

How Do Nocturnal Snakes Select Diurnal Retreat Sites?

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Theoretical and empirical studies of habitat selection suggest that reptiles should use “fixed” structural features (perch diameter, vegetation) or light intensity (sun and shade) to select thermally suitable microhabitats. But how do nocturnal species select thermally suitable diurnal retreat sites at night in the absence of visual cues? To investigate this question, we studied habitat selection by two sympatric nocturnal snakes, the endangered Broad-Headed Snake *Hoplocephalus bungaroides* and the common Small-Eyed Snake *Cryptophis nigrescens*. In the field, we investigated whether snakes selected diurnal retreat sites nonrandomly with respect to vegetation structure and rock temperature. In the laboratory, we offered snakes a choice between rocks with different crevice sizes, temperatures, and degree of shading. In the field, rocks used by snakes received significantly higher levels of incident radiation intensity (and therefore had higher temperatures) than random rocks but had similar levels of canopy cover. This apparent paradox reflects differences in the position of canopy gaps relative to the path of the sun, the most important determinant of a rock’s diurnal temperature profile. In the laboratory, snakes chose rocks with narrow crevices but did not discriminate between shaded and exposed rocks. Snakes consistently chose hot rocks over cold rocks, even though the nocturnal temperature difference between the two retreat sites was less than 4 C. Our results show that these nocturnal snakes use a fixed structural cue (crevice size) to select potential retreat sites but then use a temporally variable cue (substrate temperature) to choose among potential retreat sites.

HABITAT-SELECTION theory suggests that animals should select habitats that maximize the organism’s fitness (Fretwell and Lucas, 1970; Rosenzweig, 1981); when the costs of making a poor decision are high, animals should use proximate cues that accurately predict conditions within a habitat (Orians and Wittenberger, 1991). This is especially true for ectotherms that spend long periods sequestered in diurnal retreat sites, where the physiological and survival costs of choosing a thermally unsuitable retreat site are high (Huey, 1991). For example, an individual risks mortality if its retreat site freezes overnight or exceeds its critical thermal maximum during the day (Huey et al., 1989). Despite the important physiological consequences of habitat selection, an early review of habitat selection concluded that reptiles should use stable habitat characteristics (e.g., perch height, substrate, vegetation structure) as proximate cues (Heatwole, 1977). This assumption has been widely cited to explain observed patterns of habitat selection (Reinert, 1984; Law and Bradley, 1990; Schlesinger and Shine, 1994). However, there have been few empirical investigations of the proximate cues that reptiles use to choose habitats (Hertz et al., 1994).

Among the few studies that have elucidated mechanistic bases of habitat selection by reptiles, exceptions to the predicted dominance of

structural cues have been documented. Reagan (1974) showed that the turtle *Terrapene carolina* used temperature and humidity as cues in habitat selection. Hertz et al. (1994) demonstrated that the lizard *Anolis cristatellus* used light intensity as a proximate cue when selecting perch sites. However, most studies of reptilian habitat selection have focused on active diurnal species, especially diurnal iguanid lizards (reviewed by Heatwole, 1977; Hertz et al., 1994). Thus, our understanding of habitat selection by reptiles is based on assumptions that underlie the study of diurnal organisms: frequent references are made to the relative abundance of sun and shade; and there is an assumption that animals use visual cues that they can assess remotely, such as vegetation structure and light intensity (Castilla and Bauwens, 1991; Smith, 1996; Ramirez-Bautista and Benabib, 2001).

Obviously, visual cues might be less important for nocturnal reptiles that select habitats at night. Many nocturnal species spend long periods sequestered in diurnal retreat sites where thermal conditions will strongly influence their long-term fitness (Huey et al., 1989; Kearney and Predavec, 2000). In the present study, we used field data and laboratory experiments to investigate the proximate cues that two species of nocturnal snakes use to select diurnal retreat sites. We hypothesized that nocturnal species

use substrate temperature—a temporally variable nonstructural cue—to select thermally suitable diurnal retreat sites.

The study species, the endangered Broad-Headed Snake *Hoplocephalus bungaroides* and the common Small-Eyed Snake *Cryptophis nigriscens* are sympatric in southeastern Australia and shelter under exfoliated sandstone rocks or inside crevices during the cooler months (Webb et al., 2002). Both species of snake are small (< 90 cm snout-vent length) and are vulnerable to predation from birds and mammals. Consequently, the snakes rarely bask in the open but use diurnal retreat sites as thermoregulatory and antipredator refugia (J. K. Webb and M. J. Whiting, unpubl.). *Hoplocephalus bungaroides* is an ambush predator, often remaining in a single retreat site for several weeks at a time (Webb and Shine, 1997). By contrast, *C. nigriscens* is an active forager, frequently leaving retreat sites at dusk to forage for sleeping lizards (Shine, 1984; Downes and Shine, 2001). The two species also have very different life histories: *C. nigriscens* grows faster, matures earlier and reproduces more frequently than does *H. bungaroides* (Webb et al., 2003). Thus, we can compare habitat selection by species with different foraging modes and life-history traits and for which the costs of retreat-site selection are different: each habitat-selection event by *H. bungaroides* commits the individual for a longer time, and the costs of choosing a poor retreat site will be greater than for an individual *C. nigriscens*. We discuss our results with reference to the mechanistic basis of habitat selection and speculate about the role of foraging mode and life history in driving the observed patterns.

MATERIALS AND METHODS

Retreat-site selection in the field.—We studied snake retreat-site selection in Morton National Park, 160 km southwest of Sydney, Australia, where we have a long-term (1992–2004) mark-recapture dataset for both species of snake (Webb et al., 2002, 2003). In the cooler months of the year, both species of snake shelter inside crevices or under rocks adjacent to cliffs on the western sides of several sandstone plateaus. To determine whether snakes used retreat sites nonrandomly in the field, we visited two study sites in May 2002 and marked a 100 m long \times 15 m wide transect along the edge of westerly facing sandstone cliffs. On each transect, we randomly selected 10 rocks used by *H. bungaroides*, 10 rocks used by *C. nigriscens*, and 10 available rocks not used by snakes. Because rock size and thickness influence rock temperatures (Webb

and Shine, 1998; Kearney and Predavec, 2000), we only sampled rocks that were similar in size and thickness to those used by snakes. We followed the methods of Pringle et al. (2003) to take hemispherical photographs above each rock and used the software Gap Light Analyzer (GLA) Version 2.0 (G. W. Frazer, C. D. Canham, and K. P. Lertzman, unpubl.) to quantify canopy cover and estimate radiation intensity incident upon the rocks.

Incident radiation intensity was calculated in GLA using site-specific estimates of mean day length and mean daily sunshine hours obtained from the Australian Bureau of Meteorology. An estimate of mean radiation intensity over the eight months (April through November) that the snakes spend on the sandstone rock outcrops was used in all analyses. Because incident radiation intensity and rock temperatures are highly correlated in this system (Pringle et al., 2003), radiation intensity was used as an index of rock thermal quality. This index allowed us to compare rock categories independently of thermal fluctuations caused by local weather conditions (cloudiness, wind speed and direction, ambient temperature).

Statistical analyses were carried out using StatView Version 5.0 for the Macintosh. Prior to analyses of variance, we used *F*-tests to check that variances were heterogeneous and Kolmogorov-Smirnov tests to check that data were normally distributed. All data conformed to these assumptions, so no transformations were necessary. When a covariate was used, we ensured that the slopes of the relationship between the covariate and the dependent variables were homogeneous. Fisher's least significant difference test (LSD) was used for posthoc comparisons.

Collection and housing of snakes.—We captured snakes by hand from areas adjacent to our study sites during winter 2001 and 2002. All snakes were measured (snout-vent length, to nearest mm), sexed (by manual eversion of hemipenes), and individually marked with miniature PIT tags. Snakes were housed individually in green rectangular plastic boxes (31 \times 22 \times 10 cm high, with clear lids) with paper substrates, a plastic shelter and a small water dish. Snake cages were placed on automated heating racks (1000–1600 h) to provide a thermal gradient within each cage (17–32 C) so that snakes could thermoregulate. Lighting in the room was set to match the natural photoperiod. Small-eyed Snakes and juvenile Broad-Headed Snakes were fed 2–3 Common Garden Lizards (*Lampropholis guichenoti*) and adult Broad-Headed Snakes were fed 1–2 freshly thawed mice fortnightly. All

snakes were kept briefly in captivity (usually less than two months) and were released at their point of capture.

Retreat-site selection experiments.—Retreat-site selection experiments were carried out in a controlled temperature room and were recorded on videotape. We positioned eight test arenas in two rows of four under a low-light video camera (Panasonic WV-BL202) connected to a time-lapse video recorder (National AG6010, set to record one frame/s) in a room illuminated by a 25-W red light bulb. Each test arena consisted of an identical plastic tub (60 × 40 × 40 cm high, with ventilation holes in each side) fitted with clear perspex lids. A 30-mm entry hole was positioned in the middle of one side of the arena (2 cm from the floor) so that a holding box containing the test subject could be attached to the test arena at the start of a trial. Each holding box consisted of an identical white plastic container (20 × 10 × 10 cm high, with ventilation holes) with a 3-cm plastic pipe (30 mm diameter) attached to one corner. A plastic end-cap was attached to the end of the PVC pipe to prevent snakes from leaving the holding box prematurely.

Between 0800 and 0900 h, we placed two identical rectangular concrete paving stones (230 × 180 × 40 mm thick) on top of each other (with a crevice between them) at each end of the test arena. New paving stones were used in all trials to avoid the possibility of scent contamination from previous experiments. All pavers were rinsed with fresh water to remove concrete dust and were air dried for 48 h before use. We manipulated crevice size, temperature, and shading as explained below. Ten minutes before dusk, we gently removed each snake from its cage and placed it inside a holding box. At dusk, we turned on the video recorder and attached the holding boxes to the test arenas. 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, all plastic tubs and lids were vigorously scrubbed with a solution of hot water and detergent, soaked for 20 min in bleach solution, thoroughly rinsed with fresh water, and dried with clean paper toweling before being reused.

Crevice size.—We created a crevice between the two concrete pavers by placing a steel nut on each corner of the bottom paver. To make narrow crevices, we used four identical nuts (4.9-, 5.9-, 7.5-, or 11.0-mm thick) that closely

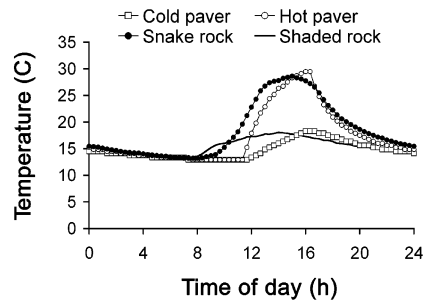


Fig. 1. Temperature profiles recorded during a 24-h period in late August (winter) underneath natural rocks at our field sites in Morton National Park and under concrete paving stones in the laboratory. The figure shows temperatures under rocks used by Broad-Headed Snakes and Small-Eyed Snakes (solid circles) and shaded rocks not used by snakes (solid line) in the field, and under hot (open circles) and cold (open squares) retreat sites created with concrete pavers in the laboratory.

matched the body diameter of the test subject. To make "wide" crevices, we placed two 2-mm thick steel washers (glued together) under each nut. All nuts were wrapped in a single layer of clean paper towel to prevent large snakes from displacing the paving stones. For each trial, we placed two pavers at each end of the test arena, one with a narrow crevice and one with a wide crevice. We randomly assigned crevices to either end of the tubs to avoid problems that might arise if snakes consistently crawled in the same direction after entering the test arenas.

Rock temperature.—To manipulate rock temperature, we placed two narrow crevices at each end of the test arena and suspended a small 40-W light globe 2 cm above one crevice. The globe above the "hot" crevice automatically switched on at 1200 h and off at 1600 h, which created a thermal profile similar to natural rocks used by snakes during late winter (August, see Fig. 1). One hour before trials commenced, we removed the light globe from above the hot rock. Both crevices had identical light sockets hanging above them during the trials. To measure the temperatures inside hot and cold crevices, we glued thermocouples to the middle undersides of the top pavers in one test arena and connected them to miniature data loggers (Hobotemp, Onset Corporation) that recorded temperatures at 15 min intervals. When trials began (approximately 15 min after sunset, 1730–1800 h) the cold rock was 4°C cooler than the hot rock, but by 0200 h temperatures under both rocks were identical (Fig. 1). Crevice and temperature trials were carried out in a con-

trolled temperature room at 16 C (range 14–17 C) during July and August 2001. Test subjects were 24 Small-Eyed Snakes (11 males: mean SVL = 453 mm, range 275–536 mm; 13 females: mean SVL = 384 mm, range 261–460 mm) and 17 Broad-Headed Snakes (6 males: mean SVL = 500 mm, range 240–653 mm; 11 females: mean SVL = 478 mm, range 235–665 mm).

Shading.—To assess whether snakes used visual cues to select retreat sites, we gave them the choice between two narrow crevices with identical temperatures (19 C) that differed in their degree of “shading.” To create a shaded rock, we placed a rectangular black card (230 × 180 mm wide) on the clear plastic lid above one of the retreat sites. Under red light the black card shaded the retreat site below, whereas the other retreat site was exposed. Trials were carried out in a controlled temperature room at 19 C, (range 18–20 C) in September 2002. Test subjects were 24 Small-Eyed Snakes (12 males: mean SVL = 512 mm, range 405–610 mm; 12 females: mean SVL = 399 mm, range 353–445 mm) and 30 Broad-Headed Snakes (19 males: mean SVL = 509 mm, range 257–635 mm; 11 females: mean SVL = 414 mm, range 244–585 mm) that were not used in previous trials.

RESULTS

Retreat-site selection in the field.—The mean percent canopy openness of random available rocks and rocks used by the two species of snake were not statistically significant (ANOVA, $F_{2,52} = 2.96$, $P = 0.06$, Fig. 2). In terms of canopy cover, the rocks selected by *C. nigriscens* were similar to those selected by *H. bungaroides* (Fig. 2). Although canopy cover was similar among the three rock categories, the rocks selected by snakes received significantly higher levels of incident radiation intensity than did random rocks ($F_{2,52} = 3.31$, $P < 0.0001$, Fig. 2). Posthoc comparisons revealed significant differences between snake retreat sites and randomly sampled rocks (LSD, $P < 0.0001$ for *C. nigriscens* rocks and $P = 0.0001$ for *H. bungaroides* rocks) but no significant difference between the rocks used by the two snake species (LSD, $P = 0.16$).

Unsurprisingly, percent canopy openness exerted a large effect on radiation intensity ($F_{1,51} = 61.85$, $P < 0.0001$). Because incident radiation intensity increases roughly as a function of increasing canopy openness (Shine et al., 2002), canopy openness was entered as a covariate in an ANCOVA to remove its effect on incident radiation intensity. Interestingly, the difference in radiation intensity between rock categories

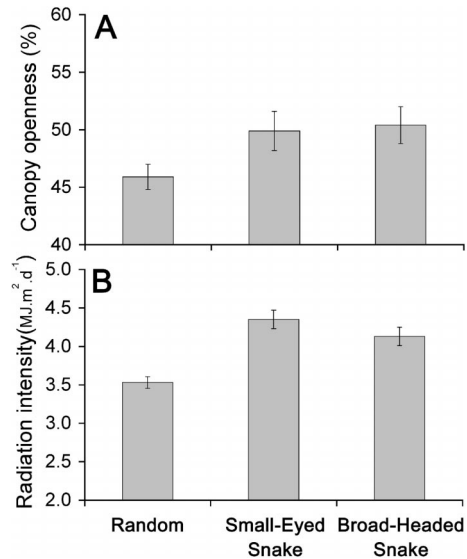


Fig. 2. Comparison of (A) vegetation canopy cover and (B) incident radiation intensity for rocks used by Broad-Headed Snakes ($n = 20$), Small-Eyed Snakes ($n = 20$) and randomly sampled rocks ($n = 20$) from two study sites in Morton National Park, New South Wales. Note that rocks selected by snakes received significantly more radiation than did randomly sampled rocks. The figure shows mean values and standard errors. Canopy cover and incident radiation intensity were calculated using hemispherical photographs and Gap Light Analyzer software.

was statistically significant even when percent canopy openness was normalized ($F_{2,51} = 16.22$, $P < 0.0001$). Posthoc comparisons showed significant differences between all three groups, although the difference was much stronger for comparisons between the two types of retreat sites and randomly sampled rocks (LSD, both P s < 0.0001) than it was between the two categories of retreat sites themselves (LSD, $P = 0.04$). Hence, snakes selected the rocks with higher incident radiation intensity (and thus, with higher temperatures) even when the analysis controlled for the effects of differing canopy coverage.

Retreat-site selection in the laboratory.—Both species of sympatric snake were highly selective with respect to retreat site crevice size and temperature but not to canopy cover (Fig. 3). When temperature was held constant, snakes selected narrow rather than wide crevices as their diurnal retreat sites (Chi-squared tests: *H. bungaroides* $\chi^2 = 8.09$, $P = 0.003$; *C. nigriscens* $\chi^2 = 10.08$, $P = 0.002$, Fig. 3A). When crevice size was held constant, snakes chose hot crevices as their diurnal retreat sites (*H. bungaroides* $\chi^2 = 8.09$, $P = 0.003$;

C. nigriscens $\chi^2 = 7.86$, $P = 0.005$, Fig. 3B). Neither species of snake showed any response to “canopy cover” and both species used shaded and exposed crevices for their diurnal retreat sites (*H. bungaroides* $\chi^2 = 0.43$, $P = 0.51$, *C. nigriscens* $\chi^2 = 0.34$, $P = 0.56$, Fig. 3C). Analysis of the videotapes showed that in all three trials, individuals of both species of snake chose their first retreat site randomly (Chi-squared tests, all $P > 0.05$) and sampled both crevices with equal frequency during the trials (paired *t*-tests, all $P > 0.05$).

DISCUSSION

In the field, the two species of sympatric nocturnal snakes selected rocks that received significantly higher levels of incident radiation than did randomly sampled rocks. Because rock temperature is highly correlated with incident radiation levels, the rocks chosen by snakes were significantly warmer than were available rocks (Pringle et al., 2003). In the laboratory, both species of snake also chose the warmest retreat sites, even though the nocturnal temperature difference between the hot and cold sites was < 4 C (Fig. 1). Collectively, these findings suggest that the two species of nocturnal snakes use rock temperature as a proximate cue to select thermally suitable diurnal retreat sites. Many diurnal reptiles use structural features or light intensity to select thermally suitable microsites (Heatwole, 1977; Hertz et al., 1994), but these cues may be less important for nocturnal species for two reasons. First, it is unclear whether nocturnal species could estimate the degree of canopy cover over a rock at night in the absence of sunlight. Although such discrimination might be possible on moonlit nights, our field and laboratory trials suggest that snakes do not use visual cues to select retreat sites. Even if they could visually assess the degree of vegetation canopy cover over a rock, our GLA analyses clearly show that canopy cover is not necessarily a good predictor of a rock’s diurnal temperature profile. That is, rocks with the same amount of vegetation cover can have very different diurnal thermal regimes, depending on where the canopy gaps are located relative to the path of the sun. For this reason, substrate temperature, particularly in the first few hours of darkness, is likely to be the best predictor of a rock’s diurnal temperature regime.

Crevice size was an important determinant of the suitability of a retreat site for both species of snake. This proximate cue is also used by the Velvet Gecko *Oedura lesueurii*, a species that also shows strong preferences for warm, narrow

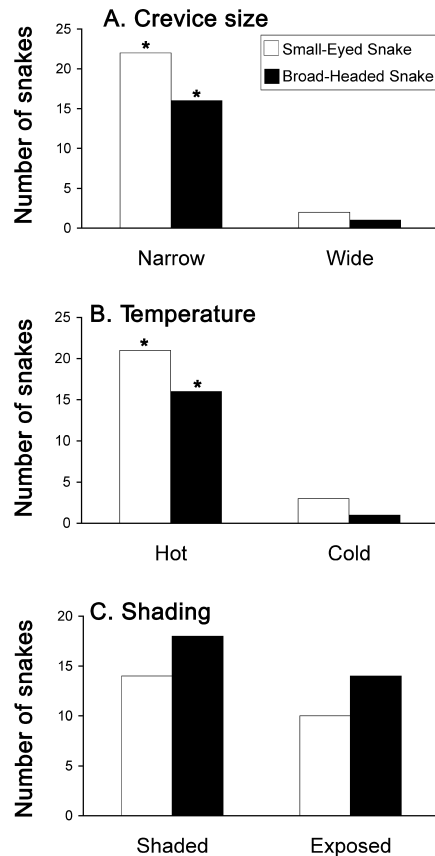


Fig. 3. Diurnal retreat sites chosen by individual Broad-Headed Snakes *Hoplocephalus bungaroides* and Small-Eyed Snakes *Cryptophis nigriscens* in laboratory retreat-site selection experiments. Both species of snake showed highly significant preferences for rocks with (A) narrow crevices over wide crevices and (B) hot rocks over cold rocks, but they did not discriminate between (C) shaded versus exposed retreat sites. An asterisk above the histogram denotes significant ($P < 0.01$) selection for the retreat site (see text for statistical details).

crevices in the laboratory (Schlesinger and Shine, 1994; Downes and Shine, 1998) and in the field (Webb and Shine, 1998). There are likely to be several benefits of choosing a rock with a narrow crevice over a rock with a wide crevice. First, narrow crevices may be safer refuges from predators than wide crevices. At our field sites, predators attacked plasticine snake replicas under rocks with wide crevices but did not attack models hidden under rocks with narrow crevices (J. K. Webb and M. J. Whiting, unpubl.). Second, narrow crevices probably offer greater thermal benefits than do wide crevices (Bustard, 1968; Kearney and Predavec, 2000). On sunny days, the underside of rocks are 5–6

C warmer than the substratum below (Webb and Shine, 1998). Thus, snakes in narrow crevices could maximize their conductive heat gain by contacting both rock surfaces, which would allow them to attain high body temperatures. Rocks with wide crevices also cool faster than rocks with narrow crevices, particularly on cold windy days (Kearney and Predavec, 2000). During rainy weather, shelter sites underneath rocks with narrow tight-fitting crevices are also drier than those under rocks with wide crevices (pers. obs.).

Previous authors have suggested that reptiles should select retreat sites using "fixed" structural cues that do not change through time (reviewed in Heatwole, 1977). By contrast, we found that both fixed and temporally variable cues were important for nocturnal snakes. Both study species used a structural cue (crevice size) to select potentially suitable retreat sites from among those available but ultimately used a temporally variable cue (temperature) to choose among that subset. In nature, animals are likely to encounter retreat sites that contain multiple temporally variable cues (e.g., predator scent, presence of conspecifics), and most animals probably use multiple cues when selecting retreat sites (Downes and Shine, 1998). Thus, temporally variable cues influence habitat selection by reptiles and may be particularly important for nocturnal species.

Our results allow us to address the question of whether differences in foraging mode influence patterns of retreat-site selection or thermoregulation in nocturnal snakes. Previous studies on diurnal snakes have found that active foragers are "thermal specialists," whereas ambush predators are thermal generalists (Secor and Nagy, 1994). Although the active-foraging Small-Eyed Snake grows faster and matures earlier than the ambush-foraging Broad-Headed Snake (Webb et al., 2003), both species of snake used rocks with very similar physical dimensions and thermal attributes (Fig. 2). Thus, foraging mode does not appear to influence diurnal retreat-site selection or thermoregulation in these two species of nocturnal snakes. Although Broad-Headed Snakes could conserve energy between meals by selecting cooler microsites (e.g., Huey et al., 1989), the snakes do not adopt this strategy in the field. Instead, the snakes select warm ambush foraging sites, presumably because such sites maximize their chances of encountering active ectothermic prey. Thus, faster growth rates in the active searcher are likely facilitated by higher food intake rates rather than by selection of higher diurnal temperatures.

Finally, our results have important implications for the conservation of the endangered Broad-Headed Snake, a species with extremely low dispersal that is currently restricted to several isolated populations. A recent study found that thermally suitable retreat sites are a limiting resource for *H. bungaroides* and suggested that local increases in vegetation density could be contributing to the decline of this endangered species (Pringle et al., 2003). Because *C. nigrescens* and *H. bungaroides* use retreat sites with similar thermal characteristics, but do not share rocks with heterospecifics (JKW, unpubl. data), they may compete for this environmental resource (e.g., Roughgarden et al., 1981; Tracy and Christian, 1986). More important, *C. nigrescens* occasionally eats other snakes (Shine, 1984) and may be an important predator of juvenile *H. bungaroides*. Theoretically, competitive or predatory interactions between *C. nigrescens* and *H. bungaroides* could negatively affect the slower growing and endangered Broad-Headed Snake. Future studies to investigate whether interspecific interactions between *C. nigrescens* and *H. bungaroides* influence patterns of habitat selection, thermoregulation, growth, or survival of *H. bungaroides* would be valuable for our understanding of snake biology and may be crucial for the long-term conservation and management of this endangered species.

ACKNOWLEDGMENTS

We thank S. Keogh, I. Scott, W. Smith, and M. Webb for their assistance in the field. S. Keogh kindly loaned his video cameras and video recorder for the laboratory experiments. We thank M. Elphick for booking cars, organizing laboratory equipment, and for her assistance with paperwork. This work was carried out in accordance with the University of Sydney Animal Care and Ethics Committee (Approval LO4/5-2003/2/3753 to JKW) and under a scientific license from the New South Wales National Parks and Wildlife Service (license S10029 to JKW). The research was supported by an Australian Research Council Discovery Grant to RS and an Academy of Science Margaret Middleton Award for Conservation of an Endangered Species, and a University of Sydney Sesqui Postdoctoral Fellowship to JKW.

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