Context-dependent avoidance of predatory centipedes by nocturnal geckos (*Oedura lesueurii*)

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Summary

Most research on the anti-predator behaviour of vertebrate prey has focused on their responses to vertebrate predators. Nonetheless, invertebrates are abundant predators in terrestrial ecosystems, and some invertebrates (e.g., centipedes, spiders) attack and consume vertebrates. We used a combination of field data and laboratory experiments to determine whether a predatory centipede (Scolopendridae: *Cormocephalus* sp.) influences habitat selection by the nocturnal rock-dwelling velvet gecko, *Oedura lesueurii*. In the field, centipedes and geckos were syntopic, and sheltered beneath rocks with similar physical dimensions, thermal regimes and degree of sun exposure. Nonetheless, geckos rarely shared rocks with centipedes in the field. In laboratory trials, both geckos and centipedes selected shelters with narrow rather than wide crevices. The presence of a centipede modified habitat selection by juvenile geckos, which preferred wide crevices without centipedes to narrow crevices containing centipedes. In contrast, adult geckos continued to select narrow crevices even if these contained centipedes. When we added centipedes to narrow crevices beneath small and large rocks occupied by geckos, both juvenile and adult geckos exited the crevice (especially if it was under a small rather than large rock). Our results show that centipedes influence habitat selection by velvet geckos, and demonstrate that anti-predator behaviours of geckos are both size- and context-dependent. Ontogenetic shifts in behaviour and habitat selection by vertebrates in response to invertebrate predators may be widespread.

Keywords: centipedes, *Cormocephalus* sp., predation, rocks, saxicolous, Scolopendridae, shelter site.

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Introduction

Predation is a major selective force that has shaped the behaviour and ecology of animals (Sih, 1987; Lima & Dill, 1990). For example, predators or the risk of predation can influence foraging time (Huey & Pianka, 1981; Bouskila, 1995), nest-site selection (Spencer, 2002) and choice of shelter sites (Resetarits & Wilbur, 1991; Downes & Shine, 1998a,b; Stapley, 2003, 2004). In many animals, the risk of predation also decreases with increasing body size because as prey size increases there are fewer predators that are physically able to consume them (Polis et al., 1989). This size-dependence in vulnerability to predators can lead to ontogenetic shifts in antipredator behaviour. For example, juvenile bluegill sunfish (*Lepomis macrochirus*) avoid larger fish predators by using structurally complex littoral zones, but larger adult sunfish inhabit open water (Werner et al., 1983). Such size dependent shifts in predator avoidance in response to vertebrate predators are well studied, but relatively little is known about the responses of vertebrates to invertebrate predators.

In terrestrial ecosystems, the most commonly studied predators occupy higher trophic levels than their prey (Clark, 1982; Bauer, 1990). Unsurprisingly, most studies on vertebrate predator-prey interactions have focused on vertebrate predators (Lima & Dill, 1990). For example, mammals, birds, and other reptiles are regarded as the most important predators of lizards (Whitaker, 1973; reviewed in Bauer, 1990). Nonetheless, invertebrates are abundant predators in most ecosystems (e.g., Lewis, 1965; Wise & Chen, 1999; Scheu et al., 2003), and larger species (e.g., centipedes, spiders, mantids) attack and consume small vertebrates (e.g., Humphreys, 1976; McCormick & Polis, 1982; Carpenter & Gillingham, 1984; Bauer, 1990; Kehr & Schnack, 1991; Anthony et al., 2007; Metcalfe & Peterson, 2007). Hence, invertebrates may influence anti-predator behaviour and habitat selection of small vertebrates.

In this study, we investigated whether predatory centipedes influence habitat selection by velvet geckos, *Oedura lesueurii*. Velvet geckos and centipedes are nocturnal, and spend the day sheltering in crevices beneath loose rocks. Given published reports of centipedes consuming lizards (reviewed in Bauer, 1990), we hypothesized that velvet geckos would avoid rocks occupied by centipedes. Juvenile geckos are smaller than adults, and may be more vulnerable to centipede predation. Hence, we predicted that juveniles would
show stronger anti-predator responses to centipedes than adults. We used a combination of field data and laboratory experiments to investigate whether juvenile and adult geckos: (1) select shelter sites in the field with similar physical and abiotic characteristics to those used by centipedes; (2) share rocks with centipedes in the field; (3) modify their choice of shelter-site in the presence of centipedes; and (4) actively avoid centipedes entering their crevices.

**Methods**

**Study species**

Velvet geckos are small (to ca. 65 mm snout–vent length) nocturnal lizards that inhabit rocky outcrops in southeastern Australia (Cogger, 2000). By day, velvet geckos shelter beneath small sandstone rocks (Schlesinger & Shine, 1994), and at night they actively forage for small invertebrates (Cogger, 2000). In the field, velvet geckos select thin rocks in sun-exposed locations; these rocks allow the animals to achieve high body temperatures during the cooler months of the year (Webb & Shine, 1998a,b; Webb et al., 2008). The centipede species that we studied (Scolopendridae: Scolopendrinae, *Cormocephalus* sp.; ca. 50–80 mm in total length) inhabits forest edges and rock outcrops within the geographic range of velvet geckos. Like most centipedes in this family, they are nocturnal, have poor vision, actively forage, and are indiscriminate and voracious predators (Summers & Uetz, 1979; Lewis, 1981; Bauer, 1990). Our study was prompted by observations of centipedes feeding on a velvet gecko and a copper-tailed skink (*Ctenotus taeniolatus*) beneath rocks. We studied velvet geckos and centipedes on sandstone rock outcrops in Morton National Park, southeastern New South Wales, Australia.

**Selection of shelter-sites in the field**

To determine whether centipedes and velvet geckos occupy similar shelter-sites, we sampled rocks at two study sites during May, August and October 2007 (see Webb et al., 2008 for site descriptions). During each sample, we carefully turned all loose surface rocks (that we could physically lift) on exposed rock outcrops near cliff edges. When we found a gecko or centipede, we numbered the underside of the rock with a paint pen, marked its location.
with a GPS unit (Garmin 12XL), recorded the length, width, and minimum and maximum thickness (to nearest mm) of the rock, and scored the substrate below (rock, soil or both). Sampling effort was equal across time (i.e., we lifted the same individual rocks during each sampling event), and because we were most interested in broad patterns of retreat-site selection (rather than site or temporal differences), we combined all data for analysis. This resulted in each individual rock being scored as used by geckos, centipedes, both, or neither.

We placed miniature thermal dataloggers (Thermochron iButtons) beneath rocks used by geckos ($N = 45$) and centipedes ($N = 16$) to quantify thermal regimes. Dataloggers recorded temperatures at hourly intervals over three consecutive days during cloudless weather in May 2007, when both species were using rocks. To test for differences in thermal regimes between species we used a repeated measures ANOVA with time as the repeated measure and temperature over one randomly-selected 24-h period as the dependent variable.

We also used hemispherical photography and gap light analysis (Frazer et al., 1999) to quantify the canopy cover above the rock, and estimate the incident radiation reaching the rock. To do this, we mounted a Nikon Coolpix 995 digital camera fitted with a Nikon FC-E8 fisheye lens to a small tripod, positioned the tripod over the rock, oriented the camera to magnetic north, pointed the lens upward, and took the photo using the camera self timer (Doody et al., 2006). We imported these photos into Gap Light Analyzer software (Version 2.0), which estimates canopy openness (%) and the amount of solar radiation (in mol/m² per day) reaching the rock (Frazer et al., 1999). These variables are calculated after manually accounting for site location (latitude/longitude, elevation) and day length (i.e., sunrise/sunset times and number of sunshine hours; daily values were obtained from a nearby weather station and averaged monthly over the entire calendar year). We compared canopy openness and incident radiation intensity between species (geckos, centipedes) using ANOVAs.

Finally, we used our field observations on rock usage to test whether geckos and centipedes share the same shelter site as expected under the null hypothesis of no avoidance. We first calculated the probability of finding a gecko or centipede alone (i.e., the number of rocks used by a gecko or centipede as a proportion of the total number of rocks lifted), and multiplied these values together to obtain the expected probability of both occurring
Predators influence lizard habitat selection

together. We then converted this probability to the number of rocks that both species would be expected to share if they are not avoiding one another (based on the number of rocks we sampled). We compared this expected value to the actual observed value using a chi-squared test.

**Animal husbandry**

We collected 44 juvenile (28–32 mm SVL), 37 adult male and 36 adult female geckos (50–61 mm SVL), and 40 centipedes (50–80 mm long) from our study sites in August 2008 and 2009. Animals were taken to the University of Sydney and housed in separate constant temperature rooms (19.5–20.5°C) with a 12:12 light/dark cycle. Geckos were housed individually in ventilated paper-lined plastic cages (200 × 140 × 55 mm) containing a water dish, plastic shelter and transparent lid. Cages were placed on timer-controlled heating racks (12:12 h on/off) that created a thermal gradient within each cage from 24.0–39.5°C. We fed lizards crickets dusted with vitamins two to three times each week and water was provided ad libitum. Individual geckos were used once in each experiment, except for the trials testing whether geckos actively avoid centipedes, where we accounted for repeat use of individuals in the analysis. In trials using adults, approximately equal numbers of males and females were used to eliminate any potential sex bias.

Centipedes were housed communally (2–4 per cage) in plastic cages (310 × 220 × 100 mm) similar to those used for geckos, but containing moist soil, leaf litter, and woody debris. The cages were misted with water once every second day. Centipedes were fed crickets dusted with vitamin powder two to three times each week. When experiments were completed, we released each animal at its capture location.

**Crevice selection in the absence of predators**

Geckos and centipedes shelter in crevices formed beneath overlying surface rocks, and the size and shape of these crevices can influence reptile retreat-site selection (Schlesinger & Shine, 1994; Croak et al., 2008). To establish whether geckos \((N = 14\) juveniles, 20 adults) and centipedes \((N = 12)\) prefer the same type of crevice, we offered them the choice between a shelter-site with a narrow versus a wide crevice. Laboratory experiments were carried out inside a constant-temperature room (25°C) with a 12:12 lighting
cycle. Each test arena consisted of a plastic tub (645 × 400 × 275 mm) containing two concrete pavers (230 × 190 × 40 mm), one at each end. One paver was raised 6 mm off the substrate to form a narrow crevice, and the other was raised 21 mm above the substrate to form a wide crevice; the location of each was randomized within a tub. At 1700 h, we placed the test subject into the centre of each tub and secured the clear lid. The next morning we scored which crevice the test subject was using as a diurnal shelter site. After each trial, all tubs, concrete pavers, and spacers were washed in a detergent solution and air-dried to eliminate the possibility that chemicals might affect subsequent trials (Downes & Shine, 1998a).

**Crevice selection in the presence of predators**

To determine whether velvet geckos modify shelter-site selection in the presence of centipedes, we used the same procedures outlined above, except that we placed a velvet gecko and a centipede together into the test arena at 1700 h. The following morning we scored the locations of the centipede and the gecko (N = 18 juveniles, 32 adults). To control for the possibility that a gecko’s behaviour might be influenced by the presence of a novel object inside the crevice, we also ran trials in which a plastic centipede was placed inside the thin crevice (N = 12 juveniles, 16 adults); live centipedes were not used in these trials. We examined the influence of stimulus type (no stimulus, plastic centipede, live centipede) and life stage (juvenile, adult) on shelter-site selection (narrow or wide crevice) using logistic regression.

**Do geckos actively avoid centipedes?**

To determine whether geckos respond to a live centipede entering their shelter site, we placed a single gecko (juvenile or adult) inside a clean plastic cage (310 × 220 × 100 mm) containing a concrete paver elevated 6 mm above the floor of the cage. The geckos were allowed to settle into the cage overnight, and all were inside the crevice the next morning. We randomly allocated geckos to one of three treatment groups: live centipede (N = 11 juveniles, 11 adults), plastic centipede (N = 12 juveniles, 21 adults), and a disturbance control (N = 12 juveniles, 20 adults). For each trial, we opened the lid of the cage and recorded the geckos’ behaviour during the next 5 min. For the live centipede trials, we allowed a centipede (>60 mm long) to crawl
inside the gecko’s crevice. Centipedes that exited the crevice were encouraged to crawl back inside. Because the presence of a novel object inside of the crevice might confound any response due to the live centipede, we also used a plastic centipede as a control. We slowly pushed a 70 mm long plastic centipede (similar in size, shape and colour to the live centipedes) inside the crevice and left it there. Before re-using plastic centipedes we soaked them in hot water for 1 h, washed them thoroughly with detergent, and allowed them to air dry. For the control trials, we simply lifted the lid of the gecko’s cage and left it open for 5 min. For each trial, we scored whether or not the gecko exited the crevice (entire body exposed) and, if so, the time taken for the gecko to exit the crevice (s). If a gecko did not leave the shelter, the time was recorded as 300 s.

We ran this experiment using both small (180 × 180 mm) and large (230 × 190 mm) shelter-sites, which allowed us to determine whether rock size influenced the likelihood of a gecko abandoning a shelter site or the time taken to abandon a shelter site. We exposed each individual gecko to both shelter sites in a randomized order, and tested for differences in propensity to abandon the retreat using a contingency table analysis (using trials with a live centipede only), and whether time to abandonment differed between juveniles and adults using a repeated-measures ANOVA with each individual treated as a repeated measure. This is the only experiment in which individual geckos were used more than once.

Results

Selection of shelter-sites in the field

We found 35 centipedes and 80 geckos (60 juveniles, 20 adults) under 112 individual rocks in the field. The rocks used by geckos (N = 70) and centipedes (N = 25) had similar physical dimensions (all p > 0.05; Table 1). Most gecko and centipede rocks were located on rock substrates (93% and 79%, respectively, χ² = 1.73, df = 1, p = 0.19), and the remaining rocks had substrates composed of both rock and soil.

Daily thermal regimes differed beneath rocks used by geckos and those used by centipedes throughout the course of the day (rock type: F₁,₅₉ = 3.61, p = 0.06; time: F₉₅,₅₆₀₅ = 556.39, p < 0.0001; rock type × time interaction: F₉₅,₅₆₀₅ = 1.54, p < 0.0006; Figure 1). Rocks used by geckos
Figure 1. Mean temperatures beneath rocks used as shelter sites by geckos (*Oedura lesueurii*, *N* = 45) and by centipedes (*Cormocephalus* sp., *N* = 16) during a sunny day in May 2007. Rocks used by geckos were on average 1.9°C warmer during midday than those used by centipedes. Error bars were too small to be visible in most cases and are not shown.

...were similar in temperature to those used by centipedes, except during the warmest part of the day, when gecko rocks were on average 1.9°C warmer.

Rocks used by geckos and centipedes overlapped considerably in canopy openness (range in canopy openness: 39.5–71.4% and 42.8–84.1%, respectively), but on average the rocks used by geckos had more open canopies (*F*$_{1,71}$ = 5.96, *p* = 0.02; Figure 2a). A similar trend was evident for solar radiation exposure (geckos, range: 8.3–14.4 mol/m$^2$ per day; centipedes, 8.5–14.1 mol/m$^2$ per day, *F*$_{1,70}$ = 5.35, *p* = 0.02; Figure 2b). The similarity in these two results reflects the high correlation between canopy openness and incident radiation (*r* = 0.72, *p* < 0.0001); more open canopies allow more incident radiation to penetrate through to the rock.

On three occasions we found geckos (two juveniles and one adult) sharing the same rock with a centipede; in one of these instances the juvenile was found dead. Under the null hypothesis of no avoidance, we would expect to observe both species sharing 20 individual rocks. Thus, geckos and centipedes shared rocks less often than would be expected by chance (*χ*$_2^2$ = 14.73, df = 1, *p* < 0.001). We also observed geckos and centipedes using the same rocks on four occasions, but in different months. Together,
these results suggest that centipedes and geckos use shelter sites that overlap in both physical attributes and thermal regimes, but that either one or both of these species avoids the other under field conditions.

**Crevice selection in the absence of predators**

When given the choice between a wide versus a narrow crevice, most centipedes chose narrow crevices as diurnal shelter-sites ($N = 11$ of 12, $\chi^2 = 8.33$, df = 1, $p = 0.004$). In the absence of predators, velvet geckos also selected narrow crevices (juvenile geckos: $N = 14$ of 14, $\chi^2 = 14.0$, df = 1, $p = 0.002$; adult geckos: $N = 16$ of 20, $\chi^2 = 7.20$, df = 1, $p = 0.007$). The preference for narrow crevices was equally strong in centipedes, juvenile geckos, and adult geckos ($\chi^2 = 3.51$, df = 2, $p = 0.17$).
Crevice selection in the presence of predators

In crevice selection trials involving a gecko plus a centipede, all centipedes selected the narrow crevice as shelter. Thus, geckos could: (1) share the narrow crevice with the predator, (2) avoid the predator by using the wide crevice, or (3) avoid the predator by clinging to the side or roof of the cage (centipedes could not climb the arena sides). A logistic regression revealed a significant interaction between ‘predator’ type (live centipede, plastic centipede, or no predator) and lizard life stage (juvenile or adult; $\chi^2 = 9.22$, $df = 2$, $p < 0.01$). When alone or exposed to the plastic centipede only, most or all geckos selected the narrow crevice, as before (Figure 3). In contrast, in trials with a live centipede, fewer juvenile geckos used narrow crevices than did adults (Figure 3). Juveniles also were less likely to share a thin crevice with a centipede than were adults ($\chi^2 = 6.38$, $df = 1$, $p = 0.01$; Figure 3). In these trials, three of 32 adult geckos (9.4%) and two of 18 juvenile geckos (11.1%) did not use retreat-sites, and were clinging to the arena walls the following morning.

![Figure 3. Proportion of juvenile and adult geckos (Oedura lesueurii) choosing a narrow crevice (6 mm high) as a diurnal shelter site when tested with a live centipede ($N = 18$ juveniles, 32 adults), a model (plastic) centipede ($N = 12$ juveniles, 16 adults), or without a centipede ($N = 14$ juveniles, 20 adults). In all trials involving a live centipede, the centipede was inside the narrow crevice the following morning; plastic centipedes were placed inside the narrow crevice.](image-url)
Do geckos actively avoid centipedes?

All juvenile and adult geckos remained inside their crevices when we opened the cages (disturbance control) or slowly inserted the plastic centipede into the crevice (visual control). In trials involving live centipedes, all of the juvenile and adult geckos abandoned the small shelter site during the 5 min observation period. Due to the consistency of these responses, we only analysed whether juveniles and adults sheltering beneath the large paver differed in their response to live centipedes. Most juveniles (64%) and adults (85%) abandoned their crevice in trials involving the large shelter site, but there was no difference with life stage (Fisher’s exact test, \( p = 0.59 \)). All geckos that remained inside the crevice moved to the side of the crevice away from the centipede; often portions of the gecko were visible at the edge of the crevice, with the animal moving around the outside of the paver. Geckos were never visible at the edge of the crevice during control trials.

Juvenile and adult geckos remained within shelter sites for similar amounts of time after a centipede entered (repeated-measures ANOVA with gecko size (juvenile, adult) and paver size [small, large] as factors, with square-root transformed time as the dependent variable: \( F_{1,20} = 0.58, p = 0.45 \)). However, both adult and juvenile geckos abandoned the small shelter site more quickly than the large shelter site (\( F_{1,20} = 9.27, p = 0.01 \); interaction term, \( p = 0.46 \)). On average, geckos abandoned small shelter sites 90 s sooner than large shelter sites.

Table 1. Comparison of mean rock sizes (±SE) used by velvet geckos (Oedura lesueurii, \( N = 70 \)) and centipedes (Cormocephalus sp., \( N = 25 \)), from field surveys in southeastern Australia. Also shown are the results of one-way ANOVAs comparing the attributes of rocks (length, width, area, minimum thickness, maximum thickness) that form the upper surface of crevices within which these two taxa shelter.

<table>
<thead>
<tr>
<th>Rock variable</th>
<th>Gecko</th>
<th>Centipede</th>
<th>( F_{1,93} )</th>
<th>( p )</th>
</tr>
</thead>
<tbody>
<tr>
<td>Length (mm)</td>
<td>454.8 ± 18.84</td>
<td>469.6 ± 28.26</td>
<td>0.17</td>
<td>0.68</td>
</tr>
<tr>
<td>Width (mm)</td>
<td>312.5 ± 13.44</td>
<td>316.2 ± 22.02</td>
<td>0.02</td>
<td>0.89</td>
</tr>
<tr>
<td>Area (mm(^2))</td>
<td>155 352.0 ± 12 629.80</td>
<td>159 775.6 ± 18 756.21</td>
<td>0.03</td>
<td>0.85</td>
</tr>
<tr>
<td>Minimum thickness (mm)</td>
<td>39.2 ± 4.13</td>
<td>31.9 ± 4.28</td>
<td>2.89</td>
<td>0.09</td>
</tr>
<tr>
<td>Maximum thickness (mm)</td>
<td>75.4 ± 5.40</td>
<td>58.2 ± 31.92</td>
<td>1.00</td>
<td>0.32</td>
</tr>
</tbody>
</table>
Discussion

Our field data show that centipedes and geckos used rocks with similar structural features (size and thickness; Table 1), daily thermal regimes (Figure 1), degree of canopy openness (Figure 2a), and exposure to solar radiation (Figure 2b). Subtle differences in habitat usage were also apparent; for example, rocks used by geckos were slightly warmer than centipede rocks (Figure 1), possibly reflecting differences in desiccation rates or thermal tolerances (Lewis, 1981). Despite this high degree of microhabitat overlap, geckos and centipedes rarely shared rocks at our field sites. This pattern is likely the result of juvenile geckos avoiding rocks used by centipedes. In laboratory trials, both adult and juvenile geckos selected narrow crevices and avoided wide crevices. However, the presence of centipedes induced juvenile (but not adult) geckos to modify their behaviour and use wide crevices (Figure 3). In combination with field studies showing that velvet geckos select rocks with narrow crevices (Croak et al., 2008), these results suggest that the presence of invertebrate predators modifies habitat selection of juvenile geckos. Similar ontogenetic shifts in antipredator behaviour occur in other lizard species, and may well be widespread. For example, juvenile water skinks (Eulamprus quoyii) avoid sheltering under refuges previously used by funnel web spiders, whereas adult water skinks do not avoid such sites (Head et al., 2002). Such size-dependent shifts in anti-predator behaviour presumably reflect differences in the vulnerability of adult and juvenile lizards to invertebrate predators. The larger, wider tails of adult velvet geckos may be more effective at directing predatory strikes away from the body than are the smaller tails of juveniles (e.g., Daniels, 1986). In velvet geckos (and many other lizard species), the tail is readily autotomised during predatory attacks, and facilitates escape from predators (Daniels, 1986).

Our laboratory trials also revealed that a gecko’s response to centipedes was influenced by the size of the shelter-site. When centipedes entered a small shelter site, the resident gecko invariably abandoned the crevice; but when the shelter was large the geckos moved around the outside of the crevice to avoid contact with the centipede. Presumably, a gecko’s response to an intruding centipede will depend on the costs and benefits associated with staying or leaving the retreat-site (Lima & Dill, 1990), which in turn will depend on factors such as the size of the overlying rock (and hence, crevice), and its proximity to other suitable shelter sites. The obvious cost
for a gecko sharing a shelter site with a centipede is the risk of predation (as we witnessed in the field), though reports of such predation events are rare (Greer, 1989; Bauer, 1990). The risk of predation is likely to be higher under small rocks than large rocks, simply because a centipede is more likely to come in contact with a gecko. Centipedes rely on tactile and chemical senses to locate prey, and because their vision is poor, they cannot pursue fast moving prey (Lewis, 1981). The dangers associated with remaining close to a centipede must be balanced against the costs of leaving the shelter-site. Geckos leaving a shelter must travel over exposed areas to find a new shelter-site, potentially increasing their vulnerability to predation or increasing the likelihood of caudal autotomy (e.g., Huey & Pianka, 1981; Downes & Shine, 2001; Webb & Whiting, 2005). Thermally optimal shelter-sites also may be in short supply, generating competition for shelter-sites (Pringle et al., 2003). Thus, even if a gecko finds another thermally suitable rock, it is likely to be occupied by another gecko (or a predatory snake), and the non-resident must then engage in a territorial dispute with the resident before it can settle under the new rock (e.g., Kondo et al., 2007). Because juvenile geckos often share rocks with other juveniles, whereas adult males do not (at least under laboratory conditions; Downes & Shine, 1998b; Schlesinger & Shine, 1994), the costs of leaving rocks and engaging in territorial disputes with residents may be higher for adults than for juveniles.

In many predator-prey systems, the risk posed by a predator depends not only on the overlap in habitat use between predator and prey, but also on ontogenetic shifts in risk that arise as a result of the potential prey item’s life stage and/or body size (Lima & Dill, 1990). Variation in the magnitude of such risks can in turn influence antipredator behaviours. In the present study, the greater vulnerability of smaller lizards appears to have favoured a stronger avoidance of predatory centipedes than is shown by adult conspecifics. The small size and reduced locomotor capacities of juvenile vertebrates often may render them more vulnerable to invertebrate predators than are larger members of the same species, suggesting that ontogenetic shifts in the nature of avoidance responses to predatory invertebrates may be widespread (Kehr & Schnack, 1991; Resetarits & Wilbur, 1991; Hickerson et al., 2004; Anthony et al., 2007).

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References


