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Note

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ABSTRACT Quantitative evaluation of control tools for managing invasive species is necessary to assess overall effectiveness and individual variation in treatment susceptibility. Invasive brown treesnakes (*Boiga irregularis*) on Guam have caused severe ecological and economic effects, pose a risk of accidental introduction to other islands, and are the greatest impediment to the reestablishment of extirpated native fauna. An aerial delivery system for rodent-based toxic baits can reduce brown treesnake abundance and heterogeneity among individuals may influence bait attraction or toxicant susceptibility. Previous baiting trials have either been simulated aerial treatments or relied on slightly different bait capsule compositions and the results of aerial delivery of toxic baits under operational conditions may not be directly comparable. We monitored 30 radio-tagged adult snakes (990–1,265 mm snout-vent length) during an aerial baiting operation in a 55-ha area using transmitters equipped with accelerometers and receivers programed to display a status code indicating mortality if a snake failed to move for >24 hours. We used known-fate models to estimate mortality and evaluate *a priori* hypotheses explaining differences in mortality based on size, sex, and treatment effects. Eleven radio-tagged snakes died in the aerial baiting treatment period (0.37, 95% CI = 0.21–0.55) and no individuals (0.00, 95% CI = 0.00–0.04) died during the non-treatment period. Our data provide strong evidence for an additive size-based treatment effect on mortality, with smaller adults (0.59, 95% CI = 0.35–0.80) exhibiting higher mortality than larger snakes (0.14, 95% CI = 0.02–0.37) but did not support a sex effect on mortality. The high mortality of snakes during the treatment period indicates that aerial baiting can reduce brown treesnake abundance, but further refinement or use in combination with other removal tools may be necessary to overcome size-based differences in susceptibility and achieve eradication. © 2021 The Authors. *The Journal of Wildlife Management* published by Wiley Periodicals LLC on behalf of The Wildlife Society.

KEY WORDS *Boiga irregularis*, Guam, invasive species, known fate models, snakes, survival estimate.

Invasive species rank as one of the greatest threats to global biodiversity (Wilcove et al. 1998) and the need to remove

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nonnatives from the landscape influences technological innovation of control measures. Quantitative evaluation of newly developed tools is fundamental to understanding their efficacy in controlling invasive target populations and to identify limitations that may indicate the need for refinement. Statistical models provide a powerful approach to assess population responses of invasive species to management actions, measured as a change in abundance or probability of survival (Jones et al. 2017, Keiter et al. 2017). Application of traditional statistical approaches for estimating population responses, such as mark-recapture models, can be costly and challenging when investigating cryptic or otherwise difficult to sample species because they generally require large sample sizes, relatively high detection probabilities, and assumptions that may be unreasonable (e.g., equal catchability; Jolly and Dickson

1983, McKelvey and Pearson 2001, Link 2003). In contrast, known-fate models provide precise survival estimates and do not require large sample sizes because encounter probabilities are assumed to be 1 by including only radio-tagged individuals (Pollock et al. 1989, Williams et al. 2002).

The brown treesnake (*Boiga irregularis*) invasion of Guam is one of the classic examples of the economic and ecological damage caused by the introduction of a nonnative species to island ecosystems and the difficulties associated with monitoring a cryptic species even with high population densities (Rodda and Savidge 2007). Brown treesnakes were likely accidentally introduced as stowaways in United States Navy salvage cargo in the 1940s (Rodda et al. 1992) and had spread over the entire island by the early 1980s (Savidge 1987, Rodda et al. 1992). Brown treesnakes caused precipitous population declines in many of Guam's native vertebrate fauna, including the extirpation of 10 of the 12 native forest bird species (Savidge 1987, Wiles et al. 2003, Rodda and Savidge 2007).

Density estimates of brown treesnakes on Guam have varied temporally and across land cover types and may have reached levels as high as 100 snakes/ha during an earlier phase of the invasion in 1985 (Rodda et al. 1992, 1999*c*). Despite being widespread and generally abundant, brown treesnake capture probabilities (p) are low ($p = 0.14$, Tyrrell et al. 2009; $p = 0.07$, Christy et al. 2010). Capture and detection probabilities are low for most snake species because of their secretive and cryptic nature, minimal or periodic activity patterns, and frequent occupation of inaccessible areas (Parker and Plummer 1987, Durso et al. 2011, Durso and Seigel 2015). It is particularly challenging to monitor brown treesnakes because they meet all criteria recognized to hamper detection in snakes and exhibit variation in detectability based on sex, body condition, size, and prey availability (Tyrrell et al. 2009; Christy et al. 2010, 2017; Siers et al. 2018).

Brown treesnakes on Guam pose an ongoing risk of accidental introduction to other islands (Fritts 1988, Stanford and Rodda 2007, Rodda et al. 2007*b*) and are an impediment to the reestablishment of extirpated native fauna. Management of brown treesnakes has primarily focused on containment (Rodda et al. 2007*a*, Hileman et al. 2021) and localized suppression in areas surrounding transportation ports (Clark et al. 2018). To a limited degree, habitat fragments occupied by native species of conservation concern undergo control in the form of snake removal, but the high cost of control programs and other factors has prevented widespread snake control to recover native ecosystems. Typically, snakes are removed using traps with live mouse lures, toxic baits placed in nontarget-excluding bait stations, and visual searching—approaches that are labor intensive and practical at small spatial scales (Rodda et al. 1999*a*). A novel system to aerially apply toxic baits may, however, provide a means to suppress brown treesnakes at the landscape scale (Siers et al. 2019*a*) that could be more cost efficient than trapping (Clark et al. 2012) and allow for treatment of areas inaccessible for ground-based

Figure 1. Deployed bait cartridge suspended within canopy vegetation. The bait mouse and acetaminophen tablet are lightly glued into the capsule and exposed for consumption by arboreally foraging brown treesnakes on Andersen Air Force Base, Guam, USA, 7, 10, and 14 June 2019. All cartridge components are biodegradable. Photo is by S. R. Siers.

methods. This system uses an acetaminophen tablet (toxicant) affixed to a dead neonatal mouse (bait) that is enclosed in a bait cartridge. Upon deployment from a helicopter-mounted automated delivery machine (ADM), the cartridge opens in the air and entangles in the canopy where the toxic bait is available to arboreally foraging brown treesnakes (Fig. 1). Acetaminophen is an approved toxicant for the lethal control of brown treesnakes (Savarie et al. 2000, Johnston et al. 2002, Sharp and Saunders 2011, van den Hurk and Kerkkamp 2019, Mathies and Mauldin 2020) and poses minimal risk to nontarget wildlife species (Johnston et al. 2002, Clark et al. 2012, Siers et al. 2019*b*). Dead neonatal mice are attractive snake baits (Shivik and Clark 1997), but rodent-based toxic baits more effectively target adults (Lardner et al. 2013) because brown treesnakes exhibit an ontogenetic diet shift with juvenile snakes (<700 mm snout-vent length [SVL]) consuming primarily lizards (Savidge 1988, Rodda et al. 1999*b*, Siers 2015) and exhibiting a strong prey preference for lizards (Lardner et al. 2009).

Several lines of indirect evidence suggest that aerial application of toxic baits suppress brown treesnake abundance at large spatial scales. Nontoxic bait take rates, for instance, have declined following experimental aerial treatment (Dorr et al. 2016, Siers et al. 2019*b*). But bait take rates are an index of foraging activity rather than a direct measure of abundance and provide no information on the traits of individuals taking baits. Surveys and monitoring of radio-tagged snakes revealed morphological and behavioral heterogeneity among

individuals such that snakes were more likely to consume a toxic bait if they exhibited lower body condition, greater activity prior to baiting applications, and were encountered more frequently foraging on the ground (Nafus et al. 2020), but in this example aerial applications were simulated by manually placing toxic baits.

We monitored brown treesnakes before, during, and after a baiting treatment using the ADM to estimate mortality probabilities during treatment and non-treatment periods using radio-telemetry and known-fate models. We developed several hypotheses to explain variation in effectiveness of baits based on previous work and aspects of brown treesnake natural history. First, we expected application of baits to increase mortality during treatment periods. Second, we predicted no sex effect on mortality because brown treesnakes do not exhibit strong sex-related differences in diet or capture probability using live mouse-baited traps (Savidge 1988, Tyrrell et al. 2009). Finally, within the range of snakes large enough to implant with transmitters, we predicted that smaller adult snakes would be more susceptible to aerially applied baits than larger individuals, for several reasons. Bait cartridges were designed to remain in the tree canopy, and although brown treesnakes are generally arboreal foragers, large individuals are more often found on the forest floor (Rodda et al. 1992, Rodda and Reed 2007, Nafus et al. 2020) where they are less likely to encounter baits. Larger individuals also exhibit decreased attraction to rodent-based carrion (Shivik and Clark 1999). Moreover, the dead neonatal mice used in aerial bait cartridges are small and offer lower prey value to larger snakes, thus likely decreasing relative bait attractiveness to the largest snakes (Lardner et al. 2013).

STUDY AREA

We conducted our study between 17 May and 5 July 2019 within a 55-ha forested plot (i.e., Habitat Management Unit; HMU) located on Andersen Air Force Base in northern Guam, which was established as a dedicated conservation area and location for biological resource studies (Siers and Savidge 2017, Siers et al. 2020a). The island of Guam experiences a warm and humid tropical climate with an average annual rainfall of 258.7 cm (Lander and Guard 2003). Approximately one third of the average yearly rainfall total (80.3 cm) occurs in the dry season from January to June with an average of 178.3 cm occurring in the wet season from July to December (Lander and Guard 2003). At approximately 150 m in elevation, the substrate of the HMU is predominately karst limestone with a vegetative understory dominated by ferns (primarily sword fern [Nephrolehis hirsutula]) and a largely uninterrupted overstory formed by a variety of trees but most commonly vitex (Vitex parviflora), screwpine (Pandanus tectorius), breadfruit (Artocarpus altilis), and coconut palms (Cocos nucifera). Dominant fauna comprises several brown treesnake prey species, including black rats (Rattus diardii), shrews (Suncus murinus), house geckos (Hemidactylus frenatus), and mourning geckos (Lepidodactylus lugubris) and 1 occasional snake predator, Mariana monitors (Varanus tsukamotoi). The dimensions of the roughly rectangular HMU measure approximately 480 m by 1,200 m. The HMU is surrounded by a snake exclosure fence allowing snake emigration but preventing movement into the treatment area. The barrier consists of a 1.8-m high chain-link fence extending 0.88 m below the surface and anchored with a continuous concrete footer. Covering the outer surface of the fence is 0.5-cm wire mesh hardware cloth that bulges outward at 1.2 m above ground level. The bulge defeats attempts by brown treesnakes to climb over the fence (Rodda et al. 2007c).

METHODS

We collected brown treesnakes between 17 May and 3 June 2019 from within the HMU using traps with live mice as a lure (Tyrrell et al. 2009) or hand-captured snakes during visual encounter surveys (Christy et al. 2010). To meet guidelines stipulating that transmitters do not exceed 5% of body mass, we included only snakes greater than 90 g in mass. We selected 30 brown treesnakes for inclusion in the study with an average mass of 123.0 ± 6.3 g ($\bar{x} \pm 1$ SE; range $= 93$–245 g) and average SVL of $1,062 \pm 11$ mm (range $= 990$–1,265 mm), including 14 females (SVL $= 1,033 \pm 8$ mm) and 16 males (SVL $= 1,086 \pm 18$ mm).

On 29 May and 4 June 2019, we anesthetized snakes via inhalation of isoflurane and surgically implanted 4.5-g radio-transmitters (MST-930-M, Lotek Wireless, Ontario, Canada) in the coelomic cavity (Reinert and Cundall 1982). Motion-sensitive transmitters displayed a code indicating mortality if motion was not detected for >24 hours, allowing us to determine the status of snakes that were not visible (e.g., snakes inside cavities or high in vegetation).

Following surgery, we observed snakes for 24 hours to allow for recovery before we returned them to site of capture on 30 May 2019 ($n = 23$) or 5 June 2019 ($n = 7$). We listened for transmitter signals from outside the perimeter of the HMU fence every Friday for 6 weeks between 31 May and 5 July 2019 using a receiver (SRX 800 m; Lotek Wireless) and either a 5-element or 3-element Yagi directional antenna (Advanced Telemetry Systems, Isanti, MN, USA). We entered the HMU to search for any signal not already acquired and to locate the carcass of any snake associated with a transmitter indicating mortality. When it was not possible to visually confirm death (e.g., individual was underground), we assumed death if a snake's transmitter consistently emitted a mortality signal that was tracked to the same location for ≥3 consecutive weeks.

On 7, 10, and 14 June 2019, we aerially applied 19,200 bait cartridges (6,600/day) over the HMU. Cartridges were ejected from the helicopter-mounted ADM at a rate of 1 cartridge/9 m along flight paths spaced 9 m apart to evenly distribute baits across the HMU and attain a target density of 120 cartridges/ha/application day (the maximum rate allowed by the Environmental Protection Agency pesticide label, Registration 56228-34). We followed all animal use protocols in our study approved by the United States Department of Agriculture, National Wildlife Research Center (NWRC) Institutional Animal Care and Use

Committee (QA-2742, QA-2610) and the United States Geological Survey Institutional Animal Care and Use Committee (2018-07). Data analyzed in the study are available online through ScienceBase, (https://doi.org/10.5066/P9WCZW5V).

Analyses

To evaluate if the size distribution of snakes sampled in the present study was representative of brown treesnakes in similar habitat on Guam, we compared our sample ($n = 30$) with reference snakes ($n = 54$) collected from 2 limestone forest sites located approximately 4 km and 32 km from our study site and with historical study site data. We restricted reference snakes to individuals >990 mm SVL (i.e., large enough to be fitted with radio-transmitters in the present study) from the reference data to make it comparable to the present study. Because data were left-truncated and non-homoscedastic (Bartlett's test of homogeneity of variance, K-squared = 9.032, df = 1, $P = 0.002$), we tested for differences in median SVL between the present study and the reference data using a 2-tailed independent-sample Mann-Whitney Wilcoxon test. We set $\alpha = 0.05$ and conducted statistical tests and data visualization using the software program R (R Core Team 2020).

We expected a 2- to 5-day lag in treatment-related mortality following each bait application. Dead neonatal mice remain viable baits for brown treesnakes for approximately 48–72 hours post-deployment. Once baits are ingested, snakes may take an additional 24–48 hours (Mathies and Mauldin 2020) or longer for larger snakes (Siers et al. 2021) to succumb to the toxin and another 24 hours following death for transmitters to broadcast a mortality signal. In accordance, we determined the effective treatment period to extend 7 days beyond the final application, or the 2-week period between 7 June through 21 June 2019. The 2 weeks prior to and following this treatment period were non-treatment periods and used to determine a baseline mortality rate.

We fit binomial known fate models to our data to estimate survival (S) probabilities using Program MARK (version 9.0; White and Burnham 1999). This modeling approach assumes that fates of individuals are known and independent of each other and that radio-transmitters do not affect survival (Williams et al. 2002). We used the logit link to constrain survival parameters between 0 and 1 and the second partial derivative method to estimate variance. For models that included covariates, we computed 95% confidence intervals using the default setting (i.e., $\hat{S} \pm SE \times 1.96$ is computed on the logit scale and then back-transformed). For models excluding covariates, we used profile likelihood confidence intervals. We set weekly intervals to 0.5 to derive cumulative 2-week mortality probabilities. We calculated mortality (M) rates as $M = 1 - S$. We modeled treatment and non-treatment effects as a binary classification factor and sex as a binary covariate. We modeled size, based on SVL, 2 ways: as a continuous covariate or a factor with 2 levels. We included a categorical size factor because our sample included 2 biologically relevant and distinct

size classes. Our smaller sized group ($1{,}019 \pm 17$ mm, range = 990–1,040 mm, $n = 15$) corresponded to the size range of snakes transitioning from juveniles to sexually mature adults (910–1,030 mm) and our larger-sized group ($1{,}104 \pm 59$ mm, range = 1,052–1,265 mm, $n = 15$) included individuals that are expected to be fully mature (Savidge et al. 2007, Siers et al. 2017a). We evaluated 5 competing models in an information-theoretic framework and used Akaike's Information Criterion adjusted for small sample size (AIC_c) for model selection (Akaike 1973) an Akaike weights (w_i) to evaluate relative likelihood.

RESULTS

We detected no difference in median SVL between our reference snakes and brown treesnakes from the present study (2-tailed Wilcoxon rank sum test with continuity correction $P = 0.75$; Fig. 2). Eleven radio-tagged snakes died during the aerial toxicant treatment period and no individuals died during the non-treatment period. We confirmed death for 10 out of 11 snakes with transmitters emitting mortality signals by recovering carcasses; we tracked 1 snake to the same location underneath a large karst outcropping for 4 consecutive weeks and assumed mortality. The transmitter in 1 of the 30 snakes malfunctioned; we removed that individual from the study in week 5 (after it survived the treatment period) and euthanized it. We censored 2 other snakes because we lost their radio signals during the study and never recovered them, 1 in week 4 and 1 in week 5 (1 during the treatment period and 1 after the treatment period). We confirmed all remaining snakes with transmitters to be alive at the end of the monitoring period through individual recovery ($n = 5$) or detection of a live signal ($n = 11$).
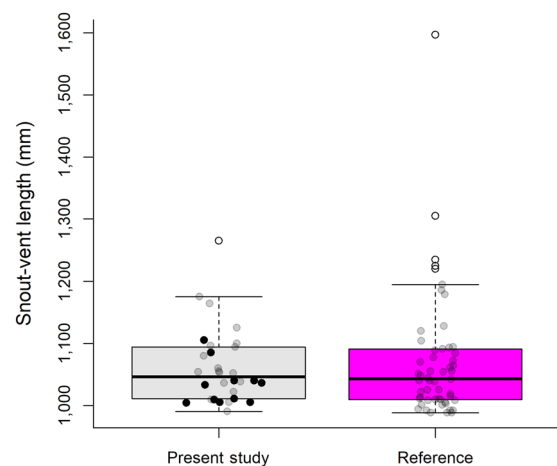
Figure 2. Comparison of brown treesnake size distribution (grey circles) in the present study (grey box) in the Habitat Management Unit (HMU) on Andersen Air Force Base, Guam, USA, 31 May to 5 July 2019, versus those from collected in 2010 and 2011 at the HMU, Northwest Field Outside, and Naval Magazine, Navy Base Guam, Guam, USA (reference; magenta box). Black circles are snakes that died during the baiting treatment and hollow circles represent outliers (i.e., rare, larger individuals). Boxes show the interquartile range, whiskers represent the minimum and maximum values, and the bold horizontal line denotes the median.

Table 1. Five candidate models considered for known fate analysis of survival (S) of brown treesnakes after aerial toxicant treatment in the Habitat Management Unit on Andersen Air Force Base, Guam, USA, 31 May to 5 July 2019. The 2 top models include a snake size variable: a categorical variable of size (small = 990–1,040 mm vs. large = 1,052–1,265 mm) or a continuous variable of snout-vent length (SVL). The treatment variable indicated periods of toxic bait treatment.

Model	AIC_c^a	ΔAIC_c^b	w_i^c	K^d	$-2 \log(\mathcal{L})^e$
S (treatment + size)	53.260	0.000	0.701	3	47.081
S (treatment + SVL)	55.811	2.552	0.196	3	49.632
S (treatment)	58.222	4.962	0.059	2	54.133
S (treatment + sex)	58.793	5.534	0.044	3	52.614
S (no treatment)	78.940	25.680	0.000	1	76.910

[a] Models are ranked in ascending Akaike's Information Criterion adjusted for small sample size (AIC_c) order.
[b] Difference between model i and the top-ranked model.
[c] Model weight.
[d] Number of parameters.
[e] Difference in $-2 \log$ likelihood of the current model and the saturated model.

Our data provided strong evidence ($w_i = 0.701$) for an additive size-based treatment effect on mortality and moderate evidence ($w_i = 0.196$) for an SVL-based treatment effect on mortality with smaller snakes exhibiting higher mortality (Table 1). There was no evidence for an additive sex-based treatment effect or a non-treatment effect on mortality. Mortality probability was higher during the treatment period (0.37, profile likelihood 95% CI [PLCI] = 0.21–0.55) than during non-treatment periods (0.00, 95% PLCI = 0.00–0.04), and the top model outperformed the no treatment model by 25.68 AIC_c units despite being penalized for having 2 additional parameters. When we considered categorical size-based treatment effects, the probability of mortality was higher during the treatment period compared with the non-treatment period for both snake size classes; however, the treatment effect was larger for smaller snakes (Fig. 3). Similarly, the model including a continuous SVL effect revealed that the probability of mortality was inversely related to snout-vent length such that larger snakes were more likely to survive the toxic baiting treatment (Fig. 4).
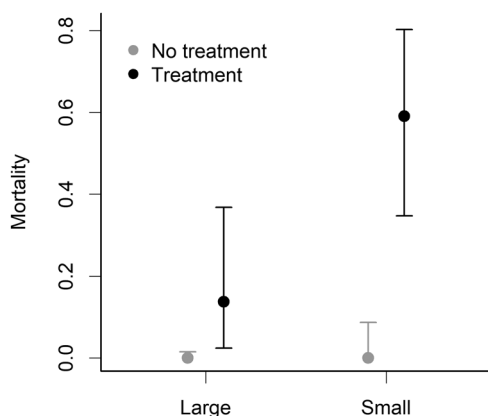
Figure 3. Two-week mortality probabilities for larger and smaller adult brown treesnakes during non-treatment and treatment periods on Andersen Air Force Base, Guam, USA, 31 May to 5 July 2019. Error bars are profile likelihood 95% confidence intervals.
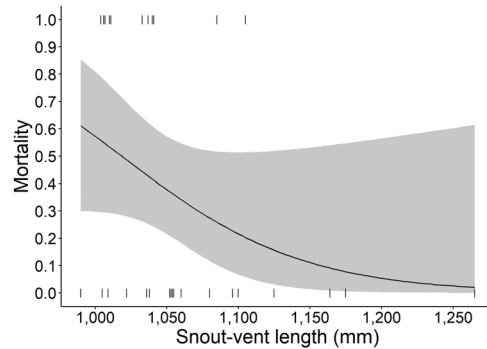
Figure 4. The effect of snout-vent length (SVL) on brown treesnake mortality probabilities (black line) surrounded by 95% confidence intervals (gray band) during the 2-week treatment period on Andersen Air Force Base, Guam, USA, 7 June to 21 June 2019. Tick marks indicate the snout-vent length of individual radio-tagged snakes that survived (0.0) or died (1.0) during the treatment period.

DISCUSSION

Our findings provide direct evidence that aerial application of toxic baits increases brown treesnake mortality at the landscape-scale, rather than indirect indices of relative abundance (Siers et al. 2020b) and supports the findings of Nafus et al. (2020). All brown treesnake mortality during the study occurred within the treatment period, indicating that deaths were likely caused by ingestion of toxic baits as opposed to other natural causes or artefacts of transmitter implantation. Adult brown treesnakes have few predators on Guam (Savidge 1991) and recovered snake carcasses, although decomposed, did not exhibit obvious signs of predation such as dismemberment. Non-movement status signals served as a reliable indication of mortality because all such snakes were confirmed dead via carcass recovery ($n = 10$) or non-movement for 4 consecutive weeks ($n = 1$) and a subsample of snakes ($n = 10$) with transmitters emitting a normal signal were visually verified to be alive during the course of the study. Moreover, we observed no indication of infection or injury during the surgical implantation of transmitters that would have contributed to snake death.

Our results suggest our sample was representative of adult brown treesnake size in limestone forest on Guam (Fig. 2) and that mortality was greater in smaller adult individuals during the treatment period. Our findings also support previous size-based effects of simulated aerial application of toxic baits (Nafus et al. 2020) and demonstrate the efficacy of this tool during an operational aerial application. Higher mortality of the smaller adult size class was expected, and several facets of brown treesnake natural history could influence increased susceptibility of this group, including greater attraction to rodent-based carrion, likelihood of arboreality, and proportionally greater prey value of neonatal mice. We cannot determine if these factors acted synergistically or which, if any, had the greatest influence on the treatment size effect we observed. We also considered the possibility that toxicant dosage influenced size-based mortality because the 80-mg acetaminophen tablet could have a larger effect on smaller snakes but concluded this

explanation is unlikely given that Savarie et al. (2001) reported an 80-mg dose orally delivered in a dead mouse to be 100% lethal for snakes ($n = 29$) <300 g in mass. Although there is evidence that some very large snakes will survive a single 80-mg dose, survival is very rare until masses exceed 250 g (Siers et al. 2021), which is larger than any subject in this trial; snakes >250 g account for <7% of males and <2% of females captured during a systematic island-wide visual sampling effort (Siers 2015, Siers et al. 2017b). Given the similar diets and lethality of acetaminophen among males and females, we found no sex-specific effect on probability of mortality. This is an important finding because females influence population growth and our results suggest toxic baits are equally effective against females and males. Further, although brown treesnakes exhibit sexual size dimorphism with males attaining maximum sizes much greater than females (Rodda et al. 1999b, Siers et al. 2017b), no snake included in our sample exceeded upper limits of female size. Greater understanding as to why smaller adults of both sexes are more susceptible to our current toxic baits may provide the key to modifying baits or baiting approaches to better target adult snakes of all size classes.

Although not directly examined here, environmental factors and aspects of snake foraging behavior likely influenced brown treesnake mortality rates during baiting treatments. Brown treesnake activity in tropical Australia is positively associated with rainfall and ambient temperature (Trembath and Fearn 2008) that may, in part, reflect greater foraging activity. Our baiting treatment in early June corresponds to the start of the wet season on Guam, during which increased foraging activity may be expected; however, brown treesnakes display a reduced response to mouse carrion lures during the wet season (Shivik et al. 2000). This apparent paradox may be explained by increased prey abundance during the wet season, possibly decreasing brown treesnake interest in carrion because available live prey is more attractive, or snakes are satiated. In support of this idea, experimental manipulation to reduce rodent abundance increased brown treesnake capture probabilities (Gragg et al. 2007) and snakes that exhibited lower body condition, suggesting recent difficulty locating prey, showed an increased susceptibility to toxic baits (Nafus et al. 2020). Moreover, brown treesnakes are more frequently in specific microhabitats, for example screwpine and sword ferns (Hetherington et al. 2008, Boback et al. 2020); however, the possible interaction between habitat use and bait encounter rates remains unexplored. Finally, stochastic weather events, such as heavy rainfall events or high wind speed during the bait application window, although not observed here, could dissolve the acetaminophen tablet (Nafus et al. 2018) and influence snake foraging behavior.

We provide a snapshot of the effects of a toxic baiting treatment, but it is difficult to forecast how mortality rates might vary in subsequent baiting operations or affect long-term population trends in treated areas. Two aerial baiting treatments occurred at our study site in the 8 months prior to the treatment examined here. Most snakes included in our sample, especially those over 1,000 SVL, were likely adults at the time of the previous drops yet survived. Multiple factors specific to individual snakes may have reduced foraging activity, thus susceptibility to baits, such as inactivity following ingestion of a large meal or prior to ecdysis (Rodda et al. 1999b, Siers et al. 2018). Brown treesnakes may also exhibit individual heterogeneity in response to rodent-based carrion, given heterogeneity in capture probabilities in traps using rodent lures (Tyrrell et al. 2009) and evidence of only capturing some individuals in traps containing avian lures despite being surrounded by rodent lure traps (Yackel Adams et al. 2019). Additional work is needed to explore this possibility, but if a subset of the population, independent of body size, exhibits little interest towards rodent-based carrion, then we might observe a pattern of decreased mortality rates during future treatments as that segment becomes a larger proportion of the population (Zavorka et al. 2018). Mortality during future treatments may also decrease if suppression of brown treesnake abundance allows for a rebound of prey populations (Campbell et al. 2012), and thus creates the scenario of increased prey abundance and decreased snake interest in carrion baits.

MANAGEMENT IMPLICATIONS

We demonstrate 37% mortality of adult brown treesnakes in a large enclosure in response to a single period (3 aerial applications) of baiting. Our identification of lower susceptibility to baits among larger snakes may aid future refinements of this management tool, such as including larger mammalian or bird-based carrion baits. We suggest aerial application of toxic baits has the potential to suppress brown treesnake abundance at large spatial scales.

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