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Original Research Article

Behavior, size, and body condition predict susceptibility to management and reflect post-treatment frequency shifts in an invasive snake

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ABSTRACT

Foraging behavior can have population-level effects that are of interest for wildlife management. For invasive species, foraging behavior has been tied to establishment ability and rate of spread and is generally of import in understanding invasion biology. A major method for controlling invasive vertebrates is using food-based baits as attractants. Tool efficacy is therefore partially driven by individual decision-making during foraging, which may also affect population response to control. We used three studies on the invasive, arboreal brown treesnake (*Boiga irregularis*) on Guam to measure 1) size, body condition, and behavioral correlates with mortality in response to control using toxic baits, 2) shifts in prevalence of those traits after control treatments occurred and, based on the prior two findings, 3) interactive relationships between size, body condition, and behavioral traits at the landscape scale for untreated populations. Each trait was selected due to a potential relationship with foraging behavior or energetic state of an arboreal snake, as a method to estimate how foraging behavior can inform control tool efficacy. We found that snakes were more likely to be killed by toxic baits if they had a lower body weight, were more active leading up to a bait application, and encountered on the ground more frequently. Across two treated populations, both body size and condition of sampled snakes increased after treatment, while the incidence of ground encounters decreased. Throughout forested habitat on Guam, ground encounter probability was positively correlated with snake size and inversely correlated to body condition. Additionally, size and condition had interactive effects such that snakes in good condition were more arboreal. Thus, body size and behavior (ground encounters) correlated with control-tool susceptibility and frequency shifts occurred in those traits within sampled post-treatment populations. Individual decision-making during foraging may thus inform population responses to bait-based control tools. Management decisions such as prey suppression are likely to directly influence removal efficacy through altered foraging behavior in snakes.

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1. Introduction

Animal behavior or individual traits are important considerations for wildlife management, because they can serve as measures of genetic variation, habitat selection, and other population patterns (Berger-Tal et al., 2011; Caro and Sherman, 2012; Palkovacs et al., 2018). For example, individual behavior can be driven by nutritional or energetic state, such that those in poorer energetic states may engage in riskier foraging activity (Caraco et al., 1980; Lima et al., 1985; Lima and Dill, 1990; Heithaus et al., 2007). When food resources are plentiful, the average individual may be more risk averse, such that populations preferentially occupy habitats with lower risk of mortality relative to when resources are scarce (Matassa and Trussell, 2014; Riginos, 2014). Therefore, behavior affects movement, presence and numerous other considerations for wildlife management and this may be especially true for behaviors related to foraging.

Foraging behavior has direct application to invasion biology and invasive species management. Dispersal rates of invaders may increase in areas with low resource availability (Lutscher and Musgrave, 2017). Behavioral traits, such as interspecific aggression, that predict resource acquisition success can also predict colony success and invasibility of Argentine ant strains (Holway and Suarez, 1999). Individual foraging choices thus have population-level effects on the invasion process that can forecast the success of an invasive species. Although behavioral decision-making is recognized as an important determinant of the invasion process (Holway and Suarez, 1999; Phillips and Suarez, 2012), there are few studies that examine relationships between population control and behavior. Yet, behavior can opportunistically be exploited to suppress and even dramatically improve the probability of eradicating invasive species (Campbell and Donlan, 2005; Smith et al., 2016). Better understanding of the relationship between animal behavior and control tool efficacy has the potential to improve management of invasive species by improving our ability to target every individual.

Foraging behavior may be of particular interest for invasive terrestrial vertebrates, because control tools often rely on attracting individuals via food-based baits or lures (Thomson et al., 2000; Orueta et al., 2001; Howald et al., 2007). For toxic baits or food-based traps to be effective, individuals must choose to seek the bait. Control-tool efficacy and eradication prospects thus have the potential to be improved by understanding how foraging behavior or other individual traits associate with responsiveness to the attractant (Ruetter et al., 2003; Hegglin et al., 2004) and whether those effects can scale up to the population. Rodent eradications, for instance, are more effective when resource conditions are low—or resource competition is high—and when control tool implementation is structured to reflect habitat use patterns of the target species (Keitt et al., 2015). Foraging behavior may thus inform susceptibility to food-based control tools depending on individual state, traits, or other factors that influence animal decision-making.

To evaluate the effect of individual traits and behaviors on the efficacy of invasive species control, we used invasive brown treesnakes (*Boiga irregularis*) on the island of Guam, USA. Indigenous to Australia, eastern Indonesia, the Solomon Islands, and Papua New Guinea, the nocturnally-active brown treesnake was a primary cause of the extirpation of many native birds, bats, and some lizard species after introduction to Guam (Savidge, 1987; Rodda et al., 1992; Wiles et al., 2003). Brown treesnakes were an appealing model due to lack of general knowledge about controlling reptile populations, as well as dependence on control tools that rely on baits. Brown treesnake control has historically relied on traps that attract snakes using a live mouse or bait tubes that contain a toxicant-laced dead rodent (Rodda et al., 1999a; Lardner et al., 2013; Clark et al., 2018). Prior research has shown that traps are more effective when associated with reduced prey availability (Gragg et al., 2007), although individuals vary in their trap entry probabilities (Tyrrell et al., 2009). Both olfactory and visual cues are known to affect brown treesnake attraction to bait (Shivik, 1998; Lindberg et al., 2000). Carrion and live prey are also equally attractive (Shivik and Clark, 1997), although individual attraction to carrion and live mice varies in a size-dependent manner (Shivik and Clark, 1999; Tyrrell et al., 2009). In general, the species is characterized by ontogenetic shifts in habitat use and prey preference, such that juveniles tend to be highly arboreal and shift from a diet composed primarily of lizards and frogs to the inclusion of birds and rodents at 700–900 mm in snout-vent lengths (SVL) (Savidge, 1988; Rodda and Reed, 2007; Lardner et al., 2009; Siers, 2015). Snakes <900 mm SVL exhibit low interest in endothermic prey, which is reflected in the size threshold at which they consistently enter traps with live rodents (Rodda et al., 2007; Tyrrell et al., 2009).

A novel mechanism to broadcast bait—a dead juvenile mouse affixed with an 80-mg acetaminophen tablet that is lethal to brown treesnakes (Savarie et al., 2000)—via an aerial delivery system (ADS) was developed to support landscape-scale control (Messaros et al., 2017; Siers et al., 2019). To measure whether size, condition, weight and behavioral traits of individuals could forecast population responses to landscape-level management action, we used three interconnected approaches. We (1) measured the relationship between size, sex, condition, weight, and behavior with survival during baited-toxicant applications, (2) determined if there was evidence for shifts in frequencies of these traits following toxicant applications in sampled populations, and (3) retroactively evaluated the interaction between behaviors and size or condition (energetic state) at the landscape scale for untreated populations of brown treesnake as an exploration into explanatory reasons for measured responses. We focused on snakes ≥ 900 mm SVL to prevent ontogenetic effects. We interpret the findings in the context of applying theories in foraging behavior relative to anticipated management outcomes and the ability of individual traits to forecast estimated population responses.

2. Materials and methods

2.1. Study sites

2.1.1. Toxicant-treated sites

We used two sites to study behavioral and morphological changes in response to bait applications on Guam (55P): Northwest Field North (NWFN, UTM: 268606, 1509098) and the Habitat Management Unit (HMU, UTM: 268865, 1504127), both on Andersen Air Force Base in Northern Guam.

NWFN was a 5-ha forested area surrounded by a snake-proof fence (1.5-m height) that prevented snake ingress or egress (Rodda et al., 2007). Toxicant applications completed at NWFN simulated ADS (Siers et al., 2019), although we distributed bait cartridges manually using telescoping poles. Each bait cartridge was comprised of a dead juvenile mouse (3–7 g) affixed to an acetaminophen tablet, with cartridges constructed of an internal paper capsule (containing the bait) attached to an external cardboard tube by a ribbon (Messaros et al., 2017; Siers et al., 2019). We followed an 8 × 10 m gridded application spacing with cartridges placed every 10 m along 27 interior forest transects each 220 m in length and spaced 8 m apart. We applied cartridges at a rate equivalent to the maximum pesticide label application of 120 baits per hectare (US EPA Registration No. 56228-34). We mimicked a 5% failure to open during deployment by withholding 30 baits per application. For each application of 570 baits, we suspended most in the tree canopy (70%, overstory; 20% mid-canopy), and placed 5% within 0.5 m of the ground. We completed three toxicant applications (31 March, 14 April, 02 June 2017) for the data analyzed herein.

The HMU was a 55 ha area enclosed by a fence (1.5-m height) that prevented ingress but not egress. From 03 September 2013–19 December 2014, the HMU was treated with 15,840 baits across eight applications to test whether aerial bait applications suppress brown treesnakes at the landscape scale (see Dorr et al., 2016 for dates and more details). Dead mouse baits with acetaminophen tablets internally inserted were attached to crepe paper streamers sandwiched between two cardboard sections, with the mouse affixed to one cardboard section via hot-melt adhesive. Thirty-six baits per hectare were manually dispensed across the HMU from a helicopter. Because baits were deployed from a helicopter we do not have data on the precise canopy distribution, although distribution was intended to primarily be in the tree canopy to reduce consumption by ground foragers such as crabs (Lima and Dill, 1990; Dorr et al., 2016).

2.1.2. Untreated sites

Untreated sites included nine locations on Guam, including Andersen Air Force Base (UTM: 1493989, 268907; years sampled: 2013, 2014), Naval Communications (UTM: 268904, 1503562; years sampled: 2013, 2014), Northwest Field (UTM: 269037, 1508928; years sampled: 2004, 2005, 2007, 2008, 2010, 2011), and Guam National Wildlife Refuge (UTM: 267581, 1509472; years sampled: 2007, 2008, 2012), as well as NWFN (2004–2016) and HMU (2013) data collected prior to toxicant control. We also completed surveys at three cave locations that have been partially redacted due to the presence of endangered species: Fachi (UTM: 2522XX, 147953X), Maemong (UTM: 2519XX, 147941X), and Mahlac (UTM: 2528XX, 147959X) from 2013 to 2016. All sites were mixed forest habitat.

2.2. Field methods and snake handling

We used nocturnal surveys conducted by teams of two visual observers using a high-power headlamp (Wilma, Lupine Lighting Systems, PA, USA) to visually scan vegetation, starting no earlier than 30 min after civil twilight. Structure of the area surveyed and transect methods varied by site. We completed visual surveys at NWFN by walking 29 maintained transects, each 220 m in length, from 2004 to 2017 at variable sampling intensity. From 24 October 2016–30 March 2017, immediately prior to the first toxicant application, we completed visual surveys of all 29 transects four times per week (94 survey nights). From 03 April 2017–18 December 2018, we conducted visual surveys of each transect every night for 10 nights following a toxicant application and twice per week during all other periods (227 survey nights). In the HMU, we conducted visual surveys from 26 March–13 August 2013, four nights per week on 18 maintained transects, each 220 m in length (69 survey nights). We conducted further surveys during (21 April – 10 June 2014; 22 survey nights) and after toxicant applications (05 January – 10 August 2015; 44 survey nights). We primarily conducted visual surveys outside of NWFN and HMU along roadside forest edge.

For each captured snake, we confirmed sex via probing (Reed and Tucker, 2012). We measured SVL and total length (mm) by gently stretching the snake along a tape measure. We weighed snakes using a Pesola® spring scale. From SVL and mass, we calculated body condition index (BCI) using a regression formula based on the ratio of individual body mass to expected mass given SVL. Expected body mass for a given length was estimated by linear regression on a logarithmic scale based on 10,000 records of length and mass of brown treesnakes captured on Guam between 1980 and 2004 (Lardner et al., 2013). BCI was thus a measure of condition as a function of SVL and mass at the time of capture, relative to the measured population on Guam. A BCI of 1 was equal to the population mean. We also recorded vertical position of snakes as ground (body of the snake on the ground, < 0.5 m off the ground) or arboreal (body of the snake > 0.5 m off the ground). Because arboreality may be conversely related to size (Rodda and Reed, 2007), the proportion of encounters on the ground relative to in the tree canopy may affect bait encounter rates of a primarily arboreally distributed bait and subsequently mortality.

We affixed very-high-frequency radio transmitters (PD-2, Holohil, Ontario Canada) to the tails of snakes ≥ 900 mm SVL captured in NWFN from 14 March–01 June 2017. The transmitter was placed roughly 8–10 caudal scutes behind the cloaca, wrapped with medical tape, and sealed in place using 3M Vetbond™ tissue adhesive, which provided 2–4 weeks of non-invasive radio attachment (Robinson et al., 2018). The complete transmitter package (transmitter, tape and glue) was $<5\%$ of the mass of the smallest snake included in the study. In the period leading up to a toxicant application, snakes were tracked twice per week between 19:00 and 23:30, the period of peak snake activity (Rodda et al., 1999b; Siers et al., 2018a). When tracked, we recorded whether some part of the snake was visible (visibility) as a coarse measure of activity. Snakes spend a significant portion of their lives inactive due to digestion, ecdysis, reproduction or otherwise and during these times are not expected to be engaged in foraging (Shivik et al., 2000; O'Donnell et al., 2004; Siers et al., 2018b). Thus, activity as measured by visibility indicates a snake is neither underground, nor holed in a tree and may encounter a bait during foraging. We also recorded their location as ground (definition described above/signal underground) or arboreal (definition described above/signal in the canopy). A few snakes lost their transmitters, probably due to normal ecdysis; we reattached the transmitter to a subset of these snakes (up to one re-attachment per snake). We avoided entering NWFN for the first 72 h after toxicant applications to minimize disturbance to snakes, after which we tracked individuals nightly for 10 days. After 72 h, baits likely were too degraded to be attractive to snakes or would have been consumed by ants. Snake and mouse handling followed institutional guidelines detailed by protocols with the U.S. Geological Survey (FORT IACUC, 2017–03) and Colorado State University (IACUC-15-5892A) Animal Care and Use Committees.

2.3. Statistical analysis

2.3.1. Objective 1

Traits associated with toxicant-mediated mortality (telemetry).—We used telemetered animals to calculate the proportion of times a snake was visible or on the ground in the two weeks leading up to a toxicant application to obtain a measure of individual visibility and arboreality. Thus, a single snake that survived multiple applications had a behavior value that was different for each application to account for temporal effects on behavior. For the survival analyses, we used mixed effect Cox proportional hazards models using the ‘Survival Analysis’ package in R (Therneau, 2014) to test the relationship between probability of survival (0) versus mortality (1) in days using visible encounters (rescaled), ground encounters (rescaled), and sex as covariates. We first verified that visibility and arboreality were independent behavioral measures using a chi-square test of independence. Because brown treesnakes are sexually dimorphic in size, we evaluated SVL as an interactive factor with sex. We used a separate model to evaluate mass as an interactive covariate with sex due to autocorrelation between the mass and SVL. Finally, we evaluated BCI as a potential explanatory variable. BCI was autocorrelated with mass and could not be included in the same model. To ensure SVL and mass models were comparable, we ran a third model that used BCI in the place of SVL or mass. We included a random intercept for subject identity in all three models, because 15 individuals were re-measured through sequential toxicant applications. We also evaluated a null model that contained only the beta estimate and a random intercept for individual to determine if parameters identified for hypothesis testing improved model fit. We used Akaike information criterion methods corrected for small sample size (AICc) to determine which body model (mass, BCI, or SVL) displayed the best fit and presented associated p-values with significance evaluated at $\alpha \leq 0.05$. Although some authors recommend against presenting p-values in association with AIC methods (Burnham and Anderson, 2002), we opted to do so because our models were testing a specific hypothesis on the importance of ground foraging, activity, size, and sex on susceptibility to toxicant applications. However, we were uncertain as to whether mass or SVL were a better measure of size traits in relation to individual survival probabilities. Size, mass, or body condition may cause dose-dependent responses to toxicant ingestion that cannot be disentangled from potential behavioral effects based on size, and thus each was explored to determine which trait was the best predictor of mortality. However, subsequent analyses focused on size and energetic traits more intensively due to their potential influence on behavior and thus value in understanding causative effects on response where a dose-dependent laboratory study was not conducted.

2.3.2. Objective 2

Trait changes post-toxicant application (visual survey).—Due to potential seasonal variation in foraging behavior (Shivik et al., 2000; Brown et al., 2002), we limited comparisons of visual surveys pre- and post-toxicant application to those completed during seasonally equivalent periods. The pre-toxicant survey period in NWFN occurred from 01 June 2016–31 January 2017 (71 survey nights) and the post-toxicant survey period used was 02 June 2017–18 December 2018 (99 survey nights). For the HMU, we completed pre-toxicant surveys from 26 March–13 August 2013 (69 survey nights). Post-toxicant surveys were conducted from 21 April–10 June 2014 (22 survey nights during the toxicant application process) and from 05 January–10 August 2015 (44 survey nights after toxicant applications had concluded).

To measure post-toxicant changes in trait frequencies we used several models. First, we used a multivariate analysis of variance (MANOVA) to compare mean SVL and BCI of snakes ≥ 900 mm SVL prior to toxicant applications to snakes sampled post-application, where SVL and BCI were included as dependent variables in the same model. We also included sex as a predictor in the model to measure and control for sex-specific effects on SVL or BCI. Both SVL and BCI were right skewed and normalized using log transformation. For this analysis, we focused on BCI to avoid autocorrelation issues between weight and

SVL and still evaluate potential changes in size and energetic state of sampled snakes. We chose to ignore potential dose-dependent effects of weight, which could be poorly characterized or captured by the observational data collected for this analysis. We also used a chi-square test to determine if there was evidence of a change in sex ratio. Finally, we used a binomial generalized linear mixed model ('lme4' package in R; Bates et al., 2013) to test the probability of encountering a snake on the ground pre- and post-treatment in response to findings from the survival analysis. The dependent variable for behavior was ground encounters (1) relative to arboreal encounters (0). We considered toxicant applications as a binomial predictor where toxicants had either been applied at some point prior to surveys (1) or had not been applied (0). We included subject identity nested within study site as random intercepts to account for repeated captures of the same individuals and included scaled SVL as an interactive term with BCI.

2.3.3. Objective 3

Relationship between body condition, size and arboreality (visual survey data; untreated sites).— To better measure the relationship between SVL, BCI, and arboreality, based on the findings of the prior analysis but in the absence of toxicant treatments, we used a binomial generalized linear mixed model using the 'lme4' package in R (Bates et al., 2013). We used data from visual surveys conducted in the nine forested sites surveyed prior to any toxicant exposure (Table 1) and classified encounters as ground (1) or arboreal (0). We included sex, SVL and BCI as fixed covariates, with an interactive term for SVL and BCI. Survey site and individual identity were included as random intercepts, such that identity was nested within site. Some locations had irregular recaptures for individuals. Although generalized linear mixed models are designed to accommodate unequal and irregular spacing of repeated measures (Cnaan et al., 1997), approximately half of snakes sampled only had one datum. To avoid overly biasing the model from unbalanced repeated measures sampling, we removed a subset of individuals with a single datum using a stratified, random approach weighted by sex and site. In the final data set, two-thirds of individuals had from 2 to 30 measures and one-third had only one measure ($n = 752$ individuals and 3344 observations). We visually presented the interactive relationship between BCI and SVL by subdividing snakes into poor ($BCI < 0.91$), roughly average ($BCI = 0.91-1.19$) and very good condition ($BCI \geq 1.20$) categories and plotted the probability of encountering a snake on the ground based on BCI category and SVL. All models use $\alpha \leq 0.05$ to determine significance.

3. Results

3.1. Traits associated with toxicant-mediated mortality (telemetry)

Of 31 snakes ≥ 900 mm SVL in NWFN with transmitters, seven died. One was consumed by a monitor lizard (*Varanus indicus*) and another by a feral cat (*Felis catus*) outside of toxicant applications. We filtered these snakes from the survival analysis because the cause of death was not related to toxicants (17% toxicant-mediated mortality). Behavioral and morphological traits were important explanatory predictors and mass yielded a better model fit than did SVL or BCI (Table 1). Male and female survival was similar overall; 16 of 19 females (82%) and 9 of 11 males (80%) survived ($z = 0.4$, $P = 0.68$, CI 95 = $-38.8, 59.2$). Heavier BTS tended to have lower mortality, although not significantly so ($z = -0.6$, $P = 0.08$, CI 95 = $-1.3, 0.1$), and that effect was equally strong for males and females ($z = -1.7$, $P = 0.98$, CI 95 = $-0.5, 0.5$). Individuals that died were visible on average more often ($49 \pm 12\%$) compared those that lived ($17 \pm 3\%$) yielding a decreased risk of mortality from reduced activity ($z = 1.9$, $P = 0.05$, CI 95 = $0.0, 8.8$); individuals that were never visible experienced zero mortality. For the five snakes that died, the mean proportion of ground encounters was $22 \pm 5\%$, while the proportion of ground encounters for snakes that lived through one or more toxicant applications was only $4 \pm 1\%$. Reduced frequency of ground encounters in the period leading up to a toxicant application resulted in a 10-fold greater probability of survival for each 1% decrease in frequency of ground encounters ($z = 2.0$, $P = 0.04$, CI 95 = $0.1, 6.3$).

3.2. Trait changes post-toxicant application (visual survey)

We encountered 170 unique snakes ≥ 900 mm SVL prior to toxicant applications (HMU: 76, NWFN: 94) from 530 total captures (HMU: 107, NWFN: 423). After toxicant applications, we documented 106 unique snakes ≥ 900 mm SVL (HMU: 43, NWFN: 63) from 504 total post-toxicant captures (HMU: 54, NWFN: 450); note that encounter tallies were not effort-corrected and do not quantify changes in population size. Based on MANOVA, SVL and BCI increased following toxicant

Table 1

Mixed effect Cox proportional hazards survival models. Predictive parameters included frequency of ground encounters (GRN), frequency of visible encounters (V) as a coarse index of activity, and sex as an interactive factor with mass, snout vent length (SVL), or body condition index (BCI), as well as a null model with no explanatory predictors. Snake ID (η) was included as a random intercept in all models.

Model	AICc	dAICc	wi
Surv[Days, Fate] ~ GRN + V + SEX * Mass + η + ϵ	20.8	0.0	0.87
Surv[Days, Fate] ~ GRN + V + SEX * SVL + η + ϵ	24.7	3.9	0.12
Surv[Days, Fate] ~ GRN + V + SEX * BCI + η + ϵ	30.2	9.4	0.01
Surv[Days, Fate] ~ η + ϵ	41.3	20.5	0.00

applications ($F_{1, 1025} = 55.1$, $P < 0.001$, $CI\ 95 = 0.07, 0.12$), but there was no difference in those traits by sex ($F_{1, 1025} = 50.2$, $P = 0.64$, $CI\ 95 = -0.02 - 0.03$). Mean SVL of captured snakes that were ≥ 900 mm SVL was 1054 ± 11 mm SVL across both sites prior to toxicant applications and 1147 ± 20 mm SVL after toxicant applications, while mean BCI of snakes increased from 1.05 ± 0.02 to 1.14 ± 0.02 after toxicant applications. There was no difference in sex ratios post-toxicant applications compared to pre-toxicant samples ($\chi^2_{(1)} = 2.4$, $P = 0.12$), although overall the captured snake sample shifted from moderately female biased (59% female) to roughly equal (49% female). Mean percentage of snakes on the ground for HMU and NWFN decreased from $27 \pm 11\%$ of all encounters prior to toxicant applications to $12 \pm 2\%$ of encounters after, a roughly 60% reduction in frequency following toxicant applications ($z = -2.6$, $P = 0.007$, $CI\ 95 = -1.1, -0.17$). Probability of encountering a snake on the ground increased by over 8-fold from the smallest to largest SVL measured ($z = -4.3$, $P < 0.001$, $CI\ 95 = 0.3, 0.7$, range: 900–1900 mm SVL). Conversely, better BCI decreased the probability of finding an individual on the ground after accounting for treatment effects ($z = -2.2$, $P = 0.05$, $CI\ 95 = -2.9, 0.2$).

3.3. Relationship between body condition, size and arboreality (visual survey data; untreated sites)

We recorded 3490 perch descriptions for 890 unique individuals for which sex of the individual was classified and SVL and mass were measured. From all captures, 704 (20%) were first detected on the ground. The mean size of snake captured on the ground was 1052 ± 6 mm SVL (range: 330–1950 mm SVL); however, 80% of ground snakes were individuals ≥ 900 mm SVL. Of the subset of 752 snakes ≥ 900 mm SVL included in statistical analysis following repeated measures bias filtering (3344 observations), males and females were found on the ground with equal probability ($z = -1.3$, $P = 0.18$, $CI\ 95 = -0.5, 0.1$). The probability of encountering a snake on the ground increased with length ($z = 8.7$, $P < 0.001$, $CI\ 95 = 0.4, 0.7$), although 75% of snake encounters were individuals less than 1132 mm SVL (Fig. 1A). BCI was inversely related to the probability of finding a snake on the ground (Fig. 1B), such that snakes in better condition were more arboreal ($z = -5.0$, $P < 0.001$, $CI\ 95 = -0.5, -0.2$). SVL and BCI interactively affected probability of encountering a snake on the ground ($z = -2.0$, $P = 0.04$, $CI\ 95 = -0.19,$

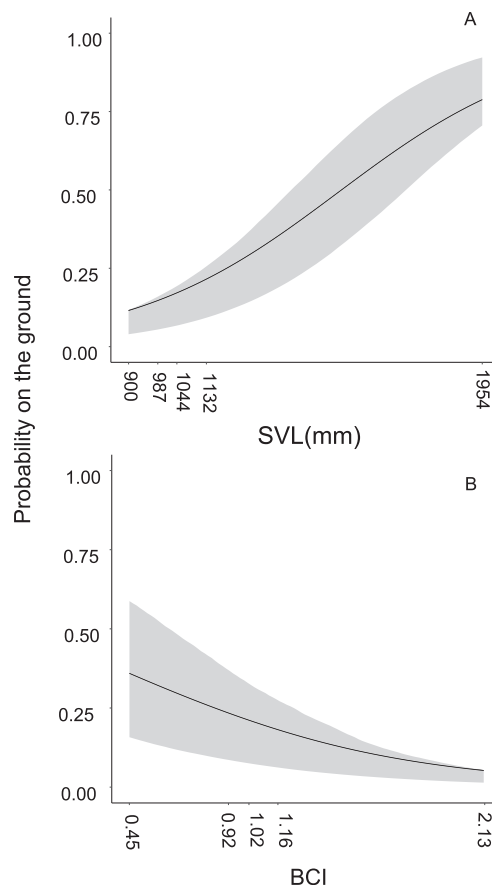


Fig. 1. Probability of encountering an arboreal brown treesnake on the ground during 14 years of visual surveys across nine untreated sites on Guam based on back-transformed snout-vent length (SVL, A) and body condition index (BCI, B). Point estimates represent minimum, first quartile, mean, third quartile, and maximum values for SVL and BCI. Shaded areas represent 95% confidence interval ($1.96 \times$ standard error) of the estimate ($n = 752$ individuals; 3344 observations).

–0.01); very large individuals (>1300 mm SVL) classified as below average BCI were more than twice as likely to be on the ground as equivalently sized animals with an above average BCI (Fig. 2).

4. Discussion

We found evidence that size (weight or SVL), condition, and behavioral traits that correlated with toxicant-mediated mortality were reflected in sampled differences in the means and frequencies of these traits in post-treatment populations. The partial consistency in findings between the telemetry study and the distribution of samples collected after toxicant application would suggest that toxicant applications were partially driving effects to the extent that they were not a result of detection bias. In addition to potential population changes due to direct mortality, density-dependent mechanisms following removal of a significant portion of the population could also have affected observed patterns. Regardless of the mechanism or causative factors for these changes, behavioral variation among individuals is often considered a nuisance variable during species management intended to affect populations (Caro and Sherman, 2012). Here we show that individual traits that predicted susceptibility to a control tool had the potential for population-level effects. Individual traits explored in this study, therefore, merit continued monitoring due to implications for use of ADS at larger spatial and longer temporal scales.

For snakes large enough to eat mouse baits, size negatively predicted survival, as reflected by the size structure of snakes detected after toxicant applications. However, the toxicant mediated mortality study used weight as an explanatory variable for size, while the post-toxicant frequency distributions focused on SVL. Correlation between weight and SVL is not perfect, but a heavier snake can generally be interpreted to be a longer snake. Within the subset of snakes that were large enough to reliably be attracted to mice, the mean size of the population increased by roughly 70 mm SVL and 140 g after toxicant applications. Larger brown treesnakes are more commonly encountered on the ground (Rodda and Reed, 2007) and thus may have lower contact rates with baits designed to catch in the tree canopy. Small carrion may be appealing prey for smaller snakes transitioning from lizards to rodents, a process thought to occur around 850 mm SVL (Savidge, 1988). Live rats or mice are inherently more dangerous prey than are small dead mice, which may drive increased attraction to carrion by small individuals (Shivik and Clark, 1999). Whether individuals encountered baits and rejected them was, however, unmeasured and this hypothesis is thus speculative. Size-based effects on foraging behavior may also be independent of effects driven by body condition. A snake foraging on the ground more often due to poor condition may have a higher probability of consuming a bait when available, irrespective of size, because they are either foraging more often or more responsive to chemical odors released by carrion. Alternatively, dose-dependent responses to toxicant exposure (Mauldin and Savarie, 2010) or preference for larger prey items by larger snakes (Savidge, 1988; Siers, 2015) could have contributed to a size bias in removal, such that smaller snakes (among those ≥ 900 mm SVL) were removed at higher rates. The change in behavior may have also resulted, in part, from prey response to brown treesnake removal. Visual sightings of small mammals increased following toxicant applications and conceivably caused accelerated growth and increased body condition (Boback et al. In Review). Three of five plausible explanations as to why toxicant applications resulted in a larger mean population length supported that under-standing size- or energetic-based variation in foraging behavior can help refine and improve management outcomes by improving understanding of why some individuals are less likely to consume baits.

Independent of size, approximated measures of foraging behavior leading up to the toxicant applications affected survival probability. Snakes that were estimated to be less active or dormant during the time leading up to an application, as estimated by visual detections, were less likely to be removed. Brown treesnake detectability is periodic and tied to digestion following a meal (Christy et al., 2010; Siers et al., 2018a). A simple explanation is thus that animals satiated from a recent meal are less active (Shivik et al., 2000; Siers et al., 2018a) and would, therefore, be expected to have a lower probability of encountering a bait. Of note, however, is that visibility of a snake to a human observer is a coarse measure of activity, because snakes high in

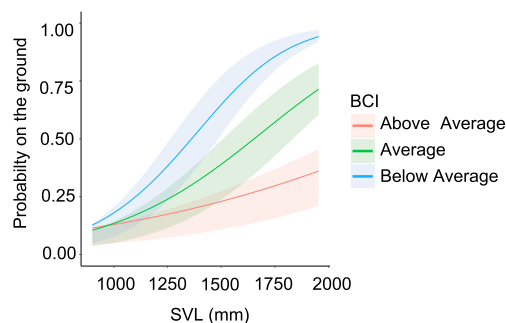


Fig. 2. Reclassification of the continuous body condition index (BCI) into categorical variables for graphical purposes of well below average (<0.90), roughly average (0.90–1.19), and well above average (≥ 1.2) demonstrates the interactive effect of BCI and size (snout-vent length; SVL [mm]) on probability of encountering mature (≥ 900 mm SVL) brown treesnakes on the ground during 14 years of visual surveys across nine untreated sites on Guam ($n = 752$ individuals; 3344 observations). Shaded areas represent 95% confidence interval ($1.96 \times$ standard error) of the estimate.

the canopy are often obscured by vegetation and not visible regardless of their activity state. A relationship between foraging behavior or activity and mortality caused by a bait-based control is intuitive.

Given, however, that larger brown treesnakes are more likely to be on the ground based on data presented here and in other studies (Rodda and Reed, 2007), our observed shift towards larger snakes represents a counter-intuitive relationship with decreased frequency of ground encounters in the post-toxicant population. Ground movement has been associated with foraging behavior in another arboreal snake (Fitzgerald et al., 2002). The average snake may thus be more likely to be foraging in untreated landscapes, perhaps as a function of increased prey competition. If small mammal abundances increased following toxicant applications due to loss of a primary predator (Holt et al., 2008), greater food availability could decrease foraging activity and improve the condition of the remaining snakes. A mean increase in condition may have subsequently also influenced habitat use. Specifically, brown treesnakes are arboreal and have behavioral, morphological, and physiological adaptations that support locomotion in the canopy (Rodda and Savidge, 2007; Jayne et al., 2015). Although terrestrial encounter frequency increased with length, the observed frequency of the behavior was influenced by the condition of the snake. Use of open, terrestrial habitats has been suggested to increase risk of predation in another species of arboreal snake (Shine and Fitzgerald, 1996; Fitzgerald et al., 2002). Although rarely investigated in snakes, poor condition has also been documented to increase risky behavioral choices and habitat use in sea turtles (Heithaus et al., 2007). Brown treesnakes in worse condition may thus spend more time on the ground because individuals in poor condition take greater risk, whether through enhanced energetic expenditure from foraging more often or increased exposure to predators in their habitat selection. We cautiously hypothesize that toxicant applications may target individuals that more willingly engage in risky behavior or are less wary of novelty, although we recommend further study. Neophobia in rodents, for example, is an explanatory variable for behaviorally-mediated bait resistance (Brunton et al., 1993). Regardless of the causative mechanism, some aspect of ground use was important for predicting susceptibility to toxicant-mediated mortality and that in turn was reflected in reduced frequency of the behavior after treatment.

5. Conclusions

Local and landscape management actions are known to cause trait changes in harvested populations, which have community-level implications important for invasive species management (Palkovacs et al., 2018; Závorka et al., 2018). Understanding the mechanism driving the patterns of susceptibility and subsequent traits of the remnant population, however, will help refine control tools. Specifically, behavioral theory, energetic states, and other individual-level traits are frequently ignored during wildlife management due to the goal of having population-level effects. However, when extreme suppression or eradication is a goal for invasive species, the variance in susceptibility across individuals has increasing importance; even the most effective management tool is likely to vary in efficacy among individuals. Understanding which factors affect individual variance in susceptibility will help maximize management effects by enabling development of complementary tools that target every individual. In this study, energetic state of the individual likely contributed to susceptibility, and thus prey control prior to and during snake suppression may have improved removal rates. Consideration of individual traits, particularly as they relate to foraging behavior, during the development of wildlife control tools is warranted due to their potential to scale up to population-level effects.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.gecco.2019.e00834>.

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