refuge (indicating different levels of predation risk) and to adjust their behaviour accordingly. For individuals that can match their predator avoidance responses to the level of threat, the long-term payoffs should be greater than for individuals that are less flexible (Mathis & Vincent 2000).

Wall lizards, *Podarcis muralis*, responded to predatory attacks from birds or mammals when out in the open by hiding inside rock crevices (Martín & López 1999b). However, smooth snakes, *Coronella austriaca*, also use these crevices to ambush their lizard prey (Rugiero et al. 1995; Galán 1998; L. Amo, P. López & J. Martín, unpublished data). Thus, *P. muralis* offers an excellent model for the study of prey adaptations to minimize risk in a multiple predator environment. The first antipredatory mechanism of many lizards to avoid snakes is the ability to detect their chemical trails (Cooper 1990; Van Damme et al. 1995; Downes & Shine 1998; Van Damme & Quick 2001). The detection of the scent of a sedentary 'ambush' predator may initially provide a strong indication of probable current danger (Kats & Dill 1998). However, chemical cues may persist after the predator has left the area, so an avoidance response to such cues may be an overestimation of the risk of predation inside the refuge. If lizards emerge quickly from a refuge containing only chemical cues, they could be exposed to the predator that hunts in the open. Therefore, according to the threat sensitivity hypothesis, wall lizards should use other cues in addition to chemical cues to assess accurately the risk of predation inside the refuge. By doing this, lizards might minimize the facilitation effects caused by both types of predators acting simultaneously.

In this study, we aimed to analyse the antipredatory strategies of lizards when simultaneously confronting two types of predators with different foraging strategies. We tested in the laboratory the ability of lizards to detect the chemical cues of smooth snakes. We then simulated a system with two predators, one that searches actively for prey in the open (simulated by the experimenter) and an ambush predator that waits for prey inside refuges (the smooth snake). We compared the propensity of wall lizards to enter the refuge, time spent in it, and variation in repeated attacks between predator-free refuges and refuges containing visual cues of a snake, chemical cues or both. We hypothesized that wall lizards should be able to discriminate the chemical cues of a snake and use them to assess the presence of a snake inside a refuge. However, an estimate of risk based only on chemical cues may be excessively conservative, so lizards might also need visual cues to assess risk level accurately, especially when emerging from the refuge is costly in terms of predation. According to the threat sensitivity hypothesis, we hypothesized that lizards should respond more accurately when they found more than a single cue inside the refuge.

METHODS

Study Animals and Maintenance

During March and April 2000, we captured by noosing 34 *P. muralis* ($\overline{X} \pm$ SE snout–vent length $= 66 \pm 2$ mm) at a rock wall (120 m long $\times$ 5 m high) near Cercedilla, Madrid Province, Spain. This lizard is a small lacertid lizard widespread in Central Europe. It is common in mountains of the northern half of the Iberian Peninsula, where it occupies soil dwellings, talus and walls in shaded zones in forests (Martin-Vallejo et al. 1995). The smooth snake is a specialist predator that feeds mainly on these lizards (Galán 1998). Its geographical distribution and habitat preferences overlap frequently with those of *P. muralis*. Smooth snakes seemed to be especially abundant on the wall at our study site. For example, during a parallel field study, we captured and marked six snakes that were often seen during the day ambushing inside crevices or occasionally basking outside very close to the crevices (L. Amo, P. López & J. Martín, unpublished data). We captured, on the same wall, two smooth snakes to be used as potential predators, and two adult male Iberian rock lizards, *Lacerta monticola*, to be used as sources of control scent stimuli. The Iberian rock lizard is insectivorous and

thus innocuous to wall lizards, but is often found in the same microhabitats.

All lizards were individually housed at 'El Ventorrillo' Field Station 5 km from the capture site in outdoor PVC terraria (60 × 40 cm and 50 cm high) containing sand substratum and rocks for cover. Every day, they were fed mealworm larvae, *Tenebrio molitor*, dusted with multivitamin powder for reptiles, and water was provided ad libitum. The photoperiod and ambient temperature were those of the surrounding region. Lizards were held in captivity at least 1 month before testing to allow acclimation to laboratory conditions.

To avoid contact with the scent and visual stimuli by lizards before they were tested, the Iberian rock lizards and the smooth snakes were housed separately. The smooth snakes were individually housed in glass terraria (60 × 30 cm and 20 cm high) with strips of absorbent paper fixed on the substrate to absorb snake scent. Species-appropriate food and water were provided ad libitum. To avoid using live lizards as food, we fed the snakes domestic crickets and small bits of minced lamb bearing the scent of live lizards (faeces and the secretion from femoral pores and skin of wall lizards). This feeding method did not affect the lizards, but their scent attracted the attention of the snakes to the meat. Because lamb is an artificial food, we also used multivitamin powder. We kept the snakes approximately 1 month in captivity. All animals were healthy during the trials. We did not observe behavioural or physiological changes from possible stress of experiments, and all maintained or increased their original body mass ($\overline{X} \pm$ SE mass increment $= 0.7 \pm 0.1$ g). All animals were returned to their exact capture sites at the end of the experiments. The experiments were performed under licence from the Madrid Environmental Agency (Consejería del Medio Ambiente de la Comunidad de Madrid).

Experiment 1: Detection of Chemical Cues from Snakes

We compared tongue-flick rates by lizards in response to stimuli arising from cotton applicators impregnated with scents of (1) smooth snake (predator), (2) Iberian rock lizard (reptile scent control), (3) cologne (pungency control) or (4) deionized water (odourless control) to test for differential responses to scents (Cooper & Burghardt 1990). Water was used to gauge baseline tongue-flick rates in the experimental situation. We prepared stimuli by dipping the cotton tip (1 cm) of a wooden applicator attached to a long stick (150 cm) in deionized water. Other stimuli were added by rolling the moistened cotton over the body surface of the snake or the Iberian rock lizard, or by dipping it in diluted cologne. A new swab was used in each trial. Every lizard was exposed to each stimulus in counterbalanced order. One trial was conducted per day for each animal ($N = 34$). Trials were conducted in outdoor conditions during May between 1100 and 1700 hours when lizards were fully active.

To begin a trial, the experimenter slowly approached the terrarium and slowly moved the cotton swab to a position 1 cm in front of the lizard's snout. The number

of tongue-flicks directed and not directed to the swab was recorded for 60 s, beginning with the first tongue-flick. Latency to the first tongue-flick was defined as the time from presentation of the cotton swab to the first tongue-flick directed at the swab. We also recorded the time that lizards remained close (within 1 cm) to the cotton swab. An increase in time spent fleeing from the cotton swab (i.e. running rapidly from the stimulus to the opposite side of the terrarium) indicated that lizards tried to escape from that stimulus.

To examine differences in number of tongue-flicks and latency to first tongue-flick between conditions, we used repeated measures one-way analyses of variance (ANOVAs) with scent stimuli as the within-subject factor. Because lizards often moved away from the stimulus, the swab had to be continuously repositioned in front of the lizard. Thus, to analyse the number of tongue-flicks directed to the swab in relation to the actual time that lizards remained exposed to the stimulus, we used repeated measures one-way analysis of covariance (ANCOVA), with the number of repositionings of the swab as a covariate to avoid possible effects of this variable. Data were log-transformed to ensure normality (Shapiro–Wilk test). Tests of homogeneity of variances (Hartley's F_{max} test) showed that in all cases, variances were not significantly heterogeneous after transformation. Pairwise comparisons were planned using Tukey's honestly significant difference (HSD) tests (Sokal & Rohlf 1995).

Experiment 2: Relative Importance of Visual and Chemical Cues

In this experiment, we compared wall lizards' use of clean refuges with those that contained chemical or visual cues of a smooth snake. We compared the propensity of the lizard to enter a refuge, time spent in it and variation in successive attacks. Each individual ($N = 20$) was tested in each of four trials in a counterbalanced sequence: (1) control treatment (odourless and empty refuge); (2) chemical treatment (refuge containing snake scent); (3) visual treatment (odourless refuge that allowed lizards to see but not to detect chemical cues from a smooth snake within the refuge); and (4) visual and chemical (combined) treatment (refuge that allowed lizards to see and detect chemical cues from a smooth snake; see below). The experiment was conducted in a terrarium (100 × 40 cm and 50 cm high) with a sand substrate and a single refuge in the middle of one end of the terrarium. The refuge was built with flat rocks, and had two openings (7 × 6 cm) that allowed entry. One entry was open, and the other was closed with the glass walls of a smaller adjacent terrarium (50 × 40 × 40 cm) that was used to house the smooth snake. This smaller terrarium was sealed to prevent lizards from detecting chemical cues from the snake. The refuge design ensured that lizards could see the snake only after they had entered the refuge.

In the control treatment, the adjacent terrarium was empty, and we applied deionized water to a clean strip of absorbent paper fixed on the substrate of the refuge. In the chemical treatment, the adjacent terrarium was also

empty, and we fixed strips of predator-scented absorbent paper moistened with deionized water to the floor of the refuge to add the predator scent. The strips of absorbent paper had been in the terrarium of the snake for at least 3 days. In the visual treatment, we used a clean strip of paper moistened with deionized water and we placed the snake into the adjacent terrarium. In the treatment with chemical and visual cues combined, we placed the snake into the adjacent terrarium and fixed predator-scented strips of absorbent paper moistened with deionized water to the floor of the refuge. We used new papers and a new refuge in each trial to avoid mixing chemical cues. After each trial, the refuges were cleaned thoroughly with water and the sand substrate was replaced.

Before each trial, a lizard was gently transferred to an experimental terrarium, where the refuge entry was initially closed. After a 5-min acclimation period, during which the lizard typically moved normally through the terrarium, the experimenter opened the entry of the refuge and simulated a predatory attack by tapping the lizard close to the tail with a brush to stimulate it to run and hide in the refuge. Lizards usually ran for some time and frequently passed several times close to the refuge without entering. An experimenter recorded the time from the beginning of the attack until the lizard entered the refuge. When the lizard hid, the observer retreated to a hidden position and recorded the time that the lizard spent in the refuge until the head emerged 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 with the same procedure and recorded data as in the first attack. Air temperature inside the refuge was maintained at $20 \pm 0.1°C$.

We used repeated measures factorial ANOVAs to assess differences in time until entering the refuge, and appearance and waiting times, between treatments and between the two attacks of each individual (both within-subject 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). Data were log-transformed to ensure normality (Shapiro–Wilk test). Tests of homogeneity of variances (Levene's test) showed that in all cases variances were not significantly heterogeneous after transformation (Sokal & Rohlf 1995).

RESULTS

Experiment 1: Detection of Chemical Cues from Snakes

All lizards responded to swabs by tongue flicking. There were significant differences between stimulus conditions in total tongue-flicks (repeated measures one-way ANOVA: $F_{3,99} = 8.32$, $P < 0.0001$; Fig. 1a). Chemicals from the snake elicited significantly more tongue-flicks than the other conditions (Tukey's test: $P < 0.01$ in all cases). Responses to deionized water, cologne and *L. monticola* were not significantly different ($P > 0.60$ in all cases).
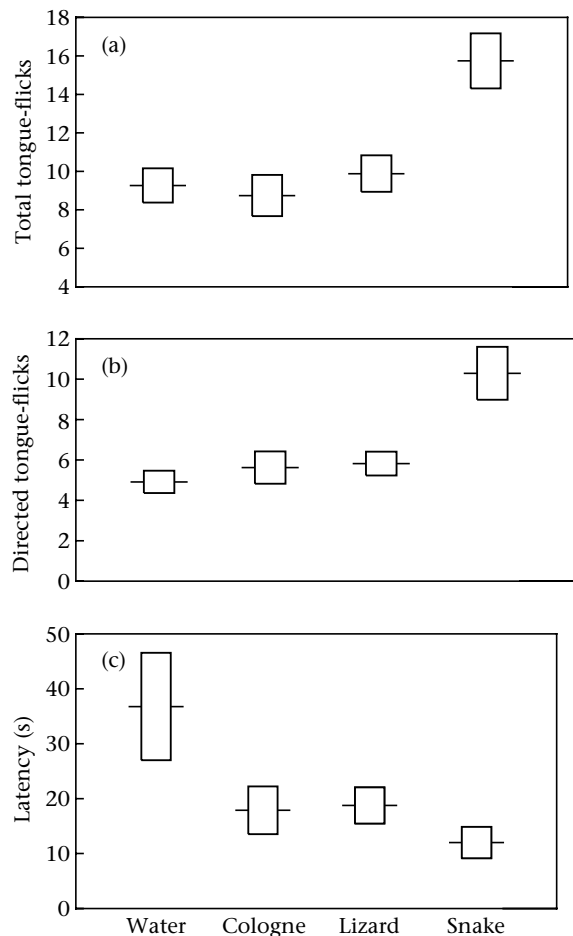

Figure 1. Mean + SE (a) total number of tongue-flicks, (b) tongue-flicks directed to swabs in relation to the time exposed to the stimulus and (c) latency (s) to the first tongue-flick by the lizard *Podarcis muralis* ($N = 34$) in response to deionized water, cologne, Iberian rock lizard, or smooth snake stimuli presented on cotton-tipped applicators.

The number of tongue-flicks directed to swabs differed significantly between treatments (repeated measures one-way ANCOVA: $F_{3,96} = 4.15$, $P = 0.008$; Fig. 1b), with more directed to swabs with snake scent than to other stimuli (Tukey's tests: $P < 0.01$ in all cases). Responses to chemicals from other conditions were not significantly different ($P > 0.90$ in all cases). The number of tongue-flicks not directed to the swab did not differ significantly between treatments (repeated measures one-way ANOVA: $F_{3,99} = 1.40$, $P = 0.25$, power = 0.40).

The time that lizards remained close to the stimulus differed significantly between treatments (repeated measures one-way ANOVA: $F_{3,99} = 4.03$, $P < 0.01$). Lizards often fled after tongue flicking the snake stimulus. Thus, lizards spent significantly less time close to the snake stimulus ($\overline{X} \pm SE = 42 \pm 3$ s) than to the other stimuli (water: 51 ± 2 s; cologne: 50 ± 2 s; *L. monticola*: 48 ± 3 s; Tukey's test: $P < 0.05$ in all cases). There were no significant differences between the other treatments ($P > 0.90$ in all cases).

Mean latency to the first tongue-flick differed significantly between conditions (repeated measures one-way

ANOVA: $F_{3,99} = 3.12$, $P = 0.03$; Fig. 1c). The latency in response to snake scent was significantly shorter than to the water (Tukey's test: $P = 0.02$), but it was not significantly different from latency to cologne ($P = 0.15$) or to *L. monticola* ($P = 0.90$). There were no significant differences between the other treatments ($P > 0.44$ in all cases).

Experiment 2: Relative Importance of Visual and Chemical Cues

Latency to enter the refuge after being attacked did not differ significantly either between first and second attacks (repeated measures two-way ANOVA: $F_{1,16} = 1.57$, $P = 0.23$, power $= 0.12$) or between treatments ($F_{3,48} = 1.73$, $P = 0.17$, power $= 0.36$). The interaction was not significant ($F_{3,48} = 2.44$, $P = 0.07$, power $= 0.39$; Fig. 2a).

Time for the head to emerge from the refuge did not differ significantly between the first and second attacks (repeated measures two-way ANOVA: $F_{1,16} = 2.97$, $P = 0.10$, power $= 0.24$), but there were significant differences between treatments ($F_{3,48} = 3.93$, $P = 0.014$), and the interaction was significant ($F_{3,48} = 3.46$, $P = 0.02$; Fig. 2b). For first attacks, time spent in the refuge was greater in the control treatment than in the chemical and visual combined treatment (Tukey's test: $P = 0.02$), but no other differences between pairs of treatments were significant ($P > 0.52$ in all cases). After the second attack, there were significant differences between the control and both the chemical and visual combined treatments ($P = 0.0004$) and the chemical treatment ($P = 0.0005$).

Waiting time did not differ significantly between the first and the second attack (repeated measures two-way ANOVA: $F_{1,16} = 0.61$, $P = 0.45$, power $= 0.20$), but treatments differed significantly ($F_{3,48} = 7.50$, $P = 0.0003$). The interaction was not significant ($F_{3,48} = 1.32$, $P = 0.28$, power $= 0.20$; Fig. 2c). Lizards left the refuge significantly later when they were hidden in a predator-free refuge than when they were in a refuge containing visual cues of a snake, either alone (Tukey's test: $P = 0.04$) or in combination with chemical cues ($P = 0.0003$), but not when it contained only chemical ones ($P = 0.38$). Lizards left the refuge sooner when they were hidden in a refuge containing both combined visual and chemical cues than when the refuge contained only chemical cues ($P = 0.02$). The visual treatment did not differ significantly from the combined chemical and visual treatment or the chemical treatment ($P > 0.29$ in both cases).

DISCUSSION

The greater tongue-flick rate and shorter latency to first tongue-flick in response to snake scents presented on cotton swabs (experiment 1) indicate that *P. muralis* is able to detect and discriminate the chemical cues of *C. austriaca* snakes. This ability is particularly important to wall lizards for three reasons: lizards are an important part of the diet of *C. austriaca* (Rugiero et al. 1995), the snake occupies the same microhabitats and is found inside refuges (Rugiero et al. 1995), and it is extremely cryptic
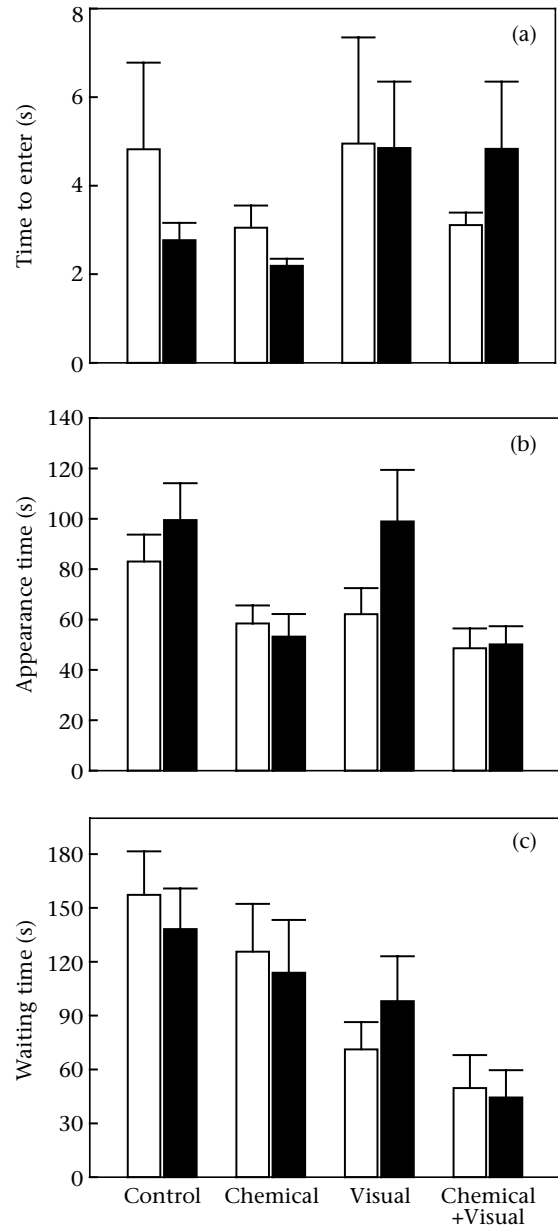

Figure 2. Mean + SE differences between (a) time to enter the refuge, (b) appearance time and (c) waiting time of the lizard *Podarcis muralis* ($N = 20$) in predator-free refuges and in refuges containing chemical cues, visual cues or both after two simulated repeated attacks (□: first attack; ■: second attack).

because it uses a sit-and-wait hunting strategy within rock crevices (Galán 1998). Hence, the ability to detect chemical cues of this snake may enable *P. muralis* to avoid entering hazardous crevices. Lizards exposed to predator chemical stimuli responded by rapidly fleeing away from the swab. This result suggests that, in a natural situation, the first response of wall lizards upon detection of chemical cues from a snake would be to flee, thereby avoiding crevices likely to contain smooth snakes.

Results of experiment 2 suggest that lizards were able to use both chemical and visual snake cues to assess the level of predation risk inside a refuge. Time to enter a refuge by

wall lizards seemed not to be influenced by the potential risk of predation inside the refuge. Regardless of the type of cue found inside the refuge, lizards sheltered quickly in both attacks. These results suggest that the actual predation risk in the open seems to be more determinant for lizards than the eventual risk of encountering a hidden snake inside the refuge. Also, assessment of risk before entering might not always be possible, especially if the lizard is fleeing from a predator. This result suggests a case of predator facilitation because predators in the exterior may force lizards to hide in potentially hazardous refuges.

However, our results also suggested that time spent in the refuge was related to the snake's cues found inside it. Appearance time in the second attack was greater when lizards found only visual cues of a snake than when there were chemical cues. This result could suggest that wall lizards discriminated the actual source of chemical cues more quickly than that of visual ones; smooth snakes are inconspicuous inside the dark crevices and their chemical stimuli may provide more important cues (Van Damme et al. 1995; Kats & Dill 1998). An alternative explanation is that lizards may have taken longer to look through the window than to tongue-flick the floor, so this result could have been caused by the cue that they encountered first. Also, lizards may have perceived that the snake was outside the refuge (W. E. Cooper, Jr, personal communication).

The results of experiment 1 suggest that lizards may assess the possible presence of a snake using only chemical cues. However, after appearing, lizards waited longer before resuming activity when the refuge contained chemical cues than when visual ones were present. Chemical detection of a snake may indicate to lizards that the refuge was risky at a certain moment, but it does not necessarily indicate a current risk. Thus, lizards left the refuge quickly only when they also saw the snake. Therefore, our results suggest that visual cues are important to confirm the uncertain level of risk implied by chemical cues.

Our results also confirm the assumption of the threat sensitivity hypothesis that multiple cues from a predator may contribute in an additive way to determine the degree of risk-sensitive behaviour. The antipredatory response of lizards was greater when they were exposed to both visual and chemical cues of ambush snakes (i.e. they appeared and emerged sooner from the refuge) than when only one cue was presented. Similar results were obtained in a study of the mosquitofish, *G. affinis*, which increased avoidance behaviour when chemical and visual cues of predatory fish were presented (Smith & Belk 2001). However, fathead minnows, *Pimephales promelas*, were most likely to react to chemical alarm cues in the absence of visual information and when the perceived risk was high (Hartman & Abrahams 2000). Larval newts, *Notophthalmus lousianensis*, distinguished between predatory and nonpredatory species only when chemical cues were available, although when only visual cues were present, newts attempted to avoid both species (Mathis & Vincent 2000). In contrast, slimy sculpins, *Cottus cognatus*, showed threat-sensitive predator avoidance when exposed only to visual cues, but not when exposed only to chemical cues

from a predator (Chivers et al. 2001). Differences between species in behavioural responses to visual and chemical predator cues should depend on ambient conditions. For example, newts and wall lizards may rely heavily on chemical cues because visibility is greatly restricted in the habitats where they may encounter their predators. Furthermore, the response of prey to different levels of information about a predator should also depend on ambient conditions. For example, yellowhammers, *Emberiza citrinella*, that heard alarm calls only from conspecifics delayed resuming activity longer than birds that saw a sparrowhawk, *Accipiter nisus*, model (van der Veen 2002). In this case, birds with less complete information perceived predation risk as being higher because they could not locate the predator. Thus, they were more cautious.

Actively foraging predators in the exterior may force lizards to increase refuge use even when the risk of predation from sit-and-wait snakes inside the refuge is high. The actual presence of a snake in the refuge may also force lizards to decrease their refuge use, exposing them to increased predation in the open. This response could enhance risk for the prey, as has been observed in other animals (Soluk 1993; Korpimäki et al. 1996). The results of this study may support this idea. Wall lizards probably could not elude the predator in the open without hiding in the refuge, and did not modify the time taken to enter the refuge in relation to the predation risk within it. However, our results also suggest that the ability to identify different cues of a predator accurately may help lizards to improve their accuracy of predation risk assessment inside the refuge. This ability may help wall lizards to reduce the risk-enhancing effects of two types of predators requiring conflicting prey defences.

References

Chivers, D. P. & Smith, R. J. F. 1998. Chemical alarm signalling in aquatic predator/prey systems: a review and prospectus. *Ecoscience,* **5,** 338–352.

Chivers, D. P., Mirza, R. S., Bryer, P. J. & Kiesecker, J. M. 2001. Threat-sensitive predator avoidance by slimy sculpins: understanding the importance of visual versus chemical information. *Canadian Journal of Zoology,* **79,** 867–873.

Cooper, W. E., Jr. 1990. Chemical detection of predators by a lizard, the broad-headed skink (*Eumeces laticeps*). *Journal of Experimental Zoology,* **256,** 162–167.

Cooper, W. E., Jr & Burghardt, G. M. 1990. A comparative analysis of scoring methods for chemical discrimination of prey by squamate reptiles. *Journal of Chemical Ecology,* **16,** 45–65.

Dill, L. M. & Fraser, A. H. G. 1997. The worm re-turns: hiding behaviour of a tube-dwelling marine polychaete, *Serpula vermicularis*. *Behavioral Ecology*, **8**, 186–193.

Downes, S. & Shine, R. 1998. Sedentary snakes and gullible geckos: predator–prey coevolution in nocturnal rock-dwelling reptiles. *Animal Behaviour*, **55**, 1373–1385.

Galán, P. 1998. *Coronella austriaca* (Laurenti 1768). In: *Fauna Ibérica. Vol. 10* (Ed. by M. A. Ramos), pp. 364–375. Madrid: Museo Nacional de Ciencias Naturales, CSIC.

Hartman, E. J. & Abrahams, M. V. 2000. Sensory compensation and the detection of predators: the interaction between chemical and visual information. *Proceedings of the Royal Society of London, Series B*, **267**, 571–575.

Helfman, G. S. 1989. Threat-sensitive predator avoidance in damselfish–trumpetfish interactions. *Behavioral Ecology and Sociobiology*, **24**, 47–58.

Kats, L. B. & Dill, L. M. 1998. The scent of death: chemosensory assessment of predation risk by prey animals. *Ecoscience*, **5**, 361–394.

Korpimäki, E., Koivunen, Y. & Hakkarainen, H. 1996. Microhabitat use and behaviour of voles under weasel and raptor predation risk: predation facilitation? *Behavioral Ecology*, **7**, 30–34.

Krupa, J. J. & Sih, A. 1998. Fishing spiders, green sunfish, and stream-dwelling water strider: male–female conflict and prey responses to single versus multiple predator environments. *Oecologia*, **117**, 258–265.

McCarthy, T. M. & Fisher, W. A. 2000. Multiple predator-avoidance behaviours of the freshwater snail *Physella heterostropha pomila*: responses vary with risk. *Freshwater Biology*, **44**, 387–397.

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. An experimental test of the costs of antipredatory refuge use in the wall lizard, *Podarcis muralis*. *Oikos*, **84**, 499–505.

Martin-Vallejo, J., García-Fernández, J., Pérez-Mellado, V. & Vicente-Villardón, J. L. 1995. Habitat selection and thermal ecology of the sympatric lizards *Podarcis muralis* and *Podarcis hispanica* in a mountain region of central Spain. *Herpetological Journal*, **5**, 181–188.

Mathis, A. & Vincent, F. 2000. Differential use of visual and chemical cues in predator recognition and threat-sensitive predator-avoidance responses by larval newts (*Notophthalmus viridescens*). *Canadian Journal of Zoology*, **78**, 1646–1652.

Rugiero, L., Capula, M., Filippi, E. & Luiselli, L. 1995. Food habits of the mediterranean populations of the smooth snake (*Coronella austriaca*). *Herpetological Journal*, **5**, 316–318.

Sih, A., Kats, L. B. & Moore, R. D. 1992. Effects of predatory sunfish on the density, drift and refuge use of the stream salamander larvae. *Ecology*, **73**, 1418–1430.

Sih, A., Englund, G. & Wooster, D. 1998. Emergent impact of multiple predators on prey. *Trends in Ecology and Evolution*, **13**, 350–355.

Smith, M. E. & Belk, M. C. 2001. Risk assessment in western mosquitofish (*Gambusia affinis*): do multiple cues have additive effects? *Behavioral Ecology and Sociobiology*, **51**, 101–107.

Sokal, R. R. & Rohlf, F. J. 1995. *Biometry*. 3rd edn. New York: W. H. Freeman.

Soluk, D. A. 1993. Multiple predator effects: predicting combined functional response of stream fish and invertebrate predators. *Ecology*, **74**, 219–225.

Van Damme, R. & Quick, K. 2001. Use of predator chemical cues by three species of lacertid lizards (*Lacerta bedriagae*, *Podarcis tiliguerta*, and *Podarcis sicula*). *Journal of Herpetology*, **35**, 27–36.

Van Damme, R., Bauwens, D., Thoen, C., Vanderstighelen, D. & Verheyen, R. F. 1995. Responses of naive lizards to predator chemical cues. *Journal of Herpetology*, **29**, 38–43.

Vanderstighelen, D. 1987. Responses of the common lizard (*Lacerta vivipara*) to visual and chemical stimuli of the viper (*Vipera berus*). In: *Proceedings of the Fourth Ordinary General Meeting of the Societas Europaea Herpetologica* (Ed. by J. J. Van Gelder, H. Strijbosch & P. J. M. Bergers), pp. 425–428. Nijmegen: Societas Europaea Herpetologica.

van der Veen, I. T. 2002. Seeing is believing: information about predators influences yellowhammer behavior. *Behavioral Ecology and Sociobiology*, **51**, 466–471.