Seasonal variability in brown tree snake (*Boiga irregularis*) response to lures

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Abstract: In continuing investigations of brown tree snake, *Boiga irregularis*, attraction to carrion odor, we hypothesized that the attractiveness of live or dead and visually apparent or concealed lures varies seasonally. We determined that lure condition (live or dead mouse lures) and sensory cues (visually apparent or concealed lure) interact among wet and dry seasons. Concealed carrion lures were more effective during the dry season than the wet season, but the effectiveness of live mouse lures showed less seasonal variability. We identified weather variables that covary with observed seasonal trends in capture rates and investigated the influence of recent feeding on snake response to lures. Data suggest that live mouse lure capture rates correlate with wind and dead mouse capture rates correlate with rainfall. Recently fed and satiated snakes were not less responsive to lures but were less active than unfed snakes. Snakes held for over 2 years were less responsive than recently captured snakes. More intensive studies will be required to determine cause-and-effect relationships between lure type, seasonality, and snake behavior.

Résumé : Au cours de nos recherches sur l'attirance de la couleuvre *Boiga irregularis* pour les odeurs de charogne, nous avons posé en hypothèse que l'attirance pour des leurres vivants ou morts et des leurres bien visibles ou camouflés varie en fonction de la saison. Nous avons conclu que la condition des leurres (souris vivantes ou mortes) et les déclencheurs sensoriels (leurres apparents ou camouflés) interagissent différemment au cours de la saison sèche et de la saison humide. Les charognes camouflées sont plus efficaces comme leurres au cours de la saison sèche, mais l'efficacité des souris vivantes comme leurres varie moins en fonction de la saison. Nous avons reconnu les variables du climat qui sont en covariation avec les tendances saisonnières des taux de capture et examiné l'influence d'un repas récent sur la réaction des couleuvres à la présence des leurres. Les données indiquent que les taux de capture de souris vivantes sont en corrélation avec le vent et les taux de capture de souris mortes, en corrélation avec les précipitations. Les couleuvres repues ou nourries récemment ne réagissent pas moins à la présence des leurres, mais sont moins actives que les couleuvres à jeun. Les couleuvres gardées pendant plus de 2 ans réagissent moins à la présence des leurres que les couleuvres capturées depuis peu. Il faudra des recherches plus poussées pour pouvoir déterminer les relations de cause à effet entre le type de leurre, la saison et le comportement des couleuvres.

[Traduit par la Rédaction]

Introduction

The brown tree snake (*Boiga irregularis*) is a nocturnal and primarily arboreal rear-fanged colubrid native to parts of Australasia, New Guinea, and the Solomon Islands (Fritts et al. 1987; Savidge 1987; Greene 1989) and was introduced to Guam in the late 1940s or early 1950s (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; Rodda and Fritts 1992). Because the brown tree snake is considered a threat to the economy and biodiversity of other Pacific islands, animal control personnel trap intensively to prevent the spread of the snake (USDA 1996). Live mice are used as lures in traps, and the development of an effective artificial lure for brown tree snakes is necessary because live mice cause logistical and animal care concerns during trapping operations. The primary objective of this study was to elucidate the sensory biology and foraging ecology of brown tree snakes to further the development of effective artificial lures.

The brown tree snake has a catholic diet (Chiszar 1990), and the snake exhibits ontogenetic shifts in diet and a variety of foraging modes (Savidge 1988; Rodda 1992; Shivik and Clark 1999*a*). Brown tree snakes possess Duvernoy's glands but normally kill larger prey mechanically rather than with venom (Rochelle and Kardong 1993). Among appetitive behavior studies, the sensory modalities reported as dominant varies. For example, visual cues alone can elicit attack behavior (Chiszar et al. 1988), and the absence of a salient visual cue lessens brown tree snake interest in chemical cues (Chiszar 1990). In contrast, brown tree snakes will enter traps baited with bird odors more often than empty traps (Fritts et al. 1989), and blind-folded brown tree snakes can efficiently attack and kill prey (Kardong and Smith 1991). Recent evidence highlights the context specificity of brown tree snake foraging behavior: the relative importance of sen-

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sory cues is a function of both the variety and quality of cues presented (Shivik and Clark 1997; Shivik 1998).

Capture rates for brown tree snakes are known to vary spatially (Engeman and Linnell 1998; Engeman et al. 1998), and one purpose of this study was to determine if capture rates from candidate lures vary seasonally. During our ongoing studies, we determined that carrion-like compounds did not attract snakes into traps (Shivik and Clark 1999*b*) and that there was considerable variability in the attraction of brown tree snakes to carrion. For many species, migrational, reproductive, and diel activity varies seasonally and we hypothesized similar seasonal changes in brown tree snake behavior. Therefore, replication of earlier research (Shivik and Clark 1997) was required in the context of seasonal weather patterns.

Methods

Seasonality in lure attractiveness

Hypothesizing a seasonal trend in brown tree snake attraction to carrion-based lures (Shivik 1999), we used and replicated work described in Shivik and Clark (1997). We set traps (Linnell et al. 1998) during 1996 and 1997 to identify components of variability in trapping data. Lures presented were live mice visually apparent (LMV), live mice concealed (LMC), dead mice visually apparent (DMV), and dead mice concealed (DMC). Live mouse and dead mouse treatments consisted of mouse lures in hardware cloth containers within traps; LMC and DMC lures were constructed using lure holders wrapped with black felt so that mouse-lure odors could permeate the fabric, but no mouse visual cue was apparent. Traps were set at Tarague Beach and in the Conventional Weapons Storage Area (Andersen Air Force Base, Guam) during April and August of 1996 and April and August of 1997. Ten traps per treatment were set for 2 nights on three trap lines in April 1996, four trap lines in August 1996, four trap lines in April 1997, and five trap lines August 1998. We examined the difference in capture rate by lure condition, sensory modality, and season using the trap line as the experimental unit. Because traps were set in the same location for 2 nights and multiple snakes could be captured in each trap, the trap location was used as the sample unit. Each trap's nightly captures were collapsed to produce the mean nightly capture rate for that location. Capture rate per trap line was the mean number of snakes captured per trap night in each trap location on a given trap line. We used a mixed-effects analysis of variance (ANOVA) and included the effects lure condition (live or dead mouse), sensory modality (visual or concealed), and season (wet or dry, which correspond with north-temperate autumn and spring months, respectively), and the accompanying interaction terms. Trap line nested within season was used as the random effect error term in the model. Analyses were performed using PROC MIXED (SAS Institute Inc. 1985). The methods for all studies were approved within protocols submitted to both the National Wildlife Research Center and Colorado State University Animal Care and Use Committees and followed the guidelines put forth by the Canadian Council on Animal Care.

Weather factors

There are no extreme seasonal trends in temperature on Guam (temperatures vary more during a 24-h period than during the year), but 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 peak in February and drop during August (Karolle 1993). Climatic variation such as wind and rain within discernable wet and dry seasons on Guam are likely to influence many aspects of brown tree snake behavior, and we designed a study to detect seasonal trends in capture rate for live and carrion lures.

We hypothesized that weather variables could influence capture rates. For example, rain may have a rinsing effect, essentially washing odors from the air around traps, making lure detection radii smaller. Additionally, winds can disperse odors quickly, resulting in a reduction in the effective odor radii. Weather data were obtained from Andersen Air Force Base, Guam, where trapping was performed. Extreme observations taken during weather patterns influenced by tropical depressions (mean rainfall >2.54 cm in 24 h, three trap lines) were not included in the analyses. We regressed mean rainfall for the 48-h period that each trap line was set and the mean maximum wind speed for the same 2 days against capture rate from live or dead and visually apparent or concealed lures using simple linear regression.

Seasonality in snake satiety

Brown tree snake activity appears to change seasonally on Guam (Rodda et al. 1999) as does prey availability (E. Campbell, personal communication, National Wildlife Research Center, Hilo, Hawai'i). We hypothesized that lure attractiveness could vary as result of seasonal changes in prey availability or vulnerability. If, during the wet season, lizards and lizard eggs are more available to foraging snakes, the resulting well-fed snakes may be less apt to investigate prey-based lures.

Tests were performed in the laboratory at Fort Collins and also replicated on Guam. We performed two studies of snake behavior to determine if recent feeding and lure type influenced snake orienting behaviors. In both studies, we 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). If a snake was not active (i.e., visibly awake) for more than 300 s during a trial, the snake was considered a nonresponder and the trial was not used in analyses. We used a two-way ANOVA to look for an effect of recent feeding (fed or unfed groups) on snake interest (i.e., proportion of time probing at, moving toward, and otherwise orienting to the lure) in lures (LMV, LMC, DMV, DMC).

In Fort Collins, 16 snakes that had been held in captivity for >3 years were tested. Snakes were held under conditions simulating ambient temperatures on Guam and given water ad libitum. Snake chambers and methods of observation were identical to those in previous studies using the same snakes (Shivik 1998). Throughout the tests, snakes remained in their cage, and we placed a $15 \times 15 \times 15$ cm acrylic treatment box (with only one transparent side) on each snake's cage during the reduced light conditions (a 25-W bulb) of the night cycle. We 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 two groups: unfed (>2 weeks since feeding) or fed (<7 days since feeding). Snakes were tested by placing mice lures in the acrylic treatment box and placing the box on the snake's cage. For concealed 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 moistened watch glass for >24 h before testing. All snakes received each combination of treatment and satiety categories in a Latin-square arrangement, but a >3 week washout 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 with those of wild-caught snakes, and the low number of snakes in Fort Collins required repeated testing of individual snakes. Therefore, we repeated the satiety effect experiment described above, this time using snakes recently captured on Guam and feeding the snakes to satiety. Snakes were captured in standard traps and randomly assigned to fed or unfed groups and treatments

Table 1. ANOVA table of capture rate per trap line by lure condition (live mouse or dead mouse), modality (visually apparent or concealed), and season (wet or dry) from data collected during 1996 and 1997 from Andersen Air Force Base, Guam.

Source	df	Type III F ratio	P
Season	1	9.84	0.0073
Lure condition	1	0.49	0.4847
Modality	1	48.49	0.0001
Season × lure	1	9.01	0.0028
Modality × lure	1	5.95	0.0150
Season × year	1	1.66	0.1980
Season × modality × lure	1	0.27	0.6026

of LMV, LMC, DMV, or DMC. All snakes were allowed to acclimate in their cages (33 × 24 × 24 cm tubs) for >5 days before testing. Snakes assigned to the Fed group were given one frozen immature mouse (mean mass, 5.1 g) nightly until each snake refused to take additional mice, and snakes that never fed were not used in experiments. Trials were run by placing a mouse lure into a hardware cloth lure container (7 × 7 × 20 cm box), putting the lure container into the snake's cage, covering the snake cage with a clear plastic cover, and then video taping snake behavior for 1 h. Concealed treatments were formed by wrapping lure holders with cloth such that odors could permeate, but mice were not visible.

Results

Seasonality in lure attractiveness

Based on the ANOVA of trap success data from Guam, there are strong interactions between the lure condition and season, and the lure condition and sensory modality (Table 1, Fig. 1). Seasonal trap success was lower during the wet season than during the dry season, especially for concealed and dead mouse lures, but the seasonal differences were not as extreme with live mouse lures (Fig. 1).

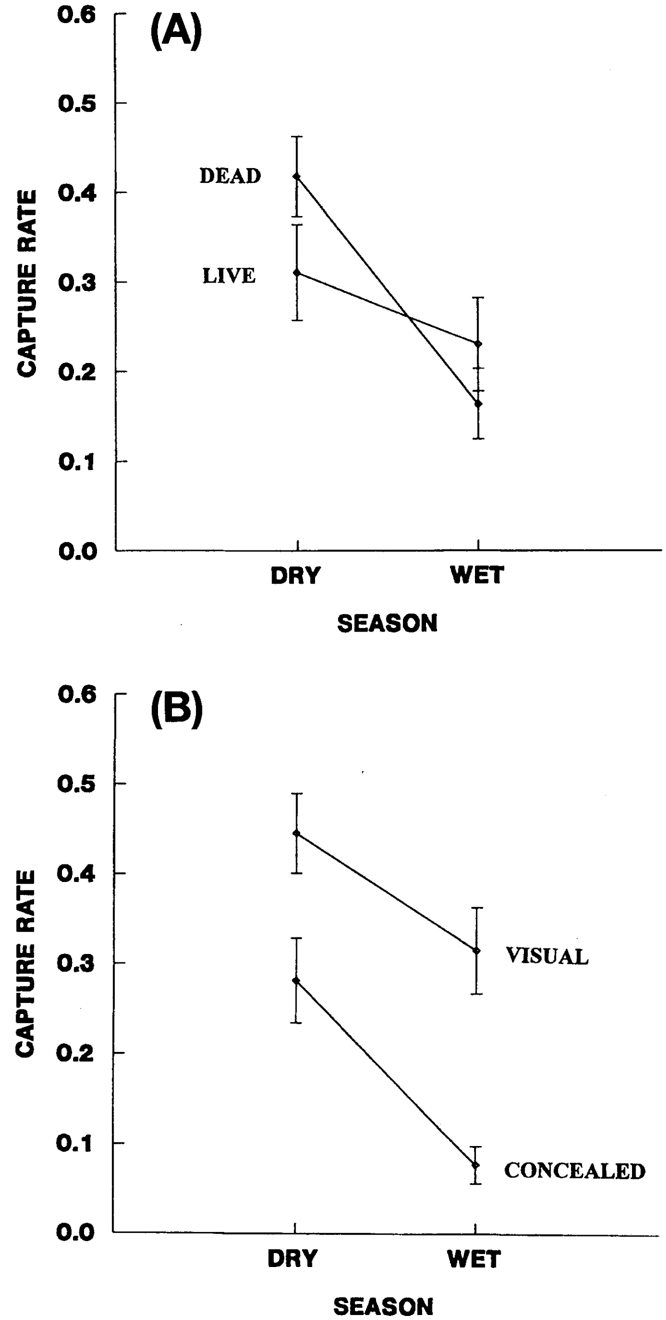
Weather factors

We examined environmental factors for correlations with brown tree snake capture rates as a means of explaining the observed interaction between season and lure type. Wind speed did not correlate with dead or concealed lures, but wind was correlated with capture rates using live and visually apparent lures. Rainfall did not correlate with live lures, but correlation with dead and both visually apparent and concealed lures was evident (Table 2) during the 2 years of trapping. The observed seasonal interaction is not explained by the correlation between wind and rainfall for these data (R^2 = 0.06, P = 0.44).

Seasonality in snake satiety

Laboratory experiments in Fort Collins were terminated before the study was completed because of the large number of nonresponding snakes and inadequate statistical power given foreseeable sample sizes. One hundred and 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 eight, except for fed DMV, fed DMC, and fed LMV, which had sample sizes of seven. Of the trials that were scored, no treatment effect was observed

Fig. 1. Interaction plots for replications of trapping using live and dead prey that were visually apparent or concealed. All trapping was performed during (A) April 1996 and 1997 (dry season) and (B) August 1996 and 1997 (wet season) on Guam. Capture rate represents the mean number of brown tree snakes captured/trap night and the error bars represent 1 SE.



by lure type ($F_{[3,54]}$ = 0.9503, P = 0.423) or feeding status ($F_{[1,54]}$ = 0.657, P = 0.421), and there was no significant interaction between these effects ($F_{[3,54]}$ = 0.897, P = 0.449, Fig. 2).

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 five snakes. We detected a difference in the proportion of time

Table 2. Regressions of mean maximum wind speed and mean rainfall against capture rates of brown tree snakes on Guam.

	R^2	P
Wind		
Live	0.191	0.026
Dead	0.024	0.451
Visual	0.167	0.038
Concealed	0.069	0.194
Rainfall		
Live	0.024	0.452
Dead	0.258	0.008*
Visual	0.151	0.050
Concealed	0.146	0.054

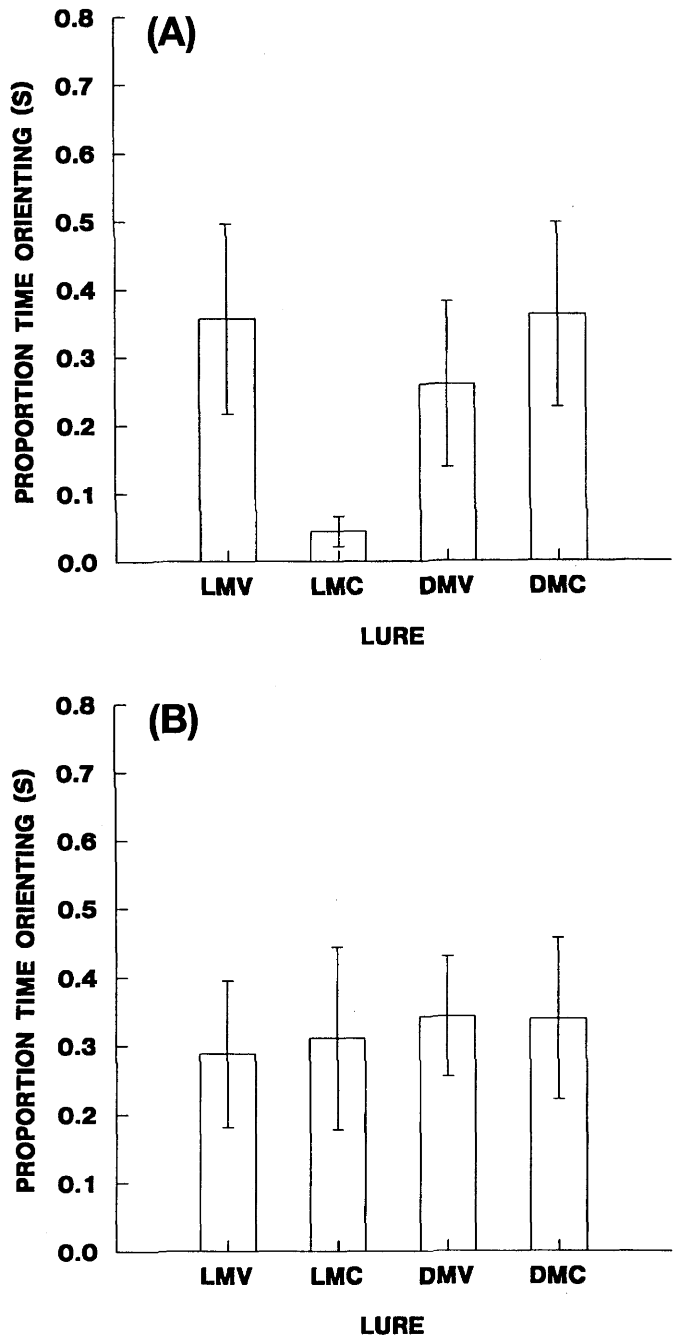
Note: Four lure types were regressed with two weather variables. Live, live mouse lure; dead, dead mouse lure; visual, visually apparent lure; concealed, visually concealed lure. n = 26 for each regression.
*Significant at α = 0.05, with a Bonferroni adjustment.

that the snakes spent orienting toward various lure types ($F_{[3,32]}$ = 12.03, P < 0.001, Fig. 3), but did not detect a significant interaction between feeding status and lure type ($F_{[3,32]}$ = 0.006, P = 0.992). Thus, satiety levels did not appear to affect attentiveness to prey.

An ancillary post hoc analysis of these data was suggested after noting apparent trends and evidence for interactions between lure condition and sensory modality (Fig. 3, fed group). We performed a two-way ANOVA of snake response to lure condition and sensory modality (similar to analyses of the capture rate data) to determine if laboratory results showed interactions between lure condition and sensory modality as indicated by field observations. Long-term captive snakes did not show differences between live and dead lures ($F_{[1,57]}$ = 0.986, P = 0.325) or visually apparent and concealed lures ($F_{[1,57]}$ = 0.373, P = 0.544), and an interaction between lure condition and sensory modality was not detected ($F_{[1,57]}$ = 1.415, P = 0.239). Short-term captive snakes, however, did exhibit responses similar to those indicated by field data. Differences between live and dead lures were detected ($F_{[1,36]}$ = 17.069, P < 0.001), as were differences between visually apparent and concealed lures ($F_{[1,36]}$ = 14.862, P < 0.001), but these results must be interpreted while acknowledging the interaction between lure condition and sensory modality ($F_{[1,36]}$ = 6.049, P = 0.019).

We further examined the data for differences in snake activity (using active time, i.e., obviously awake and moving, as the dependent variable). Long-term captive snakes in Fort Collins showed little difference in mean total activity based on feeding condition (fed = 1315 s, 37% of trial duration; unfed = 1367 s, 38% of trial duration; P = 0.844). For short-term captive snakes on Guam, however, unfed snakes were more active in trials than the fed snakes ($F_{[1,32]}$ = 7.02, P = 0.01, Fig. 4). 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).

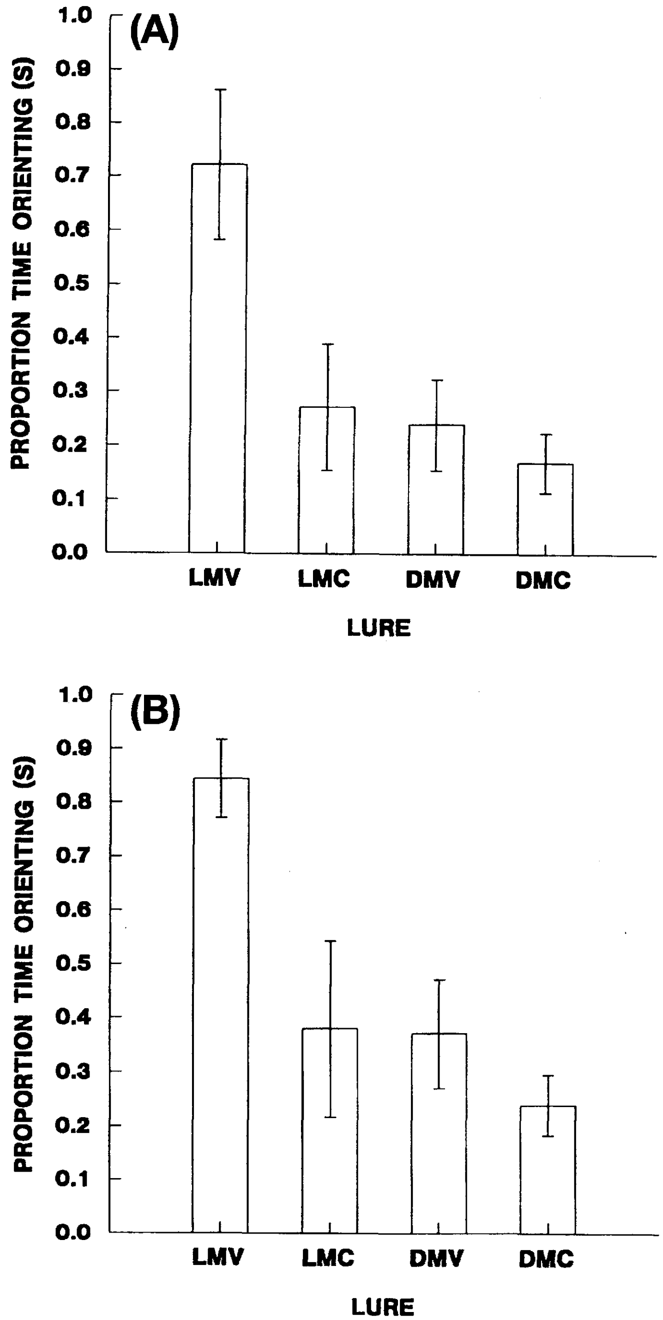
Fig. 2. Long-term captive brown tree snake (held in captivity >3 years) response to lures, measuring the proportion of time an active snake oriented toward a lure type. (A) Snakes recently fed (<7 days). (B) Snakes not recently fed (>14 days). LMV, live mouse visually apparent; LMC, live mouse concealed; DMV, dead mouse visually apparent; DMC, dead mouse concealed. Error bars represent 1 SE.



Discussion

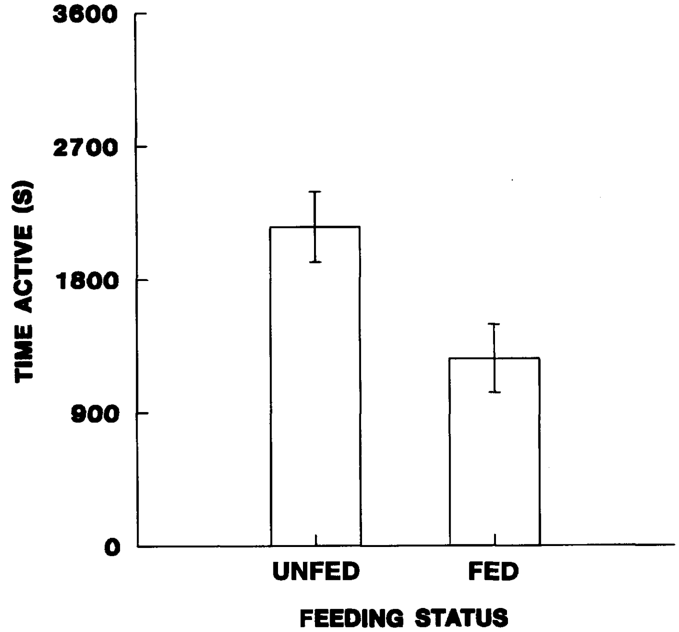
The above results suggest a seasonal component in the feeding ecology of brown tree snakes. In particular, carrion was more attractive during the dry season (Fig. 1). The seasonal trends may have resulted from changes in brown tree snake populations in the areas studied due to removal of snakes (all snakes were removed from the population after capture), or from changes in the demographics of the sampled population (Shivik and Clark 1999*a*). Some seasonality in trapping can be accounted for because brown tree snakes

Fig. 3. Short-term captive brown tree snake (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). (A) Snakes fed to satiety. (B) Snakes not fed within 5 days. LMV, live mouse visually apparent; LMC, live mouse concealed; DMV, dead mouse visually apparent; DMC, dead mouse concealed. Error bars represent 1 SE.



are more active during wet periods (Rodda et al. 1999). However, because the capture rate using live mice remained relatively constant through both seasons, we do not attribute fluctuations in capture rates using dead mouse lures to differences in local brown tree snake population sizes or movement patterns (i.e., live mice act as a positive control for these comparisons).

Fig. 4. Activity of short-term held captive brown tree snakes by feeding status. "Unfed" denotes not fed within 5 days and "fed" denotes fed to satiety. Error bars represent 1 SE.



As in previous work, we conclude that the relative importance of sensory cues to foraging brown tree snakes is doubly context specific (Shivik and Clark 1997). That is, the relative importance of visual and odor cues depends upon not only the sensory cues that are presented simultaneously but on the quality or condition of the lure (i.e., live versus dead). Our current results differ from previous results (Shivik and Clark 1997) in that the observed phenomenon is more complex than its initial appearance. We modify earlier conclusions and now conclude that the relative effectiveness of dead lure varies widely, with correspondence to a seasonal trend.

The mechanism responsible for the observed interactions is difficult to identify, and begs the question of why the dead mouse capture rate correlates with rainy weather. The results are interesting, but correlative, and other factors are likely to be responsible for the trends. For example, rainfall may cause changes in invertebrate decomposer populations. The rate and quality of decomposition is dependent upon the activity of invertebrate decomposers (Putman 1983). Because odor is important for stimulating brown tree snake response to carrion, any changes in the decomposition process could profoundly affect capture rates with carrion lures. Minor changes in the by-products of decomposition may alter the attractiveness of the rotting mice to brown tree snakes. Also, 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. A more extensive investigation of these working hypotheses would be useful because this study was correlative and the results are less certain when analyses are corrected using an overall alpha rate, but there does appear to be a link between weather factors and the attractiveness of dead mouse lures.

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, but would increase mouse vibration and movement, which may attract snakes (Shivik 1999). The importance of vibration as a lure for brown tree snakes should be more thoroughly investigated.

Prey populations could fluctuate and alter the satiety of snakes, but based on our satiety experiments, this mechanism as a complete explanation for seasonal variation in brown tree snake 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 tree snakes are more active than satiated snakes, and it would be useful to test movement patterns of recently fed or unfed snakes in a field environment. Finally, recently captured snakes respond to lures more than long-term captive snakes and they also respond to lures similarly to wild snakes. Researchers should be aware that studies of brown tree snake behavior are likely to be influenced by the duration of captivity and the level of snake satiety.

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