

Can Wall Lizards Combine Chemical and Visual Cues to Discriminate Predatory from Non-Predatory Snakes Inside Refuges?

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Abstract

The ability to use multiple cues in assessing predation risk is especially important to prey animals exposed to multiple predators. Wall lizards, *Podarcis muralis*, respond to predatory attacks from birds in the open by hiding inside rock crevices, where they may encounter saurophagous ambush smooth snakes. Lizards should avoid refuges with these snakes, but in refuges lizards can also find non-saurophagous viperine snakes, which lizards do not need to avoid. We investigated in the laboratory whether wall lizards used different predator cues to detect and discriminate between snake species within refuges. We simulated predatory attacks in the open to lizards, and compared their refuge use, and the variation in the responses after a repeated attack, between predator-free refuges and refuges containing visual, chemical, or visual and chemical cues of saurophagous or non-saurophagous snakes. Time to enter a refuge was not influenced by potential risk inside the refuge. In contrast, in a successive second attack, lizards sought cover faster and tended to increase time spent hidden in the refuge. This suggests a case of predator facilitation because persistent predators in the open may force lizards to hide faster and for longer in hazardous refuges. However, after hiding, lizards spent less time in refuges with both chemical and visual cues of snakes, or with chemical cues alone, than in predator-free refuges or in refuges with snake visual cues alone, but there were no differences in response to the two snake species. Therefore, lizards could be overestimating predation risk inside refuges. We discuss which selection pressures might explain this lack of discrimination of predatory from similar non-predatory snakes.

Introduction

The ability to discriminate between predatory and non-predatory species is a basic component of threat assessment (Mathis & Vincent 2000). This is because not responding to a predatory species is costly in terms of survival, but responding to a non-predatory species may be energetically costly and result in a loss of time for other activities (Ydenberg & Dill 1986; Stapley 2003). However, prey animals often do not have complete information about their

environment, and can make less accurate estimations of predation risk. This leads them to either over- or underestimate risk (van der Veen 2002). To minimize the negative effects of risk overestimation, prey animals should use multiple cues (e.g. visual and chemical cues) to accurately identify predators, assess the level of risk that they pose, and adjust their antipredatory behavior accordingly (McCarthy & Fisher 2000; Amo et al. 2004a).

Chemosensory cues alone may reliably reveal the presence of some predators (Chivers & Smith 1998;

Kats & Dill 1998; Chivers et al. 2001a). However, visual cues, such as predator size and activity, may provide information more specific to a predator's current motivation and threat (Smith & Belk 2001). In addition, 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; Turner & Montgomery 2003). Only a few studies have compared the relative importance of these two types of stimuli, suggesting that prey animals can combine information from both chemical and visual cues to better assess risk (Vanderstighelen 1987; Hartman & Abrahams 2000; Mathis & Vincent 2000; Chivers et al. 2001a; Amo et al. 2004a). The threat-sensitivity hypothesis assumes that multiple predator cues should contribute in an additive way to determine the degree of risk-sensitive behavior (Helfman 1989; Smith & Belk 2001). However, differences in the response to chemical and visual cues should strongly depend on the ambient conditions. For example, when visibility is low, prey animals should rely more on chemical cues than on visual ones (Mathis & Vincent 2000; Amo et al. 2004a).

Prey animals often respond to predator presence by increasing refuge use (Sih et al. 1992; Dill & Fraser 1997), but some refuges may expose prey animals to other types of predators. This may be a case of predator facilitation because antipredatory response to one predator may increase the risk of predation by another type of predator due to conflicting prey defenses (Soluk 1993; Sih et al. 1998). However, flexibility in antipredatory responses may help prey animals to avoid these risk enhancement effects (Krupa & Sih 1998; Hopper 2001). Wall lizards (*Podarcis muralis*) respond to predatory attacks from birds or mammals in the open by hiding inside rock crevices (Martín & López 1999b), but, in crevices, lizards may be exposed to predation by smooth snakes (*Coronella austriaca*), a saurophagous snake that feeds by ambush foraging hidden in rock crevices (Rugiero et al. 1995; Galán 1998). However, inside crevices, wall lizards may also encounter the harmless viperine snake (*Natrix maura*), a non-saurophagous snake that feeds mainly on aquatic invertebrates, amphibians and fishes (Braña 1998).

Many lizards avoid predatory snakes by detecting chemical cues (e.g. Cooper 1990; Downes & Shine 1998; Van Damme & Quick 2001; Downes 2002). Undisturbed wall lizards are able to detect the chemical cues of *C. austriaca* snakes presented on cotton swabs, and to discriminate them from those of

N. maura (Amo et al. 2004b). Chemical cues should be important for discriminating these snakes inside rock crevices because visibility is low and these snakes have a similar coloration. According to the threat-sensitive hypothesis (Helfman 1989), natural selection should favor individuals that take action appropriate to the magnitude of threat rather than respond to chemical cues of all predators in a similar way. Thus, the defensive responses of prey animals to chemical cues of different snakes should depend on the level of risk posed by each snake species (Stapley 2003; Amo et al. 2004b). Theoretical models suggest that the optimal time until emergence from a refuge is the time when the costs of staying exceed the costs of leaving (i.e. predation risk in the exterior) (Sih et al. 1992; Martín & López 1999a). Hence, lizards hidden in a potentially unsafe refuge (i.e. with saurophagous snake chemical cues) emerged sooner than from a snake-free refuge (Amo et al. 2004a). However, chemical cues indicate that the shelter may be used by a predator, although not necessarily at the current time (Kats & Dill 1998; Turner & Montgomery 2003; Amo et al. 2005). Therefore, if lizards only use chemical cues they could overestimate risk inside the refuge, and emerging too soon may expose lizards to the predator in the open.

Although a previous study suggested that undisturbed wall lizards can discriminate scents of different snake species (Amo et al. 2004b), we tested here whether lizards attacked by another type of predator in the open were simultaneously able to discriminate and respond differentially to dangerous and harmless snake species inside refuges, and if so, whether they used visual or chemical cues, or both. Lizards were exposed to simulated predator attacks in the laboratory, and we compared their propensity to enter a refuge, time spent in the refuge, and the variation in their response to attacks. The comparisons were made between snake free refuges, or refuges containing visual cues, chemical cues or both cues of the saurophagous smooth snake, *C. austriaca*, or the non-saurophagous viperine snake, *N. maura*. In this way we simulated a real situation in which lizards may encounter snakes inside refuges, while escaping predators in the open. As visibility is low inside refuges and both snake species have similar coloration, we hypothesized that for lizards chemical cues are more useful than visual ones in discriminating between the two snake species (Amo et al. 2004b). However, visual cues might improve the assessment of risk level. According to the threat-sensitive hypothesis, we hypothesized that lizards should respond

more accurately when they found more than a single cue of a predatory snake inside the refuge, but we did not expect differences in the response of lizards exposed to different cues of the non-saurophagous snake.

Methods

The wall lizard, *P. muralis*, 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 and walls in shaded zones in forests (Martin-Vallejo et al. 1995). Its geographic distribution and habitat preferences widely overlap with those of smooth and viperine snakes. During Mar. and Apr. 2002, we captured by noosing 28 *P. muralis* (snout-vent length, $\bar{x} \pm \text{SE} = 66 \pm 2$ mm) at a rock wall near Cercedilla (Madrid Province, Spain). Noosing is a frequently used and harmless method that entails placing a noose around the lizard's neck to capture it. Wall 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. Every day, they were fed mealworm larvae (*Tenebrio molitor*) dusted with multivitamin powder for reptiles (Reptivite; Zoo Med Laboratories, Inc., San Luis Obispo, California, USA), and water ad libitum. The photoperiod and ambient temperature followed that of the environment. Lizards were held in captivity at least 1 mo before testing to allow acclimatization to laboratory conditions.

We also captured two adult smooth snakes on the same wall, and one adult viperine snake in the nearby area to be used in the experiments. The snakes were housed in separate glass terraria (60 × 30 × 20 cm) to prevent lizards from gaining experience of the snakes before they were tested. The snakes' terraria had strips of absorbent paper fixed on the substrate to absorb snake scent. Species-appropriate food (see below) and water were provided ad libitum. To avoid using live lizards as food, we fed smooth snakes house crickets and small pieces of minced lamb bearing scent of live lizards (feces and the secretion from femoral pores and skin of wall lizards). This procedure did not affect lizards, but their scent attracted the attention of snakes to the meat. The viperine snake was fed small pieces of fish. We also dusted food with multivitamin and calcium/phosphorus supplement powder for reptiles (Reptivite, Zoo Med Laboratories, Inc.). All animals were healthy during the trials, and did not show behavioral or physiological changes due to possible stress of

experiments. They all maintained or increased their original body mass. They were returned to their exact capture sites at the end of experiments.

To analyze whether wall lizards inside refuges were able to discriminate between a predatory snake and a harmless one by using their chemical and/or visual cues, we designed a repeated measures experiment in which each individual lizard ($N = 28$) was tested in a counterbalanced sequence in all the treatments. One trial was conducted per day for each animal, and the inter-trial interval for each lizard was at least 1 d. We compared the latency to enter a refuge, time spent in the refuge, and variations in their response between two successive repeated attacks. In the control treatment the refuge was odorless and empty. In the visual cues-alone treatment the refuge was odorless and it allowed lizards to see the snake through a glass wall. In the chemical cues-alone treatment, the refuge contained chemical cues of the snake. In the combined visual and chemical cues, the refuge contained chemical cues of the snake and was visible to the lizards. Lizards were tested in these treatments with cues from either a saurophagous snake (smooth snake) or from a non-saurophagous snake (viperine snake). To avoid testing lizards too many times, we did not include in the experimental design a pungent odor (e.g. cologne). This was justified because results of previous experiments showed that *P. muralis* neither discriminate between cologne and water, nor between water and other irrelevant odors, but do discriminate between snake scent and both water and cologne (Amo et al. 2004a,b). Moreover, *P. muralis* did not modify the use of refuges containing a pungent odor, compared with an odorless control, but did modify the use of refuges containing smooth snake cues (Amo et al. 2004a).

The experiment was conducted in a terrarium (100 × 40 × 50 cm) with a sand substrate and a single refuge in the middle of one end of the terrarium. The refuge was built with flat rocks, which had two openings (7 × 6 cm) that allowed entry. One entry was open; the other was closed with the glass walls of a smaller adjacent terrarium (50 × 40 × 40 cm). This smaller terrarium was sealed to prevent lizards from detecting chemical cues from the snake, and was covered to make it darker than the experimental terrarium. This was done to simulate lower visibility in rock crevices compared with the surrounding open areas. The refuge design ensured that lizards could only see the snake after they had entered the refuge. In the 'control' treatments, the adjacent terrarium was empty and we applied some deionized

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

Lizards were allowed to bask at least 2 h before the experiments to ensure they reached an optimal body temperature. Before each trial, a lizard was gently transferred to an experimental terrarium, where the refuge entry was initially closed. After 5 min of acclimatization, during which the lizard typically moved around the terrarium, we opened the entry of the refuge, and waited until the lizard was about 50 cm from the refuge. Then, we 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. We recorded the time that the lizard was running in the terraria from the beginning of the attack until it 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 lizard's 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 $20 \pm 0.1^\circ\text{C}$.

We used repeated measures ANOVAS to assess differences in time until entering the refuge, appearance and waiting times between snake species, between treatments, and between the two attacks of each individual (all within-subject factors, because all individuals were tested in all conditions). We included the interactions in the models to test whether responses to the different treatments changed between the first and the second attack or between snake species. Data were log-transformed to ensure normality (Shapiro-Wilk's test). Tests of homogeneity

of variances (Levene's test) showed that in all cases variances were significantly non-heterogeneous after transformation (Sokal & Rohlf 1995).

Results

Lizards entered the refuge significantly sooner in the second than in the first attack (repeated measures two-way ANOVA, $F = 96.62$, $df = 1,27$, $p < 0.0001$), but there were no significant differences between snake species ($F = 0.53$, $df = 1,27$, $p = 0.47$), or between treatments ($F = 1.09$, $df = 3,81$, $p = 0.35$), and none of the interactions were significant ($F < 1.24$, $df = 3,81$, $p > 0.30$ in all cases; Fig. 1a).

The time to appearance was about 18% shorter, but not significantly so, in the second than in the first attack (repeated measures two-way ANOVA, $F = 3.04$, $df = 1,27$, $p = 0.09$). There were no significant differences between snake species ($F = 0.32$, $df = 1,27$, $p = 0.58$), but there were significant differences between treatments ($F = 4.23$, $df = 3,81$, $p = 0.008$). None of the interactions were significant ($F < 1.74$, $df = 3,81$, $p > 0.16$ in all cases; Fig. 1b). Post-hoc comparisons showed that lizards appeared significantly sooner from refuges that contained combined chemical and visual cues of a snake than from refuges that contained visual cues alone (Tukey's test, $p = 0.038$) or from control refuges ($p = 0.03$), but at similar times than from refuges with chemical cues alone ($p = 0.94$). There were no significant differences in appearance time between other treatments ($p > 0.14$ in all cases).

Waiting time did not differ significantly between first and second attacks (repeated measures two-way ANOVA, $F = 0.46$, $df = 1,27$, $p = 0.50$), between snake species ($F = 0.75$, $df = 1,27$, $p = 0.39$), or between treatments ($F = 1.65$, $df = 3,81$, $p = 0.18$), and none of the interactions were significant ($F < 0.81$, $df = 3,81$, $p > 0.50$ in all cases Fig. 1c).

Discussion

Our results do not support the threat-sensitive hypothesis, because lizards did not show a greater avoidance response when confronted with a combination of visual and chemical cues of snakes than when confronted with chemical cues alone. Therefore, it seems that lizards used chemical cues of snakes alone to assess predation risk inside refuges and that they did not respond to visual cues.

Chemical cues alone may not indicate a current risk of predation because they may persist after the snake has left the refuge (Kats & Dill 1998; Amo

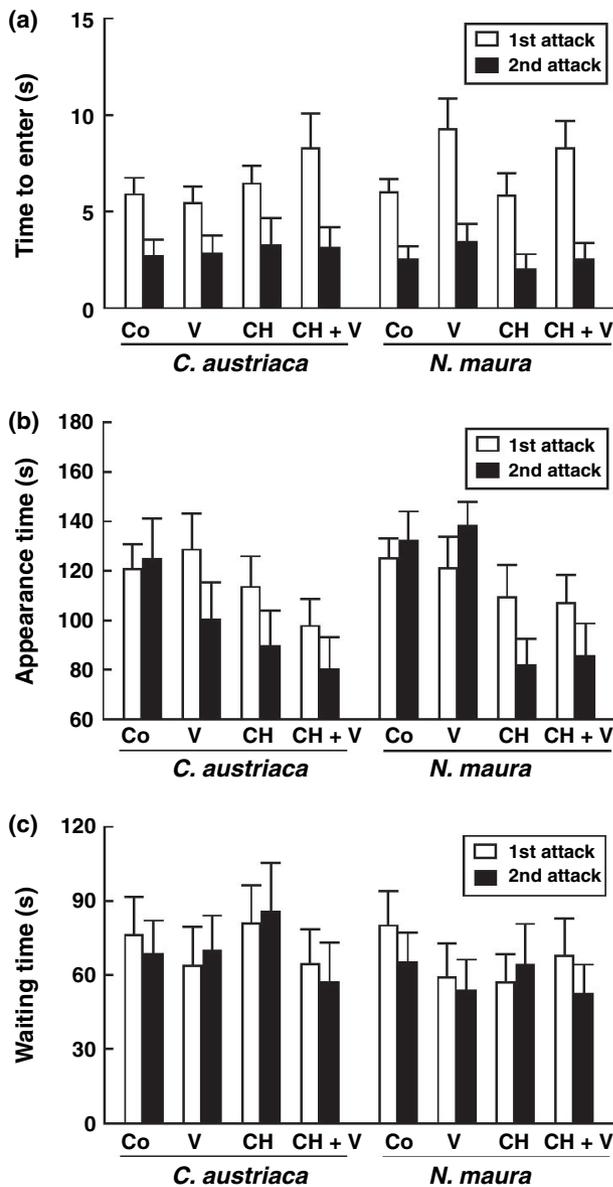


Fig. 1: $\bar{x} \pm \text{SE}$ of (a) time to enter the refuge, (b) appearance time, and (c) waiting time spent by the lizard *Podarcis muralis* ($N = 28$) in predator-free refuges (Co), or refuges containing visual cues (V), chemical cues (CH), or both cues (CH + V) of *Coronella austriaca* or *Natrix maura* snakes, when suffered two simulated repeated attacks

et al. 2005). Thus, an excessive avoidance response to snake's chemicals may cause an overestimation of risk, and if lizards leave the refuge quickly they may be captured by the predator in the open. However, although visual cues alone may indicate the current presence of a snake, these cues may not be useful enough under the low visibility conditions inside refuges. Indeed, a previous study made under good lighting conditions showed that wall lizards were

able to detect and use visual cues of smooth snakes in conjunction with chemical cues (Amo et al. 2004a). Therefore, differences in lighting conditions may determine whether lizards are able to use visual cues to identify and respond to snakes. Also in other prey species the relative importance of visual and chemical predator cues have been shown to depend on ambient conditions (Mathis & Vincent 2000; Chivers et al. 2001a). For example, the mosquitofish, *Gambusia affinis*, responded with an increase in avoidance behavior 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 alone in the absence of visual information (Hartman & Abrahams 2000). Our results suggest that wall lizards may rely heavily on chemical cues because visibility is greatly restricted inside refuges where they may encounter their predator snakes.

Our results also show that wall lizards did not discriminate between saurophagous and non-saurophagous snakes within refuges. However, results of a previous experiment showed that undisturbed wall lizards did discriminate between the chemical cues alone presented on cotton applicators of saurophagous snakes and those of harmless snakes (Amo et al. 2004b). Similarly, undisturbed mountain log skinks showed a differential avoidance response when selecting between nocturnal retreats treated with odors from different snake species (Stapley 2003). The fact that the lizards sought shelter after disturbance in the present study may account for the lack of discrimination between snake species. In the previous study (Amo et al. 2004b) the lizards were allowed to choose between odors while undisturbed. Thus it seems that stress caused by predator pressure in the open may prevent lizards from accurately assess risks in refuges. Thus, lizards sought cover faster in the second attack, because a repeated attack probably indicates enhanced risk owing to predator persistence (Cooper 1998; Martín & López 2001; Polo et al. 2005).

The kind of estimation that an animal makes about predation risk is likely to depend on local predation pressure (McCarthy & Fisher 2000; Chivers et al. 2001b). For example, the ability of some lizard species to discriminate between chemical cues of saurophagous and non-saurophagous snakes may depend on whether they are sympatric and, thus, on whether they have been submitted to a high selection pressure for discriminating between snakes (Van Damme & Quick 2001; but see Thoen et al. 1986; Van Damme & Castilla 1996 for other species).

Differences in densities of each snake species within our wall lizard study population may also have influenced the responses. Density of smooth snakes is high, whereas viperine snakes are less abundant (Luisa Amo, pers. obs.). Thus, the probability of encountering a saurophagous snake inside a refuge should be much higher. Lizards might need time to discriminate between snake species, but they should respond quickly immediately after detecting any snake cue inside a refuge, because it is very likely that most snakes found are saurophagous ones. Therefore, costs associated with a lack of discrimination of both snakes and an unnecessary avoidance of non-saurophagous viperine snakes are lower if encounters with harmless snakes are rare in the field. Furthermore, even though lizards apparently overestimated risk by appearing too soon from the refuge, they waited before emerging completely. This may allow acquisition of information on the persistence of the predator in the open (Martín & López 1999a; Polo et al. 2005). Thus, it seems that in this case an overestimation of risk in refuges might not be excessively costly.

We conclude that even if prey species are able to discriminate between predatory and non-predatory species under optimal conditions, their actual anti-predatory responses to cues of potential predators may be influenced by environmental conditions, by the local predation pressure, and by the need of avoiding simultaneously multiple type of predators requiring conflicting prey defenses.

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