

## RESEARCH PAPERS

### **Differential Avoidance of Snake Odours by a Lizard: Evidence for Prioritized Avoidance Based on Risk**

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#### **Abstract**

Most studies of predator avoidance behaviours have focussed on single-predator systems, despite the fact that prey often are confronted with predator rich environments. In the presence of more than one predator, prey may have to choose between avoiding one predator over another. How prey cope with exposure to several enemies simultaneously remains largely untested. In this study I set out to investigate if lizards showed preferential avoidance of snake odours based on the relative predation risk posed by different snake species. This relative predation risk was estimated using information on density, diet specificity and foraging habit of each snake species. I tested retreat-site selection in two-choice tests, where lizards chose between different combinations of control and snake treated retreat-sites as well as two retreat-sites treated with different snake species odours. Lizards preferred control–treated retreat-sites to those treated with snake odours and showed a differential avoidance response to refuges treated with odours from different snake species. There was strong evidence to suggest that lizards preferentially avoided refuges with the odours of the snake that posed the greatest predation risk, the white-lipped snake (*Drysdalia coronoides*). Naïve juvenile lizards were also tested and their response was similar to the adults demonstrating that the behaviour is innate and not the result of higher encounter rates of more common snake odours. To my knowledge this is one of the first studies to demonstrate that prey can prioritize avoidance to a single most dangerous predator in the face of several predators and conflicting avoidance responses.

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#### **Introduction**

The threat of predation and subsequent predator avoidance can have marked effects on a variety of prey behaviours. Most studies of predation risk have been restricted to presenting prey with a single predator or predatory cue, but in

nature, prey may be faced with multiple predators simultaneously (Sih et al. 1998). Avoiding one predator may conflict with the avoidance of another and can result in an increase in prey's exposure to both predators. For example, water striders that avoid fish by hiding under rocks may increase their susceptibility to stoneflies, which forage under these rocks (Krupa & Sih 1993). However, if the probability of being eaten differed between predator species, then prey could preferentially avoid the most dangerous predator. Although avoidance of one predator may increase vulnerability to a second, if there is a sufficient difference in the probability of being eaten between the two predators, then this may result in a net reduction in the risk of predation. No previous studies have tested if prey can make decisions based on risk in the face of multiple predators and preferentially avoid the most dangerous predator.

The fact that prey can make decisions based on risk has been demonstrated previously. When geckos faced conflicting decisions between predator avoidance, thermoregulation and social interactions, avoidance of predators was given the highest priority (Downes & Shine 1998). Furthermore, other studies have shown that when prey animals are presented with predatory cues sequentially, their response varies according to the perceived level of predatory threat associated with that cue (Helfman 1989; Licht 1989; McCarthy & Fisher 2000; Smith & Belk 2001). These examples demonstrate prey can differentially respond to different measures of risk, which could facilitate preferential avoidance of a dangerous predator in the face of multiple predators.

The likelihood of predation may vary depending on the physiological state of the predator [such as hunger levels, (Licht 1989) or time of day (Lima & Dill 1990)] and with geographical location if prey populations experience different predatory regimes (Storfer et al. 1999; Downes & Adams 2001; Hopper 2001). Importantly, predation risk may vary simply with the species of predator, if the likelihood of an attack differs between predators. Prey species often respond more strongly to abundant, active or efficient predators than to less dangerous ones (Phillips 1978; Peckarsky 1980; Dickman 1992). Therefore the relative risk associated with each species is closely linked to ecological and behavioural traits of the predators, including relative density, diet specificity and activity pattern. Accurate discrimination, on the part of the prey, is central to this hypothesis.

Discrimination among predators has been demonstrated in many animal groups and in a variety of sensory modes, the most common of which is, chemoreception (Kats & Dill 1998). Studies have shown that prey can chemically discriminate between a predator and a non-predator and only predators of significant threat elicit avoidance behaviours (Thoen et al. 1986; Cooper 1994). Therefore chemoreception provides an ideal mechanism that would enable prey to detect and discriminate between different predators. Squamate reptiles possess a highly developed chemosensory system (Schwenk 1995) and lizards have an acute ability to use chemical cues to discriminate between predatory and non-predatory snake species (Thoen et al. 1986; Cooper & Burghardt 1990). In this respect lizards and their snake predators provide an ideal system to investigate the behavioural responses of prey in the face of simultaneous multiple predator cues.

Here I test how the mountain log skink (*Pseudemoia entrecasteauxii*) copes with multiple predators. The design utilizes a two-choice test between retreat-sites that have been treated with different odours. Retreat-site selection has been used successfully in previous studies to assess the avoidance behaviours of lizards and provides a robust measure of predator avoidance (Cooper & Burghardt 1990; Downes & Adams 2001). In this study, I test if skinks differentiate between odours of three predatory snakes and avoid retreat-sites treated with odours of the most dangerous predator compared with those treated with odours from a less dangerous predator. The prediction is that when faced with retreat-sites containing control and snake odours lizards choose control retreat-sites, and when faced with retreat-sites treated with the odours of two snakes they choose refuges treated with odours of a less dangerous snake. I also test if this ability to prioritize reflects prior experience with snake odours by testing juvenile lizards that have no prior experience with snake odours. The prediction is that no difference in predator avoidance is expected if the behaviour is innate.

## Methods

### Study System

The mountain log skink, *P. entrecasteauxii*, is a small (up to 50 mm) diurnal lizard that inhabits cool temperate areas of south-eastern Australia and Tasmania (Cogger 1996). Snakes represent a significant predation threat to this species and for this study I chose three snake species that prey on *P. entrecasteauxii*. During the selection of a retreat-site lizards are likely to encounter snake chemicals, however, because of differences in the ecology and behaviour of the snakes the likelihood of an attack may vary and therefore the perceived risk of each predator will vary also. If a lizard encounters the odour of a specialist lizard feeder then the likelihood of attack from this snake is high, relative to a generalist feeder. Moreover the probability of an attack from a nocturnal feeder is lower during the day compared with at night and an attack from a common predator is more likely than from a rare predator. Hence a lizard's risk of predation from each snake can vary depending on the snake's relative density, diet specificity and foraging patterns. Using these attributes the snake species can be ranked according to their predation risk (Table 1). A lizard's risk of predation from a white-lipped snake is high as this snake is the most abundant snake in the alpine region, it specializes on scincid lizards, and is active during the day and early evenings (Shine 1981). The probability of an attack from a red-bellied black snake, on the other hand, is low as these snakes are less abundant and although they are actively foraging at the time when lizards are selecting a refuge the probability of attack is low as they feed predominantly on frogs (Shine 1977). Finally an attack from a small-eyed snake is also low as these snakes are nocturnal, and when a lizard is choosing a retreat-site prior to dusk, the small-eyed snakes are not actively foraging (Shine 1984).

Table 1: The likelihood of a predatory attack from each snake species during retreat-site selection (predation risk) based on the diet, relative density and foraging activity of the each snake species

Snake species	Proportion of diet comprising lizards	Relative density	Foraging activity	Predation risk
White-lipped snake <i>Drysdalia coronoides</i>	86% <sup>a</sup>	High <sup>d</sup>	Diurnal <sup>a</sup>	High
Red-bellied black snake <i>Pseudechis porphyriacus</i>	29% <sup>b</sup>	Medium <sup>d</sup>	Diurnal <sup>b</sup>	Low
Small-eyed snake <i>Rhinoplocephalus nigrescens</i>	89% <sup>c</sup>	Low <sup>d</sup>	Nocturnal <sup>c</sup>	Low

<sup>a</sup>Shine (1981).

<sup>b</sup>Shine (1977).

<sup>c</sup>Shine (1984).

<sup>d</sup>CSIRO Wildlife Museum records.

#### Animal Care and Husbandry

Lizards were collected from Namadgi National Park and were housed in plastic containers 42 × 32 × 22 cm (length × width × height) in a temperature-controlled room maintained at 18–20°C. The floor of the container was covered in mulch and a ceramic tile was provided as a retreat site. A temperature gradient was established by placing heating tape under one half of the container to allow animals to thermoregulate freely. The room was under a 12:12 h light:dark cycle and animals were provided with ad libitum water and food. Naïve juvenile lizards were offspring born in the lab approximately 12 wk before I began experimental trials and they had no prior experience with snake odours.

As small-eyed snakes are at such low densities in Namadgi National park and would be difficult to catch, I chose to use snakes from areas other than where the lizards were caught. A White-lipped snake (*Drysdalia coronoides*) was collected from within the Australian Capital Territory (ACT), and a Small-eyed snake (*Rhinoplocephalus nigrescens*) was collected from New South Wales (NSW). The Red-bellied black snake (*Pseudechis porphyriacus*) used in this study was a captive animal that was caught in the ACT, and housed at a nearby reptile zoo. Because of difficulties in collecting and housing poisonous snakes, a single representative of each species was used.

Although there may be inter-individual variation in scent, behavioural assays have shown that odours of conspecifics are more similar to each other than odours of individuals from different species (Heth et al. 1999; Heth & Todrank 2000; Heth et al. 2001). Thus inter-specific variation in odours is likely to be greater than inter-individual variation. Although several studies have demonstrated that prey can discriminate between individuals of a predatory species based on diet and hunger state (Licht 1989; Murray & Jenkins 1999; Belden et al. 2000; Smith & Belk 2001), no evidence for

discrimination based on other characters such as body size (Smith & Belk 2001) or population has been found (Downes unpubl. data). To minimize any dietary or hunger effects on snake odours the snakes were fasted for a week before each trial.

### Experimental Design

To investigate if lizards can prioritize avoidance according to risk and to test if this is influenced by prior experience with snake odours, separate experiments were conducted. The first investigated the retreat-site selection of adult lizards, and the second repeated this experiment with minor modifications using naïve juvenile lizards and adult lizards. Different adult lizards were used in the first and second experiment.

#### *Experiment 1: adult lizards*

The retreat-site selection of *P. entrecasteauxii* was tested for six nights in two-choice tests. Experiments were carried out in plastic tubs that were the same size as the lizard's home enclosure and had a mulch substrate. Two ceramic tiles were placed at either end of the lizard enclosures to act as retreat-sites. The trial enclosures were placed longitudinally along the heat tape to provide equal heat conditions for each tile. Under each tile a piece of odour treated paper towel was placed on top of the mulch. The paper towel was treated with one of the three snake species odours or an odourless control. Snake odours were obtained by placing the damp paper towel in the snake enclosure 2 d prior to the experimental night. The paper towel was removed from the snake's enclosure on the day of the experiment and cut into squares (100 × 100 mm), and one square was placed under each tile. Clean gloves were used when handling the paper towels to control for human odours, and gloves were changed when handling paper from other treatments to avoid cross-contamination. The odourless control paper towel was treated in the same manner but was placed into an empty plastic container 2 d prior to the experimental night. Lizards were placed into experimental cages 1 h before the heating and lights were turned off. Three hours later the retreat-site selection of the lizard was recorded and the lizards were returned to their home enclosure. Observations during a pilot study suggested that the lizards sampled each retreat-site through tongue-flicking before choosing a retreat-site.

Each individual faced all six possible two-choice combinations of odours and lizards were allocated to each two-choice test using a Latin-square design. The design ensured each lizard was tested with each of the six two-choice combinations over six experimental nights controlling for order and night effects. Within a treatment the locations of the scented and unscented towels varied such that in half the pairs the control was on the left and in the other half the control was on the right side of the enclosure. In total 24 adult male lizards were tested each night.

*Experiment 2: adult and naïve juvenile lizards*

The experimental procedure was the same as described in the first experiment, but the treatments and design differed slightly. The same odour treatments were used and a second pungency control was included to test for the possibility that lizards respond to a novel scent on the paper towel. The pungency control is particularly pertinent to this experiment as the naïve juveniles had never been exposed to snake odours and avoidance of snake treated tiles could simply be avoidance of unfamiliar odours and not snake odours. The pungency control paper towel was sprayed with dilute Eucalyptus oil (1, 8-cineole), which is a naturally occurring substance in the field, and then the paper towel was treated in the same manner as the odourless control paper towel in the previous experiment. Three snake odours and two controls (odourless and pungency retreat-sites, respectively) resulted in ten two-choice combinations. Lizards were allocated to treatments using a Latin Square designs and all lizards were tested over 10 nights with 10 different odour combinations. A total of 12 adult males and 12 naïve juvenile lizards (sex unknown) were tested.

**Statistical Analysis**

Data were analysed using the Bradley-Terry logistic regression. This model is specifically designed for paired comparisons where the response variable is categorical or ordinal (Bradley & Terry 1952), and has been used previously in several studies using two-choice tests (Boyd & Silk 1983; De'ath & Moran 1998; Head et al. 2002; Molloy & Hart 2002). The advantage of using this parametric model over other methods of analysis is that it provides a statistical measure of preference for each treatment based on the lizard's choice of retreat-site (preference rating) and it provides a single overall test rather than multiple independent tests (De'ath & Moran 1998). Most importantly, in the case of multiple treatment comparisons this model provides a rank of the treatments (expressed as the preference rating) and locates them along an underlying trait, in this case predation pressure. If the Bradley-Terry Model adequately describes the data then the preferences are uni-dimensional (De'ath & Moran 1998).

In a pilot experiment I tested if during repeated experiments lizards became acclimated to the test procedure and altered their choices. I gave 10 lizards a choice between control and white-lipped snake treated refuges for five consecutive nights and lizards consistently chose the control refuge (Stapley, J. unpubl. data). As the lizard's choice did not change across the five nights and the order of treatments in these experiments were balanced across days, repeated measures were considered independent observations to simplify the analysis.

Once the GLM was fitted, comparison of the residual deviance and degrees of freedom were conducted between models of equal preference and unequal preference, and equal preference between adults and naïve juveniles. The change in deviance between two models has a chi-squared distribution and is therefore

compared using the chi-squared statistic. The model estimates the mean treatment effects and a priori comparisons of each of these against the control were carried out ( $\alpha = 0.05$ ). Additional unplanned comparisons were also carried out and Bonferroni corrections were made to the critical p-values.

### Results

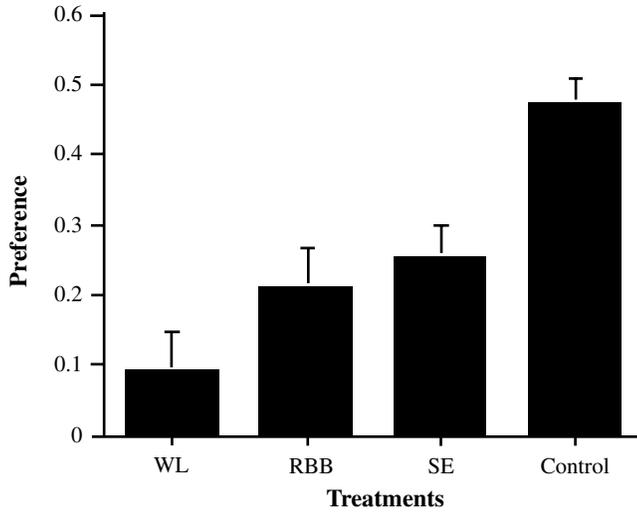
In no cases did lizards fail to select a retreat-site during the course of either of the two experiments (Tables 2 and 3). In both experiments there was a significant treatment effect on retreat-site selection, with the Bradley–Terry Model fitting the data more accurately than a model of equal preferences (experiment 1:  $\chi^2 = 26.13$ ; 3;  $p < 0.0001$ , Fig. 1; experiment 2:  $\chi^2 = 16.18$ ; 4;  $p = 0.008$ , Fig. 2). Looking at these figures the preference ratings estimated by the Bradley–Terry model show a ranking of each of the treatments and the control

*Table 2:* Total number of times adult lizards chose one of two retreat-sites treated with different odours in two choice tests ( $n = 24$ )

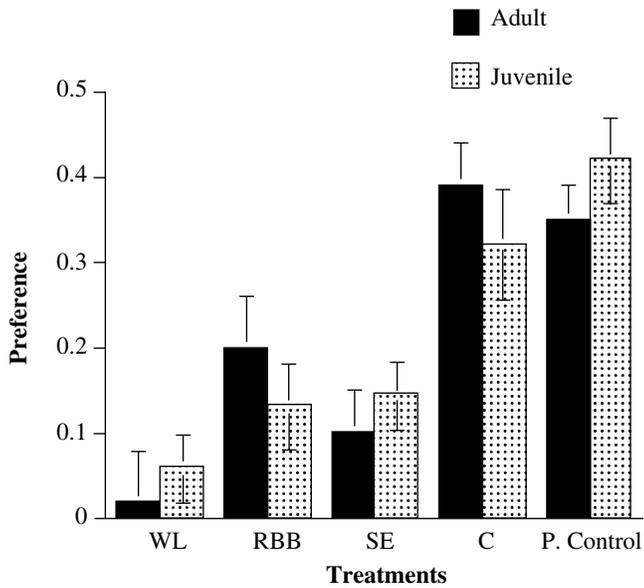
Retreat-site 1	Retreat-site 2	Choose 1	Choose 2
White-lipped snake	Red-bellied black snake	6	18
White-lipped snake	Small-eyed snake	4	20
White-lipped snake	Control	2	22
Red-bellied black snake	Small-eyed snake	14	10
Red-bellied black snake	Control	7	17
Small-eyed snake	Control	8	16

*Table 3:* Total number of times adult and juvenile lizards chose one of two retreat-sites treated with different odours in two choice tests ( $n = 12$ )

Retreat-site 1	Retreat-site 2	Adults		Juveniles	
		Choose 1	Choose 2	Choose 1	Choose 2
White-lipped snake	Red-bellied black snake	1	11	4	8
White-lipped snake	Small-eyed snake	2	10	3	9
White-lipped snake	Odourless control	1	11	2	10
White-lipped snake	Pungency control	0	12	1	11
Red-bellied black snake	Small-eyed snake	8	4	7	5
Red-bellied black snake	Odourless control	3	9	3	9
Red-bellied black snake	Pungency control	4	8	2	10
Small-eyed snake	Odourless control	2	10	4	8
Small-eyed snake	Pungency control	3	9	3	9
Odourless control	Pungency control	5	7	4	8



*Fig. 1:* Preference ratings for retreat-sites treated with snake odours (WL: white-lipped snake; RBB: red-bellied black snake; SE: small-eyed snake) and control odours. Error bars represent 95% confidence intervals



*Fig. 2:* Preference ratings for retreat-sites treated with snake odours (WL: white-lipped snake; RBB: red-bellied black snake; SE: small-eyed snake) and control and pungency control (P. Control) odours for adult and juvenile lizards. Error bars represent 95% confidence intervals

according to how often the lizards chose a particular retreat-site in the two-choice tests. In experiment one, lizards preferred the odourless retreat-site to snake retreat-sites (white-lipped snake  $t_{22} = 4.64$ ,  $p < 0.0001$ ; red-bellied snake  $t_{22} = 2.50$ ,  $p = 0.01$ ; small-eyed snake  $t_{22} = 1.97$ ,  $p = 0.03$ ). Furthermore, lizards preferred red-bellied black and small-eyed snake retreat-sites to white-lipped snake retreat-sites ( $t_{22} = 2.14$ ,  $p = 0.022$ ,  $\alpha = 0.025$ ;  $t_{22} = 2.69$ ,  $p < 0.007$ ,  $\alpha = 0.025$  respectively).

In experiment two, the response of naïve juvenile and adult lizards was not significantly different ( $\chi^2 = 0.438$ ; 1;  $p = 0.97$ , 31% power to detect a medium effect). The preference ratings show that juveniles and adults preferred control retreat-sites to snake retreat-sites (juveniles: white-lipped snake  $t_{10} = 3.35$ ,  $p = 0.003$ ; red-bellied snake  $t_{10} = 2.11$ ,  $p = 0.03$ ; small-eyed snake  $t_{10} = 2.03$ ,  $p = 0.034$  and adults: white-lipped snake  $t_{10} = 3.29$ ,  $p = 0.004$ ; red-bellied snake  $t_{10} = 1.89$ ,  $p = 0.044$ ; small-eyed snake  $t_{10} = 2.06$ ,  $p = 0.033$ ). There was no difference between the selection of retreat-sites treated with the odourless control or pungency control (juveniles  $t_{10} = 0.53$ ,  $p = 0.30$ ; adults  $t_{10} = 0.31$ ,  $p = 0.38$ ). Juvenile lizards more often selected red-bellied black and small-eyed snake refuges than white-lipped snake refuges, but this was not significant after a Bonferroni correction ( $t_{10} = 1.98$ ,  $p = 0.037$ ,  $\alpha = 0.0125$ ;  $t_{10} = 2.06$ ,  $p = 0.033$ ,  $\alpha = 0.0125$  respectively). This may be due to lack of power as the same comparison also came out as non-significant for adults ( $t_{10} = 2.15$ ,  $p = 0.028$ ,  $\alpha = 0.0125$ ;  $t_{10} = 1.96$ ,  $p = 0.039$ ,  $\alpha = 0.0125$  respectively), although a significant preference was found in the first experiment.

## Discussion

This study shows that the presence of snake odours influences the retreat-site selection of lizards. The preference ratings estimated by the Bradley–Terry Model demonstrate that lizards preferred control retreat-sites to snake refuges. Furthermore, lizards were more likely to choose red-bellied black snake and small-eyed snake refuges over white-lipped snake. This provides evidence that lizards can discriminate between the three snake species and preferentially avoid the more dangerous predator. Previous studies have demonstrated that when prey animals are presented with predator cues sequentially, they show a stronger response to cues that represent a greater threat (Helfman 1989; Licht 1989; Smith & Belk 2001). However, this is one of the first studies to demonstrate that in the face of simultaneous predator cues, prey species can preferentially avoid the more dangerous predator. These results were also replicated in naïve juvenile lizards, demonstrating that, in agreement with previous findings (Van Damme et al. 1995; Veen et al. 2000), predator recognition and avoidance behaviours are innate in these lizards. Similarly, the differential avoidance of predators by adult lizards is not simply a function of higher encounter rates of those odours in the wild.

Although the pattern of avoidance is clear, in a few occasions lizards appeared to make the 'wrong' choices, for example they chose snake retreat-sites over control retreat-sites (Tables 2 and 3). This could be because of two things,

variation in lizard responsiveness to snake scent or variation in the concentration of odour on the paper towel. When looking at the data for each lizard, no individual lizard consistently made the 'wrong' choice, instead these choices appeared to be random with respect to each individual. This would suggest then, that this result is because of variation in the concentration of snake odours on the paper towel. It is possible that snake odour was not uniformly distributed on the paper towel, although by rotating the towel within the snake enclosure the potential for this variation was minimized.

The preferential avoidance of white-lipped snake refuges to other snake refuges suggests that lizards could discriminate between the odours of white-lipped snakes and the other snakes. A previous study has shown that lizards can discriminate between the odours of different snake species and only show avoidance response to predatory snakes (Thoen et al. 1986). The lizard's preference ratings for red-bellied black snake refuges were similar to the preference ratings for small-eyed snake refuges. It is unlikely that lizards could not discriminate between their respective odours, because there is little evidence to suggest that red-bellied black and small-eyed snake odours would be more similar to each other than either is to white-lipped snake odours. First, the diets of small-eyed snakes and white-lipped snakes are more similar to each other, compared with that of red-bellied black snakes (Shine 1981; Shine 1984). Secondly, the phylogenetic relationships between the three snakes, supported by morphological and genetic data, has shown that each belongs to its own distinctive clade (Keogh et al. 1998; Keogh 1999). Therefore it is more likely that the lizard's response to red-bellied black and small-eyed snake refuges is because of the similarity in threat posed by these two snake species rather than an inability to discriminate between their odours.

Our results suggest that lizards preferred small-eyed and red-bellied black snake refuges when the alternative was white-lipped snake refuges. Why would lizards prioritize avoidance in this way? The most likely explanation is that lizards selected the refuges based on the perceived risk of predation associated with that cue. For example if a lizard encounters the scent of a white-lipped and a red-bellied black snake, the likelihood of attack from the white-lipped snake would be greater because white-lipped snakes specialize on small skinks (Shine 1981). Similarly if skinks encounter the odours of a small-eyed snake, because these snakes are nocturnal (Shine 1984) the probability of attack in the afternoon (during retreat-site selection) is less than the probability of a white-lipped snake attack. When the choice is between an odourless control and snake scented refuge lizards choose the odourless control, demonstrating that all these snakes pose some risk. However the preferential avoidance of white-lipped snake refuges, would suggest that these pose the greatest risk and lizard avoided these accordingly.

The ability of prey to preferentially avoid a single dangerous predator in the face of multiple enemies is an example of an adaptive anti-predator response, enabling prey to cope with multiple predators. This strategy may be quite widespread, as a graded avoidance response as seen in fish (Helfman 1989; Smith

& Belk 2001) and invertebrates (McCarthy & Fisher 2000) could result in prioritized avoidance when predator cues are presented simultaneously. The results of this study provide evidence that may serve to improve our overall understanding of predator prey relationships and predator population dynamics.

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### Literature Cited

- Belden, L. K., Wildy, E. L., Hatch, A. C. & Blaustein, A. R. 2000: Juvenile western toads, *Bufo boreas*, avoid chemical cues of snakes fed juvenile, but not larval, conspecifics. *Anim. Behav.* **59**, 871–875.
- Boyd, R. & Silk, J. B. 1983: A method for assessing cardinal dominance ranks. *Anim. Behav.* **31**, 45–58.
- Bradley, R. A. & Terry, M. E. 1952: Rank analysis of incomplete block designs. I. The method of paired comparisons. *Biometrika* **39**, 324–345.
- Cogger, H. G. 1996: Reptiles and Amphibians of Australia. Reed, Sydney.
- Cooper, W. E. 1994: Chemical discrimination by tongue-flicking in lizards – a review with hypotheses on its origin and its ecological and phylogenetic relationships. *J. Chem. Ecol.* **20**, 439–487.
- Cooper, W. E. J. & Burghardt, M. 1990: A comparative analysis of scoring methods for chemical discrimination of prey by squamate reptiles. *J. Chem. Ecol.* **16**, 45–65.
- De'ath, G. & Moran, P. J. 1998: Factors affecting the behaviour of crown-of-thorn starfish (*Acanthaster planci* L.) on the Great Barrier Reef: 2: Feeding preferences. *J. Exp. Mar. Biol. Ecol.* **220**, 107–126.
- Dickman, C. R. 1992: Predation and habitat shift in the house mouse, *Mus domesticus*. *Ecology* **73**, 313–322.
- Downes, S. & Adams, M. 2001: Geographic variation in anti-snake behaviour: evolution of chemically-mediated defence tactics in a gecko. *Evolution* 175–205.
- Downes, S. & Shine, R. 1998: Heat, safety or solitude – using habitat selection experiments to identify a lizards priorities. *Anim. Behav.* **55**, 1387–1396.
- Head, M. L., Keogh, J. S. & Doughty, P. 2002: Experimental evidence of an age-specific shift in the chemical detection of predators in a lizard. *J. Chem. Ecol.* **28**, 541–554.
- Helfman, G. S. 1989: Threat-sensitive predator avoidance in damselfish-trumpetfish interactions. *Behav. Ecol. Sociobiol.* **24**, 47–58.
- Heth, G. & Todrank, J. 2000: Individual odour similarities across species parallel phylogenetic relationships in the *S-ehrenbergi* super species of mole-rats. *Anim. Behav.* **60**, 789–795.
- Heth, G., Todrank, J. & Johnston, R. E. 1999: Similarity in the qualities of individual odors among kin and species in Turkish (*Mesocricetus brandti*) and golden (*Mesocricetus auratus*) hamsters. *J. Comp. Psych.* **113**, 321–326.
- Heth, G., Todrank, J., Busquet, N. & Baudoin, C. 2001: Odour-genes covariance and differential investigation of individual odours in the *Mus* species complex. *Biol. J. Linn. Soc.* **73**, 213–220.
- Hopper, K. R. 2001: Flexible antipredator behaviour in a dragonfly species that coexists with different predator types. *Oikos* **93**, 470–476.

- Kats, L. B. & Dill, L. M. 1998: The scent of death: chemosensory assessment of predation risk by prey animals (vol 5, pg 363, 1998). *Ecoscience* **5**, 361—394.
- Keogh, J. S. 1999: Evolutionary implications of hemipenial morphology in the terrestrial Australian elapid snakes [Review]. *Zool. J. Linn. Soc.* **125**, 239—278.
- Keogh, J. S., Shine, R. & Donnellan, S. 1998: Phylogenetic relationships of terrestrial Australo-Papuan elapid snakes (Subfamily Hydrophiinae) based on Cytochrome B and 16s Rrna sequences. *Mol. Phylogen. Evol.* **10**, 67—81.
- Krupa, J. J. & Sih, A. 1993: Experimental studies on water strider mating dynamics: spatial variation in density and sex ratio. *Behav. Ecol. Sociobiol.* **33**, 107—120.
- Licht, T. 1989: Discrimination between hungry and satiated predators: the response of guppies (*Poecilia reticulata*) from high and low predation sites. *Ethology* **87**, 238—243.
- Lima, A. P. & Dill, L. M. 1990: Behavioral decisions made under the risk of predation: a review and prospectus. *Can. J. Zool.* **68**, 619—634.
- McCarthy, T. M. & Fisher, W. A. 2000: Multiple predator-avoidance behaviours of the freshwater snail *Physella heterostropha pomila*: responses vary with risk. *Fresh Biol.* **44**, 387—397.
- Molloy, L. & Hart, J. A. 2002: Duiker food selection: Palatability trials using natural foods in the Ituri forest, Democratic Republic of Congo. *Zoo. Biol.* **21**, 149—159.
- Murray, D. L. & Jenkins, C. L. 1999: Perceived predation risk as a function of predator dietary cues in terrestrial salamanders. *Anim. Behav.* **57**, 33—39.
- Peckarsky, B. L. 1980: Predator-prey interactions between stoneflies and mayflies: behavioral observations. *Ecology* **61**, 932—943.
- Phillips, D. W. 1978: Chemical mediation of invertebrate defensive behaviour and the ability to distinguish between foraging and inactive predators. *Mar. Biol.* **49**, 237—243.
- Schwenk, K. 1995: Of tongues and noses - chemoreception in lizards and snakes [Review]. *Trends Ecol. Evol.* **10**, 7—12.
- Shine, R. 1977: Habitats, diets, and sympatry in snakes: a study from Australia. *J. Can. Zool.* **55**, 1118—1128.
- Shine, R. 1981: Venomous snakes in cold climates: ecology of the Australian genus *Drysdalia* (Serpentes: Elapidae). *Copeia* **1**, 14—25.
- Shine, R. 1984: Reproductive biology and food habits of the Australian Elapid snakes of the genus *Cryptophis*. *J. Herp.* **18**, 33—39.
- Sih, A., Enlund, G. & Wooster, D. 1998: Emergent impacts of multiple predators on prey. *Trends Ecol. Evol.* **13**, 350—355.
- Smith, M. E. & Belk, M. C. 2001: Risk assessment in western mosquitofish (*Gambusia affinis*): do multiple cues have additive effects? *Behav. Ecol. Sociobiol.* **51**, 101—107.
- Storfer, A., Cross, J., Rush, V. & Caruso, J. 1999: Adaptive coloration and gene flow as a constraint to local adaptation in the streamside salamander, *Ambystoma barbouri*. *Evolution* **53**, 889—898.
- Thoen, C., Bauwens, D. & Verheyen, R. F. 1986: Chemoreceptive and behavioural responses of the common lizard *Lacerta vivipara* to snake chemical deposits. *Anim. Behav.* **34**, 1805—1813.
- Van Damme, R., Bauwens, D., Thoen, C., Vanderstighelen, D. & Verheyen, R. 1995: Responses of naive lizards to predator chemical cues. *J. Herp.* **29**, 38—43.
- Veen, T., Richardson, D. S., Blaakmeer, K. & Komdeur, J. 2000: Experimental evidence for innate predator recognition in the Seychelles warbler. *Proc. R. Soc. Lond. B.* **267**, 2253—2258.

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