

Microhabitat Use by Brown Treesnakes (*Boiga irregularis*): Effects of Moonlight and Prey

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ABSTRACT.—Microhabitat selection by reptiles can be affected by a complex interplay of abiotic and biotic factors. The Brown Treesnake (*Boiga irregularis*) is an efficient nocturnal predator that hunts in the tropical forest canopy and on the ground, using visual and chemical cues. To identify the factors influencing Brown Treesnake microhabitat use, we experimentally manipulated an abiotic factor, moonlight level, and a biotic factor, prey presence. We hypothesized that (1) moonlight would affect microhabitat use and (2) the presence of prey would alter microhabitat use in various moonlight levels. Trials were conducted in a large laboratory chamber with artificial trees in simulated new, half, and full moonlight. In each trial, the snake's location in canopy, subcanopy, or open ground was recorded at 60-sec intervals for 100 min. Treesnake microhabitat use was determined in three moonlight levels without prey present and in two moonlight levels with a mouse (adult *Mus musculus*) or a Mangrove Monitor (juvenile *Varanus indicus*) present. The treesnakes used open ground areas more as moonlight decreased, and they used the canopy more as moonlight increased. No significant differences existed within a moonlight level between trials with or without prey. Thus, moonlight appeared to supercede prey availability in affecting Brown Treesnake microhabitat use. Additionally, the effect of nocturnal illumination on Brown Treesnake habitat use may also have important conservation implications regarding trapping techniques and deterring the snakes from specific areas.

Reptiles are often faced with the conflicting demands of simultaneously avoiding predation and locating food, both of which are influenced by abiotic factors. Relatively few studies have considered both biotic and abiotic factors and their effects on reptile behaviors, such as activity in particular microhabitats. In nature, the interplay between biotic and abiotic factors affecting microhabitat use can be exceedingly complex and impossible to control. Laboratory studies can increase our understanding of the selective pressures driving daily variations in habitat use by testing each variable that may be involved. In one such study, Garden Skinks (*Lampropholis guichenoti*) were found to prefer open areas for foraging and basking but avoided open areas if predator (snake) scent was present (Downes, 2001). Similarly, geckos (*Oedura lesuerii* and *Nephruroides milii*) chose retreat sites with warm temperatures that lacked predation scent in laboratory tests (Downes and Shine, 1998; Shah et al., 2004).

The objective of our study was to test the influences of an abiotic and a biotic factor on microhabitat selection in the Brown Treesnake (*Boiga irregularis*) in an experimental setting. The Brown Treesnake is a primarily nocturnal, arboreal species that uses visual and chemical cues in hunting in the tropical forest canopy and

also on the ground (Cogger, 1975; Fritts et al., 1987; Chiszar, 1990; Rodda and Fritts, 1992). Brown Treesnakes were accidentally introduced on Guam around 1950 and have proved to be formidable predators, contributing to the decimation of the island's bats, birds, and reptiles (Savidge, 1987; Rodda and Fritts, 1992; Fritts and Rodda, 1998). Visual census data on Guam have indicated that moonlight may affect microhabitat use in Brown Treesnakes (Rodda and Fritts, 1992). Moonlight intensity is a critical factor affecting the activity and habitat choice of various other nocturnal snake species. The Habu (*Trimeresurus flavoviridis*) and the Lake Tanganyika Watersnake (*Lycodonomorphus bicolor*) both exhibit increased activity with decreased moonlight (Yamagishi, 1974; Madsen and Osterkamp, 1982). Adult Prairie Rattlesnakes (*Crotalus viridis viridis*) increase activity in open ground (vs. areas with cover) as moonlight intensities decrease (Clarke et al., 1996).

Prey availability also appears to affect the activity of Brown Treesnakes, as demonstrated by the effectiveness of prey (mouse) movements and scent in trapping the snakes (Shivik and Clark, 1997; Lindberg et al., 2000). Habitat use by various other snake species is similarly affected by prey availability. In laboratory experiments, Western Rattlesnakes (*Crotalus viridis*) were shown to prefer microhabitats with prey odor and the type of cover that the prey would use in nature (Theodoratus and Chiszar,

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2000). Pigmy Rattlesnakes (*Sistrurus miliaris*) preferred areas with prey (frog) scent cues (Roth et al., 1999), whereas Gray Rat Snakes (*Elaphe obsoleta spiloides*) used visual cues of birds provisioning nestlings to focus arboreal activity on specific trees with prey (Mullin and Cooper, 1998). In the field, Water Pythons (*Liasis fuscus*) were observed to alter their habitat use to coincide with seasonal variation in habitat use by the Dusky Rat (*Rattus colletti*), their primary prey species (Madsen and Shine, 1996).

The first objective of our study was to test the hypothesis that moonlight levels affected microhabitat use by Brown Treesnakes. We predicted that a direct relationship would be observed between increased moonlight level and Brown Treesnakes' use of canopy vegetation. Our second objective was to test the hypothesis that the presence of terrestrial prey affected microhabitat use by Brown Treesnakes. We predicted that Brown Treesnakes would be observed significantly more often in open ground areas in all moonlight levels when terrestrial prey were present, compared to similar moonlight conditions when prey were absent.

MATERIALS AND METHODS

Animals.—All animals used in this study were housed in animal holding rooms at the University of Northern Colorado's Animal Facility, Greeley, Colorado, in accordance with UNC IACUC protocol 0205, ASIH/SSAR guidelines (for reptiles), and ASM guidelines (for rodents) for humane treatment. The adult Brown Treesnakes used in this study ($N = 5$) were wild-caught on Guam (U.S. Fish and Wildlife Service permit MA022452-0). Snout-vent lengths (SVLs) were 1,210–1,790 mm, and body masses were 473.5–533.0 g. Light conditions were 12 : 12 light : dark photoperiod, and room temperatures were 25–28°C. We conducted trials during the snakes' peak activity periods (2 h after lights were off). Snakes were housed separately: each snake was in a ~57-liter (15-gallon) glass terrarium with paper covering the floor and equipped with a water dish, a hiding box, and artificial foliage in one quarter of the box. Snakes were fed two adult mice (domestic *Mus musculus*) every two weeks and tested one week after feeding to control for hunger level within and among snakes.

The juvenile Mangrove Monitor, *Varanus indicus* (300 mm SVL), used in the tests was also wild-caught on Guam and maintained under a 12 : 12 light : dark photoperiod and room temperatures of 25–28°C and fed euthanized domestic mice (*Mus musculus*). The monitor lizard was housed in a ~76-liter (20-gallon) glass terrarium with paper covering the

floor and equipped with a water dish, artificial foliage, rocks for cover, and a heat lamp. The domestic mice, *Mus musculus* (30 g), used in the tests were maintained under a 12 : 12 light : dark photoperiod, 22–23°C and housed in standard lab boxes with hardwood shavings, rodent chow, and water ad libitum.

Testing Conditions.—The testing chamber was, essentially, a small room (1.76 × 3 × 2.03 m tall), constructed of wood and plexiglass. The chamber temperature was 25–28°C. The walls of the chamber were covered with plastic contact paper, and the floor was covered with hardwood shavings, which were mixed and redistributed between each test to prevent scent trailing from previous trials. Moonlight illumination was simulated using 35 light bulbs (0.05 W) in the ceiling of the chamber, and the intensity of illumination was varied using a rheostat. Simulated moonlight levels were achieved by measuring light reflectance values in the field using a standard 90% white card and a Gossen Luna-Pro light meter and then reproducing these levels in the test chamber. The snakes were tested under simulated new moon (0.05 lux, no moon, starlight only), half moon (0.35 lux), and full moon (2.10 lux). A different light level was used each night for each snake (selected using a randomized schedule) and each snake was tested only once per night at 2200 h, when they exhibited maximum activity. Brown Treesnakes have been observed to maintain nocturnal behavior in laboratory situations (Chiszar et al., 1985; Chiszar and Kandler, 1986). All snakes were tested under the situations of moonlight-only, moonlight and mouse prey, and moonlight and lizard prey. Two artificial trees (2 m tall, canopy diameter ~0.75 m) were placed in diagonally opposite corners of the chamber such that the snakes could not travel from one treetop to the other without leaving the canopy microhabitat. Because trials were conducted during the dark hours of the snakes' photoperiod, we videotaped behaviors using four Sanyo black/white video cameras with internal infrared lighting sources placed within the chamber. At the beginning of each trial, the snake was placed in the center of the chamber on the floor, and at the conclusion of each 100-min trial, the snake was returned to its home terrarium. Tapes were analyzed by scoring the location of the snake at 60-sec intervals for 100 min in (1) canopy, (2) subcanopy, and (3) open ground areas. Pilot tests revealed that the snakes were remarkably similar in their acclimation time ($P > 0.05$). After a minimum of 8 min and a maximum of 12 min, with a mean, median, and mode of 10 min, all began to move.

The effect of terrestrial prey on Brown Treesnake microhabitat use was tested in new and full moonlight conditions. During these trials, we used a live mammalian prey and a live reptilian prey. A domestic mouse or a juvenile Mangrove Monitor lizard was placed in a transparent plastic box (210 × 300 × 180 mm tall) that had numerous small holes drilled in the top and sides to allow for airflow and scent dispersal. The box was placed in the center of the chamber, equidistant from the trees, to allow equal viewing opportunities of the prey from either tree's canopy or subcanopy microhabitat. When the prey box was in place, the treesnake was released onto the floor in the center of the chamber. Trials were then conducted for 100 min under new or full simulated moonlight (hereafter, termed moonlight)

Data Analyses.—Spearman Rank correlations were used to determine microhabitat use relationships among moonlight levels. We documented the snakes' presence in the canopy, subcanopy, and open ground to determine microhabitat use. Kruskal-Wallis tests were used to compare the snakes' use of each microhabitat type between each moonlight level and between the three test situations (moonlight only, mouse prey, lizard prey). If Kruskal-Wallis tests revealed significant differences, Friedman two-way analyses of variance (a nonparametric repeated-measures test) were conducted in pairwise comparisons to identify between which conditions differences existed. Significant differences were determined at the level of $P \leq 0.05$.

RESULTS

Moonlight-Only Trials.—We observed a positive relationship between moonlight level and the snakes' use of canopy vegetation and a concurrent decrease in the snakes' use of open ground areas with increased moonlight ($r^2 = 0.88$, $P < 0.0001$, $N = 5$ snakes; Fig. 1A). In new moonlight, no significant differences existed in the snakes' use of canopy, subcanopy, and open ground areas because they were observed equally in each area ($P > 0.05$, all cases; Fig. 1A). In half and full moonlight, the snakes used canopy areas significantly more than they used open ground areas ($Q = 5.000$, $df_{n-1} = 4$, $P = 0.025$, both cases). The snakes also used the canopy more in full moonlight than they did in new or half moon light ($Q = 4.00$, $df_{n-1} = 4$, $P = 0.04$, all cases).

Prey Present Trials.—In the trials conducted with either mouse or lizard present, the snakes were not observed significantly more in open ground areas compared to conditions when prey was absent ($P > 0.10$, all cases). In full

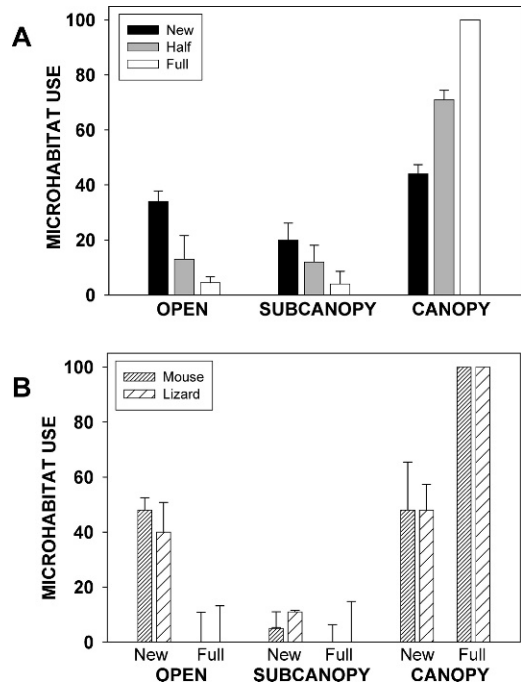


FIG. 1. Microhabitat use by Brown Treesnakes under different nocturnal illumination levels. (A) Microhabitat use (median plus 1 SE) in open, subcanopy, and canopy microhabitats under new moon (0.05 lux), half moon (0.35 lux), and full moon (2.10 lux) light levels without prey present. (B) Microhabitat use (median plus 1 SE) in open, subcanopy, and canopy microhabitats under new moon (0.05 lux) and full moon (2.10 lux) light levels with a mouse or a monitor lizard present. Microhabitat use did not change significantly when potential prey were present compared to when prey were absent.

moonlight trials with prey present, observations of the Brown Treesnakes in the canopy were not significantly greater than in trials without prey ($P > 0.10$, all cases). Also, the snakes' microhabitat use did not differ between trials with mouse prey compared to trials with the Mangrove Monitor prey ($P > 0.10$, all cases).

Similar to the moonlight-only trials, the snakes used canopy microhabitat more than open ground areas in full moonlight, even when prey was present on the ground ($Q = 5.00$, $P = 0.025$; Fig. 1B). The snakes appeared to be aware of the prey in all moonlight levels. In 60% (3/5) of the mouse trials and 40% (2/5) of the Mangrove Monitor trials conducted in new moonlight, the Brown Treesnakes wrapped their bodies around the prey box and actively tried to enter the box. This behavior was never seen in full moonlight. In full moonlight, the Brown Treesnakes extended their heads from the canopy foliage to peer at the mouse or

Mangrove Monitor in the box, but they did not descend from the canopy nor did they ever appear to seek a way out of the chamber.

DISCUSSION

Species that are both predator and prey, such as the Brown Treesnake, are confronted with a challenging array of factors when making foraging decisions. The demands of avoiding predation while locating food, both of which are influenced by abiotic factors, place a complex set of pressures on species in this trophic level. Our findings overwhelmingly indicated that moonlight is a dominant factor affecting Brown Treesnake microhabitat use, appearing to exceed terrestrial prey cues. With and without mouse or lizard prey present, the Brown Treesnakes in our tests preferred canopy vegetation and avoided open ground areas in bright moonlight. Thus, our prediction that Brown Treesnakes would exhibit an increased preference for canopy microhabitat with increased moonlight was supported. However, our prediction that prey cues would change this trend was not supported. Even in the darkest illumination (new moon = starlight only), the snakes were aware of the presence and location of the prey and they oriented toward the prey or actively tried to enter the box (in 50% of all new moon tests). However, in full moonlight, the snakes only extended their heads from the canopy vegetation and appeared to focus their gaze at the prey, demonstrating that they were aware of prey presence, but snakes never descended from the canopy microhabitat.

Precisely why moonlight so strongly affects Brown Treesnake behavior is unknown. We posit three possibilities: (1) in bright moonlight, treesnakes may be more vulnerable to predation by visually hunting predators (e.g., owls; Clarke, 1983); (2) terrestrial prey may be less available because they are avoiding the same predators (Lockard and Owings, 1974; Lima and Dill, 1990; Brillhart and Kaufman, 1991; Kotler et al., 1991), or (3) the Brown Treesnakes are less effective predators without visual cues (Mullin and Cooper, 1998; Lindberg et al., 2000; Shivik et al., 2000). Because the treesnakes left the canopy in new moonlight but not in full moonlight, even when prey was detected, we propose that predator avoidance is the principle factor contributing to their preference for canopy microhabitats in bright moonlight.

The native range of the Brown Treesnake is northern Australia, Papua New Guinea, parts of Indonesia, and nearby island chains where it has natural predators, including monitor lizards, cobras, owls, and several mammals (Rodda et al., 1992, 1999; Caudell et al., 2002).

On Guam, the natural nocturnal predators of Brown Treesnakes are absent, although snakes may be killed by dogs, cats, and pigs (Rodda et al., 1999). Apparently, the avoidance of activity in open areas in bright moonlight, a behavior associated with evading detection by visually hunting predators, has been retained by Brown Treesnakes for nearly 50 yr in their introduced habitat on Guam.

Our finding that moonlight is a major abiotic factor affecting microhabitat use by Brown Treesnakes may have practical application. Artificially increasing light levels in and around areas where the risk of snakes exiting the island (such as sea ports and airports) might be effective in preventing introgression of snakes to other tropical habitats. In those few areas on Guam where trapping is used to reduce snake numbers, capture success may be increased if capture efforts were focused in specific microhabitats during specific times (such as on the ground during new moon and in the canopy during full moon). Furthermore, the influence of nocturnal illumination on the foraging behavior of these snakes may have conservation implications regarding the effect of light pollution on the behavior of other nocturnal reptiles. In our study, Brown Treesnakes significantly altered nocturnal activity patterns with increased nocturnal illumination, and terrestrial movements were essentially eliminated; whether this change in movement pattern is affected by light pollution in the wild is unknown. The negative consequence of artificial light on hatching sea turtles is well documented (e.g., Witherington, 1997), but the impact of light pollution on other reptiles behavior and ecology is an area requiring further research.

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