EXPERIMENTAL EVIDENCE OF AN AGE-SPECIFIC SHIFT IN CHEMICAL DETECTION OF PREDATORS IN A LIZARD

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Abstract—The risk posed by predation is one of the most fundamental aspects of an animal's environment. Avoidance of predators implies an ability to obtain reliable information about the risk of predation, and for many species, chemosensory cues are likely to be an important source of such information. Chemosensory cues reliably reveal the presence of predators or their presence in the recent past. We used retreat site selection experiments to test whether the Australian scincid lizard *Eulamprus heatwolei* uses chemical cues for predator detection and avoidance. Both adult and juvenile lizards were given the choice of retreat sites treated with scents from invertebrate predators, as well as sympatric and allopatric snake predators. Some of the snake predators were known to eat *E. heatwolei*, while others did not pose a predation threat. All invertebrate predators posed a risk to juveniles, but not adults because of their size. We found that juvenile *E. heatwolei* avoided predator odors more strongly than adults. Juveniles avoided both invertebrate predators and snakes, and the strongest response was toward the funnelweb spider, the only ambush predator used in this experiment. This result may demonstrate the importance of predator ecology in the evolution of predator detection mechanisms, with chemical cues being more useful in detecting sedentary predators than active predators. Adult lizards showed no avoidance behavior toward predator odors. This result suggests an age specific shift in predator avoidance behavior as lizards get older and become too large for many predators. However, adults showed no response to the odor from the red-bellied black snake, a known predator of adult *E. heatwolei*. This finding further demonstrates the importance of predator ecology when examining communication between predators and prey. Chemical cues, which are persistent long after predators have vacated the area, may not be useful in detecting the red-bellied black snake, a wide-ranging active forager.

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INTRODUCTION

Recognition of and response to predator odors is common and widespread throughout the animal kingdom. Avoidance of predator chemical cues has been demonstrated in mollusks, arthropods, fish, amphibians, mammals, and to a much lesser extent in echinoderms, reptiles, and birds (Kats and Dill, 1998). While most prey are capable of using multiple sensory mechanisms for predator detection, there appear to be important advantages to using chemical cues (Kats and Dill, 1998). Chemical cues reliably reveal the presence of predators (or their presence in the immediate past) without the need to actually confront the predator (Van Damme and Castilla, 1996). The ability to detect predators chemically is particularly advantageous for organisms whose activity patterns or environment preclude the effective use of other sensory systems (Petranka et al., 1987).

Chemical identification of predators by lizards has received little attention. Given their well-developed chemosensory systems, the potential for chemosensory-based predator avoidance behavior appears to be considerable (Dial, 1990), although Simon et al. (1981) found no evidence for chemical detection of snake predators by the phrynosomatid *Sceloporus jarrovi*. Detection of predators via chemical cues has been reported in a number of other lizard species. These studies have shown that these lizards can detect snake predator odors, as well as distinguish between the odors of predatory snakes and nonpredatory snakes (e.g., Thoen et al., 1986; Dial et al., 1989; Cooper, 1990; Dial, 1990; Dial and Schwenk, 1996; Van Damme and Quick, 2001). Differences among populations in response to snake predator odors have been demonstrated for a number of lizards. In some species, populations living sympatrically with predators respond more vigorously to predator scent than do populations living allopatrically with the same predator (e.g., Thoen et al., 1986; Van Damme and Castilla, 1996; Downes and Shine, 1998; Downes and Adams, 2001). Moreover, age related differences in thermoregulatory behavior in response to snake predator odors have been reported in *Lacerta vivipara*, with juveniles basking less than adults when exposed to the scent of a predator (Van Damme et al., 1995). Other studies have examined lizard response to predators at different ages (e.g., Phillips and Alberts, 1992). These studies, however, concentrated on whether chemical detection of predators is innate or learned, and did not focus on age specific shifts in predator avoidance behavior.

The southern water skink, *Eulamprus heatwolei*, is a medium-size (<110 mm snout-vent length, SVL) diurnal scincid lizard that occurs in southeast Australia. They are insectivorous and can often be found basking on logs on the forest floor of sclerophyll riparian zones. To examine differences in the responses of adult and juvenile *Eulamprus heatwolei* to predator odors, we conducted retreat site

selection experiments involving a range of chemical stimuli from potential snake and invertebrate predators. Snake predator odors were obtained from snake species that are known to eat lizards and are sympatric with our population of *E. heatwolei*. To test whether lizards respond to snake odor in general or only those that naturally pose a predation threat, we also included two snake species that are allopatric with our lizard population and are not known to eat *E. heatwolei*.

In all previous studies on chemosensory based antipredator behavior, the chemical stimuli have been derived from snakes alone. No studies on lizards have used chemical stimuli from invertebrate predators, even though many arthropods are predators of small lizards, and several arthropods and lizards may be involved in cross predation (where vertebrates are sequentially the prey and later the predator of the same species of invertebrate) (McCormick and Polis, 1982). By using invertebrate predators, we have the opportunity to examine age-specific shifts in antipredator behavior as well as to examine the difference in lizard responses to vertebrate and invertebrate predator odors by both adults and juveniles. We predicted that adult lizards would not avoid invertebrate odors and may even be attracted to them, whereas juveniles should avoid these odors, as they pose a predation threat. All lizards were expected to avoid odors from sympatric, but not allopatric snakes.

METHODS AND MATERIALS

Lizards were collected in late September and early October 2000 from the Tidbinbilla Nature Reserve (Canberra, ACT, Australia, 800 m elevation). This capture period occurred immediately after spring emergence before mating began. Juveniles were caught from the field at the same time and from the same locations as adults. Based on their size, juveniles were most likely born the previous season, making them approximately 1 year old. The lizards were brought back to a laboratory at the Australian National University where they were measured, weighed, and their sex determined via hemipene eversion.

Adult lizards were housed individually in plastic boxes (43L × 32W × 23H cm) and juveniles four or five to a box. All boxes contained a bark substrate, water bowl, and a ceramic tile for shelter. A 40-W light bulb was placed at one end of the box to allow lizards to thermoregulate naturally. The light bulb was turned off at night so they experienced a natural photoperiod. During the day, when the light bulb was on, temperatures ranged from 33°C under the light bulb to 25°C at the opposite end of the cage. All lizards were provided with food (*Tenebrio* larvae and dog food) and water ad libitum.

Lizards were tested with seven potential predator species, including four snakes and three invertebrates, as well as an odorless control. Species were chosen in order to test lizard response against a range of predators that presented different threats (Table 1). Three species of elapid snakes were used. *Pseudechis*

TABLE 1. POTENTIAL PREDATORS USED IN RETREAT SITE CHOICE EXPERIMENTS AND THREAT THEY POSE TO ADULT AND JUVENILE *Eulamprus heatwolei*

Predator	Sympatric with *E. heatwolei*	Main diet	Threat Juveniles	Threat Adults	References
Red-bellied black snake (*Pseudechis porphyriacus*)	Y	Frogs, small lizards,[a] small mammals	Major	Major	Shine, 1987; Swan, 1990
White-lipped snake (*Drysdalia coronoides*)	Y	Small lizards,[a] frogs	Major	None	Shine, 1981; Swan, 1990
Small-eyed snake (*Rhinocephalus nigrescens*)	N	Small lizards,[a] frogs, snakes	None	None	Shine, 1984; Swan, 1990
Childrens' python (*Liasis maculosus*)	N	Small mammals, small lizards	None	None	Shine and Slip, 1990; Swan, 1990
Centipede (Scolopendromorpha)	Y	Invertebrates, small vertebrates	Major	None	Butler, 1970; personal observation
Funnelweb spider (*Hadronyche* sp.)	Y	Invertebrates, small vertebrates	Major	None	Mascord, 1980; personal observation
Huntsman spider (Sparrasidae)	Y	Invertebrates, small vertebrates	Minor	None	Daniels and Heatwole, 1984; personal observation

[a] The predator has been recorded to eat *Eulamprus* species.

porphyriacus (red-bellied black snake) is a major threat to both adults and juveniles (Shine, 1987). *Drysdalia coronoides* (white-lipped snake) is a major threat to juveniles, but not adults because adults are too large for them to eat (Shine, 1981). *Rhinocephalus nigrescens* (small-eyed snake) does not occur at our study site, but is known to eat *Eulamprus* spp. elsewhere (Shine, 1984; Swan, 1990). It can be regarded as an elapid control to test whether *E. heatwolei* are responding to cues of actual predators and not just a general elapid odor. *Liasis maculosus* (children's python) preys mostly on mammals and sometimes on lizards. It does not overlap *E. heatwolei* in distribution and should not pose a threat (Shine and Slip, 1990; Swan, 1990). Thus, this snake can be used as a snake control to test whether *E. heatwolei* are responding to actual predator odors or a general snake odor.

A number of invertebrates have been recorded to prey on skinks (McCormick and Polis, 1982; Daniels and Heatwole, 1984). However, there are no reports on whether lizards are able to detect invertebrate predators via chemical cues. We tested adult and juvenile *E. heatwolei* with the odors of three sympatric invertebrates that are common at our study site and have been reported to eat small skinks (Daniels and Heatwole, 1984). They all pose a threat to juveniles, but not adults. Scolopendromorpha (centipedes) are active foragers that live under moist logs. *Hadronyche* sp. (funnelweb spiders) are ambush foragers that build their funnels only in moist rotting logs. Sparassidae (hunstman spiders) are generally arboreal, but sometimes forage on the forest floor.

This experiment was designed to test whether adult and juvenile *E. heatwolei* could detect predators via chemical cues and whether there was any difference in the way the two size (and age) classes of lizards responded to predator odors. A total of 14 adult (87–96 mm SVL) and 14 juvenile (43–61 mm SVL) lizards were tested for 12 nights with various combinations of predator odors. The experimental design consisted of a linked paired-comparison design (David, 1988, p. 100). This design allowed us to balance the experiment by judges as well as by comparisons. The experiment was repeated twice for adults and juveniles, for a total of 24 nights. Each pair of odors was tested six times, and for any two lizards, there are four pairs of odors that are compared by both lizards. Each night, lizards were removed from their home boxes and placed in plastic test boxes at 17:00 hr. Four hours later, the tile under which a lizard was sleeping was recorded. Trials were run in two 12-day blocks, the first from January 25 to February 5 and the second from March 1 to 12.

Test boxes ($30 \times 15 \times 7$ cm) contained a bark substrate and two retreat sites. Retreat sites consisted of two ceramic tiles (11×11 cm) placed at either end of a test cage. Tiles were raised 1 cm off the bottom of the cage with sticks to allow lizards to crawl underneath them. A paper towel treated with the odor of one of the seven predator treatments or the control was placed under each tile. Paper towels were placed on the floor of the predators' cage for three days to obtain their odors. Paper towel used for the odorless control was handled in the same way as

for predators except that it was not placed with a predator prior to being used. Cages and tiles were washed with detergent (Morning Fresh) and dried between all trials.

To test whether preferences were the same for both size classes, we compared the fit of a model allowing different preferences for both size classes and a model with the same preferences for both size classes. If the model allowing different preferences fit the data better than the alternative model, then the size classes were analyzed separately by using the Bradley-Terry model. The Bradley-Terry model is a parametric test that allows treatments to be ordered according to preference and is specifically designed for experiments consisting of paired comparisons (David, 1988). Likelihood ratio tests were used to determine whether the data conformed to the Bradley-Terry model and whether the Bradley-Terry model fit better than a no-preference model. If the Bradley-Terry model fits the data better than the no preference model, then it shows that there were strong preferences between the treatments (De'ath and Moran, 1998). A model of no preference also was tested against the data. If both models fit the data, then the model of no preference was retained.

Our analysis represents a novel application of the Bradley-Terry model. Additionally, this model is more appropriate for our analysis than statistics such as chi-square goodness of fit tests. This model uses information from all comparisons within an experiment, simultaneously, rather than information from each of the comparisons separately (Cowling, Head, and Stapley, personal observation).

RESULTS

A significant difference existed between adult and juvenile avoidance of predators ($\chi^2 = 23.469$, $df = 7$, $P \leq 0.005$). Juveniles avoided most of the treatments, while adults showed no preference among treatments (Figure 1). For the adults, the no-preference model fit the data just as well as the Bradley-Terry model (no preference: $\chi^2 = 8.857$, $df = 7$, $P = 0.263$; Bradley-Terry: $\chi^2 = 23.919$, $df = 21$, $P = 0.296$), therefore, the no preference model was retained. This result indicates that either adults could not detect the odors of potential predators, or if they could, they did not respond (Figure 1a). For juveniles, the no preference model did not fit the data as well as the Bradley-Terry model ($\chi^2 = 29.059$, $df = 7$, $P < 0.001$), whereas the Bradley-Terry model fit the data well ($\chi^2 = 14.557$, $df = 21$, $P = 0.845$), indicating a well-ordered hierarchy of juvenile preferences. Juveniles preferred tiles treated with the odor of the small-eyed snake over the odorless control, while all other vertebrate and invertebrate predator odors were avoided in comparison to the control (Figure 1b). The odor avoided most was that of the funnelweb spider. The probability of juveniles choosing the control over the funnelweb spider was 0.835 (Table 2).
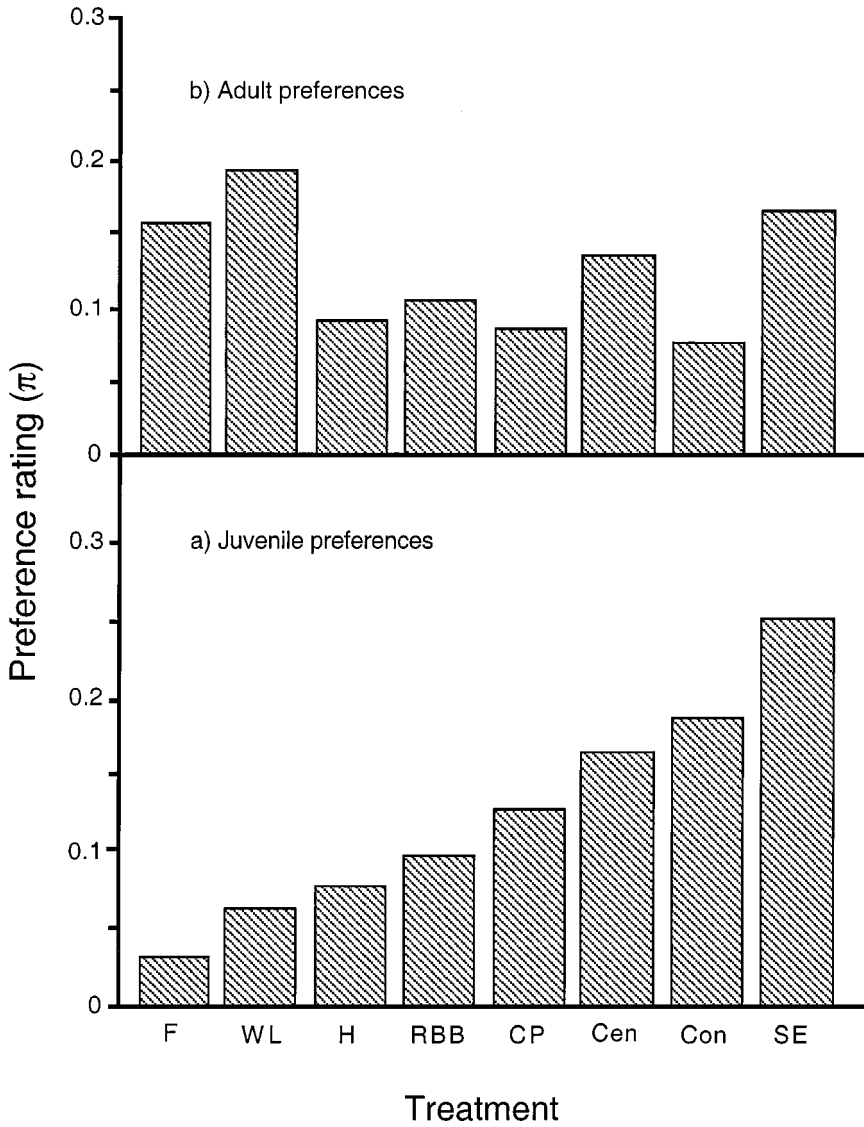
FIG. 1. Juvenile (a) and adult (b) preference ratings (π) obtained from the Bradley-Terry model. F = funnelweb spider, WL = white-lipped snake, H = huntsman spider, RBB = red-bellied black snake, CP = childrens' python, Cen = centipede, Con = odorless control, SE = small-eyed snake.

TABLE 2.   PROBABILITY OF JUVENILES CHOOSING TREATMENT 1 OVER TREATMENT 2 AS
ESTIMATED FROM BRADLEY-TERRY PREFERENCES

| | Treatment 1 | | | | | | | |
Treatment 2	Red-bellied black snake	Small-eyed snake	White-lipped snake	Childrens' python	Huntsman spider	Funnelweb spider	Centipede	Odorless control
Red-bellied black snake	—	0.720	0.405	0.569	0.446	0.248	0.628	0.656
Small-eyed snake	0.280	—	0.209	0.339	0.238	0.113	0.397	0.425
White-lipped snake	0.595	0.791	—	0.557	0.542	0.327	0.713	0.737
Childrens' python	0.431	0.661	0.443	—	0.379	0.200	0.562	0.590
Huntsman spider	0.554	0.762	0.458	0.621	—	0.291	0.678	0.703
Funnelweb spider	0.752	0.887	0.673	0.800	0.709	—	0.837	0.853
Centipede	0.372	0.603	0.287	0.438	0.322	0.163	—	0.525
Odorless control	0.344	0.575	0.263	0.410	0.297	0.147	0.475	—

DISCUSSION

Our results indicate that adults and juveniles respond differently to the chemical cues of a variety of predators and nonpredators. Adults showed no preferences between predators and nonpredators, indicating that either they could not detect predator odors or they did not avoid detected odors because they were no longer a threat. Juveniles, on the other hand, avoided all but one of the predator treatments in comparison to the control. This is the first study to show a reptile antipredator response to invertebrate predator odors. Specifically, juvenile *E. heatwolei* avoided the funnelweb spider over all other treatments.

Our knowledge of the specific chemicals that mediate antipredator responses in lizards is poor. However, evidence suggests that these chemicals are most likely lipids that originate from the integument of the predator (Dial, 1990). Integumentary lipids are thought to play an important role in communication among predator conspecifics (Simon, 1983). These substances also may be deposited on the substrate, and they have low volatility, so it is not unrealistic to expect that prey species may be able to detect these chemicals later in the absence of the predator (Schwenk, 1995).

Chemical Detection of Predators. Chemoreception is believed to be an important mechanism for detecting the presence of predators when other cues are

not available, such as in nocturnal species like geckos (Dial et al., 1989; Dial and Schwenk, 1996), or in low-visibility habitats, such as for tadpoles in turbid water (Schley and Griffiths, 1998). Low-visibility habitats also may include structurally complex habitats where prey may approach predators or be approached by them without detecting them visually. In such environments, more mobile animals such as active foragers may encounter predators at a greater rate (Anholt et al., 1996). *Eulamprus heatwolei* is an active forager that inhabits a complex habitat and uses chemoreception in social interactions. Thus, we expected that *E. heatwolei* would use chemoreception to avoid retreat sites treated with predator odors.

Adult *E. heatwolei* did not respond to red-bellied black snake odors. This result may seem surprising, as this snake species is sympatric with the lizards and is known to prey upon *E. heatwolei*. However, the ability of an individual to detect a predator is not dependent solely on aspects of the prey's ecology, but also on the behavior and ecology of the predator. For chemical cues to be useful in assessing predation risk, they must provide reliable information about the presence and identity of a predator. For example, the American toad, *Bufo americanus,* showed no response to odors of a known predator, the garter snake, *Thamnophis sirtalis* (Heinen, 1994). A lack of response may be because the substrate is likely to be permeated with the predator odors regardless of whether it is in the immediate vicinity; thus, chemicals do not provide a reliable cue. However, *Bufo cognatus* and *Bufo microscaphus* were both able to detect snake predator odors (Flowers and Graves, 1997). In this example, predator odor was a reliable cue because the snakes revisited the same foraging area daily. Chemical cues are most likely to be useful in detecting slow-moving predators that are confined to certain areas, such as ambush foragers (e.g., Gelowitz et al., 1993). Chemical information about fast moving and wide-ranging predators such as the red-bellied black snake may not be as reliable, because the chemicals will probably linger long after the snake has gone. Responding to the odors of predators that have left the area would incur unnecessary costs (Kats and Dill, 1998).

The only predator in our study that is naturally confined to a small area is the funnelweb spider, which waits at the entrance of its burrow for prey to come close. Because of its small size, the funnelweb is not a threat to adult *E. heatwolei* (in fact, observations suggest that adults may prey on funnelweb spiders). However, they do pose a predation threat to juveniles (Daniels and Heatwole, 1984). Retreat sites treated with the odor of funnelweb spiders were avoided by juvenile *E. heatwolei* more than any other scent, suggesting that chemical cues are a reliable means of detecting the risk of predation by this spider.

It is known that phylogeny can influence the distribution of chemical discrimination of prey, but there also is evidence that foraging mode affects the use of prey chemical discrimination independent of phylogeny (Cooper, 1994a). Changes in prey chemical discrimination are linked to changes in foraging mode, and this may show that prey chemical discrimination is adaptively matched to foraging mode

(Cooper, 1994b). Is chemical detection of predators also influenced by foraging mode? Published data suggest that it is. Like prey detection, the detection of predators by chemosensory means has been reported only in active foragers (however, no studies of chemical predator detection in iguanian ambush foragers have been reported) [e.g., eublepharids (Dial et al., 1989); lacertids (Thoen et al., 1986)].

A number of reasons could explain why this could be the case. First, lizards may simply be taking advantage of an already well-developed sense and applying it to other aspects of their ecology. Second, lizards that are active foragers may have other aspects of their ecology in common that influence the use of chemical predator detection. Third, foraging mode may have direct implications on the use of chemical signals for predator detection. Finally, any combination of the above may be true. Iguanian lizards may have little to gain from detecting predator odors because they tend to be sedentary species that escape predators by fleeing to known shelters rather than leaving the area. Furthermore, major predators of ambush foragers are likely to be active foragers (Cooper, 1994a). Detection of active foragers via chemical cues may not be as useful as the detection of ambush predators because odors are persistent and do not reliably indicate the location of fast-moving or wide-ranging predators. Active foraging lizards, on the other hand, are likely to encounter ambush predators, and chemical cues are likely to be reliable for detecting these predators because they are sedentary.

Our results for *E. heatwolei* support the idea that chemical detection of predators is not solely dependent on foraging mode. Adults of this actively foraging lizard species did not distinguish between the odor of predators and the control. This result is probably not a response to the inability to detect predators, but because the predator odors presented were derived from active foragers. This indicates that the absence or presence of chemical detection of predators is not the result of the lizards foraging mode directly, but that chemical cues are more useful in detecting ambush predators than active foragers and that ambush predators are more likely to pose a predation threat to active foragers. The fact that juvenile *E. heatwolei* responded most strongly to the odor of an ambush forager also supports this idea.

It has been suggested here and elsewhere (Downes and Shine, 1998) that chemical detection of predators is, in part, dependent on the ecology of the predator in question. While this idea makes intuitive sense, it remains to be demonstrated. Our study supports this idea; however, it is necessary to conduct experiments that explicitly test this hypothesis. Testing prey with the odors of numerous predators that pose an equal predation threat but differ in aspects of their ecology, such as foraging mode, may provide valuable information on this problem.

Another aspect of chemical predator detection that has been neglected is whether chemical cues are used by prey that themselves are ambush foragers. This has been looked at in the use of chemicals for foraging but not for predator

detection. Addressing this issue is pivotal to our understanding of the evolution of chemical communication. It is necessary that even negative results be published in this area if we are to gain an accurate picture of the use of chemical signals and the selection pressures that act on this mode of communication.

Age-Specific Changes in Predator Avoidance Behavior. Although not responding to predator cues appropriately can be lethal, an excessive or unnecessary response also can have detrimental effects for prey (Beldon et al., 2000). Similarly, if predators are not uniformly risky to prey, prey may respond more strongly to predators that pose a greater threat (Kats and Dill, 1998). For example, many amphibians respond only to predators that have consumed conspecifics (e.g., Wilson and Lefcort, 1993). Other evidence suggests that individuals may differ in their response to predators. For example, prey populations that experience lower predation pressures in response to different predators or predator densities respond less vigorously to predator odors (e.g., Ducey and Brodie, 1991; Mathis et al., 1993). Differential responses also may occur within populations because of changing predation pressures on different life stages. Such a phenomenon may lead to a change in antipredator responses during ontogeny (e.g., Wahle, 1992; Anholt et al., 1996). The more specific the information on potential risk, the more useful it may be in behavioral decision making.

Juvenile *E. heatwolei* avoided predator odors more than adults. Similar results have been demonstrated for other species. Some garter snakes show ontogenetic shifts in antipredator behavior in response to visual predator stimuli (Herzog et al., 1992). In lobsters, small individuals increased shelter use in response to predator odors, whereas large lobsters responded to these odors with aggressive displays (Wahle, 1992). In the common lizard (*Lacerta vivipara*), juveniles refrained from basking in the presence of predator odors, whereas adult basking behavior remained the same as in control tests (Van Damme et al., 1995). The study by Van Damme et al. (1995) differs from ours, however, in that juveniles in their study were inexperienced hatchlings and were compared to adults from the field. In our study, juveniles were caught in the field at the same time and from the same location as adults and so, presumably, would have been exposed to similar predators. Thus, previous experience is less likely to be a factor determining adult and juvenile response.

A change in antipredator response with individual size is not surprising because smaller individuals often are more vulnerable to predation than larger individuals (McCormick and Polis, 1982). This difference in predator threat is not only because more predators can eat smaller individuals, but also because a number of important antipredator mechanisms are associated with age and size. For instance, smaller individuals may not have developed a full array of defensive mechanisms present in larger individuals. Such is the case in some tadpoles, which become toxic as they increase is size (Anholt et al., 1996). In reptiles, relatively small individuals also may be less able to defend themselves because of lower stamina associated with anaerobic and aerobic capacity (Pough, 1977, 1978) and be less

able to run away from predators because size is often positively correlated with speed (Garland, 1985). Younger individuals also may be less familiar with their environment (Burger, 1990).

In conclusion, the ability of lizards to detect predators via chemical cues is not only dependent on their own ecology but also on the ecology of the predator in question. Predators must pose a sufficient threat and cues must be reliable for chemosensory mechanisms of predator detection to be an advantage. This holds true not only for different prey species or populations, but also for different life stages within a species.

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