

Predicting habitat use from opportunistic observations: a case study of the Virgin Islands tree boa (*Epicrates granti*)

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Wildlife managers must often make conservation decisions based on uncertain and incomplete information. The challenge is to make the most robust predictions of species' requirements given these limitations. This is particularly the case when the species is rare and difficult to locate and baseline data are virtually non-existent. In the absence of other data, we used 143 opportunistic observations collected over 25 years and geographical information systems to predict the habitat of the endangered Virgin Islands tree boa (*Epicrates granti*) on St Thomas, United States Virgin Islands. We compared the habitat characteristics surrounding observations to the rest of the island using logistic habitat models with varying spatial resolution. Models formed with smaller-scale presence definitions were better able to discriminate areas of occurrence from the rest of the island but were more biased towards developed areas. To investigate habitat associations below the resolution of the models, we compared microhabitat near high-certainty observations with microhabitat at nearby, random locations. Snakes were disproportionately found in low elevation (<150 m) areas with non-stony soils. Vegetation near snakes consisted of woody plants 5–10 m tall with a high degree of vegetation continuity (e.g. mangroves, drought deciduous forests, thicket/scrub). This habitat occurs primarily along the southeastern coast of St Thomas. Our multi-scale approach allowed a more informed prediction of the snakes' requirements than any single-scale approach, particularly in light of the variable resolution of the observations.

Key words: biological conservation, habitat modelling, St Thomas, United States Virgin Islands

INTRODUCTION

One of the primary challenges of wildlife conservation is the time and effort required to obtain detailed information about the ecological requirements of species. For poorly understood species the progression of a particular threat (e.g. habitat loss) could far outpace the years required to fully document patterns of resource use, much less understand the factors motivating resource selection. The challenge is compounded when a species for which baseline data is lacking is rare or otherwise difficult to locate. This issue has fuelled the development of methods to derive information from opportunistic observations of species occurrence (e.g. Graham et al., 2004; Roberts et al., 2005; Frey, 2006; Lütolf et al., 2006; Elith & Leathwick, 2007), which is often the only information available for rare and cryptic species that are of conservation concern (e.g. Freeman & Bruce, 2007). Opportunistic observations can be rapidly compiled from various sources (e.g. museum and herbarium records, government databases) but are usually biased and/or of low resolution in time and space (Elith & Leathwick, 2007). The challenge is to make the most robust predictions of species requirements given these data limitations, until more detailed information can be collected. Here we present a case study of the use of opportunistic observations and geographical information systems (GIS) to predict the habitat of the endangered Virgin Islands (VI) tree boa (*Epicrates granti*) on St Thomas, United States Virgin Islands (USVI).

The problem with using opportunistic observations to determine habitat requirements is that they are usually biased towards places where the animal is most easily observed (e.g. roads), and thus provide a skewed impression of the species' habitat (Stockwell & Peterson, 2002; Reutter et al., 2003). One approach to reducing bias is to broaden the spatial scale at which an animal is considered present based on an observation, thereby including a greater amount of potential habitat. However, a coarser presence definition may encompass some degree of unused habitat, resulting in a model with a reduced ability to discriminate used and unused areas (i.e. less discriminatory power). Both narrow and broad definitions of presence may produce inaccurate models but in different ways: narrow models by including too few variables and broad models by including too many (Boyce, 2006). We compared the discriminatory power, accuracy and bias of habitat models derived from *E. granti* observations and GIS with species presence defined on four different spatial scales. The primary objective of our study was to illustrate this multi-scale method of elucidating habitat information from opportunistic observations.

Epicrates granti is a nocturnal, semi-arboreal snake endemic to the Eastern Puerto Rican Bank. Within the USVI, the snake is only known from the eastern end of St Thomas (Nellis et al., 1983). The United States Fish and Wildlife Service listed *E. granti* as a federally endangered species in 1979 in response to the boa's fragmented distribution and development pressures on St Thomas (USFWS, 1980). In the intervening years, there have only

been sporadic sightings of this species that have produced the opportunistic observations we analyse here. Efforts to survey *E. granti*'s distribution on St Thomas more systematically have been hampered by its highly cryptic and secretive habits (Cornish, unpublished data), by the fact that much of eastern St Thomas is privately owned, and by the dense and mostly impenetrable habitat in which this species presumably resides. The rapid development of the island necessitated an immediate evaluation of the amount and location of *E. granti* habitat remaining, despite the limited information available to make that assessment. The secondary objective of our study was to promote the conservation of *E. granti* by providing updated information on its distribution and habitat requirements.

MATERIALS AND METHODS

Geographic setting

The USVI, situated near the eastern terminus of the Greater Antillean chain of islands in the northern Caribbean Sea, comprises four major inhabited islands (St Thomas, St John, St Croix and Water Island) and more than 50 smaller offshore cays. St Thomas covers an area of 83 km². The east end of St Thomas, to which the boa is restricted (Nellis et al., 1983), is composed of dry subtropical forest with a climate that is hotter and drier than the rest of the island; the moisture and temperature gradient progresses to damper and cooler towards the northwest (Thomas & Devine, 2005). The vegetation types common in this part of the island include drought deciduous forest and woodland, characterized by water mampoo (*Pisonia subcordata*), black olive (*Bucida burceras*) and Jamaican caper (*Capparis cynophallophora*), thicket/scrub characterized by seagrape (*Coccoloba uvifera*), black torch (*Erithalis fruticosa*) and locustberry (*Byrsonima lucida*), and mangroves along coastal areas.

Observations

One hundred and forty-three sightings of live or dead boas on St Thomas were reported to the USVI Division of Fish and Wildlife from 1982 to 2006. Almost half (45%) of the observations were from 2001 onwards. Virtually all snakes were observed on roads or in the vicinity of homes, businesses and resorts. In all but a few cases the location of the snake was verbally described but not referenced with spatial coordinates. Universal Transverse Mercator (UTM) coordinates were estimated for each unreferenced location based on a verbal description of the location. A spatial error was assigned to each estimate to reflect the degree of uncertainty in its position (from 10 m to 2500 m).

Defining species presence

The full suite of habitats used by a given snake will be contained within its home range; thus, we used an area equivalent to the size of a home range as the baseline unit to delineate species presence. We estimated the size of *E. granti*'s home range (about 1 ha) from a study on another island (Cayo Diablo; Chandler & Tolson, 1990). We assumed snakes were found in the centre of a circular, 1 ha

(56 m radius) home range. The exact positioning of the home range around each observation should have a minimal impact on analysis given the size of the home range (1 ha) relative to the size of the island (7116 ha). As alternate delineations of species presence, we used 1) a 10 ha (178 m radius) circular area around observations, 2) a 100 ha (564 m radius) circular area around observations, and 3) a minimum convex polygon drawn around all snake observations. For analytical purposes we used the minimum convex polygon around all observations to approximate the range of *E. granti*.

No snake locations were known with absolute certainty; all had an associated degree of spatial error. To adjust for this uncertainty, 1 m was subtracted from the radius of the presence-defining area around each snake observation per 1 m of spatial error. In effect, more area around a snake was presumed to be used by the snake if the location was known more precisely.

Creating habitat models

Elevation, Soil Nature, Soil Alteration, Vegetation, Land Use and Road GIS layers were obtained from the Conservation Data Center (CDC) at the University of the Virgin Islands. The Vegetation and Land Use layers were developed from aerial photos taken in 1994 and ground-truthed through 1999. Slope and Aspect layers were derived from the Elevation layer using the Spatial Analyst extension of ArcGIS 9.0. An urban category was superimposed onto the Soil Nature layer from the Soil Alteration layer to represent areas with no exposed soil. The Vegetation layer had a category labelled "developed". To account for the possibility of different types of development having different impacts on the tree boa (e.g. urban vs low-density residential), we relabelled all areas classified as developed with the corresponding type of development described in the Land Use layer. All map functions were performed with ArcGIS 9.0.

We used a reclassification procedure to reduce the number of inputs into the habitat model. Each variable was divided into three ordinal categories based on use relative to availability on St Thomas (high=3, medium=2, low=1), using K-means clustering to identify the major breakpoints. We used logistic regression to determine the combination of variables that best differentiated areas of snake presence from the rest of the island. Four habitat models were constructed with the four different methods of defining species presence (1 ha around observations, 10 ha around observations, 100 ha around observations, a minimum convex polygon around all observations). We comprehensively classified St Thomas into environmental variable and presence/absence combinations. The weighted frequency of these combinations by area ($n=201,018$) served as input for the regression models. To increase our confidence that unused areas represented true absences (as opposed to areas where snakes were present but not observed), we only included areas outside *E. granti*'s range (as defined by a minimum convex polygon around observations) as unused in the logistic regressions. Variables (linear and quadratic terms) were selected using forward stepwise regression (0.05 entry tolerance), with univariate *t*-tests to determine the entry

Table 1. Structural variables used to characterize Virgin Islands tree boa microhabitat on St Thomas in 2006. Radius refers to the maximum distance from the centre of the plot that the variable was measured.

Abbreviation	Radius (m)	Variable description
%CANOPY	0	Canopy closure (%) above plot
%CONTINUITY	2	Longest continuous path (%) snake could travel around centre of plot without touching ground
#STONES	2	Number of rocks with a maximum length between 25 and 60 cm
#HOLES	2	Number of holes with a minimum diameter of 2 cm and terminus not visible from the surface
#REFUGES	5	Number of objects potentially used for refuge during the day (e.g. termitaria, bromeliads)
HERBACEOUS	5	Presence (1) or absence (0) of herbaceous plants
CACTUS	5	Presence (1) or absence (0) of cacti or succulents
SHRUB	5	Presence (1) or absence (0) of woody plants with a diameter at breast height < 10 cm
TREE	5	Presence (1) or absence (0) of woody plants with a diameter at breast height > 10 cm
MAXHEIGHT	5	Height (m) of tallest woody plant within the plot

order of variables. To guard against over-fitting, we calculated the Bayesian information criterion (BIC) for each step of the regression procedure (Kass & Raftery, 1995) and retained the least parameterized model that provided at least 95% of the information of a complete model (based on the change in BIC relative to an intercept-only model). Because a weighted area ($n > 200,000$) was input into the regression models rather than actual observations ($n < 150$), model selection tended to favour more heavily parameterized models due to the appearance of a very large sample size. Both the restrictive entry tolerance of the regression and use of an information threshold relative to an intercept-only model were extra efforts to avoid selecting heavily parameterized models.

The area under a receiver operating curve (AUC) was used to compare the discriminatory power of each model. We assessed the potential for bias with each habitat model by determining the relationship between 1) snake presence and roads, and 2) disproportionately used habitats and roads, using roads as a proxy for human presence and assuming this was the major source of bias in the observations. To assess model accuracy, we compared the ability of models to successfully predict the occurrence of a subset of 23 snake locations that were known with a high degree of spatial certainty (≤ 10 m spatial error). Predicted probabilities were compared to the maximum probability possible with each model, based on the premise that more accurate models would more consistently rank used sites as high-probability occurrence areas. All statistical functions were performed with Systat Version 11 and SPSS 14.0.

Microhabitat characterization

We characterized structural microhabitat at 48 locations throughout southeastern St Thomas. Half of the locations were in or near home ranges (<100 m from an observation) and the other half were not. The characterizations served a dual purpose. The first was to test the accuracy of the GIS layers. The second purpose was to

determine what structural features, if any, differentiated locations most likely to be used by snakes (i.e. close to observations) from other locations in and around their range. To ensure that a broad range of physical features were sampled, plot locations were selected randomly with the stipulation that all range-wide locations must be more than 500 m apart and all home range locations more than 100 m apart. We sampled a simple set of structural variables that reflected the nature of the vegetation community and abundance of potential refuges (Table 1). We estimated the percent canopy closure from two digital photos taken of the canopy above each plot. Tree height was measured with a Haga altimeter.

Microhabitat associations were determined using discriminant function analysis (DFA). The variables #STONES, #HOLES and #REFUGES were log transformed prior to analyses to improve normality. Variables with mean values that clearly did not differ between groups were removed prior to DFA (univariate t -tests, $P > 0.50$). We used the jackknife procedure to determine the predictive power of DFA classifications.

RESULTS

Range

Tree boas were observed throughout the southeastern portion of St Thomas (Fig. 1). Occurrence was documented with recent records at the northern (2006) and western (2005) extremes of the range. Five snakes were observed in the Charlotte Amalie area, apart from the rest of the observations (Fig. 1). It is possible these snakes were transplanted from the southeast as the southern shore is a busy commercial route and tree boas seek out dark and concealed areas during the day (i.e. snakes may have been transported among cargo). Also, these sightings may have been misidentified corn snakes (*Pantherophis guttatus*), which were recently introduced to Charlotte Amalie (Perry et al., 2003). Because the validity of the five observations near Charlotte Amalie was

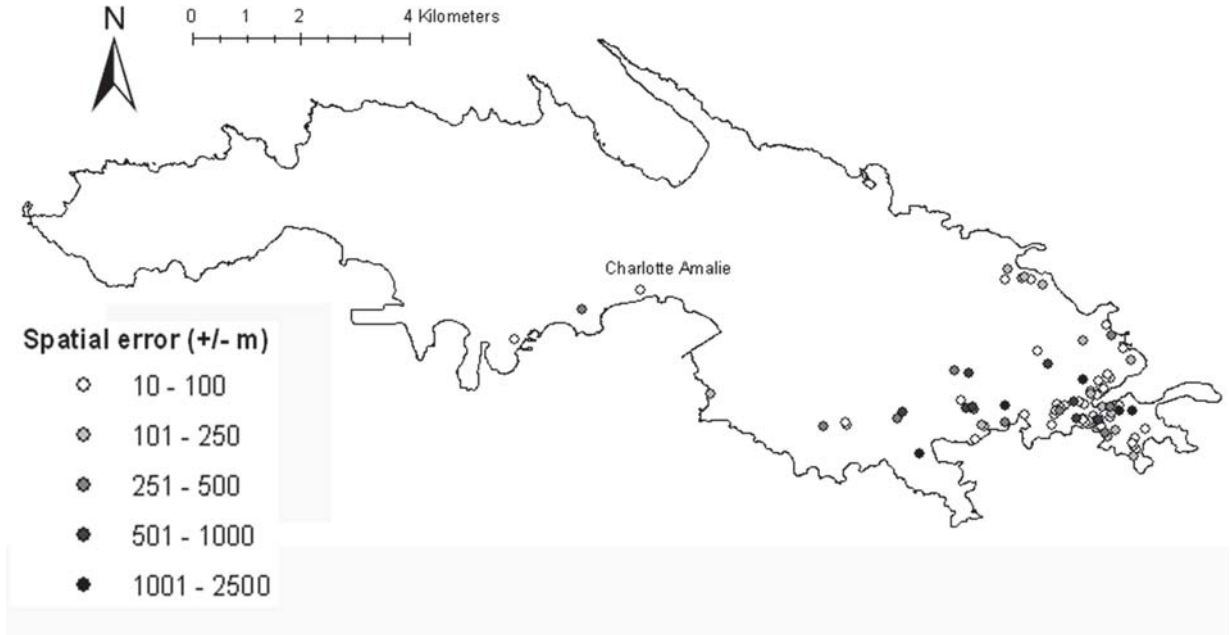


Fig. 1. Virgin Islands tree boa observations on St Thomas from 1982 to 2006.

unclear, they were excluded from the range map and further analyses.

Habitat models

At all spatial scales *E. granti* was associated with low elevation (<150 m), non-stony soils, and particular vegetation/land use communities (e.g. mangrove, thicket/scrub, hotel/resort, waterfront/marine, low density residential; Table 2). In two models, snakes were weakly associated with gentle slopes (Table 2). The discriminatory power of habitat models was greater with smaller presence definitions, but the potential for bias was also greater (Table 2). Most (57%) of the tree boa's range was within 50 m of a road. Smaller presence definitions resulted in an even stronger correlation between species presence and roads (Table 2).

A road/development bias had the greatest potential to influence the interpretation of elevation and vegetation

associations (Table 3). No snakes were observed at elevations greater than 150 m and very little (about 2%) of their range reached those heights, so the association between snakes and lower elevations was probably a real phenomenon (note that St Thomas reaches elevations of more than 450 m and there are roads throughout the island). There was a stronger association between snakes and developed areas given smaller presence definitions; in fact, snakes were associated with few natural vegetation communities given the smallest (1 ha) delineation of presence.

A model with an intermediate presence definition (100 ha around observations) was best able to predict the occurrence of a subset of observations that were known with a high degree of spatial certainty (Table 2). Smaller-scale models were tightly fit to an optimal set of habitat conditions, and thus poorly predicted occurrence in less than optimal areas. The range-wide model predicted the broadest range of habitat use; however, the probability of

Table 2. Logistic models of Virgin Islands tree boa occurrence in relation to habitat on St Thomas. The number of observations used to define species presence is referred to by *n*. Bias refers to the proportion of area defined as presence within 50 m of a road. AUC refers to the area under a receiver operator curve. Accuracy refers to mean predicted probability of occurrence for 23 observations known with spatial certainty, relative to the maximum predicted probability for that model. Veg=vegetation and ele=elevation.

Presence-defining method	Model [logit(p)=]	<i>n</i>	Bias	AUC	Accuracy
Home range	$-21.4 + 4.1\text{veg} - 0.7\text{veg}^2 + 1.5\text{ele} + 4.1\text{soil}$	42	0.82	0.95	0.58
10 ha around observations	$-21.1 + 6.0\text{veg} - 1.1\text{veg}^2 + 1.4\text{ele} + 2.7\text{soil} + 2.0\text{slope} - 0.4\text{slope}^2$	55	0.77	0.93	0.75
100 ha around observations	$-15.7 + 3.3\text{veg} - 0.6\text{veg}^2 + 4.1\text{ele} - 0.7\text{ele}^2 + 1.7\text{soil}$	92	0.66	0.86	0.85
Entire range	$-21.7 + 1.0\text{veg} - 0.1\text{veg}^2 + 6.8\text{ele} - 1.4\text{ele}^2 + 6.9\text{soil} - 1.1\text{soil}^2 + 0.4\text{slope}$	132	0.57	0.83	0.67

Table 3. Correlation (r) between the distance to roads and disproportionate habitat use given four different methods of defining Virgin Island tree boa presence on St Thomas (see text for details).

Variable	Correlation (r) with roads by presence-defining method			
	Home range	10 ha around observations	100 ha around observations	Entire range
Soil	0.04	0.04	0.04	0.04
Elevation	0.30	0.30	0.30	0.30
Vegetation	0.28	0.29	0.08	-0.16
Aspect	-0.03	0.03	0.02	0.01
Slope	0.09	0.07	0.07	0.07

occurrence within the more common habitat types was generally lower than the other models.

Microhabitat characterization

Shrubs were present in all plots and vegetation was usually continuous or nearly continuous (%CONTINUITY = $82.3\% \pm 3.5$ SE). Herbaceous plants, cacti, succulents, trees and potential refuges were common in all locations. Using DFA, the only variables with structural coefficients greater than 0.2 were #REFUGES (0.80), MAXHEIGHT (0.66) and HERBACEOUS (0.55). Locations close to snakes had fewer refuges, shorter trees and fewer herbaceous plants than random locations throughout southeastern St Thomas. Group membership could be predicted with 67% accuracy using the jackknife procedure. Locations close to snakes had fewer bromeliads (*Tillandsia utriculata*, 17) and century plants (*Agave missionum*, 37) than range-wide locations (88 and 60, respectively), but more anthropogenic debris (17 versus 9) and termitaria (5 versus 1).

GIS layer accuracy

We did not detect any major discrepancies between what was on the ground and what was specified as being there by the GIS layers in terms of elevation, slope or aspect. Some plots obviously fit their vegetation or land use classification (e.g. beach, mangrove, residential, hotel/resort, waterfront/marine, coastal hedge). We gauged the rest by comparing the maximum tree height in plots with the canopy height of the vegetation community they were classified as being within (Thomas & Devine, 2005). Snakes tended to use forested areas (drought and semi-deciduous forests and woodlands) near the low end of their respective classifications in terms of height (average = 6.9 m, range 4.6–12.6 m) and thicket/scrub communities near the upper end of the spectrum in terms of height (average = 6.5 m, range 4.0–9.7 m).

DISCUSSION

The range reported in this study extends further west and north of the range reported in Nellis et al. (1983: east of $64^{\circ}51'30''$) and is approximately four times as large. Snakes were disproportionately found in low elevation (less than 150 m) areas with non-stony soils. Vegetation near snakes

consisted of tall shrubs or short trees with a high degree of vegetation continuity (e.g. mangroves, drought deciduous forests, thicket/scrub). The approach used here to predict *E. granti* habitat could be generally applied to species for which only opportunistic observations are available.

Use of opportunistic observations

While the importance of a rigorous sampling design when making inferences about habitat use is well understood (e.g. Anderson, 2001), less attention has been paid to the scenario where inferences must be made using a non-rigorous design (e.g. opportunistic sampling). When interpreting our opportunistic observations three main sources of uncertainty needed to be addressed: 1) the temporal mismatch between the GIS habitat layers and observations collected over 25 years, 2) the spatial uncertainty in the observation locations, and 3) the uneven spatial representation of the observations due to variation in detectability. We addressed temporal uncertainty by conducting habitat evaluations to ensure the GIS layers were reasonable approximations of current conditions. To address uncertainty with regards to the location of observations, we weighted observations by their degree of spatial certainty in analyses. Observations with very vague coordinates (e.g. ± 2000 m) only informed the approximate range of *E. granti* on St Thomas. Uneven detectability was a more systemic problem with the data set and could only be accommodated rather than corrected. Our observations were almost certainly biased towards roads and developed areas because boas are easiest to find there (Reed et al., 2007). By creating habitat models with varying spatial scales, we were able to determine which habitat associations were more or less conserved as the potential impact of a road bias was increased or decreased. Engler et al. (2004) similarly advocated the use of a multi-scale modelling approach with potentially biased and uncertain observations. Quantification of *E. granti* detectability in various habitats would also allow a more rigorous interpretation of opportunistic observations.

A confounding issue with our approach is that the environmental features associated with occurrence may not be consistent across spatial scales (e.g. Rettie & Messier, 2000; Schaefer et al., 2008). In this scenario, model formation would be influenced not only by mechanical issues associated with the choice of spatial scale but by natural processes. There is some evidence that habitat selection is relatively constant across spatial scales in reptiles (Rubio & Carrascal, 1994; Harvey & Weatherhead, 2006), in which case the choice of analytical scale would be of greater importance.

We would like to emphasize that our use of opportunistic observations with low spatial certainty was born of a need for rapid information to direct conservation efforts, in addition to difficulties with access to boa habitat on private land. The utility of models formed with opportunistic observations should be gauged by their ability to provide a closer representation of the “true” distribution of species than random (Anderson et al., 2002); this utility has been demonstrated in previous studies involving the

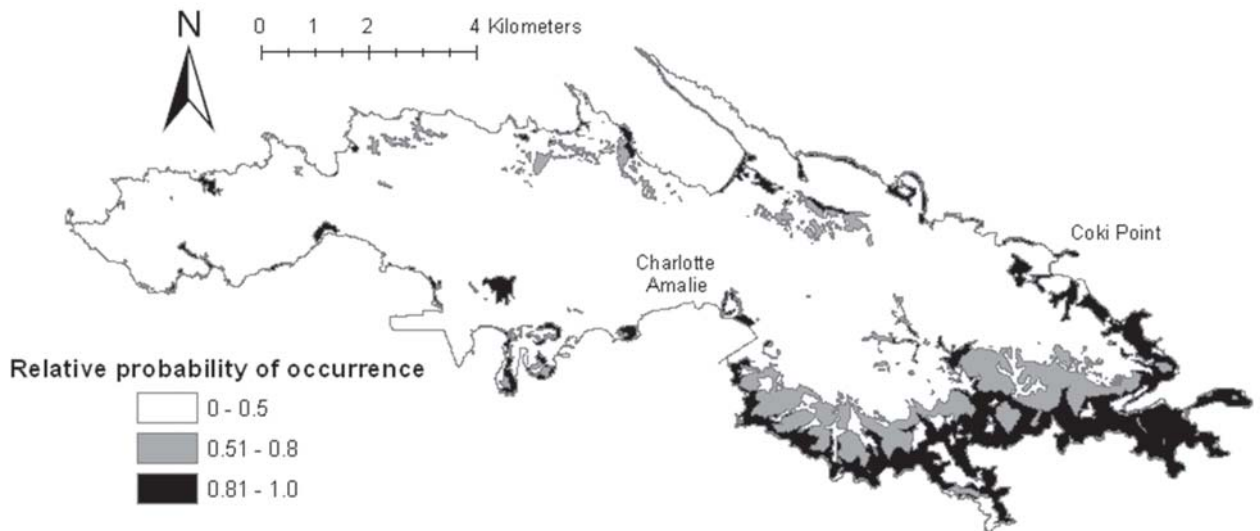


Fig. 2. Relative probability of Virgin Islands tree boa occurrence on St Thomas based on structural similarity with areas of known occurrence.

niche-based modelling of rare species (Fleishman et al., 2002; Bourg et al., 2005; Guisan et al., 2006) but has yet to be determined for our model (although the relatively high AUC value is promising).

Habitat modelling

Models formed with larger-scale presence definitions included more natural vegetation types that snakes probably used, but for which there was less evidence of use. Drought deciduous forests are a good illustration of this point. No snakes were actually observed within drought deciduous forests, but drought deciduous forests are common in close proximity to observations, rare on the rest of the island, and structurally similar to habitats that are known to be used (e.g. mangroves, thicket/scrub). This is perhaps the strongest evidence of drought deciduous forest use we could expect from opportunistic observations, given the long odds of actually encountering a snake within a drought deciduous forest.

The method used to delineate species presence did not dramatically alter the nature and relative importance of habitat variables associated with *E. granti* occurrence on St Thomas. This was probably the result of a couple of factors. First, features within *E. granti*'s range were structurally similar compared to the rest of St Thomas, so all methods of delineating presence within the range provided similar contrast to "absence" (i.e. area outside the range) habitat. Second, most features within *E. granti*'s range were only mildly correlated with developed areas (where snakes were typically seen); therefore, raising or lowering this type of bias had a minor impact on habitat associations.

Epicrates granti habitat

Habitat use on St Thomas was broadly similar to habitat use on 12 smaller islands of the Puerto Rican Bank (i.e. woody, highly continuous vegetation with a low canopy

height; Tolson, 1988). Continuous, shrub-like vegetation presumably facilitates foraging behaviour for an arboreal predator (Chandler & Tolson, 1990). Similar habitat associations (subtropical dry forest 5–6 m in height with high vegetation continuity) have been documented for the closely related Mona boa (*E. monensis monensis*) on Isla Mona, off the west coast of Puerto Rico (Tolson et al., 2007).

On Cayo Diablo, *E. granti* concealed themselves in refuges during the day (e.g. *Cocos* and *Sabal* axils, termite nests, rocks and debris) and foraged at heights of up to 4 m at night (Chandler & Tolson, 1990). Both termitaria and debris could be important refuges on St Thomas given their greater abundance near observations. *E. granti* occupied areas with trees as tall as 10 m on St Thomas; however, snakes may have been foraging on lower branches or shorter trees within these areas.

Elevation and soil type are often indirect indicators of climate conditions that are of direct relevance to reptiles (e.g. Guisan & Hofer, 2003; Anadón et al., 2006; Santos et al., 2006). Southeastern St Thomas is generally warmer, drier and windier than the rest of the island because of the steady trade winds that blow from the east (Thomas & Devine, 2005). The confluence of low elevation and non-stony soils may simply characterize the part of the island with this particular climate. Most small species of *Epicrates* appear adapted to xeric habitats (Nellis et al., 1983). Snakes could benefit from a warmer climate in a number of ways, including decreased gestation times and improved foraging conditions at night (Peterson et al., 1993).

Management implications

Of the models created, we believe the one formed with the 100-ha-around-observations presence definition provides the most useful basis for management given comparatively low bias and high accuracy. Based on

structural similarity with areas of known occurrence, *E. granti* likely occur along the southern shore of St Thomas east of Charlotte Amalie and along the eastern shore north to Coki Point (Fig. 2). Habitat models have numerous applications for conservation planning. They can be used to assess whether proposed development projects are more or less likely to impact tree boa habitat and to create preliminary mitigation guidelines. Proactively, they can be used to rank priority areas for conservation efforts. The establishment of protected areas for *E. granti* on St Thomas is a high conservation priority as virtually none of the boa's range is currently protected (Platenberg & Boulon, 2006).

Habitat access issues notwithstanding, a radiotelemetry study would fill many of the fundamental gaps in our understanding of the snakes' habits, allowing more precise modelling in addition to other benefits. More high resolution observations would provide a clearer picture of habitat associations, and studies involving non-physical factors (i.e. biotic, climatic) would improve our understanding of the causal mechanisms underlying habitat use.

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