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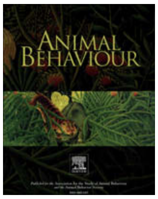

Chemical cues from both dangerous and nondangerous snakes elicit antipredator behaviours from a nocturnal lizard

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Many prey species use chemical cues to detect predators. According to the threat sensitivity hypothesis, prey should match the intensity of their antipredator behaviour to the degree of threat posed by the predator. Several species of lizards display antipredator behaviours in the presence of snake chemical cues, but how species specific are these responses? In Australia, most snake species eat lizards, and are therefore potentially dangerous. Hence, we predicted that lizards should display generalized rather than species-specific antipredator behaviours. To test this prediction, we quantified the behavioural responses of velvet geckos, *Oedura lesueurii*, to chemical cues from five species of elapid snakes that are syntopic with velvet geckos but differ in their degree of danger. These five snake species included two nocturnal ambush foragers that eat geckos (broad-headed snake *Hoplocephalus bungaroides*, and death adder, *Acanthophis antarcticus*), two active foragers that eat skinks (but rarely eat geckos) and that differ in their activity times (nocturnal small-eyed snake, *Cryptophis nigrescens*, and diurnal whip snake, *Demansia psammophis*), and a nocturnal nonthreatening species that feeds entirely on blind snakes (bandy-bandy, *Vermicella annulata*). Geckos showed similar antisnake behaviours (tail waving, tail vibration), and a similar intensity of responses (reducing activity, freezing), to chemical cues from all five snake species, even though the snakes differed in their degree of danger and foraging modes. Our results suggest that velvet geckos display generalized antipredator responses to chemicals from elapid snakes, rather than responding in a graded fashion depending upon the degree of threat posed by a particular snake species.

Predation poses a major risk for most organisms, resulting in the evolution of a complex array of antipredator tactics that involves behavioural modifications (e.g. responses to predator approach), physiology (e.g. toxins), morphology (e.g. defensive spines) and performance capacities (e.g. locomotor ability; Greene 1988; Stanford 2002; Bollache et al. 2006; Boyer et al. 2006). Evolutionary theory predicts that such modifications entail costs as well as benefits, and the degree of elaboration of antipredator traits in a specific situation will depend upon the balance between these two (Lima & Dill 1990). Because responding to predators can involve costs (e.g. loss of foraging or reproductive opportunities), there should be strong selection on prey not only to identify predators, but also to modify antipredator responses according to the level of risk posed by the predator (Helfman 1989; Lima & Bednekoff 1999). Threat-sensitive responses to predation risk occur in a wide variety of taxa, including invertebrates, fishes, reptiles, amphibians, mammals and birds (e.g. Jędrzejewski et al. 1993; Mathis & Vincent 2000; Chivers et al. 2001; Persons & Rypstra 2001; Amo et al. 2004; Palleroni et al. 2005).

Many animals use chemical cues to identify predators and to assess the risk of predation (Kats & Dill 1998), and some species show threat-sensitive responses to chemical cues. For example, goldfish, *Carassius auratus*, show stronger antipredator responses as the concentration of predator odours increases (Zhao et al. 2006). Similarly, naïve Arctic charr, *Salvelinus alpinus*, only avoided odours of predatory brown trout, *Salmo trutta*, when the predators were fed on charr (Hirvonen et al. 2000). Despite numerous studies on aquatic organisms, few studies have investigated whether terrestrial vertebrates also show threat-sensitive responses to predator chemicals. Lizards are ideal model organisms for examining this question because they have a highly developed chemosensory system and can identify predators using chemical cues (Schwenk 1993a, b; Cooper 1994). Several lizard species also display stereotyped antipredator behaviours, including tail waving, foot shaking and freezing in the presence of snake chemicals (Thoen et al. 1986; Dial & Schwenk 1996; Downes & Shine 1998). However, it is less

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clear whether lizards generally show threat-sensitive responses to predator chemicals. Some species display antipredator behaviours in response to chemicals from dangerous snakes (i.e. those that eat lizards), but not in response to chemicals from nondangerous species (Thoen et al. 1986; Dial & Schwenk 1996; Downes & Shine 1998; Van Damme & Quick 2001; Bealor & Krekorian 2002). By contrast, Amo et al. (2004) reported that wall lizards, *Podarcis muralis*, did not respond differently to chemicals of saurophagous and nonsaurophagous snakes that posed different risks and that had different foraging modes. Similarly, Stapley (2003) found that mountain log skinks, *Pseudemoia entrecasteauxii*, offered the choice between an unscented and a snake-scented refuge avoided the snake-scented refuge, irrespective of the degree of threat posed by the snake.

This variation in the responses of lizards to predator chemical cues makes it difficult to determine the causal factors responsible for the maintenance of species-specific antipredator behaviours. In the absence of predators, costly antipredator behaviours can be lost, and prey may respond only to syntopic predators (e.g. Berger et al. 2001). However, when traits are not costly, prey may show strong antipredator responses to absent or rare predators (Byers 1997; Coss 1999). The ‘multipredator hypothesis’ (Blumstein et al. 2004) predicts that when antipredator behaviours are genetically linked, or function in multiple contexts, prey species that occur with multiple predators may evolve specific behaviours to reduce predation risk in response to each predator, but their expression is not predicted to vary independently. In other words, the presence of a single predator can maintain antipredator behaviours for other predators that are rarely encountered (Blumstein et al. 2006). For example, although we might expect prey to show differential responses to predators that hunt in different ways (e.g. ambush versus active foraging) or that use different habitats, prey may show generalized antipredator behaviours (e.g. reducing activity levels) that lower their risk of predation in the presence of multiple predators (Sih et al. 1998). Provided that costs associated with antipredator behaviours are low, species-specific responses to different predators may be difficult to evolve and maintain (Coss 1999; Blumstein 2006). Mathematical models for the evolution of phenotypic plasticity under different environmental conditions predict the same result: specific responses to different enemies are difficult to evolve when prey encounter multiple predators, but each predator is only encountered rarely (Via & Lande 1985; van Tienderen 1991).

The Australian velvet gecko, *Oedura lesueurii*, is an ideal model for investigating whether lizards show threat-sensitive antipredator behaviours to odours of snake predators that differ in their dangerousness. Previous studies have shown that velvet geckos display predator-specific behaviours to chemicals from a predatory snake species that consumes geckos (the broad-headed snake, *Hoplocephalus bungaroides*) but do not respond to odours from a snake that feeds mostly on skinks (the small-eyed snake, *Cryptophis nigrescens*, Downes & Shine 1998). When velvet geckos encounter broad-headed snake chemicals, they reverse or run away from the scent, and some individuals raise their tails into the air and slowly move them from left to right (Downes & Shine 1998). This tail-waving display occurs in several other species of geckos in response to live snakes or snake chemicals (Congdon et al. 1974; Dial 1978). Experiments involving both predators and prey have shown that the tail-waving display of geckos serves to direct the predator’s attack to the tail, which is then autotomized, allowing the lizard to escape (Congdon et al. 1974; Daniels et al. 1986). Thus, tail-waving displays have probably evolved to promote prey survival during encounters with predators.

The species-specific response by velvet geckos to a single snake predator, the broad-headed snake, is unexpected, because velvet geckos are syntopic with several species of elapid snakes that prey on geckos (Cogger 2000). Some of these snakes (e.g. whip snake, *Demansia psammophis*, small-eyed snake) occur on the same rock outcrops, and use the same shelter sites (rocks) as velvet geckos, so that velvet geckos are likely to have encountered multiple snake predators over evolutionary time. Unless avoiding snake scent or tail waving involves significant energetic costs, a gecko that responds to a nondangerous snake is unlikely to be disadvantaged. More importantly, because most elapid snakes that velvet geckos encounter are potentially lethal, the optimal response by a gecko should be to treat all snakes as potentially dangerous (e.g. Amo et al. 2006), because the benefits of doing so far outweigh the costs involved with making a wrong decision (i.e. death of the gecko).

The multipredator hypothesis (Blumstein 2006; Blumstein et al. 2006) predicts that velvet geckos should display general antipredator behaviours to the scent of syntopic elapid snakes, irrespective of how frequently they are encountered, or the degree of threat they pose. In contrast, the threat-sensitive paradigm predicts that velvet geckos should ignore the scent of nonthreatening species, but should respond intensely (and perhaps even in different ways to different predator species) to snakes that pose a higher degree of threat (Helfman 1989; Downes & Shine 1998). To test between these alternative predictions, we videotaped the behaviour of adult velvet geckos in the presence of chemical cues from five species of elapid snakes that differ both in their attack strategy (ambush versus active foraging) and in their degree of danger to geckos.

METHODS

The Prey and the Predators

Velvet geckos occur in sandstone rock outcrops throughout coastal regions of New South Wales, Australia. These small (to ca. 65 mm snout–vent length) nocturnal lizards thermoregulate underneath sandstone rocks or inside crevices during the day (Schlesinger & Shine 1994; Webb 2006), and emerge at dusk to forage for invertebrate prey in leaf litter (Cogger 2000). Thus, geckos may encounter several species of ambush and actively foraging snakes that hunt in leaf litter or on rock outcrops, or that use rocks as shelter sites.

We used five species of elapid snakes that are all sympatric with velvet geckos. The bandy-bandy, *Vermicella annulata*, feeds entirely upon blind snakes (genus *Ramphotyphlops*) and hence poses no threat to geckos (Shine 1980a; Keogh & Smith 1996). Small-eyed snakes shelter under stones on rock outcrops (Webb et al. 2003), and feed mostly on sleeping skinks (Shine 1984). This species will consume velvet geckos in the laboratory, but rarely does so in the wild, apparently because both species forage at night, and alert geckos can easily escape these slow-moving predators (J.K. Webb & R. Shine, unpublished data). Whip snakes are diurnal active searchers that feed mostly on skinks, and occasionally consume velvet geckos (Shine 1980b). Whip snakes not only occur on the same rock outcrops as velvet geckos, but also shelter under rocks, therefore posing a risk to geckos. Death adders, *Acanthophis antarcticus*, ambush lizards (including geckos) and small mammals from camouflaged sites in leaf litter (Shine 1980c). Finally, broad-headed snakes feed on lizards, including velvet geckos, and shelter under rocks similar in size to those used by geckos; these ambush foragers clearly pose a major risk to the lizards (Webb & Shine 1998). With the exception of the broad-headed snake, each of these snake species has a large geographical range that overlaps with the velvet gecko’s geographical range (Cogger 2000). Broad-headed snakes have a small geographical range, which overlaps entirely