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Habitat type and structure affect trap capture success of an invasive snake across variable densities

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Abstract. Detection represents an important limitation of accurately estimating population size, abundance, and habitat suitability for wildlife, which can be especially true for cryptic animals. Moreover, for reptiles, juveniles are often less likely to be detected than later life stages. In the case of invasive species, preventing false negatives early in the invasion process can be critical for improving outcomes of control measures. We evaluated habitat structure in relation to catch per unit effort (CPUE) and mean size of trapped invasive brown treesnakes (*Boiga irregularis*) on Guam. We used a 5-ha enclosure containing a known, closed population of brown treesnakes to identify key habitat variables that related to CPUE and mean size of trapped snakes over six years. We then tested the relationship of those variables to CPUE and mean size of trapped snakes at three sites with suppressed snake populations as a proxy for low-density populations anticipated to occur during early detection of invasive populations. We found that a coarse measure of habitat structure represented by three forest types correlated with trap detections, as well as finer measures of habitat structure, such as distance to nearest branch and the type of trap support structure used. On average, smaller snakes were captured in traps placed higher in the tree canopy. Some, but not all, habitat variables identified as predictive of CPUE and mean size within the enclosed population pre-suppression were also predictive at the snake-suppressed (low-density proxy) sites. Habitat structure around the sampling unit (a trap) affected detection probability and the size of detected individuals independently of the demographic structure of the population. Measuring wildlife-habitat relationships of invaders in their novel environments may be one method to improve early detection during invasive species management.

Key words: *Boiga irregularis*; brown treesnake; density; early detection; Guam; invasive species; occupancy; presence; rapid response.

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INTRODUCTION

A fundamental parameter for wildlife management is detectability, or the probability of locating a species (species occupancy) or individual (individual detectability) that is present. Selection and application of management scenarios based on species occupancy state (presence or

absence) rely on clear relationships between presence–absence and detection or non-detection, but presence–detection relationships may be confounded by factors that affect individual detectability. Failure to detect present individuals—false negatives—during the sampling process can result in imprecise or misleading patterns of occurrence, if models do not account

for errors originating from detection biases (Ruiz-Gutiérrez and Zipkin 2011). Moreover, in the case of invasive species, established populations can exist with few to no detections of individuals, such that detection does not occur until populations are large enough that eradication is difficult, if not impossible. Each concern could be magnified in importance for species that are cryptic and by definition difficult to detect. Evaluating the relationship between detection and the structure of surveyed habitat may be one avenue toward understanding false negatives and the application of occupancy surveys for the management of land, wildlife, and invasive species, especially for cryptic organisms.

Through several distinct pathways, habitat can influence individual detectability as well as the probability of detecting any individual when some are present (Kjærsmo and Merilaita 2012, Rovang et al. 2015). Habitat quality can affect population density, and all else being equal, higher population densities should result in more detections. Population density can, however, correlate poorly with detection—measured as the per-capita probability of detecting an individual that is present. Habitat structure, for example, can influence the probability that present individuals will be seen, heard, or trapped (Melbourne 1999, Anderson et al. 2015). Dense vegetation hinders visual and auditory detection, but may promote locomotion of flightless arboreal species, thus facilitating trap capture detections. Arboreal configuration and connectivity of forest habitat in which traps are placed affects trap capture probabilities (Melbourne 1999), but could either enhance it (by steering locomotion toward the trap) or reduce it (by offering pathways to bypass the trap). More subtle effects of habitat structure are also likely to modulate detection probability; recent disturbance, for example, may disrupt a target's refugia, elevating movement rates (Driscoll et al. 2012). Conversely, recent disturbance could potentially temporarily suppress movement rates through changes in microhabitat quality, such as light, heat, and humidity levels. Additionally, changed vegetative density can alter the likelihood of visual or auditory detection. The myriad of mechanisms by which habitat can influence detectability complicate management decisions based on capture rates, especially when multiple

types of unquantified bias may be present (Beauvais and Buskirk 1999), but is of consequence for obtaining successful management outcomes.

In the case of detecting invasive species, a false negative can be extremely detrimental because emerging invasive species are easier or less costly to control early in the invasion process, a concept that resulted in development of Early Detection and Rapid Response (EDRR) programs (U.S. Department of the Interior 2016). Early Detection and Rapid Response in the context of biological invasions represents actions that support eradication of invasive species before they establish and spread to new locations (U.S. Department of the Interior 2016). Low initial population density combined with logistical or financial constraints associated with many EDRR programs can magnify the probability of a false negative. Thus, detections may not occur until the invader is established and spreading, eliminating eradication as an option. Better understanding of how habitat type and structure affect detectability of invasive species can improve the outcomes of EDRR strategies. Yet knowledge of habitat-specific detectability is rarely applied to invasive species.

We evaluated microhabitat—the habitat adjacent to the trap—to measure the effect of microhabitat type and structure on trap captures of brown treesnakes (*Boiga irregularis*), a cryptic, arboreal snake. Native to Australia, Papua New Guinea, and a number of nearby islands, they were introduced to the Pacific Island of Guam from the Admiralty Islands during or shortly after World War II (Rodda et al. 1992, Richmond et al. 2015), where they contributed to extirpations of the majority of Guam's native avifauna (Savidge 1987). After recognizing their negative ecological and economic effects, considerable investment in programs for local population control on Guam and prevention of their spread elsewhere ensued (Vice and Vice 2004, Rodda and Savidge 2007), including development and testing of multiple control tools (Clark et al. 2018). A standard trap was developed as an interdiction tool to capture brown treesnakes (Vice et al. 2005), but captures remain biased toward larger individuals (Rodda et al. 1999a, 2007, Tyrrell et al. 2009). Size-biased survey methods can produce skewed demographic results, which remains a general issue for herpetofaunal surveys (Marsh and Goicochea 2003,

Pike et al. 2008) and presents challenges for effective interdiction and EDRR (Vice and Vice 2004). Our study thus focused on relating microhabitat to trap catch per unit effort (CPUE) and mean size of individuals trapped with the purpose of identifying habitat variables likely to improve trap-based, per-capita detection probabilities.

In support of EDRR, we evaluated how microhabitat type and structure may affect detection and identified habitat variables that could increase detection probability early in an invasion. Evaluation of such relationships may improve invasive species management by improving understanding of habitat use, as well as informing habitat suitability model development. Habitat suitability models represent a developing EDRR management tool that are informed by presence-absence or presence-only surveys to predict suitability for an invasive species (Gormley et al. 2011). Within those goals, we had three primary objectives: evaluate how habitat type and structure affect (1) trap success and (2) mean size of captured individuals and (3) evaluate whether identified habitat variables that improved trap CPUE or increased the probability of capturing smaller snakes at high densities were consistent in proxy low-density populations.

METHODS

Study sites

We sampled three sites in Northern Guam at varying intensities and sampling structures from 2004 to 2017 (Table 1): (1) Northwest Field North (NWFN), (2) the habitat management unit (HMU), and (3) Guam National Wildlife Refuge (GNWR). At NWFN, a fence (1.5 m height) was erected around a 5 ha area in 2004. The fence contained a bulge at the top that prevented snakes from climbing over. Vegetation on both sides of the fence was cleared at a 1 m distance on either side to prevent snakes from crossing the fence via vegetative connectivity. The fence prevented immigration or emigration of brown treesnakes (see Rodda et al. 2007 for images of the fence). This enclosure became a focal study site in which we completed 10 yr of intensive trapping from 2004 to 2017 in a known, closed population. Population sampling followed a mark-release paradigm from 2004 to 2009. In 2011, all trapped snakes were removed, and from 2012 to 2017, NWFN was considered a suppressed population. The HMU is a 55 ha area surrounded by a barrier (1.5 m height) that prevents immigration, but allows emigration of brown treesnakes. In 2013, large-scale suppression efforts for brown treesnakes occurred via

Table 1. Trapping sites including a description of available forest types (limestone [L], degraded [D], or strand [S] forest), arrangement of trapping lines or grids (Grid), year(s) sampled, total traps deployed, duration of the trapping effort (days), and corrected catch per unit effort (CPUE) as snakes per 100 functional trap days.

Site (LAT, LONG)	Habitat	Population	Grid	Year	Trap No.	Effort	CPUE
Pre-suppression							
NWFN (13.640, 144.865)	D, L	Closed	13 × 13	2004	169	103	9.0
				2005	169	49	5.0
				2007	169	59	4.0
				2008	169	31	4.0
				2009	169	66	6.0
Post-suppression							
NWFN (13.640, 144.865)	D, L	Closed	13 × 13	2011	169	78	1.0
				2012	169	50	2.0
				2013	169	51	2.0
				2015	169	85	0.4
				2017	169	54	2.0
HMU (13.597, 144.864)	L	Semi-closed†	10 × 10 + 51‡	2015	151	29	0.3
GNWR (13.645, 144.852)	S	Semi-closed†	6 × 18	2014	108	137	1.0

Notes: HMU, habitat management unit; NWFN, Northwest Field North; GNWR, Guam National Wildlife Refuge. Blank cells indicate repeated measures of NWFN across years pre- and post-suppression efforts.

† Emigration could occur but not immigration.

‡ 51 forest edge traps in addition to a 10 × 10 interior forest grid.

baited toxicants, which resulted in a suppressed population during trap sampling in 2015 (Table 1). The GNWR site is a U. S. Fish and Wildlife Service National Wildlife Refuge located on the northern tip of Guam, which is surrounded by a degraded snake barrier. The barrier was intended to prevent immigration of brown treesnakes onto the refuge, but is likely no longer completely effective. In 2013, extensive trap-based removal of brown treesnakes was implemented by U.S. Fish and Wildlife Service. The three study sites were comprised of areas that were historically strand vegetation or limestone forest (see Fosberg 1960 for a description of forest communities) but in some cases have been highly degraded into mixed secondary native and non-native forests, interspersed with shrub scrub.

Use of a relatively small closed population (NWFN) to identify habitat features that were correlated with capture success and size allowed for the assumption that the abundance of snakes was constant throughout a trap array. Individuals could not move outside of the trap array, and some were documented to move throughout the entire enclosure. Thus, differences in CPUE by traps in NWFN were assumed to reflect modulation of per-capita detectability rather than population density heterogeneity. Comparison of results for the pre-suppression NWFN data to suppressed snake populations due to control efforts served as a proxy to evaluate whether habitat parameters identified as predictive in high-density populations were still predictive in low-density populations. All three suppressed sites were closed or semi-closed (emigration but no or low immigration) populations.

Trap design and deployment

The study sites and sampling periods varied in duration as well as number of traps, their density, and spacing (Table 1). Each trap was uniquely numbered to track trap-specific captures. We used modified crayfish traps, constructed of galvanized steel mesh with a sloping metal mesh flap and covered by gray plastic polyblend sheets to provide shade and protection for trap occupants. This trap design has been the standard trap configuration for brown treesnake research and is functionally similar to the custom-built traps used for operational snake control and interdiction (Rodda et al. 1999a, Vice

et al. 2005). All traps contained an open-ended hide tube and a live mouse inside a chamber that served as a lure. Traps were checked daily between 07:00 and 11:00. During trap checks, traps that had become non-functional as a result of doors failing to close or other mechanical failures were documented.

Trap characterization

During or immediately after each trapping bout, we categorized the microhabitat (from 0.5 to 10 m radius, depending on the habitat variable and the assumed functional relationship to capture probability). We documented whether the trap was placed in native limestone forest (Forest L, characterized by high presence of native forest trees and karst substrate), coastal strand forest (Forest S, coastal with high presence of native species and sandy soil), or degraded forest (Forest D, high presence of non-native plant species, either forest or shrub scrub, but historically, prior to anthropogenic disturbance, was limestone forest) in the 10 m radial area adjacent to the trap. We also quantified the local structure (0.5–5.0 m) of the vegetation surrounding the trap using 13 metrics. Within 5 m², we recorded the number of plant species present (SppRich) as low ($L \leq 3$ species), moderate ($M = 4–9$ species), or high ($H \geq 10$ species). Within 0.5 m² centered on the trap, we recorded the presence (Y) or absence (N) of branches of any size touching the trap (Foliage), the presence (Y) or absence (N) of branches parallel to the longitudinal axis of the trap (Suspend), and branch connectivity (Connect). Branch connectivity was rated as low ($L \leq 3$ plant parts within 200 mm of each other), moderate ($M = 4–9$ plant parts), or high ($H \geq 10$ plant parts). We measured the horizontal (HDBrnc) and vertical (VDBrnc) distance in meters to the nearest woody branch over 2 mm in diameter, which was anticipated to be the size necessary to support the weight of a brown treesnake. Each trap was hung using a wire that ran vertically through the trap top, such that each end of the wire was subsequently wrapped tightly around two support structures. We recorded the two support structures that the trap wire was attached to as one of five categories: iron reinforcing bar (Rebar), dead plant matter (dead trees, logs, or wooden posts; Dead), live trees (Tree), and vines (Vine). We recorded

trap height (Height) as the distance from the ground to the bottom of the trap (m) and the average distance (AveDist) the trap was hung from its two support structures (m). We classified season in which trapping occurred to account for demographic changes in population size or structure due to wet (May–October) or dry (November–April) season effects.

Brown treesnake trap captures

For each snake capture, we recorded trap number, assigned a unique scale clip and implanted a passive integrated transponder tag, or recorded the identity of recaptures. We measured the snout-vent length (SVL, mm) of stretched snakes. We calculated total snake captures, number of unique captures, mean size (SVL), and minimum and maximum size of all captured snakes for a given trap. Because total captures and unique captures by trap were similar (snakes rarely re-entered the same trap), we focused on total captures as the measure of trap success. For each trap, we present CPUE as captures per corrected trap night, where a trap night is defined as one trap active for one night after correcting for non-functional trap nights. Standard brown treesnake traps can capture multiple individuals at once and were functional after snake captures. Catch per unit effort was multiplied by 100 trap nights to create whole numbers of snakes.

Statistical analysis

We initially used data from pre-suppression NWFN (high population density) to measure relationships between habitat variables and two metrics of trap performance: CPUE and mean size (SVL) of snakes captured by each trap. We used categorical and regression tree models (CART) to measure the relationship between microhabitat structure and CPUE or mean size. Tree-structured data analyses are appealing for evaluating wildlife-habitat relationships for several reasons. They are a simple, yet robust statistical model that allows for missing data and unbalanced designs (De'ath and Fabricius 2000). Because CART models divide data into hierarchical groups based on the predictive power of the input predictor variables, they can be easily interpreted as a series of if-then statements directed by the presence of terminal nodes. They also make no assumptions

about data distributions, relationships among predictor variables, or form of the relationships between predictor and response variables (De'ath and Fabricius 2000). Thus, they allow interactions and non-linear relationships between dependent and predictor variables without requiring complex model development. We completed the CART analyses using the tree function from the tree package in R version 3.3.2 (Ripley 2016). We used 20-fold cross-validation and specified that a minimum of 10 samples were required to generate a split or branch and plotted number of terminal nodes in a model against its standard deviance as a measure of fit. We selected the final tree based on the number of terminal nodes that produced the lowest standard deviance. We ran two CART models: one to measure the relationship between CPUE and measured habitat variables and one to measure the relationship between mean size and measured habitat variables for traps at pre-suppression NWFN.

Because CART models are infrequently applied to analyze wildlife-habitat relationships and have a tendency to overfit relationships, we also used the step function in R package stats (R Core Team 2013) to complete forward and backward stepwise fixed-effect Poisson regression for CPUE and forward and backward linear regression for log-transformed SVL pre-suppression to test CART model performance. The function selects a formula-based model through use of Akaike's information criterion to identify the parameters that produce a best-fit model (Burnham and Anderson 2002). Regression results were used to validate significance of variables selected by the CPUE and size CART models for data collected in NWFN pre-suppression. For the categorical variables that achieved significance and contained >2 categories, we used a Tukey post hoc analysis to evaluate within treatment differences. Using the parameters selected by the fixed-effect models, we also ran mixed-effect models for CPUE and SVL using the lme4 package in R (Bates et al. 2013) to measure the effect of a random intercept for trap station, year of trapping, and season during which the majority of trapping occurred on model variance and parameter significance. Statistical outcomes for mixed-effect models are only reported for those parameters that experienced major deviation from the fixed-effect model outputs.

For a variety of reasons, organismal detection rates and factors that predict them can vary when populations exist at low densities—as would be expected in an EDRR context. Thus, we harvested the habitat parameters selected by the pre-suppression CPUE and size models and tested their ability to predict trap captures at three sites post-suppression (NWFN, HMU, and GNWR; Table 1). We used a mixed-effect Poisson regression to evaluate habitat parameters selected by pre-suppression NWFN model relationship with trap CPUE at the suppressed sites, where trap station nested by site and season was included as random effects to account for potential variation in population size by site or abundance by trap station and seasonal effects (Table 1). Likewise, we used a mixed-effect linear regression to evaluate habitat parameters selected as predictive for mean size (SVL) of captured snakes in pre-suppression NWFN and evaluated their relationship to mean size of snakes captured at the post-suppression sites. Insufficient traps in the post-suppression sample locations were categorized as high species richness, and thus, the effects of high species richness on trap CPUE could not be evaluated for suppressed populations.

RESULTS

Pre-suppression (closed population)

CPUE.—We recorded 3287 snake captures in five sampling years (308 sampling nights, 63,270 active trap nights, see Table 1 for CPUE by year and site). The regression tree for CPUE had six terminal nodes and selected five predictor variables for construction: Forest, SppRich, VDBrnch, HDBrnch, and Rebar (Table 2). Traps with the greatest CPUE were located in Forest L (Fig. 1). Within limestone forests, traps that had a VDBrnch < 0.22 m captured more snakes than those with larger distances (Fig. 1). Traps placed in Forest D captured more snakes if they were (1) affiliated with SppRich-H or (2) used at least one piece of living or dead vegetation as a support structure and had an HDBrnch < 0.55 m (Table 2, Fig. 1). In general, placing traps in limestone forest or in degraded areas with high localized plant species richness resulted in greater trap CPUE.

Forward and backward stepwise multiple regressions converged on the same final model

Table 2. The regression tree for the effect of habitat type and structure on catch per unit effort (CPUE) of snakes captured pre-suppression had six terminal nodes comprised of five habitat variables.

Split	Terminal node	<i>n</i>	Deviance	CPUE
Forest D				
SppRich-L, M				
Rebar ≤ 1				
HDBrnch < 0.55-m	1	339	8812	3
HDBrnch > 0.55-m	2	26	197	6
Rebar > 1	3	300	5337	4
SppRich-H	4	34	485	9
Forest L				
VDBrnch < 0.22-m	5	28	901	15
VDBrnch > 0.22-m	6	27	674	10

Notes: The number of samples included in a split is described by *n*, and deviance is equal to the response variable sum of squares for each node. Review text for definition of a given variable. Values are only provided for terminal nodes. Blank cells indicate non-terminal nodes. See associated Fig. 1.

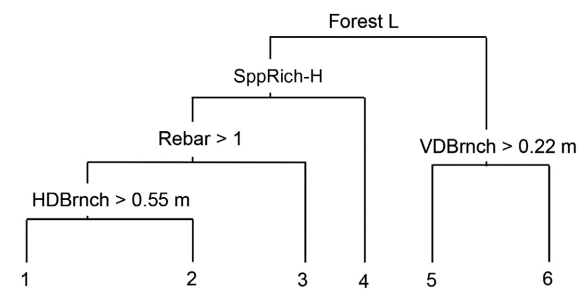


Fig. 1. Regression tree of snake catch per unit effort (CPUE; snakes per 100 functional trap days). The top is the root node and represents unpartitioned data. Each split represents two mutually exclusive groupings of a given variable until a terminal node is reached: If statement is true, move to the right branch. The values at each terminal node are the terminal node number for data associated with Table 2. Table 2 provides the number of samples (*n*), deviance (equal to the response variable sum of squares) for each node, and CPUE.

for pre-suppression CPUE, which contained nine predictor variables: Forest, SppRich, HDBrnch, VDBrnch, Dead, Rebar, Suspend, Connect, and AveDist. Of those nine, only the first seven variables had a significant relationship with CPUE, while relationships between Connect and

AveDist were non-significant (Table 3). Traps in Forest L were roughly 1.4 times more likely to capture a snake than traps in Forest D (Table 3). Traps surrounded by SppRich-H were 1.4 times more likely to capture a snake than those in either SppRich-L ($\beta = 0.36$, $SE = 0.13$, $P = 0.01$) or SppRich-M ($\beta = 0.35$, $SE = 0.04$, $P < 0.001$), but there was no difference between SppRich-M and SppRich-L CPUE ($\beta = 0.01$, $SE = 0.12$, $P = 0.99$). Catch per unit effort was greater for traps that were closer to horizontal and vertical branches. For each 1.0 m increase in the distance between the trap and the nearest branch, CPUE declined by 0.8 (HDBranch) and 0.9 (VDBranch) times (Table 3). Traps that used one Dead support were 1.1 times more likely to capture a snake than other support types, while traps that used some form of plant material (dead or live) were 1.1 times more likely to capture a snake than those that used Rebar (Table 3). A trap lacking parallel branches (Suspend N) was 1.1 times more likely to capture a snake as traps with such branches (Table 3). Although the linear regression model identified a greater number of explanatory variables during model building than did the tree regression, they overlapped in selection of five variables as predictive of CPUE: Forest, SppRich, HDBranch, VDBranch, and Rebar.

Inclusion in the generalized linear model for CPUE of a random intercept for year explained negligible model variance outside of seasonal effects. Within trap effects blocked by season in which trapping occurred explained approximately 29% of the model variance, such that CPUE was generally greater during wet season trapping. Inclusion of a season by trap random effect had minor influence on the structure of the correlation between Forest, SppRich, and HDBranch and the lack of correlation between Connect and trap CPUE. In contrast, VDBranch ($\beta = -0.06$, $SE = 0.01$, $P = 0.67$), Rebar ($\beta = -0.12$, $SE = 0.02$, $P = 0.18$), and Dead ($\beta = -0.10$, $SE = 0.04$, $P = 0.16$) lost significance as predictors for CPUE. AveDist, however, negatively predicted CPUE ($\beta = -0.24$, $SE = 0.12$, $P < 0.001$), such that up to 1.0 m, each 0.1 m increase in distance from the support structure to the trap entrance decreased CPUE by 0.8 times. Therefore, including a random intercept in the Poisson regression affected significance for two out of the three variables identified as important for CPUE by the regression tree, with the relationship between forest type, species richness, and horizontal distances to the nearest branches having consistent relationships across statistical approaches.

Table 3. Habitat variables selected by forward and backward stepwise fixed-effect Poisson regression for brown treesnake trap catch per unit (corrected) effort (CPUE) pre-suppression (NWFN) and as they relate to CPUE post-suppression† (NWFN, HMU, and GNWR) based on mixed-effect Poisson regression.

σ	β^\dagger	z^\dagger	P^\dagger	CI 95 ‡ (2.5%, 97.5%)	β^\ddagger	z^\ddagger	P^\ddagger	CI 95 ‡ (2.5%, 97.5%)
β_0 (intercept)	2.37	26.1		2.19, 2.54	-1.66	-1.8		-2.94, 0.92
Forest L	0.58	10.6	<0.001	0.47, 0.68	0.52	2.0	0.04	0.01, 1.03
Forest S					0.81	0.6	0.53	-2.85, 4.53
SppRich-H	0.36	2.6	0.01	0.10, 0.64				
SppRich-M	0.01	0.1	0.99	-0.24, 0.26	0.50	1.1	0.27	-0.01, 1.06
HDBranch	-0.18	-3.7	<0.001	-0.27, -0.08	0.53	3.4	<0.001	0.22, 0.84
VDBranch	-0.05	-2.7	0.005	-0.09, -0.01	-0.11	-2.7	0.03	-0.19, -0.03
Dead	0.11	2.3	0.01	0.01, 0.21	-0.32	-1.4	0.14	-0.79, 0.10
Rebar	-0.11	-4.1	<0.001	-0.17, -0.06	-0.26	-4.5	<0.001	-0.38, -0.14
Suspend Y	-0.07	-1.9	0.02	-0.14, -0.01	0.20	2.1	0.03	0.01, 0.40
Connect-L	-0.01	-0.2	0.80	-0.12, 0.09	0.19	1.5	0.11	-0.04, 0.44
Connect-M	-0.09	-1.6	0.09	-0.22, 0.01	0.13	1.1	0.28	-0.11, 0.39
AveDist	-0.24	-1.4	0.06	-0.48, 0.06	0.56	0.3	0.03	0.01, 1.10

Notes: HMU, habitat management unit; NWFN, Northwest Field North; GNWR, Guam National Wildlife Refuge.

Bolded beta estimates highlight parameters that were also significant in the pre-suppression categorical and regression tree models and mixed-effect Poisson regression model. Blank cells indicate habitat variables that were not included in the model due to data absence. Review text for definition of a given variable.

† Pre-suppression (high density).

‡ Post-suppression (low density).

Brown treesnake size.—The regression tree for mean size of captured snakes had five terminal nodes constructed from three predictor variables including Connect, Height, and VDBrnch. Traps > 1.2 m above ground captured smaller snakes than those <1.2 m. For traps <1.2 m, traps captured smaller snakes when Connect was high or low than Connect-M traps. For traps with Connect-M, mean size of snakes captured decreased if traps were placed >0.61 m above the ground, or if placed <0.61 m above ground and had a VDBrnch < 0.24 compared to those with a VDBrnch > 0.24. Traps placed >1.2 m above ground captured the smallest snakes (969 mm SVL on average), while traps placed in Connect-M, Height < 0.61 m, and VDBrnch > 0.24 captured the largest mean snakes at 1275 mm SVL (Table 4).

Forward and backward stepwise multiple regressions converged on the same final model for predicting mean size of individuals captured in each trap. Model-selected predictor variables included Height, Connect, VDBrnch, Suspend, and Dead. For each 1.0 m increase in Height, mean SVL of captured snakes decreased by 6% (Table 5; Fig. 2) for traps from 0.2 to 1.7 m in Height. Traps with Connect-M had a mean SVL of captured snakes that was on average roughly 3% larger than traps with Connect-H and Connect-L (Table 5), but there was no difference in

mean size between Connect-L and Connect-H traps. A positive value for Suspend (Y) resulted in an average mean SVL that was 4% smaller (Table 5). For each 1.0 m increase in VDBrnch, mean size of captured snakes increased 1% (Table 5). Thus, the fixed-effect linear regression model identified similar significant parameters as the CART model when predicting mean size of captured snakes, with smaller snakes tending to be captured in higher traps associated with high or low branch connectivity.

Inclusion in the generalized linear model for mean SVL of a random intercept for year or trap explained negligible model variance. Within season effects, however, explained approximately 50% of the variance, such that mean size of snakes captured during wet season trapping efforts were smaller on average. There was no evidence for a trap-by-season effect on mean SVL of snakes captured. Inclusion of season as a random intercept had minor effects on parameter relationships of Height and Connect to mean SVL of snakes captured and did not affect the lack of correlation between Dead supports and mean SVL. However, neither Suspend ($\beta = -0.01$, $SE = 0.001$, $P = 0.48$) nor VDBrnch ($\beta = -0.002$, $SE = 0.003$, $P = 0.54$) maintained significant relationships with mean SVL of snakes captured in the mixed-effect model. Thus, across the three models, the parameters that were most robustly supported in their relationship to mean SVL were trap height and branch connectivity.

Table 4. The regression tree on the effect of habitat type and structure on mean snout-vent length (SVL) of snakes captured pre-suppression had five terminal nodes and used three habitat variables for construction.

Split	Terminal node	n	Deviance	SVL (mm)
Height < 1.23 m				
Connect-L, Connect-H	1	503	4460000	1078
Connect-M				
Height < 0.62 m				
VDBrnch < 0.24 m	2	22	227700	1095
VDBrnch > 0.24 m	3	20	369800	1275
Height > 0.62 m	4	107	1057000	1101
Height > 1.23 m	5	21	210800	969

Notes: The number of samples included in a split is described by *n*, and deviance is equal to the response variable sum of squares for each node. Review text for definition of a given variable. Values are only provided for terminal nodes. Blank cells indicate non-terminal nodes. Indentations indicate dependent relationships between variables.

Post-suppression (low-density proxy)

CPUE.—We documented 808 total snake captures (406 sampling nights, 68,006 active trap nights) at the three sites (NWFN, HMU, and GNWR) that were sampled post-suppression. Traps placed in Forest L were 1.6 times more likely to capture a snake than in Forest D or S. For each 0.1 m increase in distance to the nearest horizontal (HDBrnch) and vertical (VDBrnch) branch, CPUE increased by 1.7 times and decreased by 0.8 times, respectively (Table 3). Traps that used some form of vegetation as support were 1.3 times more likely to capture a snake than those that used Rebar as a support structure (Table 3). Traps categorized as Suspend N were 1.2 times more likely to capture snakes than those categorized as Suspend Y. With each 0.1 m increase in AveDist up to 1.0 m, CPUE increased by 1.7

Table 5. Habitat variables selected by forward and backward stepwise fixed-effect linear regression as important for predicting mean pre-suppression (NWFN) snout-vent length (SVL, mm) of trap-captured snakes and their relationship to mean SVL at three post-suppression trapping sites based on mixed-effect linear regression.

σ	β_{\dagger}	t_{\dagger}	P_{\dagger}	CI 95 $_{\dagger}$ (2.5%, 97.5%)	β_{\ddagger}	t_{\ddagger}	P_{\ddagger}	CI 95 $_{\ddagger}$ (2.5%, 97.5%)
β_0 (intercept)	7.039	350.6		6.999, 7.078	6.932	117.2		6.856, 7.008
Connect-L	0.021	2.7	0.08	−0.046, 0.003	0.051	2.2	0.02	0.006, 0.095
Connect-M	0.033	2.5	0.01	0.007, 0.059	0.056	2.3	0.02	0.008, 0.103
VDBrnh	0.010	2.7	0.005	0.002, 0.017	0.002	0.3	0.75	−0.011, 0.002
Suspend Y	−0.022	−2.6	0.009	−0.038, −0.005	0.002	0.1	0.90	−0.037, 0.043
Height	−0.059	−2.7	0.005	−0.101, −0.017	−0.074	−2.9	0.003	−0.123, −0.024
Dead	−0.016	−1.3	0.16	−0.660, 0.090	0.016	0.4	0.66	−0.060, 0.093

Notes: NWFN, Northwest Field North

Bolded beta estimates indicate parameters that were also significant in the pre-suppression categorical and regression tree models and mixed-effect linear regression models. Review text for definition of a given variable.

\dagger Pre-suppression (high density).

\ddagger Post-suppression (low density).

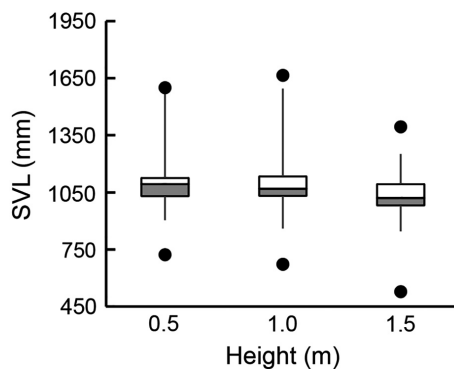


Fig. 2. Whisker plot of the mean snout-vent length (SVL) of captured brown treesnakes captured by three categories of trap height (distance above the ground: 0.5 m = heights \leq 0.5 m [$n = 53$]; 1.0 = 0.5 – 1.0 m [$n = 653$], 1.5 = >1.0 m [$n = 63$]). Minimum and maximum points are the absolute minimum or maximum SVL (mm) of any snake captured for each of the three approximate trap heights.

times. Catch per unit effort at the snake-suppressed locations was not correlated with use of Dead as a support structure. Thus, of those habitat variables identified as important predictors in the Poisson regression of trap CPUE in pre-suppression NWFN, only those variables selected by the CART model remained significant for the post-suppression trap CPUE based on Poisson regression in the post-suppression NWFN, HMU, and GNWR sites (Table 2).

Brown Treesnake mean SVL.—Mean size of captured snakes at the suppressed sites was 65 mm

smaller than in pre-suppression NWFN. Of the initial habitat variables correlated with mean size of snakes captured in pre-suppression NWFN, trap height negatively predicted mean SVL— for each 0.1 m increase in Height up to approximately 2.0 m, the mean size of snakes captured decreased by 7%. Mean SVL of snakes trapped in Connect-H traps was roughly 5% smaller than Connect-M and Connect-L traps at the post-suppression sites (Table 5).

DISCUSSION

Habitat type and components of habitat structure adjacent to a trap affected per-trap CPUE for brown treesnakes. Within the focal site, the CART model and Poisson regression selected overlapping variables as predictive of trap CPUE, with minor variation by including random intercepts for season or trap station. The results suggest some robustness between models in the habitat variables associated with CPUE, although statistical approaches did affect parameter-specific inferences. Variables that were predictive in the suppressed, low-density proxy populations did, however, show notable overlap with the variables identified by the regression tree in NWFN pre-suppression. Thus, the regression tree for CPUE in the pre-suppression, high-density population successfully identified habitat variables associated with increased detection in populations with altered demography or decreased density.

A key assumption of this study was that snakes moved broadly relative to the size of the enclosure, and thus, the density of snakes was equal across all traps, an assumption that may be supported by our own observations and reports of brown treesnake movement patterns from radio telemetry studies (Tobin et al. 1999). Differences in individual trap capture rates therefore were assumed to reflect modulation of per-capita detectability rather than population density heterogeneity within a site. Recapture patterns within NWFN strongly support the assumption that individual snakes could move throughout the enclosure and have the potential to encounter any trap present in the enclosure. Although some of the CPUE differences (especially “forest type”) could reflect microhabitat use preferences and therefore small-scale density differences within NWFN and elsewhere, the data analysis approach was not structured to measure relative density. Extrapolation of these results to inform EDRR also assumes that snakes will be attracted to traps and engage in similar habitat use patterns on a different island as was documented within our study sites. Due to aberrant behavior often associated with translocation (Pettit et al. 2017), or differences in behavior and habitat on other islands, this assumption may not be so straightforward. Overall, however, habitat structure and forest types are largely similar across the Mariana Islands (Fosberg 1960). Thus, the assumption carries reasonable justification for EDRR to detect recently established, incipient populations in the Commonwealth of the Northern Mariana Islands.

Although some of these findings may point toward size-specific habitat selection by brown treesnakes, trap CPUE appeared to best reflect an optimal balance between accessibility of the trap entrance and visibility or detectability of the rodent lure. Use of dead vegetation as a trap support structure prior to suppression efforts in NWFN, for example, had variable significance based on the inclusion of random intercepts, but positive effects on CPUE when significant. Presumably snakes do not selectively use dead vegetation, but a lack of leaves or foliage may decrease visual or chemical cue interference, or the fewer branches expected to associate with dead vegetation constrained snake movements toward the trap. Likewise, the negative effect of a

presence of branches parallel to the longitudinal axis of the trap may decrease the detection radius of the prey lure. Thus, fewer snakes are drawn to the trap, or the branches provide a pathway by which snakes may easily bypass the trap entrance. Moreover, those variables that were selected and, to some degree, their variance in the pre- and post-suppressed populations further supported balancing trap visibility with accessibility for maximizing CPUE. Therefore, trap detections reflected trap functionality as determined by the surrounding habitat, and likely also some measure of habitat use by individuals.

Attributing whether differences in capture success measured habitat use (and thus abundance) rather than detectability may, in part, be informed by species biology. Prior work has suggested that smaller brown treesnakes tend to be higher in the canopy, while larger snakes are more likely to be found on the ground (Tobin et al. 1999, Rodda and Reed 2007). Ontogenetic changes in microhabitat use occur among reptiles and may be based on thermal, prey, or predator effects (Law and Dickman 1998), such that arboreal activity can decline with size (Imansyah et al. 2008). Thus, the differences in the size of snakes captured in traps likely reflect size-specific canopy height preferences by juveniles rather than a preference by small snakes to enter traps that are further from the ground. Survey methods or control measures that are structured to encompass a gradient of available habitat or microclimates are thus more likely to target the entire population over a shorter measurement interval, although we did not test the effect of height above 2.0 m. Capture rates of juvenile arboreal species may, however, be improved by sampling at variable heights in the tree canopy.

Due to the uniform availability of all locations in NWFN, differences in CPUE among traps represented either differences in trap appeal or measures of microhabitat preference by resident snakes. However, attributing whether relationships between habitat variables and CPUE resulted from detection effects or measures of habitat preference is generally a complex task even with species-specific knowledge. Greater CPUE in limestone forest at NWFN, for instance, could be attributed to habitat preference for limestone forest by brown treesnakes. The positive effect of limestone forest on trap CPUE relative

to degraded forest (*Leucaena leucocephala* stands and open, shrubby degraded vegetation) might be due to the arboreal nature of brown treesnakes (Rodda et al. 1999b). Avoidance by an arboreal snake of degraded, open, and shrubby habitat in favor of densely forested and heavily foliated habitat of the limestone forest is reasonable. Prior visual surveys and mark-recapture density estimates of brown treesnakes have, conversely, indicated greater densities of snakes in degraded *L. leucocephala* forests (Rodda et al. 1999b). Small mammals are estimated to be more abundant in *L. leucocephala* forest than limestone forest on Guam (Wiewel et al. 2009). Traps that rely on live mouse baits to lure snakes are less effective in plots that have greater prey availability (Gragg et al. 2007). Thus, trap CPUE in limestone forest may be greater because of reduced prey availability. Alternatively, vegetation communities on Guam affect demographic structure of brown treesnakes (Siers et al. 2017a), which may contribute to density-independent differences in CPUE given size-structured trap captures (Rodda et al. 2007). Therefore, greater trap CPUE in limestone forest may only mean that snakes occupying limestone forest are easier to trap. The extent to which CPUE in distinct vegetation communities relate to relative density among habitat types is therefore difficult to measure due to potential confounding effects of detectability differences among communities.

Trap and visual survey methods each create distinct biases in detection (Rodda et al. 2007). Using multiple methods to survey populations will thus inform detection bias (Clare et al. 2017). However, the extent to which any CPUE method measures density accurately enough to make comparisons between habitats remains in question. In cases in which a land manager wishes to make comparisons among habitat types, during habitat suitability mapping, for example, capture-/recapture-based survey efforts may be required to overcome habitat-specific detection bias for cryptic organisms. Specifically, equivalent CPUE-based survey effort among habitats or locations likely does not yield accurate relative density by habitat because CPUE is a measure of detection bias as well as numbers of present individuals or occupancy state.

Differences in foraging methods or ability to detect prey based on habitat structure (Shepard

2007, Michel and Adams 2009) may also influence the relationship between habitat structure and CPUE, especially when using bait-based sampling. Within pre-suppression NWFN, the regression tree indicated habitat structural variables, such as horizontal branch distance (HDBrnh) and trap support structure (Dead or Rebar), affected CPUE in degraded forest but were not important in limestone forest. Brown treesnakes rely on chemosensory and visual stimulation to detect their prey (Shivik 1998, Lindberg et al. 2000). Habitat structure can affect the ability of predators to detect their prey (Shepard 2007), presumably as a function of visual or chemical interference. Detection of the mouse bait by a snake is an important component of trap CPUE. If, however, the relationship between CPUE and habitat structure adjacent to the trap is dependent on habitat types or other patterns (Melbourne 1999), uniformity in the application of the survey method may contribute to biased captures by habitat that are independent of population density. Although concerns have been raised about the use of CPUE to estimate relative population density (Johnson 2007), CPUE is often used as proxy for abundance or relative density in wildlife management. The variable effect of animal behavior (for instance, hyperstability effects—CPUE remains stable even as abundance declines) or local (micro) habitat structure on CPUE within the broad habitat types (Harley et al. 2001) highlights the importance of incorporating methods such as mark-recapture to verify and control for variance in detection even at small spatial scales.

Our results suggest that placing traps in dense or well-foliated forest, using vegetation as a support structure, and minimizing horizontal and vertical distance to the nearest branch may elevate the probability of capturing a brown treesnake when using bait-based trapping. When trapping occurs in areas that are predicted to have lower CPUE, greater trap effort (by number of traps or duration of trapping) may be desired to ensure detection occurs. Smaller snake captures may also be more probable when a fraction of the traps are placed higher in the canopy (>1 m).

More generally, however, our results indicate that the CPUE method applied can generate different impressions of the relative densities in different habitat types, with no clear indication of

which inference is more accurate. Combining two or more complementary occupancy sampling methods may improve detection overall (Garden et al. 2007, Otto and Roloff 2011), but may not necessarily address opposing inferences about habitat types in which populations exist at greater density without explicit efforts to characterize the population using mark-recapture. Additionally, there is little clarity as to why some habitat variables that were positively or negatively related to captures at high density (pre-suppression) had reversed relationships at low densities (post-suppression). One potential explanation may be the change in demographic structure after suppression, resulting in a smaller average population size and size-structured effects on CPUE. Alternatively, the overall effect of individual habitat variables may be weak or heavily dependent on other factors. The structure or type of habitat sampled is rarely accounted for, presumably due to the uncertainty regarding the key attributes, but can represent an important consideration for detectability (Rovang et al. 2015).

In the case of early detection of invasive species, maximizing the possibility of a detection is ultimately of greater value than accurately estimating relative densities in different habitats. Identifying methods to elevate detectability for all size classes, including information on how detection interacts with habitat, is an important step toward invasive species interdiction and control (Siers et al. 2017b). Here, we demonstrate that local habitat can bias detection and measuring wildlife-habitat relationships for invasive species may improve the probability of an early detection during invasive species management.

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