Generalization of predator recognition: Velvet geckos display anti-predator behaviours in response to chemicals from non-dangerous elapid snakes

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Abstract Many prey species detect chemical cues from predators and modify their behaviours in ways that reduce their risk of predation. Theory predicts that prey should modify their anti-predator responses according to the degree of threat posed by the predator. That is, prey should show the strongest responses to chemicals of highly dangerous prey, but should ignore or respond weakly to chemicals from non-dangerous predators. However, if anti-predator behaviours are not costly, and predators are rarely encountered, prey may exhibit generalised anti-predator behaviours to dangerous and non-dangerous predators. In Australia, most elapid snakes eat lizards, and are therefore potentially dangerous to lizard prey. Recently, we found that the nocturnal velvet gecko Oedura lesueurii responds to chemicals from dangerous and non-dangerous elapid snakes, suggesting that it displays generalised anti-predator behaviours to chemicals from elapid snakes. To explore the generality of this result, we videotaped the behaviour of velvet geckos in the presence of chemical cues from two small elapid snakes that rarely consume geckos: the nocturnal golden-crowned snake Cacophis squamulosus and the diurnal marsh snake Hemiaspis signata. We also videotaped geckos in trials involving unscented cards (controls) and cologne-scented cards (pungency controls). In trials involving Cacophis and Hemiaspis chemicals, 50% and 63% of geckos spent long time periods (> 3 min) freezing whilst pressed flat against the substrate, respectively. Over half the geckos tested exhibited anti-predator behaviours (tail waving, tail vibration, running) in response to Cacophis (67%) or Hemiaspis (63%) chemicals. These behaviours were not observed in control or pungency control trials. Our results support the idea that the velvet gecko displays generalised anti-predator responses to chemical cues from elapid snakes. Generalised responses to predator chemicals may be common in prey species that co-occur with multiple, ecologically similar, dangerous predators [Current Zoology 56 (3): 337–342, 2010].

Key words Predation risk, Chemical cues, Lizard, Elapidae, Gekkonidae, Olfaction, Multipredator

Many prey species use chemical cues to detect and discriminate among predators (Kats and Dill, 1998; Wisenden, 2000). After detecting predator chemicals or chemicals from injured conspecifics, aquatic and terrestrial animals typically reduce their activity levels and avoid using risky habitats (Chivers and Mirza, 2001; Chivers and Smith, 1998; Weldon, 1990). However, responding to predator odours can also entail costs, such as lost opportunities for foraging and reproduction (Lima, 1998; Lima and Dill, 1990). The threat sensitivity hypothesis posits that when anti-predator behaviours are costly, prey should match the intensity of their anti-predator behaviours to the degree of threat posed by the predator (Helfman, 1989). That is, in the absence of other cues, prey should show stronger responses to chemical cues of dangerous predators, but should show weaker responses to cues from harmless or non-threatening predators. Such threat-sensitive responses to predator chemicals have been documented in fish, birds, invertebrates, and lizards (Mirza and Chivers, 2001; Persons and Rypstra, 2001; Thoen et al., 1986; Turner, 2008). For example, aquatic organisms often show stronger anti-predator responses to predators which have fed on conspecifics (Chivers and Mirza, 2001). Likewise, some fish increase the duration and intensity of antipredator behaviour as the concentration of alarm or predator chemicals increases (Kesavaraju et al., 2007; Mirza et al., 2006; Zhao and Chivers, 2005). To date, most research on this topic has focused on aquatic organisms, and consequently, less is known about how terrestrial animals respond to predator chemicals.
For prey to respond adaptively to predation risk, they must first recognise and discriminate between predators that differ in threat. Intriguingly, some prey species show similar antipredator responses to novel predators that are rarely encountered. For example, black-tailed deer *Odocoileus hemionus colombianus* display antipredator behaviours to models of a cougar, their major predator, and also to models of a tiger, a novel predator. Likewise, tammar wallabies *Macropus eugeni* which were trained to recognize red foxes as predators subsequently generalized their antipredator behaviours towards models of the feral cat. These studies demonstrate that some prey species display ‘generalization of predator recognition’ (Ferrari et al., 2007). Such predator generalisation is predicted to enhance fitness in prey species that co-occur with multiple taxonomically similar predators, and in situations where predation predictability is low (Blumstein, 2006; Ferrari et al., 2007). In these circumstances, generalised rather than species-specific responses may benefit prey. For example, prey that live in an environment where most snake predators are dangerous would benefit by generalising their predator recognition to all snakes, including non-dangerous species, because failing to respond to a snake would be fatal (Webb et al., 2009).

One prey species that displays generalised antipredator behaviours to predator chemicals is the nocturnal velvet gecko *Oedura lesueurii* (Webb et al., 2009; Webb et al., 2010). This small gecko has a broad geographic range, and is sympatric with at least 10 species of lizard-eating snakes from the family Elapidae (Cogger, 2000). Recently, we found that velvet geckos exhibited similar anti-predator behaviours in response to chemicals from five species of elapid snakes, including a harmless species (bandy bandy *Vermicella annulata*) that feeds entirely on blind snakes (Webb et al., 2009). We argued that velvet geckos should show generalised antipredator behaviours towards chemical cues from elapid snakes, irrespective of their diets, because most snakes that geckos encounter consume lizards, and hence are potentially dangerous (Webb et al., 2010).

In this paper, we investigate whether velvet geckos respond to chemical cues of two additional species of elapid snakes: the harmless golden-crowned snake *Cacophis squamulosus* and the potentially dangerous swamp snake *Hemiaspis signata*. Based on available dietary and habitat-use data, *C. squamulosus* does not eat geckos, whereas *H. signata* encounters geckos very rarely because of the snakes’ preference for swampy habitats (see below). Hence, both snake species are likely to represent ‘low-risk’ predators, rarely posing a threat to velvet geckos.

## 1 Materials and Methods

### 1.1 The prey and the predators

The velvet gecko is a small nocturnal lizard (to 65 mm snout-vent length) that inhabits sandstone rock outcrops in eastern Australia. This species has a broad geographic range from southern New South Wales to Queensland, and throughout its range it co-occurs with multiple species of elapid snakes that consume lizards (Cogger, 2000). By day velvet geckos thermoregulate underneath sandstone rocks or inside crevices, and they emerge at dusk to forage for invertebrate prey in leaf litter (Cogger, 2000; Schlesinger and Shine, 1994; Webb, 2006). Thus, velvet geckos likely encounter both diurnal and nocturnal snakes that hunt in leaf litter or on rock outcrops, or which use sandstone rocks as shelter sites.

The swamp snake *Hemiaspis signata* is a small elapid snake (to 600 mm snout-vent length) that feeds mostly on lizards and frogs (Shine, 1987). Swamp snakes are active diurnally, but are also encountered foraging at night on warm evenings, and they occasionally eat geckos, which comprise less than 1% of the diet (Shine, 1987). Hence, swamp snakes are potentially dangerous to velvet geckos. The golden-crowned snake *Cacophis squamulosus* is a small (to 600 mm SVL) nocturnally active elapid that feeds mostly on skinks, and occasionally frogs (Shine, 1980). Dissections of museum specimens revealed that this species does not consume geckos (Shine, 1980), so based on its diet, it is non-dangerous to geckos. Both snake species are widely distributed along eastern Australia (Cogger, 2000) and occur in a diversity of habitat types, but swamp snakes are most abundant in swamps or riparian habitats, and hence, they probably rarely encounter velvet geckos.

### 1.2 Collection of animals and husbandry

We collected 30 adult velvet geckos (12 males, 18 females) from rock outcrops adjacent to Morton National Park during late winter and spring (August–October) 2004. We collected swamp snakes (four males, 370–473 mm SVL) and golden-crowned snakes (3 males, 352–523 mm SVL) from Olney State Forest, near Gosford, NSW. Upon capture, we placed each animal in a cloth bag and recorded the location of capture with a GPS (Garmin GPS 12XL, USA). We housed the geckos and snakes at the University of Sydney in separate temperature-controlled rooms maintained at 18°C with lighting set to match the natural photoperiod.
We housed reptiles individually in ventilated plastic cages (lizards: 22 × 13 × 7 cm; snakes: 31 × 22 × 10 cm), with a paper substrate, a plastic shelter, and a water dish. All cages were placed on automated heating racks (10:00–16:00 h) that provided a thermal gradient within each cage (18–32°C) so that the reptiles could thermoregulate. We fed geckos crickets dusted with a calcium supplement twice weekly, but snakes were not fed during their brief stay in captivity. We kept geckos in captivity for six weeks and we kept snakes for up to two weeks. At the end of the study, we released all animals to their exact site of capture in the field. All animals were collected under permits issued by the New South Wales Parks and Wildlife Service, and laboratory housing and experimental procedures were approved by the University of Sydney Animal Ethics Committee.

1.3 Behavioural trials

We conducted behavioural trials in a controlled temperature room (20°C) illuminated by a single red 25 W globe. For each trial, we used forceps to place a black piece of cardboard (110 × 100 mm) on the bottom of a clean test arena (110 × 100 × 90 mm, n = 9, with tight-fitting lids and small holes in the sides for ventilation). We thoroughly washed test enclosures with bleach, rinsed them with fresh water, and dried them with paper towelling before each trial. Snake-scented cards were used for experimental trials, unscented cards were used for control trials, and cards sprayed with cologne (Autumn Leaf, Arion Perfume & Beauty Inc.) were used in pungency control trials. To obtain snake-scented cards, we placed a fresh card inside the plastic shelter of the donor snake predator for two days. Each donor snake was used twice (i.e. deposited scent on cardboard for two trials). For each trial, we used a new card to ensure that the scent from previous trials did not influence the behaviour of the new test gecko. To begin a trial, we gently placed a gecko on the card in the test arena, closed the lid, and turned on a video recorder. We then exited the room and left the lizards undisturbed for 10 min. We carried out trials after dusk, and the order of trials was randomised.

We used a between-subjects design, whereby each gecko (n = 30) was tested once in a single trial, with eight geckos randomly allocated to each scent treatment, except in the golden-crowned snake trials (n = 6). We used this design, rather than a repeated measures design, to minimise stress to geckos, and to avoid carry-over effects that could occur if a gecko’s behaviour in multiple trials was influenced by its previous exposure to snake scent.

For each videotaped trial, we disregarded the first 10 s, and thereafter we scored the frequency (1 to 6) and duration (7 to 10) of the following behaviours: (1) Tail wave: the gecko raises its entire tail above the horizontal, and holds it stationary or slowly moves it from side to side. (2) Tail vibration: the tail or tail tip is wiggled from side to side, but is not raised above the horizontal plane. (3) Reverse: the lizard reverses either slowly or rapidly. (4) Lunge: the gecko throws its body forward and then stops. (5) Run: the gecko suddenly runs forward and attempts to escape from the test arena. (6) Freezing, ventrum raised: the gecko remains motionless, either on the floor, walls or roof of the test chamber, with its ventrum raised above the substrate. (7) Freezing, body pressed flat: the gecko remains motionless, either on the floor, walls or roof of the test chamber, with its ventrum pressed against the substrate. (8) Slow motion: the lizard crawls slowly with stalking movements, sometimes accompanied by jerky or waving movements of the forelimbs, with the belly in contact with or close to the substrate (9) Crawl: the gecko crawls slowly with the belly in contact or close to the substrate (10) Walk: the gecko displays continuous forward movement, with the ventrum raised off the substrate, typically observed in unrestrained geckos. Geckos were also observed pushing their snouts against the clear arena walls whilst walking on the arena floor and vertical walls, and this behaviour was included in our category ‘walk’.

1.4 Statistical analyses

Prior to statistical analyses, we checked that the data were normally distributed and that variances were homogeneous, and transformed data where necessary. Because a subset of behaviours (freezing body pressed flat, crawling and slow motion) were interpreted as anti-predator behaviours in a previous study on responses to broad-headed snake scent (Downes and Adams, 2001), we summed these behaviours and analysed the single variable “anti-snake locomotor behaviour” after arc-sin transformation. We square root transformed the number of tongue flicks and arc-sin transformed proportional data prior to statistical analysis. We treated controls and pungency controls as separate factors in all analyses (i.e. we did not pool results for control and pungency control trials). Hence, there were four treatments (golden-crowned snake odour, swamp snake odour, control, and pungency control) in all analyses. We used contingency table analysis to compare the proportion of geckos in each treatment that exhibited tail displays (tail waving or tail vibration) or which reversed or ran during trials.
was used to determine whether the number of tongue-flicks and proportions of time spent walking, freezing, or engaging in antisnake locomotion differed among treatments.

2 Results

The proportion of geckos which exhibited tail displays, or which ran and reversed, was higher in trials involving snake scent than in control trials (contingency table analysis, $\chi^2 = 14.70$, df = 3, $P = 0.002$, Fig. 1). However, when we excluded data from controls, the proportion of geckos which exhibited antipredator displays was similar in both snake species (tail displays: $\chi^2 = 2.43$, df = 1, $P = 0.11$; run or reverse: $\chi^2 = 0.39$, df = 1, $P = 0.53$). Geckos spent longer periods of time engaged in antisnake locomotion (freezing or crawling with the ventrum against the substrate, and slow motion) in trials involving snake scent than in control trials ($F_{3, 26} = 6.04$, $P = 0.003$; LSD post-hoc tests, all $P < 0.05$; Fig. 2). In trials involving Cacophis and Hemiaspis chemicals, 50% and 63% of geckos spent long time periods (> 3 min) freezing whilst pressed flat against the substrate, respectively. By contrast, lizards spent more time walking in control trials than in trials involving snake scent ($F_{3, 26} = 5.20$, $P = 0.006$, LSD post hoc tests, all $P < 0.05$). The proportion of time that lizards spent “freezing” with their ventrum raised off the substrate did not differ among treatments ($F_{3, 26} = 1.49$, $P = 0.24$). The number of tongue-flicks exhibited by geckos varied among treatments ($F_{3, 23} = 4.00$, $P = 0.02$), but post-hoc tests showed that means were not significantly different (Fig. 3).

![Fig. 1](image1.png)

**Fig. 1** The proportion of velvet geckos *Oedura lesueurii* that exhibited tail displays (black bars) or ran or reversed (open bars) when exposed to unscented cards (controls), cologne-scented cards (pungency controls) and cards containing chemical cues from the non-dangerous golden-crowned snake and potentially dangerous swamp snake

Geckos only displayed anti-predator behaviours in trials involving snake chemicals.

![Fig. 2](image2.png)

**Fig. 2** The proportion of the 10 min trial that velvet geckos spent engaged in anti-snake locomotion (freezing or crawling with the ventrum against the substrate, and slow motion) in trials with unscented cards (controls), cologne-scented cards (pungency controls) or cards containing chemical cues from the non-dangerous golden-crowned snake and potentially dangerous swamp snake.

Geckos spent more time using anti-snake locomotion in trials involving snake scent than in control trials. Graph shows mean values of untransformed data, and error bars denote standard errors.

![Fig. 3](image3.png)

**Fig. 3** The mean number of tongue extrusions made by velvet geckos in 10 min during exposure to unscented cards (controls), cologne-scented cards (pungency controls) and cards containing chemical cues from the non-dangerous golden-crowned snake and potentially dangerous swamp snake.

The mean number of tongue-flicks did not differ among treatments. Error bars denote standard errors.

3 Discussion

Velvet geckos showed similar antipredator behaviours to chemical cues of the non-dangerous golden-crowned snake and the potentially dangerous (but rarely encountered) swamp snake. In the presence of chemicals from both snake species, velvet geckos exhibited several overt anti-predator behaviours (running, tail waving, and freezing), and spent long time...
periods using anti-snake locomotor behaviours. Potentially, these antipredator behaviours may reduce a gecko’s risk of predation during encounters with snakes. For example, tail waving occurs in many gecko species, and functions to direct predatory attacks towards the gecko’s tail (Dial, 1978). If the gecko’s tail is grasped by the predator, the tail is rapidly autotomised, thereby allowing the gecko to escape whilst the predator chases or consumes the wriggling tail (Congdon et al., 1974). Likewise, geckos which suddenly run or lunge away from snake scent may avoid predatory strikes from hidden snakes, and geckos which press flat against the substrate may avoid detection by visually hunting snakes (Downes and Shine, 1998).

Velvet geckos responded to chemicals of the golden crowned snake, even though this species does not consume geckos. This result supports the ‘predator recognition continuum hypothesis’, which suggests that when the ratio of predators to non-predators is high, prey should generalise predator recognition, and should respond both to dangerous and non-dangerous predators (Ferrari et al., 2007). In Morton National Park, velvet geckos co-occur with nine species of elapid snakes, all of which are potentially dangerous (Cogger, 2000). Hence, geckos which fail to respond to odours of a novel snake predator would have a high probability of death. Although the present study involved filming the behaviour of geckos in small cages that prevented prey from avoiding the snake scent, experiments in larger arenas show that velvet geckos avoid retreat-sites scented by less-dangerous as well as very-dangerous snakes (Webb et al., 2010). Velvet geckos also avoid rocks chemically labelled by snakes at our field sites, suggesting that these lizards use the simple rule of thumb ‘all snakes are dangerous’ to reduce their risk of predation (Webb et al., 2010).

One unanswered question is whether geckos display innate or learnt responses to snake chemical cues. Because elapids belong to a single lineage, geckos may respond to a chemical common to the skin of all elapid snakes (Webb et al., 2009). If so, we predict that geckos from geographically distinct populations should show similar responses to elapid snakes, irrespective of the number of snake predators syntopic with geckos, or the degree of danger that they pose (Blumstein, 2006). If learning is required for geckos to recognise snake predators, then the degree of dangerousness of the snake which geckos first encounter during conditioning could affect their subsequent responses to novel snake predators (Ferrari et al., 2007). For example, Ferrari et al. (2007) showed that the concentration of conspecific alarm cues that fathead minnows encountered during conditioning affected their subsequent ability to generalise their responses to other fish predators. When minnows learnt that brown trout were a high-level threat, they subsequently generalised their responses to rainbow trout; by contrast, minnows which perceived brown trout as a low threat did not generalise their responses to rainbow trout. In the present study, we used adult geckos from a population syntopic with the highly dangerous gecko-eating broad-headed snake Hoplocephalus bungaroides. Hence, it is possible that geckos from our study population had learnt to recognise all snakes as dangerous because their initial conditioning involved a high-risk predatory snake. Experiments involving naïve geckos, similar to the recent studies on predator recognition in fish (Ferrari et al., 2007; Ferrari et al., 2008), would help us to understand which factors affect the ability of prey to recognise and respond to chemical cues of multiple predators.

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