Demography of the Puerto Rican Racer, *Borikenophis portoricensis* (Squamata: Dipsadidae), on Guana Island, British Virgin Islands

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Abstract.—Guana is a 297-ha island in the British Virgin Islands, a private wildlife sanctuary where human activity is largely restricted to small areas associated with an upscale resort hotel. Guana is free of mongooses and sustains a population of racers (*Borikenophis portoricensis*; Dipsadidae). Between 2001 and 2012 we marked *B. portoricensis* with Trovan passive integrated transponders and recorded 394 captures of 367 unique adults (males = 167; females = 200; sex ratio of 0.8 : 1) in an effective trapping area of 25.8 ha. Using contemporary capture–recapture models, we estimated annual adult apparent survival, abundance, and realized population growth. We detected no difference in apparent adult annual survival of males (0.50, 95% confidence interval [CI] = 0.34–0.66) and females (0.50, 95% CI = 0.33–0.66). Recapture probabilities of males (0.09, 95% CI = 0.04–0.18) and females (0.08, 95% CI = 0.04–0.16) were similarly indistinguishable. Annual estimates of adult abundance ranged from 368 to 540, but confidence intervals overlapped broadly between years. We estimated realized population growth as 0.98 (95% CI = 0.75–1.28) over the 12-yr study. Based on the effective trapping area (25.8 ha), average density was 19 adults/ha (range = 14–21 adults/ha). The low recapture probabilities suggest that animals spend much of their lives in areas not accessible to researchers, but we detected little evidence of substantive movement. The population on Guana appears to be healthy, suggesting that declines elsewhere are indeed the results of human activities, especially the introduction of mongooses.

At least 150 snake species occur in the West Indies (145 are endemic), but knowledge of actual conservation status is lacking for all but about 30 of those species. Despite the lack of specific information, the introduction of exotic predators clearly is one of the primary factors adversely affecting snake populations throughout the region (Tolson and Henderson, 2011). In particular, Antillean racers (Dipsadidae) do not fare well on islands also inhabited by the introduced mongoose, *Urva auropunctata*. Mongooses were introduced to West Indian islands by the owners of sugar plantations to control *Rattus* populations. The first introduction occurred on Jamaica in 1872, but other islands soon followed Jamaica's example (Hoagland et al., 1989; Henderson, 1992; Hedges and Conn, 2012). Species of *Alsophis*, *Borikenophis*, and *Erythrolamprus* have several behavioral and ecological traits in common: They are of moderate size (usually <1.0 m snout–vent length [SVL]), largely ground-dwelling, diurnal, cryptic, fast-moving, oviparous, and feed mainly on lizards and small frogs (Henderson and Powell, 2009). Several of those characteristics make them vulnerable to mongoose predation and their plight is well documented (e.g., Sajdak and Henderson, 1991; Henderson, 2004; Henderson and Powell, 2009; Caut and Jowers, 2016). Extirpations and extinctions have occurred on multiple Caribbean islands (Table 1). The seven species of *Alsophis* have suffered at least four island-level extirpations (*Alsophis antiguae* on Antigua, *Alsophis antillensis* on Marie-Galante, *Alsophis rufiventris* on St. Christopher and on Nevis, and possibly *Alsophis rijgersmaei* on St. Martin). Two of four species of *Erythrolamprus*, *Erythrolamprus cursor* and *Erythrolamprus perfuscus,* are presumed extinct, and at least one (*Erythrolamprus ornatus* on Martinique) and possibly three (*Erythrolamprus juliae* on Guadeloupe and Marie-Galante) additional island populations have been extirpated. Of three

species of *Borikenophis*, one (*Borikenophis sanctaecrucis*) is extinct, and *Borikenophis portoricensis* has suffered at least three island-wide extirpations. In sharp contrast to their inability to survive on mongoose-infected islands, racers can be abundant on mongoose-free islands, either in localized habitats or, in some cases, island-wide.

Considering their tenuous circumstances, we know remarkably little regarding the natural history of West Indian racers. The most ambitious work to date has addressed *A. antiguae* on islands satellite to Antigua where the species had been extirpated. Daltry et al. (2003, 2017) provided information on *A. antiguae* abundance and adult and subadult survivorship/mortality. In contrast, we have only a smattering of natural history information regarding other species of *Alsophis* and *Erythrolamprus*. These are based on short-term projects, fortuitous observations, or museum specimens.

Borikenophis portoricensis is widely distributed on the Puerto Rico Bank, where it occurs on about 45 islands, and is one of the most-studied snakes in the West Indies. Aspects of its natural history were summarized by Henderson and Powell (2009, and papers cited therein): It occurs in habitats ranging from xeric scrub to rainforest, as well as heavily disturbed situations; it is primarily ground-dwelling, but will ascend into trees; it actively forages and often uses venom to subdue prey; its diet consists primarily of a wide taxonomic range of lizards, but also includes small frogs, snakes, birds, and mammals; it is oviparous. In addition to mongooses, raptors and house cats are also known predators (Tolson, 1988; Henderson and Powell, 2009). Little is known about the population biology of *B. portoricensis*, although Rodda et al. (2001), Lazell (2005), and Rios-López and Aide (2007) provided short-term abundance or population density estimates. Here we present the results of a capture–recapture study conducted over a 12-yr period, with a focus on population parameters of *B. portoricensis* on a mongoose-free island. These data provide important baseline

TABLE 1. The likely impact of mongoose introductions on West Indian racers. With the exception of *Erythrolamprus*, the other genera were previously under the generic umbrella of *Alsophis* (Hedges et al., 2009). *Hypsirhynchus* is currently comprised of seven species, but only two were formerly in the genus *Alsophis* and both of those species (*Hypsirhynchus ater* and *Hypsirhynchus melanichnus*) are presumed extinct. Data were gleaned from Henderson and Powell (2009).

Distribution	*Alsophis* Lesser Antilles	*Borikenophis* Puerto Rico and St. Croix Banks	*Cubophis* Bahamas, Cuba, Cayman Islands	*Haitiophis* Hispaniola	*Hypsirhynchus* Hispaniola, Jamaica	*Erythrolamprus* Lesser Antilles
No. of species	7	3	5	1	7	4
No. of extinctions	0	1	0	0	2	2
No. of extirpations	4–5	3	1	0	0	1–3

information and reveal insights into what island populations may have been like prior to the human introduction of invasive predators.

MATERIALS AND METHODS

Study Site and Collecting Effort.—Guana Island (18°38′N, 65°25′W) is one of the British Virgin Islands (B.V.I.) and is on the Puerto Rico Bank; it has a total area of 297 ha. It is a private wildlife sanctuary where human activity is largely restricted to small portions of the island associated with an upscale resort hotel. Although mongoose-free, a small number of feral cats persist on the island despite efforts to eradicate them. Additional descriptions of Guana, including habitat, appear in Lazell (2005) and Barun et al. (2007).

The distribution of *Borikenophis portoricensis* on Guana is island-wide. Searches were made on foot, usually along trails but not restricted to them, and individuals from throughout the island were captured by hand and marked. Many of those snakes were opportunistically captured as a courtesy by researchers working on other projects. Snake-dedicated searches were concentrated in a core area of 12.75 ha (Fig. 1). We conducted searches throughout the day, from about 0800 h until about 1800 h. We occasionally encountered snakes after dark as
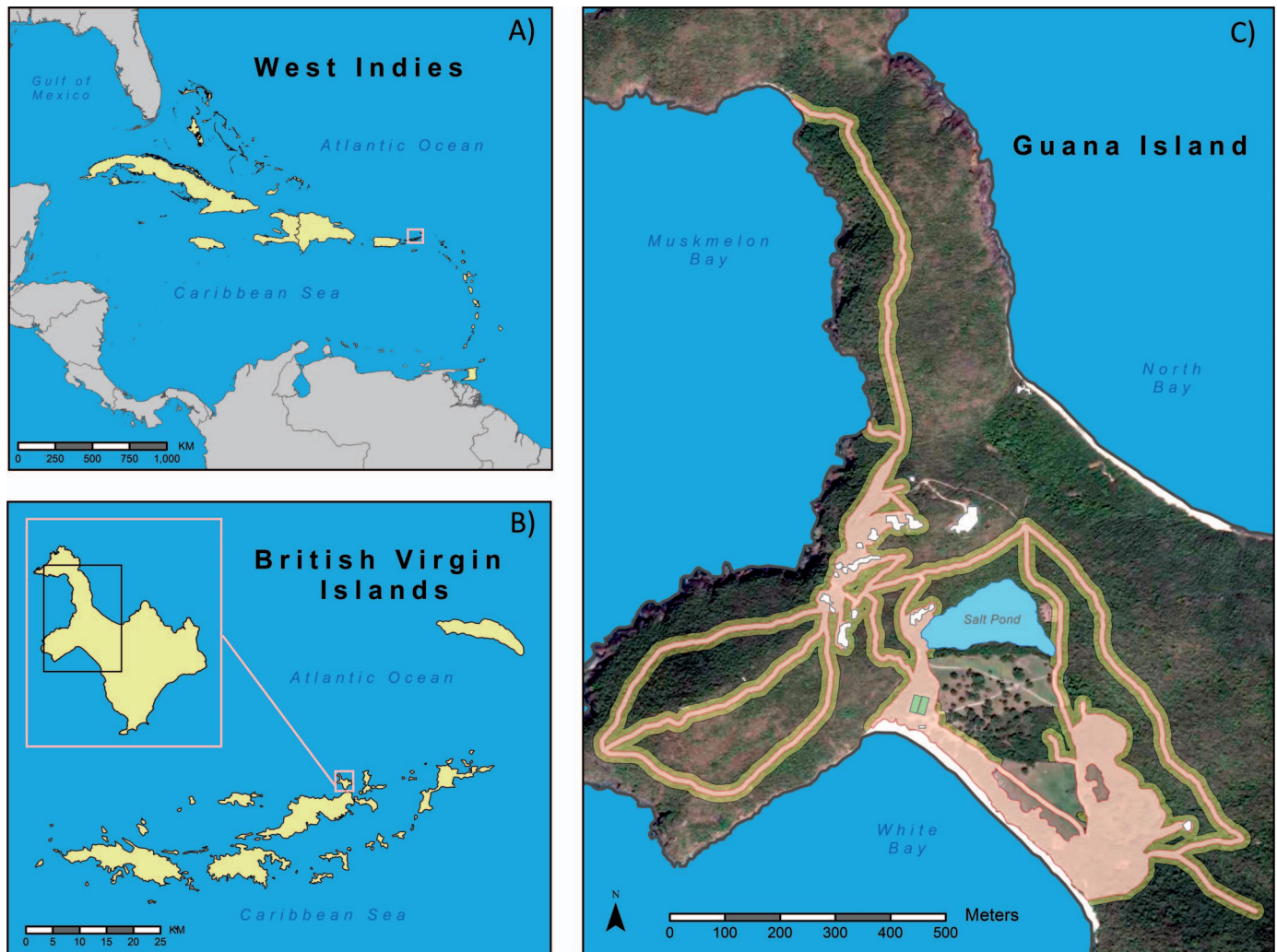

FIG. 1. The location of Guana Island in the (A) West Indies and (B) in the British Virgin Islands. (C) The core area (with buffer strip) of the *Borikenophis portoricensis* study site.

TABLE 2. Candidate models considered for adult apparent survival (CJS), abundance (POPAN), and realized population growth (Pradel) analyses. ΔAICc is the difference in AICc between the top ranked model and the next competing model. w_i is the model weight, which must sum to one for a given candidate set. K is the number of parameters for a given model. Deviance is the difference in $-2 \log(\mathcal{L})$ of the current model and $-2 \log(\mathcal{L})$ of the saturated model. Notation: (.), constant; (sex), sex effect; (t), time effect; (t-constrained), time-constrained effect.

Analysis	Model	AICc	ΔAICc	w_i	K	Deviance
CJS	Φ (.) p (.)	257.45	0.00	0.49	2	71.87
	Φ (.) p (sex)	258.92	1.47	0.23	3	71.31
	Φ (sex) p (.)	259.31	1.86	0.19	3	71.70
	Φ (sex) p (sex)	260.86	3.41	0.09	4	71.20
Popan	Φ (.) p (t-constrained) Pent (t)	334.35	0.00	1.00	16	−1,531.34
	Φ (.) p (t) Pent (t)	347.31	12.95	0.00	23	−1,533.93
	Φ (.) p (.) Pent (t)	350.77	16.42	0.00	13	−1,508.44
Pradel	Φ (0.50) p (t) λ (.)	894.82	0.00	1.00	12	36.39
	Φ (0.50) p (t) λ (t)	910.51	15.69	0.00	21	30.13

they hunted near night lights that attracted anoles seeking night-active insects (Perry and Lazell, 2000). Details of *B. portoricensis* morphometrics, activity patterns, and habitat use on Guana appear in Barun et al. (2007).

The project was carried out during the month of October during 2001–2012, with a hiatus in 2002 and intensive effort ending in 2008. Racers were captured fortuitously during the entire month, but sampling efforts varied from year to year. We marked over 600 *B. portoricensis* of all age/size classes except hatchlings. For each snake, we recorded sex, SVL, tail length, and mass. We also examined all snakes for scars. We marked each snake subcutaneously with a Trovan passive integrated transponder (PIT tag; 2.1 × 11.5 mm) and released it within 24 h at its capture site. As satellite reception on Guana was poor, we used landmark descriptions for a subset of capture locations (*n* = 24) to approximate Cartesian coordinates of snake captures with ArcGIS 10.3 (ESRI, Redlands, California, USA). We used these data to calculate a within-year mean maximum distance moved (1/2 MMDM; Wilson and Anderson, 1985) so that we could estimate an effective trapping area (i.e., our core sampling area plus a buffer).

Statistical Methods.—To determine the minimum size of sexually mature snakes, we dissected a series of 20 *B. portoricensis* from Puerto Rico and the Virgin Islands to determine their reproductive status. Based on those data, we considered males ≥542 mm SVL and females ≥513 mm SVL to be adults. We modeled population parameters using program MARK version 8.0 including only adults as defined above (White and Burnham, 1999). For model selection, we used an information-theoretic approach and Akaike's information criterion adjusted for small sample size (AIC$_c$; Akaike, 1973; Burnham and Anderson, 2002). We used model averaging and unconditional standard errors to account for model selection uncertainty unless the top-ranked model garnered 100% of the model weight (Burnham and Anderson, 2002). We used profile likelihoods to estimate 95% confidence intervals. Descriptive statistics are presented as means ± SD.

Apparent Survival.—We estimated annual adult apparent survival using the Cormack-Jolly-Seber model (CJS; Cormack, 1964; Jolly, 1965; Seber, 1965). This model estimates the fundamental parameters apparent survival (Φ) and recapture probability (p) by conditioning on captured animals. Survival is termed "apparent," because emigration is assumed to be permanent and is therefore confounded with mortality. Because of data sparseness, we included sex effects on apparent survival and recapture probability, but did not consider time effects for either parameter. This resulted in four candidate models (Table 2). We tested the global model of Φ (sex) p (sex) for adequate fit

using the deviance goodness-of-fit bootstrap method (1,000 simulations) in Program MARK (White and Burnham, 1999). We considered a goodness-of-fit *P* value ≥0.15 to meet the independent and identically distributed (*iid*) statistical assumptions adequately (Burnham and Anderson, 2002).

Abundance.—We estimated adult population size via the open population estimator Popan (Schwarz and Arnason, 1996). In this model, abundance at time *i* (N_i) is derived from estimates of apparent survival (Φ), capture probability (p), and the probability of entrance (PENT), which are estimated using maximum-likelihood theory (Schwarz and Arnason, 1996). Apparent survival (Φ) and capture probabilities (p) are similar to those in the CJS model, but are conditioned on both the marked and unmarked population. The probability of entrance can be interpreted as adult immigration and recruitment of juveniles into the adult age class. We restricted analysis to animals captured within the core sampling area so that estimates of abundance would be comparable across years. Based on results from our CJS analysis, we did not consider sex effects for our global model, but allowed capture and PENT probabilities to vary by time. We considered two additional models that were nested within our global model (Table 2). One model treated capture probabilities as constant over time. The other model constrained capture probabilities to be equal for years in which the number of unique captured snakes was similar. This resulted in four levels of capture probabilities: Level 1 treated years 2001, 2004, and 2010 as equal; level 2 treated years 2003 and 2005–2008 as equal; level 3 treated years 2009 and 2010 as equal; and level 4 included only 2012. This time-constrained model reduced the number of estimated capture probabilities from 11 (i.e., in the global model) to 4.

Realized Population Growth.—To estimate realized population growth, we used the Pradel model (Pradel, 1996). The Pradel model estimates realized population growth (λ) by simultaneously estimating apparent survival (Φ) and capture probability (p) and reading capture histories in reverse. We fixed Φ to the value estimated from the CJS analysis to reduce the number of parameters to be estimated. For this analysis, we were interested in λ, rather than Φ or p, so we maintained time-dependence for p and considered two models where λ was either time-dependent or time-constrained (Franklin, 2001).

RESULTS

Within the core research area from 2001–2012, we recorded 394 captures of 367 unique adults (males = 167; females = 200; sex ratio of 0.8 : 1). The range of SVLs for adult males was 542–855 mm (mean = 605.6 ± 43.8 mm) and for females 513–571
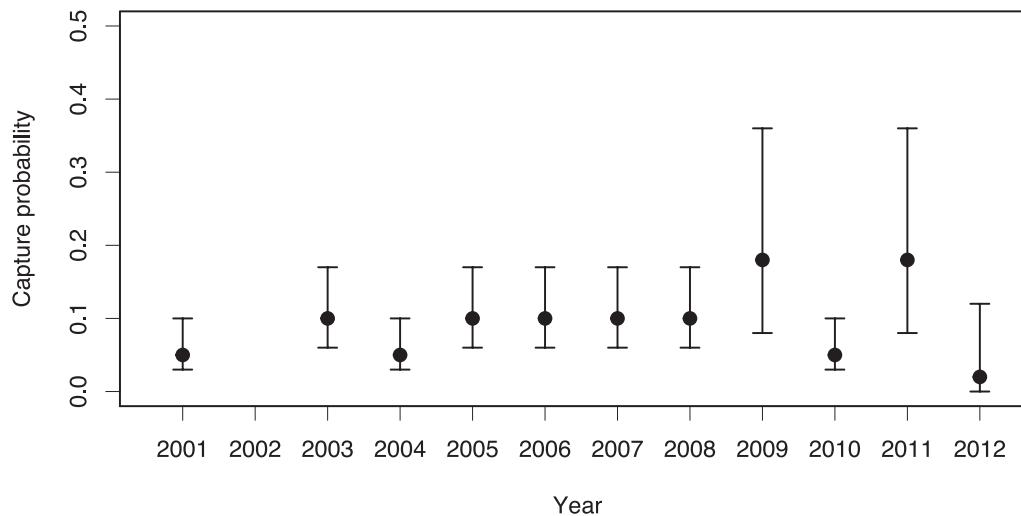
FIG. 2. Annual adult capture probabilities for *Borikenophis portoricensis* resulting from the top-ranked model in the Popan analysis. No surveys were conducted in 2002.

mm (mean = 580.6 ± 33 mm). Recaptures were surprisingly low for both males ($n = 14$) and females ($n = 13$). Recaptures almost always occurred within 10–30 m of the original site of capture.

Apparent Survival.—The deviance bootstrapped statistic revealed no evidence of violating the *iid* assumptions for the global model Φ (sex) p (sex) ($P = 0.68$). Therefore, we assumed no overdispersion and set the variance inflation factor to 1. Our top-ranked model garnered 49% of the model weight (w_i) and treated apparent survival and recapture probabilities as constant (Table 2). We detected no measurable difference in adult annual apparent survival between males (0.50, 95% confidence interval [CI] = 0.34–0.66) and females (0.50, 95% CI = 0.33–0.66). Similarly, we detected no measurable difference in adult recapture probabilities between males (0.09, 95% CI = 0.04–0.18) and females (0.08, 95% CI = 0.04–0.16).

Abundance.—From 2001 to 2012, the number of unique individuals captured per year ranged from 2 to 56 individuals. Capture probabilities were low in all years but varied across time (0.02–0.18; Fig. 2). The lowest capture probabilities were in 2012 (0.02); the highest occurred in 2009 and 2010 (0.18; Fig. 2). Our top-ranked model received 100% w_i and included time-constrained effects for capture probabilities (Table 2). Years with <12 unique captures (2004 and 2012) or uneven sampling efforts (2009 and 2011) produced unrealistically low estimates of abundance and are not reported (Table 3). Annual estimates of adult

TABLE 3. Unique number of individuals captured (M_t), abundance estimates ($\hat{N}$), and 95% confidence intervals for adults for a given year. Estimates are based on the top ranked Popan model from Table 2.

Year	M_t	$\hat{N}$	95% CI
2001	19	368	168–805
2003	55	527	316–878
2004	12	–	–
2005	45	443	254–773
2006	54	540	315–927
2007	56	529	310–905
2008	53	511	312–837
2009	39	–	–
2010	23	449	252–800
2011	36	–	–
2012	2	–	–

abundance within the core study area ranged from 368 to 540, but confidence intervals overlapped broadly between years (Table 3).

Realized Population Growth.—The model that constrained time for λ received 100% of the model weight (Table 2). This resulted in a realized population growth estimate of 0.98 and 95% CI = 0.75–1.28.

DISCUSSION

Because of their secretive habits, snakes are among the most difficult vertebrates to study under natural conditions (e.g., Mazerolle et al., 2007; Steen, 2010). Consequently, our understanding of snake ecology, especially population biology, is lacking for a majority of species, making it difficult to determine if and when conservation actions are warranted (Dorcas and Willson, 2009). Information on population dynamics is conspicuously lacking for West Indian species and for those that occur on the Neotropical mainland. The latter might reflect apparent low population densities; islands, where population densities are frequently high, however, can provide opportunities to gather information that is otherwise difficult or impossible to collect (e.g., Shine, 1987; Henderson, 2015). With the addition of this study, data are now available for eight Neotropical species that occur on islands and that represent three families and seven genera (Table 4).

Borikenophis portoricensis was ubiquitous on Guana, utilizing all major vegetative associations, landscaped areas, and built-up environments (including walkways and the outdoor dining area of the resort hotel). Although we marked more than 600 snakes (including individuals outside of the core sampling area), some we saw eluded capture as they were frequently moving when first observed. Furthermore, we are confident that we failed to detect some snakes near survey paths. The maximum-likelihood methods we used for our capture–recapture analyses are asymptotically unbiased with large sample sizes, but can result in biased estimates if sample sizes are small (Edwards, 1992). Given our small sample size for recaptures, our estimates of abundance may be underestimated.

The low adult capture probabilities were disappointing, but not unexpected (Fig. 2). We attribute the low recapture probabilities to large population size and relatively high annual

TABLE 4. Abundance and/or density estimates for species of snakes on islands in the Neotropics. L-P = Lincoln-Petersen index.

Species	Island(s) (size)	Abundance, density	Source and method
Boidae			
Boa imperator	Cays off Belize (4.52–24 ha)	8–88, 0.5–16.4/ha	Boback (2005); L-P with Chapman's modification
Boa imperator	Cayo Cochino Pequeño, Honduras (64 ha)	632 ± 143	Reed et al. (2007); L-P
Chilabothrus c. chrysogaster	Big Ambergris Cay, Turks & Caicos (400 ha)	2,241 ± 711	Reynolds and Gerber (2012); *Mt*-model
Chilabothrus granti	Cayo Diablo, Puerto Rico Bank (2 ha)	>100/ha	Tolson (1988); not specified
Corallus grenadensis	Grenada (several sites)	~4–36/ha	Henderson (2015); uncorrected count data
Dipsadidae			
Alsophis antiguae	Great Bird Island, Antigua (8.4 ha)	169.5 ± 0.9, 20.2/ha	Daltry et al. (2017); Begon's weighted mean and simulations with the use of software VORTEX; all age classes
Borikenophis portoricensis	Puerto Rico	5.6–11.1/ha	Rios-López and Aide (2007); uncorrected count data
Borikenophis portoricensis	Guana, B.V.I. (297 ha)	50/ha	Rodda et al. (2001); removal plots
Borikenophis portoricensis	Guana, B.V.I. (297 ha)	368–540 adults; ~19 adults/ha	Present study; Popan
Erythrolamprus ornatus	Maria Major, St. Lucia (9.4 ha)	17.8 ± 9.94 adults and subadults; island population <50	Williams et al. (2016); Begon's weighted mean
Viperidae			
Bothrops insularis	Queimada Grande Island, Brazil (43 ha)	55/ha	Martins et al. (2008); plot sampling
Bothrops insularis	Queimada Grande Island, Brazil (43 ha)	80–218 adults	Guimarães et al. (2014); Huggins closed capture

apparent mortality (0.50). Likely predators of the racers included soldier crabs (*Coenobita clypeatus*), birds, and rats (e.g., Daltry, 2006; Barun et al., 2007). Although the snakes are not persecuted on Guana, vehicles and mowers undoubtedly killed some racers on roads and in cleared areas, respectively; however, both road activity and mowing are infrequent, limited to small parts of the island, and unlikely to have population consequences. Despite the moderately high adult apparent mortality, our realized population growth estimate (0.98, 95% CI = 0.75–1.28) suggests a stable population size during the 12-yr study. If the population is stable, this may be due in part to the fact that our study site is not a closed system. Immigrants from outside of the focal area, along with recruitment, may help compensate for the relatively high adult turnover.

Apparent Survival.—Our survival estimates are toward the low end of values reported for temperate snakes (*Drymarchon*, *Lampropeltis*, *Thamnophis*; Hileman et al., 2015). This might be attributable, at least in part, to the active foraging mode employed by *B. portoricensis*, as active foragers are potentially more conspicuous and at greater risk of predation (e.g., Secor, 1995; Webb et al., 2003). The incidence of tail damage was high in males (69%) and females (74%), as was scarring on the body (52.7% in males, 53.3% in females; Barun et al., 2007). If a sizable number of individuals temporarily left the area over the course of the study, the low apparent survival also could be due to temporary emigration, which the CJS model does not allow (Williams et al., 2002). Such transient effects can be modeled, but were not considered here due to data sparseness (Williams et al., 2002). Although we observed no obvious differences between the sexes in terms of apparent survival, higher female mortality resulting from reproductive costs has been found in other oviparous snakes (Sperry and Weatherhead, 2009).

Abundance.—Comparisons of abundance estimates among sites are meaningless without reference to the size of the study area.

Adding 1/2MMDM as a buffer strip to the perimeter of our core sampling area (12.75 ha) resulted in an effective trapping area of 25.8 ha and an average density estimate of 19 adults/ha (range =14–21 adults/ha). Our density estimates are higher than those reported for the same species at a site in northern Puerto Rico. Stratified by habitat, density estimates of *B. portoricensis* were 5.6/ha for a reforested valley, 5.6/ha on a karst hilltop, and 11.1/ha on a karst hillside (Rios-López and Aide, 2007). Those authors used raw counts of all individuals, however, rather than detection-corrected estimates of adult abundance, and did not account for an edge effect. Moreover, predation on Puerto Rico, where the mongoose has been introduced, is likely to be considerably higher than on Guana. Therefore, comparisons between studies might not be appropriate.

On Guana, Rodda et al. (2001) sampled four 10 × 10–m plots by first removing all vegetation and then capturing all vertebrates. Racers were absent from two *Coccoloba* plots (although we frequently observed racers in such associations), but they found seven racers in two plots of early successional forest (*Leucaena* and *Acacia*). They estimated a density of 50 *B. portoricensis*/ha of all size classes in the *Leucaena* habitat, and suggested this was probably an underestimate. Our density estimate is much lower but is based only on sexually mature individuals across a variety of habitats. Similarly, our density estimate might not be comparable to that of the racer *Alsophis antiguae* on Great Bird Island (Table 4), because the latter included subadults as well as adults.

Based on several estimates of racer abundance (including that of Rodda et al., 2001), Lazell (2005) suggested that about 1,000 *B. portoricensis* occurred on Guana and that they occupied about 200 ha. Our abundance data (368–540 snakes on 25.8 ha), extrapolated to the entire island, would far exceed Lazell's estimate. Such numbers on Guana, at least in part, are facilitated by phenomenal lizard prey densities. The removal plot study by

Rodda et al. (2001) provided density estimates (ha^{-1}) of 200 *Ameiva exsul*, 1,000–1,100 *Anolis cristatellus*, 600–900 *A. stratulus*, and 13,400–52,800 *Sphaerodactylus macrolepis*.

Guana, like most West Indian islands, has had a shared history with humans; however, human-mediated habitat perturbations on the island likely have been intermittent and perhaps ephemeral. Based on a summary by Lazell (2005), the physical evidence of hunter-gatherers on Guana occurred sometime during 2000–1500 years before present (ybp) to about 1100–800 ybp. This was followed by an apparent hiatus in human occupancy that lasted until 1743–59, when several Quaker families settled on the island and partially cleared it for sugarcane cultivation. A surge of deforestation for charcoal production occurred in the B.V.I. around 1820, but we do not know to what extent Guana was affected. Although mongooses had been introduced to nearby Tortola by 1900 (Hoagland et al., 1989), the owners of Guana fortunately saw no reason to introduce them to their island. Consequently, Guana appears to have been free of major habitat alterations since the mid-18th century and may sustain a natural environment as close to that of the pre-Columbian West Indies as any island in the Eastern Caribbean. Whether racer numbers on Guana are now comparable to those of the pre-mongoose B.V.I. 250 yr ago, or even to those of the pre-Columbian B.V.I., is food for pleasant speculation.

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