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Intraguild predation, thermoregulation, and microhabitat selection by snakes

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Intraguild (IG) predation, the killing and eating of potential competitors, can be a powerful force within faunal assemblages. If both the IG predator and its prey prefer similar microhabitats in spatially structured environments, avoidance of the predator may relegate IG prey to suboptimal habitats. In southeastern Australia, the broad-headed snake (*Hoplocephalus bungaroides*) is an endangered species sympatric with the small-eyed snake (*Cryptophis nigrescens*), an abundant and geographically widespread species known to eat other snakes. Both of these nocturnal ectotherms shelter diurnally beneath thermally distinctive "hot rocks," which are in limited supply. When selecting shelter sites, broad-headed snakes thus face a trade-off between predation risk and habitat quality. In laboratory experiments, we allowed broad-headed snakes to choose between retreat sites differing in thermal regimes, in scent cues from predators, and in the actual presence of the predator. Broad-headed snakes displayed an aversion to sites with live predators and predator scent, yet nonetheless frequently selected those sites to obtain thermal benefits. In trials with live predators, adult broad-headed snakes shared hot rocks with small-eyed snakes, but most juveniles did not; data from a 16-year field study likewise suggest that broad-headed snakes only cohabit with small-eyed snakes if the two snakes are similar in body size. Our results suggest that thermoregulatory considerations are sufficient to prompt juvenile (but not adult) broad-headed snakes to risk IG predation, emphasizing the importance of microhabitat quality and body size in mediating IG predator–prey interactions. *Key words:* disturbance, endangered species, habitat selection, predation risk, refuge, snakes. *[Behav Ecol 20:271–277 (2009)]*

Intraguild (IG) predation, consumptive interactions among species that compete for shared prey, is a taxonomically widespread phenomenon in both aquatic and terrestrial ecosystems (Polis et al. 1989; Morin 1999; Arim and Marquet 2004). Pioneering theoretical work identified the coexistence of IG predators and IG prey as difficult to explain and suggested that such coexistence requires low-to-intermediate productivity levels (Mylius et al. 2001) and that the IG prey species be a superior competitor for the shared resource (Holt and Polis 1997). These predictions were difficult to reconcile with the ubiquity of IG predation in nature, stimulating recent attention to real-world complexities (such as habitat heterogeneity, disturbance, cannibalism, and omnivory) that might facilitate coexistence between predators and prey (Janssen et al. 2007; Rosenheim 2007; Rudolf 2007).

Behavioral processes are important to IG predation dynamics. Most animals modify their behavior in the presence of predators (Lima and Dill 1990; Creel et al. 2007). Hence, the ability of IG prey to respond appropriately to the presence of IG predators may facilitate coexistence (Amarasekare 2006; Kimbrell et al. 2007; Moehrenschlager et al. 2007). Prey can respond to predators in several ways. First, they can reduce their activity levels during time periods when predators are most active (Gliwicz 1986; Hays 1995; Speakman 1995). Second, prey can monitor the locations of predators and select foraging or shelter sites far away from them (Palomares et al. 1996; Durant 2000; Sergio et al. 2003; Magalhaes et al. 2005). Third, prey can avoid habitats associated with high predation risk, such as those that predators frequently use (Fedriani et al. 1999, 2000; Webb and Whiting 2005; Sergio, Blas, et al. 2007; Sergio, Marchesi, et al. 2007).

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Prey may also modify their behavior according to the degree of risk posed by the predators (Helfman 1989). In many systems, the degree of predation risk depends on the size of the IG prey relative to its predator (Polis et al. 1989; Donadio and Buskirk 2006; Sergio and Hiraldo 2008). For example, among mammalian carnivores, leopards (*Panthera pardus*) and spotted hyenas (*Crocuta crocuta*) will kill cheetah cubs (*Acinonyx jubatus*), whereas larger-bodied lions (*Panthera leo*) will kill both cheetah cubs and adults (Schaller 1972; Laurenson 1994). Thus, predator-avoidance behaviors may depend on the size or life stage of the IG prey.

Many animals shelter within refuges, which can provide a number of fitness benefits (Sih et al. 1992). However, sheltering inside refuges also can entail costs, such as loss of time and space available for mate searching and foraging (Sih et al. 1990; Dill and Fraser 1997). In ectotherms, body temperature influences nearly all behaviors (locomotion, foraging, etc.) and physiological processes (digestion, metabolism, etc.). For these animals, choosing refuges with suboptimal thermal properties can entail significant physiological and behavioral costs (Huey 1991) and can potentially decrease fitness (e.g., Christian and Tracy 1981). Because body temperature influences prey-capture success, food intake, and growth rates (Angilletta et al. 2002), the costs of selecting thermally suboptimal retreat sites may be greater for juveniles than for adults (Webb and Whiting 2006).

In southeast Australia, the endangered broad-headed snake *Hoplocephalus bungaroides* co-occurs with the small-eyed snake *Cryptophis nigrescens*. Both species feed largely on lizards, but small-eyed snakes are known to eat other snake species (Shine 1984), whereas broad-headed snakes rarely eat snakes (Shine 1983; Webb and Shine 1998). The shared prey base consists largely of scincid lizards, with broad-headed snakes also consuming geckos *Oedura lesueurii* (Shine 1983, 1984; Webb and Shine 1998). During autumn, winter, and spring, both species of these nocturnally active snakes thermoregulate during

daylight hours underneath thin exposed rocks on sandstone outcrops (Webb and Shine 1998; Webb et al. 2004). Both snake species occur on the same rock outcrops and preferentially select rocks with similar physical and thermal characteristics as retreat sites (Webb et al. 2004). Broad-headed snakes are extreme ambush foragers and spend long time periods (sometimes weeks) under the same rock (Webb and Shine 1997). This scenario sets the stage for a number of interspecific interactions (IG predation of small-eyed snakes on broad-headed snakes, competition for shared prey, and competition for thermally suitable space) and also for a heat/safety tradeoff for broad-headed snakes (e.g., Downes 2001). Although we refer to these rocks as "retreats" because they shelter both snake species from higher order predators, we emphasize that they are not refuges for the IG prey from the IG predator; instead, they are a shared resource subject to competition.

In the current study, we investigate the relative roles of thermal properties and IG predation risk in driving microhabitat selection by broad-headed snakes. Moreover, we assess whether different types of predator cues (scent only vs. physical presence) elicit different behavioral outcomes. Previously, we have shown that in the absence of predator cues, broad-headed snakes select hot rocks in preference to cold rocks (Webb et al. 2004). To assess the relative importance of thermal considerations and predation risk, we first offered snakes a choice between a hot, predator-scented versus cold, unscented retreat site (thus mimicking a common situation in nature). Then, to remove the confounding effects of temperature on retreat-site selection, we offered broad-headed snakes a choice between a hot, predator-scented versus a hot, unscented retreat site. Next, to determine whether the physical presence of the IG predator influenced a snake's choice of retreat site more than predator scent alone, we offered snakes a choice between a hot rock containing a small-eyed snake versus a cold, unoccupied, and unscented rock. We did not assess another possible treatment combination (hot, predator-present retreat vs. hot, predator-absent, unscented retreat) because several juvenile broad-headed snakes were consumed during early trials (see Results), and we could not justify risking further predation on this threatened species. However, in light of our previous results showing a strong tendency of broad-headed snakes to select the warmer of two retreat sites (Webb et al. 2004), it is unlikely that many snakes would opt to cohabit a hot retreat site with a predator when an unoccupied hot retreat site was available nearby. Finally, we evaluated a major prediction of our laboratory experiments—that only broad-headed snakes and small-eyed snakes of similar sizes will share retreat sites in nature—using data from a long-term (1992–2007) mark–recapture study.

METHODS

Collection of snakes and housing

We collected snakes by hand from sandstone rock outcrops on Crown Lands near Nowra, NSW. On capture, we placed each animal inside a numbered cloth bag and recorded its location with a global posioning system (GPS) unit (Garmin 12XL, Olathe, KS). We housed snakes at the University of Sydney in separate (by species) temperature-controlled rooms maintained at 18 °C with lighting set to the natural photoperiod. We housed snakes individually inside rectangular plastic boxes (31 × 22 × 10 cm high, with clear lids and ventilation holes) with paper substrates, a plastic shelter, and a small water dish. We placed snake boxes on automated heating racks (1000–1600 h) to provide a thermal gradient within each cage (18–32 °C) so that the animals could thermoregulate. We fed snakes freshly thawed mice or skinks, depending on their dietary preferences. After a brief stay in captivity (3 weeks), we released all snakes at their original sites of capture.

Retreat-site selection experiments: general setup

We ran behavioral trials in a controlled-temperature room maintained at 19 °C (range 18–20 °C) and recorded the trials on videotape. The lights in the room were programmed to match the natural photoperiod, and they faded in and out gradually to simulate dawn and dusk. We positioned eight test arenas in two rows of four under a low-light video camera (Panasonic WV-BL202, Sydney, Australia) connected to a time-lapse video recorder (National AG6010, Sydney, Australia, set to record one frame/s) in a room illuminated by a 25-W red light bulb. Test arenas consisted of identical white plastic tubs (60 × 40 × 40 cm high, with ventilation holes) fitted with transparent plastic lids. On the day of testing, at approximately 0900 h, we placed two identical retreat sites in the test arena, one at each end. Each retreat site consisted of two concrete paving stones (230 × 180 × 40 mm thick) placed one on top of the other. Between these stones, we placed four identical steel nuts (with thickness equal to snake body diameter) onto the bottom paving stone (one on each corner) to create a crevice (hereafter we refer to these pairs of stones as "retreat sites"). A 60-W light bulb was suspended above each retreat site. To create a hot rock, the light bulb switched on at 1000 h and off at 1600 h, thereby creating a thermal profile that was similar to a sunny rock at our field sites (see Figure 1 in Webb et al. 2004). We used new paving stones in all trials to avoid the possibility of scent contamination from previous trials.

For each trial, we placed the test subject inside a plastic holding box (20 × 10 × 10 cm high, with ventilation holes) with a 3-cm plastic pipe (30-mm diameter) attached to one corner. We placed a plastic end cap over the plastic pipe to prevent snakes from leaving the holding box prematurely. We gave snakes 10 min to settle into the holding box. At dusk, we attached the holding box to a 30-mm entry hole positioned in the middle of the test arena. Thus, snakes were able to enter the test arena (or exit it) at any time during the night. The following morning, we noted each snake's final choice of retreat site. From the videotape, we scored the snake's first choice of retreat site and the number of times that it entered each retreat site. After each trial, we thoroughly cleaned the

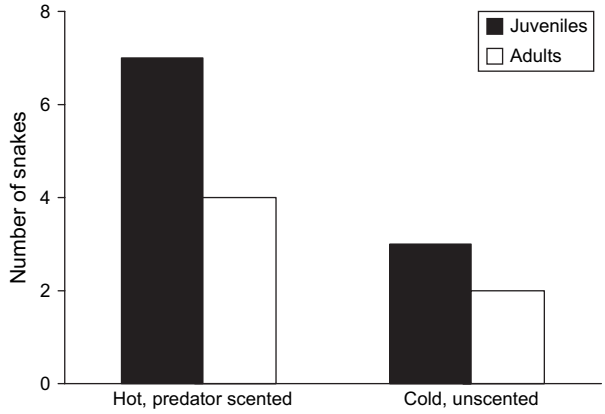

Figure 1
When given the choice between a hot, predator-scented versus a cold unscented crevice, 69% of broad-headed snakes chose the hot predator-scented crevice as their diurnal retreat site. This percentage, although high, is nevertheless significantly lower than that found in previous experiments in which snakes were offered the choice between hot and cold rocks without predator cues.

plastic tubs and lids with a solution of hot water and detergent, soaked them for 20 min in weak bleach solution, rinsed them thoroughly with fresh water, and dried them with clean paper toweling.

Hot, predator-scented versus cold, unscented retreats

To determine whether broad-headed snakes avoid hot rocks previously used by small-eyed snakes, we offered 16 snakes the choice between a hot, predator-scented retreat site and a cold, unscented retreat site. Test subjects included six adults (mean snout–vent length [SVL] = 543.5 mm, range 508–575 mm) and 10 juveniles (mean SVL = 267.9 mm, range 235–335 mm). To create the predator-scented retreat site, we placed two paving stones (with a crevice between them) in the cage of a small-eyed snake for 3 days. A different small-eyed snake ($N = 16$) was used as a scent donor for each trial. On the day of testing, we removed the retreat site (with snake inside), sealed the crevice with paper and tape, and placed the pavers inside a clean test arena at 1000 h. We placed an identical pair of clean paving stones, with crevice sealed with paper and tape (but not containing a snake), at the opposite end of each test arena. The retreat site containing the small-eyed snake heated up during the day, whereas the other retreat site did not. One hour before trials commenced, we removed the paper and tape from both retreat sites and removed the small-eyed snake from the hot retreat site. When trials commenced, the broad-headed snakes had a choice between a hot rock scented by the IG predator versus a cold, unscented rock.

Because this experiment simultaneously manipulated two variables, temperature and predator scent, we derived our expected frequencies of snakes choosing each type of rock from a separate experiment that manipulated only temperature. (This experiment was conducted at the same time as those reported here, using the same general setup, and is reported in Webb et al. 2004.) In that experiment, 16 of 17 broad-headed snakes (94%) chose the hot site as their final retreat, whereas only one (6%) chose the cold site. Thus, we expected to obtain similar frequencies in the absence of an effect of predator scent.

Hot, scented versus hot, unscented retreats

To remove the confounding effects of temperature on retreat-site selection, we offered broad-headed snakes a choice between a hot, predator-scented versus a hot, unscented retreat site. Test subjects consisted of 10 adults (mean SVL = 634.6 mm, range 558–665 mm) and 14 juveniles (mean SVL = 282.9 mm, range 235–337 mm). We created a predator-scented retreat site as described above, using 17 adult small-eyed snakes (8 males, 9 females) as scent donors. Trials were run as before, except that on the morning of testing, we switched on both light bulbs in each test arena to create a hot, predator-scented and a hot, unscented retreat site.

Hot, predator-occupied retreats versus cold retreats with no predator cues

Seventeen adult small-eyed snakes, consisting of five females (mean SVL = 382.6 mm, range 310–450 mm) and 12 males (mean SVL = 535.8 mm, range 460–610 mm) were used as residents in the experiments. To minimize the risk that small-eyed snakes might consume broad-headed snakes, we fed all small-eyed snakes 4 days before trials commenced. Three days before trials commenced, we placed a recently fed resident small-eyed snake inside a test arena containing a hot and a cold retreat site. Each day, we noted the snake's choice of diurnal retreat site by holding a small mirror beside the crevices. In all cases, the resident small-eyed snakes chose the hot rock as their diurnal retreat site. On the afternoon of testing, we replaced the cold retreat site in each test arena with an identical, cold unscented retreat site. Next, we randomly assigned a broad-headed snake to one of the resident small-eyed snake cages. Twelve juvenile (mean SVL = 269 mm, range 235–370 mm) and five adult broad-headed snakes (mean SVL = 470 mm, range 402–590 mm) were used as nonresidents.

As for the experiment above that tested preference for hot, scented versus cold, unscented sites, we derived our expected frequencies from the experiment (Webb et al. 2004) in which we offered snakes the choice between hot and cold sites without any predators or predator cues.

Long-term (1992–2008) field study

Since 1992, we have used mark–recapture methods to study broad-headed snakes and small-eyed snakes on three study plots on the western escarpment of a sandstone plateau (400 m above sea level) in Morton National Park, approximately 160 km south of Sydney, NSW. Study plots are 1.1, 1.2, and 0.7 km long; approximately 50 m wide; and are located 1.9 and 0.7 km apart (see Webb et al. 2003 for details). Vegetation on the study site consists of an evergreen mixed eucalypt forest dominated by *Eucalyptus pipperita*, *Eucalyptus gummiffera*, *Eucalyptus agglomerata*, and *Syncarpia glomulifera*. From August 1992 to November 1995, we sampled study plots once each month; thereafter, we sampled study sites at least once each year during spring. Each year, we carefully turned all suitable small rocks and other cover objects (bark, logs) on the study plots. For each snake, we recorded SVL, head length and diameter, body mass, and sex (females have thin, tapering tails; males have thick tails). We permanently marked each snake by injecting a small (11 × 2 mm) passive integrated transponder tag underneath the skin. From 1998 onwards, we also removed a scale clip from each snake for subsequent genetic analyses. All snakes were released at the site of capture. We gave each "snake rock" a unique number (with a paint pen, on the underside of the rock) and recorded its location with a GPS). From 2001 to 2008, we also surveyed snakes on several sandstone plateaus adjacent to our main study plateau, as part of a genetic study on snake dispersal (Keogh et al. 2007). We processed snakes as described above, recorded their location with a GPS, and released them at their site of capture. We carried out all research in accordance with the University of Sydney Animal Care and Ethics Committee guidelines (approval L04/5-2003/3/3753), under a scientific license from the NSW National Parks and Wildlife Service (license S10029).

RESULTS

Hot, predator-scented versus cold, unscented retreats

Due to videotape failure, we lost data on first entry and total number of entries for four snakes (three adults and one juvenile), although we knew the final choice for all 16 subjects based on where we found them on the morning after the trial. All 12 snakes for which we had data entered the hot, predator-scented retreat site at least once during the overnight trials. Seven of 12 (58%) entered the hot, predator-scented retreat site first, and 11 of 16 (69%) selected the hot predator-scented refuge as their final diurnal shelter site (67% of adults and 70% of juveniles; Figure 1). Although most snakes ultimately selected the hot retreat site, they did so less frequently than expected (~94% of the time) if they were indifferent to predator scent ($\chi^2_1 = 9.8$, $P < 0.002$). A two-by-two contingency-table analysis showed that final retreat choice did not differ by age class ($\chi^2_1 = 0.02$, $P = 0.9$). During the trials, snakes

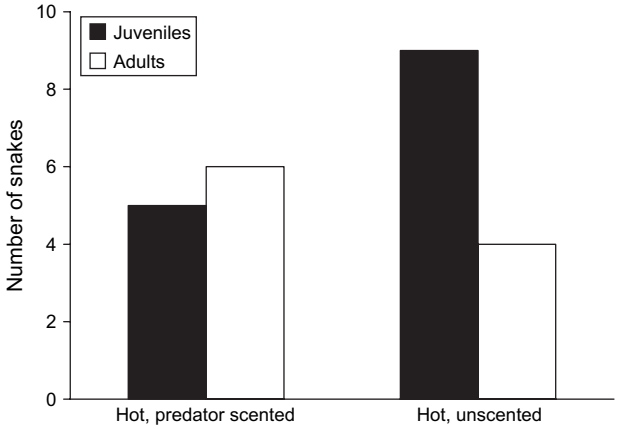

Figure 2
When given the choice between a hot, predator-scented versus a hot unscented crevice, 46% of broad-headed snakes chose the hot, predator-scented crevice as their diurnal retreat site. Patterns of retreat-site selection were similar among adult and juvenile broad-headed snakes and did not differ from the 50–50 null expectation.

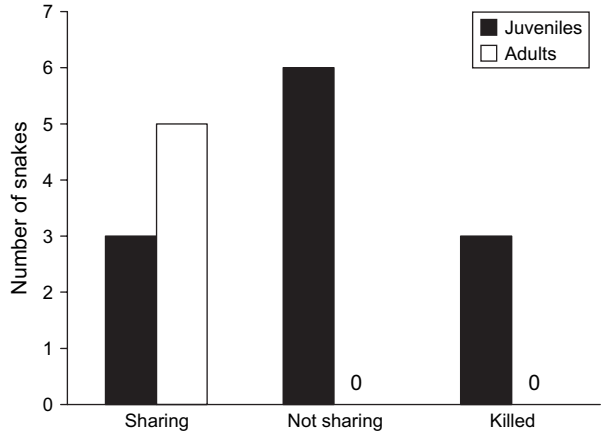

Figure 3
Outcomes of choice experiment when the IG predator occupied the hot retreat site. All adult broad-headed snakes shared the hot retreat site with the IG predator. In contrast, only 25% of juveniles shared the hot retreat site with the IG predator; 50% selected the cold retreat site, and the remaining 25% were killed by the IG predator.

entered the hot, predator-scented and the cold, unscented retreat sites with similar frequency ($N = 12$, mean number of entries = 6.17 and 4.67, respectively, paired *t*-test, $t = 1.9$, $P = 0.09$). When we analyzed juveniles separately, the tendency to enter the hot, scented sites was slightly stronger ($N = 9$, mean number of entries = 5.67 and 3.67, $t = 2.2$, $P < 0.06$).

Hot, predator-scented versus hot, unscented retreats

Of 24 broad-headed snakes, 83% entered the predator-scented retreat site at least once during the overnight trials. Overall, 58% of snakes entered the predator-scented retreat site first, and 46% used the predator-scented refuge as their final diurnal thermoregulatory site (60% of adults and 36% of juveniles). The number of snakes that chose the predator-scented crevice as their final retreat site did not differ from that expected by chance ($\chi^2_1 = 0.2$, $P = 0.7$ for all snakes, $\chi^2_1 = 0.4$, $P = 0.5$ for adults, and $\chi^2_1 = 1.2$, $P = 0.3$ for juveniles; Figure 2). A two-by-two contingency-table analysis failed to reveal any differences in final choice across age classes ($\chi^2_1 = 1.4$, $P = 0.2$). During the trials, snakes entered the predator-scented and the unscented retreat sites with similar frequency (mean number of entries = 2.96 and 3.04, respectively, paired *t*-test, $t = 0.2$, $P = 0.9$). Hence, there was again no evidence that broad-headed snakes avoided predator-scented retreat sites.

Hot, predator-occupied versus cold, unoccupied retreats

All the resident small-eyed snakes occupied the hot rocks as diurnal retreat sites when they were alone and also in the presence of nonresident broad-headed snakes. In trials involving juvenile broad-headed snakes ($N = 12$), six snakes used the cold rocks, and three snakes shared the hot rocks with the small-eyed snake (these pairs included two female–female pairs, and a male small-eyed snake and a female broad-headed snake; Figure 3). The remaining three juvenile broad-headed snakes were killed. Although we fed all resident snakes prior to the trials, two adult male small-eyed snakes (SVL = 495 and 530 mm) attacked and ate the juvenile broad-headed snakes that entered their hot retreat site (a female, SVL = 252 mm; a male SVL = 250 mm). Another male small-eyed snake killed (but did not eat) a male broad-headed snake (SVL = 245 mm) that ventured under the hot rock. Thus, 25% of the trials involving juvenile broad-headed snakes resulted in mortality for the IG prey species. In all trials involving adult broad-headed snakes ($N = 5$), the resident small-eyed snakes shared their hot rocks with the nonresident broad-headed snakes (two male–female pairs, three male–male pairs). In all of these cases, the snakes sharing rocks were similar in body size (mean difference in SVL = 76 mm).

To test whether these responses varied from those expected in the absence of a predator, we excluded the three depredated broad-headed snakes, because we do not know what their final choice would have been had they survived. Accordingly, we had 14 experimental subjects, of which eight (57.1%) chose the hot, occupied site and six (42.9%) chose the cold, unoccupied site. These frequencies diverged strongly from the expectation (94% and 6%, respectively) based on thermal preference alone ($\chi^2_1 = 15.6$, $P < 0.0001$). Moreover, contingency-table analysis indicated that the responses differed significantly across age classes ($\chi^2_1 = 7.7$, $P = 0.006$); in other words, juveniles avoided the IG predator but adults did not (Figure 3). We further tested the notion that the body size of the IG prey influenced the likelihood that it would share the hot rock with the IG predator using nominal logistic regression, with body-size difference and the sexes of the IG prey and predator as factors and the binary outcome of the trial (sharing vs. not sharing) as the dependent variable. The whole-model test was significant ($\chi^2_1 = 11.14$, $P = 0.01$) and Wald tests showed that only the body-size difference between the IG predator and prey was a significant predictor of rock sharing by IG predator and prey (parameter estimate for body-size difference = 0.024, SE = 0.01, $\chi^2_1 = 5.39$, $P = 0.02$).

We also used the results of this experiment in conjunction with those from the hot, scented versus cold, unscented trials to infer whether broad-headed snakes actually do detect IG predator scent. If they do not detect scent, then we would expect comparatively higher utilization of the hot, scented site versus the cold, unscented site relative to the utilization of hot, occupied versus cold, unoccupied site. We again excluded the three depredated juveniles and found that the relative utilization of hot, scented versus cold, unscented and hot, occupied versus cold, unoccupied did not differ significantly (68.8% vs. 31.2% and 57.1% vs. 42.9%, respectively; $\chi^2_1 = 0.9$, $P > 0.3$), suggesting that broad-headed snakes did indeed detect the scent of the IG predator.

Field data

In our laboratory trials, broad-headed snakes and small-eyed snakes were only likely to share rocks when they were similar in body size. To test whether this same pattern was evident in nature, we analyzed data from our long-term (1992–2008) field study. Over the 16-year mark-recapture study we marked and released 236 broad-headed snakes (455 total captures) and 240 small-eyed snakes (386 total captures). From 2001 to 2008, we captured an additional 73 broad-headed snakes and 85 small-eyed snakes from plateaus surrounding our main study sites (total captures = 999 snakes). However, we only found broad-headed snakes sharing rocks with small-eyed snakes on five occasions. As predicted, all of these heterospecific pairs consisted of snakes of similar body size (mean absolute difference = 89.8 mm SVL). The broad-headed snake was the larger in four instances (by 45–130 mm SVL) and was within 85 mm in the fifth. The sizes of the snakes in these five pairs were positively correlated (regression; $r = 0.91$, $F_{1,3} = 14.9$, $P = 0.03$), consistent with the idea that juvenile broad-headed snakes avoid retreat sites containing larger-bodied (and thus, potentially lethal) IG predators.

We constructed two simple null models in program R (http://www.r-project.org/) to ascertain whether this pattern was nonrandom. We used data on the SVL of all 999 snakes captured between 1992 and 2008. In the first test, we randomly drew 10 000 sets of five heterospecific pairs, calculated the mean absolute size difference in each set, and determined the number of cases in which this difference was $\leq$the observed value of 89.8 (804, indicating a 92% probability that our results differed from the null expectation). This test was conservative, because it only considered the absolute value of size differences, irrespective of species identity. In the second test, we again drew 10 000 sets of five heterospecific pairs, calculated $SVL_{small\text{-}eyed} - SVL_{broad\text{-}headed}$, and determined the number of cases in which the range of size differences was $\leq$ that in our field study (79, indicating a 99.2% probability that our results differed from the null expectation). Together, these tests strongly suggest that broad-headed snakes avoid sharing microhabitat with small-eyed snakes larger than themselves.

DISCUSSION

Although juvenile broad-headed snakes tended to avoid sites containing adult small-eyed snakes, three individuals were nonetheless killed, confirming that the latter species is an IG predator of the former. Our 16-year field data set showing the absence of heterospecific cohabitation between juvenile broad-headed and adult small-eyed snakes further suggests avoidance behavior, although it remains possible that (as in the laboratory) some juvenile broad-headed snakes were killed after entering sites occupied by small-eyed snakes. This difficulty in distinguishing between behavioral predator avoidance and consumptive removal of prey by predators is common to many studies of IG predation (Sergio et al. 2003; Sergio and Hiraldo 2008).

On balance, our results suggest that broad-headed snakes are able to distinguish IG predator scent cues. Broad-headed snakes selected hot, predator-scented sites significantly less frequently than expected if temperature were the only variable, and they used these rocks with approximately the same frequency that they used rocks occupied by actual small-eyed snakes. Although our second experiment (hot, scented vs. hot, unscented) rocks did not reveal statistically significant departures from expected frequencies, nine of 14 (64%) juveniles selected the unscented site. It may be that 14 experimental subjects did not provide adequate statistical power to detect a preference.

Avoidance behavior and predation susceptibility were greatest among juvenile broad-headed snakes, suggesting that the IG prey in this system eventually grows into a body-size refuge. Nevertheless, even predation-susceptible juvenile snakes were willing to risk predation to obtain thermally suitable retreat sites. Our previous work in both the field and the laboratory has shown that in the absence of predators, broad-headed snakes consistently choose hot retreat sites (Webb et al. 2004). This preference confers a strong functional advantage in terms of locomotion, prey capture, and juvenile growth rates (Webb and Shine 1998; Webb and Whiting 2005), making it plausible that juvenile snakes might "gamble" on a risky-but-hot microhabitat.

In these respects, juvenile broad-headed snakes appear to differ from many species that display strong predator-avoidance behavior even if it requires sacrificing habitat quality (Lima and Dill 1990; Hakkarainen and Korpimaki 1996; Downes and Shine 1998; Sergio, Blas, et al. 2007; Sergio, Marchesi, et al. 2007). Some snakes can distinguish between the odors of predatory and nonpredatory snakes, and at least one species actively avoids scent trails of ophiophagous snakes (Burger 1989). However, several other studies on snakes have found predator avoidance to be similarly weak or weaker than that observed in this study. For example, Parker (1978) reported that several species of colubrid snakes did not avoid the side of an arena that had contained an ophiophagous king snake (*Lampropeltis getulus*). Likewise, Weldon et al. (1990) showed that corn snakes (*Elaphe guttata*) did not avoid areas scented by king snakes.

"Microhabitat quality" has multiple axes, of which predation risk is only one. In nature, scent might be an unreliable indicator of the probability that an absent predator will return, or habitats might be saturated with predator scent. In such cases, other factors may dominate habitat choice. It may also be that binary choice experiments are overly simplistic, prompting subjects to disregard predator cues more often than they would in nature. In our system, however, thermally suitable microhabitat is a limiting resource (Pringle et al. 2003; Webb et al. 2005), suggesting that broad-headed snakes do indeed face such a risk-quality trade-off in the real world.

Theoretical models of IG predation hold that the IG prey must outcompete the IG predator for the shared resource in order to remain viable (Holt and Polis 1997), but in our system, the IG predator displays faster growth rates and appears to be the superior competitor (Webb et al. 2002, 2003). Here, we tested the idea that spatial habitat structure (a mosaic of discrete rock microhabitats) might provide juvenile broad-headed snakes with the opportunity to avoid small-eyed snakes behaviorally, thus minimizing the incidence of IG predation. Our experiments gave only weak support for this notion. This may be because the structural attributes in question can be used by both IG prey and IG predator, and therefore are not effective refuges. Therefore, we still lack a mechanism to account for the apparent coexistence of these sympatric species.

Recent work has emphasized the importance of alternative prey sources in stabilizing coexistence of IG predators and their prey (Holt and Huxel 2007). This mechanism might operate in our system, where both snake species consume scincid lizards, but only broad-headed snakes prey frequently on the common gecko *O. lesueurii* (Webb and Shine 1998). Coexistence can also be facilitated by disturbance (Connell 1978). In the eucalypt forests of our study site, anthropogenic fire has provided periodic disturbances for perhaps 10 000 years or more. We recently found that abundance and survival of small-eyed snakes decreased by 48% and 37%, respectively, after an intense wildfire, whereas abundance and survival of broad-headed snakes

was unaffected (Webb and Shine 2008). Fire may therefore contribute to stability of this IG predation complex.

However, it is also possible that the coexistence of these species is actually not stable—at least not any longer. The broad-headed snake is threatened and restricted to small populations within a few hundred km of Sydney; perhaps this species is en route to extinction, and IG predation by small-eyed snakes is hastening that outcome. This seems particularly likely if the effects of predation by small-eyed snakes are synergistic with other processes threatening broad-headed snakes, such as bush-rock removal (Shine et al. 1998) and vegetation encroachment resulting from fire suppression that reduces the availability of thermally suitable microhabitat (Pringle et al. 2003; Webb et al. 2005). Such reductions in microhabitat availability might bring broad-headed and small-eyed snakes into increasingly frequent contact, thus amplifying the impact of IG predation. Further research will be required, both to assess potential mechanisms of coexistence and to determine whether IG predation acts in concert with anthropogenic activity to threaten broad-headed snake populations.

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