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DISSERTATION

CARRION, CONTEXT, AND LURE DEVELOPMENT: THE RELATIVE IMPORTANCE OF SENSORY MODALITIES TO FORAGING BROWN TREESNAKES (*Boiga irregularis*)

Submitted by

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In partial fulfillment of the requirements

for the Degree of Doctor of Philosophy

Colorado State University

Fort Collins, Colorado

Spring 1999

COLORADO STATE UNIVERSITY

FEBRUARY 4, 1998

WE HEREBY RECOMMEND THAT THE DISSERTATION PREPARED UNDER OUR SUPERVISION BY JOHN A. SHIVIK ENTITLED CARRION, CONTEXT, AND LURE DEVELOPMENT: THE RELATIVE IMPORTANCE OF SENSORY MODALITIES TO FORAGING BROWN TREESNAKES (*Boiga irregularis*) BE ACCEPTED AS FULFILLING IN PART REQUIREMENTS FOR THE DEGREE OF DOCTOR OF PHILOSOPHY.

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ABSTRACT OF DISSERTATION

CARRION, CONTEXT, AND LURE DEVELOPMENT: THE RELATIVE IMPORTANCE OF SENSORY MODALITIES TO FORAGING BROWN TREESNAKES (*Boiga irregularis*)

Since the brown treesnake was introduced on Guam, it has caused the decline and extinction of avifauna and herpetofauna, numerous power outages, loss of domestic animals, and is a threat to other land masses. Trapping, using live mice as lures, is an effective method for removing brown treesnakes from an area, but using live mice in traps presents animal care and maintenance problems. These problems can be alleviated if an effective artificial lure for brown treesnakes can be developed, but effective lure development necessitates further study of the sensory biology and foraging ecology of brown treesnakes.

By performing experiments in the laboratory at Ft. Collins and in field conditions on Guam, I have determined that both visual and odor cues are important for attracting brown treesnakes when live mice are used as lures. When using mouse carrion, however, the importance of visual cues is reduced. I identified and tested major components of dead mouse odor, as well as a variety of natural compounds for attracting brown treesnakes, but did not find a single chemical that would lure snakes into traps. The attractiveness of dead mouse odor varies widely between seasons, and future lures for brown treesnakes should incorporate the concept of a "super normal stimulus suite" using multiple sensory cues from an odorized mechanical model. In light of these results, I discuss evolutionary trends in scavenging among taxa.

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ACKNOWLEDGMENTS

I express my appreciation to the many people and organizations that enabled me to complete this dissertation. First, I thank the United States Air Force for the Legacy funds (Project # 1281, "Development of chemical control methods for brown treesnakes management") that made my research possible. I also thank Heidi Hirsch and all personnel at Andersen AFB, Guam for providing much needed logistical support. This work simply could not have been completed without the assistance and insights provided by Dan Rodriguez, Mike Linnell, Mike Pitzler, and Dan Vice of Wildlife Services, Guam. Pete Savarie's discussions and assistance were extremely important and I thank him and Joe Brooks for running the traps during the first carrion experiment. Ali Lindberg helped me greatly by running the first moving model trials and I appreciate all of her help with research and for introducing me to Finadene. I am grateful to Rick Bruggers for his input but also for obtaining the funding and guiding it through the National Wildlife Research Center to my project. Many people at the Center were instrumental in the success of this degree program. I thank Jean Alleman for the necessary administrative assistance that transported me safely to and from Guam and the Animal Research Building, John Johnston who provided me access to his instruments in the Chemistry building, and Bruce Kimball, who's assistance was vital to the successful completion of the gas chromatography. Mike Fall was kind enough to accept me into the working world while I wrote this dissertation: I am now able me to forever abjure the graduate student fare of Ramen noodles for breakfast, lunch and dinner.

At CSU, Joan Herbers graciously accepted me into the graduate program and found me office space. I hope the office staff at the Department of Biology, especially Kathy, Nadine, and Sunny will forgive me for the many headaches that I caused them while trying to do my research (I hope that I am not the sole reason the Department is on its third budget administrator since I started at CSU). There are too many graduate students to mention with which I shared the numerous beers, kayaks, hikes, climbs and discussions that make the graduate experience, even with all its associated misery, actually quite fun.

I appreciate the help, guidance, and support of my graduate committee. It was wonderful to have a committee that helped me pursue my research in an efficient manner. They allowed me to publish as I progressed and encouraged me to focus primarily on the most important thing in a graduate program: the research. I thank Dr. Gary Packard for wonderful statistical discussions within and without of his herpetology seminar. I owe Dr. William Andelt a few pink frough-frough drinks for helping me to remember my roots studying human-wildlife conflicts and coyotes. I appreciated Dr. Gordon Rodda's (the resident brown treesnake world-expert) faith in me and his ability to talk with me about my data; I am extremely happy to see he made it through Pineview enough times to sign the cover-page of this dissertation. I thank Dr. William Wright for accepting me and my exotic project into his stable of graduate students. He opened up the sensory world of synapses and impulses, but I most appreciate learning from his teaching style and his keen understanding of ecology. I was lucky to have Dr. Larry Clark as an advisor and colleague. His extensive skills and knowledge in a variety of fields allowed me to successfully put together an interdisciplinary doctoral dissertation that was always exciting to work on. Most of the ideas for this work came out of great long discussions filled with sesquipedalian jargon and poetic repetitions of words like *salient sensory stimuli, or conditioned taste aversion, trigeminal, unconditional*, and the effects of *bradykinin*. Because of his guidance

I feel uniquely qualified to speak to and understand Chamorros, herpetologists, and the most erudite of chemosensory biologists.

General thanks go to Brad Coupe for instruction on wrestling techniques before important presentations, Alfred Peet for the concoction that rejuvenated me through 6 years of graduate study, Bombay Sapphire, GTDS and MDA for a few fun moments on Guam, Perception Kayaks, Garrison Keilor, Tom and Ray and Guam Public Radio for helping me to remember what life was like at home when I was so far away. I thank my parents, John and Roberta Shivik and all of my siblings for their support through the years and for not thinking me too weird in my chosen career. Special mention goes to Uncle Bob and Aunt Celia for suggesting alternative techniques for prophylactic snake control. Most importantly I thank Perth and Mary for their smiles, encouragement, and enthusiastic support. Gretchen (the prodigy) went far beyond the call of duty to help me understand sensory biology and animal behavior while devotedly obtaining cans of beer.

PREFACE

Much of the work within this dissertation has been previously presented in numerous individual reports, presentations, and publications. However, more recent research will be immediately prepared for future publication. Therefore, individual sections of this dissertation were written in a form ready for journal submission. A reader may find a certain amount of repetition as study areas and methods are similarly described in all chapters. However, these data have not previously been bound into a cohesive scholarly document, and I have attempted to organize various papers and presentations as chapters and subsections within this work. I believe that this presentation will most efficiently allow a reader to understand the methods, results, and details of each section by its present organization.

I have taken advantage of the dissertation format to add in useful ancillary data that did not necessarily appear in previous publications related to this work, but many of the results and conclusions of individual sections are published or in press. I encourage the reader to examine the journal articles. For Chapter I, see the 1997 *Journal of Wildlife Management* 62:105-111. For Chapter II, see the 1997 *Journal of Experimental Zoology* 279:549-553. Some discussion of data in Chapter III are scheduled for the volume in press, "Advances in Chemical Communication in Vertebrates", edited by Robert E. Johnston, Deitland Müller-Schwarze, and Peter Sorensen, Plenum Press, New York, 1999. Similarly, some data in Chapter IV are in press for the 1999 *Journal of Herpetology*.

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CHAPTER I. BROWN TREE SNAKE RESPONSE TO VISUAL AND OLFACTORY CUES.

Abstract. The brown treesnake (*Boiga irregularis*), an exotic on Guam, is a primarily arboreal colubrid that is thought to be responsible for the decline and extinction of many avian species. Brown tree snakes on Guam are currently trapped, using live mice 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. The purpose of this study was to identify whether visual or chemical cues most stimulate appetitive behavior in brown treesnakes, and to test the effectiveness of artificial lures for capturing snakes. Using trials in both a laboratory and field setting, I determined that visual and olfactory cues are equally important for trapping brown treesnakes. The effectiveness of a live mouse lure diminishes with the loss of either sensory cue. Developing simple artificial lures based on the cues provided by live mice is likely to be difficult; lures may require complex odor and visual stimuli to be effective.

The brown treesnake is a nocturnal, primarily arboreal, rear-fanged colubrid native to parts of Australia, Indonesia, New Guinea, and the Solomon Islands (Fritts et al. 1987, Savidge 1987, Greene 1989, Fritts 1988). 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

treesnake'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, McCoid 1991, Fritts and McCoid 1991, Rodda and Fritts 1992). An intensive control program is underway on Guam because the brown treesnake endangers the fauna of Guam and other ecosystems (U.S. Dept. Agric. 1996).

Trapping is an effective method for removing brown treesnakes from an area, and control personnel currently use live mice as lures for snakes (U.S. Dept. Agric. 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 treesnakes can be developed, but effective lure development necessitates further study of the sensory biology and foraging ecology of brown treesnakes.

A variety of chemosensory inputs is 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, Duvall et al. 1990, Chiszar et al. 1990,). Gopher snakes (*Pituophis catenifer*; Eichholz and Koenig 1992), rat snakes (*Elaphe obsoleta*; Neal et al. 1993) and the brown treesnake (Fritts et al. 1989, Rodda 1992) may use both visual and chemical cues to locate distant prey.

For the brown treesnake, 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 treesnakes 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 treesnakes with the anticipation that this information will assist in the efficient development of artificial lures.

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), Ft. 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 15x15x15-cm 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 proportion 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 treesnakes in natural habitats on Guam. I placed 5 trap lines 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 trap line contained 40 traps, randomly 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. The filter allowed the mouse to breathe, but I could not detect any mouse odors emanating from the bottle. For the odor treatment, I placed a mouse in a bottle and vented air through 1.0- x 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 trap line for 2 nights and calculated the capture rate as the number of captures per trapnight for each treatment on each trap line. 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 trap line 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 trap lines, each run for 2 nights, and used the trap location (5 traps/treatment/trap line) 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 trap lines 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 treesnakes. I ran 3 trap lines during August 1996. Each trap line 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; (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.

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 towards the presented stimulus ($F_{3,30} = 4.64$, $P = 0.009$). In the multiple comparisons, snakes oriented toward the combined stimuli 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 odor stimuli ($P = 0.88$) more than the negative control (Fig. 1.1).

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, odor only, visual only, 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 (all P-values < 0.005; Fig. 1.2). 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 ($F_{5,35} = 8.18$, $P < 0.001$). Among treatments, the live mouse was better at capturing snakes than all other model and odor treatments (all P-values < 0.001), but I could not detect any difference between the other treatments and the negative control (all P-values > 0.77; Fig. 1.3).

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.1.4).

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 or absent) and odor cue (present or absent).

Using the collected lab and field data, I 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, 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. A significant interaction term would indicate a nonconstant relationship between the effect of visual and chemical cues which would be 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 exist ($F_{1,196} = 3.04$, $P = 0.08$; Fig. 1.5).

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.

I was able to add snake response to lure types within each trap line to examine these data for evidence of synergy. I summed the capture rates from visual and chemical stimuli per trap line (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 treesnakes. 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 treesnake interest in a stimulus and the continued use of laboratory studies for analyzing the behavior of brown treesnakes.

My results may explain conflicting reports of the relative importance of sensory modalities to the brown treesnake (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 treesnakes with only odors, whereas Chiszar et al. (1988) found that only a visual cue would elicit strikes. I captured significantly more brown treesnakes with only odor cues than with an empty trap (Fig. 1.2). However, when

the sensory input is incomplete, the intensity of appetitive behavior is low; single stimuli were significantly less engaging to brown treesnakes 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). For example, a snake is less likely to respond to mouse odor with appetitive behavior unless a mouse is visible. 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. 1.5). Furthermore, recent data (Shivik and Clark, 1997) suggest that the relative importance of cues dependent upon not only 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 treesnakes, odors from rotting mice can 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 treesnakes is context specific (the importance of a sensory cue is dependent upon the other stimuli that occur, or do not occur, simultaneously); and more specifically, (2) combined sensory cues add together 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 treesnakes 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. Furthermore, 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 possibly 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.

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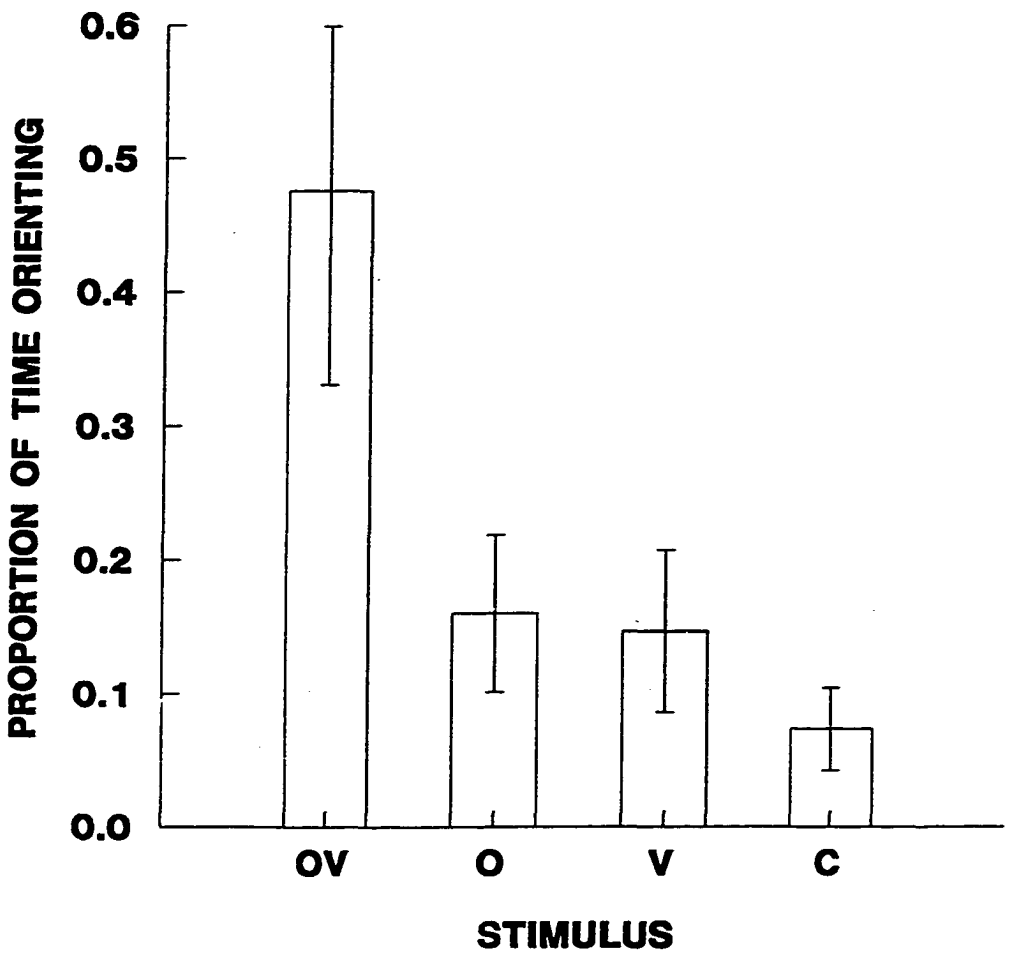

Figure 1.1 Proportion of time (time orienting/time active) 34 active captive brown treesnakes spent orienting toward the stimulus presented during March-June 1996. OV = simultaneous odor and visual stimuli of a live mouse (n = 8); O = live mouse odor only (n = 8); V = live mouse, visually apparent only (n = 9); C = negative control (n = 9). Bars represent 1 SE. OV > C (P = 0.008); OV > V (P = 0.04); all others: P > 0.05.

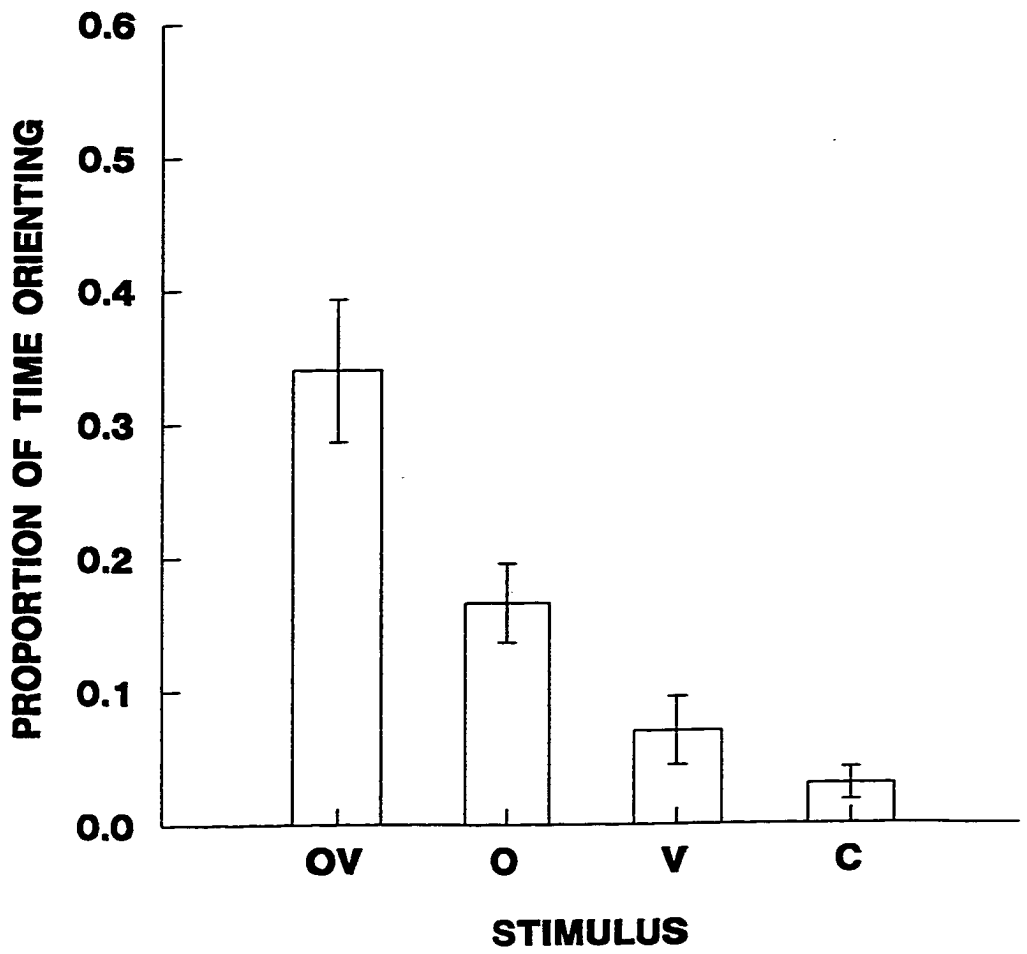

Figure 1.2. Capture rates by stimulus presented to brown treesnakes captured at 5 trap lines adjacent to Tarague and Haputo beaches, Guam, during August 1996. OV = simultaneous odor and visual stimuli of a live mouse; O = live mouse odor only; V = live mouse, visually apparent only; C = negative control (empty trap). Bars represent 1 SE as calculated from 50 trap locations/treatment. OV > O, V, C ($P < 0.005$); O > C ($P = 0.04$), all others: $P > 0.05$.

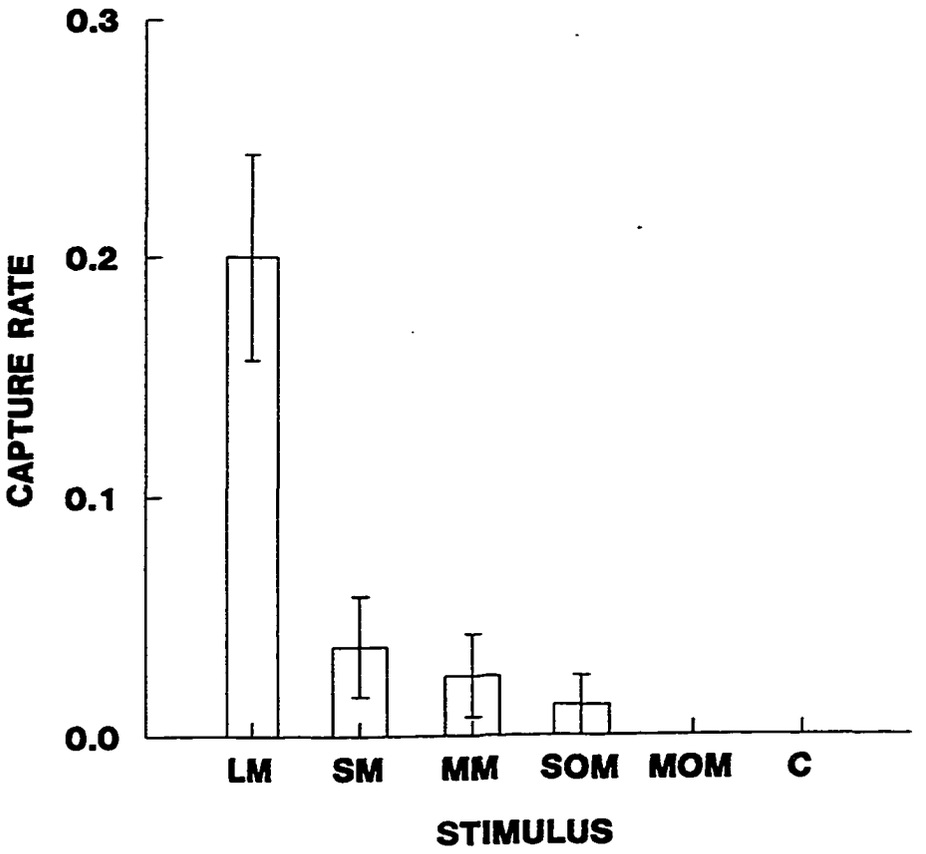

Figure 1.3. Capture rates for each stimulus presented to brown treesnakes captured on 8 trap lines on Andersen Air Force Base, Guam, during January 1996. LM = live mouse; SM = static mouse model; MM = moving model; SOM = static odorized model; MOM = moving odorized model; C = empty control trap. Bars represent 1 SE as calculated from 40 trap locations/treatment. LM greater than all other treatments ($P < 0.005$); all others: $P > 0.05$.

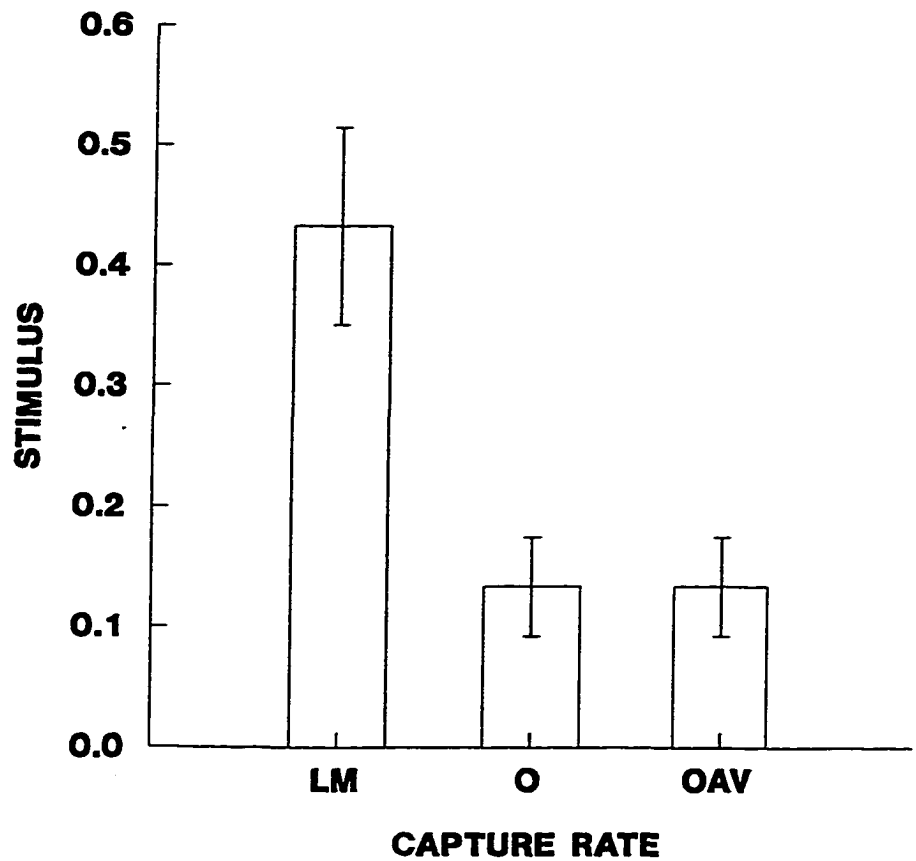

Figure 1.4. Capture rates for each stimulus presented to brown treesnakes captured on 3 trap lines adjacent to Tarague Beach, Guam, during July-August 1996. LM = live mouse; O = live-mouse odor; OAV = live-mouse odor with an artificial visual stimulus (a mouse model). Bars represent 1 SE as calculated from 30 trap locations/treatment. LM > O, OAV ($P = 0.001$); all others: $P > 0.05$.

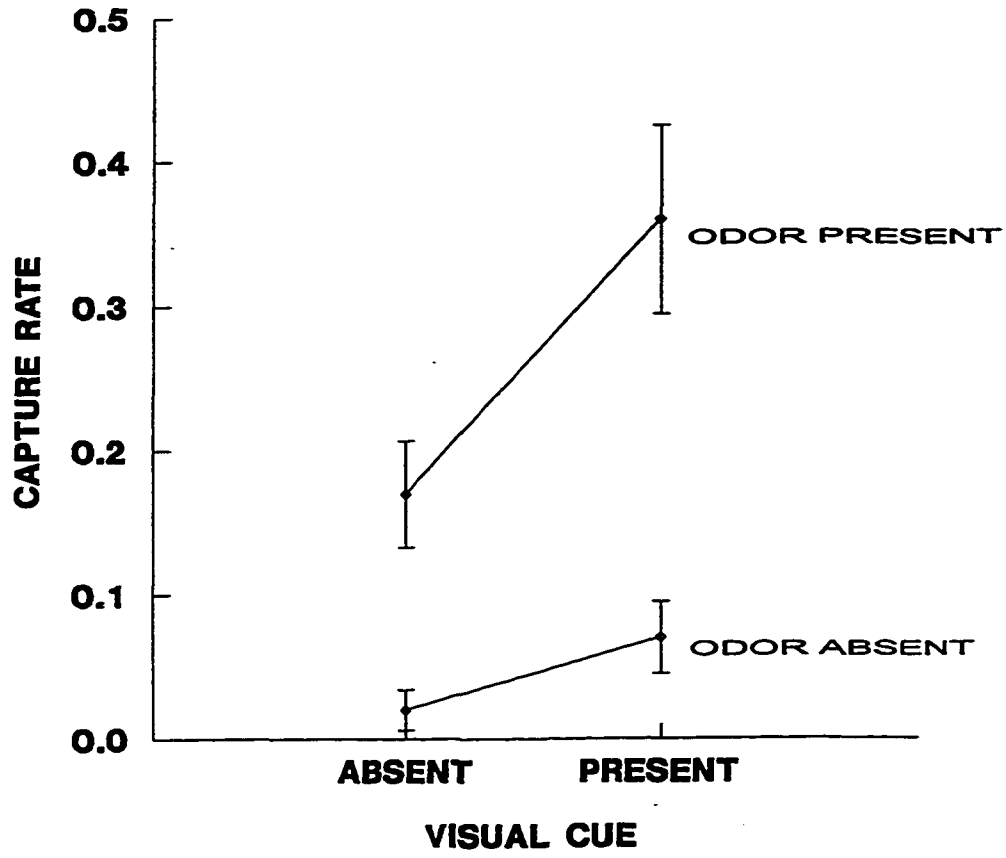

Figure 1.5. Profile plot of capture rates of brown treesnakes based on the presence or absence of visual or odor cues. Snakes were captured on 5 trap lines adjacent to Tarague and Haputo Beaches, Guam, during August 1996. Bars represent 1 SE.

CHAPTER II. CARRION SEEKING IN BROWN TREESNAKES: IMPORTANCE OF OLFACTORY AND VISUAL CUES.

Abstract. After hypothesizing that brown treesnakes (*Boiga irregularis*) were attracted to carrion, I performed a field experiment to examine the relative importance of visual and chemical cues of live or dead prey to foraging snakes. Brown tree snakes were attracted to carrion and entered traps baited with dead mice as readily as traps baited with live mice. Chemical cues were the most important for acquiring dead prey, but visual cues were required to sustain appetitive behavior in brown treesnakes searching for live prey. Thus, the relative importance of chemical and visual sensory stimuli to brown treesnakes is context specific. My study presents the first experimental field evidence showing carrion to be attractive to an ophidian predator.

Visual and chemical stimuli provide critical information to snakes about type and location of prey. The importance of one stimulus over another varies according to the species of snake and the context of the stimulus. For example, chemical cues stimulate appetitive behavior in gartersnakes and rattlesnakes (*Thamnophis* spp. and *Crotalus* spp., Burghardt, 1969; Burghardt et al., 1988; Chiszar et al., 1990; Cowles and Phelan, 1958; Duvall et al., 1990; Ford and Low, 1984; Golan et al., 1982; Heller and Halpern, 1981). Gopher snakes (*Pituophis catenifer*) and rat snakes (*Elaphe obsoleta*) use visual and/or chemical cues to find arboreal prey (Eichholz and Koenig, 1992; Neal et al., 1993). Brown treesnakes may respond to olfactory

cues, be primarily visually guided, or switch between modalities when cues are ambiguous (Chiszar et al., 1988; Chiszar, 1990; Fritts et al., 1989; Lankford, 1989). The relative importance of visual and olfactory stimuli to foraging brown treesnakes appears to be dependent upon which cues are simultaneously presented (Chiszar, 1990), but recent data suggest that, at least for live prey, visual and odor cues act synergistically to promote foraging behaviors in brown treesnakes (Shivik, 1998).

On Guam, the brown treesnake feeds on a variety of prey as it does in its native range, and the snake is known for its wide diet including anecdotal observations of unique objects such as spareribs (Fritts, 1988; Savidge 1988; Chiszar, 1990). The diversity of prey taken by brown treesnakes reflects shifts in diet as snakes grow; smaller size brown treesnakes prey upon lizards and lizard eggs, whereas large snakes prey primarily on mammals, birds, and bird eggs (Savidge, 1988). Rodda (1992) reported that these snakes actively search for and ambush prey while residing in the lower layers of the forest canopy, but that they will move to the ground when arboreal prey in an area are exterminated. Mildly venomous, the brown treesnake kills large struggling prey by constriction (Rochelle and Kardong, 1993), and the snake is an aggressive predator. It is responsible for the extinction of numerous avian species on Guam (Savidge, 1987).

To reduce the risk of accidentally transporting this species to other islands, efforts to control brown treesnake populations are being carried out on Guam by the U.S. Department of Agriculture, Wildlife Services (USDA, 1996). An important tool in this effort is the use of snake traps baited with live mouse lures (Linnell et al. in press). During the course of the U.S. Department of Agriculture's trapping program, I noted that the mice used as lures would, upon occasion, die, and that traps containing dead mice would often capture snakes. Did these captures represent an uncommon opportunistic exploitation of a potential food source, or does

attraction to carrion represent a broader pattern of snake foraging behavior? If carrion is attractive to brown treesnakes, it might be possible to develop an effective artificial attractant based on carrion odors.

The amount of carrion in the diet of snakes is thought to be inconsequential, unknown, or not acknowledged (Wright and Wright, 1957; Porter, 1972; Behler and King, 1979; Mushinsky, 1987; Shine, 1991; Arnold, 1993; Zug, 1993). In general, snakes are not thought to forage for carrion, but only to consume it in opportunistic or husbandry situations (Mattison, 1995). Gasc (1994) reports that the only snake thought to occasionally eat carrion is the cottonmouth (*Agkistrodon piscivorous*). However, *Crotalus* spp. prefer dead prey (Cowles and Phelan, 1958) because viperid predatory behavior involves envenomating, tracking, and finally consuming dead prey items. Thus, such venomous predators are believed to be more inclined to scavenge than species that kill prey by constriction (Patten and Banta, 1980; Gillingham and Baker, 1981; Lillywhite, 1982; Diller, 1990). However, non-venomous colubrid snakes, which kill by constriction, have also been observed to eat carrion (Bedford, 1991; Norton, 1993; Mattison, 1995). In general, snakes are thought not to actively forage for carrion because they are poorly equipped for the task compared with avian and mammalian species (Mattison, 1995). In this study, I experimentally quantified the attraction to carrion by wild brown treesnakes and examined the relative importance of vision and olfaction in the context of foraging for live or dead prey.

MATERIALS AND METHODS

Two field experiments were conducted. One experiment was designed to determine whether brown treesnakes are attracted to carrion. Another experiment was performed to describe the importance of visual and odor cues in attracting brown treesnakes to live or

decomposing prey. For both experiments, I 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 near Tarague Beach, Guam. To prevent snakes from eating lures, we enclosed the lures within hardware cloth boxes (7x7x20 cm boxes of 6 mm mesh) before placing them inside traps. To minimize extraneous biological odors, all traps and bait boxes were cleaned with a high-pressure water spray and then soaked in a 1:60 bleach:water solution for > 2 hours. Traps were sun-dried before baiting and placement.

I ran each trap-line for 2 nights and each line contained 10 traps/treatment type (randomly ordered). Traps were checked every morning, but because each trap on each trap-line was set for two nights in one location, all trap-nights were not independent. Therefore, the sample unit was the mean capture rate at each trap location and not an individual trap night. The capture rate was a measure of both a snake's ability to detect a lure, as well as a snake's interest (i.e., foraging behavior intense enough to result in trap entry) in the lure. I used analysis of variance to detect differences in capture rate between treatments. Statistical assumptions of the ANOVAs were evaluated using residual plots and multiple comparisons were made using the Tukey procedure (Ott, 1993).

To determine if wild brown treesnakes were attracted to carrion, I ran 4 trap-lines, during March and April, 1997, at the Guam study area. The treatments were traps baited with a live mouse (a positive control), a quartered and decomposing dead mouse, or an empty trap (a negative control). Mice were euthanized in the early afternoon before trap placement according to National Wildlife Research Center (NWRC) guidelines (SOP WRC-128.R4) and trapping was performed with the approval of NWRC (QA479) and Colorado State University (95-247A-01) animal care and use committees. I recorded nightly captures, and all captured snakes were removed from the study area.

To determine the attractiveness of visual and odor cues of live and dead mice to brown treesnakes, I placed 3 trap-lines, during March and April, 1996, in the Guam study area. I assessed the capture rates of live mice (the positive control), dead mice, live mice visually obscured, and dead mice visually obscured. Dead mice were euthanized in the early afternoon, as described above, but were left whole. Mice were visually obscured by wrapping black felt around the lure holder such that the mouse was not visible, but odors could permeate the fabric.

RESULTS

During 240 trap-nights (120 trap stations), I captured 54 brown treesnakes using live mice, quartered dead mice, and empty traps. I detected a difference in capture rate by lure type ($P < 0.001$) (Fig. 2.1). Live mice and quartered dead mice were more attractive to brown treesnakes than empty traps ($P = 0.001$ and 0.003, respectively).

I examined the likelihood that the capture of a snake during the first night's trapping influenced the capture of a snake during the second night's trapping at each trap station. Eighty four trap stations caught no snakes either night and 6 caught snakes both nights. Eleven trap stations captured snakes on night 1, but not night 2. However, nineteen trap stations captured snakes on night 2, but not night 1. Therefore, I found no evidence that a capture on night 1 increased the probability of a capture on night 2 ($X^2 = 2.511$, $P = 0.113$). There was no apparent attraction of snakes to traps that had previously held snakes.

For the test of visually apparent and visually obscured live and dead prey, I captured 97 brown treesnakes during 240 trap-nights (120 trap stations). I detected a difference in capture rate by bait type ($P = 0.019$). Dead mice, and dead mice obscured captured more brown treesnakes than live mice obscured ($P = 0.047$, and 0.023 respectively) (Fig. 2.2).

DISCUSSION

These data present the first experimental field evidence of a snake being attracted to decomposing prey. In these experiments, brown treesnakes were attracted to decomposing and quartered mice that bore little resemblance to a living mouse, as gauged from human eyes and olfaction.

Reports of carrion foraging by snakes have been met with some resistance (Hammerson, 1981; Patten, 1981) and rare mention of carrion as a food source in herpetological texts leads one to believe that it is not an important food resource for snakes in general (Wright and Wright, 1957; Porter, 1972; Behler and King, 1979; Mushinsky, 1987; Shine, 1991; Arnold, 1993; Zug, 1993). Reports of carrion feeding are generally viewed as curiosities and aberrant foraging behavior. Notwithstanding the popular belief that carrion is not an important food source for snakes, scavenging is anecdotally reported for viperids (Wharton, 1966; Patten and Banta, 1980; Gillingham and Baker, 1981; Lillywhite, 1982; Diller, 1990; Hamel, 1996;) and colubrids (Bedford, 1991; Norton, 1993; Mattison, 1995). This is the first field study to experimentally show that a snake is attracted to carrion, and that the attractiveness of decomposing prey is similar to that of live prey. The number of anecdotal reports, combined with these field experiments, suggest that carrion feeding by snakes may be much more common than widely believed.

The brown treesnake is a colubrid that is thought to primarily rely on constriction rather than venom to subdue and kill large prey; the mechanism proposed that explains viperid interest in carrion (i.e., they are "used to" previously envenomated and long-dead animals, Patten and Banta, 1980; Gillingham and Baker, 1981; Lillywhite, 1982; Diller, 1990) does not apply. As with predators of various other taxa (e.g. *Canis*, *Haliaeetus*, *Chelydra*), carrion can provide an important food resource to ophidian predators. Snakes are likely to actively (albeit not

exclusively) search for and eat carrion. For both active foragers and sit-and-wait predators, finding prey, whether live or dead, is an opportunistic event. However, the decreased handling-time involved with ingesting carrion improves its cost:benefit ratio and will favor its inclusion in the diet of all snakes.

The presence of a visual cue had less bearing on the attractiveness of dead prey, but was very important for live prey. Obscured dead prey were more attractive to brown treesnakes than visually obscured live prey. Thus, I infer that odor was an important sensory cue used to locate carrion. In contrast, the loss of the visual cue for live mice lures resulted in reduced trap success. This observation indicates that vision is an important sensory system modulating appetitive foraging behavior for locating live prey. These observations indicate that the relative importance of vision and olfaction to foraging brown treesnakes is context specific in terms of the stimuli presented (Chiszar, 1990). For example, the presence of odors characteristic of live prey signal that a potential prey item was at one time at a given location. However, odors left by live prey do not ensure that the prey item is still nearby. Thus, for live prey, odor cues may increase appetitive behavior in a snake, but visual cues are needed to fully motivate active foraging. If carrion odors are present, e.g. emanating from a hole, it is highly likely that a carcass is still within the hole. Thus, if carrion is an acceptable food, odor alone should be a sufficiently potent cue to promote heightened appetitive behavior. Alternatively, carrion odor may be "louder" and simply provide a more long distance signal to foraging snakes than live mice --which are best found visually. Under either hypothesis, the conclusion remains that brown treesnakes are attracted to carrion and odor alone is a sufficient stimulus to draw them to it. Interestingly, ongoing studies of brown treesnake attraction to carrion indicate that mouse carrion is consistently attractive to brown treesnakes, but a carrion odor lure varies through time in its effectiveness (Chapter V).

Snakes may be unable to effectively compete with many mammalian and avian scavengers for the carcasses of large animals (Mattison 1995). However, snakes are better suited to probe cavities where small prey species find refuge and are likely to die from causes other than predation. The carrion resource that small prey species provide is likely to be exploited by many snake species and the importance of the resource is a subject requiring further study. For example, I hypothesize that upon detecting carrion odors, both active foragers and sit-and-wait foragers will search for carrion; only in the context of live-prey trails will sit-and-wait predators assume an ambush posture.

ACKNOWLEDGMENTS

I thank P. J. Savarie and J. E. Brooks for assistance in the field, and M. A. Linnell, M. E. Pitzler, D. Rodriguez, and H. Hirsh for logistical assistance on Guam. I thank R. Bruggers and A. K. Holloway for reviews of an earlier version of the manuscript. This project was conducted with funds provided to the National Wildlife Research Center and the Department of Biology, Colorado State University, by the U.S. Department of Defense under DOD MIPR-064-95.

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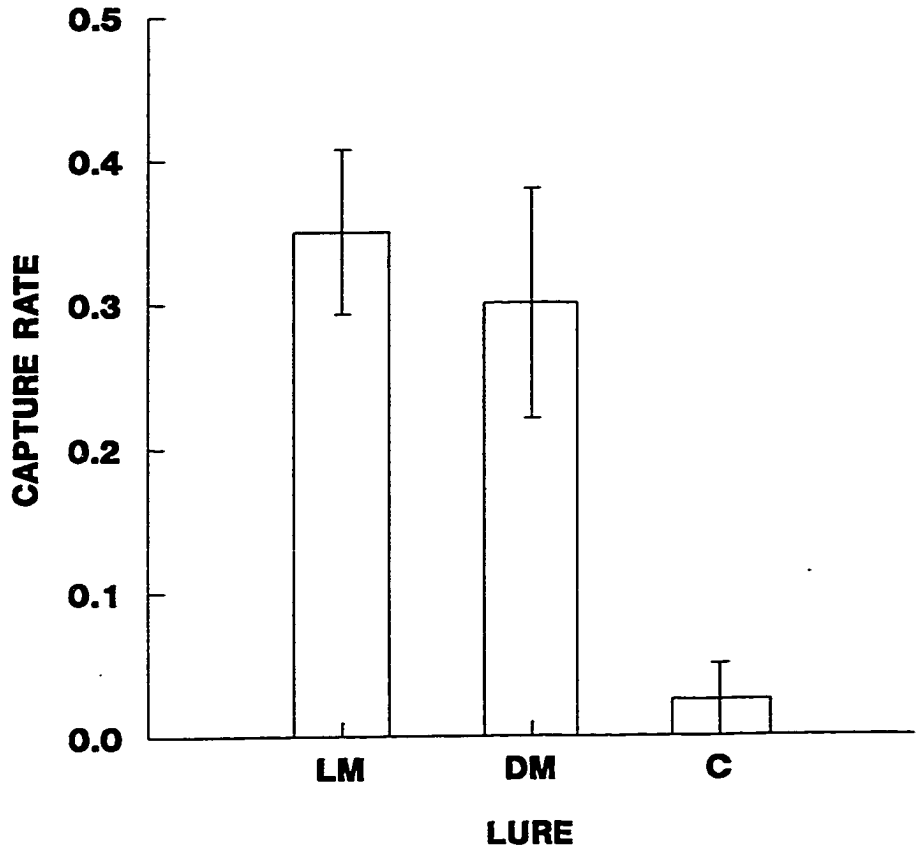

Figure 2.1. Capture rates of brown treesnakes on Guam by lure type. LM = live mouse; DM = quartered dead mouse; C = empty control trap. Error bars represent one standard error. Sample sizes were 40 trap-locations per treatment.

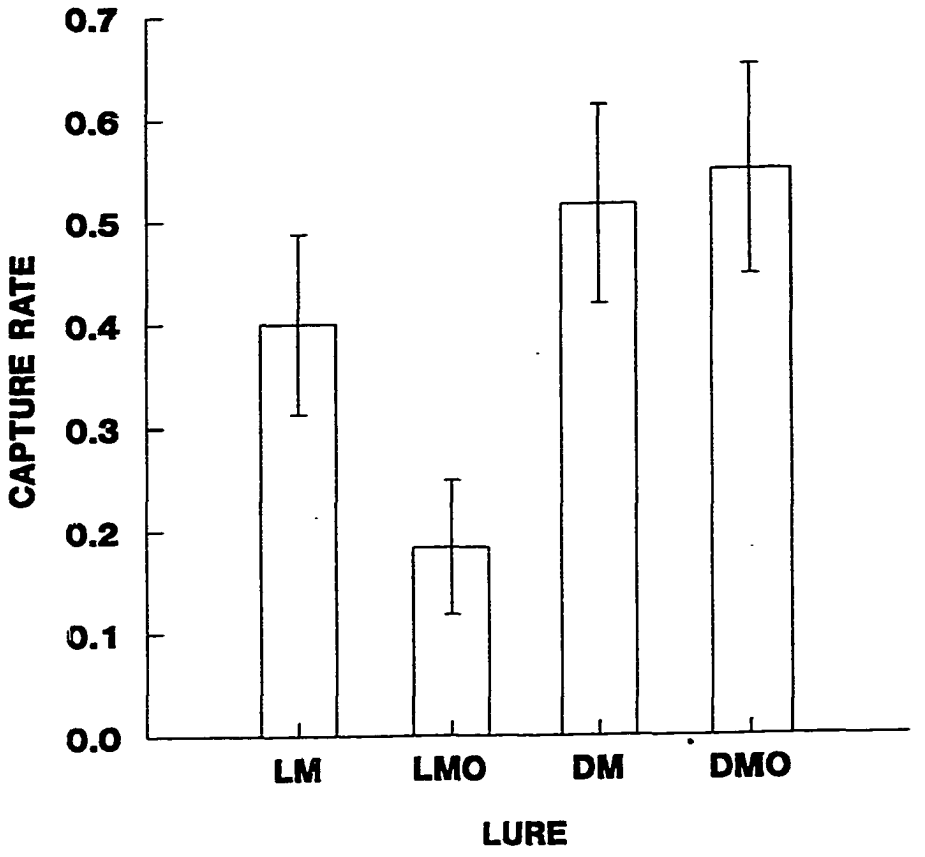

Figure 2.2 Capture rates of brown treesnakes on Guam by stimulus presented. LM = live mouse; LMO = live mouse, visually obscured; DM = dead mouse; DMO = dead mouse, visually obscured . Error bars represent one standard error. Sample sizes were 30 trap-locations per treatment. Based on the 97 snakes captured, DMO > LMO ($P = 0.023$); DM > LMO ($P = 0.05$). The P-value for the LM, LMO comparison was 0.32.

CHAPTER III. THE DEVELOPMENT OF CHEMOSENSORY ATTRACTANTS FOR BROWN TREESNAKES

Abstract. Concern that the brown treesnake (*Boiga irregularis*) may be inadvertently transported in cargo shipments from Guam has resulted in management programs aimed at limiting the likelihood of snake stowaways. A primary tool used to capture snakes is a trap containing a live mouse lure. Because the care of live mice presents logistical and animal care and use problems, it is desirable to develop an effective inanimate lure. Previous studies indicate that brown treesnakes are attracted to carrion odors. Here, I present the results of several pilot studies examining the attractiveness of cadaverine, dimethylamine, dimethyl disulfide, dimethyl sulfide, ethanethiol, trimethylamine, and putrescine (all components of carrion odor) to brown treesnakes. Results indicate that the major components of carrion odor, as defined by human perception, are not necessarily salient odors to brown treesnakes. I encourage a more systematic approach to the isolation of specific brown treesnake attractants by testing serial fractions of carrion odor for bioactivity.

Since arriving on Guam in the late 1940's or early 1950's, the brown treesnake (*Boiga irregularis*) has virtually extirpated the island's avifauna (Savidge 1987, Fritts 1988). There is concern that the snake may further extend its range via incidental transport in cargo and cause similar ecological disruptions elsewhere. The Department of Agriculture and Wildlife Resources

of Guam, the Biological Resources Division of the U. S. Geologic Survey, and the U. S. Department of Agriculture's Wildlife Services Program have all implemented research and control programs aimed at minimizing the risk of brown treesnakes being accidentally transported in cargo. Control efforts largely focus on creating "snake-free" zones in the areas adjoining cargo and areas targeted as sites for the preservation and reintroduction of endemic species of avifauna.

A variety of control methods have been explored and implemented on Guam. The Wildlife Services program uses trained Jack Russell terriers to identify cargo containing brown treesnakes. Barrier systems have been developed that decrease the likelihood of snakes crossing over protected areas (Campbell 1996). Fumigants for treatment of outward bound cargo have been tested. However, due to the cost and logistical difficulty of fumigating all cargo, fumigants have not been implemented as a general control strategy (J. E. Brooks & P. J. Savarie, unpublished data; P. J. Savarie, J. E. Brooks & Wood, unpublished data). Similarly, studies investigating the usefulness of dermally delivered toxicants have been performed, but a safe and long lasting snake toxicant and toxicant delivery system has not been developed (J. E. Brooks, P. J. Savarie & J. J. Johnston, unpublished data). Nighttime surveys, during which perimeter fences around cargo areas and airports are patrolled, are a part of normal snake control operations; snakes are removed individually from fences during the patrols. Perhaps the most effective method, but also the most labor intensive, has been the Wildlife Services program of trapping snakes, thus intercepting snakes before they can slither into cargo areas (Linnell, Engeman, Pitzler, Watton, Whitehead & R. C. Miller, in press; U. S. Dep. Agric. 1996).

The lures used for capturing snakes are live mice placed within holding compartments within traps. Maintaining mice imposes logistical constraints and the cost of maintaining mice in traps is high because mice must be fed and watered on a regular basis. More traps could be set

if an artificial lure were used, and improving the efficiency of trapping efforts has remained a high priority. Also, animal welfare concerns reduce the desirability of using a live animal lure. Thus, there is a clear need for the discovery, development, and implementation of a highly effective inanimate lure for brown treesnakes.

Identifying the specific cues which stimulate appetitive foraging behavior in snakes will enable the efficient development of an effective inanimate lure. Various snakes, including the brown treesnake, may use visual and/or chemical cues to locate distant prey (Eichholz & Koenig, 1992; Fritts, Scott & Smith, 1989; Neal, Montague & James, 1993; Rodda, 1992). For the brown treesnake, the cues that are reported as dominant vary between studies. Chiszar, Kandler & Smith (1988) noted that visual cues alone would elicit attack behavior and that visual cues are important because if a lure-container is visibly empty, attractive effects of chemical cues may be lost (Chiszar, 1990). However, Fritts et. al (1989) showed that brown treesnakes will enter traps baited only with bird odors (bird cage litter).

Lately, efforts to identify chemical lures for brown treesnakes have focused on reproductive signals (M. J. Greene & R. T. Mason, unpublished data) and cues from prey (Fritts et. al 1989; Shivik & Clark, 1997; Shivik, 1998). Relevance of behavioral assays to field applications is clearly an important issue. For example, laboratory investigations typically use the frequency of tongue flicks as a metric of interest by snakes for a specific chemical stimulus (Burghardt, 1969). The threshold for this assay is low and many chemical stimuli are identified as candidate lures in the laboratory, only to be discarded as ineffective lures in the field (G. H. Rodda & D. Chiszar, unpublished data). In the continuum of appetitive foraging behaviors, the tongue flick is a low-effort, low-cost behavior of snakes that has utility as an information gathering tactic.

The tongue flick, therefore, is a questionable behavioral index for evaluating a snake's willingness to pursue prey, and it is not an appropriate index of a snake's probability to enter a trap. Shivik (1998) showed that orientation behavior, i.e., directional probing of the head, was an easily monitored behavior that gave good concordance between laboratory studies and field trapping data. Orientation and probing behaviors presumably require higher motivational levels in the appetitive foraging process, and thus better reflect the salience of a stimulus. Most importantly, however, orientation behaviors are consistent with the behaviors required for a snake to enter a trap during the appetitive foraging process. Studies aimed at developing effective lures for brown treesnakes must use a metric that is directly applicable to the problem of trapping brown treesnakes. Appropriate methods include recording duration of orientation behavior of snakes in the laboratory or measuring capture rates on Guam. One objective of this paper is to examine possible lures using trap success as a basic metric.

Earlier studies showed that both visual and odor cues were important for investigatory behavior of live prey by brown treesnakes (Shivik, 1988). The combination of cues produced more intense investigatory behavior and higher trapping success than when either component was tested alone. Other studies showed that carrion was a suitable lure (Shivik & Clark, 1997). In contrast to live prey lures, carrion odor alone (i.e., with no visual prey stimulus) was sufficiently potent, yielding trap success equivalent to that using live mouse lures in initial studies. Actual carrion is not a useful lure because mice rot away too fast in field conditions to enable efficient long-term trapping. Therefore, I set out to identify salient components of carrion odor with the goal of developing an effective inanimate lure. Initial efforts at identifying attractive stimuli, the subject of this report, focused on amine and sulfur compounds associated with the decomposition of flesh.

METHODS

I hypothesized that compounds that attract brown treesnakes could be those that are considered major components of the odor of carrion. These include cadaverine, dimethylamine, dimethyl disulfide, dimethyl sulfide, ethanethiol, trimethylamine, and putrescine, (Eskin, Henderson & Townsen, 1971; Stager, 1964). For testing, I chose odor concentrations that were easily detectable, but not overpowering, to the human nose.

I performed trapping experiments on Guam to determine if compounds characteristic of decomposition are attractive to brown treesnakes. All traps were cleaned with cool, high-pressure water and soaked in a cold-water bleach solution (10% chlorine bleach) for > one hour to minimize extraneous odors. Trap-lines were set along forest edges with control and treatment traps randomly distributed within each trap-line. Traps were hung approximately 1.5 m high in trees.

Because these were pilot studies and sample sizes were limited (satisfaction of ANOVA assumptions could not be effectively evaluated), I assessed differences in trapping rates using a loglikelihood test. These experiments were reviewed and approved by Colorado State University and National Wildlife Research Center Animal Care and Use Committees.

In the first experiment, dimethylamine, trimethylamine and cadaverine were tested. I used 20 ml of a 20% solution of each chemical, diluted them to 200 ml in a spray bottle and sprayed the solution onto fur-covered mouse models (commercially available cat-toys). Four traps containing the soaked models, and five traps containing live mice, were placed in traps above Haputo Beach during August, 1996. This trap-line was run for two nights and capture rates were based on eight trap-nights for chemical lures and ten for live mice. Live mice were used as a positive control and the effectiveness of each lure was measured by capture rate per treatment. In this and all trapping experiments, captured snakes were removed from the area.

In a second experiment on Guam in May of 1997, 80 ml of 0.5% putrescine was wicked into absorptive cotton and then placed into traps in the forest adjacent to Tarague Beach. Seven traps of each treatment type (live mouse, putrescine, empty trap) were run for two nights resulting in 14 trap-nights/treatment.

In a third experiment, I used permeation tubes (HRT type, Kin-tek, Laurel, TX) to slowly release the sulfur compounds ethanethiol, dimethyl disulfide, and dimethyl sulfide from within traps. I placed permeation tubes (one tube of each chemical) within black-felt covered lure holders within each brown treesnake trap. I set a series of trap-lines adjacent to Scout Beach during August 1997 to examine the attractiveness of these chemicals. I set three chemical lure traps, three live mouse lure traps, and three empty control traps in four trap-lines. Trap-lines were moved daily for four nights to produce 12 trap-nights per treatment.

For my fourth experiment, I used singly presented sulfur compounds as lures. Trap-lines were run adjacent to Scout Beach Guam during August of 1997. I set three traps of each treatment type. The treatments were ethanethiol, dimethyl disulfide, dimethyl sulfide (in permeation tubes), live mice, and empty control traps. Trap-lines were moved daily for five nights to produce 15 trapnights per treatment.

RESULTS

In the first experiment, four snakes were captured with live mice (40% capture rate), but none were captured with the chemical treatment. The dimethylamine, trimethylamine and cadaverine treatment was much less successful in capturing brown treesnakes than live mice ($G = 5.61$ $P = 0.02$).

In the second experiment, ten snakes were captured with live mice (71% capture rate), one snake was captured with putrescine, and one with an empty trap (7% capture rate).

Putrescine was of very limited effectiveness for capturing brown treesnakes compared to live mice ($G = 19.09$; $P < 0.001$). The capture rate of putrescine was 10% that of live mice in traps, and it was not different than the capture rate using empty traps (Fig. 3.1).

In the third experiment, using ethanethiol, dimethyl disulfide, and dimethyl sulfide compounds simultaneously was not as effective as live mice in luring brown treesnakes into traps ($G = 11.95$; $P = 0.003$; Fig. 3.2). I captured one snake in 12 trapnights using the chemical lures and their capture rate was 16% as effective as live mice, with which I captured six snakes (50% capture rate).

In the fourth experiment, when the compounds were presented individually, differences were more striking ($G = 50.93$; $P < 0.001$). Twelve snakes were captured with mice (80% capture rate), but none were captured with ethanethiol, dimethyl disulfide, dimethyl sulfide or in the control traps.

DISCUSSION

The purpose of this study was to make an initial evaluation of the effectiveness of odors normally associated with decomposition for attracting brown treesnakes. I must eschew broad inference from these results because although the compounds I tested were not attractive in these pilot studies, one of these compounds could still be an essential component of an attractive chemical stimulus. My results firmly suggest, however, that a simple chemical attractant is unlikely to be found by examining individual compounds perceived by humans as important components of the odor of decomposition. More comprehensive testing is required before stronger inference can be made as to the influence these compounds have on appetitive foraging behavior of brown treesnakes, but I do not believe that these compounds will prove useful as artificial lures.

I caution against undue optimism regarding the quick discovery of simple chemical signals for an artificial lure system, especially if the candidate lures are compounds that are selected on the basis of human perception. Human perception is likely to be an inappropriate basis for sensory studies of other animals. For example, many procellariiform birds are attracted to the odors of a variety of fish oils and fish by-products (Clark and Shah, 1992). To humans, these food items have a distinctly "fishy" smell largely attributable to the methylamine compounds. However, when fractions were prepared from krill and field tested for attractiveness using Leach's Storm Petrels (*Oceanodroma leucorhoa*), the carboxylic acid extracts were the most attractive component of krill. Extracts dominated by phenols or amines were less attractive, and in fact, did not statistically differ from the negative control (water) in their ability to lure petrels to a target (Clark & Shah 1992). Thus, the compounds which signal "krill" to humans are substantially different than the compounds that signal "krill" to petrels. Similarly, compounds salient to humans (in the appropriate concentrations for humans) do not seem to be salient to brown treesnakes, based on the experiments reported here.

Whole odors of decomposition are attractive to brown treesnakes, but various amine and mercaptan components of carrion odors do not appear to be (Clark, in press). Testing individual odors is not an efficient method of lure development. Nearly 10 years of this inductive approach has failed to produce a strong candidate lure. For future studies, I urge a more systematic method to identify effective components for lures. A standard fractionation and assessment for biological activity is required. Researchers should concentrate on serially fractionating (e.g. using a variety of chemical solvents) carrion odors until salient components can be deduced rather than taking a "shotgun" approach, hoping that one snake-attracting chemical may serendipitously be found.

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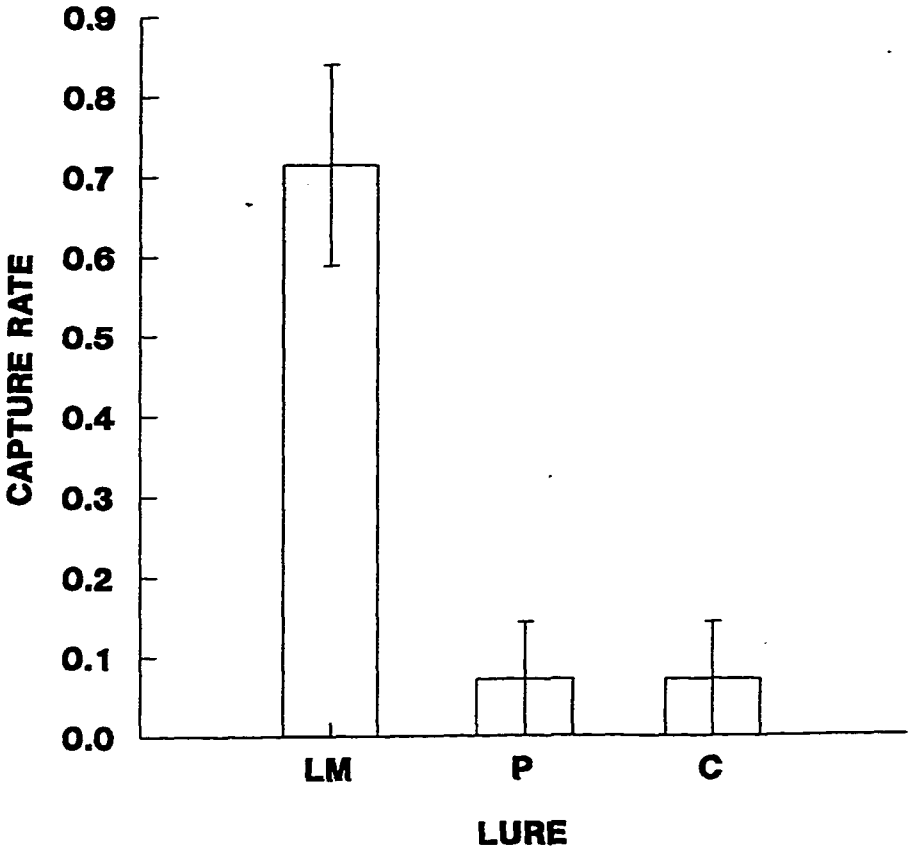

Figure 3.1. Capture rate by lure provided for brown treesnakes on Guam based on 14 trapnights per treatment. M = live mouse, P = putrescine soaked cotton, C = empty, clean trap control. Bars represent one standard error. LM > P, C ($P < 0.001$).

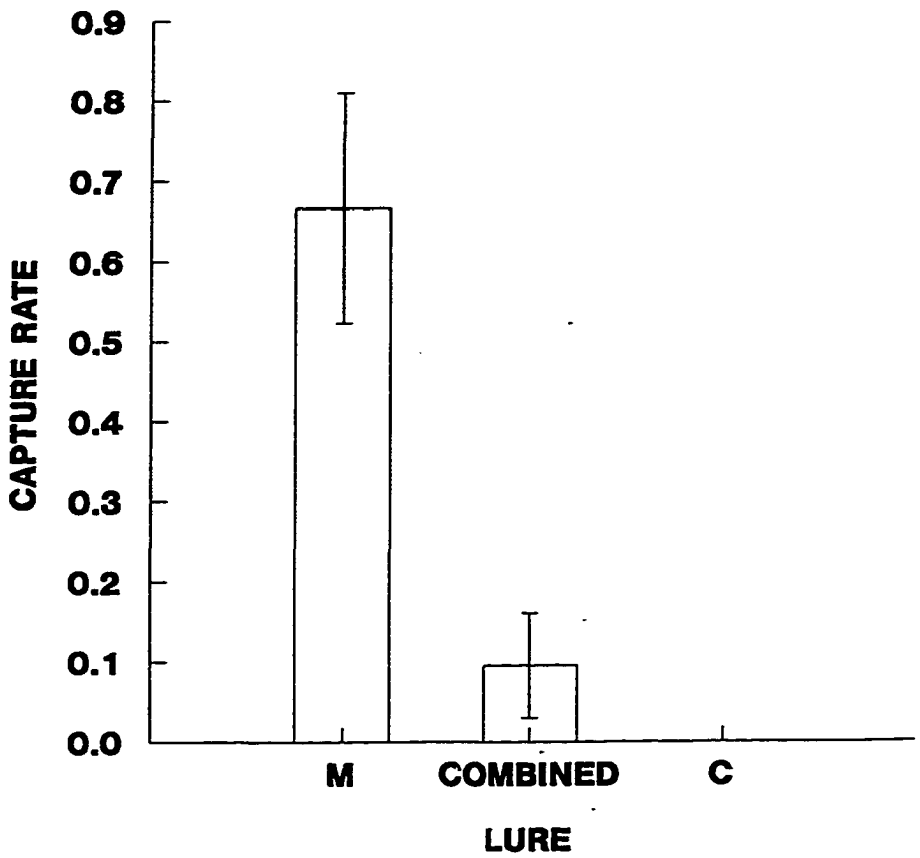

Figure 3.2. Capture rate by lure provided for brown treesnakes on Guam based on 12 trapnights per treatment. M = live mouse, Combined = ethanethiol, dimethyl disulfide, and dimethyl sulfide presented simultaneously, C = empty, clean trap control. Bars represent one standard error. M > Combined and C, LM > P, C ($P < 0.001$).

CHAPTER IV. ONTOGENETIC SHIFTS IN CARRION ATTRACTIVENESS TO BROWN TREESNAKES

Abstract. Because brown treesnakes (*Boiga irregularis*) have caused extensive changes to the ecosystem of Guam, extensive programs are underway to prevent the inadvertent dispersal of the snake. Scientific studies thus far have described brown treesnake populations and rated the effectiveness of various inanimate trap lures. Because brown treesnakes exhibit ontogenetic shifts in diet, as well as attraction to carrion, I tested the hypotheses that brown treesnakes varied their attraction to carrion based by sex and size class. In two separate studies on Guam, I found no differences between sexes, but noted that snakes captured with carrion were smaller than snakes captured with live mice. I conclude that care should be taken against size-class biases in snake capture data and that inanimate attractants can be developed that target specific size classes of snakes.

The brown treesnake (*Boiga irregularis*) is a nocturnal, primarily arboreal, rear-fanged colubrid native to parts of Australasia (Savidge, 1987; Greene, 1989). Throughout their range, brown treesnakes 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 treesnake 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 treesnake'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. Dept. Agric., 1996).

Managers use live mouse lures in brown treesnake traps. The desire to avoid using mice has given rise to a quest for inanimate attractants for brown treesnakes (Fritts et al., 1989). 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 with live mice were relatively ineffective in field trials because live prey odors require a simultaneous visual cue to attract brown treesnakes 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 treesnakes (Shivik and Clark, 1997).

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

METHODS

Snakes were collected during two studies on Guam. For both studies, I 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, I enclosed lures within hardware cloth boxes (7x7x20 cm boxes of 6 mm mesh) to prevent snakes from eating lures. To minimize extraneous biological odors, I 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. I 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, I set 90 traps containing live mice, quartered dead mice, or empty control traps (10 traps per lure type in three trap lines). 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, I replicated an earlier study (Shivik and Clark, 1997) and collected sex and length data on captured snakes. I 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. I set 160 traps (10 traps per lure type in four trap lines) in March and 200 traps (5 trap lines) during August 1997.

I examined differences in snake snout vent length (SVL) using analysis of variance (ANOVA). In Study 1, I performed a one-way ANOVA to determine if snake size varied by lure type. Also, I used a log-likelihood chi-square to determine if captures differed by lure type and

sex. In Study 2, I performed a two-way ANOVA examining the effects of a live or dead lure and a visual and odor or an odor only lure. I used a Mantel-Haenszel chi square (Kirby, 1993; Ott, 1993) to determine if male and female snakes showed differential attraction to trap lures.

RESULTS AND DISCUSSION

In the first study, I captured 22 snakes using live mice, 14 snakes using dead mice, and two snakes in 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 were larger ($\bar{x}$ = 92.8 cm; SE = 2.7; range = 70-109 cm) than those captured with quartered dead mice ($\bar{x}$ = 81.5 cm; SE = 3.3; range 58-103; $F_{1,34} = 6.99$; P = 0.012; Fig. 4.1). I did not detect a difference in the attractiveness of live or dead lures to male or female snakes ($\chi 2 = 0.45$, df = 2, P = 0.50)

In the second study, I captured 152 snakes. Snout vent length of snakes captured with visually apparent lures (n = 113; $\bar{x}$ = 93.8 cm; SE = 1.2) were not significantly larger than snakes caught with only odor lures (n = 39; $\bar{x}$ = 90.8; SE = 2.0; $F_{1,148} = 1.7$, P = 0.20). However, snakes captured with dead mice were smaller (n = 74; $\bar{x}$ = 90.0; SE = 1.6; range = 51-120) than those captured with live mice (n = 78; $\bar{x}$ = 95.7; SE = 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-Haenszel test, male and female snakes did not show differential attraction to any lure type ($\chi 2 = 1.08$; df = 1 ; P = 0.30). In regard to carrion foraging, male and female brown treesnakes appear to have similar preferences, because I did not detect a difference in capture rates when using live prey versus carrion, nor did I detect a difference in proportions captured with live or dead and visually apparent or visually obscured prey. These results are consistent with previous brown treesnake studies on Guam that did not detect a difference in male and female food habits (Savidge, 1988).

In contrast, I 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 treesnake, show ontogenetic shifts in feeding habits (Savidge, 1988; Greene, 1989, 1997; Arnold, 1993), and my data suggest the behavioral mechanism for these observations. The 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 treesnakes may eat a wide variety of prey and be considered opportunistic, it is interesting to note that individual variation occurs within the brown treesnake population on Guam. Throughout their range, brown treesnakes may eat a wide variety of prey, but individual snakes and size classes may be much more specialized and less opportunistic.

I have, in two separate experiments, demonstrated that live or dead lures are biased to catching different sized snakes. In these 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 accurately determined with present trapping methods, I am unable to fully interpret the ecological significance of the observed difference in capture rates by size class.

Researchers performing population analyses on brown treesnakes should use sampling methodologies that account for the possible under sampling 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 treesnakes. For control programs, it may be important to target certain age classes of brown treesnakes. 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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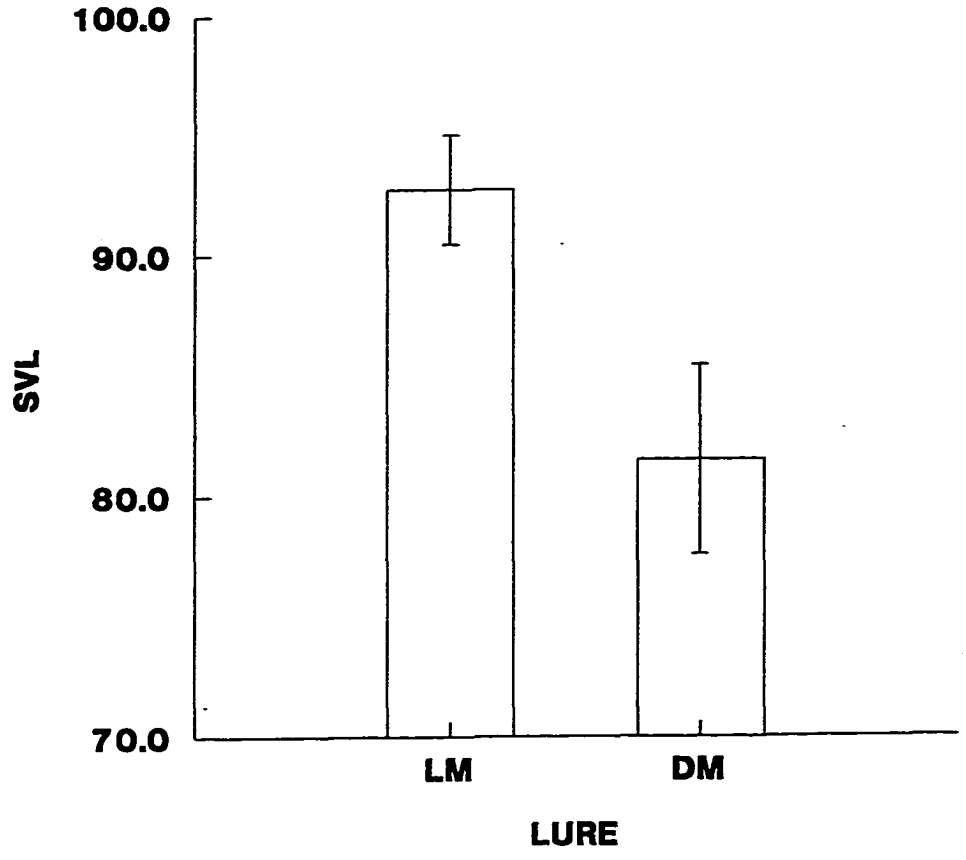

Figure 4.1. Mean snout vent length (SVL) and SE of snakes captured using live mice (LM; n = 22) and quartered dead mice (DM; n = 14) in traps set adjacent to Tarague Beach, Guam during April 1997. LM > DM, $\underline{P} = 0.012$.

CHAPTER V. BROWN TREE SNAKE RESPONSE TO INANIMATE LURES: VARIABILITY, TRENDS, AND SOLUTIONS

Abstract. I identified and tested major components of dead mouse odor, as well as a variety of natural compounds for attracting brown treesnakes, but did not find a single chemical that would lure snakes into traps. The attractiveness of dead mouse odor varied widely over a 2-year period with a trend consistant with seasonality. Lures for brown treesnakes should incorporate the concept of a "super normal stimulus suite" and use visual cues from the moving model described herein and appropriate fractions of carrion odor.

The brown treesnake (*Boiga irregularis*) is a nocturnal and primarily arboreal rear-fanged colubrid native to parts of Australia, New Guinea, and the Solomon Islands (Fritts et al. 1987, Savidge 1987, Greene 1989, Fritts 1988) and was introduced to Guam in the late 1940's or early 1950's (Savidge 1987, Rodda et al. 1992). The snake achieves population densities of 50-100 snakes/ha in some parts of Guam (Rodda et al. 1992), has caused declines and extinctions of avifauna and herpetofauna, and is responsible for a variety of other negative impacts (Fritts et al. 1987, Savidge 1987, McCoid 1991, Fritts and McCoid 1991, Rodda and Fritts 1992). Because the brown treesnake is a considerable threat to the economy and biodiversity of other pacific islands, animal control personnel use live mice as lures in extensive trapping efforts (U.S. Dept. Agric. 1996). Development of an effective artificial lure for brown treesnakes is necessary

because live mice in traps present logistical and animal care difficulties. The primary objective of this study was to elucidate the sensory biology and foraging ecology of brown treesnakes to allow the development of effective artificial lures.

The brown treesnake has a catholic diet (Fritts 1988, Chiszar 1990), and the snake exhibits ontogenetic shifts and a variety of foraging modes (Rodda 1992, Savidge 1988, Shivik and Clark, in press). Brown tree snakes possess a Duvernoy's gland, but normally kill larger prey mechanically rather than with venom (Rochelle and Kardong 1993). In appetitive behaviors, which sensory modalities are reported as dominant varies among studies. Visual cues alone can elicit attack behavior (Chiszar et al. 1988), and the absence of a salient visual cue lessens brown treesnake interest in chemical cues (Chiszar 1990). In contrast, brown treesnakes will enter traps baited with bird odors more often than empty traps (Fritts et al. 1989), and blindfolded brown treesnakes can efficiently attack and kill prey (Kardong and Smith 1991) . Recent evidence highlights the context specificity of brown treesnake foraging behavior: the relative importance of sensory cues is dependent upon both the variety and quality of cues presented (Shivik 1998, Shivik and Clark 1997).

Testing of Candidate Lures for Brown Tree Snakes: Pilot Studies

Brown tree snakes are attracted to carrion odors (Shivik and Clark 1997), blood (Chiszar et al. 1992, 1993), saliva (Chiszar et al. 1997), and bird odor (Fritts et al. 1989). Although some of the chemical components of carrion odor (cadaverine, dimethylamine, dimethyl disulfide, dimethyl sulfide, ethanethiol, trimethylamine and putrescine) have been examined (Shivik and Clark, in press), there is a paucity of published information examining the effectiveness of other possible attractants for capturing brown treesnakes. Here, I performed several pilot studies to examine candidate compounds for attractiveness to brown treesnakes. The methods for all

studies were approved within protocols submitted to the National Wildlife Research Center and Colorado State University Animal Care and Use Committees. Unless otherwise noted, I performed statistics using the program SYSTAT and made all multiple comparisons with the Tukey procedure. Analyses of candidate lure captures were performed using log-likelihood tests.

Prey Components—Blood and saliva appear to be attractive to brown treesnakes in laboratory studies (Chiszar et al. 1992, 1993, 1997), and I hypothesized that the serum from prey species may be attractive to wild snakes. I tested mouse serum and chicken serum (Sigma Chemicals) as lures for brown treesnakes on Guam. For this pilot study, I added 2 μl of lyophilized serum to 10 ml of water and applied the mixture to 5 cotton wicks. I used modified commercially minnow traps for capturing snakes (Linnell et al. in press). Five traps were set containing mouse serum, and 5 traps containing chicken serum and all ten traps had a mouse model visual cue (Shivik 1998) suspended within the trap. Five traps containing mice were set as a positive control with the treatment traps at Tarague Beach, Guam, during January 12 and 13, 1996.

Carrion Odors—Because brown treesnakes are attracted to the odors of carrion, I hypothesized that various substances and absorptive matrices could be used to attract snakes into traps. I examined the possibility that organic fibers could be used to absorb rotten mouse odors. I used bulk cotton and wool fibers as odor-delivery matrices for attracting brown treesnakes into traps. Two mice were allowed to begin decompose for 48 hours in a loosely covered 13 x 24 x 10 cm plastic boxes containing 9.5 cm strands of wool and 19 cm strands of cotton. Ten traps containing odorized cotton, 10 traps containing odorized wool, and 10 traps with live mouse lures were randomly ordered in a trap line at Tarague Beach, Guam, on July 14 and 15, 1996.

Aqueous extractions of rotted mouse could also be attractive to brown treesnakes, and I tested two matrices for holding the solution in traps. First, I decomposed 2 mice for 48 hours

(under ambient conditions on Guam), blending them with 350 ml of water and absorbing the slurry onto 10 tampons. Treated tampons were used as trap lures and their effectiveness at capturing brown treesnakes was compared to that from live mouse lures. Ten traps of each treatment were randomly placed in three different trap lines that were run for a total of 11 nights at Tarague Beach and Finegyan housing area, Guam, during July of 1996. Second, I formed a soft gel composed of 5 g carrageenan, 5 g locust bean gum, and 1 L of odorized water. Water was odorized by blowing air over decomposing mice and bubbling it through a container of water (using a home-aquarium aerator) for 48 hours. Odorized water was warmed to near-boiling, mixed with gelling agents and divided into 200 ml portions in plastic cups where gels solidified. Gels were removed from cup molds and placed in ten traps at Tarague Beach during April of 1997. Ten live mouse, ten gel, and ten empty control traps were set for two nights on two trap lines, yielding 40 trap nights per treatment.

PseudoCorpse II (Sigma Chemicals) is a chemical formulation based on components of carrion odor that is used to train search dogs to find carrion. Search dogs equate its odor with corpse odor, but the chemical composition is proprietary and not available for this paper. I performed a pilot study of PseudoCorpse II as an attractant for brown treesnakes. Ten traps containing 1 ml of PseudoCorpse II on filter paper and ten traps containing live mice lures were set at Tarague Beach, Guam, during 2 nights in July of 1998 (20 trap nights per treatment).

Predator attractants—Many compounds found in mouse carrion also occur in carnivore attractants and herbivore repellents (e.g., Deer Away™, Bullard et al. 1978a, Bullard et al. 1978b). I set 5 traps for two nights at the Naval Computer and Telecommunications Area Master Station (NCTAMS), Guam. These traps contained mouse models dipped in Deer Away™, and 5 traps that contained live mice. I also chose rotted eggs as an attractant because eggs are known to be eaten by brown treesnakes and because the sulfur compounds that are released from rotting

eggs are common components of decomposition odors (Bullard 1982, Dainty 1996). Eggs were soft-boiled to prevent cracking and the loss of shell contents and then were rotted for two days before being placed in traps. Ten traps containing eggs, ten containing live mice, and ten empty control traps were set on 7 separate trap lines from August 4th through August 10, 1998, at Tarague Beach, Guam.

Milk—Because rotten milk may be attractive to brown treesnakes (Brad Coupe, pers. commun., The Ohio State University) I also formulated a milk-based gel for pilot testing as an attractant for brown treesnakes. I formed ten milk-gels by rotting 2 L of whole milk for 48 hours at ambient temperature. The milk was mixed with 0.7% locust bean gum (by weight), and 0.3% carrageenan, and allowed to solidify in 200 ml cups. Ten milk-gel traps were set at Tarague Beach during April, 1997.

Pilot Studies: Results and Discussion

None of the prey components, carrion odor compounds, predator attractants, or milk formulations proved attractive to brown treesnakes (Table 5.1). In this dissertation, I present these data as pilot data, and not as an thorough examination of each possible lure type. Sample sizes were low, preventing strong statistical inference, but the data indicate that few of the attractants tested may warrant further testing. Sulfur compounds from readily available fermented egg products (Dear Away™) were not attractive (Fig. 5.1), nor were eggs (Fig. 5.2).

None of the compounds tested in these pilot studies is sufficient for attracting brown treesnakes into traps. Although a variety of compounds promote interest by brown treesnakes, a single odor source that effectively and consistently attracts brown treesnakes into traps has yet to be identified. The goal of my preliminary investigation of candidate compounds was to identify and test a logically derived list of readily available possible lures. As noted previously (Chapter

III) this inductive "shotgun" approach to problem solving is an inefficient method for resolving complex scientific questions. Testing several easily obtainable compounds gives scientists a more thorough grasp of the complexity of the problem, but this result is not useful because the complexity of nature is self-evident. Although the sufficiency of various agents for attracting brown treesnakes has been tested, the above trials did not indicate the necessity of any particular compound. Given evidence of synergy between visual and odor cues, similar synergies are likely to exist within a combination of odor cues. Also note that although the tested chemicals may not be attractive singly, some but may be necessary components in a more complex and effective chemical attractant.

Chemical Characterization and Evaluation of Mouse Carrion Volatiles

Because brown treesnakes are attracted to the odors of decomposing mice (Shivik and Clark 1997), I used the odors emanating from decomposing mice as the basis for a chemical analysis of possible lure compounds. The analysis was designed to identify and quantify the predominant chemical components of mouse-carrion odor.

Chemical analysis methods—Dead mice that have been decomposing for two to three days appear to be the most attractive to brown treesnakes (Chapter VI). Therefore, I sampled the head space (i.e., the air surrounding the decomposing mouse) from a mouse carcass that had been decomposing for 56 hours to determine components of the suite of chemicals that may be attractive to brown treesnakes. A frozen mouse was thawed in a watch-glass and allowed to rot under a hood at room temperature. The bottom of the glass was kept moist to increase the humidity proximal to the carcass. Samples were taken during February and March, 1998 at the National Wildlife Research Center, Ft. Collins with equipment suited for the analysis of volatile compounds. I used a Tekmar 3000 Purge and Trap Concentrator to collect head space samples.

Components were separated using a Hewlett Packard 5890 Series II gas chromatograph and identified using a Hewlett Packard 5972 Series Mass Selective Detector. Head space samples were taken during a 40 minute purge at 40° C onto a column K trap. The trap was desorbed at 250° for 3 minutes into 30 m DB5 column (He carrier, 0.250 mm diameter, 33 kPa 1.0 ml/min flow rate). The column was chosen for its sensitivity for volatile compounds. Oven temperature was set at an initial temperature of 0° and ramped to 300° at a rate of 15°/min.

Compounds within the head space were initially identified using their mass spectra. Reference compounds were run in later trials to positively identify peaks and retention times. To estimate relative abundances of compounds within the sample, I repeated runs of known quantities of reference chemicals and used linear regressions to back-calculate relative abundances of chemicals in the initial sample.

Chemical analysis results—Numerous compounds were identified in the mouse carrion head space analysis (Fig. 5.3). I did not attempt to make a thorough examination of every component of mouse carrion odor, but was successful in identifying the predominant components of the head space samples (Table 5.2). The list of compounds generated by this analysis suggested a formulation that was possibly attractive to brown treesnakes, and I used this information to construct an artificial dead mouse odor.

Dead mouse formulation bioassay—I used the components and estimated quantities of carrion odor components (Table 5.2) to develop an artificial formulation of carrion odor. Qualitatively, the combination of chemicals in the listed proportions resulted in a strong smelling mixture reminiscent of the odor of decomposition. I constructed a dead mouse formulation (DMF), using the data generated from gas chromatographic analysis and tested this formulation for biological activity. The DMF testing was done on Guam during June of 1998. Ten traps containing the dead mouse formulation were set with ten traps containing live mice, ten with

dead mice, and ten empty control traps in 2 trap lines, for 4 nights at Tarague Beach, Guam. I recorded the capture rate per treatment and performed a log-likelihood test to detect if brown treesnake capture rates differed by lure type. Based on 40 trap nights per treatment, I detected a difference in capture rates between lure types ($G = 23.47, df = 3, P < 0.001$). I captured no snakes with the DMF, however, and conclude that it was not an effective attractant (Fig. 5.4).

The gas chromatographic investigation of dead mouse odors is extremely limited in interpretational value. I can use these data to confirm presence of compounds in rotting mice, but do not assert that the components listed in Table 5.2 are a recipe for the exact smell of rotting mice. I qualitatively compared, using human olfaction, the smell of DMF to actual dead mice. The DMF certainly was reminiscent of the odor characteristic of carrion, but could be readily recognized as only an approximation of the true odor or rotting mice. Therefore, future research should concentrate on partitioning active components and dilutions of whole dead mouse odor rather than trying to reconstruct odors from a MS GC "big peak" supposition. Assuming that the size of a peak in a gas chromatograph corresponds to the biological relevance of the chemical is a fallacy and is detrimental to an efficient process of elucidating the biologically relevant components of odors to brown treesnakes.

Variability in Lure Effectiveness for Brown Tree Snake Capture

Temporal variability—A more thorough examination of brown treesnake attraction to carrion was required because candidate carrion-like compounds did not attract snakes into traps, and my ongoing studies indicated variability in the attraction of brown treesnakes to carrion. Therefore, replication of earlier research (Shivik and Clark 1997) was required to understand variability in foraging behavior, and I set traps during 1996 and 1997 in order to identify components of variability in trapping data.

Traps containing live mice (LM), live mouse odors (LMO), dead mouse (DM), and dead mouse odor (DMO), were set at Tarague Beach and on the Conventional Weapons Storage Area, Andersen Air Force Base, Guam, during April and August of 1996 and April and August of 1997. These experiments were replications of the work performed in Chapter II (Shivik and Clark 1997) and incorporate those data. Ten traps per treatment were set for two nights on 3 trap lines in April 1996, 4 trap lines in August 1996, 4 trap lines in April 1997, and 5 trap lines in August, 1998. I examined the difference in capture rate by treatment, year, and season using the trap line as the experimental unit. Because traps were set in the same location for two nights, the trap location was used as the sample unit and each trap's nightly capture rate was collapsed to produce the mean capture rate for that location. Capture rate was the mean number of snakes captured per trapnight in each trap location. I used a mixed-effects ANOVA and included the effects Lure (LM, LMO, DM, DMO) , Season (Wet or Dry which correspond with north-temperate Autumn and Spring months, respectively), Year (1996 or 1997), and the accompanying interaction terms. Trap line, which was nested within Year and Season, was used as the random effect error term in the model. Analyses were performed using PROC MIXED (SAS Institute 1996).

Based on the ANOVA, there is a strong lure effect, a strong seasonal effect, and an interaction between the season and lure type (Table 5.3). Reasons for these statistical results can be inferred from the data presented seasonally (Fig. 5.5). Seasonal trap success was lower during the wet season than during the dry season, especially for dead mice and dead mouse odor, but the seasonal differences were not as extreme with live mouse lures. The seasonal trends may have resulted from changes in brown treesnake populations in the areas studied due to removal of snakes (all snakes were removed from the population after capture), or due to changes in the demographics of the sampled population (Chapter IV). Because of these seasonal trends in

capture rate data, I explored specific mechanisms for the observed results, i.e., weather and changes in snake motivation due to changes in prey availability.

Weather factors—There are no extreme seasonal trends in temperature on Guam (temperatures vary more during a 24-hr period than during the year) and seasonality is most obvious in wind and rainfall trends (Karolle 1993). On Guam, mean monthly rainfall peaks in September (approximately 38 cm) and drops to approximately 11 cm in April; mean monthly wind speeds also show a seasonal trend with winds peaking in February and dropping during August (Karolle 1993). Climatic variation and discernable wet and dry seasons on Guam are likely to influence many aspects of brown treesnake behavior, and I designed a study to detect seasonal trends in temporal variability.

I hypothesized that weather variables could influence capture rates. Wind and rain can influence the effectiveness of lure odors. For example, rain may have a rinsing effect, essentially "washing" odors from the air around traps, making lure detection radii smaller. Moisture levels can influence decomposition rates and snake movement, and winds can disperse odors quickly, resulting in a reduction of odor radii. I examined environmental factors for correlations with changes in brown treesnake capture rates as a means of explaining the observed interaction between season and lure type.

Weather data were obtained from Andersen Air Force Base, Guam, on which trapping was performed, and extreme observations taken during weather patterns influenced by typhoons (mean rainfall > 2.54 cm in 24 h, 3 trap lines) were not included in the analyses. I regressed mean rainfall for the 48 hr period each trap line was set and the mean maximum wind speed for the same two days against capture rate from each lure type using simple linear regression.

Wind speed did not correlate with dead mouse or dead mouse odor lures, but wind was positively correlated with capture rates using live mice and live mouse odor lures (Table 5.4, Fig.

5.6) on the 12 trap lines set during 2 years. The observed seasonal interaction between carrion and live lures is partly explained by the differential result of weather variable correlation. The influence is more interesting, because of the lack of colinearity between wind and rainfall for these data ($R^2 = 0.06$, $\underline{P} = 0.44$). The mechanism responsible for the observed trend is difficult to identify: Why do live mice capture more snakes in windy weather and dead mice capture fewer snakes in rainy weather? The results are convincing (38 and 42% of variability is explained by wind with live mice lures and 28 and 30% of variability is explained by rain with dead mouse lures), but correlative, and other factors are likely to be more responsible for the trends. For example, high winds may be associated with barometric pressure drops and the approach of storm systems may influence brown treesnake activity and capture rates.

Wind may influence live mouse lures by influencing mouse behavior. Rocking traps may keep mice more active and more attractive to brown tree snakes. This effect would have no influence on dead mouse lures, as seen in the analyses. Rainfall did not correlate with live mouse capture rates, but correlated negatively with carrion lure capture rates. Rainfall and humidity may influence carrion lures by altering the decomposition process and rate. It is possible that rain "washes" the air proximal to traps holding carrion lures and thus lessens the effective radius of the lures during rainy periods. If odor is important for stimulating brown tree snake response to carrion, any changes in the decomposition process could profoundly affect capture rates using carrion. Again, this study was correlative and a more extensive investigation of these working hypotheses would be useful.

A post-hoc analysis that I used to more thoroughly investigate the observed trends was to examine the capture rates using each lure type in each season, but incorporating wind and rain as covariates in the models. The results (Table 5.5), futher show the effect of wind on live mouse lures and the effect of season on dead mouse odor lures and account for the significant

lure*season interaction shown in Table 5.3 . Live mouse capture rates are influenced by some factor correlated with wind speed and dead mouse odor is influenced by a trend consistant with seasonality.

Seasonal Differences in Snake Satiety

Prey availability appears to change seasonally on Guam (Earl Campbell, pers. commun. National Wildlife Research Center, Hilo, HI). I hypothesized that observed differences in carrion odor lure attractiveness were related to seasonal changes in prey availability or vulnerability. Specifically, I hypothesized that during the wet season, lizards and lizard eggs may be more available to foraging snakes. I assumed that well-fed snakes are less motivated to investigate carrion odors and tested this satiety mechanism for the observed seasonal differences in brown treesnake attraction to carrion odor. Tests were performed in the laboratory at Ft. Collins and replicated on Guam.

Methods—I performed 2 studies of snake behavior to determine if recent feeding and lure type influenced snake orienting behaviors. In both studies, I used video recordings of snakes in their home cages to determine the amount of time an active snake oriented toward a potential food item (Shivik 1998). I used a 2-way ANOVA to look for an effect of recent feeding (Fed or Unfed) on snake interest (proportion of time orienting toward the lure) in lures (live mouse, live mouse odor, dead mouse, or dead mouse odor).

In Ft. Collins, 16 snakes which had been held in captivity for > 3 years were tested. Snakes were held in conditions simulating ambient temperatures on Guam and given water *ad libitum*. Snake chambers and methods of observation were identical to previous studies using the same snakes (Shivik 1998). Throughout the tests, snakes remained in their cage, and I placed a 15x15x15-cm acrylic treatment 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 into the snake cage with a 10-cm-diameter dryer hose and a low-volume fan. Snakes were randomly divided into 2 groups (fed or not-fed). The snakes in the Fed group were fed 1-2 freshly euthanized adult mice every three weeks. Snakes were either tested "unfed" (> 2 weeks since last feeding) or "fed" (< 7 days since last feeding) when exposing them to one of four treatments: live mouse, live mouse odor, dead mouse, and dead mouse odor. Snakes were tested by placing mice in the acrylic treatment box, and placing the box on the snake's cage. For odor treatments, an opaque side faced the snake and for visually apparent treatments, the clear side faced the snake. Dead mice were thawed and decomposed at room temperature under a hood in a watch glass with a moistened bottom for > 24 hours before testing. All snakes received each combination of treatment and satiety categories in a latin-square arrangement, but a > 3 week "wash out" period was ensured between testing trials to reduce repeated measures effects (Ott 1993). Studies began in October of 1997 and were discontinued in May of 1998.

Snakes held in captivity for long periods of time may alter their behaviors compared to wild-caught snakes, and the low number of snakes in Ft. Collins required repeated testing of individual snakes. Therefore, I repeated the satiety effect experiment done in Ft. Collins, this time using recently captured snakes on Guam. Snakes were captured in standard traps and randomly assigned to Fed or Not-fed groups and treatments of live mouse, dead mouse, live mouse odor, and dead mouse odor. Odor treatments were formed by wrapping lure holders with cloth such that odors could permeate, but mice were not visible. All snakes were allowed to acclimate in their cages (33 x 24 x 24 cm tubs) for > 5 days before testing. Snakes assigned to the Fed group were given 1 frozen immature mouse (mean weight 5.1 g) nightly until snakes refused to take additional mice, and snakes that never fed were not used in experiments. Experimental trials were run by video taping snake behaviors for 1 hour after lures (protected

within 7 x 7 x 20 cm hardware cloth holding boxes) were placed in the holding cages of individual snakes.

Results and Discussion—Laboratory experiments in Ft. Collins were ended before the study was completed due to the large number of non-responding snakes and inadequate statistical power given foreseeable sample sizes. One-hundred sixteen trials were run but snakes only responded during 61 (53%) trials. All treatments had sample sizes (i.e. the number of snakes that responded) of 8, except for fed snake-dead mouse, fed snake-dead mouse odor and, fed snake-live mouse treatments, which had sample sizes of 7. Of the trials that were scored , no treatment effect was observed by lure type ($F_{3,54}$= 0.9503, P = 0.423) nor feeding status ($F_{1,54}$ = 0.657, P = 0.421), nor was there a significant interaction between effects ($F_{3,54}$ = 0.897, P = 0.449, Fig. 5.7).

Recently captured snakes on Guam were more responsive to experimental trials. Out of 55 trials performed, 40 snakes responded (73%) and all treatments had sample sizes of 5 snakes. I detected a difference in the proportion of time snakes spent orienting toward various lure types ($F_{3,32}$ = 12.03, P < 0.001, Fig. 5.8), but did not detect a significant interaction between feeding status and lure type ($F_{3,32}$ = 0.006 df = 3, P = 0.992).

I further examined the data for differences in snake activity (using time active, i.e. obviously awake and moving, as the dependent variable). Long-term captive snakes showed no difference in total activity based on feeding condition (Fed = 1315 s activity, Unfed = 1367 s of activity, P = 0.844). For short-term captive snakes, however, unfed snakes were more active (i.e., spent more time moving about their cage) in trials than fed snakes ($F_{1,32}$= 7.02, P = 0.01, Fig. 5.9). Unfed snakes had a mean activity of 2152 s (60% of trial duration) and fed snakes had a mean activity of 1264 s (35% of trial duration).

Seasonally, capture rates using live mice were relatively constant during all trapping periods and variability was greatest for dead mouse lures (Fig. 5.5). Because the capture rate using live mice remained relatively constant through all seasons, I do not attribute fluctuations in capture rates using dead mouse lures to differences in local brown treesnake population sizes or movement patterns (i.e., live mice act as a positive control for these comparisons). Prey populations could fluctuate and alter the satiety of snakes, but this mechanism as a complete explanation for seasonal differences in brown treesnake attraction to carrion is insufficient. More likely, seasonal differences in microbial decay or other factors intrinsic to the carcass may drive seasonal differences in carrion attractiveness. Of note is that hungry brown treesnakes are more active than satiated snakes, and it would be useful to test movement patterns given feeding rates for snakes in a more field-like environment.

A Moving Model Attractant for Brown Tree Snakes

Visual and odor stimuli may add synergistically to stimulate foraging behavior from brown treesnakes although odor by itself is a sufficient inducement in some contexts (Chapters 1 and 2). Therefore, the composition of the most effective lure should incorporate elements of visual as well as odor stimuli. To test the importance of movement to brown treesnakes, I constructed an artificial mechanical mouse and tested snake response to the moving model using recently captured snakes on Guam.

Methods—Mechanical mice were constructed by gluing a 1.5 V motor to a AA battery holder and unevenly weighting a flywheel attached to the motor. The device, approximately the size of a mouse, wobbles constantly and rapidly when powered with an AA battery. The treatments examined were a fake fur covered mechanical mouse, a mechanical mouse covered with an unwashed mouse skin (that was removed from a frozen mouse), a live mouse, or an

empty control lure chamber. Recently captured snakes were allowed to acclimate in their holding chambers (33 x 24 x 24 cm tubs) for > 5 days before testing. Snakes were tested by placing a lure (protected by a 7 x 7 x 20 hardware cloth box) in the snake chamber and video taping behavior for 1 hr. Tapes were then scored at a later date. Experiments were performed on Guam during July and August of 1998. I used 1-way ANOVA to detect differences in the proportion of time active snakes spent orienting toward each stimulus (live mouse, moving model with fake-fur, moving model with mouse skin, and empty lure chamber), and used the Tukey method of multiple comparisons.

Results and Discussion—I detected a difference in snake response to the various treatment types ($F_{3,35}$= 12.38, $P < 0.001$; Fig. 5.10). Snakes oriented toward live mice more than moving models ($P < 0.025$) and control treatments ($P < 0.0001$). Snakes oriented toward moving models more than empty containers ($P < 0.017$).

Perhaps the broadest implication of this research is the significance of finding an artificial visual cue uncoupled from biological odors that is attractive to brown treesnakes. Especially with live mice, visual and odor cues act synergistically to lure brown treesnakes into traps (Shivik 1998). However, a mechanical mouse model produced considerable interest in laboratory snakes (59-73 % as intense as a live mouse). Dead mouse odor, albeit of variable attractiveness, elicits a similar response from brown treesnakes in trapping studies (overall, a capture rate 51% as high as live mice). Both single stimuli are much greater than their negative controls (non-moving model, or live mouse odor) and studies of these cues in tandem are required.

Although visual and odor cues are both important to foraging brown treesnakes, I have found odors that attract brown treesnakes independent of visual cues and visual cues that attract brown treesnakes independent of biological odors. Partitioning entire sensory cues into salient

components is performed by all animals and the cues relevant to an animal are not necessarily relevant to humans. Tinbergen (1972) thoroughly examined gull (*Laurus ridbundus*), nestling blackbird (*Turdus merula merula*), and thrush (*Turdus ericetorum ericetorum*) response to incomplete sensory images, and found that eliciting egg shell removal behaviors depends upon a variety of perceptual stimuli which may or may not be important relative to human perception, e.g., a nesting gull will eject a bottle cap from a nest but will incubate a "D" size battery (Tinbergen 1972, Beer 1961).

A level of appetitive behavior that will bring brown treesnakes into traps is likely to be constructed based on a variety of sensory stimuli. The use of models for studying animal response is a common method in ethology and has been used to study the courtship of ruffed grouse (*Bonasa umbellus*) (Allen 1934), and Gould's manakin (*Manacus betellinus vitellinus*) (Chapman 1935) as well as to study aggression in European Robins (*Erithacus rubecula*) (Lack 1943). Esch (1967) and Moffett (1990) used a motor-driven model to research food location in honey-bees. Hunsaker (1962) used a machine to control head bobbing movements of lizards (*Sceloperus* sp.). As with any research tool, models should be used with caution (Lehner 1996), but through the use of motorized models researchers should be able to identify a combination of the sensory stimuli that will best heighten appetitive behavior in foraging snakes.

The concept of a super-normal stimulus is well described (Alcock 1984) and an expanded version of this concept should be applied to brown treesnake lure development. Whereas previous researchers varied single sensory stimuli, and often identified a super-normal stimulus, I propose that a "super-normal stimulus suite" may be identified that will elicit intense appetitive behaviors in brown treesnakes. A super-normal stimulus suite is a combination of sensory stimuli that act through numerous sensory modalities to elicit a response greater than the

sum of the individually stimulated sensory modalities or greater than that from the combined natural stimuli. That is, by combining a number of stimuli that are each super-normal or nearly so, I hypothesize that the combinded cues will synergize to elicit a stronger response than that elicited from whole natural prey cues.

For instance, mice are not active constantly through the night and if artificial movement is attractive to snakes, it follows that artificial movement throughout the night may be more attractive than live mouse movement. By altering periodicity and amplitude of mechanical lures an extremely attractive visual cue may be developed. Similarly, continued investigation into the odors of dead mice is likely to identify the attractive components of this attractive odor. The combination of the best movement and odor cues may result in a suite of artificial stimuli that is more attractive to brown treesnakes than a natural mouse lure.

There will be a physiological limit to the response of an animal to any stimulus, and more of a stimulus does not necessarily result in an increased response. For example, odors that are attractive in low concentration can be repellant in high concentration, but the super-normal stimulus suite concept relates to maximizing the quality of the various cues and not necessarily their quantity or intensity. Based on these results, I hypothesize that an appropriate combination of visual and odor components can be constructed that will result in a lure with greater attractiveness than live mice, thus making the use of mice in traps obsolete.

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SUBSTANCE	DATE TESTED	TRAP NIGHTS	ARTIFICIAL LURE CAPTURES	LIVE MOUSE CAPTURES	LIKELIHOOD P VALUE	RELATIVE EFFICIENCY
Aqueous solution, gel	April 1997	40	2	20	< 0.001	0.10
Aqueous solution, tampon	July 1996	110	5	34	< 0.001	0.147
Carrion odor wool	July 1996	20	1	8	0.005	0.125
Carrion odor cotton	July 1996	20	0	8	< 0.001	0
Chicken serum	Jan 1996	10	1	2	0.53	0.50
Deer Away	Aug 1997	10	1	4	0.112	0.125
Milk gel	April 1997	40	0	--	--	--
Mouse serum	Jan 1996	10	0	2	0.084	0
Pseudo Corpse	June 1998	20	0	3	0.036	0
Soft Boiled Eggs	Aug 1997	70	2	14	0.001	0.143

Table 5.1. Summarized results of several pilot studies used to examine possible brown treesnake attraction to candidate odors and matrix formulations. The relative efficiency category was calculated by dividing the number of captures using an artificial lure by the number of captures in concurrently set live mice traps and is an index of the effectiveness of the lure relative to standard live mouse lures.

Compound	Estimated Quantity (*ul*)
Acetaladehyde	0.0047
Benzaldehyde	0.00004
Dimethyl Disulfide	0.02
Ethanol	0.0073
Ethyl acetate	0.001
Hexanal	0.0002
Hexane	0.0006
Hexanol	0.00003
3-Methyl Butanol	0.00028
Heptadecane	0.0007
Pentane	trace
Pentanal	0.00065
Octanal	0.0006

Table 5.2. Major chemical components of mouse carrion odor as determined from gas-chromatographic analysis of a 56 hour old mouse carcass. See text for equipment and conditions.

SOURCE	DF	TYPE III F RATIO	P-VALUE
LURE	3	17.3	0.0001
SEASON	1	9.68	0.009
YEAR	1	1.38	0.263
LURE*SEASON	3	4.41	0.004
LURE*YEAR	3	2.30	0.077
SEASON*YEAR	1	0.13	0.721
LURE*SEASON*YEAR	3	2.12	0.097

Table 5.3. ANOVA table of capture rate per trap line by LURE (live mouse, dead mouse, live mouse odor or dead mouse odor), SEASON (wet or dry), and YEAR (1996 or 1997) data collected from Andersen Air Force Base, Guam.

	LURE	COEFFICIENT	R-SQUARE	P-VALUE
WIND				
	LM	0.036	0.375	0.026
	LMO	0.020	0.417	0.017
	DM	0.018	0.095	0.306
	DMO	0.013	0.038	0.526
RAIN				
	LM	-0.060	0.056	0.438
	LMO	-0.025	0.035	0.543
	DM	-0.136	0.303	0.051
	DMO	-0.150	0.282	0.062

Table 5.4. Statistics for regressions of wind and rainfall during trapping of brown tree snakes.

	SOURCE	P-VALUE
LIVE MOUSE	SEASON	0.699
	RAIN	0.613
	WIND	0.053
LIVE MOUSE ODOR		
	SEASON	0.371
	RAIN	0.682
	WIND	0.033
DEAD MOUSE		
	SEASON	0.475
	RAIN	0.297
	WIND	0.526
DEAD MOUSE ODOR		
	SEASON	0.050
	RAIN	0.608
	WIND	0.837

Table 5.5. Post-hoc analysis of live and dead mouse apparent and odor lure capture rates by season (wet or dry) using concurrent rainfall (mm) and windspeed (m/s) as covariates.

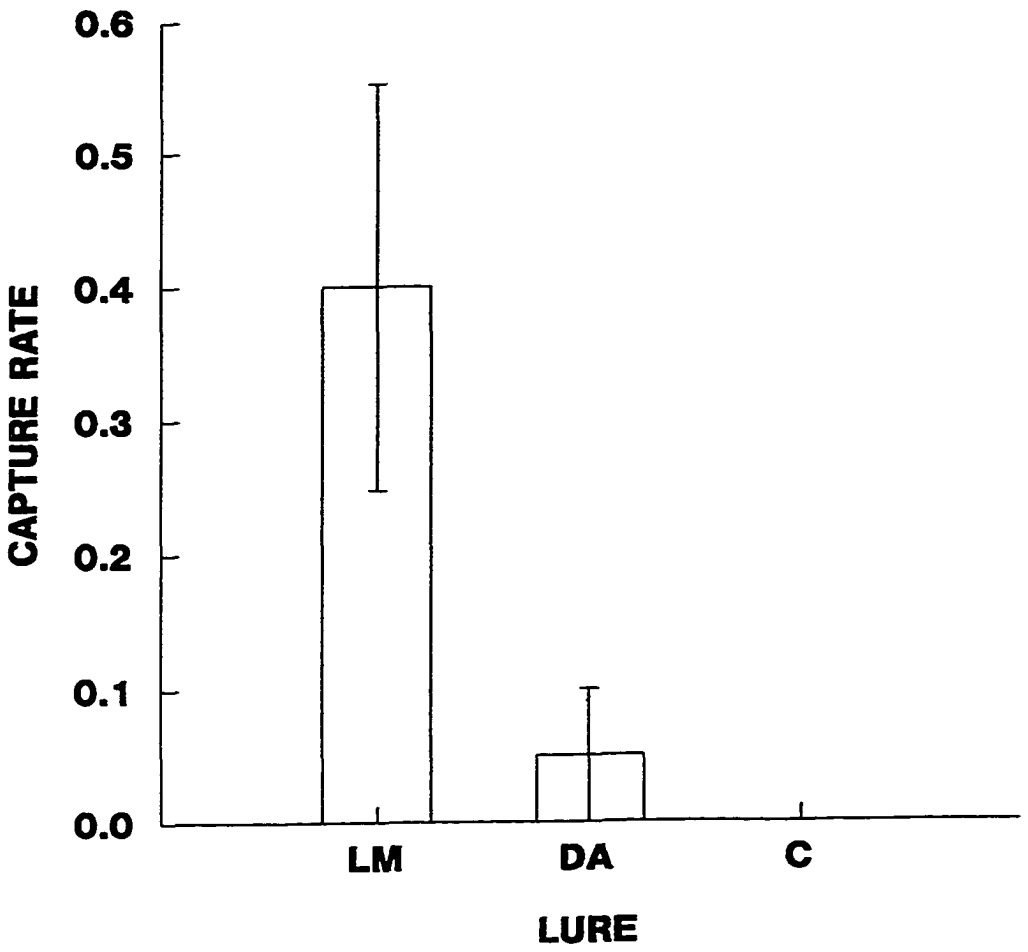


Figure 5.1. Test of Live mice (LM), Deer Away™ (DA) and empty control traps (C). Ten traps per treatment on two trap lines (20 trapnights per treatment) set on Guam during August 25 and 26th 1997.

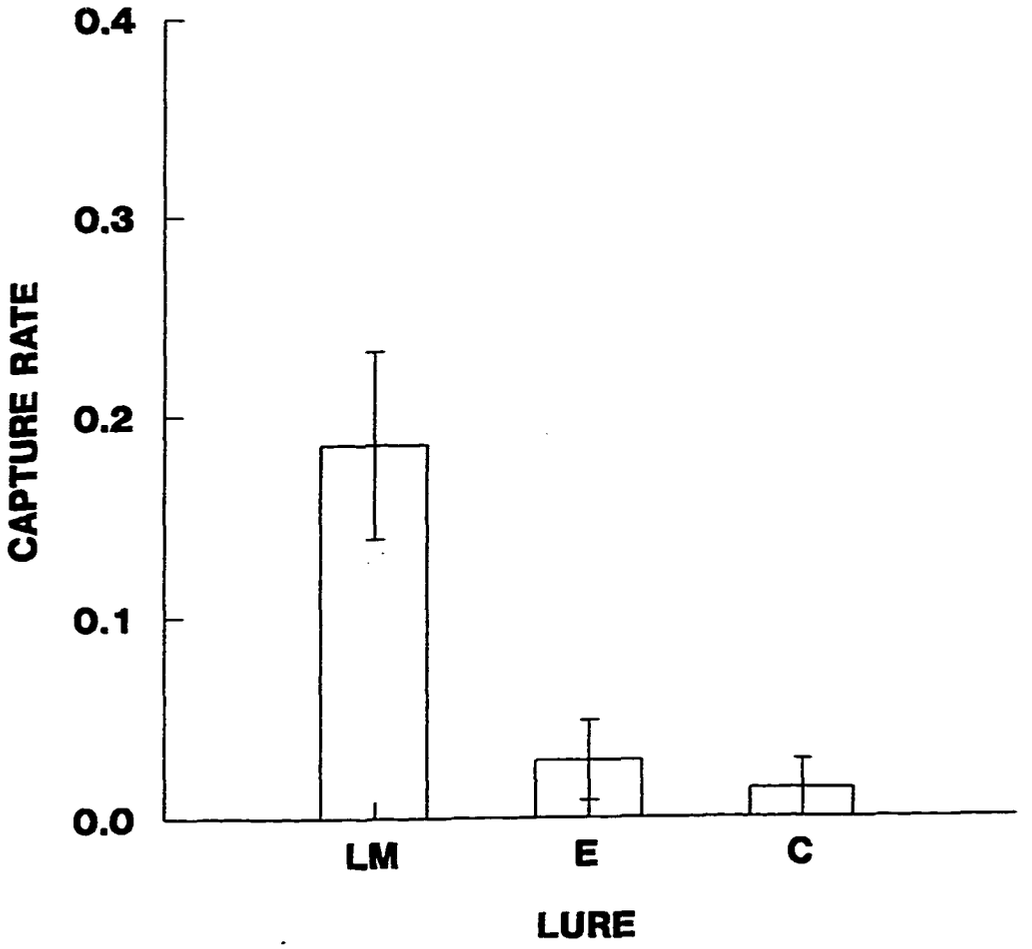


Figure 5.2. Capture rate of brown treesnakes on Guam using rotted eggs (E), live mice (LM), or empty control traps (C).

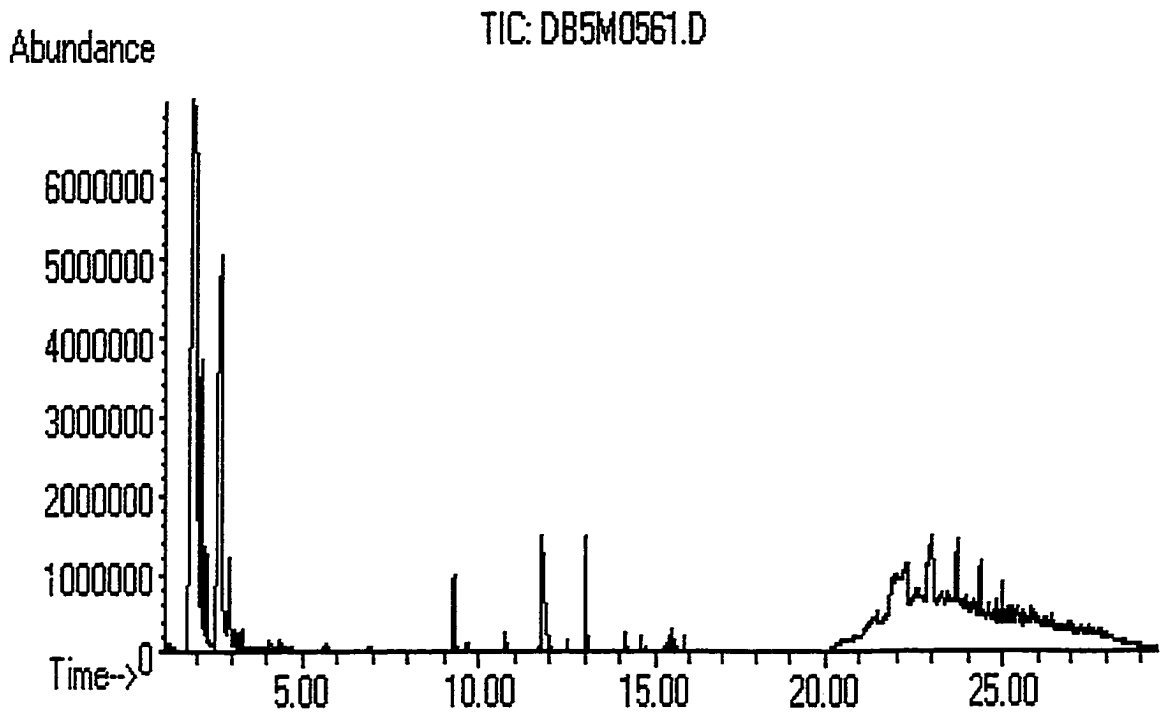


Figure 5.3 Gas chromatograph of 56 hour old mouse carrion odor as determined from gas-chromatographic analysis. See text for equipment and conditions.

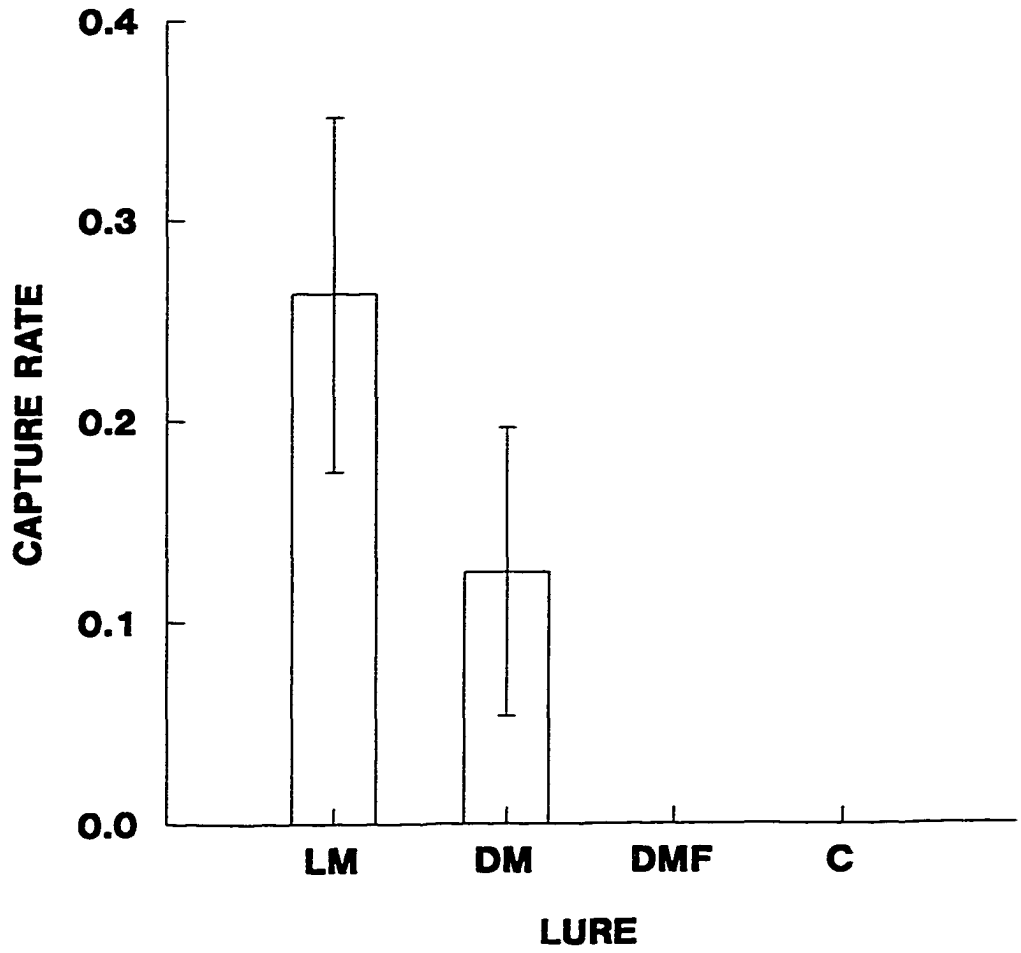


Fig 5.4. Capture rates of brown treesnakes using a dead mouse formulation (DMF) of compounds found in volatiles observed in headspace over a dead mouse. C = empty control trap, DM = dead mouse, LM = live mouse.

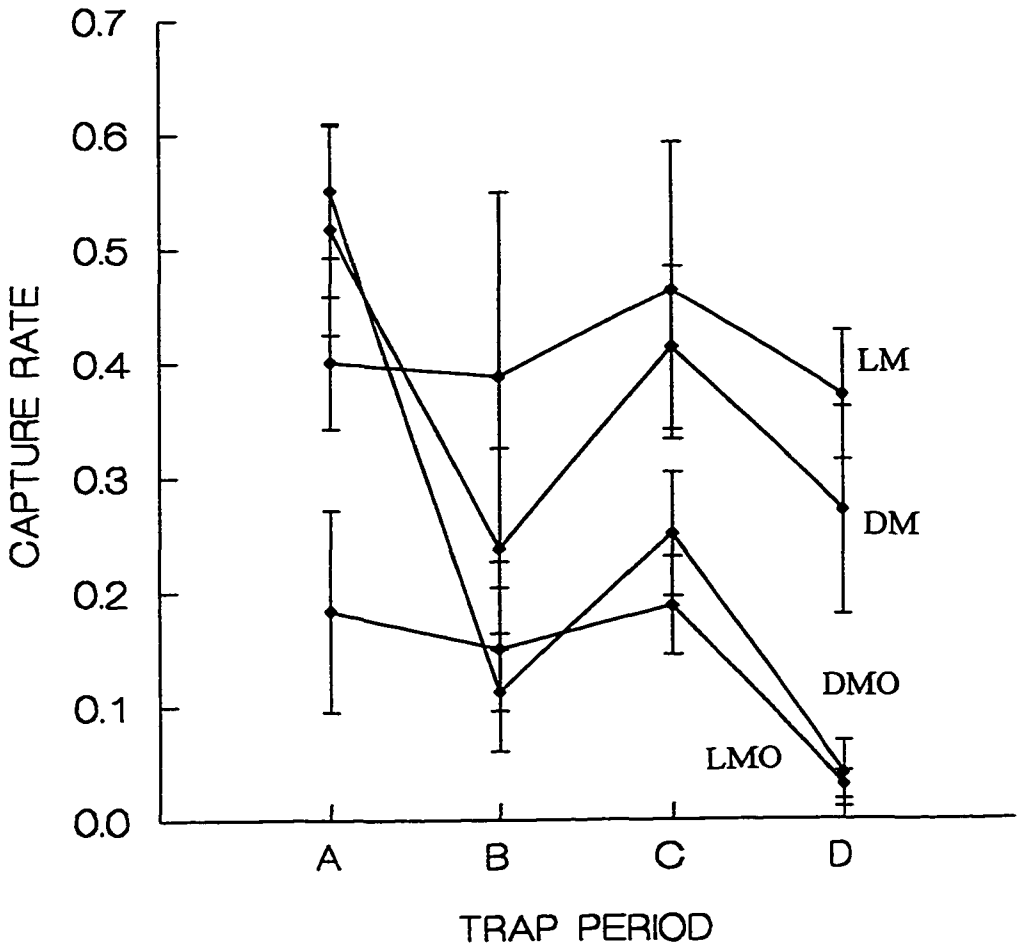


Figure 5.5. Replications of live mice, live mice odor, dead mice and dead mice odor by season. DM = dead mouse, DMO = dead mouse odor, LM = live mouse, LMO = live mouse odor. Trapping was performed during the dry season of 1996 (A), the wet season of 1996 (B), the dry season of 1997 (C) and the wet season of 1997 (D) on Guam.

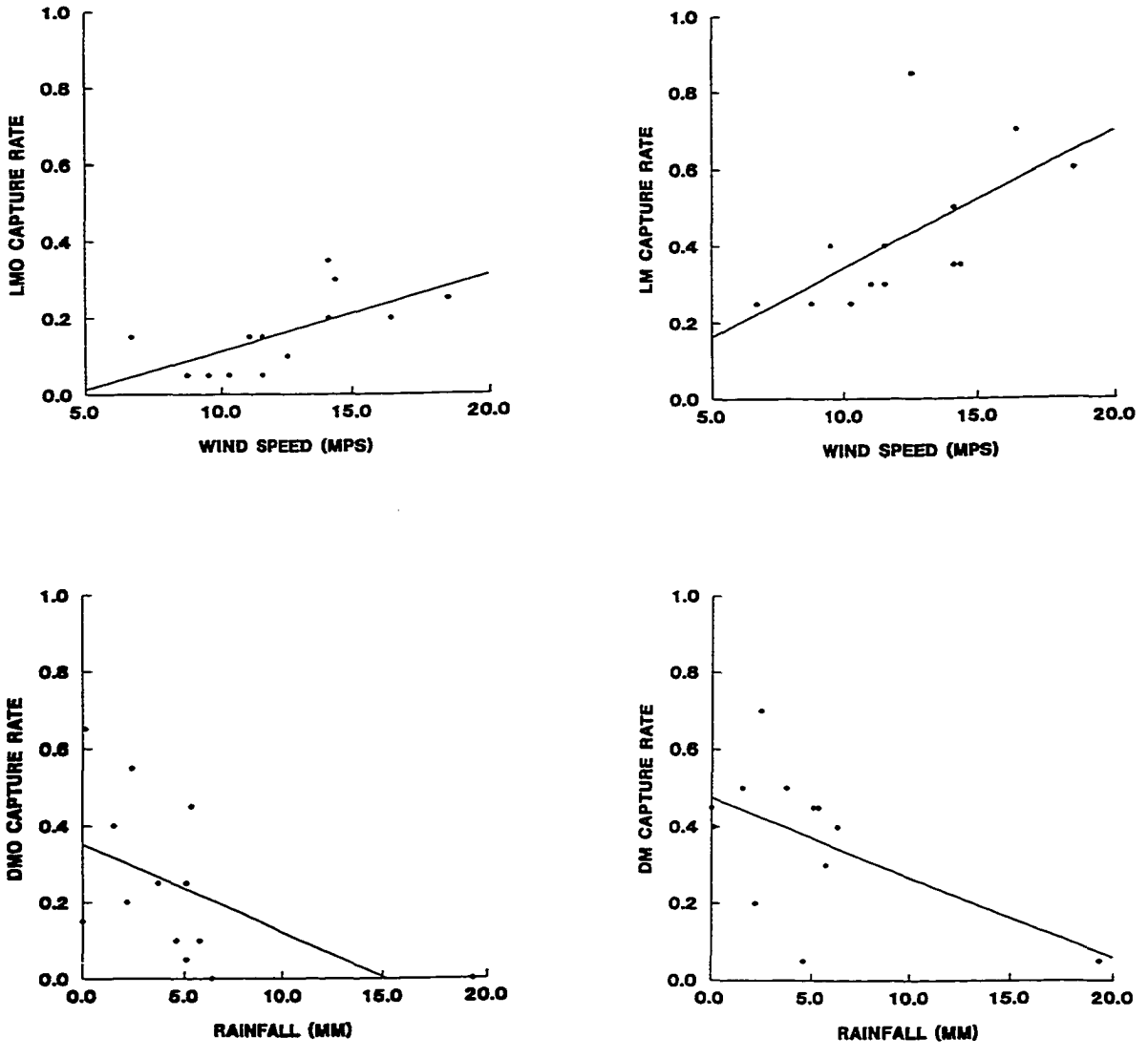
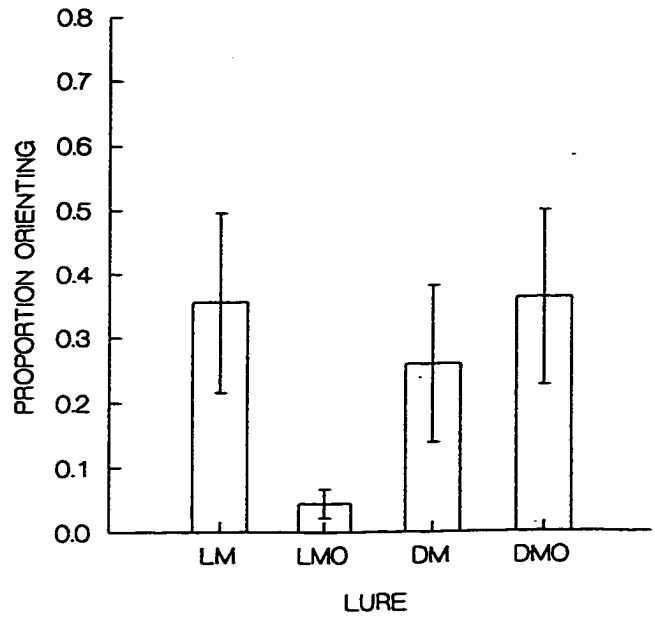


Figure 5.6. Regression of brown treesnake capture rate using live mouse, live mouse odor, dead mouse, or dead mouse odor against average wind speed (m/s) and rainfall (mm)during April and August, 1996 and April and August, 1997 on Andersen Air Force Base, Guam.

A. Recently Fed Snakes



B. Unfed Snakes

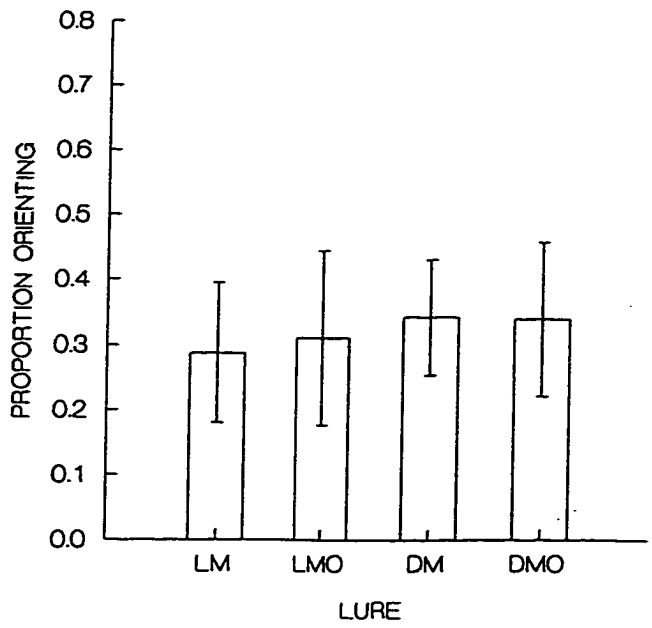
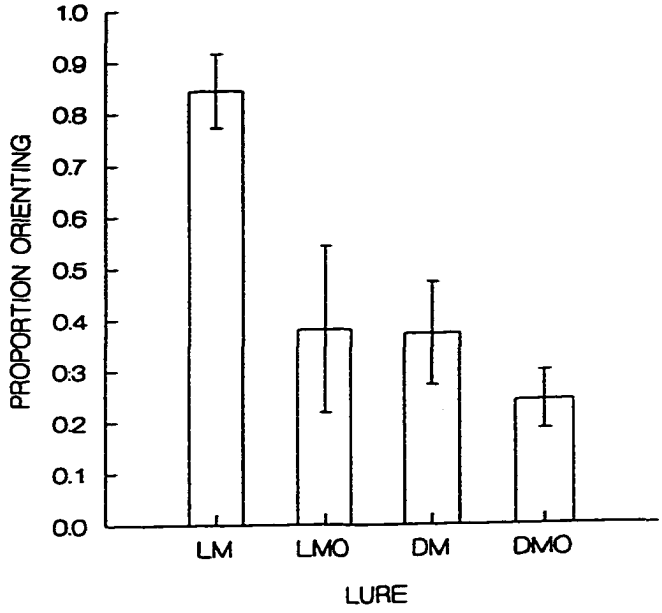


Figure 5.7. Long-term captive brown treesnake (held in captivity >3 years) response to lures, measuring the proportion of time an active snake oriented toward a lure type. LM = live mouse, LMO = live mouse odor, DMO = dead mouse odor, DM = dead mouse.

A. Recently Fed Snakes



B. Unfed Snakes

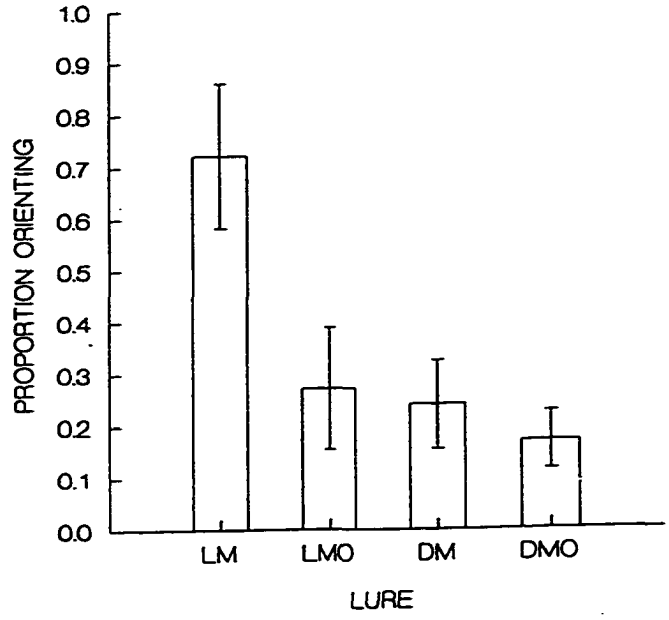


Figure 5.8. Short-term captive brown treesnake (held in captivity < 3 weeks) response to lures, measuring the proportion of time an active snake oriented toward a lure type (n = 5 per treatment). LM = live mouse, LMO = live mouse odor, DMO = dead mouse odor, DM = dead mouse.

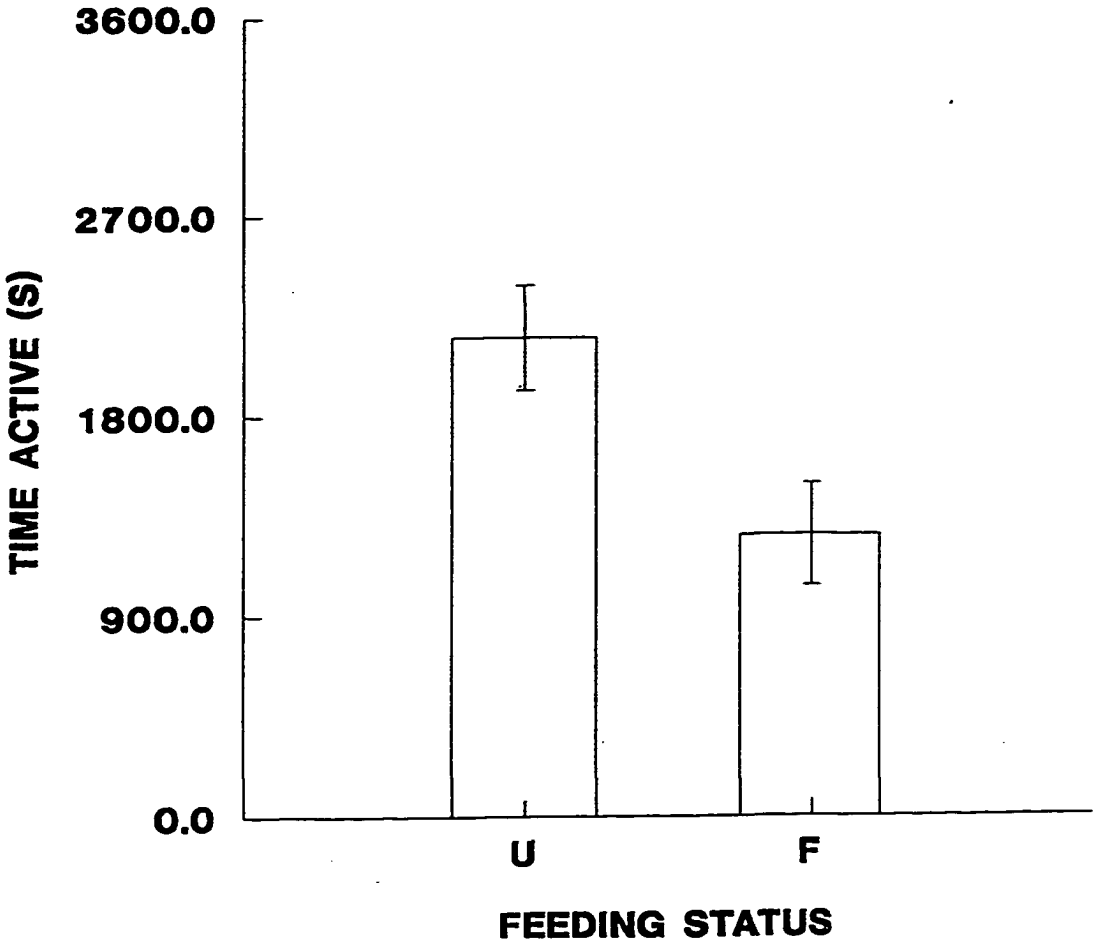


Figure 5.10. Activity of short-term held captive brown treesnakes by feeding status. U = unfed (not fed withing 5 days), F = fed (fed within 24 hours).

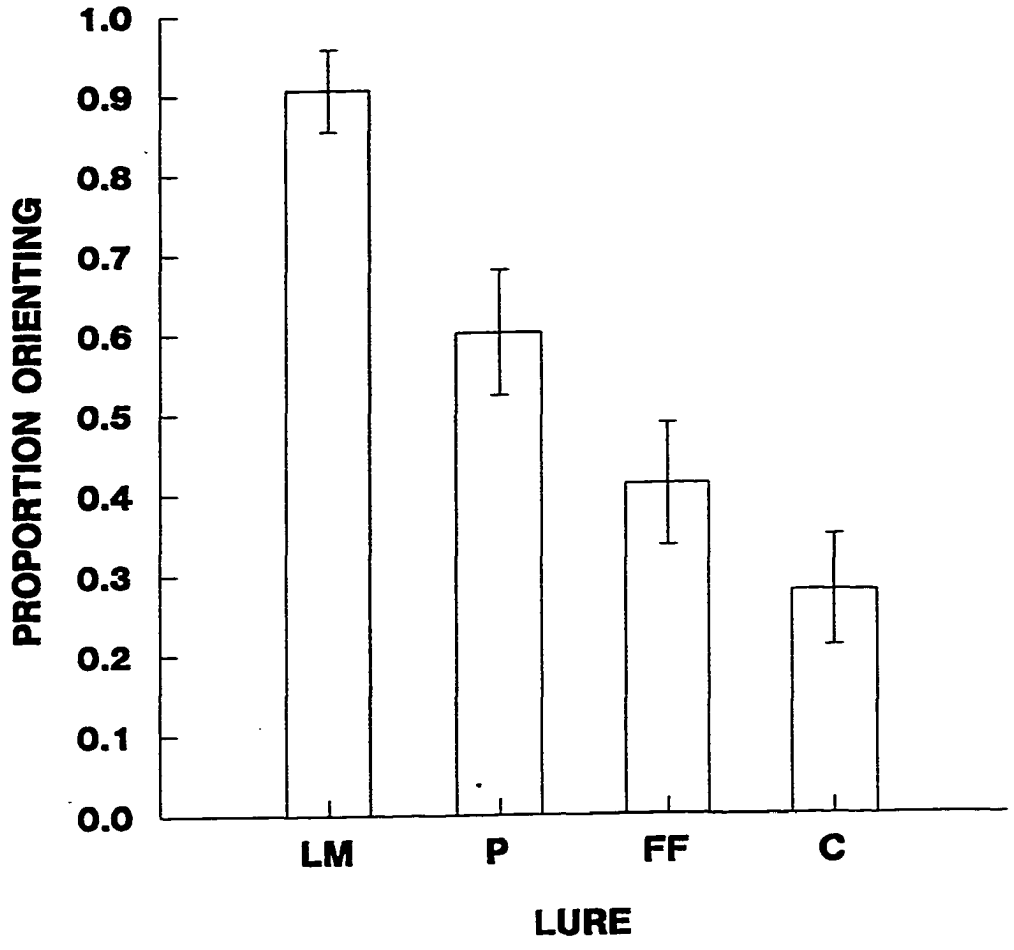


Figure 5.10. Proportion of time recently captive brown treesnakes spent orienting toward a live mouse (LM, n = 10), a mouse-pelt covered mechanical model (P, n = 11), and empty control trap (C, n = 8), or a fake-fur covered mechanical model (FF, n = 8).

CHAPTER VI. WHY BROWN TREESNAKES EAT CARRION: EVOLUTION OF CARRION CONSUMPTION AMONG TAXA

ABSTRACT: The subject of foraging by predators and herbivores is well studied, as is the competition between frugivores and the microbes that rot fruit. However, a paucity of empirical observation and theory exists because of human aversion to rotted carcasses, bias that scavengers are anti-charasmatic, and difficulty in identifying scavenged material in predator food habits studies. Because students of animal behavior or managers of endangered species are not aware that they should expect scavenging, the importance of carcasses and carcass use in ecological systems is grossly underrepresented even though a large proportion of the energy from animal biomass initially passes first through a scavenger, and not only a microbial intermediary. Numerous similarities exist between the ecology of plant chemical defenses and microbial chemical defenses for the patchily distrubted, but non-mobile resources of plants or carcasses, and the availability of herbivore carcasses provides an evolutionary pathway from herbivore to scavenger to carnivore. A gap in ecological knowledge has resulted becuase scavenging by snakes has only been remotely addressed in natural history studies, and I use a nutritive value-detectability model to describe the evolutionary pressures impinging upon the behavior of a scavenging snake species, *Boiga irregularis*.

Numerous authors in unrelated studies have reached the conclusion that a particular predator probably eats more carrion than would be surmised from the literature (Gochfeld and Burger 1980, Caro 1982, Squires 1995, Sheffield and Jobe 1996,Shivik and Clark 1997). Still, for decades, authors have been surprised when observing a supposedly obligate predator eat carrion. Twenty years after noting that one of the most unappreciated classes of interspecific competition occurs between microbes and large organisms over newly dead animals (Janzen 1977), this phenomenon is still unappreciated. The subject of decomposition is not without discussion, but the subject of fleshy fruits and seeds have been far more palatable to researchers than carcasses; chemical compounds in plants have inspired volumes of research (Rosenthal and Janzen 1979), but other than Putman's (1983) exploration of the subject, elaborate studies of the evolutionary importance of dead animals are far too few. Thus, the phenomenon is viewed as a curiosity rather than an important ecosystem process.

For a variety of reasons, carrion foraging by vertebrates is a phenomenon frequently noted but infrequently described, and references to it are often oblique and qualitative (Wilton 1986). Carrion use is methodologically difficult to quantify because typical techniques used for food habits studies often preclude determining whether ingested prey was killed or scavenged. For example, scat analysis does not identify carrion ingested, because fecal remnants of killed and scavenged prey are nearly identical. The use of stomach content analysis may be limited as well, unless special attention is paid to evidence of carrion eating (e.g. maggots mixed with stomach contents). Carrion is usually omitted from lists of commonly eaten items, and is not observed in some studies because it is simply not looked for. Natural history and foraging studies are often organismal in their approach and carrion is not a "species" normally studied.

Even when a species is studied intensively, observations typically end with the death of an individual and do not necessarily trace the fate of the animal's carcasses.

Another reason for the lack of scavenging studies is because of a human aversion to rotted substances. The term scavenger connotes a less than noble life-style and "charismatically-challenged" species often suffer from a paucity of basic natural history data. Even when predators are studied fairly intensively, descriptions of carrion use are relegated to anecdotal accounts or minor mention. Also, charismatic species such as the Gyrfalcon (*Falco rusticolus*) are given a classically biased description in older works, e.g., the "Gyrfalcon is noble and this aristocratic bird lives only on warm-blooded living prey, preferably birds, and never eats carrion," although a preponderance of recent evidence demonstrates the importance of carrion in actual diets (Tommeraas 1989). It is apparently not so desirable to study an ignoble and pedestrian scavenger. It is important to overcome methodological and cultural biases against detecting carrion feeding by vertebrate predators to allow objective and scientific descriptions that are accurately reflective of a species' natural history.

My objective in this paper is to demonstrate that carrion use is much more important than conventional theory addresses, and is not a curiosity of animal behavior, but a key ecological process. I hope to stimulate studies of scavenging behaviors, and to show how selective pressures may influence the development of carrion foraging behavior.

The carrion resource is important ecologically because the only way materials taken into the animal part of the ecological system can be released and recycled is through decay of carrion and animal wastes (Putman 1983). The importance of carrion is *fait accompli*, as exhibited by the plethora of scavengers in every ecosystem, from skuas (*Stercorarius* spp.) and arctic foxes

(*Vulpes* spp.) in tundra, to coyotes (*Canis latrans*) and badgers (*Taxidea taxus*) in more temperate zones or jackals (*Canis* spp.) and vultures (*Cathartes* spp.) in tropical regions (Putman 1983). Moreover, the high degree to which scavengers compete with each other for the carrion resource suggests how important the carrion resource is ecologically (Anderson and Horwitz 1978, Herman 1981, Houston 1987, Wallace and Temple 1987).

Although one is tempted to believe that decomposers are the primary reason the earth is not covered knee-deep in carcasses, the importance of scavengers cannot be denied because scavengers usually digest the carcasses first: they undoubtedly account for recycling far more of the available carrion than popularly supposed. In one study, vertebrate scavengers removed 75% of placed House Sparrow and Brown-headed Cowbird carcasses, while insects and bacteria caused the decay of only 13 % of the carcasses (Tobin and Dolbeer 1990). Vertebrate scavengers take the vast majority of all small mammal carcasses, e.g., crows , foxes and badgers have been estimated to take between 75-100% of carcasses, depending on the season (Putman 1983).

In any scientific exploration there is an infinite number of alternative hypotheses that we must actively disprove to move towards some confidence in the knowledge that we have gained. By not being aware of major categories of theory, we will be at a loss to explain observed phenomena, merely because the biases we have against certain behaviors prevent us from considering them as viable alternative hypotheses. We are limited in our interpretations of foraging behavior by being caught up in dogmatic assumptions.

In the current age of conservation, understanding the use of carrion resources by declining species is important. Misunderstanding the cycle of carrion is dangerous for

conservation efforts because many endangered species may scavenge frequently. Carrion placement is a strategy that has already been used to supplement food supplies of endangered species such as Bald Eagles (*Haliaeetus leucocephalus*) and California Condors (*Gymnogyps californianus*) (Marr et al. 1995). Carcasses may be important for many other at-risk species as well.

Costs and benefits of carrion foraging behavior

A variety of costs and benefits selecting toward or away from carrion use impinge upon the foraging behavior of animals. By not having to chase and kill dead prey, predators gain a food source that is handled relatively safely and easily. Carcasses are stationary and do not have innate defensive tactics, and are thus preferentially used by predators. For example, in a study where hyaenas (*Crocuta crocuta*) encountered 2.8 prey groups per hour, they hunted on only 8% of these occasions (Gasaway et al. 1991). In contrast, of the 0.6 carrion items per hour hyaenas encountered, they fed on 39% of the carcasses. Even though there was not as much energy return from the carcasses due to decomposition (hyaenas only obtained 25% of their food biomass from scavenging), not having to chase and kill a carrion item allows for energy savings relative to killing live prey.

Carrion foragers are spared some negative elements of predator-prey evolutionary dynamics (i.e., the constant evolution of predator adaptations to overcome constantly evolving prey defenses) because selective pressure does not act upon dead animals. Natural selection can act though competition between carrion eating species, but a predator that is eating carrion is spared the concurrent predator-prey coevolutionary "arms race." Carcasses do not defend

themselves and are relatively easy to handle, but the resource is not without inherent costs. A certain level of competition between a vertebrate scavenger and the invertebrates that decompose a carcass is to be expected. The microbes that are attempting to take advantage of the resource should play an evolutionary and ecological game with toxins and substrate degradation (Janzen 1977). Most invertebrate members of the carrion-community must rapidly discover and colonize carcasses in order to use the resource maximally (Braack 1987). The microbe must rapidly convert the carcass nutrients into an inedible, unwanted, or toxic substance to vertebrates and this is most easily done by producing a few objectionable materials rather than converting all edible materials to less desirable molecules (Janzen 1977). For example, *Clostridium perfrigens, Clostridum botulinum, Escherichia coli, Staphylococcus aureus, Shigella dysenteriae, Salmonella typhi and Bacillus stearothermophilus* all produce toxins that are dangerous to mammalian and avian species that are exposed to them. Aposematically, the wide variety of amines and sulfur compounds characteristic of rot by these species also allow a human mammal to immediately identify a piece of meat as being fetid and inedible (Janzen 1977).

The vertebrate scavengers must out-compete the microbe by obtaining the carcass faster, or by detoxifying or otherwise avoiding the chemical defenses of the microbes (Janzen 1977). Vertebrate scavengers must assume the fixed cost of developing detoxicating enzymes and associated morphological structures to protect themselves from bacteria and the metabolic cost of the detoxicating process itself (Feeny 1973).

Vertebrates that become scavengers reduce the need for the specialized structures and behaviors of a predatory animal, but require adaptations to overcome competitive pressures from other vertebrate and invertebrate scavengers. Interestingly, the realized benefits and costs of

eating carrion are equivalent to those of eating plants except that a herbivore is largely coevolving with the plants it is eating (the herbivore must constantly counter newly evolved plant chemical defenses) but a carrion eater is competing not with the carcass itself but with the invertebrate scavengers which tend to produce a similar suite of toxic and thus defensive products of metabolism. Micro-scavengers defend themselves and their resource in much the same way that plants do. Relatively sessile bacteria and fungi produce chemical compounds that reduce the attractiveness of the carrion resource to vertebrate scavengers. The dynamic equilibrium that can be assumed between plants and their enemies (Dethier, 1954) cannot exist between a carcass and its decomposers, but the competition is likely to exist between the various taxa of macro- and micro-scavengers that attack the carcass (Cole 1972, Wilton 1986). Interspecific competition is evident because the carrion resource is always recycled, and no one species or taxon dominates its use.

There is direct competition between macro-scavengers and invertebrate scavengers. In temperate zones during winter, vertebrate scavengers have an advantage, obtaining most carcasses. In the summer, the invertebrate scavengers may wholly consume most of the available carcasses (Putman 1983). Warmer temperatures allow more rapid bacterial and fungal growth, and insects steepen carrion decay curves by transporting decomposers to carcasses while insect pupae tunnel and aerate carcasses (Payne 1965, Putman 1978).

Carrion Eating by Vertebrates: Evolution and Patterns

A carrion eater, like an obligate herbivore, does not have to evolve weapons such as strength, size, specialized teeth, claws, and a relatively fearless disposition to secure its food (although such structures may be helpful to defend a carcass from other scavengers), but it

requires specializations for the efficient and safe ingestion and digestion of decomposing matter. The mix of costs and benefits results in a continuum of specific characteristics that allow carrion use to some degree. Many animals, such as cheetah (Bond and Lindburg 1990), otter (O'Sullivan et al. 1992), herons (Klapste 1991), newts (Morey 1987), pheasants (Knox and Buckland 1983), and a variety of corvids, raptors and gulls (Wilkinson 1982, Skaggs 1983, Heinrich 1988, Hiraldo et al. 1991, McKinstry and Knight 1993, Squires 1995, Sheffield and Jobe 1996) have been observed to eat carrion when conditions are appropriate. Therefore, the realized distribution of vertebrate behavior between plant, live prey, or carrion foraging strategy is a continuum with selective pressures operating to shift foraging behavior between the foraging strategies (Fig. 6.1, Table 6.1).

Evolutionarily, the first wholly terrestrial vertebrates were herbivorous and insectivorous because carnivorous terrestrial vertebrates could not exist until the land was populated with potential prey. It was not just a simple matter of terrestrial carnivores waiting to have some of their "placental cousins develop into harmless herbivorous types upon which they might prey" (Romer 1941), but a series of intermediate steps. Notwithstanding the other likely intermediate of insectivory between herbivory and carnivory, scavenging may have been an important evolutionary step for some taxa. Largely because of the commonalities between carrion and plant foraging, a parsimonious evolutionary path is from herbivory to scavenging to predation rather than directly to predation from herbivory. As previously discussed, plants and carrion are similar in their lack of mobility. A relatively simple behavioral adaptation would be for a herbivorous species to begin opportunistically sampling dead animal material. A rapid evolution of the necessary enzymes needed to digest this animal material more efficiently is a likely result

of such scavenging behavior. Given the enzymes required for efficient digestion of animal matter, a scavenging herbivore should next develop structures such as carnassial teeth and claws for ripping carcasses which would, in turn, allow the evolution of active predatory behaviors. As a scavenger shifts from herbivory through scavenging toward predation, the reduction of structures initially developed to aid in the digestion of plant material will result in a modern predator.

Competition will favor adaptations that make a particular species a more effective competitor for a food resource (Anderson and Horwitz 1978; Houston 1979; Wallace and Temple 1987). A specialist feeder may be dependent upon the ephemeral resource of carrion, but behavioral and physiological mechanisms that allow it to find the resource more efficiently reduces competition within its "adaptive zone" (Feeny 1973). Death of a small animal in a nook or cavity makes the carcass unavailable to many vertebrate scavengers. However, the resource may then present a niche for species with reduced body-forms such as snakes. Large predators may not be able to obtain many tree-dwelling animals and as a result most arboreal organisms probably die of disease, parasites, accidents, old age, or food shortages rather than from predation. In healthy forests, one animal dies in each square mile every day (Houston 1994) and in a tropical site such as Barro Colorado Island, about 2 kg of animal mass per km^2 dies every day (Houston 1986). This provides a tremendous amount of biomass for an arboreal predator that is willing and capable of taking advantage of this unpredictable but easily handled resource.

Few vertebrates that are scavengers feed exclusively on carrion. Most scavengers are predators that indulge as they are able (Putman 1983). Indeed, members of the Carnivora and other predatory orders generally eat whatever they can get (Ewer 1973), and most North

American carnivores will scavenge if the opportunity presents itself (Wilton 1986).

Carrion is extremely ephemeral in nature and species are expected to exhibit adaptations toward more efficient use of the resource. The temporal patchiness of carrion may preclude many instances of evolution towards specialization for carrion foraging behavior. For example, the species best specialized for carrion use are avian because of low costs of search efforts in soaring locomotion. Because soaring requires less energy than running (Schmidt-Nielson 1972), an avian scavenger is at an advantage when compared with mammalian or reptilian scavengers (Houston 1979). The greater efficiency of birds relative to other vertebrates is because they find and consume carrion more rapidly (Kruuk 1967, Pennycuick 1971, Houston 1974, Houston 1979, Hiraldo et al. 1991, Prior and Weatherhead 1991). Indeed, members of most other vertebrate taxa are unlikely to travel as some ravens, that fly at least 90 km / day to feed (Heinrich 1988). Only among birds do we find species adapted to survive on carrion alone, and all of these bird species have the similar characteristics of large wingspans, a soaring habit, keen eyesight, and a reduction of feathers around the head that would otherwise crust with putrefying and potentially toxic material (Putman 1983).

In systems with productive large herbivore populations (e.g., African systems), carrion is abundant and predictable enough to produce carrion specialists such as highly adapted vultures, but the availability may still be such that no large mammal could survive on carrion alone (Braack 1987, Heinrich 1988, Putman 1983). No mammal has ever evolved to be an exclusive scavenger, as many bird species have done (Houston 1994). Mammalian carnivores will consume a carcass whenever they find one (Houston 1986) but birds can usually out-compete mammalian scavengers, except at night when carnivores such as coyotes can monopolize carrion

resources (Prior and Weatherhead 1991). Turkey Vultures consumed 90-95% of placed carcasses (Houston 1986), and in a similar study, vultures located 63% of provided carcasses compared to mammalian scavengers which only found 5% (Gomez et al. 1993). Ravens (*Corvs corvax*) and golden eagles (*Aquila chrysaetos*) accounted for 90% of the activity around carcasses placed for bears (*Ursus arctos*) (Elgmork and Tjørve 1995).

Niche separation remains evident within vultures, as various vulture species partition the use of a carcass (König 1983). Mountain-dwelling species of vultures, where the food supply is more irregular have developed larger body sizes to be able to fast longer between meals and to be able to defend the use of the larger carcasses found (König 1983).

On a grand ecological scale, birds are likely to out-compete other species for available carcass biomass. However, it is important to note that the importance of a prey item in an individual species' diet is not necessarily proportional to the amount of that prey item that is eaten. That is, even though bird species may consume the majority of carcasses, carcass feeding by other vertebrate scavengers may easily mean the difference between life, death, and reproduction of a mammalian or ophidian predator. Grizzly bears (*Ursus arctos*), for instance, obtain 70% of the meat they eat by scavenging (Mattson 1997), and the survival and reproduction of a poikliotherm with relatively few meals a year (e.g., a bushmaster, *Lachesis muta,* may only require 5-6 rats per year) may be solely dependent upon a single carrion meal (Gillingham and Baker 1981, Greene 1997). Especially with poikliotherms, the quantity of carrion consumed does not necessarily scale to the importance of the resource: consumption proves importance.

Model of Selective Pressures on Carrion Foraging

In the preceding discussion, I outlined evolutionary reasons and processes that have resulted in observed scavenging and predatory adaptations. My objective in the following section is to outline proximate evolutionary mechanisms at the species level. The proximate environmental factors that determine whether an opportunistic species will detect and consume a carrion item include nutritive value (i.e., the nutrition inherent in the food must outweigh the costs of digestion of the food), detection distance (which presumably increases as carrion rots), and toxicity of the products of decomposition. The shape of the nutritive value curve will be related to carcass weight and is sigmoidal in shape (Payne 1965), and the odor radius curve will be related to gases, such as CO_2, which emanate over time in a bell-shaped concentration curve (Putman 1978) (Fig. 6.2).

As bacterial and fungal organisms digest a carcass, compounds useful to scavengers are metabolized. Through time, the nutritive value of the carcass degrades. Furthermore, the products of decomposition are often toxic, thus further minimizing the usefulness of a carcass to a scavenger. Other products of decomposition have an opposite, beneficial effect for a scavenger. Low molecular weight compounds such as hydrogen sulfide, putrescine, etc., are characteristic of decomposition and signal the presence of carrion to scavengers (Stager 1964). The products of decay are both attractive and repulsive to scavengers, depending upon concentration, and will result in an optimum detection-consumption model for prediction of carrion use by a scavenger through time (Fig. 6.2). The attractiveness (i.e., the detectability and desirability of a carcass to a scavenger) of a carcass will reach an optimum when the carcass is odoriferous enough to be detected at great distances, but still retains much non-fetid biomass.

Vultures, which are one of the few scavenging species intensely studied, exhibit foraging behavior consistent with this optimum detection-consumption model. First, detection rates begin low, become high and then drop off again as carcasses age (Fig. 6.3, Houston 1986). However, as the carcass ages, it also becomes less attractive to a vulture: 24 hour old carcasses are preferred over 120 hour old carcasses in two-choice consumption studies (Fig. 6.4, Houston 1986).

Brown tree snake behavior also fits the detection-consumption model. The brown treesnake is a carrion-eating generalist species with a catholic diet (Savidge et al. 1988, Shivik and Clark 1997). To examine the suitability of the detection-consumption model, I performed a trapping study of brown treesnakes on Guam to compare the attractiveness of mouse carrion (of several ages) to brown treesnakes. Traps were set August 14-18, 1997, above Haputo Beach, Guam, and capture rates per treatment type were recorded. Frozen "feeder" mice (Fink's Rats and Mice, Anaheim, CA) were thawed and rotted at ambient conditions on Guam. Mice were rotted in a staggered fashion to provide dead mice that were 1-5 days old for each trap line.

High variability in the data prohibit a thorough test of the carrion use hypothesis (Fig. 6.5), but the results of this experiment support the model of carrion foraging proposed in Figure 6.2. Given support of the detection-consumption model of selective pressures operating on an animal's use of carrion, I can expand the interpretation of the model to describe within-species adaptations that result in specialization toward carrion use.

In the model, the size of the realized usage area can be increased in two ways: 1) Shifting the nutritive value curve up and right, and 2) shifting the detectable odor radius curve up and left. Nutritive value can be shifted through the development of improved enzymes that

minimize micro-scavenger competition and the detectable odor curve can be increased by improving sensory structures or mobility adaptations that increase the distance at which carrion odor can be detected (Fig. 6.6).

Snakes as Scavengers

Manipulating the nutritive value and detection radius curves allows understanding of the limitations of individual species on the scavenging continuum. The ultimate scavengers are vultures and other avian scavengers. Birds have the unique adaptation of soaring flight which maximizes detection radii while minimizing the costs of long-distance foraging. Species such as snakes and mammalian carnivores are expected to scavenge, but they are limited in their scavenging abilities relative to birds. Snakes and mammals cannot sustain soaring flight and are best able to compete as scavengers by shifting the detection curve through the development of improved sensory structures and by developing improved enzyme systems for more efficient digestion of rotted meals.

Snakes are favored as scavengers in some situations and therefore scavenging behaviors are retained in ophidian predators. Snakes have a body form that allows them to probe small cavities and arboreal locations where small animals are likely to die but that other scavengers cannot access. Snakes are widely thought to be specialized hunters, but many, such as Racers (*Coluber constrictor*), Common Kingsnakes (*Lampropeltis getula*), Eyelash Pitvipers (*Bothriechis schlegelii*), and Indigo Snakes (*Drymarchon corais*), have very broad diets. Among amateur and beginning herpetoculturists, species that feed easily and on a wide variety of prey are well-know and popular and they consume carrion readily as is evident from the wide use of

frozen mice as feed. The cottonmouth (*Agkistrodon piscivorous*) occasionally eats carrion (Gasc 1994) and rattlesnakes *(Crotalus* spp.) prefer dead prey (Cowles and Phelan 1958). Venomous predators are believed to be more inclined to scavenge than species that kill prey by constriction because eating previously envenomated dead prey is normal to them (Patten and Banta, 1980, Gillingham and Baker 1981, Lillywhite 1982, Diller, 1990). However, non-venomous colubrid snakes, which kill mechanically, have also been observed to eat carrion (Bedford 1991, Norton 1993, Mattison 1995). Among snakes, I hypothesize that mobile predators such as Gopher Snakes (*Pituophis catenifer*), and Common Kingsnakes, that travel considerable distances among clusters of sessile prey (Greene 1997) are as likely to contain significant amounts of carrion in their diets as well as sit and wait predators. It is interesting to note that the snake best known for carrion eating is a sit and wait predator, the rattlesnake, *Crotalus viridis* (Cowles and Phelan 1958, Gillingham and Baker 1981). I hypothesize, however, that rattlesnakes will forage actively when detecting carrion odors and adopt an ambush position when they detect fresh odors of live prey.

The commonly hypothesized proximate use of snake venom is to aid in subduing prey. The toxicity and thus ability of venom to perform this task is usually thought of in human or mouse terms and is divorced from the ecological context within which many snakes operate (Kardong 1996). Indeed, human saliva, if injected cutaneously, will produce local pain, erythema and edema, but humans are not accurately described as a venomous species (Kardong 1996). The context of use, then, is of utmost importance when considering evolutionary explanations for observed physiological properties of snake oral secretions. Although toxicity in colubrids may be more widespread than commonly appreciated, the function of oral glands

should not be assessed purely based on its toxicity (Kardong 1979). Oral gland secretions may help to condition teeth and promote oral hygiene, aid in the digestion of prey, and prevent its putrefaction (Gans 1978, Kochva et al. 1983). Snake oral secretions are cytotoxic, and digestive enzymes contained within them are common in other body tissues (Kochva et al. 1983). It follows that these toxic substances with other uses besides subduing live prey only developed into venoms after the structures that aid in grasping and swallowing prey (e.g., enlarged posterior maxillary teeth) evolved (Kardong 1979).

Many colubrids have a Duvernoy's gland and its associated toxic secretions, but the gland did not evolve for prey-killing (Kardong 1979). Furthermore, species with a well developed Duvernoy's gland, such as the brown treesnake, kill primarily mechanically (Rochelle and Kardong 1993, Rodda 1992). In my casual observations of brown treesnakes eating, they subdue prey by constricting and clamping with their mouths. Swallowing is a series of chewing-like mandibular protractions which may act to slowly and more completely introduce oral secretions into and over the carcass. I hypothesize that one function of the Duvernoy's gland is to slow bacterial, fungal, and parasitic growth on carcasses to allow safer digestion. The secretion, whether or not it is defined as a venom (Kardong 1996), is likely to have a number of functions and venoms in general are composed of a variety of components, including many cytolytic compounds (Tu 1996). These compounds may act on specific bacteria, fungi, and their toxins, or may act to kill insects and parasites that could otherwise harm a carrion eater. Most herpetologists do not think that the Duvernoy's gland evolved to enable safer carrion eating, and I do not believe that this is its only likely function, but given the context of the generalist diets of many colubrids, this is a hypothesis which should be explored.

The brown treesnake is of particular note as a generalist scavenger because of its disruption of bird life on Guam (Savidge 1987). The tremendous densities of scavenging brown treesnakes (Rodda 1992) may have had undetected effects on the Mariana crow. Above and beyond the direct predation on crow eggs and hatchlings, the large numbers of snakes may actually be consuming carrion biomass that would otherwise be available almost exclusively to crows. Brown tree snakes removed 30-40% of mouse carcasses placed in Guam forests, and the effect of this voracious scavenger is likely to have other far-reaching effects (P. Savarie, National Wildlife Research Center, pers. commun.).

Indeed, the brown treesnake did not only influence the Guam ecosystem by direct predation: they are likely to have altered the overall chain of energy. Small carcasses now flow through brown treesnakes rather than through another scavenging species.

Given anthropomorphic and research biases, the actual consumption or importance of the consumption of carrion by snakes is likely under represented. In an ecological system, everything that is organic dies, but energy is converted and conserved. More energy moves through ecological processes with a carrion intermediary than with a predated intermediary. Although the concept seems trivial, it is not, and although the answer to the question seems flippant, it is not. The reason snakes, and all predators, eat carrion, is because it is available.

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Common Name	Scientific Name	Veg.	Prey	Carrion
Burrowing Owl[a]	*Speotyto cunicularia*	0	99	1
Coyote[b]	*Canis latrans*	27	61	12
Feral cat-Kinchenga[c]	*Felis catus*	0	99	1
Feral cat-Highlands[c]	*Felis catus*	0	99	1
Feral cat-Mallee[c]	*Felis catus*	0	98	2
Feral cat[d]	*Felis catus*	0	48	52
Hyenna[e]	*Crocuta crocuta*	0	77	33
Hyenna[f]	*Crocuta crocuta*	0	75	25
Lion[e]	*Pantera leo*	0	91	9
Mountain Lion[g]	*Felis concolor*	0	85	15
Skunk, spring[h]	*Mephitis mephitis*	39	61	0
Skunk, winter[h]	*Mephitis mephitis*	54	30	15

Table 6.1. Source data for relative percent food habits of selected species used to generate Fig. 6.1. Data were collected from papers in which carrion were listed as occurring in diets (e.g., pure predators, scavengers, and herbivores, or those studies not monitoring scavenging were not included). [a]Plumpton and Lutz 1993; [b]Dixon 1925; [c]Jones and Coman 1981; [d]Apps 1983; [e]Houston 1979; [f]Gasaway et al. 1991., [g] Dixon 1982; [h]Godin 1982.

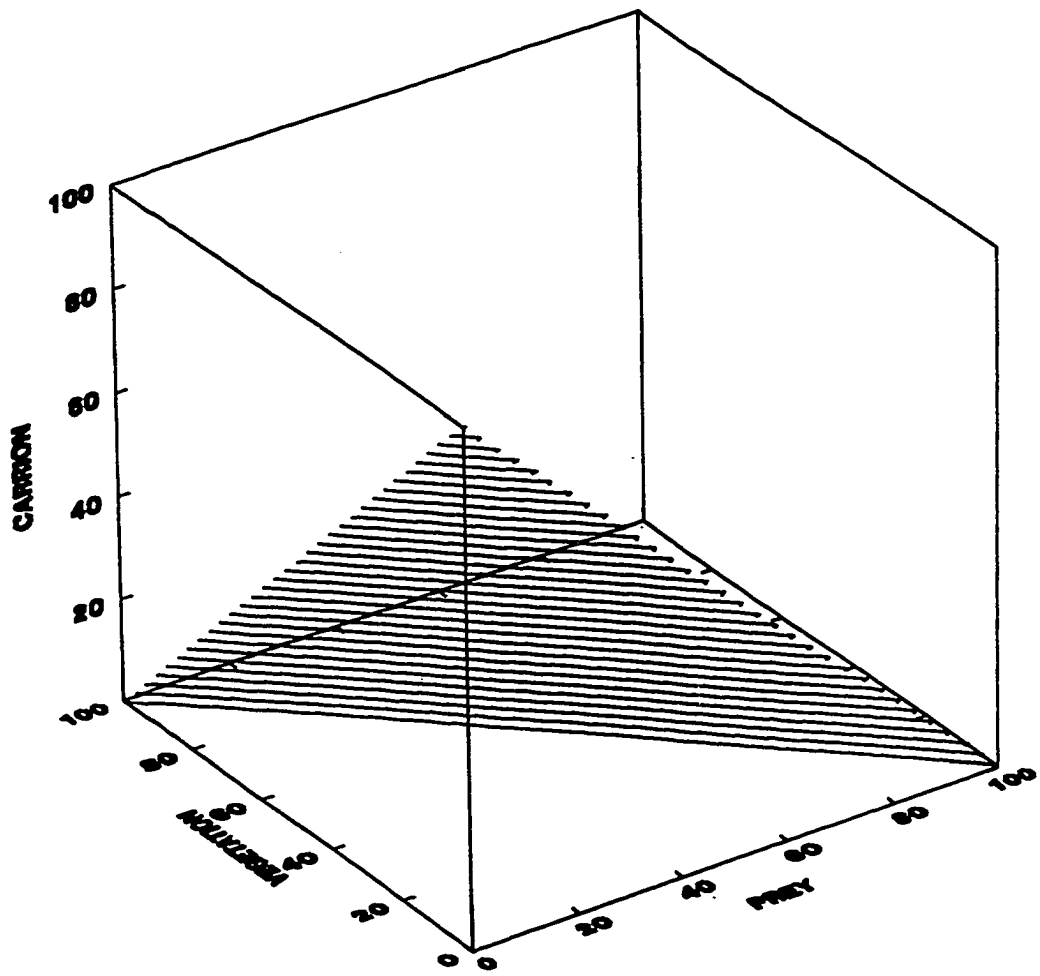

Figure 6.1. Three-dimensional surface formed using percent of diet data from food habits studies (Table 6.1). Vegetation = plant matter, Prey = live prey killed, Carrion = prey scavenged. All animals fall on the continuum of the surface.

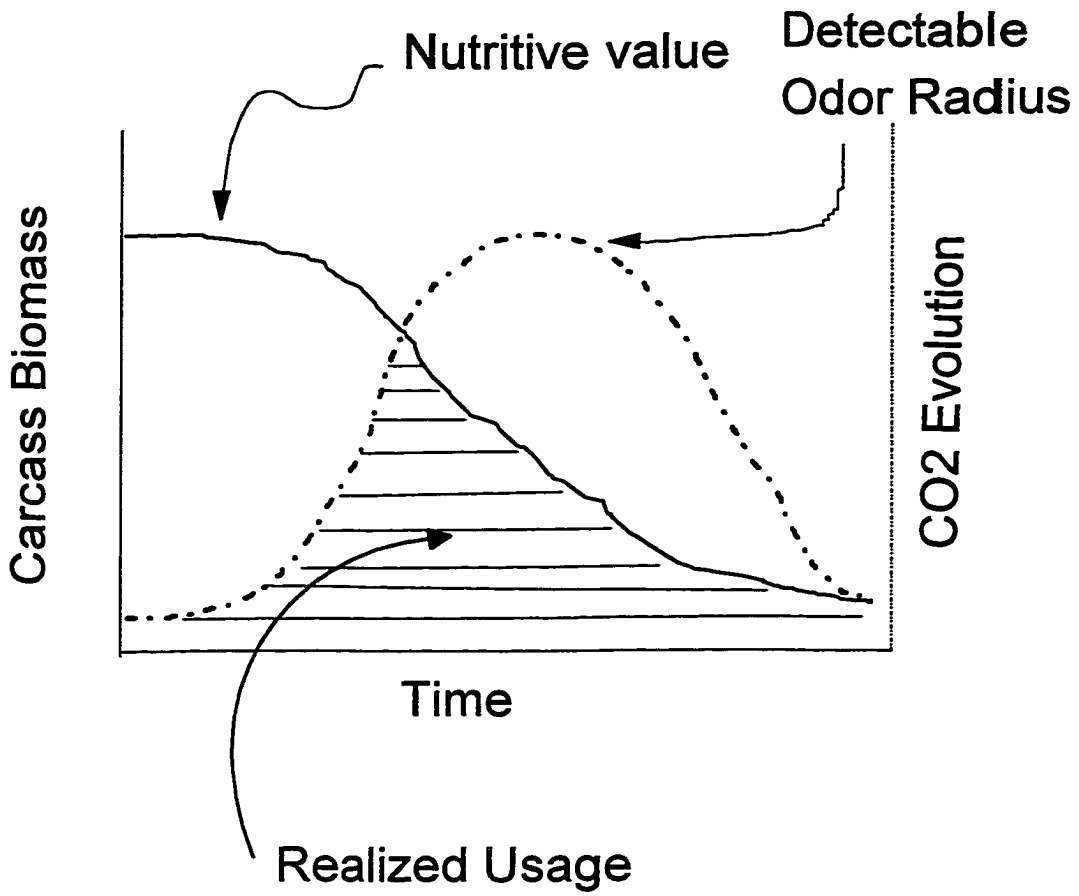

Figure 6.2. Generalized model of proximate environmental factors impinging upon a predator's decision or ability to detect and consume carrion. As time and bacterial and fungal decay progress, the detectability of the carrion presumably increases as odors are increasingly emanated. Concurrently, decay reduces the nutritive value of the carrion while increasing the amount of toxic byproducts of decay. Therefore, attractiveness (i.e., the likelihood of a scavenger detecting and deciding to consume a carrion meal) of carrion will follow a curve shaped by combining odor and nutritive curves.

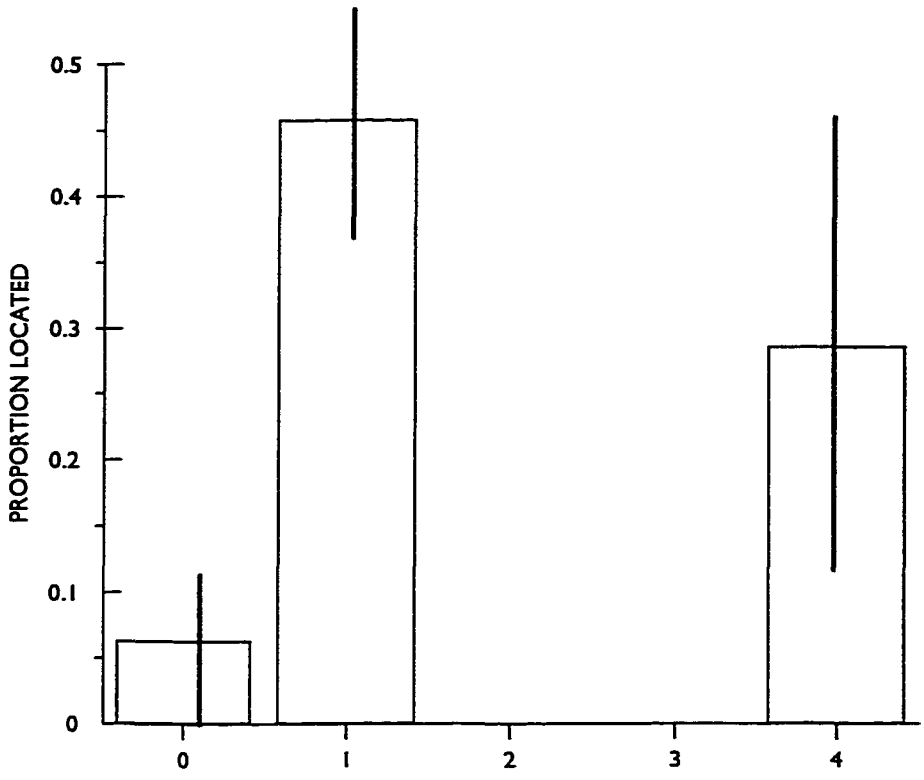

Figure 6.3. Carcass location by turkey vultures (*Cathartes aura*) by carcass age. Location rate begins low, grows higher as the carcass ages and then drops lower as the carcass putrefies. Vultures were less efficient at locating fresh bait than one day old carcasses ($\chi^2 = 7.16$, $P \leq 0.1$) The graph was constructed using data reported by Houston (1986). Bars represent one standard error.

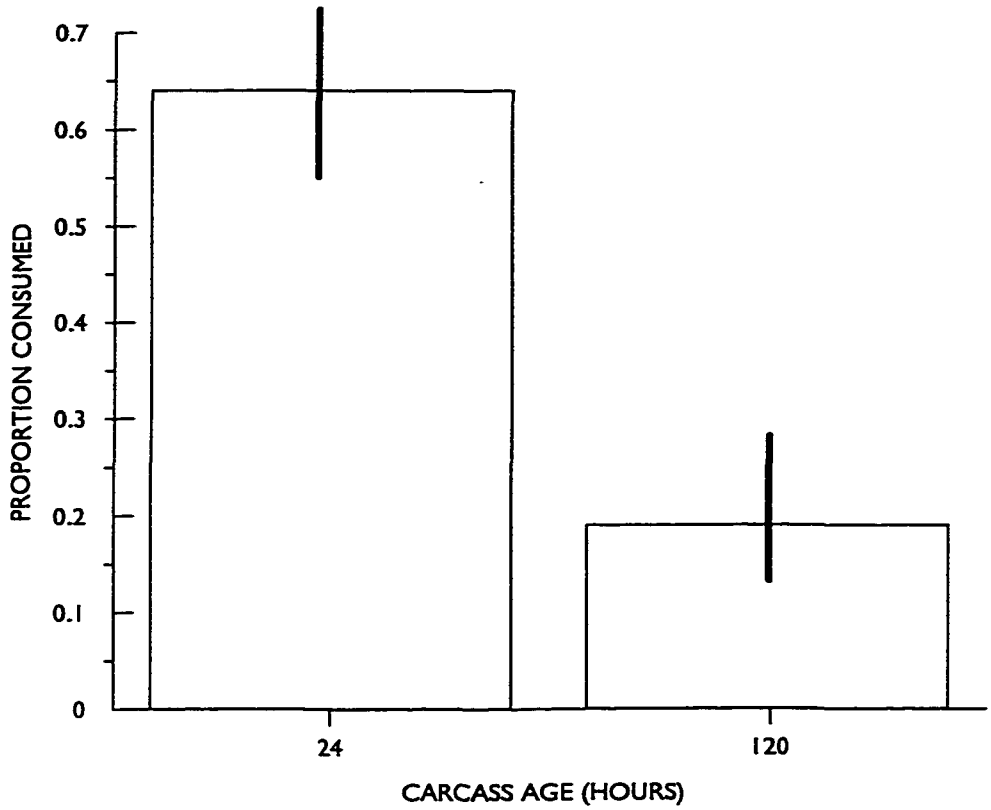

Figure 6.4. Carcass consumption by turkey vultures (*Cathartes aura*) by carcass age. Turkey vultures were given the choice of a 24 h or 120 h old carcass and preferred fresher carcasses to older ones (Mann-Whitney U test, $P < 0.01$). The graph was constructed using data reported by Houston (1986). Bars represent one standard error.

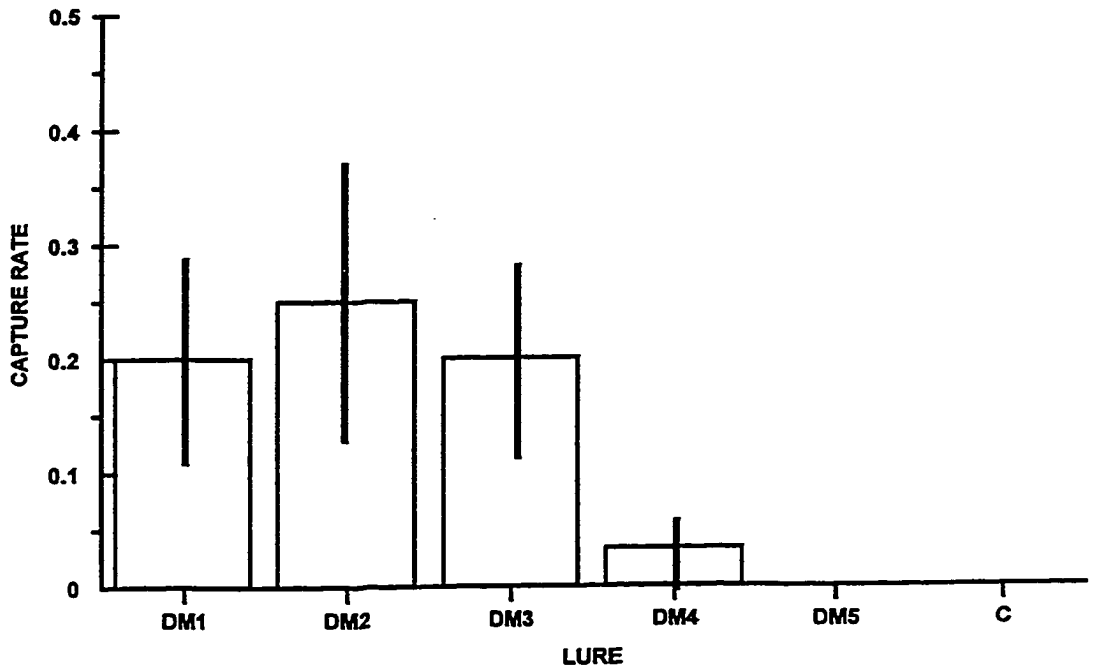

Figure 6.5. Brown tree snake capture rate by age of rotting mice. DM1 = Dead mouse first night, n = 20; DM2 = Dead mouse second night, n = 20; DM3 third night, n = 20; DM4 fourth night, n = 30; DM5 fifth night, n = 20; C = Empty control trap, n = 40.

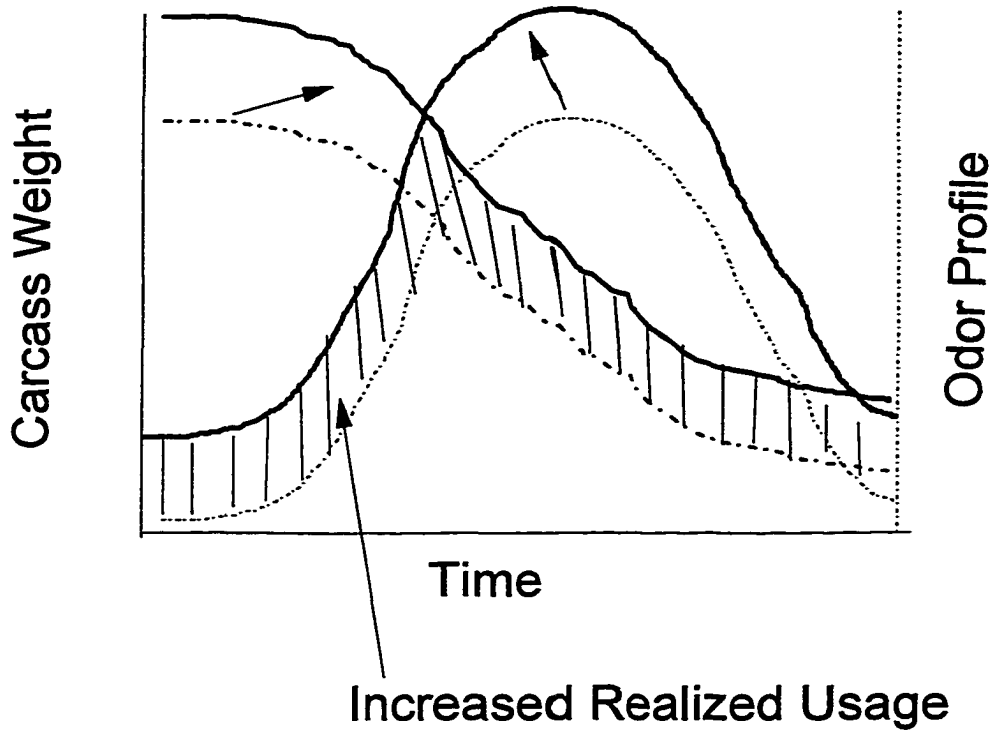

Figure 6.6 Specific adaptations allowing animals to increase efficiency in carrion foraging. The shaded area in the inset is the predicted increased amount of time an animal can efficiently use a carcass by shifting the theoretical curves. Efficiency of carcass use can be increased by shifting the nutritive value curve up and right (e.g., with more efficient digestive enzymes), or by shifting the detectable odor radius curve up and left (e.g. with improved sensory structures). Dotted curves represent the model proposed in Figure 6.2 and solid curves represent adaptations that increase realized carcass usage by an animal.