January 1999

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Ontogenetic Shifts in Carrion Attractiveness to Brown Tree Snakes (*Boiga irregularis*)

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The brown tree snake (*Boiga irregularis*) is a nocturnal, primarily arboreal, rear-fanged colubrid native to parts of Australasia (Savidge, 1987; Greene, 1989). Throughout their range, brown tree snakes eat a variety of prey, including lizards, rats, and birds (Greene, 1989; Shine, 1991; Rodda, 1992; Rodda et al., in press). Brown tree snakes on Guam have a wide diet consisting mainly of lizards and lizard eggs, but a variety of other items were found in snake stomachs, including odd items such as cooked spareribs (Savidge, 1988). Savidge (1988) noted an ontogenetic shift in Guam brown tree snake diets; small snakes consumed lizards and lizard eggs and larger snakes consumed birds, bird eggs, and mammals.

Brown tree snakes were introduced to Guam in the late 1940s or early 1950s as a passive stowaway in cargo (Savidge, 1987; Rodda et al., 1992). Since the brown tree snake's introduction on Guam, its population has irrupted: population densities may occasionally reach 50–100 snakes/ha (Rodda et al., 1992). The snake has virtually extirpated the island's avifauna (Savidge, 1987), and concern that the snake will invade elsewhere has spawned intensive trapping programs (U.S. Dep. Agric., 1996).

Managers use live mouse lures in brown tree snake traps. The desire to avoid using mice has given rise to a quest for inanimate attractants for brown tree snakes (Fritts et al., 1989; Shivik and Clark, in press). Substances such as blood and saliva have shown promise in laboratory studies (Chiszar et al., 1992, 1993, 1997, in press), but have proven ineffective in the field (Rodda et al., 1997). Therefore, it is important to validate laboratory methods with field tests. Furthermore, previous lures based on odors associated

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with live mice were relatively ineffective in field trials because live prey odors require a simultaneous visual cue to attract brown tree snakes into traps (Shivik, 1998). Carrion lures produce capture rates similar to live mice lures; however, carrion does not need to be coupled with a visual cue in order to attract brown tree snakes (Shivik and Clark, 1997).

It is important to investigate thoroughly the use of carrion-based odor as an inanimate attractant prior to incorporating this technique into a management strategy. Here, we hypothesized that lure type, specifically a live or dead lure, could attract different size classes and sexes of brown tree snakes. The objective of this study was to test brown tree snakes on Guam for an ontogenetic shift in the attractiveness of carrion.

Snakes were collected during two studies on Guam. For both studies, we used wire mesh minnow traps fitted with one-way doors, and placed traps 20 m apart (Linnell et al., in press). Trap lines were established in forest edge along roads and trails. In traps, we enclosed lures within hardware cloth boxes (7 × 7 × 20 cm boxes of 6 mm mesh) to prevent snakes from eating lures. To minimize extraneous biological odors, we cleaned traps with a high-pressure water spray, soaked them in a 1:60 bleach: water solution for ≥two hours, and sun-dried them before placement. We ran each trap-line for two nights and each line contained 10 traps/treatment type (ordered randomly). Traps were checked every morning, and snakes were brought to a laboratory for measuring and sexing (probing hemipenes).

In the first study, we set 90 traps containing live mice, quartered dead mice, or empty control traps (10 traps per lure type in three traplines). Traps were set during April, 1997 adjacent to Tarague Beach, Guam (Shivik and Clark, 1997). For dead-mice traps, commercially purchased frozen mice were defrosted early in the day and allowed to rot in traps for two nights.

Because previous work showed that the importance of a visual cue was dependent upon whether lures were live or dead mice, we replicated an earlier study (Shivik and Clark, 1997) and collected sex and length data on captured snakes. We hypothesized that different size classes of snakes may be attracted differentially to live or dead prey (as examined in Study 1), or to visually apparent or visually obscured prey. Traps contained live mice, dead mice, live mice obscured, or dead mice obscured. Lures were obscured by wrapping their holders in black felt. Traps in the second study were set adjacent to Tarague Beach and Haputo Beach, Guam. We set 160 traps (10 traps per lure type in four trap lines) in March and 200 traps (five trap lines) during August 1997.

We examined differences in snake snout–vent length (SVL) using analysis of variance (ANOVA). In Study 1, we performed a one-way ANOVA to determine if snake size varied by lure type. Also, we used a log-likelihood chi-square to determine if captures differed by lure type and sex. In Study 2, we performed a two-way ANOVA examining the effects of a live or dead lure and a visual and odor or an odor only lure. We used a Mantel-Haenszel chi square (Kirby, 1993; Ott, 1993) to determine if male and female snakes showed differential attraction to trap lures.

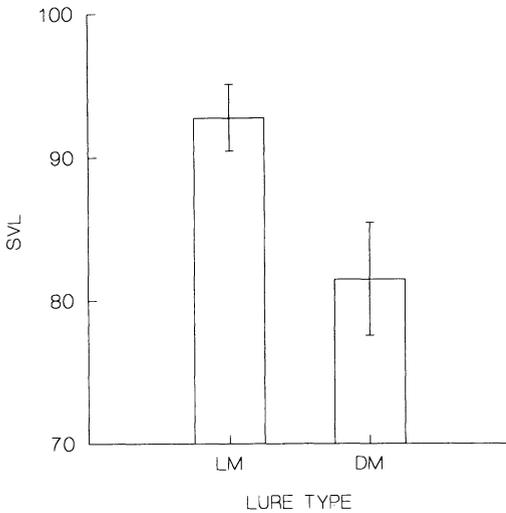In the first study, we captured 22 snakes using live mice, 14 snakes using dead mice, and two snakes in

FIG. 1. Mean snout–vent length (SVL) and SE of snakes captured using live mice (LM; N = 22) and quartered dead mice (DM; N = 14) in traps set adjacent to Tarague Beach, Guam during April 1997.

control traps. Because only two snakes were captured in control traps, the control treatment was removed from the SVL analysis. Snakes captured with live mice lures ($\bar{x}$ = 92.8 ± 2.7 [SE] cm, range = 70–109 cm) were larger than those captured with quartered dead mice ($\bar{x}$ = 81.5 ± 3.3 cm; range 58–103, $F_{1,34}$ = 6.99, P = 0.012; Fig. 1). We did not detect a difference in the attractiveness of live or dead lures to male or female snakes (χ^2 = 0.45, df = 2, P = 0.50).

In the second study, we captured 152 snakes. Snout vent length of snakes captured with visually apparent lures (N = 113, $\bar{x}$ = 93.8 ± 1.2 cm) were not significantly larger than snakes caught with only odor lures (N = 39; $\bar{x}$ = 90.8 ± 2.0; $F_{1,148}$ = 1.7, P = 0.20). However, snakes captured with dead mice (N = 74, $\bar{x}$ = 90.0 ± 1.6, range = 51–120) were smaller than those captured with live mice (N = 78, $\bar{x}$ = 95.7 ± 1.7; range = 58–119, $F_{1,148}$ = 3.8, P = 0.05). No interaction between visual and odor or odor only cues and live or dead lure types was apparent ($F_{1,148}$ = 0.24; P = 0.62). Using the Mantel-Haeszel test, male and female snakes did not show differential attraction to any lure type (χ^2 = 1.08; df = 1; P = 0.30).

In regard to carrion foraging, male and female brown tree snakes appear to have similar preferences, because we did not detect a difference in capture rates when using live prey versus carrion, nor did we detect a difference in proportions captured with live or dead and visually apparent or visually obscured prey. These results are consistent with previous brown tree snake studies on Guam that did not detect a difference in male and female food habits (Savidge, 1988).

In contrast, we found evidence that lure type (i.e., live versus carrion) differentially affected capture rate as a function of snake size. Snakes captured with carrion lures were smaller than snakes captured with live mice lures. Various snakes, including the brown tree snake, show ontogenetic shifts in feeding habits (Savidge, 1988; Greene, 1989, 1997; Arnold, 1993), and our

data suggest the behavioral mechanism for these observations. Our observed difference in snake size indicates prey preference (i.e., a higher degree of motivation to enter a trap that contains a particular prey type). Further studies in the laboratory should be performed to examine this phenomenon more thoroughly because differential prey preference will influence the effectiveness of inanimate lures.

Even though brown tree snakes may eat a wide variety of prey and be considered opportunistic, it is interesting to note that individual variation occurs within the brown tree snake population on Guam. Throughout their range, brown tree snakes may eat a wide variety of prey, but individual snakes and size classes may be much more specialized and less opportunistic.

We have, in two separate experiments, demonstrated that live or dead lures are biased to catching different sized snakes. In our studies, snakes captured with live mice were 23% and 8% longer than those captured with dead mice, relative to the range of the snakes captured. The mean size of captured snakes is influenced by the lure used as well as by the underlying distribution of snakes sampled (Rodda and Fritts, 1992). Given current trapping methods, it will be difficult to estimate the actual numbers of snakes in each size class because different size classes have different susceptibilities to different trap lures. Ironically, because the size distribution of local populations cannot be determined accurately with present trapping methods, we are unable to fully interpret the ecological significance of the observed difference in capture rates by size class.

Researchers performing population analyses on brown tree snakes should use sampling methodologies that account for the possible undersampling of small snakes (Rodda and Fritts, 1992; Rodda et al., 1992). However, differential attractiveness of inanimate lures may enable development of artificial lures that target specific size classes of brown tree snakes. For control programs, it may be important to target certain age classes of brown tree snakes. Therefore, future studies should report the size classes of snakes captured with various lure types in order to understand potential biases, and lure developers should develop lures that target specific size classes of snakes.

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Reproductive Cycle of the Tropical Night Lizard *Lepidophyma pajapanensis* from Veracruz, México

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The family Xantusiidae is represented by the viviparous genera *Xantusia*, *Lepidophyma*, and *Cricosaura* (Crother et al., 1986). Only the reproductive biology of *Xantusia vigilis* (Miller, 1948; Zweifel and Lowe, 1966) and *X. riversiana* (Goldberg and Bezy, 1974) have been studied in detail. In both species, reproductive events (gametogenesis, mating, ovulation, gestation, and parturition) occur during spring and summer, but slightly earlier in *X. riversiana*. There is no information on the reproductive biology of *Cricosaura*, and information about the reproductive biology of *Lepidophyma* is limited. According to Telford (1970) only parthenogenetic females of *L. flavimaculatum* were found in a population from Panama. Gestation takes place in January and females give birth from April to early June; litter sizes varied from one to five young. In México, Alvarez-del Toro (1982) found that *L. flavimaculatum* give birth from five to eight young in June or July. In *L. tuxtlae*, gestation is initiated in February, parturition occurs by late June or July, and litter size varies from three to six (Greene, 1970; Castillo-Cerón and López-González, 1990). The present study describes the reproductive biology of *Lepidophyma pajapanensis*, a night lizard that inhabits the Mexican tropics, and that exhibits asynchrony in the reproductive phenology of females and males.

The study area, Estación de Biología Tropical "Los Tuxtlas", is located in Veracruz, México (95°04'W, 18°36'N), between 300 and 400 m, and the vegetation is a tropical rain forest (González-Soriano et al., 1997). Temperature variation through the year is low; the dry season occurs in the spring, and the rest of the year is wet (Fig. 1).

A total of 62 adults (29 females and 33 males), and