Efficacy, effort, and cost comparisons of trapping and acetaminophen-baiting for control of brown treesnakes on Guam

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Abstract: Brown treesnakes (*Boiga irregularis*) are an invasive species to the island of Guam. Because they have extirpated the native forest avifauna on Guam and are a threat to other Pacific islands, the development of efficient and cost-effective methods to control them is desired. We compared the efficacy, cost, and effort required to remove brown treesnakes on 6-ha plots in forest scrub on Guam, using 2 methods: trapping and poison baiting. Toxic baits consisted of dead neonatal mice adulterated with 80-mg acetaminophen. To assess efficacy, we used mark-recapture methods to estimate snake abundance on plots 12 days before and 12 days after treatment. We also monitored bait-take or trap success for 20 days during treatment. From 6,304 trap-nights, we recorded 801 captures of 504 snakes on 6, 6-ha plots during a 51-day period. Snake populations on plots ranged from 41 to 107 prior to treatment. Using trapping to gauge survival of marked snakes, the 2 methods (trapping and baiting) had similar efficacies (0.05 to 0.1). Based on trapping, post-treatment population estimates ranged from 26 to 40, yielding reductions from estimated pre-treatment populations of 7 to 68% for both types of snake-removal treatments. Using post-treatment bait-take of unadulterated mice as an index of efficacy, poisoned baiting was twice as effective as trapping in diminishing snake activity. Trapped plots had post-treatment bait-take rates similar to reference plots (75%), whereas poison-baited plots had bait-take rates of 38%, suggesting that some snakes cannot be trapped and that baiting affects a wider range of the snake population. Because of the potential for baiting to impact more snakes, this method was about 1.67 times more cost effective than trapping. If baiting were to occur via aerial drop rather than via bait stations, the economic incentive for using baiting as a control strategy would be even greater. These observations will prove useful for managers making decisions about appropriate methods for control of brown treesnake populations.

Key words: acetaminophen, baiting, *Boiga irregularis*, control, cost efficiency, human–wildlife conflicts, trapping

Brown treesnakes (*Boiga irregularis*) are nocturnal, primarily arboreal, rear-fanged, mildly venomous colubrids native to Australia, Indonesia, New Guinea, and the Solomon Islands. Brown treesnakes were probably introduced onto Guam in the late 1940s or early 1950s (Savidge 1987). Since that time, their population has irrupted, at times reaching densities of 50 to 100 snakes/ha (Rodda et al. 1992). Consequences of this population increase include the decline and extinction of avifauna and herpetofauna (Savidge 1987, Rodda and Fritts 1992), power outages (Fritts et al. 1987), loss of domestic animals (Fritts and McCoid 1991), and threats to human health and safety (Fritts et al. 1994). Because of concern that these snakes may be transported to other island ecosystems, considerable effort is being invested in snake control and containment programs and research (McCoid et al. 1994, Rodda et al. 1998, Fritts et al. 1999). Currently, the primary management tools used in containment programs include traps containing live mouse lures, hand capture, and detector dog teams (Engeman and Linnell

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1998, Engeman et al. 1998*a*, 1998*b*, Linnell et al. 1998, Rodda et al. 1999*a*, Vice and Pitzler 2002). Other methods, such as barriers, fumigants, and toxicants also have been investigated (Savarie et al. 1999, Savarie et al. 2001, Savarie et al. 2005). Additional concerns focus on reducing snake density on the island of Guam, toward the goal of repatriating forest birds currently being held in captive breeding programs at other locations.

Engeman et al. (1998*b*) evaluated the effectiveness of different snake control methods (e.g., trapping, detector dogs, hand-capture). Shivik and Clark (1997) documented the attractiveness and practical use of mouse carrion as an inanimate lure and bait for brown treesnakes, and Savarie et al. (2001) demonstrated the practicality and efficacy of using dead mice laced with a snake toxicant, acetaminophen, to reduce survivorship of snake populations on small plots (~ 6 ha) to zero. How poisoned baiting compared to trapping in efficacy and cost was the objective of this study.

Study area

We carried out evaluations of control techniques on plots of approximately 6-ha in size on the munitions storage area, Andersen Air Force Base, Guam. Forested scrub plots used within the Munitions Storage Area are transected by access roads in a regular grid pattern, providing for semi-isolated plots of approximately equal size (Figure 1).

Methods
Study plots 6 months after previous control efforts

Plots on the munitions storage area were selected based on availability relative to ongoing military base activity. This necessitated us having to use plots that were used in previous experiments. In February 2000 and prior to initiating the experiment, we monitored bait-take on study plots 1 to 6 to assess whether these areas recovered from previous snake removal activities that occurred during the summer of 1999 (Savarie et al. 2001). We placed unadulterated, dead neonatal mice inside bait stations along the forest perimeters on the study plots at 20-m intervals. A record of mouse bait-take was made at the same time
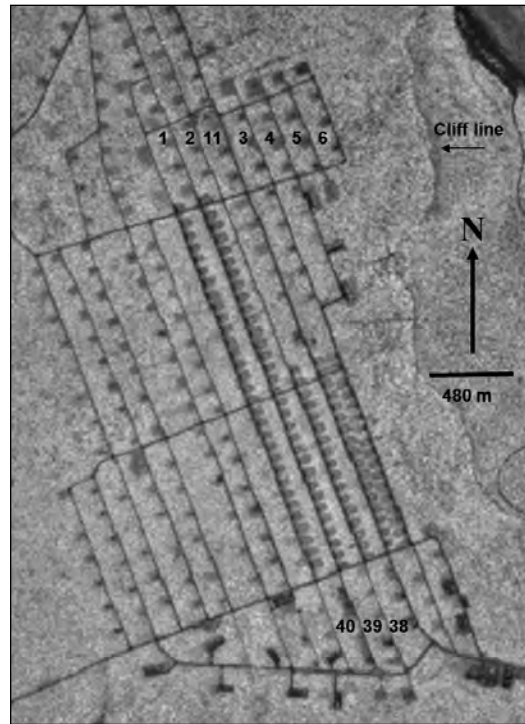
Figure 1. Spatial layout of plots in the munitions storage area, Andersen Air Force Base, Guam, during the summer of 2000.

of day every other day over a 6-day period. During the first and second checks, old baits were removed, and all bait stations received new baits. Owing to variations in plot size, the number of bait stations varied (n = 64, 60, 60, 62, 60, and 63, respectively). We used a fixed effects, 3-way, repeated measures analysis of variance to partition experimental effects, where the rate of disappearance of baits was the dependent variable, the between measures effect was treatment history (Savarie et al. 2001; 2 levels—acetaminophen plots and matched nontreated reference plots) and the repeated (within) measures effects were day (3 levels—day 2, 4, and 6) and month (2 levels—August 1999 and February 2000).

We do not report on the entire model because many of the terms are biologically uninteresting or trivial. Rather, we report on 3 specific biological questions of interest, using simple orthogonal contrasts: (1) did UMB-take, and by implication, snake numbers, on the acetaminophen-treated plots increase after control efforts were discontinued (i.e., the within acetaminophen post-treatment comparison of UMB-take between August 1999 and February

2000); (2) did bait-take on the reference plots change after control efforts were discontinued (i.e., the within reference treatment comparison of bait-take between August 1999 and February 2000); and (3) did the post-experimental UMB-take differ among plots as a function of control history (i.e., the within February 2000 comparison of bait-take of the reference and acetaminophen treated plots)? The precondition of no carry-over effect was met (see below), and the main experiment is described below.

Plot assignments

We define experimental controls as reference plots; and we use the term, control, as the methods of snake removal (i.e., trapping or poisoning by baiting with acetaminophen-laced dead neonatal mice). Plot assignment to treatment type was random for plots 1 to 6. Treatments consisted of removal by trapping (plots 1, 6), removal by poisoning (plots 4, 11), and no removal (plots 38, 40). Buffer plots were used to minimize experimental carryover effects of treatments (plots 2, 3, 5, 39). Reference plots 38 and 40 were selected as being isolated from previous and ongoing treatment assignments and to further control for removal carryover (migration) effects during the observations.

Experimental time course

The experiment proceeded along the time course of cumulative test days (CTD): pretreatment mark-recapture (CTD 1 to 12), treatment (CTD 13 to 32), post-treatment mark-recapture (CTD 33 to 44), and post-treatment UMB-take indexing (CTD 45 to 51).

Bait stations

We used 10-cm diameter multiplied by 30-cm length sections of white PVC pipes as bait stations suspended about 1.5 m high in vegetation. During the treatment period (CTD 13 to 32), we used the proportion of baits taken as an index of snake activity on the poisoned plots (plots 4, 11); mouse baits contained 80 mg acetaminophen per mouse. All laboratory and field evidence indicated that snakes ingesting this dose die within 48 hours (Savarie et al. 2001). To match removal effort of bait station to traps, stations were placed at 30-m intervals (Engeman and Linnell 2004). During the post-treatment period (CTD 45 to 51), we used the proportion of baits taken as an index of snake activity on all plots. Surveys of bait stations were conducted at the same time every other day over 6 days, as described above.

Traps

We used standard, 1-piece U.S. Department of Agriculture, Wildlife Services' (WS) brown treesnake traps, which are similar to modified minnow traps ,with 1-way flap doors (Vice et al. 2005). Following WS procedures, we suspended traps about 1.5 m high in vegetation to capture snakes (Linnell et al. 1998). We used live adult laboratory mice (*Mus musculus*) as the lure. Mice were contained in an inner cage within the trap and were provided a food block of mixed grain in paraffin and a potato as a source of water. Spacing of traps depended upon the objective (mark-recapture or removal; see below).

Comparison of trapping and baiting as control methods

Mark-recapture. We estimated snake abundance and survivorship for each plot by trapping, marking, and recapturing snakes. During the pre- (CTD 1 to 12) and post-treatment (CTD 33 to 44) trapping periods, we placed trap stations at 40-m intervals in lines along the perimeter of each plot (Engeman and Linnell 2004). Owing to variations in plot size, plots 1, 4, 6, 11, 38, and 40 contained 31, 28, 29, 28, 41, and 34 traps, respectively. Each trap was hung about 1.5 m high on woody vegetation. Traps were checked daily. Brown treesnakes were captured and marked by inserting microchips subcutaneously, under ventral scales proximal to the vent, so that all captures resulted in our ability to identify individuals. Upon capture, all snakes were scanned with a microchip reader (AVID). Snakes were identified using a unique electronic identifier, scored for sex (by probing hemipenes), measured for snout-to-vent length (SVL), and weighed before they were released at the capture site. For empirical descriptions of trapping patterns per plot, we defined capture rate as the number of snakes captured per night divided by the number of traps per plot.

We used program MARK (White and Burnham 1999) to analyze snake-encounter histories. Specific parameters of interest included number and survival of snakes on control and treated plots pre- (CTD 1 to 12)

and post-treatment (CTD 33 to 44). We used the robust design model (Kendall and Nichols 1995; Kendall et al. 1995, 1997) to determine survival (probability of survival multiplied by probability that the animal remained on the study area) between pre- and post-trapping sessions, population size (N) before and after treatment on each plot, as well as initial capture (p) and recapture (c) probabilities. Because only 2 primary trapping sessions were available, the probability of leaving the trapping grid conditional on being on the trapping grid during the previous primary session (y″) was set to zero, and the probability of remaining off the trapping grid conditional on being off the trapping grid during the previous session (y′) never appeared in the model. Models were ranked using AICc and were averaged to determine final parameter estimates using AICc weights (Burnham and Anderson 1998).

Experimental treatments. During CTD 13 to 32, we assigned plots to one of 3 treatment levels: removal by trapping (plots 1 and 6), removal by poisoning (plots 4 and 11), and no removal as monitored in spatially isolated reference plots (plots 38 and 40). These latter plots allowed us to track snake activity through time without potential confounding carryover effects that occur when reference plots are adjacent to plots where snakes are removed.

For the removal by trapping treatment, we spaced traps at 30-m intervals, resulting in 43 traps each for plots 1 and 6 (Engeman and Linnell 2004). We checked traps every 3 days (except the last check, which was made on the second day) and removed snakes for sacrifice when they were present. We collected vital statistics on snakes as described above. For the plots where we effected removal with adulterated mouse baits (AMBs), we spaced bait stations at 30-m intervals, resulting in 42 and 44 bait stations for plots 4 and 11, respectively. We increased the distance between bait stations over that employed by Savarie et al. (2001) to reduce the likelihood of multiple bait-takes by individual snakes and to increase logistic efficiency. At bait station intervals of 25 m, Campbell and Sugihara (2001) showed that snakes from marked populations in 2 field studies took an average of 1.13 toxic baits per night. Snakes died between 24 to 36 hours after ingestion, thus, precluding the possibility that additional baits

would be consumed by those snakes (Clark and Savarie 2012). We checked bait stations every other day and noted the presence or absence of baits, after which we added new baits to empty stations, or replaced uneaten baits with new baits. No activity occurred at the isolated reference plots during the treatment period. It should be noted that we employed fewer bait stations per unit area (~ 6 ha) and conducted removal by poisoned-baits for a shorter time (i. e., 20 versus 30 days) relative to the Savarie et al. (2001) study. However, the 30-m spacing interval for traps and bait stations assured an equal spatial effort for snake removal.

Post-treatment bait-take. Very small (<700 mm SVL) and very large snakes (>1500 mm SVL) may be underrepresented using the USDA trap design (Rodda et al 2007). Video analyses of bait-take in our laboratories suggest that the open design of bait stations is more broadly accessible to all size classes of snakes (L. Clark, U.S. Department of Agriculture, personal observation). Thus, we used bait-take of untreated mice presented in bait stations as an alternative index of snake activity on all plots following the conclusion of the post-treatment trapping mark-recapture period. (CTD 45 to 51). We spaced bait stations at 30-m intervals. Plots 1, 4, 6, 11, 38, and 40 had 43, 42, 43, 44, 57, and 48 bait stations, respectively. We checked and replaced unadulterated baits every other day.

Cost estimates for control method. The cost-effectiveness (CE) of each control method was based on a cost per snake captured or killed basis (Caudell et al. 2010) and described by:

$$C_{E,i} = (C_{M,i} + C_{L,i}) / S, \qquad (1)$$

where $C_{M,i}$ and $C_{L,i}$ are the monetary costs of material and labor for method, i, respectively, and S was the number of snakes killed or captured. For the baiting control method, the number of snakes killed was estimated as the number of baits taken divided by the mean number of baits taken per snake (i.e., 1.4 baits persnake). Most of the relationships involved in computing $C_{M,i}$ and $C_{L,i}$ are fixed or derived in a straightforward manner, as indicated below.

The term for materials for method *i* was defined as

$$C_{M,i} = (c_{w,i} + c_{f,i} + c_{l,i} + c_{d,i}), \qquad (1.1)$$

where $c_{w,i}$ was the cost of the water source required to support the lure used for method i, (e.g., potato for the live mice); $c_{f,i}$ was the cost of materials and labor for the manufacture of the food source for method i, (e.g., bait blocks for live mice); $c_{l,i}$ was the daily prorated cost of the lure for method i; and $c_{d,i}$ was the daily prorated cost of the device for method i. These terms are defined as

$$c_{w,i} = w_i \cdot N_i \cdot (D_i / r_i), \qquad (1.2)$$

where w_i was the average market price of a single potato, r_i was the day interval for checking the device, D_i was the number of days devices are deployed, and N_i was the number of devices used;

$$c_{f,i} = f_i \cdot N_i \cdot (D_i / r_i) \qquad (1.3)$$

where f was the average price of material and labor needed to produce the food source for the lure;

$$c_{l,i} = N_i \cdot D_i \cdot (l_i / e_{l,i}), \qquad (1.4)$$

where l_i was the cost of the lure, in this case either a live or dead mouse, and $e_{l,i}$ was the average life expectancy of the lure; and

$$c_{d,i} = N_i \cdot D_i \cdot (d_i / e_{d,i}), \qquad (1.5)$$

where d_i was the cost of the device and $e_{d,i}$ was the average life expectancy of the device in the field, owing to destructive forces such as damage by corrosion, wind, pigs, and ungulates. Substituting the terms into Equation 1.1 and rearranging the equation yields:

$$C_{M,i} = D_i \cdot N_i \cdot [(w_i/r_i) + (f_i/r_i) + (l_i/e_{l,i}) + (d/e_{d,i})]. \quad (2)$$

The cost of the labor required to maintain devices in the field was based on the effort of 2 investigators who recorded the time required to walk the perimeter of trapped and baited plots and maintain those devices.

The method to calculate the labor cost required to check and process traps (i = trap) was slightly more complex, and can be expressed as

$$C_{L,i} = (\sum T_{j,k} \cdot W) / FTE, \qquad (3)$$

where T was time in minutes for the jth plot and k^{th} maintenance interval; W was the annual salary and benefits of a full-time technician at the time of the study (US $ 32,841); and FTE was the annual full time equivalent in minutes of the salaried employee (1.248×105). Normally, operational personnel check traps every 7 days. However, we checked traps every 3 days during the course of this study. To standardize the labor costs patterned after a normal operational program, we regressed the time we spent checking the trapped plots against the number of snakes captured on those plots and found the linear relationship ($R^2 = 0.879$):

$$T_{j,k} = b + m \cdot S_{j,k}, \qquad (4)$$

where the b was the minimum time (64.48 minutes) required to walk the perimeter of each experimental 6-ha plot and maintain the live mice; m was the number of minutes required to process a snake (5.19), and $S_{j,k}$ was the number of snakes captured for the jth plot and k^{th} sampling interval.

The above approach represents the cost-effectiveness of control operations where the control effort is spatially defined and temporally finite and allows for a direct comparison of the control methods (trapping and acetaminophen baiting) used in this study, given study parameters. Other approaches to cost effectiveness of control programs, overall economic impacts, and cost-benefit ratios can be taken but are not directly considered in this study. All values are expressed as mean ± standard error unless otherwise noted.

Results
Study plots 6 months after previous control efforts

Savarie et al. (2001) showed that baits reduced densities of snakes on treated plots. Despite this success, bait-take returned to pretreatment levels 6 months after the end of the experiment (Figure 2). The within-acetaminophen-plot contrast between August 1999 and February 2000 for rate of unadulterated bait-take was F = 26.96; df = 1,4; P < 0.01, where the average rate of bait-take at the end of the Savarie et al. (2001) study in August 1999 went from 0.15 on poisoned plots to 0.64 in February 2000. By comparison, there was no temporal change

Table 1. Disappearance rates of baits from stations as a function of treatment received in 1999 and during a survey 6 months after the end of the 1999 study.

| Plot	Treatment[c]	September 1999[a]			February 2000[b]	
		n[d]	Mean[e]	SE	Mean[e]	SE
1	Acetaminophen	64	0.10	0.02	0.37	0.05
4	Acetaminophen	62	0.13	0.02	0.75	0.04
6	Acetaminophen	63	0.21	0.04	0.78	0.02
2	Control	60	0.96	0.01	0.73	0.04
3	Control	60	0.98	0.01	0.89	0.05
5	Control	60	0.89	0.01	0.93	0.01

[a] The proportion of unadulterated baits taken at the end (post-treatment period) of the Savarie et al. (2001) study.
[b] The proportion of unadulterated baits taken during the 6-month post treatment evaluation.
[c] The method of snake control used on plots during the Savarie et al. (2001) study was acetaminophen laced baits or unadulterated baits (control).
[d] Number of bait stations per plot.
[e] Means and standard errorswere calculated as the proportion of baits taken per plot, averaged over 3 sampling intervals.
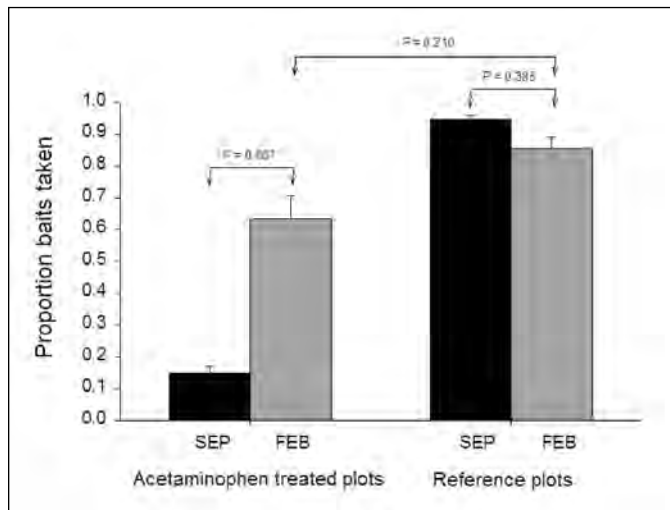
Figure 2. The proportion of unadulterated baits taken from bait stations as a function of plot type. Plot type refers to the treatment the plots received 6 months prior to the current evaluation. Unadulterated baits were presented in bait stations on reference plots. Acetaminophen-adulterated baits were presented in bait stations on acetaminophen-treated plots.

in the rate of bait-take for plots previously designated as controls (F = 0.95; df = 1,4; P = 0.38). Indeed, by February 2000, 6 months after snake control efforts ended, there was no indication that previous experimental treatment had any effect on the rate of bait-take (Table 1; F = 2.23, df = 1,4, P = 0.21).

Characterizations of snakes captured

Between May 22 and July 5, 2000, we captured 504 individuals over 6,304 trap nights, with 178 snakes of those captured >2 times, yielding 801 captures during the study. Snakes ranged from 587 to 1,395 mm SVL (Figure 3), with a mean length of 1,017 + 7 mm. Previous control efforts did not appear to impact the size distribution of snakes (χ^2 = 0.79, P > 0.37). On average, snakes weighed 121 + 3 g and ranged from 23 to 663 g at initial capture (Figure 4). Brown treesnakes larger than 1,000 mm SVL are considered to be mature and capable of breeding (Mathies et al. 2010). Approximately 53% of the snakes we captured were mature.

Pre- and post-treatment comparison of snake abundance using the trap success index

The effects of control varied as a function of treatment, space, and time. The minimum AICc robust design model included survival rate varying between the reference plots and the 4 removal plots combined, initial capture probabilities varying by session, recapture probabilities constant across days within a session, and population size estimates for each plot before and after treatment (Table 2). Both methods of removal, trapping and poisoning, reduced the post-treatment trapping success relative to the within-plot pre-treatment trap success, and relative to the reference plots (Figure 5). The level of effect was similar for the 2 types of removal method.

Snake removal lowered the estimated snake population size per plot. Estimates of the initial population sizes for the study plots based on model-averaged values were 41 to 107 snakes during the pre-treatment period

Table 2. Model parameters and AICc values for robust design models examining brown treesnake survival and population size from 6 plots (2 treated by trapping and removal, T; 2 treated with acetaminophen, A; or 2 untreated control plots, C) during pretreatment or post-treatment intervals on Andersen Air Force Base, Guam, during summer 2000.

Model	Δ AICc	AICc weights	Number of parameters	Deviance
{S(Combined) p(Session) c(.) N(Session*Plot)}[a]	0.00	0.59	17	864.56
{S(Treatment) p(Session) c(.) N(Session*Plot)}[b]	1.56	0.27	18	864.00
{S(Combined) p(.) c(.) N(Session*Plot)}[c]	4.29	0.07	16	871.00
{S(Plot) p(Session) c(.) N(Session*Plot)}[d]	4.75	0.05	21	861.00
{S(Treatment) p(.) c(.) N(Session*Plot)}[e]	8.13	0.01	16	875.00
{S(Plot) p(.) c(.) N(Session*Plot)}[f]	9.01	0.01	20	867.20
{S(Combined) p(.) = c(.) N(Session*Plot)}[g]	9.14	0.01	15	877.92

[a] Survival varies among control plots and the 4 treatment plots combined with initial capture probability varying by session, recapture probability constant and estimating population size for each session and plot combination.
[b] Survival varies by treatment, with initial capture probability varying by session, recapture probability constant, and estimating population size for each session and plot combination.
[c] Survival varies among control plots and the 4 treatment plots combined with initial and recapture probabilities constant and estimating population size for each session and plot combination.
[d] Survival varies by plot with initial capture probability varying by session, recapture probability constant and estimating population size for each session and plot combination.
[e] Survival varies by treatment, with initial and recapture probabilities constant and estimating population size for each session and plot combination.
[f] Survival varies by plot with initial and recapture probabilities constant and estimating population size for each session and plot combination.
[g] Survival varies among control plots and the 4 treatment plots combined holding initial capture and recapture probabilities constant and equal while estimating population size for each session and plot combination.

Table 3. Population estimates (N) for brown treesnakes on 6 study plots on Andersen Air Force Base, Guam, during the summer of 2000.

| Plot[a]	Pretreatment		Post-treatment	
	N[b]	SE	N[b]	SE
1-T	41	4	38	19
6-T	107	9	40	20
4-A	81	7	26	13
11-A	85	7	40	20
38-R	61	6	69	33
40-R	62	6	78	37

[a] Treatments consisted of snake removal by trapping (T) on plots 1 and 6, baiting with acetaminophen (A) on plots 4 and 11, and no removal on reference Plots 38 and 40 (R).
[b] Estimates are from model-averaged robust design models in program MARK.

(Table 3). During the post-treatment period, we estimated the population size within the reference plots to be 69 to 78. During the post-treatment period, we estimated the snake population in acetaminophen treated plots to be 26 to 40 snakes per plot and for the trapped plots to be 38 to 40 snakes per plot. Apparent survival of snakes between pre- and post-treatment trapping sessions was lower on plots experiencing snake control (~0.10) relative to the reference plots (0.63; Table 4).

Patterns of snake activity during treatment

Despite differences in the number of snakes per plot prior to the start of removal, the profiles for the rates of snake capture and bait-take during the treatment period (CTD 13-32) were similar (Figure 6). Snake capture and bait-take converge to minimum asymptotic levels of 0.10 to 0.20 (Table 5), suggesting that an equilibrium between removal and encounter to the control method (perhaps owing to immigration) was achieved within 10 to 14 days (Figure 6).
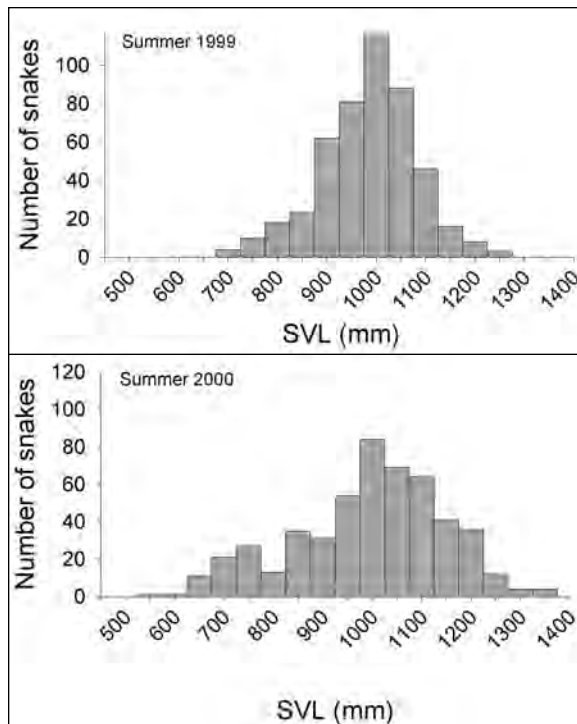
Figure 3. Frequency distribution of snout-to-vent lengths (SVLs) of brown treesnakes captured on Andersen Air Force Base, Guam, 1999 and 2000.

Table 4. Apparent survival estimates during the study period for each plot for brown treesnakes on 6 study plots on Andersen Air Force Base, Guam during the summer of 2000.

Plot[a]	S[b]	SE
1-T	0.10	0.05
6-T	0.10	0.06
4-A	0.12	0.07
11-A	0.12	0.07
38-R	0.63	0.30
40-R	0.63	0.31

[a] Between the 2 trapping sessions, snakes were removed by trapping (T) on plots 1 and 6. Baits containing acetaminophen (A) were placed onto Plots 4 and 11. No removal treatment occurred on plots 38 and 40, the reference plots (R).
[b] Estimates were constructed using model-averaged robust design models in program MARK with confidence intervals based on a logit transformation. Estimates do not account for movement of snakes out of the study area and onto treatment plots.

Empirical bait-take patterns during post-treatment

The trapping data suggest that both trapping and poisoned baiting were equally effective in reducing snake populations on the experimental plots relative to the reference plots. However, using bait-take as an index of snake presence on the plots suggests that this may not be the case. The average disappearance rate of UMBs on the reference plots was 0.78 snakes per day. Surprisingly, the average disappearance rate of UMBs on plots where snakes were previously removed by trapping was 0.76, and the disappearance rate of UMBs on previously baited plots was 0.38. Population estimates for brown treesnakes on acetaminophen plots 4 and 11 were 81 and 85 snakes, respectively. However, the total number of baits taken on these plots was 145 and 150, respectively. We infer from these patterns that many more snakes still remained on the trapped plots after control efforts relative to the baited plots.

Comparative cost-effectiveness of the 2 control methods

The use of poisoned baits in this study was a more efficient way to reduce snake numbers relative to trapping (Tables 6, 7). The prorated, per capita cost of capturing a snake using traps was $4.08 per snake trapped. The cost of trapping was 1.67 times the cost of snake removal using poisoned baits (i. e., $2.45 per snake killed), assuming a 1:1.13 ratio of bait taken to snakes killed. Trapping was more costly across all labor and material categories relative to baiting, with the exception of the cost of the mouse lure-bait (Table 7). Because of this asymmetry in cost between the 2 methods, the total costs for deployment are approximately equal for the baiting versus trapping. However, bait stations appear to remove more snakes than do traps; hence, baiting is a more efficient method of removal.

Discussion
Measures of efficacy

Raw capture rates and mark-recapture methods for estimating population and survivorship of snakes caught by traps are the most frequently used indices for evaluation of efficacy of control management methods. Using only these indices, it was clear that removal both by trapping and poisoned baiting were equally effective control methods. Raw captures rates
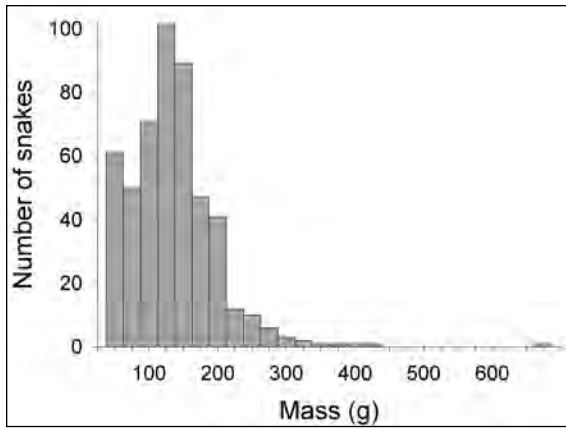
Figure 4. Frequency distribution of mass of brown treesnakes captured on Andersen Air Force Base, Guam, 2000.

Table 5. Parameter estimates and associated standard errors for the curves relating rate of capture of brown treesnakes or rate of bait disappearance attributable to snakes during the treatment period for study plots on Andersen Air Force Base, Guam, during the summer of 2000. R^2 is the proportion of the variance in capture rate explained by the model.

Parameter[a]	Trap		Acetaminophen	
	Plot 1	Plot 6	Plot 4	Plot 11
R^2	0.94	0.93	0.92	0.90
$a \pm$ SE	0.21 ± 0.04	0.53 ± 0.11	1.79 ± 3.00	0.48 ± 0.09
$b \pm$ SE	-0.20 ± 4.75	-0.52 ± 4.02	-6.63 ± 7.87	-1.35 ± 1.19
$x_o \pm$ SE	20.80 ± 4.77	20.75 ± 2.01	13.97 ± 11.02	20.22 ± 0.69
$y_o \pm$ SE	0.10 ± 0.02	0.20 ± 0.01	0.19 ± 0.04	0.19 ± 0.04

[a] Parameters were estimated using the Marquardt-Levenberg algorithm for the Gompertz equation of the form, $y = yo + a.exp(exp(-((x - xo)/b)))$ (STATISTICA 1994).

Table 6. Variable values used in calculating costs for the control method.

Method, i	N_i (#)	D_i	r_i (Days)	$e_{l,i}$	$e_{d,i}$	l_i	w_i	d (US $)	f_i
Trapping	86	21	7	180	720	2.50	0.15	57.00	0.50
Baiting	86	20	1	2	720	0.50	0.00	1.20	0.00

Not surprisingly, the other measures of treatment effects parallel these findings. Estimates of survival from the pre- to post-treatment period were around 5 to 10% for the 2 types of removal plots and 65% for the reference plots. In addition, population estimates for the removal plots decreased, while the population estimate increased for the reference plots.

A question remains as to the fate of snakes marked on the study plots but never seen again. They may have left the plots, or they may have reduced their activity owing to quiescence attributable to satiety or oviposition. It is likely that some combination of movement and quiescence may influence apparent disappearance of marked snakes and appearance of new snakes occurring on plots (Savarie et al. 2001, Clark and Savarie 2012). Previous research has shown that brown treesnakes move <70 m over relatively short time periods (<40 days), even after consuming treated baits (Tobin et al. 1999, Shivik et al. 2002) While brown treesnakes will become inactive if satiated, our observations over the years on the prey base exploited by these snakes and laboratory feeding trials suggest that the snakes never become satiated for natural prevailing conditions on Guam. If the new snakes are immigrants, then any control effort must be accompanied by efforts to prevent further intrusion into the controlled area (e.g., barriers). This was clearly important, given that bait-take on acetaminophen-treated plots returned to pretreatment levels within 6 months after the treatment ended. If the snakes captured during the post-treatment period are derived from within the plot, then questions arise about improvements in the control method or amount of time such a method is employed.

decreased by about 77% from the pre- to post-treatment periods for the 2 methods of removal. Although there was some indication for a time effect in the AICc models, as evidenced by a 44% decrease in raw capture rates on the reference plots, the larger negative change in capture rate for the treated plots suggests some level of efficacy for both removal techniques.

Table 7. Summary of costs in U.S. dollars (2000) associated with snake control methods on Andersen Air Force Base, Conventional Weapons Storage Area, Guam.

Cost category	Combined cost of trapping n = 86	Combined of cost baiting n = 86
Materials		
c_w	$ 38.70	$ 0.00
c_f	$129.00	$ 0.00
c_l	$ 25.08	$430.00
c_d	$142.98	$ 3.01
Subtotal	$335.76	$433.01
Pro-rated cost/unit	$ 3.90	$ 5.03
Labor	$321.69	$209.99
Total	$657.45	$643.00
Snakes captured or killed	161	262[b]
Efficiency ($/snake removed)	$ 4.08	$ 2.45

[a]Materials: *cw* (water source), *cf* (bait), *cl* (lure), *cd* (device)
[b]Number of baits taken (295) divided by the mean number of baits taken/snake (1.13; from Campbell and Sugihara 2001).

Resolution of these questions is critical in the development of an effective management plan.

Another problem to consider in evaluating the efficacy of control measures is the method of estimating success. Mark-recapture techniques using robust design estimates for survival and population levels assume closed systems and equal probability for all individuals to be captured. There is evidence from our laboratory that this is not the case. Infrared videography (L. Clark, U.S. Department of Agriculture, unpublished data) showed that only 20% of visits by snakes to traps result in capture, yet, >90% of visits to a bait station result in bait-take by snakes. These observations are consistent with the notion that some snakes are untrappable or difficult to trap.

While we do not know how the index for bait-take relates to extant populations on plots, we suggest that trapping rates and bait-take rates provide differing benchmarks of success for a control program. The raw capture and bait-take rates indicate that the elimination of snakes during the treatment period are parallel, suggesting that the 2 methods are equally effective to about the same level (Figure 6). Moreover, when post-treatment trapping was used to assess survivorship of marked individuals and to provide population estimates, the equality of the techniques was borne out (Figure 5). However, when an index for bait-take was used as a comparative post-treatment measure of efficacy, we found that the 2 methods of control are not equally effective (Figure 7). Thus, despite similarities in post-treatment trap success, the bait-take on plots where removal was achieved by trapping was similar to the reference plots and was substantially greater than the bait-take recorded on plots where the removal method was achieved by the use of acetaminophen-laced baits.

The difference may stem from the greater accessibility of snakes to bait tubes relative to the trap. Considering the geometry and source of foraging signals for snakes of the 2 capture devices, when presented in a tube, the bait is visible only from the 2 open ends, and the odor source of the carrion is being emitted only from these ends. Moreover, even though the source of the signals (i.e., the 2 ends of the tube) relevant to foraging snakes is only 10% of the total surface of the bait tube, these ends represent 100% of the signal source. Snakes approaching bait stations show directed investigatory
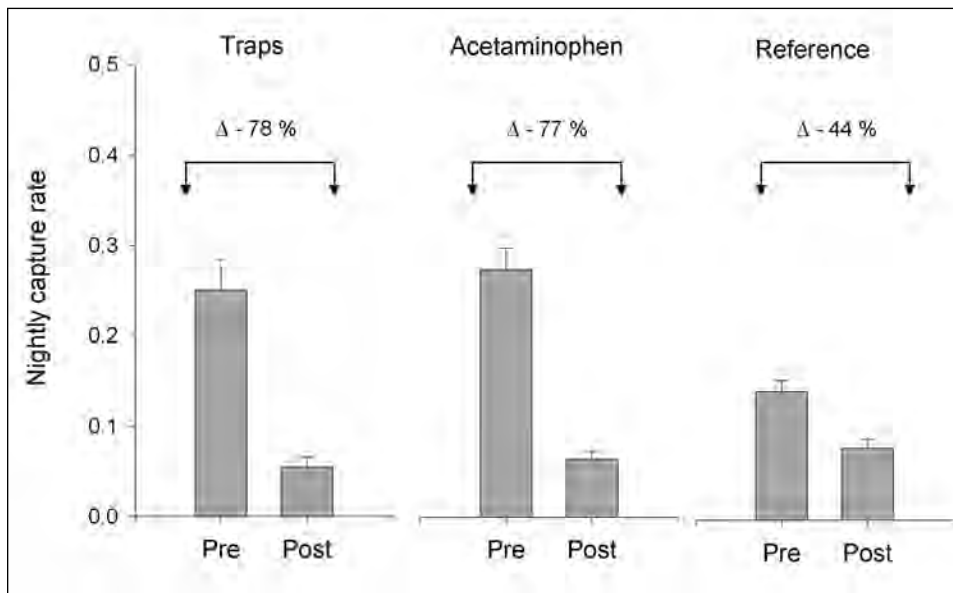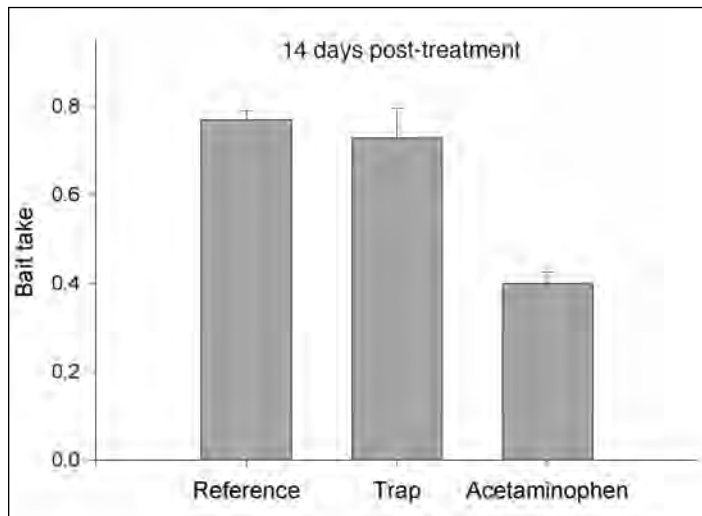
Figure 5. Comparison of pre- and post-treatment nightly capture rates of brown treesnakes in traps as a function of plot treatment on Andersen Air Force Base, Guam, 2000: removal by trapping (trap), removal by poisoned baiting (acetaminophen), and no removal method (reference). Values depict means + SE.
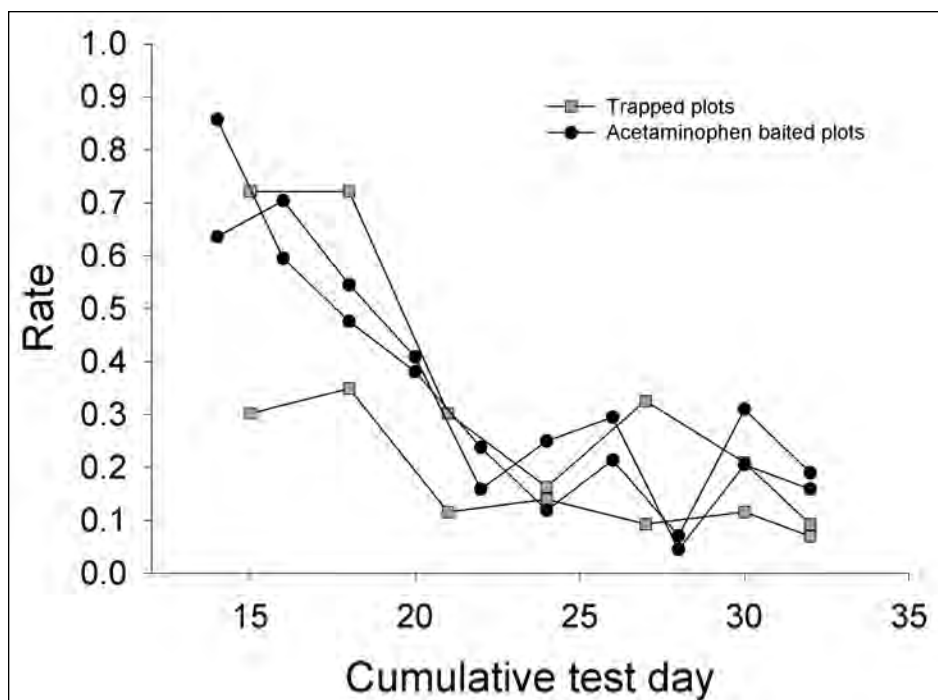
Figure 6. Comparison of trapping rate and bait-take rate of brown treesnakes as a function of time during the treatment (i.e., removal) period on Andersen Air Force Base, Guam, 2000.

behavior that brings them in contact with the bait very quickly. In contrast, the visual and chemical signals for a live-mouse lure in a trap are derived from 75% of the total surface area of the trap. Yet, the surface area available for trap entry is only 2% of the surface area available for the signal source. As a consequence, a snake will spend more time investigating areas of the trap that do not offer the opportunity for capture (L. Clark, U. S. Department of Agriculture, unpublished data).

Figure 7. The rate of bait-take for unadulterated baits as a function of plot treatment on Andersen Air Force Base, Guam, 2000, 14 to 20 (CTD 45 to 51) days after the treatment period. Treatments consisted of removal by trapping, removal by poisoned baiting, and no removal method (control). Values depict means + SE.

yet, 864 baits were taken during the treatment period. Hence, Savarie et al. (2001) reported that 312% more snakes were killed than were estimated on the treated plots, assuming a bait-take rate of 1.13 baits per snake. One inference from the above discussions was that baiting was a more effective method for snake control relative to trapping, assuming that baiting encompasses the snakes that would be trapped. Our previous study (Savarie et al. 2001) and this study support this conclusion, in so far as survivorship on the baited plots was <10% and did not differ from the other experimental plots where trapping was used as the method of control. Together, these observations suggest that snake removal by trapping may catch only about half the snakes present on a plot.

Costs and comparative efficiency of the control method

For the effort and duration of this study, traps had a lower prorated unit cost for materials but a higher cost for labor. As a consequence, the total cost for the control methods was similar. Because baiting affected more snakes than trapping; in this study, control by baiting was 1.67 times more cost effective than trapping. Though this study reports finding 10 years old, the 1-piece traps used in this study have become the operational standard; thus, the results should still be applicable (Vice et al. 2005). However, trapping minimizes possible impacts to nontarget species relative to baiting and may be the only viable option in some circumstances. Lastly, the comparison presented here does not represent all possible trapping and baiting scenarios, which could vary significantly both spatially and temporally and by technique (e.g., hand delivery by walking transects versus use of ATVs or aerial application).

Regardless, baiting was at least as efficient as trapping in this study, and steps to reduce labor costs in the implementation of baiting programs, such as aerial delivery over large areas (Shivik et

Finally, the data for captures and baits taken further suggest that baiting affects more snakes in treated areas. Based on trapping and mark-recapture estimates, the combined pretreatment estimated population size of snakes was between 122 and 175 snakes on the trapped plots and 135 and 195 on baited plots. During the treatment period, 161 snakes were removed by traps on the trapping plots, and 295 baits were taken on the baited plots. The number of snakes removed by trapping was consistent with the estimated population size based on the mark-recapture data. However, more baits were taken relative to the estimated population size derived from trapping for the baited plots. Campbell and Sugihara (2001) showed using similar baiting methods that the average rate of bait-take was about 1.13 baits per snake per night. Because snakes die within 48 hours of consumption of poisoned baits (Clark and Savarie 2012), the estimated number of snakes killed by acetaminophen baiting, adjusting for multiple bait-takes, was 262 snakes. Thus, the number of snakes killed with AMBs was 59% greater than the population estimate based upon mark-recapture trapping.

Similar trends were observed by Savarie et al. (2001) who reported that a combined mark-recapture population estimate of trapped snakes on acetaminophen-treated plots was 245;

al. 2002, Clark and Savarie 2012), will only tend to favor the use of acetaminophen-laced baits in terms of cost effectiveness. We, therefore, conclude that acetaminophen baiting should be considered as a viable alternative to trapping as a means of snake control not only because it was cost competitive, but because it has the potential to impact more snakes in a treated area. Issues of how long such baiting programs need to be maintained still need to be resolved.

Management implications

Despite our having achieved a reduction in estimated snake populations in the short term, our data show that reinvasion of treated areas occurs within a few months. Thus, if eradication or long-term population reduction is an endpoint of management, it is critical that the areas to be treated be isolated from additional sources of snakes. This isolation may be achieved through artificial barriers (e.g., snake fences) or through the use of natural barriers (e.g., low-quality snake habitat). Strategies for snake control would best employ area-wide snake reduction throughout the targeted area, with a subsequent shift of control efforts to bottle-necked peripheral areas. Such a strategy would concentrate and deploy control efforts to areas of higher risk while protecting areas where control efforts had already been deployed. Finally, other tactics to increase area of coverage and decrease labor costs, such as aerial application of baits, would improve the cost efficiency of the baiting method over trapping even further. Such a strategy will prove critical if island-wide control of brown treesnakes is to be effected. Finally, we emphasize that any aerial baiting for snake population reduction would occur prior to repatriation of endangered birds to forest habitat. This strategy would minimize the exposure of nontargets to acetaminophen.

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