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Tools and Technology

Effectiveness of Bait Tubes for Brown Treesnake Control on Guam

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ABSTRACT In 2008, we studied simulated toxicant efficacy to control invasive brown treesnakes (*Boiga irregularis*) using bait tubes (elongate bait stations that reduce non-target bait take) in a 5-ha enclosure in Guam (U.S. Territory) with a known population of snakes. Instead of toxicants, we implanted radiotransmitters in small (6.6 ± 1.4 g) and large (21.8 ± 2.9 g) bait-mouse carcasses, offered from 2 types of bait tubes over a 3-month period. The known snake population allowed us to characterize not only the snakes taking bait, but also those evading our mock control effort. Tube design had no effect on take rate, but snout–vent length was a strong predictor of bait take: none of the 30 snakes <843 mm in length took any bait, whereas 77 of the 126 snakes ≥843 mm in length took 164 baits. While medium-sized snakes preferentially ingested small bait (and the largest snakes tended to take large mice more frequently), some of the smallest snakes that took bait ingested large mice. Snake body condition was positively correlated to take rate, but snake sex had no discernible effect. Our data show that there is a relatively narrow size (and, thus, time) gap between the size at which the snakes become susceptible to bait-mouse take and the size at which they become sexually mature. This has implications for the timing of repeated baiting efforts, if the goal is eradication rather than suppression. Published 2013. This article is a U.S. Government work and is in the public domain in the USA.

KEY WORDS bait station, *Boiga irregularis*, eradication, Guam, invasive, size selectivity, snake, toxicant.

Invasive species can have dramatic ecosystem impacts and entail high costs to society. A well-known example is the brown treesnake (*Boiga irregularis*), which was accidentally introduced to the island of Guam (U.S. Territory) shortly after World War II. Since its introduction, the snake has caused the extinction of most native forest birds, numerous power outages, and severe cases of envenomation in young children (Savidge 1987, Rodda and Savidge 2007). Guam is a transportation hub of the Western Pacific and there is risk of the snake spreading and causing similar damage elsewhere. In the past 2 decades, there have been numerous brown treesnake sightings on other islands in the Pacific and Indian Oceans, in North America, and as far away as Spain—all believed to be snakes originating as stowaways from Guam (Stanford and Rodda 2007). This is of grave concern to more than conservation biologists; should the snake colonize Hawaii, the economic damage alone (i.e., ignoring the ecological damage) has been projected at US$0.6–2.1 billion annually (Shwiff et al. 2010). Because of the high stakes, a brown treesnake control program is in place in Guam to prevent snakes from entering the transportation network and being transported off the island (Engeman and Vice 2001). In addition to preventing snakes from spreading beyond Guam, a goal is to suppress or locally eliminate snakes in Guam to allow restoration and repatriation of native species, and ultimately to eradicate the snake throughout Guam (Engeman and Vice 2001, Colvin et al. 2005).

Brown treesnake interdiction in Guam focuses on perimeter trapping around ports and airports and eliminating snakes from aircraft and cargo with the aid of detector dogs (Engeman and Vice 2001). Given the size of Guam (543 km^2) and the immense labor required to maintain a trapping program for large areas (Vice and Pitzler 2002), island-wide eradication by trapping has not been judged practical. With the registration of acetaminophen as an oral toxicant for brown treesnake control on Guam (U.S. Environmental Protection Agency reg. no. 56228-34), large-scale suppression or eradication now may be possible (Savarie et al. 2001). The toxicant is delivered in pellet form inside a bait matrix, typically a dead juvenile mouse. Studies are underway to develop aerial delivery systems that will help spread the bait over large and inaccessible areas (Shivik

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et al. 2002, Savarie and Tope 2004, Savarie et al. 2007), but thus far, bait tubes have been the main method of delivery (Fig. 1). Bait tubes minimize bait access by non-target species such as monitor lizards (*Varanus indicus*), feral and domestic cats, hermit crabs (*Coenobita* spp.), coconut crabs (*Birgus latro*), and Mariana crows (*Corvus kubaryi*), while allowing the slender snakes to reach the bait inside the tube. Unlike aerial delivery, bait tubes may also offer a means of distributing toxicants in residential areas that is both safe and acceptable to the public.

Traditional brown treesnake control has been by means of funnel traps baited with live mice. Although traps (Rodda et al. 1999*b*, Vice et al. 2003) currently capture thousands of snakes annually, they have been largely ineffective for snakes <700 mm snout–vent length (SVL), and only partially effective for snakes 700–900 mm SVL (Rodda et al. 2007). Size-specific trap efficacy may be partially due to snakes being gape-size-limited predators (i.e., attractant mice in traps are perceived by the snakes as too large to swallow), or because juvenile brown treesnakes might not consider live adult mice suitable prey. Juvenile brown treesnakes on Guam consume lizards, but shift to eating endotherms at 700–1,200 mm SVL (Savidge 1988), and the smallest brown treesnakes show a strong preference for lizard prey when offered lizards and mice simultaneously (Lardner et al. 2009). However, brown treesnakes do scavenge (Savidge 1988) and at least some sizes of snake readily consume dead mice (Shivik and Clark 1997). Furthermore, use of dead mice as a toxicant vector makes it possible to use smaller bait (very young mice are not normally used in traps because they have a low survival rate when used as an attractant). Hence, smaller snakes can potentially be more easily attracted with bait tubes (which can be baited with a small mouse carcass) than with a live adult mouse attractant, such as that used in traps.

In this study, we investigated the effectiveness of 2 bait-tube designs developed by the U.S. Department of Agriculture (USDA). Our objectives were 1) to test whether the tube designs were equally effective for snakes of different sizes; 2) to evaluate whether bait mice of different sizes would help control snakes of a wider size range; and 3) to investigate the influence of snake body condition and sex on bait-take rate.

Figure 1. Bait tubes used to deliver dead mice to brown treesnakes in Guam (U.S. Territory), 2008, were of 2 designs. Pictured lower right is the narrow tube that was suspended horizontally, with the bait placed in the center. The other tube was suspended vertically and a perforated end cap (here seen removed from the tube) forced snakes to access bait, placed on a metal wire shelf near the top, from below.

STUDY AREA

Our research was conducted in a 5-ha snake enclosure located on a limestone plateau near the northwestern tip of Guam (N13°38′, E144°52′). The snake enclosure, which also acted as an exclosure to prevent ingress by snakes from outside the population, was described in Rodda et al. (2007) and Tyrrell et al. (2009). The vegetation inside the enclosure consisted primarily of degraded, 5- to 10-m-tall forest dominated by the introduced Tangan–Tangan tree (*Leucaena leucocephala*).

METHODS

Bait-Tube Design and Bait-Mouse Sizes

We focused on the 2 most promising field-tested bait tubes developed by USDA-Wildlife Services: 1) a 300-mm-long polymerized vinyl chloride plastic tube with an inner diameter of 52 mm, suspended horizontally with the aid of cord attached to holes drilled at the ends of the tube, and 2) a 200-mm-long, 76-mm-diameter tube that is hung vertically (this study) or at a 45° angle with an end cap containing multiple holes, allowing bait scent to diffuse out while preventing non-target access to the bait from above (Fig. 1). Our bait-tube deployment practices mirrored those of USDA except that we attached a magnet to the location where the bait mouse was placed; the magnet kept radiotransmitters deactivated until the mouse was removed by a snake. To test for a bait size effect, we used both small (mean ± SD mass before transmitter implant = 6.6 ± 1.4 g) and large (21.8 ± 2.9 g) mice.

Baiting and Snake Telemetry

Our snake enclosure had 169 (13 × 13, at 16-m intervals) bait (or trap) stations. Because we had a 2 × 2 experimental design (2 tube types × 2 bait size classes), we randomly assigned each of the 4 treatments to 42 replicates drawn from 168 stations (stations were treatment replicates and we discarded one station to achieve a balanced design). Because logistics allowed us to bait only a fraction of the stations at any given time, we randomized the order with which the stations were used. In some cases, snakes took fresh baits from tubes on the first night. We re-baited those tubes during the latter part of our study, following the same bait-station attendance order and using pre-aged transmittered mice. On the morning after baiting with these aged mice, we checked for take and removed bait still present. By the end of the study, each of the 168 positions had thus offered bait for 2 nights each; once with fresh bait and once with aged bait.

We conducted field trials between 8 September and 3 December 2008. When baiting with fresh mice, the procedure was as follows. On Day 1, we thawed frozen mice,

implanted a radiotransmitter (Holohil BD2-HX [Holohil Systems Ltd., Carp, ON, Canada]; mass 1.9 g) in the abdominal cavity of each mouse, and sealed the incision with surgical glue. The transmitters had a smooth coating and were narrow enough to be passed by snakes smaller than any taking bait in this study. The number of bait mice prepared and placed in tubes on Day 1 varied between weeks, primarily due to transmitter availability (some were still in snakes), but we normally baited with 25 mice. We recorded transmitter frequency, mouse net mass (hence, bait size class), bait-tube type, and its location. On Day 2, we checked for bait takes and started tracking snakes that had ingested bait. Mice not taken from tubes were left for another night. On Day 3, we checked for additional bait takes, removed any mice still not taken from tubes, and continued tracking snakes. We repeated this baiting and tracking in weekly cycles. During the latter part of the study, pre-aging of mice in snake-proof outdoor cages for 24 hours meant we baited tubes on Day 2 and removed mice not taken on Day 3.

To locate snakes, we used Communication Specialists Inc. (Orange, CA) R1000 receivers fitted with Telonics Inc. (Mesa, AZ) RA-14 antennae. All snakes that took transmittered bait and subsequently were captured during our study had been captured and marked previously. We recorded snake net mass (excluding transmitter and mouse mass), SVL, and sex. If we could not capture and identify a snake (some were inside tree trunks, underground, or in tall forest canopy), we made repeated attempts, during day and/or night, to catch it before it passed the transmitter. All successfully tracked snakes were released at their point of capture.

Study Population

We used mark–recapture data from trapping, visual searches, and incidental encounters of snakes to define the study population at 156 snakes. Snakes in the enclosure have been studied since the area was closed to immigration and emigration in 2004, primarily by trapping (prior to this study, for 306 nights totaling >50,000 trap-nights) and visual searching for snakes at night (prior to this study, for 3,466 person-hr). Upon first capture, snakes are marked with a passive integrated transponder (PIT tag) and a series of unique ventral-scale clips and promptly released at their point of capture. Just prior to our study we conducted a 32-night trapping effort identical to that described in Rodda et al. (2007) and Tyrrell et al. (2009) in all respects except the number of trap-nights. Subsequent to our study, we conducted visual searches over 4.5 months. Visual searches are the only known tool for detecting snakes of all sizes and can therefore act as a census of the population (Rodda et al. 2007, Christy et al. 2010). Searches were conducted at night by biologists experienced with searching for brown treesnakes, walking along 28 transects and using headlamps to detect (catch, measure, mark) snakes. We continued to monitor for undetected snakes by searches until 16 December 2010.

Snakes not seen after 2006 were considered dead at the time of this study (2008). Twenty-nine snakes were seen after 1 January 2007, but not encountered after the onset of the bait-tube study. These snakes either died before, during, or after the bait-tube study, or they may have survived undetected (unlikely). To evaluate whether these snakes were present during the study, we characterized each snake's detection probability (based on prior context-specific mark–recapture analyses of this population) and survival probability (also based on this population) in conjunction with its capture history in different efforts (trapping, visual searching), its size, and its body condition trend. Based on these factors, we predicted the probability that the focal snake would have gone undetected before, during, and after the bait-tube study. In 23 of the 29 cases we had strong evidence to believe that the focal snake had died before the onset of the bait-tube study (19 individuals) or was alive during the study (4 individuals). We were less certain regarding the fate of the remaining 6 snakes. Of these, we estimated that 2 snakes were most likely still alive during the study (both juv when last seen) and 4 (2 F and 2 M; all ad when last seen) were most likely dead. Field methods were approved by the Colorado State University Institutional Animal Care and Use Committee (IACUC protocol 03-249A-05; snake population census data were also collected under IACUC 03-249A-01-03-249A-06 and 09-237A-01-09-237A-02).

Analyses

We used Poisson regression (LIMDEP v. 9.0; Econometric Software, Inc., Plainview, NY) to analyze bait-take counts, using both a full data set (all snakes present in the enclosure; $n = 156$) and, to evaluate body condition index and sex, using the subset of snakes $\geq$843 mm SVL ($n = 125$). In essence, this is a mixed Poisson model where a random snake individual effect is added by allowing the intercept for each snake to vary randomly according to a gamma distribution (preferred because it is the conjugate prior to Poisson and it allows an analytic solution of the integral in the likelihood; Hilbe 2007:208). Although there is independence from snake to snake, repeated observations from an individual snake are correlated. The correlation structure between the dependencies of multiple observations from an individual snake is handled by the correlation structure of the random effect. Because we analyzed tube design, bait size, and also accounted for the effect of bait age (first night vs. second night)—all factorial variables with 2 states—there were $2^3 = 8$ treatment combinations for each snake individual. Each contrast used a snake's covariates (SVL, SVL^2, and body condition index [BCI] subjected to z-transforms so that the mean = 0 and SD = 1), interpolated to the midpoint of the study, and the snake's sex −1, +1).

For each snake, we modeled SVL as a function of time to obtain an interpolated (or extrapolated) size at the midpoint of the study (20 Oct 2008), often using data collected before and after this study to help improve interpolation. For 16 snakes found on too few occasions to allow size estimation based on individual growth patterns (mainly small snakes not encountered until after the bait-tube effort), we calculated their expected size at the midpoint of the bait-tube study from the mean sex-specific growth functions of snakes from

this population. Body Condition Index was calculated as midpoint mass as a proportion of the expected mass for a snake of that length, based on a regression of (log) body mass on (log) snake SVL, using over 10,000 records from Guam between 1980 and 2004. Mass varies more than length on a short time scale, so for 9 snakes ≥843 mm SVL (see below) with mass data too sparse to allow reliable interpolation, we assumed they had the mean body condition index for snakes of their size in the population at the time of the study. We determined snake sex with reasonable reliability (from repeated probing of hemipenial pockets) for 153 of the 156 snakes. Information on sex was missing for only 1 snake ≥843 mm SVL; therefore, this snake was excluded from the analysis that used sex as a covariate.

To evaluate gape-size limitation, we plotted snake SVL for each bait-take event as a function of the mass of the bait mouse ingested. This evaluation was primarily descriptive, so we ignored pseudoreplication caused by repeated takes by some snakes. We also compared the size of snakes taking bait from tubes (and those not taking bait) to those captured (and not) during the 32-night trapping period that preceded the bait-tube study ($n = 157$ snakes). Because the midpoints of these efforts were separated by >2 months, we interpolated SVL to estimate size for the midpoint of the trapping period (13 Aug 2008). In comparing the efficacies of traps and bait tubes, we contrasted "captures" with "bait takes," either of which would be fatal in an operational context.

Model Selection, Model Building, and Estimation of Effect Sizes

We used the log-likelihood values to calculate Akaike's Information Criterion (AIC) as in Burnham and Anderson (2002:61), where the parameter count included an intercept and the random effect (α; each contributing $K = 1$). The model with the smallest AIC value is considered best, and plausible models generally have a $\Delta AIC < 7$ (Burnham et al. 2011). To help assess the relative importance of alternative models, we used ΔAIC to calculate Akaike weights (w_i); these can also be used to compute evidence ratios between pairs or groups of models (Burnham and Anderson 2002:75). For top models, we present the 95% CI of the effect coefficients to assess whether a variable had a strong effect (i.e., 95% CI did not span zero). We present only plausible models (95% confidence set) in Tables 1 and 3 based on summed Akaike weights from largest to smallest until ≥0.95 (all models listed in Supplementary Appendices A and B, available online at www.onlinelibrary.wiley.com).

Using the full data set (all 156 snakes), we evaluated 27 models and focused on the 3 experimental design factors (tube design, bait size, and bait age) affecting the physical limitations on which snakes took bait, rather than the rate at which bait was taken. In addition to these 3 experimental design variables, we used snake size (SVL and SVL^2) as the sole snake covariate (both z-transformed). Because gape limitation should be correlated with snake size, and is therefore relevant to the bait size variable, we included the interaction of Bait × SVL and Bait × SVL^2. To reduce the number of models considered, we assessed the relative support for snake size using a linear versus a polynomial effect of snake size (SVL alone, or SVL and SVL^2) in the most complex model, and used the best-supported length metric in subsequent models. Our most complex model had interactions between the experimental design variables (tube type, bait size, bait age) and snake size (SVL and SVL^2). We reduced the full model by focusing on one of the 3 design variables of management interest at a time.

Using a subset of the data (snakes ≥843 mm SVL; truncating at the smallest snake taking bait in the study), we evaluated the effects of BCI, sex, and biologically sensible interaction terms by adding these terms to the most plausible model from the analysis of the full data set. Because this analysis contained only larger snakes, we re-evaluated whether the snake-length effect was best described by SVL alone or by a second-degree polynomial expression in the most plausible model from the full data set, and used the most supported metric in subsequent models. We evaluated 7 non-hierarchical models where the interaction effect with snake size was nonlinear while the main effect of snake size was linear. Such models were interpretable because we had a

Table 1. Random-effect Poisson models (95% confidence set, Burnham and Anderson 2002:169) used to evaluate data set of bait-take rates of 156 brown treesnakes, Guam (U.S. Territory), 2008 (all models listed in Supplementary Appendix A, available online at www.onlinelibrary.wiley.com).

Rank	Variables in model[a]							K[b]	AIC[c]	ΔAIC	w_i[d]
1	B A S S2		B × A	B × S				8	948.814	0.000	0.387
2	B A S S2		B × A	B × S	B × S2			9	950.445	1.631	0.171
3	B A S S2		B × A			A × S		8	952.123	3.310	0.074
4	T B A S S2		B × A	B × S	B × S2			10	952.226	3.412	0.070
5	B A S S2			B × S	B × S2			8	952.296	3.482	0.068
6	B A S S2		B × A					7	952.760	3.946	0.054
7	T B A S S2	T × B	B × A	B × S	B × S2			11	953.234	4.420	0.042
8	B A S S2		B × A			A × S	A × S2	9	953.837	5.023	0.031
9	A S S2							5	954.590	5.776	0.022
10	B A S S2							6	954.610	5.797	0.021
11	T B A S S2		B × A			A × S	A × S2	10	955.617	6.803	0.013

[a] T, tube type; B, bait size; A, bait age; S, snake snout–vent length (SVL); S2, SVL2.
[b] K is the parameter count including the intercept (1) and the random effect (1), denoted by α in Table 2.
[c] Akaike's Information Criterion.
[d] Akaike weight.

balanced data set with standardized size measures to achieve independence.

RESULTS

Of 168 mice cumulatively available for take on the first night (when still fresh), 38% ($n = 63$) were taken by snakes of known identity (one more was assumed to have been taken by a snake that we failed to capture). The second night, which included the pre-aged mice, had a cumulative take rate of 60% ($n = 101$; another 6 aged mice were assumed to have been taken by snakes that we failed to capture). Had there been no compensatory re-baiting with pre-aged mice, these take rates (and our baiting intensity) would have translated to a cumulative 71% of the baits being taken by snakes after 2 nights. This does not include the 7 cases where we suspect a snake took the bait, which would have increased the take to 78%. Ninety-one of the 164 baits taken by snakes of known identity (55%) were small mice, while 85 baits (52%) were taken from the narrow, horizontal bait tubes. The mean size of snakes taking small bait was 988 ± 93 mm SVL, while the corresponding mean for large bait was 1,025 ± 103 mm SVL. The r^2 value indicated that bait mass explained only 5% of the snake's size. Even the smallest snakes taking bait were physically able to ingest bait of the large size class (note the equality of SVL minima between low and high bait-mouse mass classes in Fig. 2).

Modeling Physical Limitations to Bait Take (Full Data Set)

When considering all snakes (those that took bait and those that did not), the quadratic function for snake size received the most support (ΔAIC > 10 for the linear counterpart). As illustrated in the top model (Akaike wt = 0.387; Table 1), the strongest effect was that of non-linear snake size (Table 2). Bait mice were taken at a higher rate on the second night they were available (in a progressed state of decomposition) and, overall, small mice were taken more frequently than were large mice (Table 2). However, bait size interacted with both snake size and bait age; the largest snakes took large mice more frequently than small mice, and large mice were taken at a disproportionally low rate unless aged (Table 2; Fig. 3A).

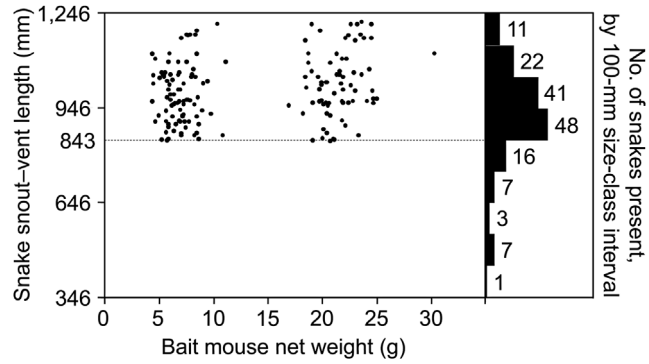

Figure 2. Size of brown treesnakes (interpolated to the midpoint of the 12-week study in Guam [U.S. Territory], 2008) ingesting bait as a function of the respective bait's mass (excluding a 2-g transmitter; scatterplot to the left), in light of the size distribution of snakes present in the population (histogram to the right). In the scatterplot, one snake individual may be responsible for >1 bait take.

Models that included a tube effect generally had little support (ΔAIC = 3.41 for the highest ranked model; Table 1) and the confidence interval of the main tube effect widely overlapped zero in all models. The highest ranked model with any tube effect had less than half as much support as the same model excluding the tube effect (Akaike wt 0.171 vs. 0.070; evidence ratio = 0.41). None of the models with tube interactions had strong support, and all interactions with tube effects had confidence intervals widely overlapping zero. To assess model fit of our top model, we evaluated the 95% CI coverage of its variables (Table 2) and compared its maximum log likelihood (L) of −466.4 and AIC = 948.8 (Table 1) with a random intercept-only model ($L = -500.2$; AIC = 1004.3) and an ordinary Poisson model version of our top model ($L = -471.8$; AIC = 957.5). As indicated by AIC, our mixed-effects model with covariates fitted our data substantially better than did either the random intercept model (55.5 ΔAIC units higher than the best model) or the ordinary Poisson model (8.7 ΔAIC units higher than the best model).

Table 2. Variables in the top-ranked model of bait-take rate for full (Table 1) and subset (Table 3) brown treesnake data sets, Guam (U.S. Territory), 2008.

	Full data set ($n = 156$)				Subset ≥843 mm SVL ($n = 125$)			
			95% CI				95% CI	
Variable[a]	Effect size	SE	Upper	Lower	Effect size	SE	Upper	Lower
Intercept	−2.804	0.245	−2.324	−3.284	−1.938	0.117	−1.709	−2.167
Bait size	−0.316	0.116	−0.089	−0.543	−0.195	0.091	−0.017	−0.373
Bait age	0.260	0.083	0.423	0.097	0.260	0.082	0.420	0.099
SVL	8.989	3.187	15.236	2.742	0.305	0.115	0.529	0.080
SVL^2	−7.137	2.727	−1.792	−12.482				
Bait size × Bait age	0.161	0.079	0.316	0.006	0.161	0.077	0.312	0.009
Bait size × SVL	0.320	0.138	0.590	0.050	0.183	0.083	0.346	0.020
Body condition					0.260	0.096	0.449	0.072
α	0.443	0.235	0.904	−0.018	0.325	0.200	0.716	−0.067

[a] Design variables (bait size, bait age) were effect-coded as [−1, +1], while snake size (SVL, SVL^2) and body condition were z-transformed to have a mean of 0 and a standard deviation of 1. α denotes the random effect. Note that design and individual variables have 95% CIs that do not include zero; this indicates strong effects as well as an explanatory model.

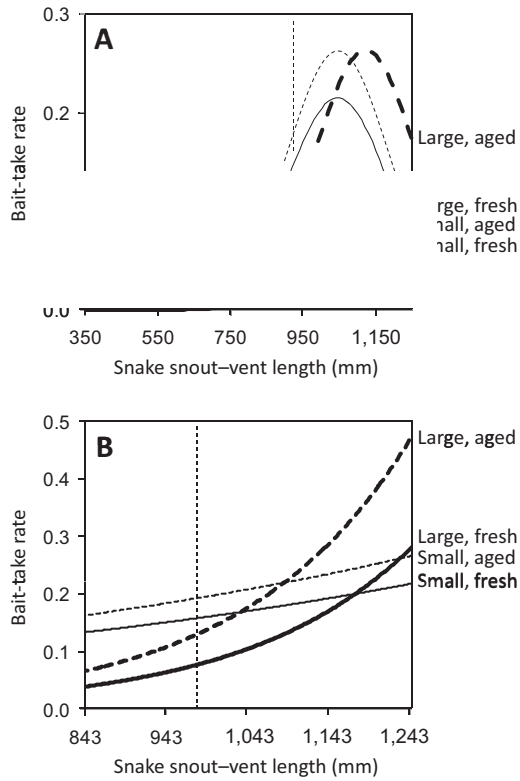

Figure 3. Bait-take rates by brown treesnakes in Guam (U.S. Territory), 2008, of small and large mice that were fresh versus aged, as predicted by the highest-ranked models for (A) the full 156-snake data set, and (B) the subset of 125 snakes of ≥843 mm SVL. Shown here are back-transformed snake snout–vent lengths; analyses were conducted on z-transformed SVL and (for the 156-snake data set) SVL^2 values. The mean snake size is indicated by vertical dashed lines. For (B), the snake body condition effect is fixed at the population mean.

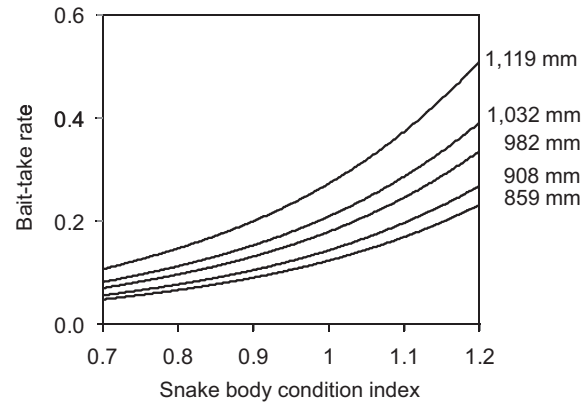

Figure 4. Bait-take rate by brown treesnakes in Guam (U.S. Territory), 2008, as a function of body condition index, for snakes exceeding the observed 843-mm snout–vent length bait-take threshold. Shown are model predictions from the top-ranked model for snakes of the mean size (982 mm) as well as the 10th, 30th, 70th, and 90th percentile snout–vent lengths. Bait size and bait age are fixed at a level intermediate to their binomial states.

Modeling Effects of Snake Body Condition and Sex on Bait-Take Rate (Data Subset)

When evaluating bait take in snakes larger than the apparent size threshold (≥843 mm SVL), we considered 15 models varying in complexity with regard to body condition index and sex effects (Table 3 provides the 95% confidence set of these models). The top model (Akaike wt = 0.316) was similar to a linear version of the top model from the full data set, but also included BCI. The second- and third-most high-ranked models also had substantial support and included interaction terms between BCI and snake size (as a polynomial and a linear effect, respectively). Body Condition Index was positively correlated with bait-take rate in all plausible models (Fig. 4). The main effect of BCI had a 95% confidence interval excluding zero in all models, but confidence intervals for the interaction terms of BCI × SVL or BCI × SVL^2 were asymmetrical in the second-ranked model (BCI × SVL = −5.94 to 0.20; BCI × SVL^2 = −0.21 to 5.73), suggesting a slightly elevated bait-take rate among the smallest snakes with BCI values >1. However, model predictions for small snakes with BCI values >1 would need to be interpreted with caution because we had few small fat snakes in the population. The confidence interval for the linear size interaction with BCI in the third-ranked model was almost centered on zero and inclusion of this term did little to improve model fit (1.81 ΔAIC units higher than the top-ranked model with the addition of a single parameter).

When snake sex was added to the top-ranked model, it did not result in an improvement (1.94 ΔAIC units below the

Table 3. Random-effect Poisson models (95% confidence set) used to evaluate data subset of brown treesnake bait-take rates (125 snakes ≥843 mm SVL), Guam (U.S. Territory), 2008 (all models listed in Supplementary Appendix B, available online at www.onlinelibrary.wiley.com).

Rank	Variables in model[a]							K[b]	AIC[c]	ΔAIC	w_i[d]
1	B A S C	B × A	B × S					8	930.665	0.000	0.316
2	B A S C	B × A	B × S	C × S	C × S2			10	932.132	1.466	0.152
3	B A S C	B × A	B × S	C × S				9	932.473	1.807	0.128
4	B A S C G	B × A	B × S					9	932.605	1.940	0.120
5	B A S C G	B × A	B × S			G × S		10	933.796	3.131	0.066
6	B A S C G	B × A	B × S	C × S	C × S2			11	934.031	3.366	0.059
7	B A S C G	B × A	B × S	C × S				10	934.438	3.773	0.048
8	B A S C G	B × A	B × S			G × S	G × S2	11	934.867	4.202	0.039
9	B A S	B × A	B × S					7	936.045	5.380	0.021

[a] B, bait size; A, bait age; S, snake snout–vent length (SVL); S2, SVL^2; C, body condition index (BCI); G, sex.
[b] K is the parameter count including the intercept (1) and the random effect (1).
[c] Akaike's Information Criterion.
[d] Akaike weight.

top model with the addition of a single parameter; a pretending variable [Anderson 2008]); the 95% CI for sex included zero. The summed Akaike weight for the 11 models including a BCI effect (0.954) was about twice that of the 11 models including a sex effect (0.426).

These models had the same qualitative effects as the top-ranked model from the full data set in that bait size interacted with bait age and snake size (which was positively correlated to bait-take rate). The higher take rate of aged mice than of fresh mice was more pronounced for large bait mice but, overall, small mice bait were taken more frequently. Additionally, large snakes took large mice more frequently than small mice (Table 2; Fig. 3B).

Size Selectivity of Bait Tubes Compared With Traps

We were interested in what proportion of snakes in different size classes took bait from tubes compared with the corresponding cohort proportions captured by the trapping effort preceding this study. Although these sampling periods involved different levels of effort (>5,000 trap-nights vs. 336 bait-tube nights), they yielded similar percentages of the snake population (52% and 49%, respectively). For both methods, the smallest snakes were not trapped or baited, and the mid-sized snakes (800–1,000 mm SVL) were trapped or baited at a lower (but progressively increasing) rate than were snakes >1,000 mm SVL (Fig. 5). Considering the bait-tube data alone, 30 out of 156 snakes present in the population were <843 mm SVL (the size of the smallest snake that took any bait). Had snakes of all sizes removed baits at the same rate, we would have expected about 32 bait takes by snakes <843 mm SVL.

DISCUSSION

This study reaffirmed that a toxicant inserted into a dead mouse, presented in a bait tube, can be an efficient means of controlling invasive brown treesnakes (Savarie et al. 2001). Had we not compensated for bait removal during first night offerings by re-baiting with aged bait, but instead returned only after 2 nights, >70% of the bait would have been ingested by snakes. This figure is slightly inflated in that our mock poisoning did not remove snakes that took bait. The bait-take rates we obtained were representative only of a first round of operational baiting for this particular population density and demography and at this particular baiting intensity. Even so, we reached approximately the same proportion of the snake population with 336 bait nights as we did with >5,000 trap-nights. Caution is warranted regarding such comparisons because the rate of baiting in our study did not mimic the trap density used in trapping studies (e.g., Rodda et al. 2007, Tyrrell et al. 2009). Shivik et al. (2000) documented that concealed dead mice are, for unknown reasons, particularly effective in attracting snakes during the dry season. We conducted our study during the wet season; so, in a seasonal context, our take rate estimates may be conservative, and the year-round efficacy of bait tubes even higher.

Despite this success, there are limits to the efficacy of bait tubes, as we failed to reach the smallest snakes in the population. Gape-size limitation seems not to be the prime reason for failed bait take of snakes <843 mm SVL. For example, juvenile brown treesnakes as small as 560 and 570 mm SVL, kept in the laboratory, successfully swallowed dead mice weighing 13.6 and 14.0 g, respectively; and a 665-mm SVL snake ingested a 20.3-g mouse (B. Lardner, unpublished data). Extrapolating from those data suggests that snakes ≤500 mm SVL may be physically able to ingest mice the size of the small bait we offered ($\bar{x}$ mass = 6.6 g, excluding the transmitter). However, of the 26 snakes present in the population that were between 500 and 843 mm SVL, none ingested bait mice. In the wild, these small snakes feed primarily on lizards (Savidge 1988). Small brown treesnakes prefer geckos (*Hemidactylus*) and typically

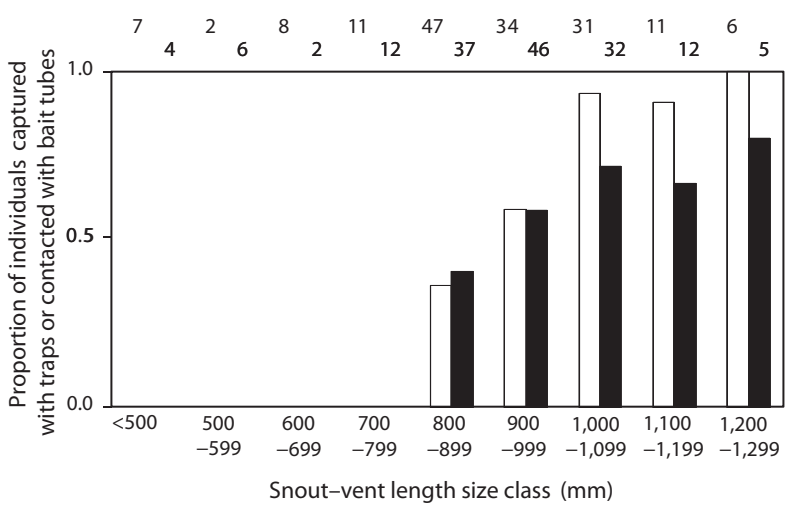

Figure 5. Proportion of brown treesnake individuals in different size classes captured with traps using a live mice attractant (white bars; $n = 82$ out of 157 snakes, in >5,000 trap-nights) and targeted with bait tubes baited with dead mice (black bars; $n = 77$ out of 156 snakes, in 336 bait-tube nights) in Guam (U.S. Territory), 2008. Numbers above the panel are the estimated numbers of snake individuals in the respective size class present during the trapping (upper row) versus the bait-tube effort (lower row).

avoid neonatal mice as well as skinks (*Carlia*) when geckos are available (Lardner et al. 2009). Geckos were abundant in the area at the time of our study (B. Lardner et al., unpublished data). Additionally, some small brown treesnakes will refuse to feed on mice even in the absence of alternative food sources (Lardner et al. 2009). Therefore, the lack of bait take by small snakes may be attributable at least partially to their aversion to the prey type we offered. We have no quantitative data to test whether additional factors may have played a role. For example, little is known about the foraging strategy of small brown treesnakes (Rodda 1992), and telemetry studies on brown treesnakes (Santana-Bendix 1994, Tobin et al. 1999) have not focused on small snakes. If small snakes are ambush foragers then they would rarely encounter stationary baits. Similarly, if larger snakes are faster at removing prey, they might out-compete small snakes by exploitative competition. Indeed, we provided far fewer prey targets than were available to snakes during our trap studies (Rodda et al. 2007, Tyrrell et al. 2009). At this study's baiting rate—about 25 mice/week for a population of 156 snakes, 126 of which were above the apparent threshold size—there was some degree of exploitation competition among snakes. We note that the density of wild rodents at the site was extremely low during our study (B. Lardner et al., unpublished data). Even so, >60% of the fresh bait and >35% of the aged bait were not taken and were therefore available to the small snakes. Despite this fact, no small snake took any bait.

We sampled a population that, at the time, had a low proportion of snakes below the apparent size threshold at which mice baiting becomes effective. Had the baiting effort been significantly higher, or had there been more small snakes, it is possible that we would have seen smaller snakes take the occasional bait. Indeed, in studies similar to ours (C. Clark, unpublished data) but that employed a larger baiting effort in an open population, snakes smaller than 800 mm SVL frequently took bait mice. We do not fully understand this apparent discrepancy, but note the following factors may contribute to the difference seen among the studies: 1) the snake measurement procedure differed between studies (snake length measured unstretched post mortem vs. stretched alive); 2) Wildlife Services removed snakes, whereas we released snakes that took bait (this potentially affects competition for bait, which may be size-biased); and 3) small mice used by Wildlife Services were smaller than ours ($\bar{x}$ mass approx. = 5 g vs. 6.6 g). Perhaps most importantly, 4) Wildlife Services had no information on the demography of the populations they sampled, so the proportion of snakes in different cohorts they targeted remains unknown.

The similarity of the lower snake size threshold for effectiveness of traps and poison bait, and the similarity in the shapes of these tools' efficacy functions (Fig. 5), imply that the primary cause of the tools' ineffectiveness for small snakes is something associated with the common target (small brown treesnakes) or common attractant (mice) rather than something uniquely associated with the design of either bait tubes or traps. This inference is strengthened by other trap-capture analyses (where snake size has been used as a covariate) that showed greatly reduced capture probabilities for the smallest snakes (Rodda et al. 1999*b*, 2007; Gragg 2004; Boyarski et al. 2008; Tyrrell et al. 2009). The sole study deviating from this pattern was based on a small sample and a suspiciously low modeled population estimate of snakes <800 mm SVL (4% of the population; Rodda et al. 1999*a*). Given the aversion to rodent ingestion often exhibited by small snakes in the laboratory (Lardner et al. 2009), our study in combination with the trap studies in aggregate indicate that it is highly unlikely that any eradication tool for small snakes will be successful if based solely on a rodent attractant. Gecko attractants have not produced yields for small snakes approaching those achieved with rodents for large snakes (Rodda et al. 1999*b;* G. Perry and G. Rodda, U.S. Geological Survey, unpublished data; Boyarski et al. 2008; B. Lardner et al., unpublished data), which suggests that some other factor must also be involved. A predilection of small snakes for sit-and-wait foraging methods would account for the poor yields in both trapping studies and the present work (stationary foragers do not readily encounter stationary control devices).

In addition to snake size, bait age had a strong effect on take rate. Higher bait take rate on the second night was seen in a previous study of brown treesnakes offered dead mice (Jojola-Elverum et al. 2001), and confirms their scavenging tendencies noted by Savidge (1988). Because cumulative take rate is higher the longer the bait is available for take, we see no obvious management benefits of withholding bait until it is in a progressed state of decomposition.

To target the largest snakes at the highest possible rate, large mice would be effective, especially after they start to decay. However, to target somewhat smaller snakes most effectively, adding small mice to the bait offered may result in a wider segment of the population being susceptible to a finite baiting effort. This highlights the value of knowing the target population demographics, and realizing that the optimal balance between different bait sizes might change during the course of an eradication effort.

Both tube types appeared to elicit bait takes equally well. The horizontal tubes were easier to manufacture and easier to bait, and had no disadvantages with regard to bait removal rate by snakes. However, in sites where entry by rats or crabs is common and non-target bait take is a problem, Mathies et al. (2011) recommended using the vertical tubes. We found no evidence that either tube type was better or worse for any particular snake size cohort, but that inference is limited to the larger snake size classes that took the bait. We do not think the lack of bait take by small snakes was due to their inability to reach mice in the tubes, because the horizontal tubes, at least, should be easy for snakes of any size to enter via the cords that suspend them from the vegetation.

Our data showed a positive correlation between snake body condition and bait-take rate. This result could not be easily predicted, because one can hypothesize a condition effect in either direction: skinny and hungry snakes may forage more actively and widely, resulting in a negative correlation; or energetically stressed snakes could preserve energy by using a

sit-and-wait predation strategy, resulting in a positive correlation. Indeed, trap-based studies with live mouse attractants have shown a body condition effect in the opposite direction of what we found here (Gragg 2004, Boyarski et al. 2008; see also Tyrrell et al. 2009). Should our results be representative of control methods using dead mice as bait, it would provide an opportunity for brown treesnake interdiction on recently colonized islands, where prey abundances would still be high. In such places, snakes will most likely be fat. Our results suggest that large fat snakes may be readily attracted with mouse carcasses.

Trapping brown treesnakes with a live mouse attractant, Tyrrell et al. (2009) found males to be 13% less trappable than females, but Boyarski et al. (2008) found the opposite pattern. Perhaps these contradictory results reflect populations at different points in females' modal reproductive cycles. Our analysis failed to show that either sex is more susceptible to dead mouse bait. Contrasting brown treesnake trap-capture rates using dead versus live mice, Shivik and Clark (1999) found no difference between the sexes in bait type effect; however, snakes they trapped with dead mice were smaller than those trapped with live mice.

Knowing the identity of all snakes in a geographically closed population allowed us to characterize not only snakes that took bait, but also individuals that did not. Snake body condition was positively correlated with take rate, but sex had no discernible effect; nor did bait-tube design. Most notably, none of the 30 snakes of <843 mm snout–vent length took any bait. Medium-sized snakes preferentially ingested small bait mice, whereas the largest snakes tended to take large mice more frequently. However, among snakes that took bait, some of the smallest individuals ingested large mice. Thus, our failure to "control" snakes <843 mm in length did not appear to be caused by gape-size limitation.

MANAGEMENT IMPLICATIONS

Although we studied take rates from bait tubes, the observation that small snakes are difficult to target with both traps and toxic bait suggests that the snake size effect is independent of the bait delivery method. Thus, our results indicate a possible limit to the effectiveness of dead mouse bait in proposed aerial broadcasts on Guam. If eradication or suppression is dependent on control tools using rodent attractants, its effectiveness may be largely limited to the snake size cohort we have identified (>843 mm SVL). After an initial baiting effort, it is therefore essential that follow-up toxicant applications be timed so that residual snakes are eliminated before they reproduce. To estimate the safe window between bait application efforts (assuming all snakes above the size threshold have already been successfully eliminated), one should take into consideration bait acceptance as a function of snake size in both male and female snakes; similar functions for sexual maturity; and the growth-rate functions for fast-growing male and female snakes. This window may correspond to a snake length increase of <100 mm (Savidge et al. 2007). If some snakes are refractory to dead mouse bait at sizes >850 mm SVL, or if some snakes become sexually mature earlier than is typical, the window of opportunity shrinks accordingly. A worst-case scenario for snake eradication efforts is that some snakes will not become vulnerable to mouse bait until after they become sexually mature. If snakes are capable of reproducing at small sizes, then it may be impossible to eradicate a brown treesnake population with mouse bait alone, and dedicated bait for small snakes would be required. Such a bait is not currently available. This would also be relevant if chronic control of larger snakes caused selection for early maturation.

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LITERATURE CITED

Anderson, D. R. 2008. Model based inference in the life sciences: a primer on evidence. Springer-Verlag, New York, New York, USA.

Boyarski, V. L., J. A. Savidge, and G. H. Rodda. 2008. Brown treesnake (*Boiga irregularis*) trappability: attributes of the snake, environment and trap. Applied Herpetology 5:47–61.

Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference: a practical information-theoretic approach. Second edition. Springer-Verlag, New York, New York, USA.

Burnham, K. P., D. R. Anderson, and K. P. Huyvaert. 2011. AIC model selection and multimodel inference in behavioral ecology: some background, observations, and comparisons. Behavioral Ecology and Sociobiology 65:23–35.

Christy, M. T., A. A. Yackel Adams, G. H. Rodda, J. A. Savidge, and C. L. Tyrrell. 2010. Modelling detection probabilities to evaluate management and control tools for an invasive species. Journal of Applied Ecology 47:106–113.

Colvin, B. A., M. W. Fall, L. A. Fitzgerald, and L. L. Loope. 2005. Review of brown treesnake problems and control programs. U.S. Department of the Interior, Office of Insular Affairs unpublished report, Honolulu, Hawaii, New York, USA.

Engeman, R. M., and D. S. Vice. 2001. Objectives and integrated approaches for the control of brown tree snakes. Integrated Pest Management Reviews 6:59–76.

Gragg, J. E. 2004. Rodent reduction for enhanced control of brown treesnakes (*Boiga irregularis*). Thesis, Colorado State University, Fort Collins, USA.

Hilbe, J. M. 2007. Negative binomial regression. Cambridge University Press, New York, New York, USA.

Jojola-Elverum, S. M., J. A. Shivik, and L. Clark. 2001. Importance of bacterial decomposition and carrion substrate to foraging brown treesnakes. Journal of Chemical Ecology 27:1315–1331.

Lardner, B., J. A. Savidge, G. H. Rodda, and R. N. Reed. 2009. Prey preferences and prey acceptance in juvenile brown treesnakes (*Boiga irregularis*). Herpetological Conservation and Biology 4:313–323.

Mathies, T., R. Scarpino, B. A. Levine, C. Clark, and J. A. Savidge. 2011. Excluding nontarget species from brown tree snake, *Boiga irregularis* (Reptilia: Colubridae), bait stations: experimental tests of station design and placement. Pacific Science 65:41–57.

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

Rodda, G. H., T. H. Fritts, and E. W. Campbell, III. 1999*a*. The feasibility of controlling the brown treesnake in small plots. Pages 468–477 *in* G. H. Rodda, Y. Sawai, D. Chiszar, and H. Tanaka, editors. Problem snake management: the habu and the brown treesnake. Cornell University Press, Ithaca, New York, USA.

Rodda, G. H., T. H. Fritts, C. S. Clark, S. W. Gotte, and D. Chiszar. 1999*b*. A state-of-the-art trap for the brown treesnake. Pages 268–283 *in* G. H. Rodda, Y. Sawai, D. Chiszar, and H. Tanaka, editors. Problem snake management: the habu and the brown treesnake. Cornell University Press, Ithaca, New York, USA.

Rodda, G. H., and J. A. Savidge. 2007. Biology and impacts of Pacific island invasive species. 2. *Boiga irregularis*, the brown tree snake (Reptilia: Colubridae). Pacific Science 61:307–324.

Rodda, G. H., J. A. Savidge, C. L. Tyrrell, M. T. Christy, and A. R. Ellingson. 2007. Size bias in visual searches and trapping of brown treesnakes on Guam. Journal of Wildlife Management 71:656–661.

Santana-Bendix, M. A. 1994. Movements, activity patterns and habitat use of *Boiga irregularis* (Colubridae), an introduced predator in the island of Guam. Thesis, University of Arizona, Tucson, USA.

Savarie, P. J., T. C. Mathies, and K. A. Fagerstone. 2007. Flotation materials for aerial delivery of acetaminophen toxic baits to brown treesnakes. Pages 218–223 *in* G. W. Witmer, W. C. Pitt, and K. A. Fagerstone, editors. Managing vertebrate invasive species: proceedings of an international symposium. U. S. Department of Agriculture, Animal and Plant Health Inspection Service, Wildlife Services, National Wildlife Research Center, Fort Collins, Colorado, USA.

Savarie, P. J., J. A. Shivik, G. C. White, J. C. Hurley, and L. Clark. 2001. Use of acetaminophen for large-scale control of brown treesnakes. Journal of Wildlife Management 65:356–365.

Savarie, P. J., and K. L. Tope. 2004. Potential flotation devices for aerial delivery of baits to brown treesnakes. Pages 27–30 *in* R. M. Timm, and W. P. Gorenzel, editors. Proceedings of the 21st vertebrate pest conference. University of California, Davis, USA.

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

Savidge, J. A. 1988. Food habits of *Boiga irregularis*, an introduced predator on Guam. Journal of Herpetology 22:275–282.

Savidge, J. A., F. J. Qualls, and G. H. Rodda. 2007. Reproductive biology of the brown tree snake, *Boiga irregularis* (Reptilia: Colubridae), during colonization of Guam and comparison with that in their native range. Pacific Science 61:187–195.

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

Shivik, J. A., and L. Clark. 1999. Ontogenetic shifts in carrion attractiveness to brown tree snakes (*Boiga irregularis*). Journal of Herpetology 33: 334–336.

Shivik, J. A., P. A. Savarie, and L. Clark. 2002. Aerial delivery of baits to brown treesnakes. Wildlife Society Bulletin 30:1062–1067.

Shivik, J. A., W. G. Wright, and L. Clark. 2000. Seasonal variability in brown tree snake (*Boiga irregularis*) response to lures. Canadian Journal of Zoology 78:79–84.

Shwiff, S. A., K. Gebhardt, K. N. Kirkpatrick, and S. S. Shwiff. 2010. Potential economic damage from introduction of brown tree snakes, *Boiga irregularis* (Reptilia: Colubridae), to the islands of Hawai'i. Pacific Science 64:1–10.

Stanford, J. W., and G. H. Rodda. 2007. The brown treesnake rapid response team. Pages 175–187 *in* G. W. Witmer, W. C. Pitt, and K. A. Fagerstone, editors. Managing vertebrate invasive species: proceedings of an international symposium. U. S. Department of Agriculture, Animal and Plant Health Inspection Service, Wildlife Services, National Wildlife Research Center, Fort Collins, Colorado, USA.

Tobin, M. E., R. T. Sugihara, P. A. Pochop, and M. A. Linnell. 1999. Nightly and seasonal movements of *Boiga irregularis* on Guam. Journal of Herpetology 33:281–291.

Tyrrell, C. L., M. T. Christy, G. H. Rodda, A. A. Yackel Adams, J. A. Savidge, K. Dean-Bradley, and R. Bischof. 2009. Evaluation of trap capture in a geographically closed population of brown treesnakes on Guam. Journal of Applied Ecology 46:128–135.

Vice, D. S., R. M. Engeman, and D. L. Vice. 2003. A comparison of three trap designs for capturing brown treesnakes on Guam. Wildlife Research 32:355–359.

Vice, D. S., and M. E. Pitzler. 2002. Brown treesnake control: economy of scales. Pages 127–131 *in* C. Clark, editor. Human conflicts with wildlife: economic considerations. National Wildlife Research Center, Fort Collins, Colorado, USA.

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at the publisher's web-site.

Supplementary Appendix A: Random-effect Poisson models used to evaluate data set with all 156 brown treesnakes, Guam, 2008. This table lists *all* models estimated, as opposed to the 95% confidence set (Burnham and Anderson 2002:169; model ranks 1–11; shown in Table 1 of the paper).

Supplementary Appendix B: Random-effect Poisson models used to evaluate data subset (125 snakes $\geq$843 mm SVL), Guam, 2008. This table lists *all* models estimated, as opposed to the 95% confidence set (Burnham and Anderson 2002:169; model ranks 1–9; shown in Table 3 of the paper).

Appendix A. Random-effect Poisson models used to evaluate data set with all 156 brown treesnakes, Guam, 2008. This table lists *all* models estimated, as opposed to the 95% confidence set (Burnham and Anderson 2002:169; model ranks 1–11; shown in Table 1 of the paper).

Rank	Variables in model[a]													K[b]	AIC[c]	ΔAIC	w_i[d]
1		B	A	S	S2		B×A			B×S				8	948.814	0.000	0.387
2		B	A	S	S2		B×A			B×S	B×S2			9	950.445	1.631	0.171
3		B	A	S	S2		B×A					A×S		8	952.123	3.310	0.074
4	T	B	A	S	S2		B×A			B×S	B×S2			10	952.226	3.412	0.070
5		B	A	S	S2					B×S	B×S2			8	952.296	3.482	0.068
6		B	A	S	S2		B×A							7	952.760	3.946	0.054
7	T	B	A	S	S2	T×B	B×A			B×S	B×S2			11	953.234	4.420	0.042
8		B	A	S	S2		B×A					A×S	A×S2	9	953.837	5.023	0.031
9			A	S	S2									5	954.590	5.776	0.022
10		B	A	S	S2									6	954.610	5.797	0.021
11	T	B	A	S	S2		B×A					A×S	A×S2	10	955.617	6.803	0.013
12			A	S	S2							A×S	A×S2	7	955.667	6.853	0.013
13		B	A	S	S2							A×S	A×S2	8	955.687	6.873	0.012
14	T		A	S	S2									6	956.370	7.557	0.009
15	T		A	S	S2			T×S						7	958.364	9.550	0.003
16	T	B	A	S	S2	T×B	B×A	T×S	T×S2	B×S	B×S2	A×S	A×S2	15	958.405	9.591	0.003
17	T		A	S	S2			T×S	T×S2					8	959.586	10.772	0.002
18	T	B	A	S	S2			T×S	T×S2					9	959.606	10.792	0.002
19	T	B	A	S	S2	T×B		T×S	T×S2					10	960.614	11.801	0.001
20				S	S2									4	961.475	12.662	0.001
21		B		S	S2									5	961.496	12.682	0.001
22	T			S	S2									5	963.256	14.442	0.000
23			A											3	997.446	48.632	0.000
24		B	A											4	997.466	48.652	0.000
25	T		A											4	999.226	50.412	0.000
26		B												3	1,004.352	55.538	0.000
27	T													3	1,006.112	57.298	0.000

[a] Variable abbreviations: T (tube type), B (bait size), A (bait age), S (snake snout-vent length, SVL), S2 (SVL^2).
[b] *K* is the parameter count including the intercept (1) and the random effect (1), denoted by alpha in Table 2.
[c] Akaike's Information Criterion.
[d] Akaike wt.

Appendix B. Random-effect Poisson models (95% confidence set) used to evaluate data subset (125 snakes ≥843 mm SVL), Guam, 2008. This table lists *all* models estimated, as opposed to the 95% confidence set (Burnham and Anderson 2002:169; model ranks 1–9; shown in Table 3).

Rank	Variables in model[a]														K[b]	AIC[c]	ΔAIC	w_i[d]
1	B	A	S	C		B×A	B×S								8	930.665	0.000	0.316
2	B	A	S	C		B×A	B×S	C×S	C×S2						10	932.132	1.466	0.152
3	B	A	S	C		B×A	B×S	C×S							9	932.473	1.807	0.128
4	B	A	S	C	G	B×A	B×S								9	932.605	1.940	0.120
5	B	A	S	C	G	B×A	B×S			G×S					10	933.796	3.131	0.066
6	B	A	S	C	G	B×A	B×S	C×S	C×S2						11	934.031	3.366	0.059
7	B	A	S	C	G	B×A	B×S	C×S							10	934.438	3.773	0.048
8	B	A	S	C	G	B×A	B×S			G×S	G×S2				11	934.867	4.202	0.039
9	B	A	S			B×A	B×S								7	936.045	5.380	0.021
10	B	A	S		G	B×A	B×S								8	936.877	6.212	0.014
11	B	A	S	C	G	B×A	B×S	C×S	C×S2	G×S	G×S2	C×G×S			14	937.249	6.583	0.012
12	B	A	S	C	G	B×A	B×S	C×S	C×S2	G×S	G×S2				13	937.264	6.598	0.012
13	B	A	S		G	B×A	B×S			G×S					9	938.352	7.686	0.007
14	B	A	S	C	G	B×A	B×S	C×S	C×S2	G×S	G×S2	C×G×S	C×G×S2		15	939.115	8.450	0.005
15	B	A	S		G	B×A	B×S			G×S	G×S2				10	939.838	9.172	0.003

[a] B (bait size), A (bait age), S (snake snout-vent length, SVL), S2 (SVL^2), C (body condition index; BCI), G (sex).
[b] *K* is the parameter count including the intercept (1) and the random effect (1).
[c] Akaike's Information Criterion.
[d] Akaike wt.