

PREY PREFERENCES AND PREY ACCEPTANCE IN JUVENILE BROWN TREESNAKES (*BOIGA IRREGULARIS*)

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Abstract.—On the Pacific island of Guam, control of the invasive Brown Treesnake (*Boiga irregularis*) relies largely on methods that use mice as bait. Juvenile *B. irregularis* feed primarily on lizards and their eggs, but little is known about their prey preference. We conducted an experiment to investigate preferences for, and acceptance of, dead geckos, skinks, and neonatal mice, in juvenile *B. irregularis* ranging from 290 mm to ca. 700 mm snout-vent length (SVL). Snakes of all sizes showed a preference for geckos over skinks and neonatal mice. Geckos were the first prey chosen in 87% of 224 initial trials (56 snakes subjected to four trials each; 33% would be expected from a random choice). The smallest snakes had the most pronounced preference. Although many of the snakes accepted neonatal mice and/or skinks, some snakes of all sizes were reluctant to feed on anything but geckos, especially when well fed. We also addressed the hypothesis that repeated encounters with a particular prey type increase a snake's preference for that prey. Our study does not support this hypothesis. Our results suggest that control methods relying solely on rodent bait may be inefficient for targeting snakes < 700 mm SVL and that individual heterogeneity in prey preference may cause a significant part of this juvenile cohort to be completely refractory to capture with rodent bait, even if the bait is dead and small enough to be readily swallowed.

Key Words.—*Boiga irregularis*; Brown Treesnake; *Carlia aylanpalai*; *Hemidactylus frenatus*; *Mus musculus*; prey acceptance; prey preference.

INTRODUCTION

Since the accidental introduction of the Brown Treesnake (*Boiga irregularis*) to the island of Guam about 1950, this nocturnal, semi-arboreal colubrid has had vast negative effects on the island biota (Savidge 1987; Wiles 1987; Rodda et al. 1997; Fritts and Rodda 1998) and has caused substantial revenue loss due to snake-caused power outages (Fritts 2002). Because the density of Brown Treesnakes on Guam is high (Rodda et al. 1999b) and the island is a transportation hub for much of the western Pacific, there is a risk of snakes from Guam establishing populations on other islands. Indeed, reports of Brown Treesnakes occur on several other neighboring Pacific islands; probably from snakes being transported in cargo and vessels from Guam (Fritts 1987; McCoid and Stinson 1991; Fritts et al. 1999; Kraus and Cravalho 2001; Stanford and Rodda 2007).

During the last two decades, much effort was allocated to investigating ways to reduce risk of snakes departing Guam. Preventive efforts include snake-proof barriers around sensitive areas, canine teams trained to detect snakes in outbound cargo, visual searches for snakes on fence lines surrounding airports and harbors, and an extensive snake trapping program around ports and cargo holding areas (Engeman and Vice 2001). With the registration of acetaminophen as an oral

toxicant for Brown Treesnake control on Guam (US EPA Reg. No. 56228-34), there is renewed hope that large scale eradication or severe island-wide suppression may one day be possible (see Savarie et al. 2001). Recent work by the US Department of Agriculture has focused on distributing the toxicant in dead mice delivered either from bait stations or by aerial drops (Savarie et al. 2007).

Most snakes intercepted in and around cargo facilities and ports in Guam have been captured in traps that use live mice as bait (Engeman and Vice 2001). However, the traps used for operational control are inefficient for catching snakes < 700 mm snout-vent length (SVL) and only partially effective for snakes 700–850 mm SVL (Rodda et al. 1999c, 2007; Rodda and Dean-Bradley 2004). Additionally, the Brown Treesnake population on Guam exhibits an unusually large proportion of juveniles (Rodda et al. 1999b), many of which are smaller than the 700 mm SVL trapping threshold. Hence, there is particular risk of these small snakes evading capture and transportation to other islands (Vice and Vice 2004).

Although reducing snake densities on Guam may reduce risk of snakes being transported to other islands, complete eradication requires that every individual in the focal population is targeted at some point during its lifetime. Moreover, it would be advantageous if snakes

could be targeted before reaching sexual maturity and reproducing. This calls for identifying an attractant that targets the widest possible size range of snakes and effectively attracts a large proportion of the individuals within the size class(es) it is designed to target.

Based on stomach content analyses, Savidge (1988) concluded that Brown Treesnakes < 700 mm SVL ate primarily lizards and lizard eggs, and similar data were given by Rodda et al. (1999b). Stomach content analyses, however, are biased towards what prey is available, and Brown Treesnakes are often considered very catholic feeders (Savidge 1988). Most native forest birds were already extinct in Guam by the mid 1980's (Savidge 1987) and small mammal densities in Guam are currently lower than on nearby islands (Wiewel et al. 2009). It seems likely that the diet of juvenile snakes today is largely limited to geckos and skinks (see Fig. 2.9 in Rodda et al. 1999c), with the possible addition of recently introduced frogs (Christy et al. 2007). However, the extent to which juvenile snakes will prey on small rodent bait, such as dead neonatal mice, remains unknown. Ontogenetic shifts in prey preference and prey acceptance in small (< 700 mm SVL) Brown Treesnakes have not been studied in detail (but see Qualls and Hackman 2004). We therefore conducted a controlled experiment to address the following four questions: (1) Which prey is preferred by juvenile Brown Treesnakes of different sizes?; (2) Will all snakes accept non-preferred prey, or could some individuals be completely refractory to capture with some potential prey types at certain snake body sizes?; (3) Does snake hunger level affect acceptance of non-preferred prey?; and (4) Does previous experience with a particular prey type make them more inclined to accept that prey (cf. Burghardt 1992)? The latter could have implications for bait effectiveness and control opportunities on islands that differ in prey community composition.

MATERIALS AND METHODS

Snakes, cages, and monitoring equipment.—We collected snakes by hand at night from forested areas of northern Guam. We measured snout-vent length (SVL) to the nearest mm by gently stretching snakes along a measuring tape, at the beginning and end (when a snake had completed all trials ≥ 18 weeks later) of the experiment. At the beginning of the study, snakes ranged from 290 mm to 702 mm SVL, with a mean SVL of 551 mm (SD = 102 mm).

We housed the snakes in a room with a clock-shifted 12:12 h light cycle at ambient temperature (27.4–29.5°C), which is similar to year-round outdoor temperatures in Guam. They were kept individually in 21-l (5 gallon) plastic buckets (diameter 255–290 mm, height 360 mm), with four ventilation holes covered with



FIGURE 1. Partial view of the experimental setup to test food preference in Brown Treesnakes (*Boiga irregularis*). The prey presentation dishes are not yet attached inside the buckets, but are sitting on top of the glass lids. When this photo was taken, most snakes were in the experimental T1 phase when each snake was offered three prey types simultaneously.

aluminum screen (total area 0.01 m²) near the bottom of the bucket. We presented prey on plastic Petri dish lids (diameter 146 mm) fitted with three rigid metal wires that latched onto short sections of plastic hose that we had attached to the wall of the bucket, 50 mm from the rim. To make prey items more visible when the entire set-up (Fig. 1) was filmed with surveillance cameras, we painted the dishes white. Square pieces of glass served as bucket lids. Each bucket was lined with paper and furnished with a water bowl that doubled as a hide box. A twig was provided for climbing opportunity and as a shedding aid. We misted the cages with water two to three times per week and cleaned the day before a weekly trial and when deemed necessary. We recorded trials in infrared light with ceiling-mounted surveillance cameras. Each camera monitored no more than a block of 4×3 buckets.

Test schedule and procedures.—We collected and incorporated snakes into the experiment from 22 August to 20 November 2007. A snake was allowed to acclimate to captive conditions for 7–13 days before its first trial. To test for food preference, we ran four consecutive trials one week apart (denoted the T1 phase, with trials T1-1 through T1-4). In each trial the snake was offered three prey items simultaneously presented on a dish: a Common House Gecko (*Hemidactylus frenatus*), a Curious Skink (*Carlia aylanpalai*), and a neonatal lab mouse (*Mus musculus*). All prey items were offered dead, so prey behavior had no effect on trial outcome. We collected geckos and skinks by hand on Guam (where these non-native species are abundant), killed them by CO₂ inhalation, wrapped them in plastic film, placed them in air-tight plastic containers, and

stored them at -18°C . Mice were provided by a commercial breeder (FrozenRodent.com; Blum, Texas, USA), already vacuum-packed and frozen. All prey handling by investigators was conducted so that cross contamination of scent from one prey type to another was avoided. We tried to size-match the three prey items offered to a snake, so that prey scent rather than prey size would be the basis for choice. We also tried to offer prey groups of suitable size to the different snakes tested, so that larger snakes were offered larger prey items than were smaller snakes. These efforts were to some extent limited by the size variation of prey we had available. There is also the question of the metric a snake might use when evaluating prey size (i.e., length, diameter, volume, mass, etc.). For a gape-limited predator such as a snake, prey diameter is probably a relevant metric. We therefore tried to match prey items by body diameter for the skinks and mice, while using head width for geckos (unlike skinks and mice, geckos often had heads that were wider than the body). Calipers were used to measure prey to the nearest 0.1 mm, and we recorded the mass (to 0.1 g precision) of every prey item offered to the snakes. Based on 478 prey trio offerings, mice were slightly wider than geckos and skinks (mean difference \pm SD across all pairwise comparisons: $8.9 \pm 9.5\%$ and $9.1 \pm 13.1\%$ wider, respectively); whereas, geckos were only marginally wider than skinks ($0.5 \pm 10.7\%$). Although mice were wider than lizards, their short body length made them lighter in weight than both skinks and geckos ($54 \pm 15\%$ and $78 \pm 18\%$ of the respective lizard weights).

On days of trials, we size-matched prey items as described above while they were still frozen, and then allowed them to thaw at room temperature for 1–2 h. Before the lights in the snake room switched off at noon we misted the buckets lightly with water and suspended prey dishes from the hose sections attached to the bucket walls. We then turned on the cameras and switched off the lights. After two hours the trial was terminated. We entered the room, turned on the lights and recorded which prey items each snake had consumed, after which we removed the dishes. Afterwards, we turned off the lights and re-activated the light cycle timer. We recorded the order that each snake consumed the different prey.

After a snake had been subjected to four of the above multiple-prey offer trials, it entered what we call the ‘forced diet phase.’ During this phase, a snake was offered only one particular prey type (skinks, geckos, or mice) for 10 consecutive weekly meals, denoted F1 – F10. Five snakes were subjected to nine such meals due to scheduling errors, and one died after the F4 trial. We tried to generate groups of snakes with comparable size distributions across the three treatment groups. This was done at the time snakes were brought to the lab, before we knew snakes’ individual prey preferences. Snakes

assigned to the mouse treatment group had a mean \pm SD SVL of 547 ± 103 mm (range 330–692 mm); the corresponding sizes for snakes in the gecko and skink groups were 569 ± 101 mm (range 387–702 mm) and 537 ± 104 mm (range 290–690 mm), respectively. The F phase served two purposes. First, we wanted to investigate how prior feeding experience might affect prey preference. By forcing snakes to eat just one prey type, which might in some cases not be a preferred type, and then repeating the preference trials, we might tell if their preference shifted towards the prey type that was recently offered. Second, the forced diet phase could tell us if a snake’s repeated refusal of a particular prey during the initial preference trials was a ‘hard’ or a ‘soft’ refusal. Hard refusals were when a snake did not consider the item offered as potential prey, regardless of how hungry it was. A soft refusal could occur when the snake was not very hungry, such as after having eaten one or two prey items of a preferred prey type. From the initial preference trials, it was difficult to judge if refusals were soft or hard. This was particularly true for the smallest snakes, as these snakes frequently became satiated before consuming all of the prey offered. The forced diet phase allowed us to evaluate this question by forcing all snakes to choose between going hungry or eating a less preferred prey type (cf. Cueto et al. 2001).

The majority of snakes readily ate the sole prey item assigned to them during the forced diet phase. The few that repeatedly refused to eat were eventually force-fed prey of the assigned type by holding the rear of the snake’s head with three fingers and persuading the snake to bite the prey item, presented with forceps. The prey was then slowly and gently pushed into the mouth. Once the prey item was far enough for the snake to close the mouth, we gently massaged the prey down the throat. Because food refusal might have been related to ecdysis cycles, or simply because the snake was not yet hungry enough to consider less preferred prey, we allowed a snake two attempts of the F1 trial before force-feeding. Two attempts were also allowed for the F2 trial, but we did not want to starve the snakes and only allowed one attempt for the F3 to F10 trials. The exception to the latter rule was when a snake had eaten the prey on a previous F-trial as an occasional refusal could be due to ecdysis. These snakes, too, were given a second chance on the F-trial in question before being force-fed. Once a snake had been force-fed, it was considered to have completed the F-trial in question, and thus moved one step forward in the test schedule. Skipped meals that did not require force-feeding did not move snakes forward in the test schedule. The forced diet phase was followed by one more bout of preference trials, denoted the T2 phase. The procedure for the T2 phase was identical to the first bout of four trials per snake.

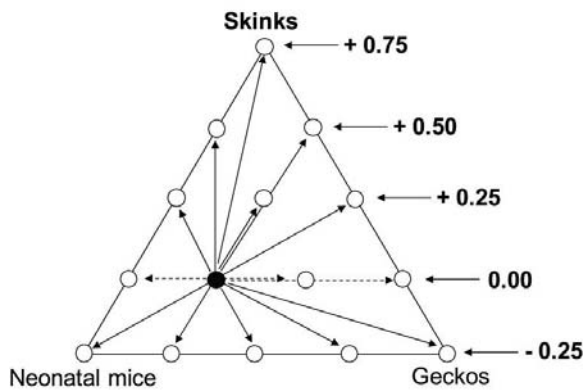


FIGURE 2. Scoring changes in Brown Treesnake prey preference after the forced diet phase. For the snake in the example shown here, the first prey taken during each of the initial four trials was a gecko (once), a skink (once), and a mouse (twice). The mean preference for the T1 trial phase is therefore as indicated by the black symbol. We offered this snake nothing but skinks for 10 feeding events. Arrows and empty symbols show the potential changes in preference registered during the following T2 phase (i.e., another four preference trials). The numbers on the right side of the diagram indicate the stepwise increase, decrease, or lack of change because this snake was ‘trained’ on skinks the stepwise increase, decrease, or no change in preference for skinks.

Analysis.—We used multinomial logistic regression to model the ontogeny of prey preference. Preference was scored by the food items first chosen by a snake during its four T1 trials. We used a cluster specification in software LIMDEP v. 9.0 (Econometric Software, Inc., Plainview, New York, USA) to correct standard errors and *P*-values for the repeated measures conducted on individual snakes. The number of observations was constant across clusters (i.e., snakes) and the effect sizes were not affected by this correction. Mice were used as a baseline against which we contrasted the functions for skinks and geckos. Following the methods of Agresti (2002), we then used the effect estimates obtained to plot the preference probabilities for the three prey categories as functions of SVL.

Prey acceptance was judged by prey consumption histories during the T1 and F trial phases. For descriptive purposes, we grouped snakes in three categories, showing different degrees of reluctance to accept a particular prey: snakes that refused a prey type only when the other two prey types were present; those that also refused it when it was the sole prey offered; and those that still refused it (on a majority of the occasions it was offered) after having been force fed that prey on > 2 occasions.

To analyze if the forced food treatments caused snakes to shift preference towards the prey type to which they had recently been confined, we plotted mean preference for first prey taken during the first four preference trials (i.e., the T1 phase) in a triangular diagram (Fig. 2, solid black circle). We then plotted the corresponding

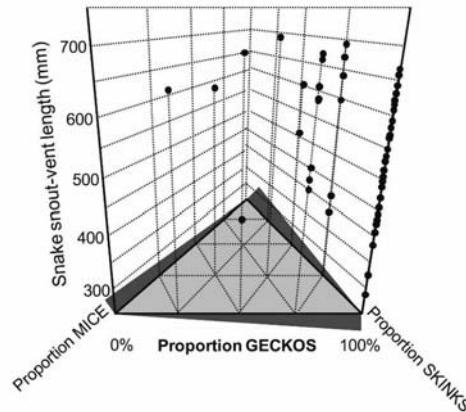


FIGURE 3. Triangular diagram showing, for each Brown Treesnake, what proportion of trials ($N = 4$ per snake; the T1 phase of the experiment) different bait types were chosen first, in relation to snake length. The front axis shows the proportion geckos taken; hence symbols over the right (front) apex represent snakes taking the gecko first in four out of four trials. The left apex correspond to a preference for dead neonatal mice; the rear apex a preference for skinks.

location resulting from the final four preference trials (the T2 phase) in the same diagram. Knowing what prey the snake had been ‘trained’ on during the F phase, we scored the change in mean preference between the two preference trial phases as steps towards / parallel to / away from the forced diet prey type. Fig. 2 shows the potential scores for a snake that during the T1 phase initially consumed a gecko once, mouse twice, and skink once, and then was offered only skinks during the F phase. The potential score for the snake illustrated would be constrained to $-0.25, 0, +0.25, +0.5,$ and $+0.75$, but possible values range from -1 to $+1$ in increments of 0.25 . Looking for a general effect of prey experience on food preference, we first pooled the scores of snakes from all three prey treatments. To evaluate if the scores were positive, as predicted from an experience-modulated preference, we used Wilcoxon’s sign ranked test (Sokal and Rohlf 1995). To evaluate if experience with just one or two prey types were likely to enhance the preference, we also analyzed the three prey treatments separately. For all statistical tests, results were considered significant at $\alpha = 0.05$.

RESULTS

Prey preference.—The gecko was the first prey chosen in 87% of the 224 initial trials in the T1 phase of the experiment (56 snakes tested four times each). Of the 56 snakes, 35 (62%) ate the gecko first in all four T1 trials. Only two snakes preferred a prey different from

TABLE 1. Parameter estimates for multinomial logistic regression of prey preference in juvenile Brown Treesnakes. Dead neonatal mice (subscript *M*) are used as a baseline to which we compared skinks (*S*) and geckos (*G*).

Prey	Logit	intercept	SE (intercept)	<i>P</i>	SVL	SE (SVL)	<i>P</i>
Gecko	$\log(\pi_G/\pi_M)$	6.40	2.35	0.006	-0.0070	0.0038	0.069
Skink	$\log(\pi_S/\pi_M)$	1.21	3.16	0.702	-0.0026	0.0052	0.618

the gecko (i.e., the mouse or the skink) in a majority of their trials (Fig. 3).

Analyzing the first prey taken during the 224 trials with multinomial logistic regression, a preference for geckos over neonatal mice was evident over the entire range of snake sizes tested, although the gap was smaller for the larger snakes (Fig. 4). Although the cluster adjustment used to ameliorate pseudoreplication resulted in a weak snake size effect, the difference in intercept between the gecko and mouse preference probability functions nevertheless stood out as a strong effect (Table 1). Preference for skinks and mice was indistinguishable.

Prey acceptance: distinguishing reluctance from refusal.—Snakes may prefer one prey, but that does not necessarily mean they are disinclined to consume other prey. Although most snakes showed a preference for geckos during the experimental T1 phase, the majority continued eating one or both of the additional prey items after the gecko. Twenty-eight snakes took at least one mouse and one skink during the T1 phase, in addition to the gecko, but 14 never took any mouse, six never took any skink, and eight snakes never ate anything but the gecko. There was a clear tendency for the smallest snakes tested to fall into the latter category (Appendix 1), but two relatively large snakes (617 and 667 mm SVL) stopped eating in all four T1 trials, after having taken the gecko. Conversely, one small snake (483 mm SVL) habitually ate three prey items in succession.

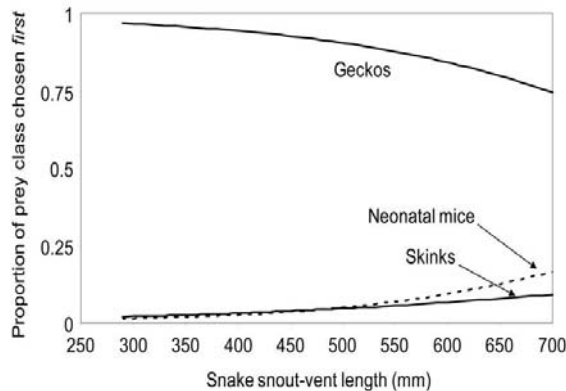


FIGURE 4. Preference probability functions generated from multinomial logistic regression based on first prey chosen by 56 Brown Treesnakes in four trials each. Preference for neonatal mice (hatched curve) is a baseline to which preference for skinks and geckos are compared.

The F phase offered an opportunity to see whether refusals of particular prey in the T1 trials were definite (hard), or if the snakes would consider less preferred prey when nothing else was offered (soft). Twenty-two of the 56 snakes had a T1 phase prey acceptance history suggesting that they might refuse mice (either all the time or unless very hungry), but only eight of these 22 snakes were subsequently restricted to a neonatal mouse diet during the F phase. Of these eight snakes, two immediately and voluntarily ate the mice offered, while six had to be force-fed on at least the first occasion (i.e., after having refused a mouse on two consecutive weekly

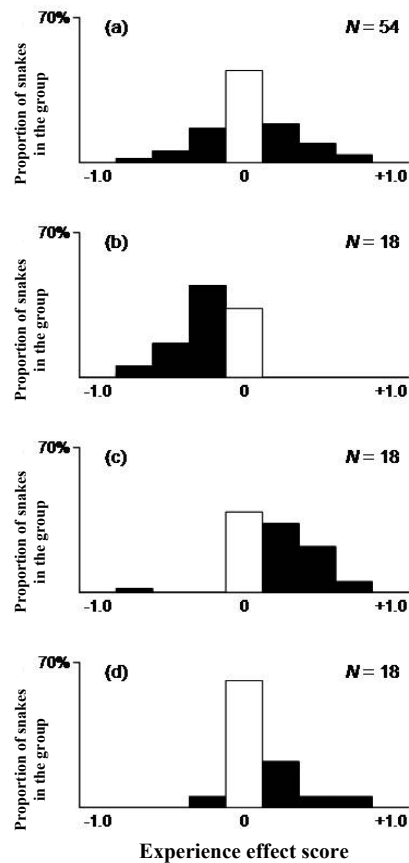


FIGURE 5. Frequencies of experience effect scores from Appendix (1) pooled for (a) the entire data set, (b) gecko treatment snakes, (c) skink treatment snakes, and (d) mouse treatment snakes. Positive scores indicate snakes increasing preference of prey they had encountered during the forced diet phase; negative scores indicate a stronger avoidance resulting from previous prey experiences (but see the text for sources of bias that may cause the patterns seen in panel b – d).

trials). Of these six, three started eating mice voluntarily after one or two force-feedings, but three had to be force-fed regularly. Rating the strength of mouse refusal in three categories, 39% (22 out of 56) initially showed a soft refusal of mice. When alternative food was no longer offered, this figure dropped to 32% (six out of 19 mouse treatment snakes) or, calculated slightly differently, 29%. The latter figure is calculated as follows. First we recognize that also soft refusal of mice seen in 22 out of 56 snakes during the T1 phase (the majority of which did *not* end up in the F phase mouse treatment) can give clues to what proportion of the snakes might eventually have shown hard mouse refusals had they all been subjected to the F phase mouse treatment. That is because we know that six out of eight snakes that had not taken mice during the T1 phase required force-feeding when subsequently confined to a mouse diet. By multiplying these two fractions ($22/56 \times 6/8 = 0.29$) we make an inference about predicted hard mouse refusals in the full sample of 56 snakes, not just the snakes in the mouse treatment. Even if facing more severe hunger, 15–16% of the snakes (3/19; or calculated as $22/56 \times 3/8$) would seemingly refuse a mouse.

Making the same tabulations and calculations for skink refusal, 25% of the snakes (14 out of 56) did not take skinks when other food was available. Only one of 18 skink-treatment snakes (6%) did not eat when only a skink was offered to it. With the alternative calculation method, one out of six of the soft refusals transformed into hard refusals, and based on the total number of snakes showing soft skink refusals, this suggests that 4% ($14/56 \times 1/6$) of the snakes may actually have shown hard skink refusal. The snake showing a hard refusal had a SVL of 435 mm at the beginning of the experiment. By the time it had completed all trials, having reached a size of 505 mm SVL, it had voluntarily eaten nothing but geckos and mice. The corresponding estimate for soft, intermediate, and hard refusal of geckos was 0%, regardless the method of calculation.

Effect of experience on prey selection.—When we pooled the experience scores from all three prey treatments, there was no experience effect (Wilcoxon's sign rank test: $N = 29$ non-zero scores, $P = 0.38$; Fig. 5a). Analyzing the three prey treatments separately, however, indicated that experience with skinks resulted in a stronger preference for skinks ($N = 11$ non-zero scores, $P < 0.001$; Fig. 5c). Conversely, restricting diet to geckos appeared to decrease their attractiveness to snakes over time ($N = 12$ non-zero scores, $P < 0.001$; Fig. 5b), while snakes in the mouse treatment showed no significant change in preference ($N = 6$ non-zero scores, $P = 0.078$; Fig. 5d). A bias that is obscured in our analyses of experience effects is that snakes grew during the experiment. The mean \pm SD increase in SVL during the experiment was 74 ± 33 mm, but one snake (#52)

increased its SVL by 207 mm. Because the snakes tended to increase consumption of skinks and mice as they grew (Fig. 4), we would expect to see our experimental snakes exhibit the patterns of the same directions as seen in Fig. 5c and 5d without invoking experience effects.

DISCUSSION

Operational control of Brown Treesnakes has historically relied to a large extent on traps baited with live, adult mice. Unfortunately, these traps are almost completely ineffective for catching snakes < 700 mm SVL (Rodda et al. 2007). Although it would seem reasonable for a small snake to avoid a relatively large rodent (which might bite back), dead neonatal mice do not pose a real, and probably not even a perceived threat to a snake. In a previous study, the smallest Brown Treesnake that voluntarily ate a dead neonatal mouse was 415 mm SVL (Fiona J. Qualls and Jason D. Hackman, unpubl. data), a size within the upper range of hatchling sizes (Linnell et al. 1997, Rodda et al. 1999c). To widen the range of snake sizes targeted by control efforts it would therefore seem logical to use dead neonatal mice containing a toxicant such as acetaminophen (Savarie et al. 2001).

Our results, however, indicated that small snakes have a strong preference for geckos. Although even hatchling-sized snakes seem physically able to consume neonatal mice, many snakes < 700 mm SVL were reluctant to do so. In most cases, this seemed to be a soft refusal in the sense that snakes rejected neonatal mice (as well as skinks) only when they had already consumed a gecko. We tried to offer smaller snakes smaller prey, but availability of small prey (small neonatal mice in particular) limited the size matching possibilities and caused smaller snakes to be offered a larger total meal size relative to their own weight. However, one 483 mm SVL snake habitually ate all three prey items in succession. A snake > 600 mm SVL would easily have been able to take at least a second prey, and probably all three prey items offered.

As a snake becomes hungrier, a truly soft refusal means the snake will gradually become more inclined to take less preferred prey. Depending on snake hunger level, our data suggest that 15 to 40% of snakes < 700 mm SVL might be refractory to control methods using neonatal mice as bait. We can only speculate what proportion of juvenile snakes in the field will be hungry enough to consider feeding on less preferred mice, and what proportion would rather wait for another gecko. The hunger level may differ depending on prey (especially gecko) availability at the focal site, and thus differ between islands as well as among habitats within an island (Rodda and Dean-Bradley 2002). It should also be pointed out that our figures on mouse acceptance

levels are based on a particular snake size distribution. The opportunity to target small snakes with neonatal mice will be better if the size distribution is more skewed towards larger sizes and worse if more skewed towards hatchlings. Such demographic properties may differ over the course of a year due to the degree of reproductive seasonality exhibited by the focal snake population.

Our study was not designed to test the extreme limits for hard refusals (i.e., snakes refusing a particular prey type regardless how hungry they are). It nevertheless seemed as if a small fraction of the snakes starved rather than consume a non-preferred prey type. This was most pronounced in the smallest snakes that were offered mice (Appendix 1), but even a snake that measured 660 mm SVL at the beginning of the experiment only voluntarily consumed a mouse once during the experiment (during the F2 trial). Only one snake refused to eat skinks. Because we did not restrict snakes to different diets in consecutive order, we cannot tell if there are juvenile Brown Treesnakes that are monophagous gecko feeders. It seems likely some are effectively so, provided geckos are common.

Although perhaps of limited use for operational control, it may be that visual stimuli offered by moving prey elicits a strike and prey consumption even if the prey may not be preferred on basis of its scent (Chiszar et al. 1988). Even so, the abundant (Rodda et al. 2005) skink *C. aitanpalai* is diurnal and normally sleeps hidden under vegetation or debris on the forest floor, thus rarely offering a visual cue to nocturnal snakes. Also, neonatal rodents are not visually stimulating unless a snake encounters them in their nest, which would generally necessitate scent trailing and an interest to start with. The common geckos of Guam, *Hemidactylus frenatus*, *Lepidodactylus lugubris*, and *Gehyra mutilate*, are primarily arboreal (Rodda and Fritts 1992) and nocturnal. It is striking that small snake preference for geckos neatly match the microhabitat where both snakes and geckos forage: during visual searches for Brown Treesnakes at night, > 95% of snakes < 1,000 mm total length (corresponding to ca < 785 mm SVL) are found perched above ground, while larger snakes are more frequently found on the ground (Rodda and Reed 2007).

Several studies have investigated the effect of prey experience on juvenile snake prey preferences. Naïve neonatal snakes typically become more prone to investigate and attack prey as they gain experience with that prey type (Arnold 1978), but the opposite effect has also been observed (Burghardt 1992). The extent to which prey preference and acceptance can be modified may depend on the energetic demands of the focal snake (cf. Waters and Burghardt 2005). In our study, snakes in the mouse treatment group received the smallest food rations relative to snake body size, and would thus be expected to be most prone to have a more liberal prey

acceptance when entering the second preference trial phase. Even so, there was no conclusive evidence that the previously non-preferred mice became more acceptable in the latter trials. Some may argue that force feeding may cause the subject to associate the prey with a negative experience and therefore become even more reluctant to eat that prey. This is contraindicated by the fact that three out of six snakes that we force fed mice started to accept mice after 1–2 mouse meals. It is also a common procedure among experienced snake breeders to force or assist-feed snakes with dead neonatal mice (or parts thereof) before they voluntarily eat them on their own.

Our test of the experience effect suffered from an inherent bias in that most snakes started out with a complete preference for geckos. Such snakes that were trained on geckos had experience effect scores constrained to either no change or negative values, because they could not get a stronger preference for geckos. Adding a random error will inevitably result, on average, in a negative score for snakes that initially had a complete preference for geckos. Similarly, we would expect these snakes to get an overall positive experience effect score if trained on prey other than the preferred geckos. When we pooled all treatments, the score was at zero, indicating no overall experience effect. However, when analyzing the food treatments separately, snakes in the gecko and skink treatments exhibited the patterns expected from the systematic constraints. In addition, we would expect snakes to grow increasingly tolerant of, or attracted to, skinks and mice the longer the experiment progressed because the snakes grew larger.

Acknowledging that the experimental design was not immune to bias and interpretation problems, we cannot claim to see any evidence for the prey training phase having an effect on food preference during the second preference trial. In particular, there seemed to be no positive experience effect of the mouse treatment: snakes did not increase their preference for mice despite the two sources of bias that could lead to such a result. This suggests that small Brown Treesnakes in places where rodents are more abundant than in Guam (e.g., in the nearby Northern Mariana Islands; Wiewel et al. 2009) may have the same preference for geckos and that control efforts there may prove just as challenging as on Guam, should neonatal mice be the bait used.

In conclusion, using rodents as bait will only target part of the juvenile Brown Treesnake population, even if the bait offered is small enough for a small snake to ingest. Although a majority, though not all, of the snakes < 700 mm SVL may accept neonatal mice, they do not prefer them. Small snakes seem especially reluctant to accept rodent bait when they are well-fed, as would be expected at sites rich in lizard prey. Unfortunately for Brown Treesnake control efforts, oceanic islands often have dense lizard populations

(Rodda et al. 2001; Rodda and Dean-Bradley 2002). If the goal is to target the entire snake population, and not just medium sized and large snakes, it would be desirable to enhance the attractiveness of the bait used. One could either offer the bait preferred by small snakes (live or dead geckos) or find a way to apply gecko scent to rodent bait. Large numbers of geckos are more difficult and more expensive to obtain than neonatal mice. However, gecko-based solutions may prove an integral part of efforts to target all snake size classes and all individuals within the smaller size classes. The alternative is to acknowledge that we cannot target the entire population, but instead aim for repeated rodent baiting until all snakes have reached a size where their soft preference for rodents approaches or exceeds that for geckos. Brown Treesnakes mature at 910–1030 mm SVL (Savidge et al. 2007), and to restrict control efforts to larger snakes may increase the risk of reproduction occurring before every individual has been successfully targeted. This is perhaps less of a problem if the goal is merely snake suppression, but may compromise the opportunities for large-scale eradication.

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- Erratum:* Due to a publishing error, this article was accidentally supplanted with a different article (Bull 2009) on the initial release of this issue. The correction was made on 9 December 2009.

Lardner et al.—Prey preference in Brown Treesnakes.



BJÖRN LARDNER received his Ph.D. in Animal Ecology from Lund University. Much of his research has focused on Swedish frogs and tadpoles, but he has studied frog vocalization in Borneo and conducted reptile and amphibian surveys in Borneo and Sulawesi. He is currently a postdoctoral researcher with Colorado State University, stationed on the island of Guam where he works on control of the invasive Brown Treesnake. (Photographed by Björn Lardner)



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APPENDIX 1. Snake snout-vent length at the start (SVL-1) and end (SVL-2) of the experiment; prey treatment during the F phase, where G = gecko, S = skink, and P = neonatal mouse; number of the different prey types taken *first* during T1 vs. T2 trials ($\Sigma=4$ per phase); experience effect score; total prey consumption during the T1 phase; prey acceptance / rejection history during the ten ‘forced’ feeding events following after the phase 1 preference trials (0 = prey rejected and snake force fed; bold score **1** indicates the snake ate during a second trial attempt w/o any force feeding; score 1 (non-bold) that snake ate right away); and total prey consumption during the T2 phase.

Snake ID#	SVL-1 (mm)	SVL-2 (mm)	Prey treat.	FIRST PREY CHOSEN		Experience effect score	Phase 1 total consumption (G:S:P = Σ)	‘Forced’ diet acceptance / rejection history	Phase 2 total consumption (G:S:P = Σ)
				Phase 1 (G:S:P)	Phase 2 (G:S:P)				
21	290	435	S	4:0:0	2:2:0	+ 0.50	4:1:0 = 5	1111111111	3:4:1 = 8
53 [†]	330	DD	P	4:0:0	DD	DD	4:0:0 = 4	0000-----	DD
39	387	462	G	4:0:0	4:0:0	0.00	4:2:0 = 6	1111111111	4:3:0 = 7
45	387	478	P	3:1:0	3:1:0	0.00	4:3:0 = 7	0101111111	4:3:1 = 8
33 ^{**}	410	DD	G	4:0:0	[3:0:0]	[0.00]	4:0:0 = 4	1111111111	[3:1:0 = 4]
52	422	629	S	3:1:0	1:3:0	+ 0.50	4:4:0 = 8	1111111111	4:4:0 = 8
30	425	494	P	4:0:0	3:1:0	0.00	4:2:0 = 6	0111111111	4:3:1 = 8
49	432	500	G	2:0:2	1:3:0	- 0.25	3:0:4 = 7	1110111111	2:3:0 = 5
15	433	563	S	4:0:0	2:0:2	0.00	4:2:0 = 6	1111111111	4:4:2 = 10
38	435	505	S	4:0:0	4:0:0	0.00	4:0:2 = 6	0000000000	4:0:3 = 7
37	445	488	P	4:0:0	3:1:0	0.00	4:0:0 = 4	0000000000-	4:4:0 = 8
50	450	543	G	4:0:0	4:0:0	0.00	4:0:0 = 4	1111111111	4:1:0 = 5
54	456	556	S	4:0:0	3:1:0	+ 0.25	4:0:0 = 4	1111111111-	4:3:0 = 7
25	470	602	S	4:0:0	4:0:0	0.00	4:0:3 = 7	1111111111	4:1:2 = 7
32	483	583	G	3:0:1	0:3:1	- 0.75	4:3:4 = 11	1111111111	4:4:4 = 12
34	490	565	P	4:0:0	1:0:3	+ 0.75	4:4:2 = 10	1111111111	4:4:4 = 12
56	498	546	P	4:0:0	4:0:0	0.00	4:1:2 = 7	1111111111	4:0:3 = 7
42	499	593	S	3:0:1	3:1:0	+ 0.25	4:1:1 = 6	1111111111	4:4:0 = 8
35	503	549	G	4:0:0	4:0:0	0.00	4:0:0 = 4	1111111111	4:0:0 = 4
23	507	560	P	2:2:0	2:2:0	0.00	4:4:1 = 9	1111111111	4:4:1 = 9
41	516	570	P	4:0:0	2:1:1	+ 0.25	4:0:2 = 6	1111111111	4:4:3 = 11
55	517	562	G	4:0:0	3:1:0	- 0.25	4:3:1 = 8	1111111111	4:2:0 = 6
36	520	641	S	3:0:1	0:4:0	+ 0.75	3:3:3 = 9	1111111111	4:4:4 = 12
51	530	651	P	4:0:0	4:0:0	0.00	4:3:1 = 8	1111111111	4:4:4 = 12
01	540	670	S	4:0:0	3:1:0	+ 0.25	4:3:1 = 8	1111111111	3:4:4 = 11
47	548	641	G	4:0:0	2:2:0	- 0.50	4:3:0 = 7	1111111111	4:3:0 = 7
07	550	594	P	4:0:0	2:2:0	0.00	4:3:1 = 8	1111111111	4:4:3 = 11
27	550	600	P	4:0:0	3:1:0	0.00	4:3:0 = 7	1111111111	4:3:0 = 7
17	569	665	S	4:0:0	3:1:0	+ 0.25	4:3:0 = 7	1111111111	4:3:0 = 7
22	571	641	G	4:0:0	3:0:1	- 0.25	4:3:1 = 8	1111111111	4:3:3 = 10
31	582	660	S	4:0:0	4:0:0	0.00	4:2:0 = 6	1111111111	4:4:0 = 8
03	593	652	G	4:0:0	4:0:0	0.00	4:3:0 = 7	1111111111	4:4:0 = 8
46	600	648	P	3:1:0	3:0:1	+ 0.25	4:3:1 = 8	1111111111-	4:4:2 = 10
40	605	709	S	2:2:0	0:2:2	0.00	4:4:4 = 12	1111111111	4:4:4 = 12
14	610	650	G	4:0:0	2:2:0	- 0.50	4:2:4 = 10	1111111111	4:3:4 = 11
24	617	685	S	4:0:0	2:2:0	+ 0.50	4:0:0 = 4	1111111111	4:3:0 = 7
09	620	710	S	1:1:2	1:1:2	0.00	4:4:4 = 12	1111111111	4:4:4 = 12
26	622	665	P	3:0:1	1:0:3	+ 0.50	4:0:3 = 7	1111111111	4:2:4 = 10
05	623	706	S	4:0:0	3:1:0	+ 0.25	4:3:0 = 7	1111111111	4:4:0 = 8
04	625	677	P	3:0:1	1:3:0	- 0.25	4:4:3 = 11	1111111111	4:4:4 = 12
11	635	673	P	4:0:0	2:1:1	+ 0.25	4:4:2 = 10	1111111111-	4:4:3 = 11
13	637	691	S	1:0:3	2:1:1	+ 0.25	3:0:4 = 7	1111111111	4:3:4 = 11
29	640	699	G	3:1:0	3:1:0	0.00	4:4:2 = 10	1111111111	4:4:1 = 9
18	642	738	G	4:0:0	3:1:0	- 0.25	4:4:3 = 11	1111111111	4:4:4 = 12
08	643	726	G	3:0:1	3:1:0	0.00	4:2:4 = 10	1111111111	4:4:4 = 12
48	644	704	G	4:0:0	3:0:1	- 0.25	4:2:2 = 8	1111111111	4:3:3 = 10
20	654	730	S	4:0:0	2:2:0	+ 0.50	4:3:1 = 8	1111111111	4:4:4 = 12
44	660	704	P	4:0:0	3:1:0	0.00	4:4:0 = 8	0100000000	4:4:0 = 8
06	663	732	G	4:0:0	2:2:0	- 0.50	4:3:4 = 11	1111111111	4:4:4 = 12
19	667	664	P	4:0:0	3:1:0	0.00	4:0:0 = 4	1111111111	4:3:0 = 7
16	670	722	P	3:1:0	4:0:0	0.00	4:3:0 = 7	0111111111	4:4:1 = 9
12	680	752	G	3:0:1	2:2:0	- 0.25	4:3:3 = 10	1111111111	4:4:4 = 12
43	688	748	G	3:0:1	2:2:0	- 0.25	3:3:4 = 10	1111111111	4:4:4 = 12
10	690	745	S	2:0:2	4:0:0	0.00	4:2:4 = 10	1111111111-	4:4:3 = 11
02	692	728	P	3:1:0	2:1:1	+ 0.25	3:3:4 = 10	1111111111	4:4:4 = 12
28	702	753	G	2:1:1	1:3:0	- 0.25	3:3:4 = 10	1111111111	4:4:4 = 12

[†] Snake #53 passed away after the F4 trial.

^{**} Snake #33 only completed three T2 trials before escaping; experience score based on incomplete T2 phase and not used in analyses.

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Erratum: Due to a publishing error, Bull 2009 was accidentally posted instead of Lardner et al. 2009 on the initial release of this issue. The correction was made, and Bull 2009 was deleted from this issue on 9 December 2009. Bull 2009 appears in Vol. 4, Issue 2 (http://www.herpconbio.org/Volume_4/Issue_2/Bull_2009.pdf)



Brown Treesnake (*Boiga irregularis*). (Photographed by Gordon Rodda).