# BROWN TREE SNAKE RESPONSE TO VISUAL AND OLFACTORY CUES

JOHN A. SHIVIK,[1] Department of Biology, Colorado State University, Fort Collins, CO 80523, USA

***Abstract:*** The brown tree snake (*Boiga irregularis*), an exotic on Guam, is primarily an arboreal colubrid thought responsible for the decline and extinction of many species. Brown tree snakes on Guam currently are trapped, with live mice as lures, to minimize the likelihood of the snakes being transported elsewhere. It is desirable to end the use of live mice in traps, but the successful development of inanimate lures requires initial knowledge about snake foraging behavior. I tested whether visual or chemical cues most stimulate appetitive behavior in brown tree snakes, and I examined the effectiveness of artificial lures for capturing snakes. Using trials in both a laboratory and field setting, I determined that both visual and olfactory cues were important for trapping brown tree snakes. The effectiveness of live mice as a lure greatly diminished with the loss of either sensory cue, apparently because of synergy between combined cues. Development of simple artificial lures based on the cues provided by live mice is likely to be difficult. Lures based on cues associated with live mice may require complex odor and visual stimuli; however, odors from other sources may lure snakes without a visual stimulus.

***JOURNAL OF WILDLIFE MANAGEMENT 62(1):105–111***

***Key words:*** artificial lure, *Boiga irregularis*, brown tree snake, Guam, olfaction, sensory modalities, vision.

The brown tree snake is a nocturnal, primarily arboreal, rear-fanged colubrid native to parts of Australia, New Guinea, and the Solomon Islands (Fritts et al. 1987, Savidge 1987, Fritts 1988, Greene 1989). The snake was 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 occasionally reach 50–100 snakes/ha (Rodda et al. 1992). The snake has caused the decline and extinction of avifauna and herpetofauna, numerous power outages, the loss of domestic animals, and is likely to be transported elsewhere (Fritts et al. 1987, Savidge 1987, Fritts and McCoid 1991, McCoid 1991, Rodda and Fritts 1992). An intensive control program is underway on Guam because the brown tree snake endangers the fauna of Guam and other ecosystems (U.S. Department of Agriculture 1996).

Trapping is an effective method for removing brown tree snakes from an area, and control personnel currently use live mice as lures for snakes (U.S. Department of Agriculture 1996). Use of live mice in traps presents animal care and maintenance problems. These problems can be alleviated if an effective artificial lure for brown tree snakes can be developed, but effective lure development necessitates further study of the sensory biology and foraging ecology of brown tree snakes.

A variety of chemosensory inputs are available to snakes (Gillingham and Clark 1981, Fritts et al. 1989, Cooper and Burghardt 1990). Stimulation of these senses can produce typical behaviors such as ambush positions or trail-following behaviors of garter snakes (*Thamnophis* spp.; Burghardt 1969, Heller and Halpern 1981, Ford and Low 1984, Burghardt et al. 1988) and rattlesnakes (*Crotalus* spp.; Cowles and Phelan 1958, Golan et al. 1982, Chiszar et al. 1990, Duvall et al. 1990). Gopher snakes (*Pituophis catenifer*; Eichholz and Koenig 1992), rat snakes (*Elaphe obsoleta*; Neal et al. 1993) and the brown tree snake (Fritts et al. 1989, Rodda 1992) may use both visual and chemical cues to locate distant prey.

For the brown tree snake, however, reports vary as to which sensory cue is dominant. Visual cues alone can elicit attack behavior and are important because if a container is visibly empty, attractive effects of chemical cues may be lost (Chiszar 1990). In contrast, brown tree snakes will enter traps baited only with bird odors (Fritts et al. 1989). My objective was to examine the effects of visual and olfactory cues on the appetitive behavior of brown tree snakes with the anticipation that this information will assist in the efficient development of artificial lures.

[1] E-mail: jshivik@lamar.colostate.edu

## METHODS

### Importance of Cues to Captive Snakes

I measured the relative importance of visual and chemical cues by videotaping each snake's response to a 1-hr presentation of 1 of 4 treatments: a negative control, a visual stimulus, an odor stimulus, and a combined odor-visual stimulus. I used 16 captive snakes maintained in individual cages at the National Wildlife Research Center (NWRC), Fort Collins, Colorado. All experiments were performed according to protocols approved by the NWRC (QA458) and Colorado State University (95-247A-01) animal care and use committees. Snakes originally were captured on Guam but were maintained in captivity for >1 year. I kept snakes on a 12:12-hr light-dark cycle and fasted them 5–9 days before testing. Throughout the tests, snakes remained in their cage, and I placed a 15- × 15- × 15-$cm^2$ acrylic box (with only 1 transparent side) on each snake's cage during the reduced light conditions (a 25-watt red bulb) of the night cycle. I vented the treatment box with a 10 cm diameter dryer hose and a low-volume fan. For the vision, odor, and combined stimuli treatments, I placed a live mouse in the box during testing. I cleaned the box with hot water and scrubbing and let it air-dry before control trials.

For the control treatment, I positioned the empty box, clear side facing the snake, and vented the box into the snake cage. For the visual treatment, I put the mouse in the box, clear side facing the snake, but vented the box to the room. For the odor treatment, I put a mouse in the box with a dark side facing the snake and vented the box into the cage. For the combined stimuli, I put a mouse in the box, placed the clear side towards the cage, and vented the box into the cage.

Each snake was tested repeatedly; therefore, I used a Latin square, cross-over design (Ott 1993) to cancel possible effects of treatment order on snake behavior. I randomly assigned snakes to 4 groups, then presented each treatment to each group of snakes in the order determined by the counter-balanced design. Thus, I conducted 64 trials using 16 snakes during March-June 1996.

Because the response to sensory cues by a foraging snake was the parameter of interest, I used the proportion of time an active snake spent orienting toward a stimulus as the dependent variable. A snake was active if it was uncoiled and moving (i.e., visibly "awake") within its cage during the 1-hr trial. I defined orienting behavior as an active snake aiming its head toward the stimulus; this behavior included tongue-flicking and probing box and vent-tube edges.

I used videotapes to record snake behavior and subsequently scored the behaviors. When scoring trials, I was blind to the experimental conditions (i.e., the stimulus presented to the snake was not in the video frame and was unknown when I scored the trials). I used a 1-way analysis of variance (ANOVA) to detect significant differences in the amount of time snakes spent orienting toward each stimulus. For this and all other experiments, I checked ANOVA assumptions using residual plots and made multiple comparisons using the Tukey method.

### Importance of Cues to Free-Ranging Snakes

*Natural Visual and Odor Cues.*—I also performed an experiment to determine the relative importance of visual and odor cues to brown tree snakes in natural habitats on Guam. I placed 5 traplines during the first half of August 1996 along forest edge adjacent to roads and trails near Tarague and Haputo beaches, Guam. Traps were wire-mesh minnow traps fitted with 1-way doors and were placed 20 m apart (Linnell et al. In press). Each trapline contained 40 traps, arranged with 4 treatments of 10 traps each. The control treatment was an empty trap. For the visual treatment, I placed a mouse in a plastic bottle and vented air through an organic-chemical gas mask filter. For the odor treatment, I placed a mouse in a bottle and vented air through 1.0- × 0.5-cm holes spaced approximately 1 cm apart around the entire bottle. I then covered the bottle with black felt such that the mouse was not visible, but odors could permeate the fabric. For the combined stimulus, I placed a mouse in a clear, uncovered, vented bottle. Mice within traps were provided with potato slices and grain as a source of food and water.

I ran each trapline for 2 nights and calculated the capture rate as the number of captures per trapnight for each treatment on each trapline. Because each trap was left in a single location for 2 nights (trapnights were not independent), absolute trapping effort could not be considered the sample unit. Instead, I used the individual trap location as the sample unit; thus, the sample size for each treatment was 50. In this and all other field studies, I used a 2-way mixed-effects ANOVA based on a randomized complete block design (with each trapline as a block within which treatments were randomly allocated) to determine if there was a difference in capture rate among treatments. All statistical analyses were conducted using SYSTAT (Kirby 1993) and SAS (SAS Institute 1985).

*Artificial Visual and Processed Odor Stimuli.*—I investigated the effectiveness of artificial lures with an artificial visual stimulus that was stationary, moving, or either stationary or moving and coupled with chemical cues derived from mouse feces. During January and February 1996, I placed 8 traplines, each run for 2 nights, and used the trap location (5 traps·treatment$^{-1}$·trapline$^{-1}$) as the sample unit (thus $n$ = 40 for each treatment). I measured the capture rate from each of 6 treatments: (1) the positive control was a live mouse; (2) the static model was a mouse model that was a commercially available, fur-covered cat toy; (3) the moving model was a mouse model suspended within the trap by a safety pin, such that wind or rocking the trap would cause movement of the model; (4) the static odor model was a mouse model that was soaked in an aqueous extraction of mouse feces; (5) the moving odor model was a mouse model soaked in feces extract and suspended by a safety pin; and (6) empty traps were the negative control. To prevent snakes from eating the lures, I enclosed live mice and models in lure-holders of hardware cloth within each trap, but lures were readily visible through the mesh.

*Artificial Visual and Natural Odor Stimuli.*—I ran additional traplines to test the efficacy of natural mouse odors (rather than an aqueous extraction of mouse feces assumed salient to foraging snakes in the previous experiment) combined with a simple visual stimulus for capturing brown tree snakes. I ran 3 traplines during August 1996. Each trapline contained 3 treatments and was composed of 30 traps (10 traps/treatment): (1) a live mouse in a trap was a positive control; (2) the odor treatment was a live mouse in a trap, but obscured visually with felt; and (3) the artificial visual and natural chemical treatment was a live mouse that was visually obscured, but this treatment included a visually apparent mouse model as an artificial visual stimulus.

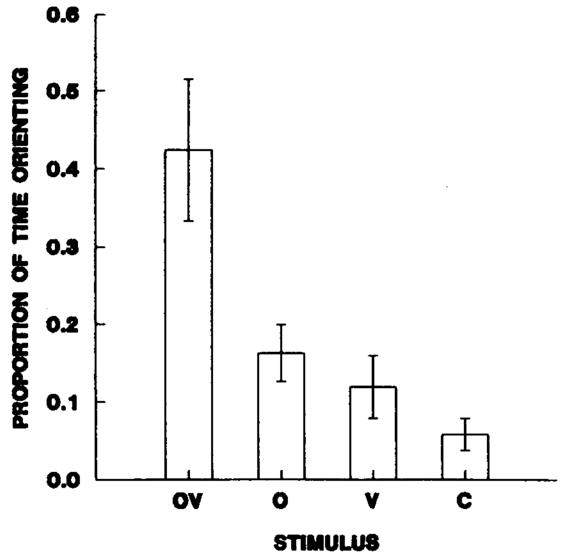


Fig. 1. Proportion of time (time orienting/time active) captive brown tree snakes spent orienting toward the stimulus presented during March-June 1996. OV = simultaneous odor and visual stimuli of a live mouse ($n$ = 8); O = live mouse odor only ($n$ = 8); V = live mouse, visually apparent only ($n$ = 9); C = negative control ($n$ = 9). Bars represent 1 SE.

# RESULTS

## Relative Importance of Cues to Captive Snakes

For the 34 trials where snakes were active, I detected a difference in the amount of time snakes spent orienting toward the presented stimulus ($F_{3,30}$ = 4.64, $P$ = 0.009). In the multiple comparisons, snakes oriented toward the combined stimulus more than the negative control ($P$ = 0.008) and the visual treatment ($P$ = 0.04). However, snakes did not orient toward the visual ($P$ = 0.91) and chemical stimuli ($P$ = 0.88) more than the negative control (Fig. 1).

## Relative Importance of Cues to Free-Ranging Snakes

*Natural Visual and Odor Cues.*—From the capture of 60 snakes, I detected a difference between the combined, chemical, visual, and control treatments ($F_{3,12}$ = 16.36, $P$ < 0.001). In the multiple comparisons, the capture rate of the combined stimulus was greater than all other treatments ($P$s < 0.005; Fig. 2). I could not detect a difference between trapping rates with only chemical and visual stimuli ($P$ = 0.30), but the odor treatment was different than the control ($P$ = 0.04).

*Artificial Visual and Processed Odor Stimuli.*—I detected a difference between treatments for the 22 snakes I captured ($F_{5,35}$ = 8.18, $P$ <

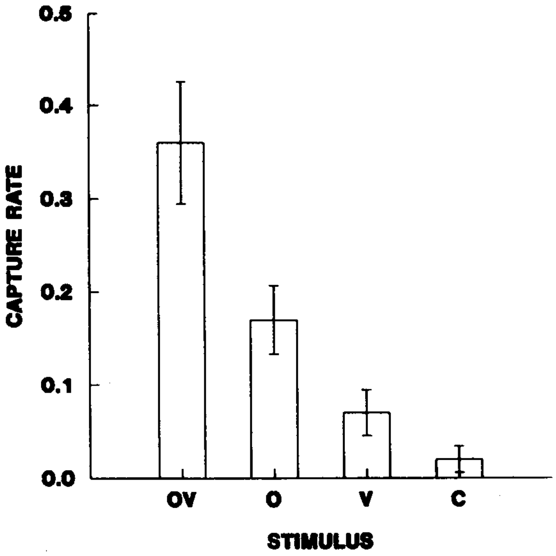


Fig. 2. Capture rates by stimulus presented to brown tree snakes captured at 5 traplines adjacent to Tarague and Haputo beaches, Guam, during August 1996. OV = simultaneous odor and visual stimuli of a live mouse; O = live mouse odor only; V = live mouse, visually apparent only; C = negative control (empty trap). Bars represent 1 SE as calculated from 50 trap locations/treatment.

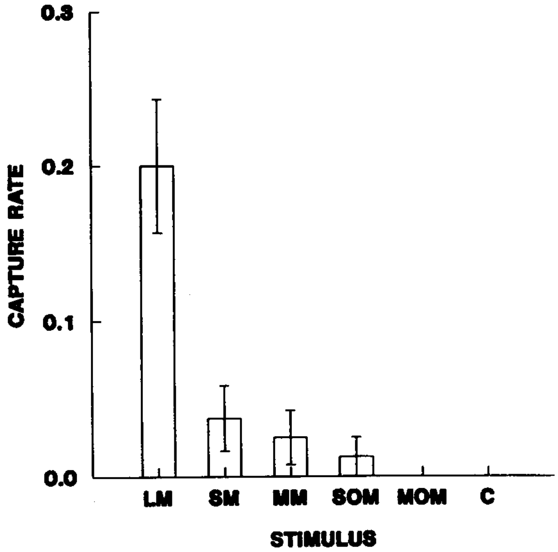


Fig. 3. Capture rates for each stimulus presented to brown tree snakes captured on 8 traplines on Andersen Air Force Base, Guam, during January 1996. LM = live mouse; SM = static mouse model; MM = moving model; SOM = static odorized model; MOM = moving odorized model; C = empty control trap. Bars represent 1 SE as calculated from 40 trap locations/treatment.

0.001). Among treatments, the live mouse was better at capturing snakes than all other model and odor treatments ($Ps < 0.001$), but I could not detect any difference between the other treatments and the negative control ($Ps > 0.77$; Fig. 3).

*Artificial Visual and Natural Odor Stimuli.*—I detected a difference between capture rates per treatment ($F_{2,4} = 27.27$, $P < 0.001$) based on the 42 snakes captured. Between treatments, the live mouse was better than the treatments of odor only and odor with an artificial visual stimulus ($P = 0.001$). I could not detect a difference between the treatments of mouse odor and artificial visual stimulus ($P > 0.99$; Fig. 4).

*Ancillary Analyses.*—Odor and visual cues may vary in relative importance, depending upon which other stimuli are available simultaneously, and this phenomenon may lead to a synergistic effect when combining sensory cues. Therefore, I conducted 2 subsequent analyses to determine if the data I collected showed evidence of context-specific relative importance of sensory modalities or evidence of synergy when sensory stimuli are combined. I constructed 2-way ANOVAs to examine the relative interest snakes showed in visual or chemical stimuli. The "treatments" in this ancillary analysis were visual cue present, visual cue absent, odor cue present, and odor cue absent.

I used the collected data and combined snake response to individual stimuli into 2 visual categories: visual cue present (originally the odor and visual cues combined and visual cue only treatments) or visual cue absent (originally the odor only and control treatments). Similarly,

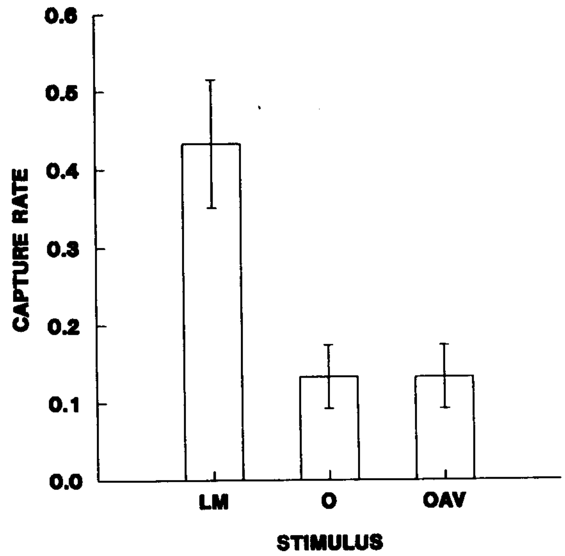


Fig. 4. Capture rates for each stimulus presented to brown tree snakes captured on 3 traplines adjacent to Tarague Beach, Guam, during July–August 1996. LM = live mouse; O = live-mouse odor; OAV = live-mouse odor with an artificial visual stimulus (a mouse model). Bars represent 1 SE as calculated from 30 trap locations/treatment.

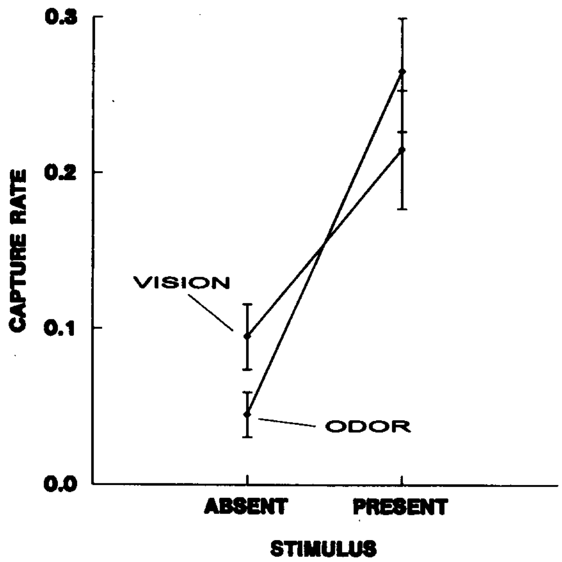


Fig. 5. Profile plot of capture rates of brown tree snakes based on the presence or absence of visual or odor cues. Snakes were captured on 5 traplines adjacent to Tarague and Haputo beaches, Guam, during August 1996. Bars represent 1 SE as calculated from 50 trap locations/treatment.

treatments were combined to be odor present (originally the odor and visual cues combined and odor only treatments) or odor absent (originally the vision only and control treatments). This ANOVA identified differences in mean response between treatments where mouse visual and odor cues were present or absent. The interaction term indicated a nonconstant relation between the effect of visual and chemical cues. That is, a significant interaction between responses to visual and chemical treatments indicated that visual and chemical effects were nonadditive, which was evidence of context-specific differences in the relative importance of sensory modalities.

I saw little evidence of an interaction between the presence or absence of visual and chemical stimuli based on the analysis of laboratory data ($F_{1,30}$ = 2.20, $P$ = 0.15). However, field data indicated that an interaction may actually exist ($F_{1,196}$ = 3.04, $P$ = 0.08; Fig. 5).

Another method of identifying synergistic effects between visual and chemical stimuli is to compare snake response to individually presented visual and chemical stimuli (summed together) with the response to simultaneously presented visual and odor stimuli. The mean proportion of time orienting in response to visual and odor cues (minus the mean proportion of time spent orienting in the control trials) was 0.159 min. The summed response was less than the time spent orienting toward combined cues (minus the mean proportion of time spent orienting in the control trials), which was 0.402 min. The mean time orienting in control trials was subtracted from other orienting times only to examine the effect of single or paired stimuli and not the effect of these stimuli combined with the effect of the experimental apparatus (evidenced by some snakes orienting toward an empty box). Because all snakes were not active in all lab trials, I could not meaningfully add snake response to single cues and statistically compare this sum to snake response to combined cues.

However, I performed an analysis on the field data to determine if the existence of synergy between visual and chemical cues is likely. I summed the capture rates from visual and chemical stimuli per trapline (minus the capture rates in the control traps) and used a paired sample $t$-test ($n$ = 5) to determine if summed scores were different than the scores recorded from combined stimuli (minus the capture rate from control traps). There was evidence of synergy between visual and olfactory cues ($t_4$ = 2.69, $P$ = 0.05).

## DISCUSSION

Many animals, when kept in captivity and deprived of the various stimuli they would encounter in a natural setting, may respond differently if not captive. This phenomenon has frustrated past efforts at developing effective inanimate lures for brown tree snakes. However, results were consistent between my laboratory and field experiments. Thus, my field experiments support the use of orientation time as a measure of brown tree snake interest in a stimulus and the continued use of laboratory studies for analyzing the behavior of brown tree snakes.

My results may explain conflicting reports of the relative importance of sensory modalities to the brown tree snake (Chiszar et al. 1988, Fritts et al. 1989, Lankford 1989, Chiszar 1990). A single sensory cue, either chemical or visual, can cause investigative behavior by snakes. For example, Fritts et al. (1989) caught brown tree snakes with only odors, whereas Chiszar et al. (1988) found that only a visual cue would elicit strikes. I captured significantly more brown tree snakes with only odor cues than with an empty trap. However, when the sensory input is incomplete, the intensity of appetitive behavior is low; single stimuli were significantly less engaging to brown tree snakes than combined stimuli.

Brown tree snakes may be primarily visually guided when searching for prey, but can switch between modalities when the visual cue is ambiguous or irrelevant (Lankford 1989, Chiszar 1990). Because of the phenomenon of switching between sensory modalities, identification of the relative importance of single sensory cues is an oversimplification of foraging behavior; snakes react to single cues based on the context in which the cues are presented (Chiszar 1990). Interactions between visual and chemical cues appear to occur, and the loss of a particular cue (e.g., odor) may not be equivalent to the loss of another cue (e.g., vision; Fig. 5). Furthermore, recent data (Shivik and Clark 1997) suggest that the relative importance of cues are not only dependent upon what other cues are available, but also upon the nature of the cue itself. For example, although odors of live mice require a visual cue to promote appetitive behavior in brown tree snakes, odors from rotting mice elicit appetitive behavior without a simultaneous visual cue (Shivik and Clark 1997).

My ancillary analyses were formed after initial examinations of the data, and are therefore not completely valid in a strict statistical sense. However, these analyses suggest the following hypotheses, which remain to be thoroughly tested: (1) the relative importance of sensory modalities to brown tree snakes is context specific (the importance of a sensory cue is dependent upon the other stimuli that occur, or do not occur, simultaneously); and (2) combined sensory cues interact synergistically.

## MANAGEMENT IMPLICATIONS

Either a visual or an olfactory cue will stimulate interest in a snake, and each cue is important biologically. However, in terms of trapping for control purposes, each sense is equally important; when either cue was missing, trap success was significantly lowered. The results of this study suggest it will be difficult to develop a simple, yet effective, inanimate lure for brown tree snakes based on the stimuli provided by live mice. Indeed, even if the chemical components of live mouse-odor that are salient to a foraging snake are identified, the success of the chemical attractant is not likely to approach that of a real mouse. The visual cue is also required. However, as shown by the third and fourth experiments, trapping success is likely to be low unless an elaborate visual cue is included.

My static and moving models and aqueous feces extractions were not meant to represent every possible artificial stimulus that could be developed, but to demonstrate that the complexity of an effective artificial lure based on the stimuli provided by live mice may have to be elaborate to equal the capture rate of live mice in traps. An effective lure that mimics live mice may need to include an appropriate odor, a realistic model with mouse-like movement, and heat. Therefore, odors that do not require a complex visual stimulus (e.g., from other prey types or carrion) should be identified to efficiently develop an inanimate snake attractant.

## ACKNOWLEDGMENTS

I thank L. Clark for assistance with the design and implementation of these studies, P. J. Savarie for assistance in the field, and H. Hirsh, M. A. Linnell, M. E. Pitzler, and D. V. Rodriguez for logistical assistance on Guam. I thank J. E. Brooks, R. L. Bruggers, L. Clark, R. M. Engeman, and P. J. Savarie for helpful reviews of the manuscript. This project was conducted with funds from the Department of Biology, Colorado State University, and the National Wildlife Research Center, through the U. S. Department of Defense Legacy Project Number 1281.

## LITERATURE CITED

BURGHARDT, G. M. 1969. Comparative prey-attack studies in newborn snakes of the genus *Thamnophis*. Behaviour 33:77–114.

———, S. E. GOSS, AND F. M. SCHELL. 1988. Comparison of earthworm- and fish-derived chemicals eliciting prey attack by garter snakes (*Thamnophis*). Journal of Chemical Ecology 14:855–880.

CHISZAR, D. 1990. The behavior of the brown tree snake: a study in applied comparative psychology. Pages 101–123 *in* D. A. Dewsbury, editor. Contemporary issues in comparative psychology. Sinauer Associates, Sunderland, Massachusetts, USA.

———, K. KANDLER, AND H. M. SMITH. 1988. Stimulus control of predatory attack in the brown tree snake (*Boiga irregularis*) 1. Effects of visual cues arising from prey. Snake 20:151–155.

———, T. MELCER, R. LEE, C. W. RADCLIFFE, AND D. DUVALL. 1990. Chemical cues used by prairie rattlesnakes (*Crotalus viridis*) to follow trails of rodent prey. Journal of Chemical Ecology 16:79–86.

COOPER, W. E., AND G. M. BURGHARDT. 1990. Vomerolfaction and vomodor. Journal of Chemical Ecology 16:103–105.

COWLES, R. B., AND R. L. PHELAN. 1958. Olfaction in rattlesnakes. Copeia 1958:77–83.

DUVALL, D., D. CHISZAR, W. K. HAYES, J. K. LEONHARDT, AND M. J. GOODE. 1990. Chemical and behavioral ecology of foraging in prairie rattlesnakes (*Crotalus viridis viridis*). Journal of Chemical Ecology 16:87–101.

EICHHOLZ, M. W., AND W. D. KOENIG. 1992. Gopher snake attraction to birds' nests. Southwestern Naturalist 37:293–298.

FORD, N. B., AND J. R. LOW, JR. 1984. Sex pheromone source location by garter snakes: a mechanism for detection of direction in nonvolatile trails. Journal of Chemical Ecology 10:1193–1199.

FRITTS, T. H. 1988. The brown tree snake, *Boiga irregularis*, a threat to pacific islands. U.S. Fish and Wildlife Service Biological Report 88(31).

———, AND M. J. MCCOID. 1991. Predation by the brown tree snake *Boiga irregularis* on poultry and other domesticated animals in Guam. Snake 23: 75–80.

———, N. J. SCOTT, JR., AND J. A. SAVIDGE. 1987. Activity of the arboreal brown tree snake (*Boiga irregularis*) on Guam as determined by electrical outages. Snake 19:51–58.

———, ———, AND B. E. SMITH. 1989. Trapping *Boiga irregularis* on Guam using bird odors. Journal of Herpetology 23:189–192.

GILLINGHAM, J. C., AND D. L. CLARK. 1981. Snake tongue-flicking: transfer mechanics to Jacobsen's organ. Canadian Journal of Zoology 59:1651–1657.

GOLAN, L., C. RADCLIFFE, T. MILLER, B. O'CONNELL, AND D. CHISZAR. 1982. Trailing behavior in prairie rattlesnakes (*Crotalus viridis*). Journal of Herpetology 16:287–293.

GREENE, H. W. 1989. Ecological, evolutionary, and conservation implications of feeding biology in old world cat snakes, genus *Boiga* (Colubridae). Proceedings of the California Academy of Sciences 46:193–207.

HELLER, S., AND M. HALPERN. 1981. Laboratory observations on conspecific and congeneric scent trailing in garter snakes (*Thamnophis*). Behavioral and Neural Biology 33:327–377.

KIRBY, K. N. 1993. Advanced data analysis with Systat. Van Nostrand Reinhold, New York, New York, USA.

LANKFORD, J. D. 1989. Stimulus control of foraging in brown tree snakes (*Boiga irregularis*) Journal of the Colorado-Wyoming Academy of Sciences 21:12.

LINNELL, M. A., R. M. ENGEMAN, M. E. PITZLER, M. O. WATTON, G. F. WHITEHEAD, AND R. C. MILLER. In press. An evaluation of two designs of stamped metal trap flaps for use in operational trapping of brown tree snakes (*Boiga irregularis*). Snake.

MCCOID, J. M. 1991. Brown tree snake (*Boiga irregularis*) on Guam: a worst case scenario of an introduced predator. Micronesica 3:63–69.

NEAL, J. C., W. G. MONTAGUE, AND D. A. JAMES. 1993. Climbing by black rat snakes on cavity trees of red-cockaded woodpeckers. Wildlife Society Bulletin 21:160–165.

OTT, R. L. 1993. An introduction to statistical methods and data analysis. Duxbury Press, Belmont, California, USA.

RODDA. G. H. 1992. Foraging behaviour of the brown tree snake, *Boiga irregularis*. Herpetological Journal 2:110–114.

———, AND T. H. FRITTS. 1992. The impact of the introduction of the colubrid snake *Boiga irregularis* on Guam's lizards. Journal of Herpetology 26:166–174.

———, ———, AND P. J. CONRY. 1992. Origin and population growth of the brown tree snake, *Boiga irregularis*, on Guam. Pacific Science 46:46–57.

SAS INSTITUTE. 1985. SAS user's guide: statistics. Version 5. SAS Institute, Cary, North Carolina, USA.

SAVIDGE, J. A. 1987. Extinction of an island forest avifauna by an introduced snake. Ecology 68: 660–668.

SHIVIK, J. A., AND L. CLARK. 1997. Carrion seeking in brown tree snakes: importance of olfactory and visual cues. Journal of Experimental Zoology 279: 549–553.

U.S. DEPARTMENT OF AGRICULTURE. 1996. Brown tree snake control activities on Guam. Environmental assessment. U.S. Department of Agriculture, Washington D.C., USA.

*Received 23 September 1996.*
*Accepted 24 March 1997.*
*Associate Editor: Fairbrother.*