

Sedentary snakes and gullible geckos: predator–prey coevolution in nocturnal rock-dwelling reptiles

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Abstract. We investigated (1) the importance of chemical cues for predator detection by the nocturnal, rock-dwelling velvet gecko, *Oedura lesueurii*, and (2) how the lizards' responses to snake odour may have exerted selection on the foraging behaviours of a nocturnal elapid snake. This snake species (broadheaded snake, *Hoplocephalus bungaroides*) feeds primarily on velvet geckos, and does so by means of a distinctive foraging behaviour: the snakes remain sedentary in rock crevices for days or weeks, waiting to ambush geckos. Behavioural assays showed that geckos that are sympatric with this sedentary 'ambush' predator can detect and respond to the scent of the snake. Retreat-site selection experiments showed that geckos are less likely to enter crevices if the snake's scent is distributed over the entire rock surface, rather than localized to a central portion. Together, these data support the notion that the 'ambush' predator benefits by remaining sedentary within a retreat-site for long periods, because it thereby minimizes the extent to which it spreads its scent over the rocks forming the crevice. Geckos from a population sympatric with the 'ambush' predator responded strongly to the snake scent, but those from an allopatric population did not. Additionally, geckos from sympatric populations were able to detect the scent of a nocturnal snake that does not eat geckos (small-eyed snake, *Rhinoplocephalus nigrescens*), but did not modify their retreat-site selection or locomotory behaviours in response to this cue. Lizards from allopatric populations apparently did not detect the scent of small-eyed snakes. Collectively, our findings support an interpretation of predator-prey coevolution in the present system, and emphasize the importance of chemosensory cues to these rock-dwelling reptiles.

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Predators are believed to be important agents of selection and to elicit a remarkable variety of adaptations in the organisms upon which they prey (for reviews see [Edmunds 1974](#); [Curio 1976](#); [Morse 1979](#); [Vermeij 1987](#)). If so, selection to maintain or enhance traits that minimize vulnerability to predation is likely to occur in the vast majority of prey populations. Other things being equal, such selection should be stronger in populations that are exposed to high levels of unsuccessful predation attempts, than in populations that (because they are easy victims or live in habitats with few predators) sustain low levels of unsuccessful attack ([Abrams 1986](#)). The theory of evolution by natural selection predicts that prey defences should improve at the same time that predator efficiency increases ([Vermeij 1994](#)). There

is also some evidence that prey can balance the costs and benefits of predator avoidance by distinguishing between hunters with different predatory abilities, and responding more strongly to abundant, active, or efficient species than to less dangerous ones (e.g. [Walther 1969](#); [Peckarsky 1980](#); [Soluk & Collins 1988](#); [Dickman 1992](#)).

Although much theory exists on the coevolution of predators and prey (for reviews see [Vermeij 1982](#); [Futuyma & Slatkin 1983](#); [Vermeij 1994](#)), there are relatively few good empirical examples that support these models, especially for vertebrates. Three types of evidence are needed to support such an interpretation. First, the prey's behaviours should suit the predator's foraging tactics: for example, guppies, *Poecilia reticulata*, minimize predator risk during courtship by shifting visually conspicuous display to times of the day when the risk from visually oriented predators is minimal ([Endler 1987](#)). Second, the predator's

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foraging tactics should suit its prey's features: for example, the garter snake, *Thamnophis sirtalis*, is resistant to the chemical defences of its prey (the toxic newt, *Taricha granulosa*; Brodie & Brodie 1990, 1991). Finally, these 'coevolved traits' should be absent in areas where the predator-prey interaction is not significant (i.e. in areas where predator and prey are allopatric: Dickman 1992).

Snakes and lizards offer an excellent system for studying many aspects of predator-prey coevolution. Vision and chemoreception are the two primary senses by which lizards can recognize the proximity of a potential snake predator. For many species, keen vision allows detection of moving hunters at a distance sufficient for the lizard to avoid detection, or evade the attacking snake. However, because snakes (especially nocturnal hunters) are not always visible to their prey, chemical stimuli from predators may provide other important cues (for examples see Berry 1974; Thoen et al. 1986; Dial et al. 1989; Cooper 1990; Van Damme et al. 1990, 1995; Phillips & Alberts 1992). Hence, the ability to detect chemical cues of predators may be particularly important for nocturnal lizards, and the chemical senses of these reptiles might have evolved to enable very specific responses to snake predator odours. In such cases, we might expect lizards to be particularly sensitive to the odour of cryptic 'sit-and-wait' snake predators; unlike active foragers (which move over large areas), the scent of a sedentary 'ambush' predator provides a strong and reliable indication of danger. In response, it would be of benefit to such predators to evolve behaviours that minimize their chance of disseminating scent which may be detected by prey. We might also expect lizards to be able to distinguish between the scents of predatory and non-predatory snakes so that they could balance the costs and benefits of predator avoidance.

In this paper, we describe the results of two complementary laboratory studies that investigate (1) the importance of chemical cues for predator detection by a nocturnal rock-dwelling gecko, and (2) how the lizards' responses to snake odour might have exerted selection on the foraging behaviours of a nocturnal snake that employs an extreme sit-and-wait foraging strategy. We first investigated whether geckos are able to detect and discern the odours of two species of nocturnal snakes that also inhabit rock outcrops. One of the species preys heavily on these lizards, whereas the

other species (although also saurophagous) does not consume geckos. We also tested the ability of the geckos to detect snake scent that is localized within a central portion of a retreat-site versus spread more widely over a larger portion of the rock, because this distinction has strong implications for movement patterns by the snakes. For both of these experiments, we tested the responses of geckos from two populations, only one of which was sympatric with the snakes.

MATERIALS AND METHODS

The Study System

Our study animal is a small (in our study populations, up to 60 mm snout-vent length) nocturnal, terrestrial lizard (velvet gecko, *Oedura lesueurii*) which occurs in rocky outcrops from northern Queensland to southern New South Wales in eastern Australia (e.g. Cogger 1957; Swan 1990). During the day, these geckos remain in diurnal retreat-sites beneath sandstone (Schlesinger & Shine 1994; Webb 1996). They emerge to forage actively at nightfall, and assess a wide range of structural, microclimatic and social aspects of potential shelters before selecting suitable retreat-sites for the following day (Schlesinger & Shine 1994).

Broadheaded snakes, *Hoplocephalus bungaroides*, and small-eyed snakes, *Rhinoplocephalus nigrescens*, are relatively small (on average, 50–60 cm snout-vent length), nocturnal, rock-dwelling, saurophagous elapids that occur sympatrically with velvet geckos over most of their range (e.g. Cogger 1994; Webb 1996). There is considerable overlap in the types of retreat-sites selected by the geckos and the snakes (Webb 1996), and thus a high potential for the coevolution of behaviours associated with predation. Analyses of the stomach contents of broadheaded snakes indicate that this species feeds primarily on velvet geckos (J. Webb, unpublished data). Moreover, when given the choice between similar-sized velvet geckos and scincid lizards, *Lampropholis* spp., captive broadheaded snakes consistently choose the former as their first item of prey (S. Downes, personal observation). In contrast, small-eyed snakes do not consume geckos; scincid lizards make up most of their diet (Shine 1984; J. Webb, unpublished data), and captive snakes consistently refuse to feed on velvet geckos

(S. Downes, personal observation). We predicted that it would be advantageous for the geckos to be able to distinguish between the scents of these snakes, because they would benefit not only from avoiding broadheaded snakes, but also by recognizing that small-eyed snakes are not a threat, and hence not a reason to compromise their selection of optimal habitats. Additionally, recent studies have shown that broadheaded snakes employ an unusual foraging strategy to capture their prey: they are extremely sedentary sit-and-wait hunters, with most radiotracked snakes spending long periods (up to 4 weeks) under the same rocks waiting for lizards to venture near or under their crevice (Webb 1996, unpublished data). Why are these snakes so remarkably sedentary? One likely explanation (which stimulated this study) is that this foraging tactic minimizes their chance of disseminating scent that may be detected by a gecko assessing suitable retreat-sites. The foraging behaviour of small-eyed snakes is less well known, but is thought to involve active searching for sleeping prey (diurnally active skinks) from within or under logs and rocks (Shine 1984; Webb 1996).

To sustain an interpretation of predator-prey coevolution, we needed information about the responses of lizards obtained from different populations that were sympatric and allopatric with broadheaded snakes and small-eyed snakes. We collected 19 adult geckos from each of two locations in coastal and near-coastal New South Wales, during July and August 1996: Cape Banks (151°15'E, 34°01'S) and Sassafras (150°20'E, 35°06'S). Mean snout-vent length (mm) and mass (g) were: 50.0, 3.4 and 50.6, 4.1, respectively. Cape Banks is an exposed coastal rock platform 20 km southeast of Sydney, at the edge of Botany Bay National Park. Broadheaded snakes and small-eyed snakes do not currently occur at Cape Banks, to the best of our knowledge (Shine et al. 1995), but historical records suggest that they were present at the time of the European invasion of Australia (Krefft 1869). Sassafras is a sandstone outcrop surrounded by dry sclerophyll forest 160 km south of Sydney, in Morton National Park, and contains large numbers of both broadheaded snakes and small-eyed snakes (Webb 1996). In August 1996, we captured two broadheaded snakes (385 and 495 mm snout-vent length) and two small-eyed snakes (585 and 757 mm) from Sassafras.

Animals and their Maintenance

We housed the geckos and snakes at the University of Sydney in separate temperature-controlled rooms maintained between 17 and 22°C, and all of the animals were provided with a heat source (that attained 35°C) between 0800 and 1600 hours (to mimic the range of operative environmental temperatures selected in their natural environment). The light cycle was the natural cycle of the surrounding area. The lizards were kept in individual soil-filled plastic cages that contained a sandstone shelter, and fed mealworms once a week. The snakes were maintained individually in identical plastic tubs (62 × 41 × 28 cm), the floor of which was lined with paper. A shelter was positioned at each end of the tub, and the constituent portions were used in our experiments (see below). Each shelter measured 20 × 20 × 1.5 cm, and was made from two layers of unglazed sandstone slabs (either, one measuring 20 × 10 × 1.5 cm abutting three measuring 6.6 × 10 × 1.5 cm; or two abutting slabs of 20 × 10 × 1.5 cm), separated vertically by squares 1 mm thick (20 mm²) of plastic sheet. We varied the thickness of the crevice to ensure that each snake made contact with both the upperside of the bottom slab and the underside of the top slab. To ensure that the snake used both retreat-sites within its cage, we moved the heat source (one 75-W bulb) over one or other shelter several times throughout the day; the snake would typically follow. All of the animals were supplied with water ad libitum.

Small-eyed snakes were fed on skinks as they do not eat laboratory mice. We first attempted to use humanely culled lizards but the snakes also refused to eat these. An adult skink was confined in the half of the cage that did not contain the snake shortly before the dark period and allowed to settle in the vacant retreat-site. We would have removed skinks that showed any signs of distress but this did not occur. The cage divider was removed after the lights were switched off to allow the snake to forage. The predation event was instantaneous when the snake encountered the sleeping skink.

Broadheaded snakes were also fed on live skinks to avoid any potentially confounding effects of predator diet on the geckos' responses to scent (e.g. Laurila et al. 1997 and references within). Since we succeeded in capturing only

immature broadheaded snakes, and intended to return these to the wild at the end of the study, it was also necessary to feed them on live lizards rather than pre-killed prey items. Although it is possible to feed juvenile snakes on pre-killed day-old mice (Shine & Fitzgerald 1989), this involves force feeding which can be stressful to the snakes and involves significant risk of injury to their mouths and danger to the handler. We thus kept the snakes for the minimum period required for the study and attempted to minimize any suffering experienced by their prey. The skink and snake were confined to the same half of the snake's cage and the lizard was always consumed within 5 min of entering the snake's retreat-site (the time limit after which uneaten prey would have been removed). The predation event was instantaneous and the skinks were killed very quickly by the potent venom of the snake.

Experimental Procedure

Chemical detection of predators

We placed a gecko on to a treated rock (two abutting sandstone slabs measuring $20 \times 10 \times 1.5$ cm) covered with a clear plastic test box ($21 \times 21 \times 8$ cm). The rock had been treated in one of six ways: (1) fresh (neutral control), the rocks had never been covered with snake scent; (2) cologne (chemical pungency control), the rocks had been sprayed with a 1:1 solution of commercial cologne ('Confess') and distilled water; (3) small-eyed snake control, the rocks had been used for shelter by a small-eyed snake but had been thoroughly washed (see below); (4) broadheaded snake control, the rocks had been used for shelter by a broadheaded snake but had been thoroughly washed (see below); (5) small-eyed snake, the rocks had been used as shelter by a small-eyed snake; and (6) broadheaded snake, the rocks had been used as shelter by a broadheaded snake. We included treatments (3) and (4) to confirm the efficiency of our cleaning method (see below), so that we could be confident that the geckos in the retreat-site selection experiment (see below) were in fact responding to the immediate treatment, and not to the residual scent from a previous trial.

Observations started ca 10 s after transfer of the lizard to the test box. The lizard's behaviour was then observed continuously for 12 min from behind a blind. We directly recorded on to com-

puter (using an event recorder created using Microsoft QuickBASIC) either the frequency (1 to 8) or duration (9 to 13) of the following behavioural acts and locomotor patterns.

- (1) Tongue-extrusion: the lizard extrudes and rapidly retracts its tongue, regardless of whether the tongue touches the substrate or is 'waved' in the air.
- (2) Tail-raise: the entire tail is raised above the horizontal, but is not moved laterally.
- (3) Tail-vibration: the entire tail, or its posterior, is moved rapidly from side to side.
- (4) Stand up: the lizard stands in an upright position against the wall of the test box and attempts to adhere to this vertical wall with its forelegs.
- (5) Reverse: the lizard rapidly moves backwards, often over a short distance.
- (6) Eye-lick: the lizard slowly extrudes its tongue and passes it over an eye.
- (7) Lunge: the gecko throws its body forward and then comes to a halt.
- (8) Run: very fast movement, often over a short distance.
- (9) Walk: continuous, relatively fast forward movement with the ventrum >5 mm from the rock surface. This is the locomotor pattern typically observed in unrestrained geckos.
- (10) Slow motion: the lizard proceeds by very slow, stalking movements, most often accompanied by jerky or waving movements of the forelimbs. The back is slightly arched and the ventrum is >5 mm from the rock surface.
- (11) Crawl: the lizard crawls slowly with its ventrum adhering closely to the rock surface.
- (12) Stationary, ventrum raised: the lizard stands still, its ventrum not resting on the rock (this pattern can be accompanied by movement of the head, tail or forelimbs).
- (13) Stationary, ventrum not raised: as for (12), except that the ventrum of the lizard is resting on the rock.

After each trial, we soaked all of the rocks for 2 h in hot soapy water. They were then vigorously scrubbed, soaked for a further 30 min in hot water, scrubbed, and then rinsed and air-dried. After this procedure, all of the slabs from treatments (5) and (6) became available for use as control rocks for small-eyed snakes and broadheaded snakes, respectively. Fresh rocks and cologne-scented rocks were always cleaned in

separate basins, and became available for use as their original treatment after washing.

The experiment was performed over 10 nights: 26 and 29 August; 3, 5, 6, 8, 14 and 17 September; and 9 and 10 November. All trials were conducted between 1800 and 0030 hours (the period when velvet geckos are most active: [Schlesinger & Shine 1994](#)) within a temperature-controlled room maintained at 18°C (to simulate the operative environmental temperature of retreat-sites during the night in a natural environment; see [Webb 1996](#)). We randomly selected 24 lizards, 12 each from Sassafras and Cape Banks, from those collected. At most, lizards were tested once only on any night, and each lizard experienced all six tests. The treatment was randomly chosen from those that had not previously been presented, and each lizard was tested with a rock that had not been used in a trial on that night.

We separately analysed the data for the fresh, control small-eyed and control broadheaded rocks (analysis 1) and fresh, cologne, small-eyed snake and broadheaded snake rocks (analysis 2) using split-plot ANOVAs. If there was a significant population by treatment effect, separate two-factor repeated measures ANOVAs were performed on data from each population. For both types of ANOVA, we made comparisons for within-treatments effects using Tukey-Kramer Honestly Significant Difference (HSD) comparisons tests.

Retreat-site selection

Our retreat-site selection experiments were conducted in large plastic tubs (62 × 41 × 28 cm), and recorded on videotape. We positioned eight of the tubs side-by-side, in two rows of four, inside a temperature-controlled room (maintained at 18°C) devoid of other animals. A low-light Panasonic video-camera was positioned directly above, and connected to a National AG6010 time-lapse video-cassette recorder (set to take one frame/s) and monitor. Four portable lights were taped to the ceiling above the arena: three were fitted with clear 100-W globes and connected to a gradual light dimmer designed to simulate artificial dusk and dawn over a 20-min period (see also [Graham & Hutchinson 1977](#)), and the fourth had a 25-W red globe and was used to aid recording.

Late in the afternoon, we constructed a retreat-site measuring 20 × 30 cm at each end of each tub.

We constructed them from a bottom layer of treated rocks (two outer slabs of 20 × 10 × 1.5 cm flush with three central slabs of 6.6 × 10 × 1.5 cm), and a top layer of rocks that had never been in the cage with a snake (one slab of 20 × 20 × 1.5 cm and one of 20 × 10 × 1.5 cm). The rocks were separated to a height of 5 mm (1 mm greater than the average minimum crevice width of adult geckos; see [Schlesinger & Shine 1994](#)) using 20 mm² squares of plastic. We conducted three separate experiments using the scent from each species of snake, and we hereafter refer to these as: (1) control versus all; (2) centre versus control; and (3) centre versus all. The slabs making up the bottom layer of the retreat-site in the 'control' treatment had been used previously in a trial but had been thoroughly washed, whereas those for the 'all' treatment had been covered with the scent of snake; and only the central slab of the 'centre' treatment had been covered with the scent of snake. Thus, we created artificial crevices with: no snake scent (to mimic a crevice that does not contain a snake); scent restricted to a small central area (to mimic a crevice that contains a sedentary snake); and scent spread over the entire floor area of the crevice (to mimic a crevice that contains a snake that moves around within the crevice).

Soon after constructing the retreat-sites, we placed a gecko under a small temporary rock in the centre of the tub and a transparent plastic cage on top of this rock so as to enclose it, thereby preventing the gecko from haphazardly selecting a retreat-site. Ten minutes before the artificial dusk (around 1800 hours), the video-camera was activated, the cage was removed, and a clear plastic lid was fastened to the tub. Once all animals were active, we slowly dragged the temporary rock to the side of the tub (by pulling an attached string that had been fed through a hole in the top of the tub) and raised it until vertical. We left the lizards undisturbed until the following morning when they were removed and their retreat-site selection recorded (final retreat). It was important to conduct experiments overnight to assess the final retreat choice of the geckos in addition to their initial response. After each trial, all of the rocks were washed using the method adopted in the previous experiment (see above). After this procedure, all of the slabs from the bottom of a retreat-site became available for use as control rocks, and those from the top layer remained as

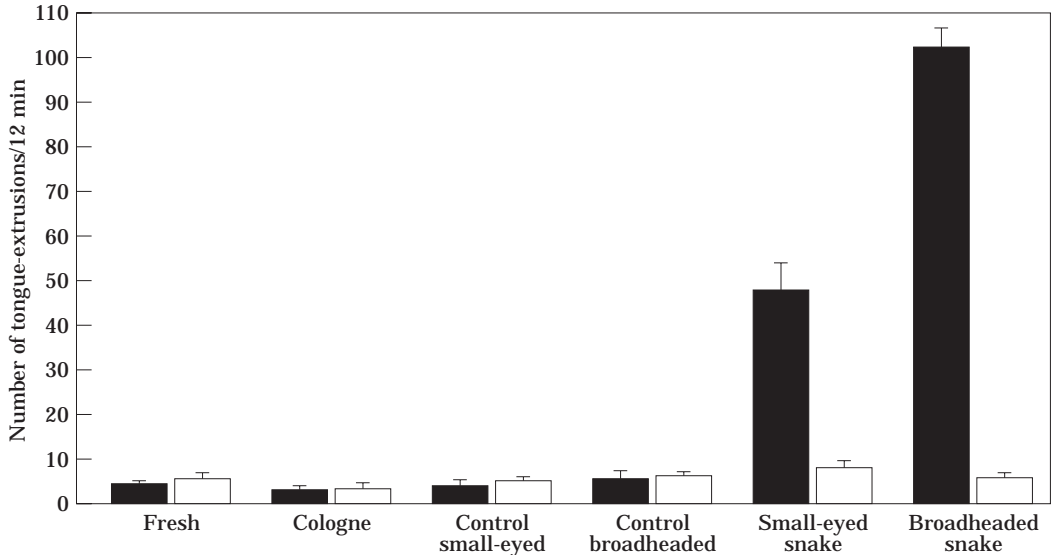


Figure 1. Mean (\pm SE) frequency per 12 min of tongue-extrusions for velvet geckos in the six experimental situations. ■: Lizards collected from Sassafras ($N=12$); □: Cape Banks lizards ($N=12$). We separately analysed the data for the fresh, control small-eyed and control broadheaded rocks (analysis 1) and fresh, cologne, small-eyed snake and broadheaded snake rocks (analysis 2). For both analyses, there was little variation in tongue-extrusion frequency among animals from the same source population (ANOVA: analysis 1, $F_{22,44}=1.73$, NS; analysis 2, $F_{22,66}=1.00$, NS).

fresh rocks. All of the tubs were thoroughly scrubbed and rinsed with hot water after each trial.

We performed the experiments concurrently with the first, between 23 August and 28 September 1996. We tested the same lizards that were used in the first experiment, and the remaining seven from each population. Each lizard was tested once in each of the six experimental combinations, with a minimum of 5 days between trials. At least 24 h elapsed between trials when the gecko had been recently tested in the first experiment. The position of the crevices in the tubs was always randomized, as was the order in which animals were tested, the treatment combination assigned to each tub, and the selection of the slabs that made up each crevice.

From the videotapes, we noted: (1) the first retreat-site selected by the gecko (first retreat); (2) the amount of time the gecko spent under each retreat-site throughout a trial (as a proportion of the total time the animal spent in either crevice, but timing ceased once the animal had chosen its final retreat-site; % time); (3) the number of times a gecko entered each crevice (times entered); and (4) the mean time the gecko spent under a crevice

per visit (mean time). For each experiment, we scored the number of geckos with a greater response in one direction versus the other, and analysed these data using chi-square two-way contingency tables. The data for animals from Sassafras and Cape Banks were also separately analysed using chi-square goodness-of-fit tests.

RESULTS

Chemical Detection of Predators

Only geckos from Sassafras responded strongly to the scent of broadheaded snakes, and were able to distinguish between a novel scent (the chemical pungency control), the scent of a sympatric predatory snake (broadheaded snake) and the scent of a sympatric non-predatory snake (small-eyed snake) using tongue-extrusion (ANOVA: Sassafras, $F_{3,33}=156.23$, $P<0.01$; Fig. 1). The lizards extruded their tongues most often when presented with the scent of broadheaded snakes, and least often when presented with either non-scented or cologne-scented rocks (Tukey-Kramer HSD: Sassafras, difference=98.50, 99.58 [critical difference=14.23], $P<0.01$ for broadheaded

snakes versus non-scented and cologne-scented rocks; Fig. 1). Geckos also extruded their tongues more often when presented with the scent from small-eyed snakes, at a rate that was markedly lower than their response to broadheaded snake scent (Tukey-Kramer HSD: Sassafras, difference=54.33 [critical difference=14.23], $P<0.01$; Fig. 1), but higher than to the cologne or fresh rock treatments (Tukey-Kramer HSD: Sassafras, difference=45.25, 44.16 [critical difference=14.23], $P<0.01$ for small-eyed snakes versus cologne-scented and non-scented rocks; Fig. 1). Regardless of population, the geckos did not respond strongly (in terms of tongue-extrusion rate or other behavioural acts) to fresh rocks or to rocks that had previously been in the cage with a snake but thoroughly washed, and there was very little variation in response between these treatments (Table I, Fig. 1).

In addition to the tongue-extrusion response, some striking behaviours were observed for the lizards from Sassafras presented with the scent of a broadheaded snake: indeed, the run, lunge and tail-vibration behaviours were observed only in these geckos, and significantly higher frequencies or durations of the stand up, walk, (ANOVA: Sassafras, $F_{3,33}>15.5$, $P<0.01$; Tukey-Kramer HSD: difference>critical difference for broadheaded snake versus fresh, cologne and small-eyed snake rocks), crawl and stationary, ventrum not raised behaviours (ANOVA: Sassafras, $F_{1,23}>25.6$, $P<0.01$) were displayed in response to the scent of broadheaded snake when compared with the other treatments (Table I). There was no significant variation between animals from either population in the duration of the slow-motion behaviour displayed in response to any of the treatments (Table I). Except for lizards from Sassafras responding to the scent of broadheaded snake, the geckos from both populations showed few striking behavioural responses to any of the treatments (Table I).

Retreat-site Selection

For the large majority of cases, the geckos from Sassafras and Cape Banks differed markedly in their retreat-site selection responses to the scent of broadheaded snake (Fig. 2). Lizards from Sassafras showed strong and consistent aversion to scented crevices, but those from Cape Banks selected retreat-sites without regard to whether

they were scented or clean (Table II). This variation in behavioural responses of geckos from the different populations was less pronounced in trials offering retreat-sites that were partially covered versus not covered with the scent of broadheaded snake (Fig. 2). There were no significant differences in the behavioural responses of geckos from either population to the scent of small-eyed snakes ($\chi^2_1<2.66$, NS, for all behaviours in all three experiments; Table II): the scent appeared to have little or no effect on the retreat-site selection behaviours of geckos.

When the alternative was a rock completely covered with the smell of broadheaded snake, all of the geckos from Sassafras selected crevices that were not labelled with scent (Table II). Additionally, these geckos never entered the scented crevice prior to entering the non-scented retreat-site, and avoided visiting or spending large amounts of time within the scented crevice (Table II). Similarly, the Sassafras geckos preferred final retreat-sites that were partially covered with broadheaded snake scent when the alternative rock was completely covered with scent, and this trend was evident for all of the retreat-site selection behaviours that we scored (Table II). Finally, the Sassafras geckos chose crevices that were not covered with broadheaded snake scent in preference to those that were partially covered, and this pattern was consistent for all but one of the behaviours: the exception was that geckos selected their first retreat-site at random (Table II).

DISCUSSION

Our retreat-site choice experiments were designed to mimic the situations that geckos experience in their natural habitat (see Schlesinger & Shine 1994; Webb 1996). Hence, our results are likely to provide an accurate reflection of retreat-site selection by velvet geckos. We employed several procedures to reduce potentially confounding 'carry-over' effects associated with our experimental designs. We randomly allocated geckos to the treatments, randomly selected the slabs for each retreat-site, and randomly positioned alternative retreat-sites within each tub. Moreover, we were able to confirm the efficiency of the cleaning methods that were adopted. Additionally, we discarded the slabs that were used for our chemical detection experiments after each trial to avoid the

Table 1. Mean (\pm SE) frequency* or duration† (per 12 min) of distinct behavioural acts displayed by velvet geckos in the six experimental situations

| Behaviour | Treatment | | | | | | ANOVA | | | |
|-------------------------------------|------------------|------------------|---------------------|----------------------|------------------|-------------------|------------|---------------------|-----------|-----------------------|
| | Fresh | Cologne | Control, small-eyed | Control, broadheaded | Small-eyed snake | Broadheaded snake | Population | Animal (Population) | Treatment | Population* Treatment |
| Stand up* | 3.6 \pm 0.7 | 1.7 \pm 0.5 | 3.3 \pm 0.7 | 3.5 \pm 0.8 | 3.8 \pm 0.7 | 13.8 \pm 1.1 | 10.28 | 2.02 | 33.03 | 15.96 |
| Tail-raise* | 4.0 \pm 1.4 | 2.0 \pm 0.5 | 3.2 \pm 0.9 | 3.5 \pm 1.1 | 4.5 \pm 0.8 | 5.2 \pm 1.0 | <0.01 | 0.15 | <0.01 | <0.01 |
| Tail-vibration* | 0 | 0 | 0 | 0 | 0 | 7.1 \pm 1.8 | — | — | 14.91 | — |
| Reverse* | 0 | 0 | 0 | 0 | 0 | 0 | — | — | <0.01 | — |
| Eye-lick* | 0 | 0 | 0 | 0 | 0 | 1.0 \pm 0.3 | — | — | — | — |
| Lunge* | 0 | 0 | 0 | 0 | 0.1 \pm 0.1 | 8.2 \pm 1.4 | — | — | 33.61 | — |
| Run* | 4.4 \pm 1.5 | 2.3 \pm 0.9 | 6.5 \pm 1.3 | 4.0 \pm 1.1 | 3.0 \pm 1.1 | 0 | 1.80 | 0.81 | <0.01 | 1.35 |
| Walk† (s) | 3.7 \pm 1.3 | 2.8 \pm 1.1 | 3.0 \pm 1.0 | 4.3 \pm 1.4 | 4.0 \pm 1.1 | 0 | 0.18 | 0.70 | 1.29 | 0.27 |
| Slow motion† (s) | 0 | 0 | 0 | 0 | 0 | 7.8 \pm 0.8 | — | — | — | — |
| Crawl† (s) | 0 | 0 | 0 | 0 | 0 | 0 | — | — | — | — |
| Stationary, ventrum raised† (s) | 216.3 \pm 37.6 | 333.4 \pm 29.7 | 255.3 \pm 36.3 | 293.8 \pm 33.6 | 193.8 \pm 35.4 | 5.8 \pm 4.2 | 38.38 | 1.01 | 16.01 | 5.51 |
| Stationary, ventrum not raised† (s) | 409.2 \pm 37.8 | 315.0 \pm 26.3 | 210.8 \pm 30.0 | 224.6 \pm 30.8 | 364.6 \pm 40.1 | 237.1 \pm 38.0 | <0.01 | 0.47 | <0.01 | <0.01 |
| | 65.8 \pm 22.2 | 66.6 \pm 15.2 | 113.3 \pm 19.8 | 82.5 \pm 23.5 | 89.1 \pm 17.6 | 167.9 \pm 37.6 | 0.06 | 0.66 | 1.36 | 1.61 |
| | 99.6 \pm 41.6 | 110.8 \pm 15.7 | 126.3 \pm 33.4 | 107.5 \pm 30.4 | 78.8 \pm 29.8 | 97.1 \pm 27.0 | 0.94 | 0.90 | 0.26 | 0.20 |
| | 0 | 0 | 6 \pm 5 | 0 | 8.3 \pm 3.7 | 257.9 \pm 39.2 | 44.74 | 0.96 | 41.83 | 41.45 |
| | 0 | 0 | 2 \pm 1 | 0 | 0.8 \pm 0.8 | 34.2 \pm 34.2 | <0.01 | 0.52 | <0.01 | <0.01 |
| | 437.9 \pm 42.4 | 320.0 \pm 39.2 | 345.4 \pm 33.3 | 343.8 \pm 25.1 | 422.5 \pm 30.8 | 385.0 \pm 50.5 | 0.21 | 0.69 | 5.37 | 23.44 |
| | 211.3 \pm 26.3 | 294.2 \pm 26.8 | 380.8 \pm 32.8 | 387.9 \pm 39.7 | 275.8 \pm 29.6 | 254.2 \pm 35.3 | 0.65 | 0.83 | <0.01 | <0.01 |
| | 0 | 0 | 0 | 0 | 6.4 \pm 4.6 | 0 | — | 0.83 | 50.21 | — |
| | 0 | 0 | 0 | 0 | 0 | 0 | — | — | <0.01 | — |

For treatment, the first and second lines for each variable show the responses of lizards from Sassafra (N=12) and Cape Banks (N=12), respectively. For ANOVA, the first and second lines correspond to F- and P-values, respectively, from analyses performed on data from the fresh, cologne, small-eyed snake and broadheaded snake treatments only (analysis 2), and significant results are highlighted in bold. There was no significant variation in the behavioural responses of geckos towards the fresh, control small-eyed and control broadheaded treatments (ANOVA, analysis 1: $F < 2.17$, ns, for population (df=1,44), animal (population) (df=22,44), treatment (df=2,44), treatment*population (df=2,44) for all behaviours).

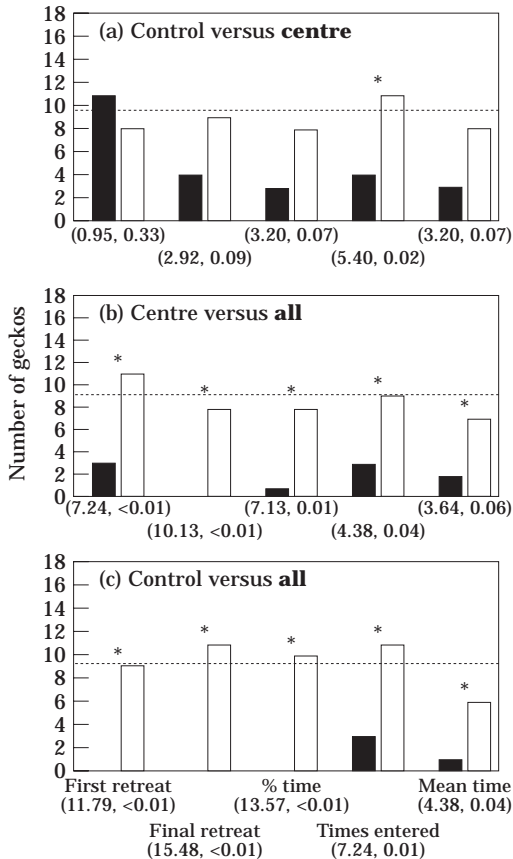


Figure 2. Variation in retreat-site selection behaviours (the first and final retreat-site selected, the percentage of time spent in the retreat-site, the number of times a site was entered, and the mean time spent in it) of velvet geckos collected from two populations. The lizards were given a choice between rocks partially (centre), completely (all) or not (control) covered with scent of broad-headed snakes. ■: Lizards collected from *Sassafra* ($N=19$); □: Cape Banks lizards ($N=19$). The number of lizards showing a bias in response towards the retreat covered with the largest area of scent (highlighted in bold in each figure) are shown. The dotted line indicates the number of geckos expected in each retreat-site according to chance. An asterisk above the histograms indicates a significant interaction as indicated by two-way contingency tables (with population and behavioural response as factors), and chi-square and P -values are given in parentheses under each variable.

potentially confounding effects of gecko scent on the responses of subsequent lizards. This procedure has been adopted only rarely in previous studies of chemical cue detection.

Collectively, our data provide evidence to sustain an interpretation of predator-prey coevolution in the present system. First, our data suggest that the behaviours of velvet geckos might have evolved in response to the foraging tactics of predatory broadheaded snakes: geckos that were sympatric with broadheaded snakes detected and responded strongly to the scent of this sit-and-wait predator. Indeed, they displayed several novel behaviours in response to broadheaded snake chemical cues, and performed a number of movements at much higher rates than in response to any other treatment (see below). Similar behaviours have been noted for several other species of lizard in response to snake chemicals (e.g. Dial et al. 1989; Cooper 1990; Van Damme et al. 1990, 1995). In most cases, the ability to detect the scent of a predator is likely to be of significant selective advantage to the prey. For velvet geckos however, the ability to detect the scent of a broadheaded snake is particularly important for three reasons: this snake is a major predator of the geckos; it occupies the same microhabitats; and it is extremely cryptic because it employs a sit-and-wait hunting strategy from within rock crevices. Hence, the ability to detect the chemical cues of such a predator would provide a great selective advantage for velvet geckos, because it enables them to avoid crevices containing these snakes.

A second criterion for an interpretation of predator-prey coevolution is that the foraging tactics employed by a predator match the anti-predatory tactics used by its prey. Broadheaded snakes are extreme sit-and-wait predators, remaining sedentary under the same rock for up to 4 weeks at a time (Webb 1996, unpublished data). Our results strongly support the notion that the advantage of this foraging mode to broad-headed snakes is that immobility will minimize the extent to which the snake's scent is spread over the rocks forming the crevice. Our geckos were able to detect this scent, and strongly avoided crevices in which the fresh scent of broadheaded snakes was widely disseminated across the entire retreat-site. However, when the same stimulus was localized to a central portion of the retreat-site (as would be the case with broadheaded snakes in a real situation), the same lizards were apparently unable to detect the scent until after they had first entered the retreat-site. In the field, even a brief penetration into such a crevice might substantially improve the opportunity for the snake to seize the

Table II. The retreat-site selection behaviour of velvet geckos from Sassafras (N=19) and Cape Banks (N=19) when given a choice between rocks partially (centre), completely (all) or not (control) covered with scent of snake

| | Broadheaded snake | | | Small-eyed snake | | |
|-----------------------------------|------------------------------|-------------------------------|-------------------------------|-----------------------|----------------------|----------------------|
| | Control versus centre | Centre versus all | Control versus all | Control versus centre | Centre versus all | Control versus all |
| | | | | | | |
| Sassafras | | | | | | |
| First retreat entered | 8-11 (0.47, 0.50) | 16-3 (8.86, <0.01) | 19-0 (19.00, <0.01) | 8-11 (0.47, 0.50) | 12-7 (1.31, 0.27) | 10-9 (0.05, 0.83) |
| Diurnal retreat | 15-4 (6.37, 0.01) | 19-0 (19.00, <0.01) | 19-0 (19.00, <0.01) | 10-9 (0.05, 0.83) | 11-8 (0.47, 0.50) | 11-8 (0.47, 0.50) |
| Proportion of time under retreat | 16-3 (8.86, <0.01) | 18-1 (16.11, <0.01) | 19-0 (19.00, <0.01) | 8-11 (0.47, 0.50) | 7-12 (1.31, 0.27) | 11-8 (0.47, 0.50) |
| No. times retreat entered | 15-4 (4.56, 0.03) | 16-3 (8.86, <0.01) | 16-3 (8.86, <0.01) | 10-9 (0.05, 0.83) | 7-12 (1.31, 0.27) | 11-8 (0.47, 0.50) |
| Mean time under retreat per visit | 16-3 (8.86, <0.01) | 17-2 (12.56, <0.01) | 18-1 (16.11, <0.01) | 7-12 (1.31, 0.27) | 13-6 (2.78, 0.11) | 9-10 (0.05, 0.83) |
| Cape Banks | | | | | | |
| First retreat entered | 11-8 (0.47, 0.50) | 8-11 (0.47, 0.50) | 10-9 (0.05, 0.83) | 10-9 (0.05, 0.83) | 10-9 (0.05, 0.83) | 11-8 (0.47, 0.50) |
| Diurnal retreat | 10-9 (0.05, 0.50) | 11-8 (0.47, 0.50) | 8-11 (0.47, 0.50) | 10-9 (0.05, 0.50) | 10-9 (0.05, 0.50) | 8-11 (0.47, 0.50) |
| Proportion of time under retreat | 11-8 (0.47, 0.50) | 11-8 (0.47, 0.50) | 9-10 (0.05, 0.50) | 12-7 (1.31, 0.27) | 9-10 (0.05, 0.50) | 10-9 (0.05, 0.50) |
| No. times retreat entered | 8-11 (0.47, 0.50) | 10-9 (0.05, 0.50) | 8-11 (0.47, 0.50) | 9-10 (0.05, 0.50) | 11-8 (0.47, 0.50) | 8-11 (0.47, 0.50) |
| Mean time under retreat per visit | 11-8 (0.47, 0.50) | 12-7 (1.31, 0.27) | 13-6 (2.78, 0.11) | 12-7 (1.31, 0.27) | 8-11 (0.47, 0.50) | 10-9 (0.05, 0.83) |

The first line for each variable shows the number of lizards with a greater response in one direction or the other. Significant results from goodness-of-fit tests (with behavioural response as the factor) are printed in bold, and chi-square and P-values are given in parentheses under each value.

lizard. Thus, remaining sedentary for long periods of time under the same rock may be an effective predatory strategy for rock-dwelling hunters that consume prey that inhabit similar microhabitats, but are sensitive to the chemical cues of predators. This notion is further supported by the fact that the geckos respond strongly to rocks labelled with the scent of broadheaded snake, some weeks after they have been removed from a snake cage (S. Downes, personal observation).

Perhaps the strongest support for an interpretation of predator-prey coevolution, however, is our observation that some components of the putatively coevolved interaction are absent in an area where the predator-prey interaction is not significant. Although geckos sympatric with broadheaded snakes responded strongly to snake scent, those that were allopatric did not. The mechanism driving these behaviours may be heritable or learnt. It is not implausible to imagine that the behaviours are learnt given that these geckos frequently and easily autotomize their tail (and therefore may escape from predation events a good deal of the time). If the behaviours are genetically determined, an absence of behavioural response may be the 'ancient' condition and the ability to detect the scent of broadheaded snakes may evolve independently in each sympatric population (a traditional adaptationist view). Alternatively, the response might have originally been present in all populations, and has been lost in allopatric populations upon relaxation of predation pressures. This second scenario implies that there is a cost associated either with the ability to detect the snake scent or with the elicited response (e.g. perhaps the scent of broadheaded snakes closely resembles that of some other part of the biota?). Unfortunately, areas that are inhabited by broadheaded snakes but not by velvet geckos probably do not exist (Shine et al. 1995). Thus, we cannot test whether broadheaded snakes employ an extreme sit-and-wait foraging strategy in the absence of velvet geckos.

Several of the behaviours that the geckos from *Sassafra* frequently displayed in response to scent of broadheaded snakes are likely to aid predator avoidance. The most consistent behavioural response to the scent was that the geckos would press their ventrum flat against the rock substrate during locomotion (crawl) and while stationary (stationary, ventrum not raised). Pressing close to

the rock surface may reduce the chance of the gecko being detected as it enters a crevice containing a snake, and/or make it more difficult for the snake to seize the gecko. Similarly, the reverse and run behaviours may increase the chance of a gecko escaping a retreat-site if it encounters a broadheaded snake once it has entered. Perhaps the most predictable behavioural responses to the scent of a threatening snake predator were the tail-vibration and tail-raise behaviours. However, while predator-specific tail-vibration behaviour (the arching of the tail from a horizontal to a vertical position, with slow undulation) has been reported in many other species of lizard (e.g. *Lacerta vivipara*: Thoen et al. 1986; *Coleonyx variegatus* and *C. brevis*: Dial et al. 1989; *Eumeces laticeps*: Cooper 1990), the tail-raise behaviour has not. The tail-raise behaviour may be a modified tail-vibration response that effectively overcomes the restrictions imposed on the movement of a gecko's tail by the enclosed retreat-site habitat. This behaviour is likely to serve a similar anti-predatory function to the tail-vibration behaviour: that is, to redirect the predator's attack from the body to the tail (Dial 1978).

The lack of behavioural response by sympatric geckos to the scent of small-eyed snakes can be interpreted in at least two ways. Most probably, velvet geckos have evolved the ability to distinguish between very specific predatory chemical cues. Our results may thus reflect the ability of these lizards to recognize and avoid the scent from sympatric predatory (broadheaded snake) but not sympatric non-predatory snakes (small-eyed snake; see also Walther 1969; Peckarsky 1980; Soluk & Collins 1988; Dickman 1992). An alternative explanation is that our geckos can detect, but fail to respond to, the scent of snakes that employ an active foraging mode because the scent of such an animal provides minimal information about the current location of the snake. Small-eyed snakes are nocturnal foragers which typically seek out inactive skinks from under logs and rock crevices. Thus, these snakes are likely to disseminate their scent over a relatively large area, and are less likely than an 'ambush' predator to remain in the vicinity. In our laboratory, captive small-eyed snakes consistently refused to feed on velvet geckos, suggesting that the former hypothesis is the most probable. However, the ability to distinguish between a sit-and-wait predator and an actively foraging hunter (of the same or

different species) using chemical cues is likely to be important for many prey.

The foraging tactics employed by a lizard may be an important determinant of its ability to detect predatory scents. Among reptiles, only lizards that adopt an active foraging mode possess a vomeronasal system that enables discrimination between various chemical cues (for a review see Cooper 1994). Presumably, this trend reflects the fact that employing an 'ambush' foraging strategy precludes lingual sampling of a wide area by a lizard, and tongue-flicking disrupts the crypticity required for successful ambush predation (Cooper & van Wyk 1994). Our data suggest an additional reason for the strong correlation in lizards between foraging mode and the presence of lingually mediated chemical discrimination: the ability to detect potential predators chemically is more important for lizards that actively forage for their prey (and hence, are likely to move into an 'ambush' predator's post) than for ambushing lizards (which are not likely to enter an 'ambush' predator's post). Consequently, the foraging tactics employed by a species (both predator and prey) may considerably influence the ways in which selection acts on chemosensory capabilities.

Collectively, our results provide some evidence supporting the reciprocal adaptation of a snake predator (broadheaded snake) and its lizard prey (velvet gecko). Although our conclusions are based on just two populations, the results are clear-cut and convincing. Our data highlight the importance of chemosensory cues for predator detection in these rock-dwelling geckos, and provide us with clues as to why broadheaded snakes employ such an unusually extreme sit-and-wait foraging strategy. Detailed ecological studies on broadheaded snakes suggest that this species' reliance on 'ambush' predation has had major consequences for other ecological traits. The combination of low feeding rate and high survival rate (because of low exposure to predation) has resulted in unusually low growth rates, delayed sexual maturation and low reproductive frequencies in adult females (J. Webb, personal communication). Low reproductive rates may in turn have contributed to the endangered status of broadheaded snakes because of the species' consequently low ability to tolerate habitat destruction (Webb 1996). If indeed there has been an evolutionary arms race between broadheaded snakes and velvet geckos, the outcome

may have significantly influenced other aspects of the ecology of the predator in this particular system.

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