

**Puerto Rican Boa**  
*(Epicrates inornatus)*

**5-Year Review:  
Summary and Evaluation**



**U.S. Fish and Wildlife Service  
Southeast Region  
Caribbean Ecological Services Field Office  
Boquerón, Puerto Rico**

**September 2011**

**5-YEAR REVIEW**  
**Puerto Rican Boa (*Epicrates inornatus*)**

**I. GENERAL INFORMATION**

**A. Methodology used to complete the review:** This 5-year review for the Puerto Rican boa was prepared by the lead recovery biologist in the Caribbean Ecological Services Field Office. It summarizes new information that the Service has gathered on the species and is based on reviewed literature, survey reports written by local herpetologists, unpublished data, and field observations. Public notice was given of this review in the *Federal Register* on September 12, 2005, and a 60 day comment period was opened. In this notice, we requested new information concerning the biology and status of the species. Two comment letters were received, one from Iniciativa Herpetológica, Inc., and another from the Caribbean National Forest (US Forest Service). Comments received during the comment period were addressed as appropriate in the review.

**B. Reviewers**

**Lead Region:** Kelly Bibb, Southeast Region, (404) 679-7132

**Lead Field Office:** Jan P. Zegarra, Caribbean Ecological Services Field Office,  
Boquerón, Puerto Rico, (787) 851-7297 ext. 220

**C. Background**

- 1. Federal Register Notice citation announcing initiation of this review:**  
September 12, 2005; 70 FR 53807.
- 2. Species Status:** Stable (2011 Recovery Data Call) Although current population estimates are not available, based on the information collected the species' distribution is broader than previously thought and seems to be more abundant than what was known. Efforts should be taken to conduct comprehensive surveys and to establish a methodology for estimating population levels. Efforts to protect the northern karst region should continue.
- 3. Recovery Achieved:** 1 (0-25%) of species' recovery objectives achieved.
- 4. Listing History**
  - Original Listing
  - FR notice: 35 FR 16047
  - Date listed: October 13, 1970
  - Entity listed: Species
  - Classification: Endangered

**5. Associated rulemakings:** None

**6. Review History:** The Final Rule to include the Puerto Rican boa (PR boa) in the United States List of Endangered Native Fish and Wildlife was published on October 13, 1970. The Recovery Plan developed for this species was approved and signed on March 27, 1986 (USFWS 1986). The PR boa Recovery Plan (Plan) includes information about distribution, habitat, feeding, reproductive biology, activity patterns, and status of the species. The Plan mentions possible causes of population decline such as habitat loss, direct human impacts such as mortality caused by medicinal use of snake oil and overall populace feelings against snakes, and depredation by mongoose. The objective of the Plan is to attain population levels at which the species can be delisted.

The Service conducted a five-year review for the PR boa in 1991(56 FR 56882). In this review, the status of many species was simultaneously evaluated with no in-depth assessment of the five factors or threats as they pertain to the individual species. The notice stated that the Service was seeking any new or additional information reflecting the necessity of a change in the status of the species under review. The notice indicated that if significant data were available warranting a change in a species' classification, the Service would propose a rule to modify the species' status. No change in the boa's listing classification was found to be appropriate.

Recovery Data Call: years 2000 through 2011.

**7. Species' Recovery Priority Number at start of review (48 FR 43098):** 11c. At the time of listing, the PR boa was recognized as a species with moderate degree of threat. Recovery potential was considered to be low.

**8. Recovery Plan:**

Name of plan: Puerto Rican Boa Recovery Plan.

Date issued: March 27, 1986.

## **II. REVIEW ANALYSIS**

### **A. Application of the 1996 Distinct Population Segment (DPS) policy**

- 1. Is the species under review listed as a DPS?** No.
- 2. Is there relevant new information that would lead you to consider listing this species as a DPS in accordance with 1996 policy?** No.

## B. Recovery Criteria

1. **Does the species have a final, approved recovery plan containing objective, measurable criteria?** No. Although the species has an approved final recovery plan, it does not contain measurable criteria. The objective of the recovery plan was to attain population levels at which the species could be delisted. No quantitative criteria were defined due to the absence of information on population sizes and limiting factors. The recovery plan recommends conducting a comprehensive status survey and ecological studies of the species before determining specific recovery actions.
2. **Adequacy of recovery criteria.**
  - a. **Do the recovery criteria reflect the best available and most up- to-date information on the biology of the species and its habitat?** No. The recovery plan did not include objective measurable criteria and recommended conducting comprehensive surveys and ecological studies to determine specific and quantified recovery goals.
  - b. **Are all the 5 listing factors that are relevant to the species addressed in the recovery criteria?** Not applicable. The recovery plan did not include objective measurable criteria.

## C. Updated Information and Current Species Status

1. **Biology and Habitat**
  - a. **Is there relevant new information regarding the species' abundance, population trends (e.g. increasing, decreasing, stable), demographic features (e.g. age structure, sex ratio, family size, birth rate, age at mortality, mortality rate, etc.), or demographic trends?** Yes.

Various attempts have been carried out by researchers to determine the PR boa's population status. However these investigations have either been conducted on specific areas, are based on counts and do not reflect population estimates, or the results are mostly based on anecdotic reports. According to Reagan (1984), the PR boa is probably less abundant than it was in Pre-Columbian times, when Puerto Rico had an extensive forest cover. More recent reports indicate that the PR boa apparently is not as rare as previously thought (Moreno 1991, Bird-Picó 1994, Wunderle et al. 2004). However, some of these authors explained that the apparent abundance increment may be an artifact of increased encroachment into ever reducing habitats (Moreno 1991, Bird-Picó 1994, Puente and Vega 2005).

In 1991, a study to determine the status of the PR boa was conducted as part of the Costa Isabela development project in the coastal area between the municipalities of Isabela and Quebradillas (Lebrón Associates 1992; Figure 1 at the end of this review). During the months of June, July and August, the consultants positively identified 45 PR boas distributed along the project's property. They concluded that there was an abundant population of boas in the property and that the species was widely distributed within the study area (Lebrón Associates 1992).

From July 1992 to December 1994, Bird-Picó (1994) conducted a status survey of the PR boa to determine its presence mostly in the northern part of Puerto Rico. In his report, he did not provide a population estimate. The report makes reference to a questionnaire based survey by Rivero and Seguí (1992), of which 32 out of 76 municipalities responded. Less than 10% of surveyed people that responded reported the boa as abundant, more than 25% reported the boa absent from their localities, another 25% reported the boa as rare, and the other 37.5% reported that the snakes were occasionally seen. Although Bird-Picó (1994) emphasized that interviewed citizens had a tendency to exaggerate the species' abundance, the findings of his study support the idea that the PR boa has a broader distribution than what had previously been documented (e.g., Tolson and Henderson 1993).

Bird-Picó (1994) was able to document a maximum of 24 snakes during one night at Culebrones Cave (Mata de Plátano Nature Reserve) in the municipality of Arecibo (Figure 1). It is common to see boas in this particular cave, where Puente-Rolón and Bird-Picó (2004) captured nine snakes for a radio telemetry study. Puente-Rolón and Bird-Picó (2004) indicated that Culebrones Cave represents a highly productive habitat, where food is concentrated in a particular area and available to the snakes, thus explaining the boa's common occurrence at the site. Rodríguez-Durán (1996) also observed boas at Culebrones Cave ranging from 2 to 21 boas on a given night.

Wunderle et al. (2004) also conducted a radio telemetry study with the PR boa at El Yunque National Forest in eastern Puerto Rico. Besides monitoring twenty-four snakes for their tracking study, Wunderle et al. (2004) tagged a total of 70 PR boas with transponders (pit-tags). Boas were found incidentally during daylight and evening hours while walking or driving to sites with radio-marked boas. Nevertheless, no population estimate was calculated. According to Wunderle et al. (2004), much of the boa's apparent rarity is related to the observer's ability to visually detect this cryptic species within the forest. As an example, Wunderle et al. (2004) failed to visually detect telemetry-tracked boas an average of 85 percent of their telemetry relocations. They indicated that given this detection difficulty in the forest, it is likely that the PR boa is more abundant than generally perceived.

The only published density estimate for the PR boa is from Ríos-López and Aide (2007). They surveyed herpetofauna within five different types of habitats (i.e., deforested valley, reforested valley, old valley, karst hill top, karst hillside) along a 50 m transect for each habitat type in the municipality of Toa Baja (Figure 1). Ríos-López and Aide (2007) estimated a mean monthly density of 5.6 boas per hectare for the reforested valley, the old valley and the karst hill top. They did not encounter boas in the deforested valley nor at the karst hillside habitats. Although, this estimate may provide a rough idea of how many boas one may encounter in similar areas, it may not be extrapolated to the whole karst region. The area where Ríos-López and Aide (2007) conducted their study is a small somewhat isolated karst fragment surrounded by urban and commercial development, a herbaceous wetland, and primary and secondary roads. Karst and other types of forest where boas occur are dynamic and the occurrence of this species within such habitats also depends on other factors (e.g., forest complexity and composition, abundance and availability of prey, climate).

- b. Is there relevant new information regarding the species' genetics, genetic variation, or trends in genetic variation (e.g. loss of genetic variation, genetic drift, inbreeding, etc.)? No.**
- c. Is there relevant new information regarding taxonomic classification or changes in nomenclature? No.**
- d. Is there relevant new information regarding the species' spatial distribution, trends in spatial distribution (e.g. increasingly fragmented, increased numbers of corridors, etc.), or historic range (e.g. corrections to the historical range, change in distribution of the species within its historic range, etc.)? Yes.**

Various attempts to update the distribution of the PR boa have been carried out after the approval of the Plan in 1986. Published information prior to the Plan was scarce and much of it was anecdotal rather than rigorously scientific (Reagan and Zucca 1982). More recent publications concur with previous studies (Schwartz and Thomas 1975), indicating that although the PR boa was considered rare since the beginning of the 20<sup>th</sup> century, as reported by Grant (1932; 1933), the Puerto Rican boa is widespread in Puerto Rico.

Pérez-Rivera and Vélez (1978) provided a map of the distribution of the PR boa. The map was based on previous boa reports, the authors' observations, and collection specimens from the Biology Museum of University of Puerto Rico. The reports confirm PR boa occurrence in the following municipalities or regions: Caguas, Humacao, Bayamón, Río Piedras, El Yunque, Utuado, haystack hills of San Juan, haystack hills of Toa Alta, forest in Dorado, Aibonito, Cayey, Isabel, Aguadilla, Moca, Adjuntas, Fort Buchanan, Arecibo, Roosevelt Roads in Ceiba, Yabucoa, and Cabo Rojo (Figure 1).

Bird-Picó (1994) made reference to a map from Tolson and Henderson (1993), which situates the PR boa mainly in the eastern and western part of the Island. Later, Bird-Picó (1994) reported a broader distribution of the PR boa, adding several more locations to those previously reported. These locations are within the municipalities or regions of Barceloneta, Guajataca Commonwealth Forest in Isabela, San Germán, Juncos, Mayagüez, and Quebradillas (Figure 1). The presence of the PR boa in these municipalities was corroborated by Bird-Picó (1994) either by finding boas during searches, through a questionnaire based survey, and through information provided by local people who contacted the author. According to Bird-Picó (1994), boas are found throughout the karst region, on the periphery of coastal plains, and in the mountain regions. Mostly directing his research efforts towards the northern part of the Island, Bird-Picó (1994) found that the highest number of anecdotal reports and boa findings derived from areas associated to the haystack formations, which are the dominant geo-ecological features of the north-northwestern part of the Island. The haystack formations or “mogotes” are collectively within the northern karst belt and cover an extensive region from the western part of Bayamón towards the west into the Aguadilla-Moca area (Figure 1).

Rivero (1998) indicated that the PR boa is distributed throughout the Island, being more abundant in the “mogotes” of the north (from Bayamón to Aguadilla) and much less abundant in the dry southern region of the Island. Rivero (1998) confirmed southern collection reports from Cabo Rojo, Lajas, Ponce, Salinas, and Guayama (Figure 1).

Wiley (2003) collected data from 1973 through 1986 and reported several new localities to the PR boa distribution, also showing that boas are widespread in Puerto Rico. Although mostly from the Sierra de Luquillo (within the Caribbean National Forest), PR boa individuals were also reported from Arecibo, Guánica, Ceiba, Cidra, Dorado, Maricao, Río Abajo Forest in Utuado, and Toa Alta (Figure 1).

The Puerto Rico Gap Analysis Project developed an occurrence map and predicted distribution map for the PR boa (Figures 2 and 3; Gould et al. 2008). They described the PR boa as widespread in its distribution, but uncommon. For their analysis, a species record of occurrence was confirmed when associated to a credible observation, including the location, observation date, and observer’s name. Gould et al. (2008) also based the species probable occurrence on published range maps, location descriptions, confirmed occurrence of habitat, and expert opinion that the species is likely to occur in a particular area. Species habitat models were linked to specific mapped land cover units or other information for which they have reliable spatial information.

The PR boa predicted habitat includes 46.3% (414,379 ha; 1,023,952.81 acres) of the Island, of which 9% occurs within protected areas (Figure 3 at the end of this

review). However, this does not exclude PR boa occurrence outside of the predicted habitat. In fact, based on a strong likelihood, GAP illustrates the entire island of Puerto Rico as having a probable occurrence of boas (Figure 2 at the end of this review; Gould et al. 2008).

The Service also has information from species experts, site visits and personal communications about PR boa occurrence. For example, we know that boas have been sighted in several caves within the karst areas of the island. We also have reports from several state and private forests as mentioned above (Figure 1; Río Abajo, Guajataca, Camabalache, and Vega Commonwealth Forests, Mata de Plátano Nature Reserve in Arecibo, and El Convento Caves in Guayanilla). Previous elevation distribution for the PR boa has been characterized as from sea level to less than 400 m (1,312 ft). However, Grant (1932, 1933) reported boas at 450 m (1,476 ft) and near the headwaters of the Luquillo mountains, which Reagan (1984) noted would be at an elevation of 700 m (2,296 ft). This last report is based on Reagan's interpretation of Grant's habitat description. This report in elevation is considerably higher than any previously known boa locality. Schwartz and Henderson (1991), and Henderson and Powell (2009) described the PR boa's elevation range from sea level to 1,050 m (3,445 ft). The highest elevation Wiley (2003) encountered was 480 m (1,575 ft) in the Sierra de Luquillo. Mean elevation in the Sierra de Luquillo, where most individuals were found, was 250.8 m (823 ft).

**e. Is there relevant new information addressing habitat or ecosystem conditions (e.g. amount, distribution, and suitability of the habitat or ecosystem)? Yes.**

According to the status survey of the PR boa conducted by Bird-Picó (1994), the species has a wide distribution in a variety of habitats including wooded areas, open pastures, shrubs, and cave entrances and interiors. The presence of boas on cave entrances and interior areas is usually attributed to its feeding behavior (Rodríguez and Reagan 1984, Rodríguez-Durán 1996, Puente-Rolón 1999). Bird-Picó (1994) indicated that the localities where the boa was described as abundant are the ones where construction and urban development are taking place at a high pace. He further explained that as Moreno (1991), and Tolson and Henderson (1993) mentioned the apparent increase in abundance has probably resulted from the encroachment of the boas into ever reducing habitats.

Puente-Rolón (1999) conducted habitat characterization for 73 PR boa locations. He identified a total of 47 plant species during the habitat measurements, and also found that boas did not show a specific preference on two locations where plant species were the same.

Wiley (2003) collected data on the PR boa from the Sierra de Luquillo (within El Yunque), and from the Río Abajo Commonwealth Forest in Utuado, Cidra, and



some coastal areas. Although his observations were biased toward habitats next to roads and areas where boas were killed as threats to livestock or out of fear, they support previous reports showing that boas are widespread in Puerto Rico, inhabiting a wide variety of wet and moist forested habitats, as well as areas of human habitation near natural areas. During his research, most animals were found in two of the four forest types [tabonuco (*Dacryodes excelsa*) and palo colorado (*Cyrilla racemiflora*) zones] of the Sierra de Luquillo (montane wet forest). No boas were encountered by Wiley (2003) in the two higher zones of the forest, the sierra palm and dwarf forest. However, sampling was not similarly conducted because these forest types have few roads. According to Wiley (2003), habitat types that have been documented to be used by boas include mangrove forest (Ceiba), wet limestone forest (Río Abajo Commonwealth Forest, Utuado), remnant coastal rain forest (Dorado Beach), pastureland with patches of exotic trees (Cidra), and suburban and urban areas, where boas occurred in outbuildings and houses. One individual was reported as collected in the Guánica Commonwealth Forest (dry limestone karst), possibly indicating that the species is tolerant to xeric environments. Another boa was found on a mangrove cay (Montalva Bay, Guánica) about 0.5 km off the mainland.

Wunderle et al. (2004) studied habitat use of the PR boa at the Luquillo Experimental Forest (LEF, currently El Yunque National Forest) in eastern Puerto Rico. His findings indicate that, although boas were located in a variety of microhabitats at LEF (i.e., vine enclosed broadleaf trees and shrubs, vine tangles, sierra palm [*Prestoea montana*], tree ferns [*Cyathea* spp.], bamboo [*Bambusa vulgaris*], dead trees, stream, building, and miscellaneous cultivated plants), the highest mean percentage of fixes for telemetrically followed boas occurred in broadleaf trees (52.8%), followed by ground or belowground sites (34.9%).

According to the findings of Wunderle et al. (2004), habitat use differed significantly among sexes with females spending more time on or below ground than males. As stated by these authors, thermoregulation requirements of gravid females may contribute to use of exposed terrestrial debris piles. However, the role of thermoregulation in microhabitat selection is largely unknown, although both sexes were observed basking in both terrestrial and arboreal sites.

Wunderle et al. (2004) also observed that broadleaf trees in which boas were located differed from randomly selected broadleaf trees in a number of traits. For example, trees with boas differed from random trees by having larger diameter trunks (DBH); being taller; having more crown contact with neighboring crowns; being closer to other broadleaf trees; being surrounded by a higher density of understory vegetation; and having a lower percentage canopy cover than random trees. It was vine cover, however, that especially characterized trees used by boas, as these trees had more vines (both attached and

unattached to the trunk), the nearest free vines were closer to the trunk and had larger diameters than vines on randomly selected trees.

Vines are important for gaining access to trees from either the ground or from other trees or shrubs and provide dense cover for foraging and resting (Wunderle et al. 2004). Moreover, vines were more abundant on large trees in the LEF, which partially explains the presence of boas in trees of larger DBH relative to randomly sampled trees. Also, big trees are likely to provide larger diameter perches used by heavy snakes and tree cavities, which are more common and bigger in trees with larger DBHs. Tree cavities may be used by boas for resting or prey location. Also, large trees may have bigger crowns, increasing the likelihood of contacting the crowns of neighboring trees and thereby providing the vegetation continuity required for arboreal snake movements in the canopy. Rarity of vegetative continuity, including vine coverage, and structural aspects may have limited boa use of palms and tree ferns despite their abundance in the LEF.

Gould et al. (2008) stated that the PR boa predicted habitat model includes the following land cover types: moist and wet forest, woodland and shrubland mangrove, *Pterocarpus*, mature dry forest, and dry forest near water bodies, at or below 1,000 m of elevation (Figure 3).

**f. Is there any other relevant information on the species? Yes.**

Puente-Rolón and Bird-Picó (2004) utilized radiotelemetry to determine the home range, activity, and movement patterns of the PR boa in the Mata de Plátano Nature Reserve in Arecibo. This reserve is located in the limestone karst region of north-central Puerto Rico. Eleven snakes (6 females, 5 males) were fitted with transmitters and tracked for ten months. Home range size, mean distance per move, and mean distance moved per day were tested for difference between sexes. They found that home range areas varied from 138.9 m<sup>2</sup> (1,495 ft<sup>2</sup>) to 18,380 m<sup>2</sup> (197,840.7 ft<sup>2</sup>). Home ranges of males and females did not differ significantly. However, females tended to have larger mean home range areas (7,890 m<sup>2</sup>; 84,927 ft<sup>2</sup>) than males (5,000m<sup>2</sup>; 53,820 ft<sup>2</sup>). Male 50% core activity area [ranging from 20m<sup>2</sup> (215 ft<sup>2</sup>) to 653m<sup>2</sup> (7,029 ft<sup>2</sup>)], and female core activity area [ranging from 6m<sup>2</sup> (65ft<sup>2</sup>) to 664m<sup>2</sup> (7,147 ft<sup>2</sup>)] did not differ statistically. Puente-Rolón and Bird-Picó (2004) attributed their findings to highly productive habitats, since home ranges have been found to be smaller in this type of habitat. Culebrones Cave (Figure 1, Mata de Plátano Nature Reserve), where this study was specifically conducted, represents a highly productive habitat where food is concentrated in a particular area and is available to the snakes. This may explain why individuals were confined to the proximity of the cave. In areas where food resources are more dispersed or in lower densities, the PR boa needs larger home ranges (Puente-Rolón and Bird-Picó 2004).

Wunderle et al. (2004) conducted studies about the Puerto Rican boa spatial ecology in a subtropical wet forest from October 1996 to July 2001. Analyses of movement and home range were based on 18 snakes for which they had approximately one year of data on three tracking periods: pre-hurricane, hurricane, and post hurricane. Monitored boas moved an average of 12.9 m (42.3ft) daily between fixes (fix= telemetry relocation). No significant differences in daily movement per fix were found between males [mean of 15.2 m (49.9 ft) and females mean of 10.5 m (34.4 ft)]; however a significant interaction between sex and period was found. This interaction indicates that mean daily movement per fix by males was greater than those for females in the pre- and post-hurricane periods [pre-hurricane mean of 14.8 m (48.6ft) vs. mean of 9.9 m (32.5ft); post-hurricane mean of 19.6 m (64.3 ft) vs. mean of 7.3 m (24 ft)], but in the hurricane period males moved less than females [mean of 7.2 m (23.4 ft) vs. mean of 13.7 m (44.9 ft)].

Wunderle et al. (2004) also found that although some individuals changed behavior following the hurricane, response of individual boas to the storm were not consistent. For example, the median daily movement per fix of one of the tracked females was significantly higher after the storm than before. This response however, may have been correlated to the hurricane and was due to changes in movement associated with the birth of young slightly after the storm.

Wunderle et al. (2004) also provided detailed information on immobility in addition to daily and monthly movements of boas. According to their findings, boas moved an average of 26.4 m (86.6 ft) daily per move. However, most of the time boas were immobile as evidenced in a mean of 10.2 consecutive days without movement between fixes.

Female boas were immobile for more days and were located more frequently on the ground than males, as might be expected given the constraints or requirements of gestation. Gravid females of the PR boa are known to use exposed terrestrial debris piles for thermoregulation (Tolson and Henderson 1993), which may contribute to greater use of ground sites by females. Consistent with this was a female that showed a marked shift to ground use when gravid (97% of fixes) compared to its non-gravid period (23% of fixes). A marked difference was not shown in other females possibly because about half of its time was spent at ground sites anyway.

Immobility of gravid females was expected due to reduced locomotor performance of gravid snakes, especially before parturition. Reduction in movement was indeed evident in the minimum immobile periods of 60 and 118 days each documented prior to parturition in the two females of known reproductive status.

In general, movement of boas during a fix was observed significantly more often at night than during daylight hours. Mean daily movement per month varied significantly among months. Sex differences in mean daily movement per month were significant with greater values for males than females. A significant interaction between sex and month was detected, with males showing a bimodal peak in monthly movement during April and June in contrast to females in which movement peaked in July.

Wunderle et al. (2004) found that home range of individual boas shifted considerably in size and geographic position over the approximately one-year period in which snakes were followed. Expansion of home range size was expected to correspond with the increased boa movements documented during the reproductive period and in some cases was observed, especially for males but less frequently for females. Fidelity to a specific site was usually low, as boas only revisited a small percentage of the sites in the home range during the approximate one year each boa was studied.

In summary, sex differences in movements were detected as found in previous studies. Males moved farther than females based on results of mean daily movement per move, mean daily movement per month, and mean daily movement per fix. In contrast to males, females were immobile for significant longer average time periods. The sexes did not differ significantly in home range size, although their sample size was small (potentially limiting statistical power).

PR boa movements were consistent with previous studies in reflecting a seasonal pattern of reproduction. Mating of Caribbean *Epicrates* occurs from January through May (Tolson and Henderson 1993). Within the LEF, mating is believed to occur at the beginning of the wet season (April-May; Grant 1932, Reagan 1984), which was confirmed by observations of copulating pairs (Grant 1932, Reagan 1984). Furthermore, a 153-176 gestation period (Huff 1978) supports the observations of Grant (1932) and Reagan (1984) on the birth of young boas during September-October and a mating period between April-May. Furthermore, Wunderle et al. (2004) found an increase in movements of male boas from April through June, suggesting that males actively search for females during this period, which also corresponds with the mating period previously reported. It is less obvious why female movements peaked in July following the male peak, but it partly represents increased foraging to sustain embryo growth as well as shift to environments appropriate for gestation and parturition. The April to July peak in boa movements also corresponded approximately to the period of reproductive activity in some boa prey abundance and vulnerability.

Although seasonal patterns of boa movements in the LEF may be most attributable to reproductive behavior, the overall patterns of movement likely reflect foraging behavior. Alternation of immobile periods with active movement as observed in this study is consistent with an opportunistic foraging

strategy involving both active search and ambush strategies of a generalist predator. Wunderle et al. (2004) suspected that prey were occasionally ambushed by boas during immobile periods as well as captured while moving between sites.

Wunderle et al. (2004) compared their results and observations with the previous home range study conducted by Puente-Rolón and Bird-Picó (2004). Their analysis indicate that snakes foraging in productive food patches are expected to have smaller home ranges than those in less productive patches (Stickel & Cope 1947). Consistent with this prediction are the studies at a bat cave (productive area) in the karst region of north-central Puerto Rico (Puente-Rolón and Bird-Picó 2004), which indicate smaller home range sizes than those in the LEF. Although telemetry fixes were obtained more frequently at the cave site than in El Yunque (48h vs. 4-5d), and boas were studied for fewer months (10 vs. 12), it is likely that the substantial differences in home range size between the two sites resulted from differences in prey abundance and dispersion. These differences in boa home range are consistent with an expectation of smaller home ranges associated with a rich food environment, represented by abundant bats at the cave, in contrast to the larger home ranges at the LEF, where prey were likely more widely dispersed and occur at lower densities.

## **2. Five Factor Analysis (threats, conservation measures, and regulatory mechanisms)**

### **(a) Present or threatened destruction, modification, or curtailment of its habitat or range:**

Based on the above discussion on species' distribution and habitat use, the PR boa appears to be widely distributed throughout Puerto Rico and utilizes a wide variety of habitats, ranging from mature forest to plantations and disturbed areas. Various authors concurred that this species is most often found in the northern limestone karst region of Puerto Rico, known from both protected areas (Cambalache, Río Abajo, and Guajataca Commonwealth Forests) and privately owned lands (Mata de Plátano Nature Reserve). Additional areas have been acquired for conservation by non government organizations such as the Puerto Rico Conservation Trust. Moreover, since 2001, the Service's Partners for Wildlife Program has restored about 89 ha (220 acres) of private land previously impacted mostly by agricultural activities in an effort to provide suitable habitat for the PR boa and other species.

However, despite the above conservation efforts and additional proposals to protect the northern karst region of Puerto Rico by non-government organizations, part of this area is still in private ownership. This region has been previously affected by deforestation and land movement for agricultural purposes, commercial, industrial, highway, and urban development. At present,

habitat modification is still occurring within the region, transforming the karst landscape by removing haystacks (“mogotes”), filling sinkholes and caves, filling wetlands, and paving over surfaces to facilitate intense uses of the land (Lugo et al. 2001).

Although the PR boa seems to occupy a wide variety of habitats not only in the karst region but also throughout the Island, wild individuals seem to prefer specific habitat arrangements in forested areas. Besides rocks and trees in forested areas, light gaps provided by forest openings and forest edge situations are frequently used for basking by boas (Reagan 1984). The species has also been reported to be very common along streams on tree branches (Schwartz and Henderson 1991). Throughout project evaluation processes, the Service has identified that riparian areas along streams are prone to direct and indirect impacts by poor development practices during and after project construction.

Joglar et al. (2007) discussed how habitat loss and landscape fragmentation have become another concern in the conservation of the PR boa. The authors explained that habitat destruction is increasing and may disrupt natural population dispersal and gene flow. Due to the PR boa’s protected status, translocation (i.e., movement of wild individuals from one part of their range to another) has become a common practice when boas are found in human settlements, and sometimes recommended if found in project areas under construction. A study on how the translocation influences thermoregulation, movement and survivorship is in progress. Preliminary data show that translocated snakes expand their home ranges when compared to non-relocated individuals (Puente-Rolón, unpubl. data).

Based on the above discussion, although efforts are being carried out to preserve and restore areas in which the PR boa is commonly found, habitat modification and destruction in privately-owned areas still occur. Moreover, the effect of translocation on boas as a result of habitat modifications has not been determined. Hence, it could be a management tool that might be affecting the species instead of protecting it. We believe that this factor is the main threat to the species, at this time.

**(b) Overutilization for commercial, recreational, scientific or educational purposes:**

Illegal hunting of boas for oil and meat is reported in the literature. The hunt of PR boas to extract its fat was reported in the 1930s by Grant (1933) and supported by Rivero (1998), indicating that snake “oil” is used as a medicinal remedy. Illegal hunting has been identified as a factor contributing to the species’ decline (Pérez-Rivera and Vélez 1978). More recent authors, after conducting interviews with local people during their investigations, agree that this practice still continues to date (Reagan 1984, Puente-Rolón 1999, Joglar

2005). In addition, Bird-Picó (1994) reported a case in which snake meat was used for human consumption. We believe that these anecdotal reports do not constitute over utilization of the species for commercial and recreational purposes. There is no evidence that boas have been over utilized for scientific and educational purposes. Although both Federal and local laws and regulations currently prohibit commercial and recreational utilization of boas and their products, there are no reported cases in which law enforcement officials have intervened. In addition, the extent or effect of illegal hunting is not known.

**(c) Disease or predation:**

Depredation by Indian mongoose (*Herpestes auro punctatus*) was listed as one of the causes for this species' decline (USFWS 1986). However, according to Rivero (1998), the mongoose does not appear to have caused serious losses to the boa population. Reagan and Zucca (1982) suggest that a mongoose might occasionally eat a small boa, but studies of mongoose food habits in Puerto Rico and throughout the Caribbean have not documented any such predation (Pimentel 1955, Henderson 1992). Wiley (2003) found the remains of a dead boa with tooth impressions consistent with depredation by the Indian mongoose; however, this author states that this may be a result of scavenging. Besides the mongoose, house cats may also represent a depredation threat.

Rivero (1998) mentioned pigs as implacable enemies of snakes and that large birds of prey can also eat them. Small snakes can be victims of cats, toads, lizards, and even chickens (Rivero 1998). Reagan and Zucca (1982) mentioned birds such as the red-tailed hawk (*Buteo jamaicensis*), pearly-eyed thrasher (*Margarops fuscatus*), red-legged thrush (*Turdus plumbeus*), and Puerto Rican lizard cuckoo (*Coccyzus vielloti*) as possible predators of juvenile boas, but evidence to support this is lacking.

According to Reagan and Zucca (1982) observations while conducting studies in the Caribbean National Forest, a few mites were noted on some of the specimens examined, but heavy infestations were not apparent. Individuals of PR boa found in an area close to cattle and horse grazing pastures in northern Puerto Rico have been reported as being infested by cattle ticks (*Amblyoma* spp. and *Boophilus* spp.) by Bird-Picó (1994). He also found few individuals infested with the red mite (*Ornithodoros portorricensis*). Besides these reports, no other diseases have been documented for the PR boa.

Since parasite infestation has only been reported in isolated cases, no disease has been documented for this species, and mongoose depredation on the PR boa has not been documented. Therefore, we do not have evidence to suggest that disease and predation are presenting threats to this species.

**(d) Inadequacy of existing regulatory mechanisms:**

In 1999, the Commonwealth of Puerto Rico approved the Law No. 241, known as the “Nueva Ley de Vida Silvestre de Puerto Rico” (New Wildlife Law of Puerto Rico). The purpose of this law is to protect, conserve, and enhance both native and migratory wildlife species; declare property of Puerto Rico all wildlife species within its jurisdiction, regulate permits, hunting activities, and exotic species, and to avoid inadequate modifications of habitat, among other activities. Based on this law, in 2004 the Puerto Rico Department of Natural and Environmental Resources (PRDNER) approved the “Reglamento para Regir el Manejo de las Especies Vulnerables y en Peligro de Extinción en el Estado Libre Asociado de Puerto Rico” (Regulation 6766 to Regulate the Management of Threatened and Endangered Species in Puerto Rico). This regulation explicitly prohibits the possession, transportation, taking, destruction, hunting, and killing, of any wildlife species listed as threatened or endangered. Regulation 6766 also prohibits modifications of habitat designated by the PRDNER as critical and critical essential. Although the PR boa has no critical habitat designated, Law No. 241 prohibits the modification of natural habitat without a mitigation plan approved by the PRDNER.

The Puerto Rican boa was included in the list of protected species and designated as “vulnerable”: A2 (c and e) under Regulation 6766. The PRDNER listing criteria are based on the IUCN Red List Categories and Criteria. Thus, the PR boa was categorized as vulnerable with reduction in population size based on: an observed, estimated, inferred, or suspected population size reduction of  $\geq 30\%$  over the last 10 years or three generations, whichever is the longer (up to a maximum of 100 years) based on: (c) a decline in area of occupancy, extent of occurrence and/or quality of habitat and (e) the effects of introduced taxa, hybridization, pathogens, pollutants, competitors or parasites.

In addition, various other laws have been approved by the Commonwealth of Puerto Rico to protect the karst region of the Island, which has been described as the type of habitat where the PR boa is more commonly found. Law No.292, known as “Ley para la Protección y Conservación de la Fisiografía Cársica de Puerto Rico” (Law to Protect the Karst Physiography of Puerto Rico) was approved in 1999 to protect the karst area as one of the most valuable natural resources of the Island. Hence, this law indirectly protects the PR boa and all other species that occur in the karst as well.

Based on the presence of local laws and regulations protecting this species and its habitat, we believe that inadequacy of existing regulatory mechanisms is not a threat to the species.



**(e) Other natural or manmade factors affecting its continued existence:**

Intentional killing of this species due to superstitious beliefs was first reported by Rivero (1978). Throughout the years, various researchers have interviewed people in immediate areas of their research sites corroborating that killing boas due to innate fear, religious prejudice and ignorance persists (Bird-Picó 1994, Puente-Rolón and Bird-Picó 2004, Joglar 2005). Boas are also being killed because they regularly eat poultry and their eggs (Wiley 2003). Boas are also accidentally killed by vehicles each year while crossing roads within the Caribbean National Forest and elsewhere in the island (Reagan and Zucca 1982, Wiley 2003).

In view of the above, we believe that illegal take of the PR boa likely still occurs and is a threat to the species. Incidental and or direct road kills of boas by vehicles also occurs and is considered a threat. Both of these threats are not reported to any authority routinely. However based on the few existing anecdotal reports and the fact that this snake in general occupies a large home range and has wide distribution, we believe the extent and degree of this threat is low.

**3. Synthesis**

The PR boa was apparently abundant in Puerto Rico during the early years of colonization. Boa populations presumably declined in both size and distribution during a period of intense deforestation on Puerto Rico in the late 1800s. This decline and apparent rarity prompted the Federal government to include the PR boa in the Endangered Species list in 1970. Various causes for this species population decline have been stated, including habitat loss, intentional killings, captures of individuals to be sold as pets, road killings, and the accidental and planned introductions of exotic species.

After the approval of the Recovery Plan for the PR boa, various investigations have been conducted on foraging behavior, home range, movement patterns and habitat use, contributing to the knowledge on the species' ecology. Additionally, although some attempts have been carried out to determine this species' status and distribution, the investigations have been conducted in restricted areas (providing information only for the specific site where the research was conducted), and information obtained is principally anecdotal and does not provide population estimates.

Much of the lack of information and the PR boa's apparent rarity has been attributed to observer's difficulties in visually detecting the species due to its cryptic coloration and habits. Some authors have established that based on the amount of individuals they found in their study area, and given the species detection difficulty, the PR boa is more abundant than generally perceived. In fact, this species has been reported in about 90% of the municipalities of Puerto

Rico (<http://ecos.fws.indexPublic.do>), and the Puerto Rico GAP Analysis Project illustrates almost the entire Island as having a probable occurrence of boas. In addition, there is a general consensus that the boa is not as rare as previously thought. However, there is still not enough information regarding the islandwide population status of this species. At best, we can state that the PR boa has a widespread distribution and is more common in the karst region of the north-northwest portion of the Island.

According to the five factor analysis performed for this review, the Puerto Rican boa is still threatened by habitat destruction and modification and other manmade factors such as intentional killing for snake oil extraction and general prejudice against snakes, and accidental road kills. Nonetheless, a number of laws and regulations have been approved by the Commonwealth of Puerto Rico in recent years to protect threatened and endangered species, including the PR boa; and to protect the karst region of Puerto Rico where this species has been reported as more commonly found. In addition to these regulatory mechanisms, land in the karst region has been set aside for preservation and acres of agricultural land have been restored through reforestation to provide potential habitat for the species. Certainly the PR boa is widely distributed and has benefitted from the conservation measures previously mentioned and the occurrence of the species on protected land. Nevertheless, there is no current population data or models that support a downlisting recommendation at this time.

### III. RESULTS

#### A. Recommended Classification:

- Downlisting to Threatened
- Uplist to Endangered
- Delist
- No change is needed

**B. New Recovery Priority Number:** 11c. Based on the information gathered and analyzed in the five factor analysis conducted in this review, we believe that the degree of threat is moderate and the species has a high recovery potential.

**C. If applicable, indicate the Listing and Reclassification Priority Number:** N/A

#### IV. RECOMMENDATIONS FOR FUTURE ACTIONS

- a. Conduct quantitative efforts to estimate the relative abundance of the PR boa.
- b. Revise and update the PR boa Recovery Plan with current information on the species and establish delisting criteria.
- c. Investigate the effect habitat loss fragmentation on the PR boa.
- d. Refine habitat description and suitability habitat models for the PR boa based on GAP analysis and other geographical related tools.
- e. Investigate if translocation is an effective tool for protecting the PR boa when jeopardized by habitat destruction.
- f. Promote research on the PR boa through the academia.
- g. Develop public education and outreach programs aimed at reducing the public prejudice against the PR boa.
- h. Develop more cooperative agreements with local partners (i.e., federal and Commonwealth agencies, NGOs, and private landowners) for the conservation and protection of more habitat for the PR boa.

#### V. LITERATURE CITED

- Bird-Picó, F.J. 1994. Final report on *Epicrates inornatus* survey throughout Puerto Rico. Cooperative agreement between the U.S. Department of the Interior, Fish and Wildlife Service and the Department of Biology, University of Puerto Rico, Mayagüez Campus. Cooperative agreement #14-16-0004-92-958. 42pp.
- Grant, C. 1932. Notes on the boas of Puerto Rico and Mona. J. Dept. Agric. Porto Rico 16:327-329.
- Grant, C. 1933. Notes on *Epricrates inornatus* (Reinhardt). Copeia 1933:224-225.
- Gould, W.A., C. Alarcon, B. Fevold, M.E. Jimenez, S. Martinuzzi, G. Potts, M. Quinones, M. Solarzano, E. Ventosa. 2008. The Puerto Rico Gap Análisis Project. Volume 1: Land Cover, Vertebrate Species Distributions, and Land Stewardship. U. S. Department of Agriculture, Forest Service, International Institute of Tropical Forestry. General Technical Report IITF\_GTR-39.
- Henderson, R.W. and R. Powell. 2009. Natural History of West Indian Reptiles and Amphibians. Univ. Press of Florida, Gainesville, FL.

- Huff, T.A. 1978. Breeding the Puerto Rican boa at the Reprtile Breeding Foundation. Int. Zoo. Yrbk. 18:96-97.
- Joglar, R.L. 2005. Reptiles, p. 99 – 190. In: Joglar, R.L. (Ed.) Biodiversidad de Puerto Rico: Vertebrados Terrestres y Ecosistemas. Serie de Historia Natural. Editorial Instituto de Cultura Puertorriqueña, San Juan, P.R. 563pp.
- Joglar, R.L., A.O. Álvarez, T.M. Aide, D. Barber, P.A. Burrowes, M.A. García, A. León-Cardona, A.V. Longo, N. Pérez-Buitrago, A. Puente, N. Ríos-López, and P. Tolson. 2007. Conserving the Puerto Rican herpetofauna. Applied Herpetology 4: 327-345.
- Lugo, A.E., L. Miranda-Castro, A. Vale, T. López, E. Hernández-Prieto, A. García-Martinó, A.R. Puente-Rolón, A.G. Tossas, D.A. McFarlane, T. Miller, A. Rodríguez, J. Lundberg, J. Thomlinson, J. Colón, J.H. Schellekens, O. Ramos, and E. Hunter. 2001. Puerto Rican Karst-A Vital Resource. U.S. Forest Service Gen. Tech Report WO-65. 100pp.
- Moreno, J.A. 1991. Accounts of those species considered to be of concern, p. 9-10. In: J.A. Moreno (ed.). Status y distribución de los reptiles y anfibios de la región de Puerto Rico. Publicación Científica Miscelánea No1. Departamento de Recursos Naturales, San Juan. 67pp.
- Pérez-Rivera, R.A. and M.J. Vélez, Jr. 1978. Notas sobre algunas culebras de Puerto Rico. Science-Ciencia 6(1):68-73.
- Pimentel, D. 1955. Biology of the Indian mongoose in Puerto Rico. J. Mammal. 36:62-68.
- Puente-Rolón, A.R. 1999. Foraging behavior, home range, movement, and activity patterns and habitat characterization of the Puerto Rican boa (*Epicrates inornatus*) at Mata de Plátano Natural Reserve, Arecibo, Puerto Rico. M.S. thesis, University of Puerto Rico, Mayagüez Campus. 62pp.
- Puente-Rolón, A.R. and F.J. Bird-Picó. 2004. Foraging behavior, home range, movements and activity patterns of *Epicrates inornatus* (Boidae) at Mata de Plátano Reserve in Arecibo, Puerto Rico. Caribbean Journal of Science 40(3):343-352.
- Puente-Rolón, A.R. and S.I. Vega-Castillo. 2005. Comments letter to the USFWS. Nov. 14, 2005.
- Reagan, D.P. 1984. Ecology of the Puerto Rican boa (*Epicrates inornatus*) in the Luquillo mountains of Puerto Rico. Caribbean Journal of Science 20 (3-4):119-126.
- Reagan, D.P. and C.P. Zucca. 1982. Inventory of the Puerto Rican boa (*Epicrates inornatus*) in the Caribbean National Forest. CEER T-136, 42 pp.

- Ríos-López, N. and T.M. Aide. 2007. Herpetofaunal dynamics during secondary succession. *Herpetologica* 63(1): 35-50.
- Rivero, J.A. 1998. Los anfibios y reptiles de Puerto Rico. University of Puerto Rico Press, Río Piedras, Puerto Rico. 510 pp.
- Rodríguez-Durán, A. 1996. Foraging ecology of the Puerto Rican boa (*Epicrates inornatus*): bat predation, carrier feeding and piracy. *Journal of Herpetology* 30 (4):533-536.
- Rodríguez, G. and D.P. Reagan. 1984. Bat predation by the Puerto Rican boa (*Epicrates inornatus*). *Copeia* 1984 (1):219-220.
- Schwartz, A. and R. Thomas. 1975. A check-list of West Indian amphibians and reptiles. *Carnegie Mus. Nat. Hist. Spec. Publ.* 1:1-214.
- Schwartz, A. and R.W. Henderson. 1991. Amphibians and reptiles of the West Indies: descriptions, distributions, and natural history. Univ. Florida Press, Gainesville, 720pp.
- Stickel, W.H. and J.B. Cope. 1947. The home ranges and wanderings of snakes. *Copeia* (2):127-135.
- Tolson, P.J. and R.W. Henderson. 1993. The natural history of West Indian boas. R. & A. Publ. Limited, 125pp.
- Wiley, J.W. 2003. Habitat association, size, stomach contents and reproductive conditions of Puerto Rican boas (*Epicrates inornatus*) in a hurricane impacted forest. *Caribbean Journal of Science* 39(2): 189-194.
- Wunderle, J.M., J. Mercado, B. Parresol, and E. Terranova. 2004. Spatial Ecology of Puerto Rican boas (*Epicrates inornatus*). *Biotropica* 36(4): 555-571.
- U.S. Fish and Wildlife Service. 1986. Puerto Rican Boa Recovery Plan. Atlanta, Georgia. 21pp.



## **APPENDIX A: Summary of peer review for the 5-year review of the Puerto Rican boa (*Epicrates inornatus*)**

Marelisa T. Rivera, CESFO Deputy Field Supervisor, reviewed this 5-year review internally and provided editorial and technical comments that were included in the document. Additionally, we sent this 5-year review to four outside peer reviewers (see below). Reviewers were selected based on their qualifications and knowledge of the species. We indicated our interest in all comments the reviewers may have had on the PR boa, particularly any new information on the status and current threats to the species. We did not ask peer reviewers to comment on the listing classification of the species.

Only one of the independent peer reviewers, Mr. Alberto Puente-Rolón, answered our request. Most comments and recommendations provided Mr. Puente -Rolón were incorporated into the document and cited accordingly. The reference of these peer review comments was included in the Literature Cited section of the 5-year review and is available in the file of the Puerto Rican boa in our office.

### **List of Peer Reviewers**

Mr. Alberto Puente-Rolón, MS  
President  
Iniciativa Herpetológica, Inc.  
P.O. Box 1112  
Ciales, Puerto Rico 00638  
E-mail: [albertonski@hotmail.com](mailto:albertonski@hotmail.com)

Miguel A. García, Ph.D.  
Director  
Bureau of Fish and Wildlife  
Department of Natural and Environmental Resources  
P.O. Box 366147  
San Juan, Puerto Rico 00936  
E-mail: [magarcia@drna.gobierno.pr](mailto:magarcia@drna.gobierno.pr)

Neftalí Ríos-López, Ph.D.  
University of Puerto Rico  
Humacao Campus  
Department of Biology  
CUH Station  
Humacao, Puerto Rico 00791  
E-mail: [neftalirios@yahoo.com](mailto:neftalirios@yahoo.com)

Fernando Bird-Picó, Ph.D.  
University of Puerto Rico  
Mayagüez Campus  
Department of Biology  
P.O. Box 9000  
Mayagüez, Puerto Rico 00681  
E-mail: [fbird@uprm.edu](mailto:fbird@uprm.edu)



Figure 1. Municipalities, forests, natural reserves, and karst regions within the island of Puerto Rico

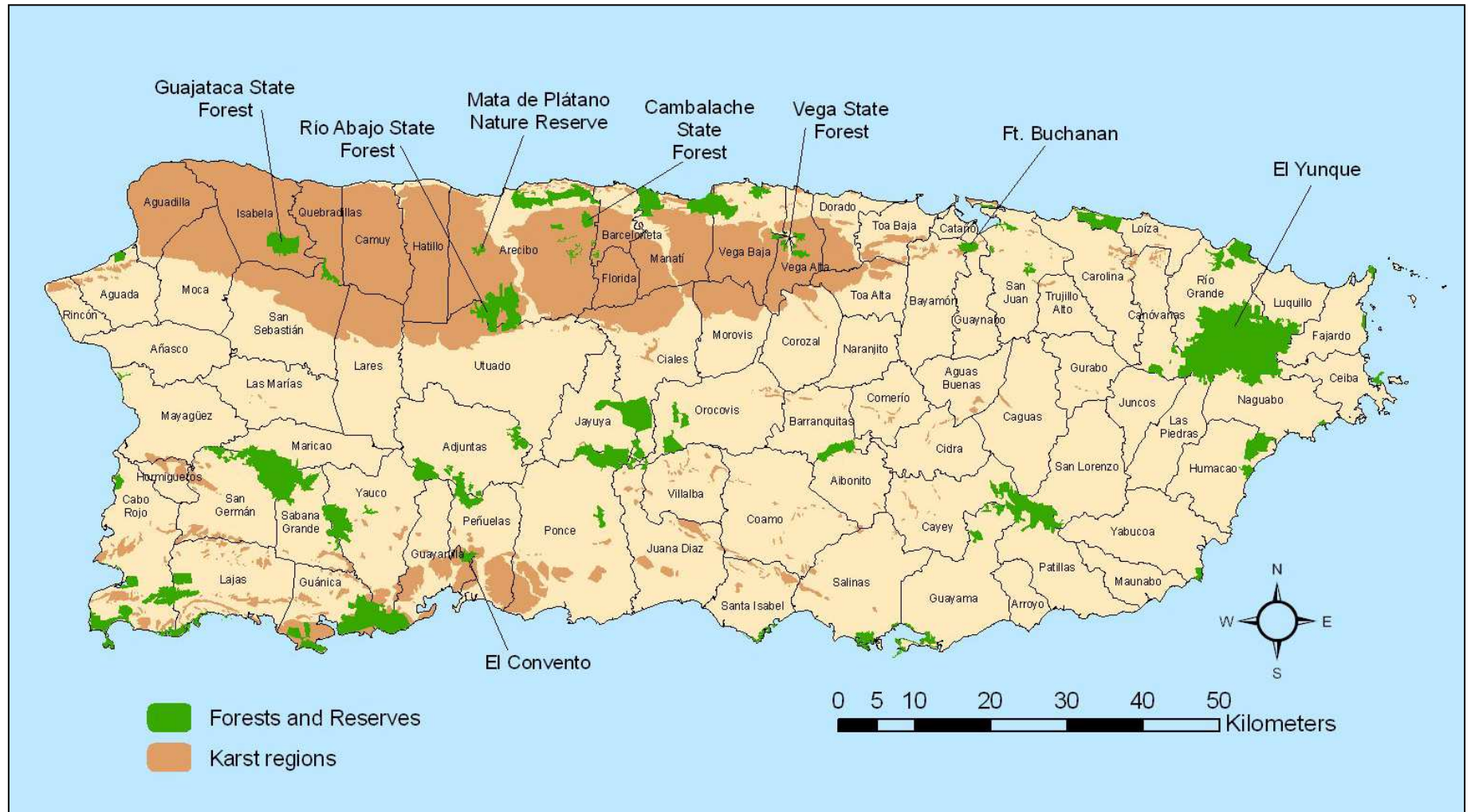


Figure 2. GAP Puerto Rican boa hexagon occurrence map (Gould *et al.* 2008).

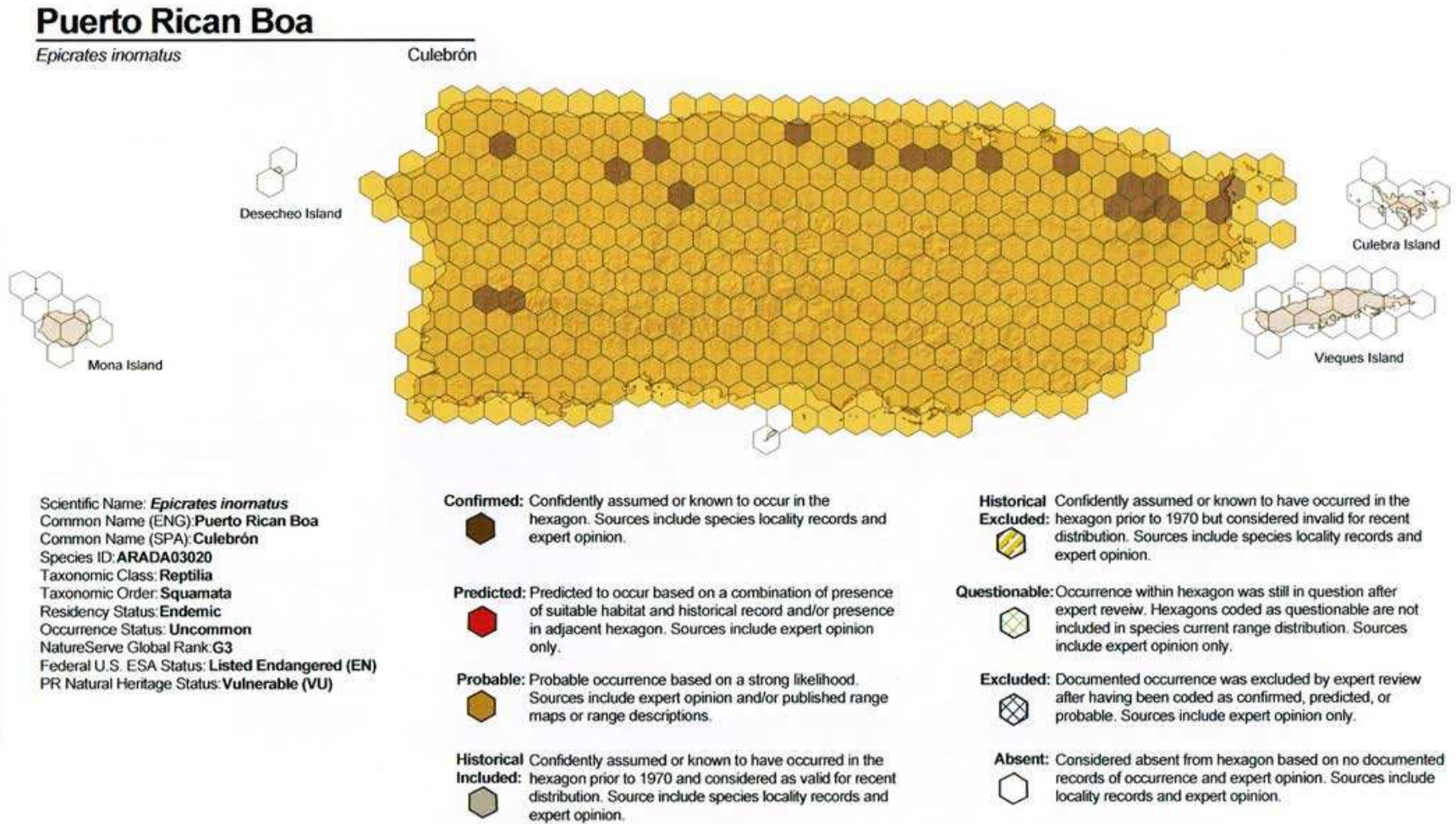
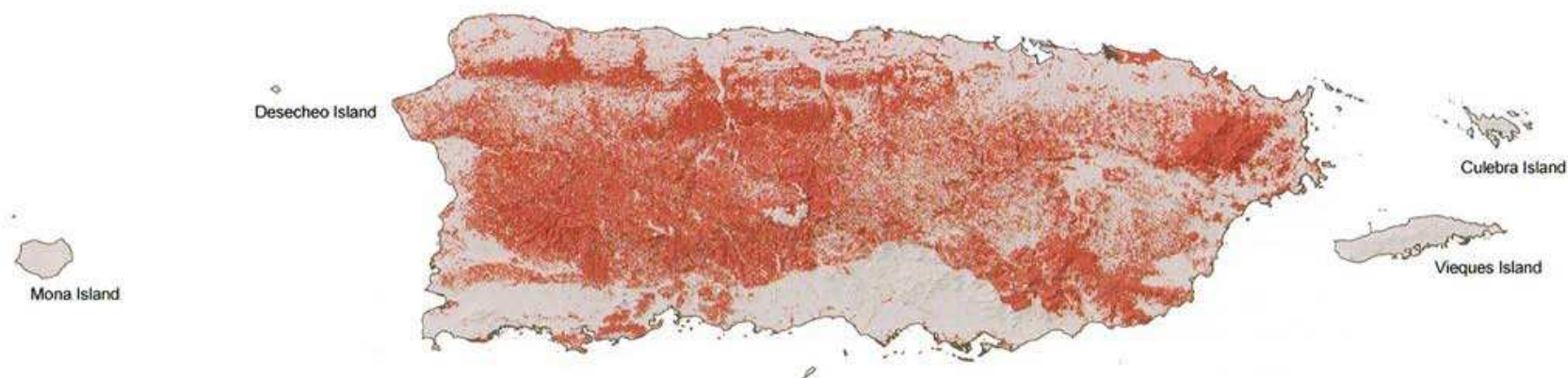


Figure 3. GAP Puerto Rican boa predicted distribution map (Gould *et al.* 2008).

## Puerto Rican Boa

*Epicrates inornatus*

Culebrón




Scientific Name: *Epicrates inornatus*  
 Common Name (ENG): Puerto Rican Boa  
 Common Name (SPA): Culebrón  
 Species ID: ARADA03020  
 Taxonomic Class: Reptilia  
 Taxonomic Order: Squamata  
 Residency Status: Endemic  
 Occurrence Status: Uncommon  
 NatureServe Global Rank: G3  
 Federal U.S. ESA Status: Listed Endangered (EN)  
 PR Natural Heritage Status: Vulnerable (VU)



Photo courtesy of Javier Mercado

### Species Predicted Habitat:

 Predicted habitat model includes the following land cover types: moist and wet forest, woodland, and shrubland mangrove, *Pterocarpus*, and mature dry forest and dry forest near water bodies, at or below 1000 m of elevation. This species habitat includes 46.3% (414379 ha) of the island, of which 9% occurs in protected areas (PRGAP Status 1 and 2).

### Species Accounts Summary:

The Puerto Rican boa is more commonly found in the northern lime stone karsts belt extending from the town of Bayamón west to Aguadilla and less abundant in the dry southern region<sup>1</sup>, although there are collection records from towns of Cabo Rojo, Lajas, Ponce, Salinas, and Guayama<sup>1</sup>. For this reason, it is believed that this boa is widespread in its mainland distribution<sup>3</sup>. It occupies wet montane forest to dry forest environments<sup>1</sup> and also lowland wet forest, mangrove forest, wet limestone karst, and offshore cays, remnant coastal rainforest, pastureland with patches of exotic trees, tabonuco and palo colorado forest types, plantations, and second-growth forests<sup>3</sup>. It is known to feed on domestic fowl, bath, rodents, lizards, insects, and other invertebrates<sup>1,2</sup>.

1. Rivero, J.A. 1998. Los anfibios y reptiles de Puerto Rico/The amphibians and reptiles of Puerto Rico. Segunda Ed. Universidad de Puerto Rico, Editorial Universitaria, San Juan, Puerto Rico. 510 p.
2. Schwartz, A. and W.R. Henderson 1991. Amphibians and reptiles of the West Indies. Descriptions, distributions, and natural history. Gainesville, FL: Univ. Press Florida, 720 p.
3. Wiley, W. James. 2003 Habitat association, size, stomach contents, and reproductive condition of Puerto Rico boas (*Epicrates inornatus*). Caribbean Journal of Science. 39(2): 189-194.