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A demographic projection model to support conservation decision making for an endangered snake with limited monitoring data

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Abstract

Conservation planning for rare and threatened species is often made more difficult by a lack of research and monitoring data. In such cases, managers may rely on qualitative assessments of species risk that lack explicit acknowledgement of uncertainty. Snakes are a group of conservation concern that are also notoriously difficult to monitor. Here, we demonstrate a quantitative population projection for a data-deficient species, the Puerto Rican boa (*Chilabothrus inornatus*) using expert knowledge and published information about species life history and threats to persistence. Using this model, we simulated population dynamics over 30 years under four scenarios of future urbanization and found that there was an increased probability of population decline as urbanization rates increased. We conduct a sensitivity analysis to evaluate the sensitivity of outcomes to model inputs, a practice that may also be useful in recovery planning. The sensitivity analyses also provide insight into how the future trajectories would change if the elicited demographic rates are incorrect. Even when data are sparse, quantitative methods can often be used to produce rigorous and reproducible estimates of future status with quantifiable uncertainty.

Introduction

For many rare and threatened species, little research or monitoring data exist to inform conservation decision-making (Karanth *et al*., 2003; Good *et al*., 2006; Brito, 2010). Despite a lack of data, managers still need to make predictions about the effects of potential management actions in order to make decisions (Conroy & Peterson, 2013). In such situations, decision makers often rely on qualitative assessments of species risk which may be subjective and lack explicit acknowledgement of uncertainty (McCarthy *et al*., 2004). Although qualitative methods are useful in some circumstances, there may be many cases where even some knowledge of the species' life history and ecology can be used to develop demographic projection models that result in quantitative assessments of resiliency, extinction risk, and associated uncertainties. There are many sources of uncertainty in population projections (Williams *et al*., 2002), and failing to explicitly acknowledge them can lead to overly precise predictions and misunderstandings about risks to species persistence (Gregory & Keeney, 2002; McGowan *et al*., 2011). Quantitative projections allow for the explicit acknowledgement and incorporation of uncertainty and provide decision makers with more nuanced results upon which to base their decisions.

Snakes are notoriously persecuted by humans worldwide and are a group of conservation concern (Mullin & Seigel, 2009; Böhm *et al*., 2013). A recent analysis of a randomly selected subset of reptile species showed that up to 33% of snake species worldwide may be threatened (Böhm *et al*., 2013). For many species there exists data about species distribution only, and information about population trends is lacking. However, an analysis of 17 snake populations in Europe, Australia, and Nigeria found that 11 (65%) declined sharply over the ~20 year study period (Reading *et al*., 2010). Habitat loss due to urbanization and human development is one of the main threats facing snake populations (Gibbons *et al*., 2000; Böhm *et al*., 2013). Additionally, as humans move into previously natural areas snakes face increased threats as result of human interactions (Burghardt *et al*., 2009).

Snakes and many other reptiles are difficult to monitor, leading to data deficiency for many species (Böhm *et al*., 2013). Many snakes are cryptic and difficult to detect, exhibit low activity, and are not commonly captured using standardized sampling protocols (Winne *et al*., 2007; Steen, 2010). As a result, quantitative assessments of perceived declines are lacking (Bland & Böhm, 2016). Lack of monitoring data also makes it difficult to quantify relationships between environmental stressors and population dynamics (Gibbons *et al*., 2000). These factors present many challenges for conservation planning and assessment.

The Puerto Rican boa (*Chilabothrus inornatus*) is a terrestrial/arboreal boa endemic to the island of Puerto Rico. This species has been classified as Endangered in the United States since 1970 and listing under the Endangered Species Act requires periodic assessment of the species status to inform possible reclassification decisions and recovery planning. Despite widespread accounts of species occurrence, there are no estimates of historic or current population size and limited field studies on population status, trends, or demographics. However, demographics and life history of captive populations are well-understood. We used expert opinion and published studies to develop a demographic projection model, which was used to assess the predicted future status of the Puerto Rican boa (hereafter, PR boa) under several potential scenarios. This model allowed us to incorporate many sources of uncertainty to produce quantitative estimates of quasi-extinction risk and population growth. This type of model, despite lack of data, will still be useful for status assessment, reclassification decisions, recovery planning and prioritizing future research and monitoring.

Materials and methods

Focal species

The PR boa is a large boa that grows to an average size of 1.5 m and lives up to 32 years. Females reproduce biennially, producing 18–32 eggs per clutch (Huff, 1978; Tolson, 1992; Puente Rolon, 2012). After hatching, young reach sexual maturity at around 5 years (Huff, 1978). Diet and behavior vary across life stage, with smaller boas remaining in trees and shrubs to forage on small lizards and frogs, gradually moving to the ground as they grow and begin to also consume rodents, birds, and bats. Small boas may be predated by mongoose, cats, and some birds, but the main sources of larger boa mortality are road strikes, human persecution, and habitat loss.

Expert meeting

On March 5–6, 2018, a team of species experts met to develop a modeling framework that could be used to inform an upcoming status assessment. The team of nine participants included researchers from academic and nonprofit institutions as well as the U.S. Fish and Wildlife Service Caribbean Ecological Field Office. Participants had experience working with PR boas and/or sister taxa (e.g., Cuban boa) either in field studies or captivity. During that meeting the team developed a life cycle model (Fig. 1), identified key threats, and estimated demographic rates by consensus. If experts did not initially agree on demographic rate estimates, differing estimates were discussed until participants agreed on an average value. Experts agreed that the PR boa species should be considered a single population unit comprising the island of Puerto Rico, noting homogeneity in genetics, morphology, and behavior across the island.

Demographic matrix model

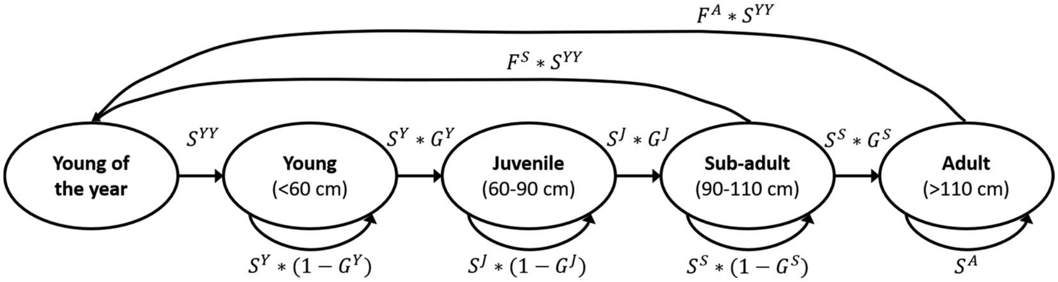
Based on the life history diagram, we developed a stage-based Lefkovitch matrix model (Caswell, 2001) for this population that grouped individuals into stages based on total length (Fig. 1). We considered five life stages: young of the year (<60 cm), young (<60 cm, born in a previous year), juveniles (60–90 cm), subadults (90–110 cm), and adults (>110 cm). We elicited the probabilities of annual survival, growth to the next size class, and fecundity (average number of offspring per individual) for each size class from the expert team or, where applicable, drew from the available literature (Table 1). The experts used personal experience, unpublished data, and inference from captive zoo populations to provide estimates of average productivity, survival, and growth rates for the wild population. The experts also directed us to graduate theses and dissertations that were completed but not widely available through literature searches.

We used the stage-specific estimates of survival and growth to calculate the transition rates in the diagram and matrix in Fig. 1. These demographic rates are summarized in a matrix:

$$\begin{bmatrix} N_t^{YY} \\ N_t^{Y} \\ N_t^{J} \\ N_t^{S} \\ N_t^{A} \end{bmatrix} = \begin{bmatrix} 0 & 0 & 0 & 0.6 & 1.35 \\ 0.1 & 0.1 & 0 & 0 & 0 \\ 0 & 0.2 & 0.4 & 0 & 0 \\ 0 & 0 & 0.5 & 0.54 & 0 \\ 0 & 0 & 0 & 0.18 & 0.9 \end{bmatrix} \times \begin{bmatrix} N_{t-1}^{YY} \\ N_{t-1}^{Y} \\ N_{t-1}^{J} \\ N_{t-1}^{S} \\ N_{t-1}^{A} \end{bmatrix}$$

Habitat availability

The Puerto Rico Gap Analysis Project (Gould *et al*., 2008) developed habitat suitability models for a suite of species. That analysis estimated a total of 414 379 ha of suitable habitat for the PR boa. However, there are no clear records of PR boa above 700 m, so we only considered areas below 700 m to be suitable habitat, resulting in 379 029 ha of habitat. We were also interested in determining the proportion of habitat that fell in developed, urban areas, as experts believed boas experience different pressures in those areas (see *Differences Between Natural and Urban Habitat*, below). We used a raster dataset developed by Martinuzzi *et al*. (2007) to determine the proportion of suitable habitat falling within developed areas (Fig. 2). Martinuzzi *et al*.



$$\begin{bmatrix} N_t^{YY} \\ N_t^Y \\ N_t^J \\ N_t^S \\ N_t^A \end{bmatrix} = \begin{bmatrix} 0 & 0 & 0 & F^S * S^{YY} & F^A * S^{YY} \\ S^{YY} & S^Y * (1 - G^Y) & 0 & 0 & 0 \\ 0 & S^Y * G^Y & S^J * (1 - G^J) & 0 & 0 \\ 0 & 0 & S^J * G^J & S^S * (1 - G^S) & 0 \\ 0 & 0 & 0 & S^S * G^S & S^A \end{bmatrix} x \begin{bmatrix} N_{t-1}^{YY} \\ N_{t-1}^Y \\ N_{t-1}^J \\ N_{t-1}^S \\ N_{t-1}^A \end{bmatrix}$$

Figure 1 Life cycle and stage-based matrix model for the Puerto Rican boa. N_t^X is the number of individuals in stage *X* in year *t*. Survival (*S*), growth (*G*), and fecundity (*F*) are all stage-specific, with superscripts indicating stages (*YY* = young of the year, *Y* = young, *J* = juvenile, *S* = subadult, *A* = adult). Demographic rates are defined in Table 1.

Table 1 Stage-specific demographic rates for the Puerto Rican boa

Demographic rate	Description	Average	Rationale
S^{YY}	Survival – Young of the year	0.1	Expert opinion, informed by studies of Cuban boa[a]
S^Y	Survival – Young	0.3	Expert opinion, informed by studies of Cuban boa[a]
S^J	Survival – Juvenile	0.9	Expert opinion
S^S	Survival – Subadult	0.72	Expert opinion – survival of this stage is lower than the juvenile or adult stage because individuals begin dispersing widely and face more threats
S^A	Survival – Adult	0.9	Expert opinion and estimates from radio-tracked translocated snakes[b]
G^Y	Growth – Young to Juvenile	0.67	Expert opinion – approximately 2/3 of the young of the year grow enough to become juveniles in the next year.
G^J	Growth – Juvenile to Subadult	0.5	Expert opinion – juvenile stage typically lasts two years
G^S	Growth – Subadult to Adult	0.25	Expert opinion – subadult stage typically lasts four years
F^A	Fecundity – Adult	4.5	Average clutch size is 18 (range = 12–32)[b,c] This clutch size is multiplied by 0.5 because only females produce young (assumes a 50:50 sex ratio) and multiplied by 0.5 again because females reproduce biennially[c]
F^S	Fecundity – Subadult	2	Expert opinion – some larger subadults may breed, but with a lower breeding probability

Survival (*S*) and growth rates (*G*) are annual probabilities and fecundity (*F*) is the average number of young produced per adult in a given year. Superscripts indicate stage-specific values (*YY* = young of the year, *Y* = young, *J* = juvenile, *S* = subadult, *A* = adult). Average values were determined by the expert team or drawn from available literature.

[a] Tolson (1992).

[b] Puente Rolon (2012).

[c] Huff (1978).

(2007) used remote sensing data and information from the U.S. Census Bureau to define three land use types across Puerto Rico: urban, densely-populated rural, and sparsely-populated rural. Human persecution is a key threat to this species, so we considered habitat within sparsely populated areas to be “natural”, i.e. minimally disturbed, and habitat within either urban or densely populated areas to be “developed”. Of the estimated 379 029 ha of suitable habitat, 43% falls within developed areas (Fig. 2). Spatial analyses were performed using QGIS version 3.6.3 (QGIS Development Team, 2019).

Carrying capacity

We imposed density dependence on this population in the form of a simple population ceiling (Morris & Doak, 2002). Published estimates of PR boa density range from 1 to 5.6 boas/ha (Tolson, 1997; Rios-López & Aide, 2007; Mulero Oliveras, 2019). If all available habitat was used (379 029 ha), this corresponds to a maximum population size ranging from 379 029 to 2 274 174 individuals. Although some studies have estimated higher boa densities in some areas (6 boas/ha; Tolson, 1997; Rios-López & Aide, 2007),

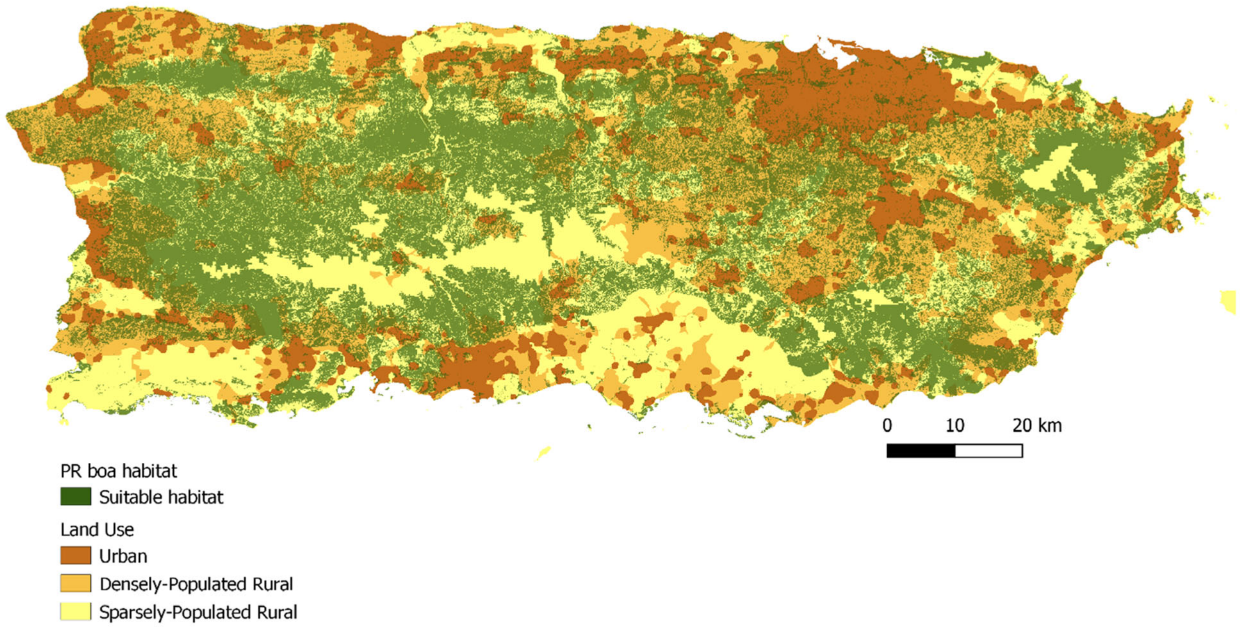


Figure 2 A map of the island of Puerto Rico showing habitat availability for Puerto Rican boas. Suitable habitat (green) was based on the PR Gap Analysis and only includes pixels at less than 700 m elevation. Land use raster based on remote sensing and U.S. Census Bureau data was used to determine the proportion of habitat falling within developed (urban and densely-populated rural) versus natural (sparsely-populated rural) areas.

all available estimates are from the northern part of the range where the species is considered more abundant than in the dry southern region of the Island. To account for variation in density and habitat quality across the island, we chose to set the maximum island-wide density at 3 boas/ha, for a maximum carrying capacity of 1 137 087 boas. We compared model outputs for simulations with varying maximum densities and found that these input values had little to no effect on resulting probabilities of population growth or quasi-extinction (Appendix B).

For each model replication, we randomly drew a carrying capacity from a Uniform distribution bounded by this minimum and maximum (379 029–1 137 087 boas). We assumed that reproduction would cease if the ceiling was reached, and therefore imposed a rule that set fecundity equal to zero if the total population size reached (or exceeded) the ceiling. It is likely that approaching and exceeding carrying capacity would affect multiple demographic processes, but we do not have data to estimate these effects and so implementing a simple fecundity reduction ceiling function allows us to limit population growth without speculating on the functional form of density dependence (Morris & Doak, 2002; McGowan *et al.*, 2017).

Initial population size

The current population size of PR boas is unknown, and little data exists to inform estimates of current abundance. Therefore, for each model replication, we randomly drew an initial population size from a predetermined range. The range for possible current abundance was estimated using published estimates of boa density and input from the expert team, and we assumed a range of 0.1–0.5 boas/ha across all available habitat as a starting density, which corresponds to a range of 37 903 to 189 515 boas in the current population. We chose a maximum current density lower than that estimated by published studies from the northern part of the island (up to 6 boas/ha) to account for the fact that densities are likely lower in other parts of the range. We assumed that the population started at the stable stage distribution, calculated using the popbio package for R (Stubben & Milligan, 2007; R Core Team, 2019). The final population size depends in part on the initial population size, so we present projection results as the change in population size from the first year.

Uncertainty in demographic rates

At the expert meeting described above the team approximated the average value of each rate, but we did not conduct a formal elicitation to obtain estimates of uncertainty in those estimates (Burgman, 2005). We followed the recommendations of McGowan *et al.* (2011) to introduce parametric uncertainty into the replicates of our model simulations. To incorporate uncertainty in our estimates of the average demographic rates, we assumed that the error in our mean estimate was 15% of the average value approximated by the team. We wanted to introduce parameter uncertainty and variability and chose a value between 10% and 20% following the guidance of Kremer (1983). For example, the team estimated average adult survival probability as 0.9, so we assumed a standard deviation of $0.9 \times 0.15 = 0.135$. For each transition probability, we randomly drew an average value for each iteration from a Beta distribution, using the method-of-moments method to convert the mean and standard deviation into shape parameters (Morris & Doak, 2002). For the fecundity rates, we randomly drew an average value from a log-normal distribution with the expert-estimated mean and derived standard deviation (Morris & Doak, 2002). A log-normal distribution was used for the fecundity rates to allow for a continuous random variable with a lower bound of zero.

Temporal variation in demographic rates

Realized demographic rates often vary annually based on stochastic variation in environmental conditions. To allow for temporal variation in realized rates, we assumed the standard deviation in realized annual rates was 15% of the mean. We used these replication-specific mean and standard deviation to define the distributions from which annual rates were drawn. A conceptual diagram of this hierarchical process is provided in Appendix A. Survival and growth probabilities were drawn from a Beta distribution and fecundity rates were drawn from a Log-normal distribution.

Differences between natural and urban habitat

PR boas occur in many different habitats across the island and experience different conditions in each habitat type. For this projection, we assumed that boas could occupy either natural or urban (developed) habitat. Natural habitat was defined as all suitable habitat falling within sparsely populated areas and urban habitat was defined as all suitable habitat within densely populated or urban areas, as defined by Martinuzzi *et al*. (2007). Experts believed that in more developed areas boas experience higher mortality due to human persecution, road strikes, and the occurrence of feral cats. Therefore, we assumed that all realized demographic rates would be lower in urban habitats than in natural (undeveloped) conditions. There was some uncertainty in the magnitude of this effect with some experts believing that survival and growth rates in urban areas would be as low as 50% of the same rates in natural areas while others arguing that increased availability of small prey could mitigate threats. Therefore, we allowed this effect to vary among replications. For each replication we calculated average rates in urban habitats as the average baseline rate multiplied by a randomly drawn habitat effect with a minimum of 0.5 and a maximum of 1. This allowed the demographic rates in urban areas to be lower than those in natural settings by up to 50%.

Sensitivity analysis

Most of the demographic rates used in this model have not been empirically estimated for this population, therefore we relied on elicited estimates by the expert team. To evaluate the sensitivity of model outputs to these input values, we ran simulations in which we randomly drew values for survival and fecundity from a wide range of possible values. For survival rates, we drew values between 0.01 and 0.99, and for fecundity we drew values between 1 and 20. For each demographic rate we randomly drew 1000 values, holding all other rates constant at the average values in Table 1. We simulated 1000 replications of the population projection at each value, keeping the initial population size and carrying capacity fixed at 113 709 and 758 058, respectively, which were the midpoints of the ranges used in the full population projection. For each projection we determined whether the population remained stable or grew by determining whether the population size in the final year was greater than or equal to the initial population size. We also calculated the probability of quasi-extinction at a threshold of 5000 individuals by finding the proportion of replicates in which the population size fell below 5000. Our purpose was to quantify the expected change in model outputs as each model input parameter changed and to identify thresholds for viability for each input demographic parameter.

We also evaluated the sensitivity of model outputs to the input ranges of possible current abundance and carrying capacity. We compared four different iterations of the simulation model that set the upper bound for current density at either 1 boa/ha or 0.5 boa/ha and set the upper bound for carrying capacity at either 6 boas/ha or 3 boas/ha. We projected the population for 1000 replicates per scenario, holding all demographic rates constant at their average values, and compared the probabilities of population growth, decline, and quasi-extinction.

Future scenarios

Predicting the status of a species under different future conditions is a key part of building management plans for an endangered species. Current ecosystem dynamics may change and current threats to viability may worsen or abate in the future, so simulating multiple future scenarios can help inform management planning and decision-making. The expert team agreed that the key threats to the PR boa are habitat loss and human interactions, both of which are linked to increased development and conversion of natural areas into urban areas. PR boas can persist in islands of habitat within an urbanized matrix (Mulero Oliveras, 2019), but not in a purely developed landscape. We considered future scenarios that included changes in land cover such that developed areas would encroach upon natural areas, resulting in both an increased proximity of natural areas to development and loss of overall habitat area. Each scenario had a different urbanization rate, which was implemented as the rate at which both overall suitable habitat area declined and the rate at which the percent of available habitat falling within developed areas increased. Habitat area directly influenced the carrying capacity, and the percent of habitat within developed areas influenced the proportion of the population subject to the randomly varying habitat effect described above. By simulating simultaneous habitat loss and land cover change, these scenarios represent the most extreme way that urbanization could impact PR boa populations.

A recent analysis of past rates of urbanization in proximity to protected natural areas in Puerto Rico (Castro-Prieto *et al.*, 2017) found that urban growth increased at a rate of 16% over 2000-2010. For a best-case scenario, we assumed no future urban growth (0% per decade), and therefore that the percent of habitat within developed areas would remain the same as current conditions (43%) and that the total amount of habitat would remain constant (379 029 ha). We next considered a scenario in which the rate of urbanization was reduced by half to a rate of 8% per decade, and therefore that both the proportion of habitat falling in an urban matrix would increase by 8% every ten years and the total habitat area would decrease by 8% every 10 years. For a status quo scenario, we assumed that the rate of urbanization would continue at 16% per decade, and the total amount of available habitat would decrease by 16% every 10 years. For the worst-case scenario, we assumed that the rate of urbanization would increase by half to rate of 24% per decade. To implement these changes in land cover in the model, we calculated the expected rate of development per year and used this to calculate the predicted total habitat availability and proportion in urban areas. This assumes that development occurs gradually each year.

Population projection

We projected the population for 100 000 replications per scenario. For each replicate, we randomly drew the initial population size, carrying capacity, and average demographic rates. The initial population size in each habitat type was equal to the iteration-specific initial population size multiplied by proportion of the available habitat in that type. We projected each population for 30 years, starting in the stable stage distribution as calculated from the replicate average matrix using the popbio package for R (Stubben & Milligan, 2007; R Core Team, 2019). The time horizon of 30 years was chosen by the team as a reasonable representation of the "foreseeable future" for this species (U.S. Department of the Interior, 2009; Smith *et al.*, 2018). For stochastic projections with many sources of uncertainty, shorter time horizons are recommended to minimize error propagation (Beissinger & Westphal, 1998). For each year, we calculated annual realized demographic rates as described above and calculated the population size by multiplying the year-specific matrix by the population size in the previous time step. We summed the number of individuals in each stage to determine the total population size and calculated the change in population size from the first year by subtracting the initial population size from the projection population size. We calculated the average population growth rate (λ) for each replicate by finding the geometric mean of the year-specific growth rates $\left(\lambda_t = \frac{N_{t+1}}{N_t}\right)$. We calculated the probabilities of population growth and decline for each scenario as the proportion of replicates in which the average population growth rate was greater than or equal to 1 or less than 1 respectively.

Quasi-extinction threshold

The quasi-extinction threshold is the population size below which either the population cannot recover because it enters an "extinction vortex" (Gilpin & Soulé, 1986), or the plausible management alternatives would drastically change (e.g., switching from habitat management to captive breeding). Selecting an appropriate quasi-extinction threshold for a specific population is often challenging due to uncertainties about how demographic feedbacks and management actions influence realized population dynamics. Therefore, we assessed quasi-extinction risk at four thresholds: total population size of 50, 500, 1000, or 5000. For each scenario, we calculated the probability of the population falling below these thresholds as the proportion of replicates in which this occurred. A conceptual diagram of the simulation model is provided in Fig. 3. We ran this model using R version 3.6.1 (R Core Team, 2019) and all model code is available in the Supporting Information.

Results

Sensitivity analysis

Changes in adult survival probability had the strongest influence on both the probability of quasi-extinction and of population growth (Fig. 4). Quasi-extinction probability was ~0 for all iterations in which adult survival was >0.75. This analysis also indicated some thresholds at which we expect population dynamics to change. For example, the probability of population growth declined drastically as fecundity fell below ~4.5 young per adult per year (Fig. 4).

Changing the input for maximum current density and maximum carrying capacity density had little effect on simulation model outcomes (Figure B2). Reducing the upper bound for initial population size (current density) resulted in slightly higher quasi-extinction probabilities, but probability of quasi-extinction was ~1% at the highest threshold and under the worst urbanization scenario. Reducing the upper bound for carrying capacity resulted in little to no change in probabilities of population growth and lower probabilities of population decline (Table B1).

Population projection

Our projection model indicated that the population is most likely to decline over a 30-year period under the status quo scenario, i.e. if the current rate of urbanization were to continue (Table 2, Fig. 5). Under the current rate of urbanization (16% per decade) the model predicted a 64.3% probability of decline and 35.7% probability of stability or growth. Lower rates of urbanization were associated with a greater probability of population stability or growth, but the probability of growth was only 50.2% under the best-case scenario (no further urbanization), which may be unlikely to occur. However, quasi-extinction probability was low, likely due to the possibility of a large current population size (initial population size range from 37 903 to 189 515 individuals, see

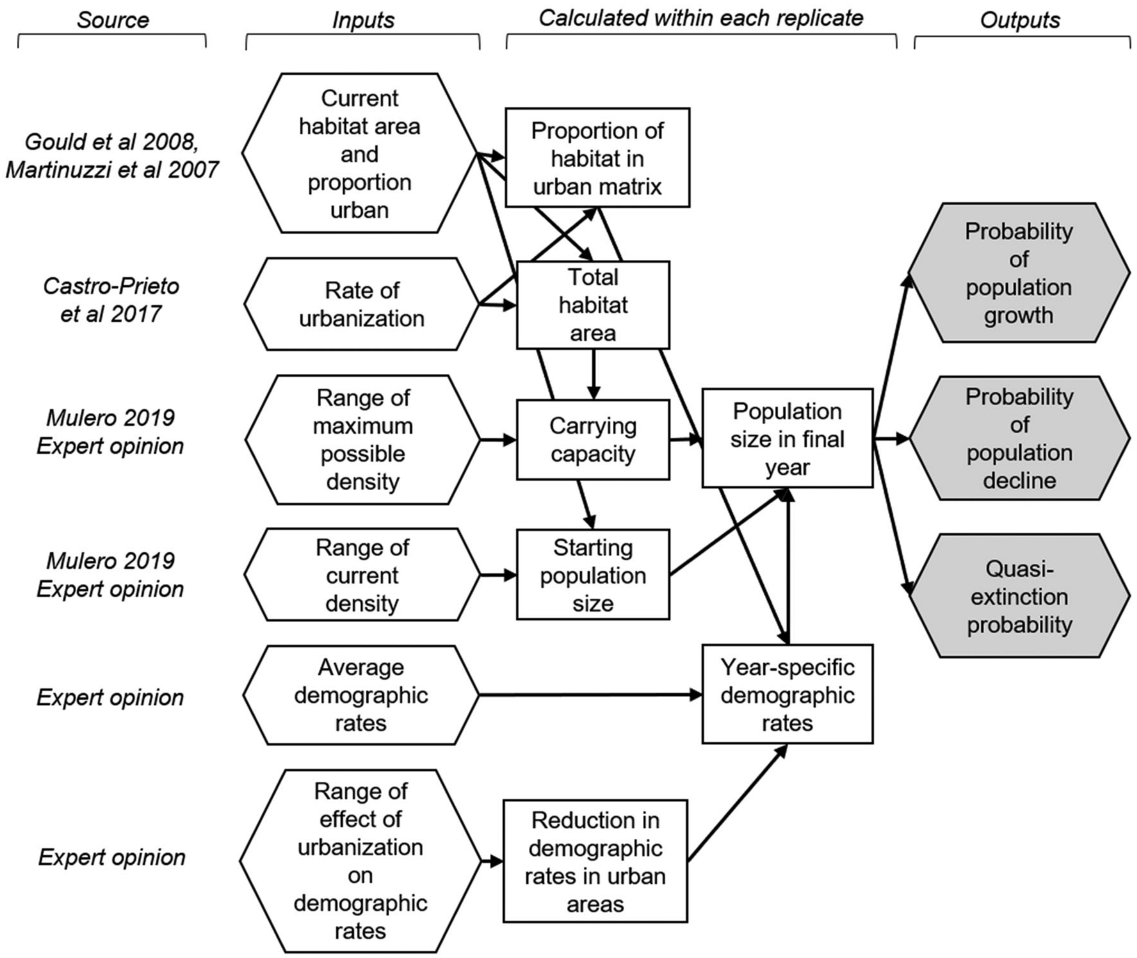


Figure 3 Conceptual diagram of the stochastic simulation model used to assess the future condition of PR boas under different rates of urbanization. White hexagons on the left represent model inputs and gray hexagons on the right represent model outputs. Rectangles represent values calculated within each replication of the simulation.

Initial Population Size above), and was less than 5% for all scenarios and thresholds (Table 2, Fig. 5).

Discussion

Conservation planning requires predictions about the future status of species and populations, which is challenging for data-deficient species. We developed a demographic projection model for the PR boa that incorporated many sources of uncertainty regarding current population status and population vital rates, despite a lack of monitoring data to inform past or current abundance. Using this model, we simulated population dynamics over 30 years under four scenarios of future urbanization and found that there was an increased probability of population decline as urbanization rates increased. The probability that the population would remain stable or grow was greater than 50% only when urbanization rates fell to 0%. Increasing rates of urbanization were also associated with an increased quasi-extinction probability, especially at the highest quasi-extinction threshold (5000 individuals). Quasi-extinction probabilities were low for most scenarios due to the possibility of a large initial population size, which buffers the population from falling below the quasi-extinction thresholds within 30 years. If the true current population size is lower than our projected minimum of 37,903 individuals, quasi-extinction probability may be greater.

This model is largely built based on the personal knowledge and opinion of species experts, with support from published studies. The sensitivity analyses serve to evaluate the effect of key model inputs on our estimates of the probability of quasi-extinction or population growth. These sensitivity analyses can help managers see how predictions would change if model inputs are incorrect, identify how incorrect model inputs would have to be before management decisions would change, and establish priorities for future research. Methods exist to formally elicit demographic parameter estimates and relationships from experts, but those are also time-consuming and can be expensive, or not feasible if few people are experts on the species biology, as was the case

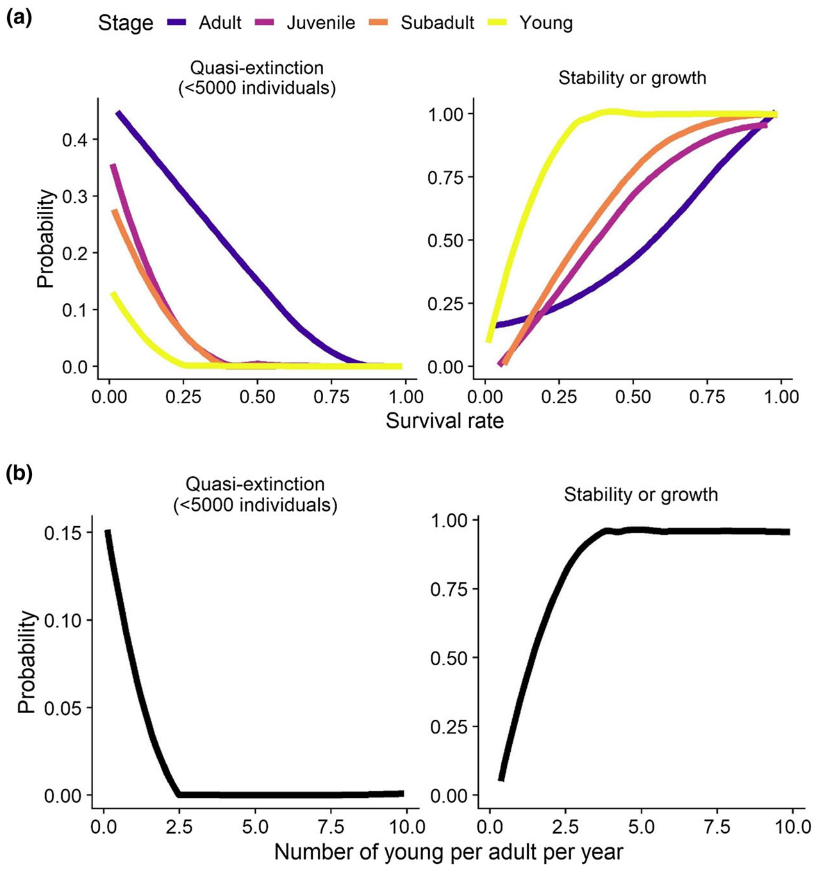


Figure 4 Sensitivity analysis of the effects of demographic rate inputs on model outputs. Simulated probabilities of quasi-extinction and of population growth over the range of possible survival rates for each stage (a) and fecundity (b). The quasi-extinction probability is calculated as the proportion of replicates in which the population size fell below 5000 individuals. The probability of stability or growth is the proportion of replicates in which the average population growth rate (λ) was $\geq$1.

Table 2 The probabilities of quasi-extinction, population growth, and population decrease for the Puerto Rican boa under four urbanization scenarios, based on projections of a matrix population model. We evaluated quasi-extinction probability at four thresholds due to our uncertainties about how that threshold should be determined. The probability of population growth and decline are the proportion of replicates in which the average population growth rate (λ) was greater than 1 or less than 1, respectively. Average population growth rate and percent change in population size are presented as the median and 95% quantiles among all replicates

	Quasi-extinction probability				Probability of population stability or growth ($\lambda \geq 1$)	Probability of population decline ($\lambda < 1$)	Average population growth rate (λ)
Urban growth	50	500	1000	5000			
0%	0	0	0	0.005	0.502	0.499	1.00 (0.933, 1.06)
8%	0	0	0	0.006	0.435	0.565	0.994 (0.927, 1.06)
16%	0	0	0.0001	0.011	0.357	0.643	0.987 (0.921, 1.05)
24%	0	0	0	0.015	0.285	0.715	0.981 (0.916, 1.04)

for the PR boa (Martin *et al*., 2012; Drescher *et al*., 2013; Burgman, 2016). Such methods are especially useful for eliciting estimates of uncertainty in demographic rates, i.e. variance or 95% CI. Here, we applied a blanket uncertainty of 15% to all demographic rates because we did not have expert elicitation results, but our projection would be improved by including explicit estimates of uncertainty for each demographic rate. Our model structure incorporated parametric uncertainty such that each replicate of the simulation drew different mean values from the distribution set up using expert elicited means and the 15% C.V. With this added layer of prediction uncertainty, our simulations account for the possibility that the elicited average values are incorrect. With or without those expert-elicited estimates of parametric uncertainty, a sensitivity analysis like the one presented here can help identify which demographic rates contribute the most to realized population trajectories, and can provide decision makers with target thresholds (e.g.,

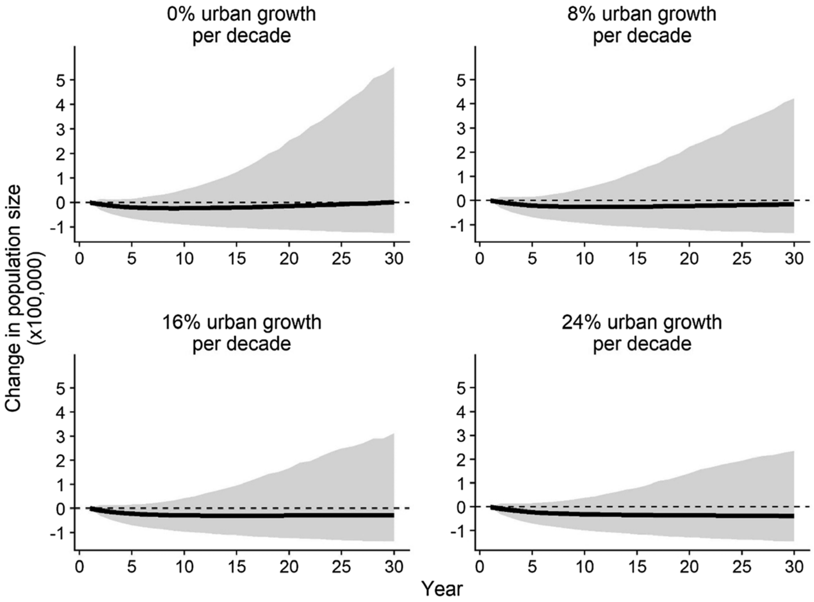


Figure 5 Projected change in population size over 30 years for four potential scenarios of land cover change. Solid black lines show the medians among all replicates, and shaded gray regions show the 95% quantiles (95% of replications fell within this range). The dashed line is at 0, indicating no change in population size.

adult survival >0.75) that may be useful in recovery planning.

Without demographic information, occupancy models can be useful for predicting species presence across its range. However, abundance can change without affecting occupancy, and therefore occupancy status may not reveal declines. Additionally, occupancy alone may not be sufficient to understand responses to future threats because animals often exist in suboptimal habitat (Schlaepfer *et al*., 2002; Battin, 2004). For the PR boa, there are opportunistic sightings from across the range, most frequently in human-dominated areas. That alone might indicate that urbanized habitat is suitable for boas, but species experts agreed that those areas are likely population sinks in which boas experience increased mortality due to road strikes and direct human persecution. By modeling the proportion of habitat in urbanized areas and allowing for a large range in the negative effect of urbanization, we were able to capture this nuance that might be lost if we analyzed occurrence records alone.

Density dependence presents a challenge in developing demographic projections because the mechanisms and functional form of population responses to increased density are still poorly understood for many species. Especially for an island endemic, we thought it important to restrict population growth but had no data to inform carrying capacity or population responses to increased density. By using published estimates of boa density and home range size, we calculated a reasonable range of possible carrying capacities for the island of Puerto Rico. We imposed density dependence in the projection using a simple ceiling function, though in reality population response to density is likely more complex and nuanced. However, our sensitivity analysis indicated that, for our projections, changing this ceiling had little effect on population trajectories.

The sensitivity analyses were an important outcome of this modeling effort. However, we note that this sensitivity analysis is conducted assuming that only one demographic rate changes independent of the others, while, in reality, threats likely influence more than one rate simultaneously. Methods that allow multiple rates to vary simultaneously, e.g. Latin hypercube sampling (Fordham *et al*., 2016; Bradke *et al*., 2018), may be better suited to capture nuances of parameter interactions. However, our approach still provides insight into how the future trajectories would change if the elicited demographic rates are incorrect. For example, we found that all simulations with adult survival >0.75 had no extinction risk, meaning that our experts would have to be wrong about the average adult survival rate by 0.15 in order to change the risk for this species. Estimates of adult boa survival rates using mark–recapture or known fate models would improve confidence in our model predictions and utility for decision-making. Additionally, this analysis is useful at prioritizing future research. In this case, the expert-estimated average fecundity (4.5 offspring/female) is very close to the threshold at which projected probability of stability or decline changes drastically (Fig. 4). Future research to refine this estimate would help reduce our uncertainty in the future trajectories for this species.

This analysis synthesized information from the published and grey literature with expert opinion to develop a quantitative projection model despite many uncertainties about current population status and demographic rates. Because we explicitly incorporated those uncertainties in the simulation model, the outputs reflect our best predictions given those uncertainties. Even when data are sparse, quantitative methods can often be used to produce rigorous and reproducible estimates of future status with quantifiable uncertainty.

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Authors' contributions

AMT, NAF, CPM, and JPZ conceived the ideas; NAF and AMT designed methodology and analyzed the data with input from CPM, JPZ, and EMO; AMT led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

Code availability

All code can be found in the Supporting Information and online at http://www.github.com/annamtucker/puerto-rican-boa.

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Supporting information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Appendix A. Simulation model diagram.
Appendix B. Sensitivity analysis.
Data S1. R code for population projection model.