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Living in the City: Reproductive and Population Ecology of Green Iguanas, *Iguana iguana* (Linnaeus 1758), in an Urban Landscape in Colombia

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Abstract.—Understanding how species persist in urban landscapes can provide insights into the fate of biodiversity affected by rapid and unplanned urbanization. While the ecological and conservation implications of urbanization have been reasonably well studied for temperate species, relatively little is known for those in tropical latitudes, especially Neotropical lizards. We investigated the life history, habitat use, and reproductive seasonality of Green Iguanas (*Iguana iguana*) inhabiting an urban area in Colombia. Our analysis of age structure showed that the sex ratio in this population was approximately 1:1 at birth and adulthood, suggesting that both sexes are experiencing similar selective pressures over time. The presence of individuals of all size classes throughout the year is indicative of a stable population. Density estimates based on linear transect data indicated that iguanas in the studied population occur at higher densities than those in rural areas. This increased density might be related to some benefits of urbanization, including human trophic subsidies and decreased predation and competence. The estimated growth rate was also higher than those reported for populations in natural habitats, likely reflecting increased food availability. Iguanas in the study area apparently reproduce twice per year, a pattern that might be explained by rainfall regime. Occupancy modeling revealed that contrary to rural populations, urban green iguanas successfully exploit open grassy areas for feeding and basking, with tree cover and built-up areas being key predictors of their occurrence. The ability of urban iguanas to modify some traits of their basic ecology to cope with the challenges imposed by urbanization may be crucial for this species to persist or even thrive in cityscapes.

Urbanization is a growing global phenomenon that exposes wildlife to novel conditions that differ radically from those in their natural environments (Grimm et al. 2008; Birnie-Gauvin et al. 2016; Ouyang et al. 2018; Batabyal and Thaker 2019). Urban habitats are hostile for most species as they impose strong selection pressures that challenge individual survival and population persistence (Ouyang et al. 2018; de Andrade 2020; Vanek et al. 2019; Tiatragul et al. 2020). Indeed, urbanization is expected to act as an ecological filter for most species (McKinney 2008; Shochat et al. 2006; de Andrade 2020), but in some cases cityscapes can introduce wildlife to novel resources and habitat conditions (e.g., abundant food, new supplementary habitats, and reduction in predation risk) that could result in ideal situations for populations of some species (e.g., Francis and Chadwick 2012; Møller et al. 2012; Eötvös et al. 2018; de Andrade 2020; Putman and Tippie 2020). Understanding how species can persist in urban landscapes is therefore crucial for predicting and mitigating future biodiversity loss due to human-driven modifications of natural habitats (Dirzo et al. 2014; Vanek et al. 2019; de Andrade 2020; Putman and Tippie 2020).

Studies of organisms responding to urbanization are centered primarily on birds and mammals in temperate regions (de Andrade 2020; Putman and Tippie 2020; Zuñiga-Palacios et al. 2021). Species inhabiting cityscapes are expected to display rapid responses to novel conditions via plasticity or flexibility in morphology, physiology, and behavior (Lapiedra 2018; Batabyal and Thaker 2019; Tiatragul et al. 2020). The ability to cope with urbanization also has been linked to some attributes that confer a competitive advantage over similar

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species, such as high population densities, high fecundity, wide niche breadth, effective competitive and anti-predator abilities, and effective learning processes (Shochat et al. 2010; Møller et al. 2012; Batabyal and Thaker 2019; de Andrade 2020). In addition, species living in cities often are successful invaders, suggesting that human-caused habitat alterations within their native range induce evolutionary changes that could favor niche expansion (Stepkovitch et al. 2019).

Factors that might influence tolerance of or aversion to cities in reptiles have not been studied extensively (French et al. 2018; de Andrade 2020; Collins et al. 2021; Brum et al. 2023). Only a few recent studies have explored how aspects of urbanization affect Neotropical lizard biology (Marnocha et al. 2011; Winchell et al. 2018; de Andrade 2020; de Andrade et al. 2019). For some lizards, urbanization brings reproductive benefits leading to increased fitness. This is the case of urban Neotropical Lava Lizards (*Tropidurus hispidus*) in northeastern Brazil, which occur at higher densities than in rural areas (de Andrade 2020). Yet, urbanization in the same area has apparently contributed to the decline and local extinction of teiid lizards (de Andrade et al. 2019). The ecological challenges posed by urban habitats also can lead to functional and morphological shifts in some lizards. For instance, urban Caribbean anoles (genus *Anolis*) have larger bodies, longer limbs, and improved locomotor performance on both artificial and natural substrates than those in forested areas (Marnocha et al. 2011; Winchell et al. 2018). Understanding the full spectrum of ecological impacts that city-life imposes on natural populations is a pressing objective in biodiversity research.

The Green Iguana, *Iguana iguana* (Linnaeus 1758), provides an exceptional opportunity to investigate the effects of urbanization. It is naturally distributed in the Neotropics, from northern Mexico to the Tropic of Capricorn in Paraguay and Brazil on the mainland as well as many associated islands (Bock 2014). Thanks to its wide distribution and economic importance, this species is perhaps the best known of all Neotropical squamates (Bock et al. 2016). It occupies a wide variety of habitats throughout its native range, including urban areas (Powell and Henderson 2005; Falcón et al. 2012). This species also is a successful invader outside its natural distribution (e.g., the United States and Puerto Rico), where it has become established and often reaches greater densities than native iguana populations (Falcón et al. 2012). Several aspects of its basic biology have been widely studied (e.g., demography, morphology, reproduction, diet, and behavior) in many native populations in natural environments (Burghardt and Rand 1985; Rand et al. 1990; Rodda 1992; Bock et al. 1998, 2016; Muñoz et al. 2003), which allow for comparisons with populations inhabiting novel habitats such as those in urban areas.

Determining ecological aspects of urban biodiversity is critical to design integrated management projects aimed at enhancing sustainability and resilience in anthropogenic landscapes. Herein we characterized the basic ecology of a native Green Iguana population inhabiting an urban area in Colombia. This species is one of the most common and abundant lizards in natural environments close to the study area (Ramos-Pallares and Meza-Joya 2018), so it is expected to be a successful city dweller (see Møller et al. 2012). In such environments, this arboreal lizard spends much of its life high in the canopy (Greene et al. 1978; Bock 2014); thus, urban iguanas are predicted to occupy areas resembling those they occupied in nature. Since iguanas in this population apparently enjoy abundant and stable food resources and low predation risk (see below), their population density and body growth rates are expected to be higher than in rural populations. We also anticipated that iguanas in this urban population reproduce once per year, as reported for populations in natural habitats (Wiewandt 1982; Bock et al. 1998, 2016).

Materials and Methods

Study site.—We studied the iguana population at Club Miramar, located in an industrial zone in the Municipality of Barrancabermeja, Department of Santander, Colombia (Fig. 1; 7.073333, -73.871667, elev. 73 m asl). Most of the 6-ha private club is a golf course surrounded by the Miramar Swamp, gardens, infrastructure (i.e., buildings, offices, and facilities), and small patches of remnant arboreal vegetation and scattered fruit trees, mainly *Mangifera indica*, *Terminalia catappa*, and *Syzygium malaccense*. This anthropogenic landscape is a mosaic of open vegetation dominated by the golf course (49.7%), infrastructure (28.5%), and tree cover (21.8%). The climate in this area is highly seasonal, with a bimodal rainfall pattern, with rains peaking in April–May and again in September–November. The months with the least precipitation are December–March, and June– August. Mean annual rainfall is 2,766 mm, and mean annual temperature is 28.2 °C (IDEAM 2018).

The iguanas are iconic visual attractions for visitors; therefore, human-animal interactions might favor them over other native species. On weekends, iguanas obtain direct human trophic subsidies in the form of food leftovers (mainly vegetables), with such supplementary feeding inducing short-term (few hours) aggregations usually dominated by the largest males. Predation of adult iguanas likely is reduced given that the only native predators in the study area targeting this age class (*Caiman crocodilus*) occur in very low numbers and are repelled by staff members when seen approaching adult iguanas. Protection from humans is granted as hunting is prohibited, and peripheral fencing excludes some alien predators such as free-ranging dogs.

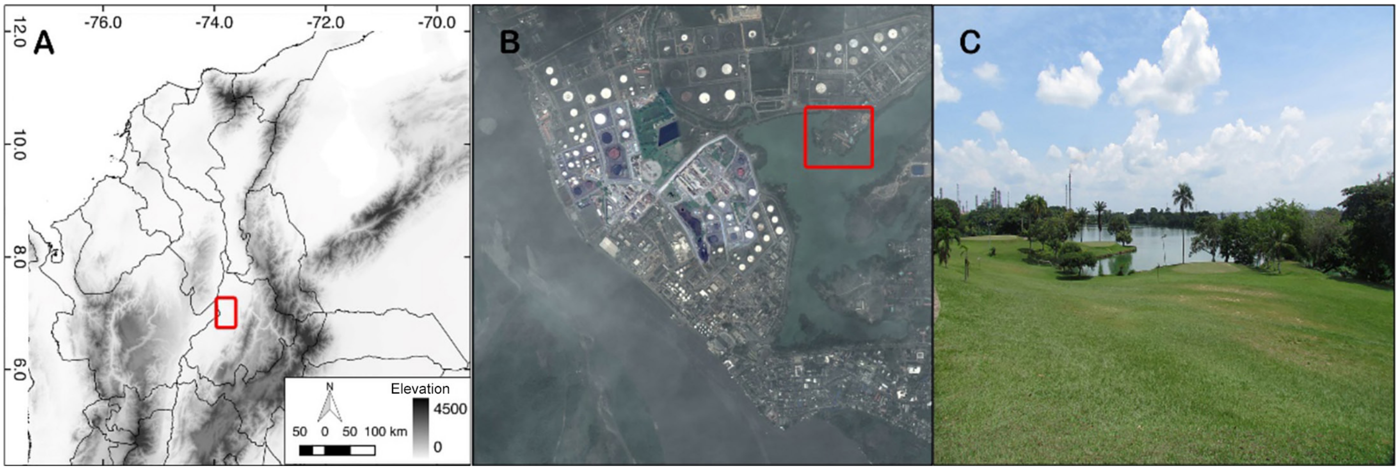

Figure 1. Map of Colombia showing the study area (red square) in Santander Department (A). Satellite image from Google Earth Pro (https://www.google.com/earth) showing the location of Club Miramar (red square) in west Barrancabermeja urban area (B). Picture of the Miramar golf course (C). Photograph by Eliana Ramos.

Monitoring and marking.—We conducted monthly surveys from January to December 2013. Each eight-day trip consisted of daily mark and recapture sampling between 0800 and 1800 h. Monitoring was limited to weekdays to avoid biases related to animal aggregations triggered by human trophic subsidies on weekends. Iguanas were captured using telescoping fiberglass poles, fishing nets, or by hand. Each captured lizard was marked with a unique number using two methods: a temporary mark consisting of a number on both flanks of the animal using non-toxic indelible paint and a permanent mark with a unique combination of colored beads (numeric code) attached to the dorsal crest (Rodda et al. 1988; Hayes et al. 1999). For all captured and recaptured iguanas, we measured snout-vent length (SVL) with a measuring tape to the nearest 1 mm and body mass with a series of dynamometers to the nearest 0.5g or 5 g, depending on the lizard's size. Sex was determined based on sexual dimorphism for adults (e.g., body size, length of nuchal and dorsal spines, and size of femoral pores) and cloacal inspection for juveniles and neonates (Fitch and Henderson 1977; Rodda 1992; Rivas and Ávila 1996). The reproductive status of adult females was determined by abdominal palpation to detect the presence of follicles or eggs, and then categorizing them as gravid or non-gravid (Morales-Mávil et al. 2016). Females were considered post-reproductive once oviposition, indicated by abdominal shrinkage, had occurred.

Age structure.—The age structure of the studied population was characterized for each sampled month based on sex, age class, and reproductive condition. For this, we assigned captured individuals to three age classes based on external morphology and body size: neonates (SVL < 150 mm), juveniles (150 mm > SVL < 250 mm), and adults (SVL > 250 mm). Sex (male and female) and reproductive condition (gravid, non-gravid, or post-reproductive) were defined as previously mentioned. We used a G-test to examine significant differences in age structure between months. Juveniles were excluded from this analysis because of small sample size (n = 18).

Reproduction and nesting.—We classified nesting sites as solitary or communal (Rand 1968; Mora 1989). Solitary nests were single-entrance burrows located along the margins of the swamp and used by a single female. Communal nests were multi-entrance burrows, where females congregated to oviposit, found mainly on the golf course. Nesting activity was inferred when females were observed arriving at nesting areas, digging, entering, and back-filling burrows after egg laying (Rand 1968). We did not witness actual oviposition, but it was inferred when females emerging from burrows exhibited a much shrunken (concave) abdomen (Rand 1968). Clutch size was determined by counting eggshells from six solitary nests. We estimated the proportion of gravid females in every sampled month. We used chi-square (χ^2) tests to examine monthly variation. The relationship between the number of reproductive females and monthly precipitation was determined using Spearman's rank correlation. The length of the reproductive and nesting period was determined based on field observations. We used data loggers (WatchDog 1200, n = 5) to remotely monitor the internal temperature (depth = 50 cm) of the two main nesting areas within the golf course (one exposed directly to the sun and the other in partial shade) from December to March.

Growth.—The instantaneous growth rate (IGR) for each specimen was estimated as the difference in SVL between two consecutive captures, divided by the number of days elapsed between such captures (Zúñiga-Vega et al. 2005). To avoid non-independence in the data, only one growth rate per lizard was estimated. We used nonlinear regressions to fit three widely used growth models to the relationship between IGR and the average SVL between captures: logistic-by-length, logistic-by-weight, and von Bertalanffy (von Bertalanffy

1957; Schoener and Schoener 1978; Andrews 1982). Each model was fitted separately for females and males. The best-fitting model was chosen based on Akaike's Information Criterion (AIC) using the R package AICcmodavg version 2.3-1 (Mazerolle 2020). We used the differential equation from the best-fitting model for estimating the characteristic growth parameter (r) and the estimated asymptotic size (A_1) for each sex.

Density.—We used the line-transect distance sampling method (Lancia et al. 1994) for estimating population density. For this, we surveyed a total of four randomly distributed 600-m transects. We walked each transect twice per sampling trip at a constant speed (~0.6 km/h) between 0900 and 1600 h when iguanas were most active. When a lizard was detected, the distance and angle to the transect along with perch height were recorded with a laser distance measurer (Bosch GLM 50 C). The population density was estimated using the software DISTANCE 6.2 (Thomas et al. 2010), which fits a detection function to the observed distances and provides an estimate of the number of individuals in the area (Thomas et al. 2010). To increase precision in our estimates, we first ran an exploratory analysis to truncate the data by removing the largest 5% of distances from our dataset (Buckland et al. 2001). We assessed the functions half-normal key and hazard-rate, both with cosine and simple polynomial adjustments (Thomas et al. 2010). We included perch height as a covariate term using a multiple covariate distance sampling approach. Density was estimated for each sampling trip and the complete sampling period. A nonparametric bootstrap was used to estimate the variance of our density estimations (Buckland et al. 2001). The best-fitting model was selected based on Akaike's Information Criterion (AIC) with the R package AICcmodavg version 2.3-1 (Mazerolle 2020).

Occupancy and detection modeling.—We defined 18 randomly distributed monitoring sites (30 × 30 m = 900 m^2 grid cells) throughout the study area using a Geographic Information System (GIS), with a maximum of four sites per hectare. To ensure independence among sites, a circular buffer with a radius of 55 m (9,503 m^2) was established around the centroid of each site. This metric corresponds to nearly twice the average home range reported for this species (~4,294 m^2; Rand et al. 1989; Morales-Mávil et al. 2007) and almost twice the average distance traveled by individual iguanas in the study area as recorded in our field surveys (40 m). We considered each sampling survey to be a single survey period; hence, we had 12 survey periods for each site. We used single-season occupancy models (MacKenzie et al. 2002) to investigate the occupancy and detectability of iguanas. This method estimates rates of site occupancy (ψ) and detectability (p) based on repeated surveys at a site and accounts for imperfect detectability to obtain unbiased estimates of occupancy (Gu and Swihart 2004). We fit models using a maximum likelihood implementation of single-season occupancy analysis within the R package *unmarked* version 1.1.1 (Fiske and Chandler 2011). This approach comprises two modeling procedures, one for the occupancy component (ecological process; ψ) and the other for the detection component (observation process; p).

We considered four covariates expected to influence occupancy of iguanas: percent tree cover (native or orchard trees), percent infrastructure (built-up area), percent open areas (short grasses), and distance to the nearest body of water (Table S1). We included the ordinal day of year and percent tree cover as detection covariates. We did not include sampling effort as a covariate due to the low variability of sampling effort between survey periods. All covariates were standardized to have zero mean and unit variance. Due to the large number of potential models, we used step-down selection to reduce the size of the final model set (Burnham and Anderson 2002). To do so, we first modeled occupancy while holding detection constant and then modeled detection using the top-ranked occupancy model (MacKenzie et al. 2017). We ranked models based on Akaike's Information Criterion (AIC) corrected for small sample sizes (AICc) with the R package *AICcmodavg* version 2.3-1 (Mazerolle 2020). We considered models with ΔAICc < 2 as having less support than the top-ranked model (Burnham and Anderson 2002). We evaluated the goodness of fit of the best global model (i.e., the model with all significant covariates) using a Pearson chi-square test (MacKenzie and Bailey 2004) with a parametric bootstrap approach (5,000 re-sampling).

Results

Age structure.—We marked 659 iguanas, 414 hatchlings, 18 juveniles, 118 adult males, and 109 adult females. Adults were collected during all months of the year, juveniles were collected through eight months but were observed year-round, and neonates were found only during March, April, and May (Fig. 2). We did not find any differences in the occurrence of adult males and females throughout the year (males $G_{0.05, 13}$ = 3.12, p = 0.43; females $G_{0.05, 13}$ = 4.60, P = 0.32). The sex ratio (male:female) did not vary significantly from 1:1 (0.5 binomial test, P = 0.33) when pooling data from all months. Yet, significant female-biased sex ratios were detected in December (1:1.6, 0.5 binomial test, P < 0.006) and January (1:1.3, 0.5 binomial test, P < 0.001), when nesting female aggregations occurred. Similarly, significant male-biased sex ratios were detected in October (1.4:1, 0.5 binomial test, P = 0.022) and November (1.6:1, 0.5 binomial test, P = 0.004), when males became more territorial and displayed courtship and copulation behaviors (see below). Adult iguanas in this population exhibited sexual dimorphism in size, where males were larger and had larger heads than females (ANOVA $F_{1, 120}$ = 28.4, P < 0.001; ANCOVA $F_{1, 120}$ = 5.42, P = 0.002, respectively).

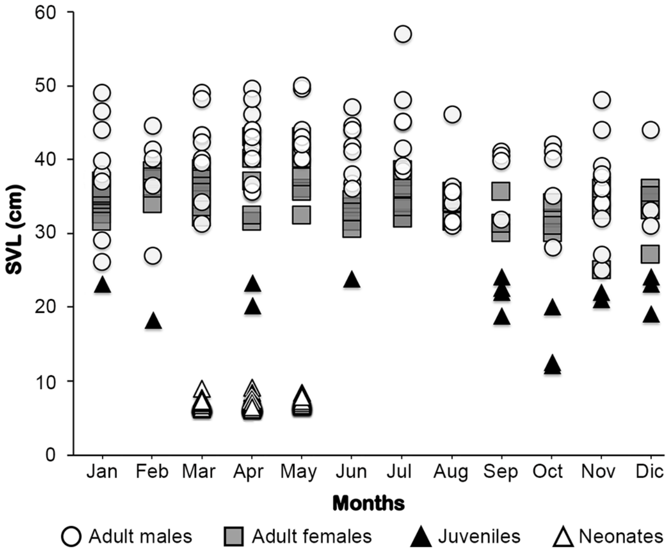

Figure 2. Monthly distribution and sizes (SVL) of adult male, adult female, juvenile, and neonatal Green Iguanas (Iguana iguana) at Club Miramar, Municipality of Barrancabermeja, Department of Santander, Colombia.

Mean SVL was 38.3 cm ± 5.4 SD (n = 118) for adult males and 33.5 cm ± 3.1 SD (n = 109) for adult females. Mean head length was 9.67 cm ± 0.98 SD (n = 118) for adult males and 6.65 cm ± 0.85 SD (n = 109) for adult females.

Reproduction and nesting.—Reproductive activity in this population began between October and November with agonistic interactions between males and courtship and copulation behaviors. The smallest gravid female was 25.8 cm SVL. We collected 109 adult females, with 62% of them being non-gravid, 6% post-reproductive, and 32% gravid. No significant differences in the occurrence of non-gravid females throughout the year were significant ($\chi^2_{0.05,\,12}$ = 6.0, P < 0.873). However, gravid ($\chi^2_{0.05,\,12}$ = 22.5, P < 0.001) and post-reproductive ($\chi^2_{0.05,\,12}$ = 12.8, P < 0.001) females were found during few months of the year (Fig. 3A). Although the highest percentage of gravid females was concentrated between November and February, females in this stage were also recorded from July to August (Fig. 3A). Gravid females had a significantly higher body weight than non-gravid females (ANCOVA $F_{1,\,85}$ = 11.5, P = 0.021). We found a negative correlation between precipitation and the number of gravid females (Spearman R = -0.62, P = 0.01; Fig. 3).

The main nesting season extended from mid-December to mid-February, with a second but less intense nesting period between mid-June and mid-August (Fig. 3B). The peak in nesting activity was between late December and early January, with 8–12 females per day per nesting site. We did not observe any instances of nest guarding, as females departed from the nesting area soon after laying. We recorded nine communal nesting sites within the study area, six of which were located on the golf course (close to sand bunkers, sand traps, and greens) and the remaining three were on the margins of the swamp. Incubation temperatures inside the nest exposed directly to the sun ranged between 29.8 and 32.1 °C (mean = 31.05 °C ± 0.25 SD), while the nest under partial shade ranged between 28.0 and 31.3 °C (mean = 29.8 °C ± 0.55 SD). We did not find significant differences in incubation temperatures between the two nests (Z = 1.87, P = 0.97).

The hatching season extended from March to April (Fig. 3B). Average clutch size was 25 eggs ± 7.34 SD (n = 6). The sex ratio (male:female) for hatchling iguanas did not vary significantly from 1:1 (0.5 binomial test, P = 0.403). Hatchling SVL was 7.0 cm (± 3.87 SD). Once hatching occurs, neonates move to adjacent shrubs, herbs, and/or abundant litter and organic matter, forming small groups of 5 to 20 individuals. The maximum perch height of hatchlings did not exceed 2.5 m. Despite the large number of neonates marked during the hatching and dispersal season (414 individuals), few were recaptured (~6%).

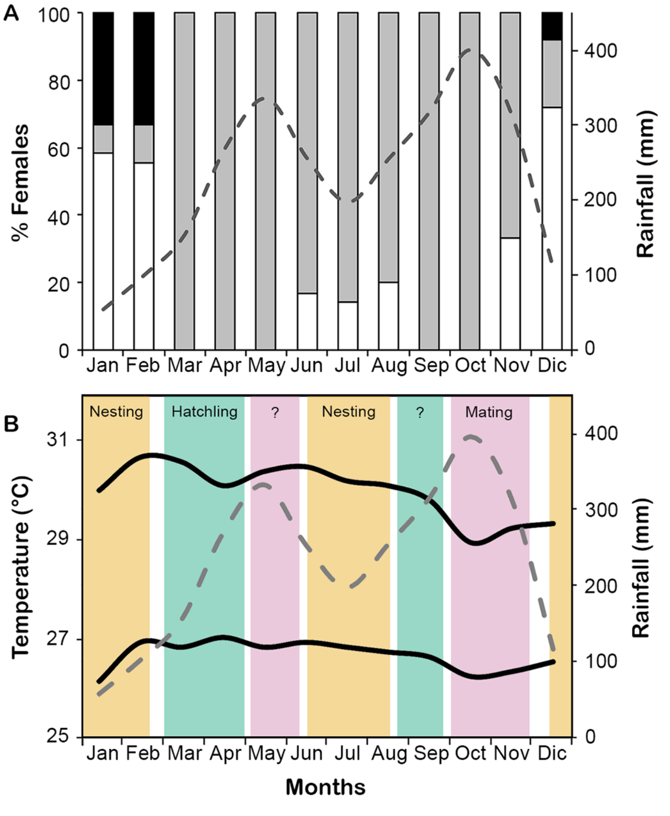

Figure 3. Annual reproductive cycle of Green Iguanas (*Iguana iguana*) at Club Miramar, Municipality of Barrancabermeja, Department of Santander, Colombia, during the study period (Jan–Dec 2013). (A) Monthly distribution of reproductive stages of mature females: non-gravid (gray bars), gravid (white bars), post-reproductive females (black bars), mean rainfall (dashed line). (B) The annual cycle is characterized by two reproductive peaks during dry seasons, with a first intense peak during the drier months (December–February). Mean rainfall (dashed line) and maximum and minimum temperatures (solid lines) are shown. Colors indicate the duration of reproductive events throughout the year (i.e., mating, nesting, and hatching). Question marks indicate the expected (not recorded) mating period (pink bars) during 'veranillo' and subsequent hatching (green bars).

Growth.—Mean growth rates (Fig. 4A) varied between young (SVL < 250 mm = 0.26 mm day^{-1} ± 0.08 SD, n = 30) and adult iguanas (SVL > 250 mm = 0.07 mm day^{-1} ± 0.05 SD, n = 70). The von Bertalanffy growth model provided the best fit to our growth data for both sexes (Table 1). Adult females and males did not vary significantly in the characteristic growth parameter (r for females = 0.0006 [CI = 0.0005–0.0009], n = 38; r for males = 0.0007, [CI = 0.0006–0.0008], n = 40) and in the asymptotic body size (A_1 for females = 403.7 [CI = 400–593], n = 38; A_1 for males = 485.3 [CI = 446–537], n = 40). Therefore, we constructed a single growth curve combining data for both sexes. Parameters estimated for the final model were A_1 = 473.62 mm and r = 0.0007 mm day^{-1} (Fig. 4B).

Density.—The density of adult iguanas estimated for the study area during the whole survey period varied between 41.84 and 47.69 individuals per hectare (ind*ha^{-1}) for all models. The model with half-normal detection function, cosine fit term, and perch height as a covariate had the best fit to the data as judged by its AIC score (Table 2). According to this model, adult iguana density at Club Miramar during the whole survey period was 47.69 ind*ha^{-1} (36.65–58.01). The density estimates per month were also variable for the best-fitting models, ranging from 37.75 to 74.87 adult ind*ha^{-1}. In most cases, the models with the best fit included height as a covariate, except for September and October (Table S2). The months with the highest density were November, December, and January (between 67.54 and 74.87 adult ind*ha^{-1}). We found a negative correlation between the density of adult individuals and precipitation (Spearman R = -0.64, P = 0.02).

Occupancy and detection modeling.—We found two top-ranked occupancy models with similar levels of support based on AICc scores (ΔAICc = 1.51): ψ(infrastructure) and ψ(water). Yet, the former model had nearly twice the model

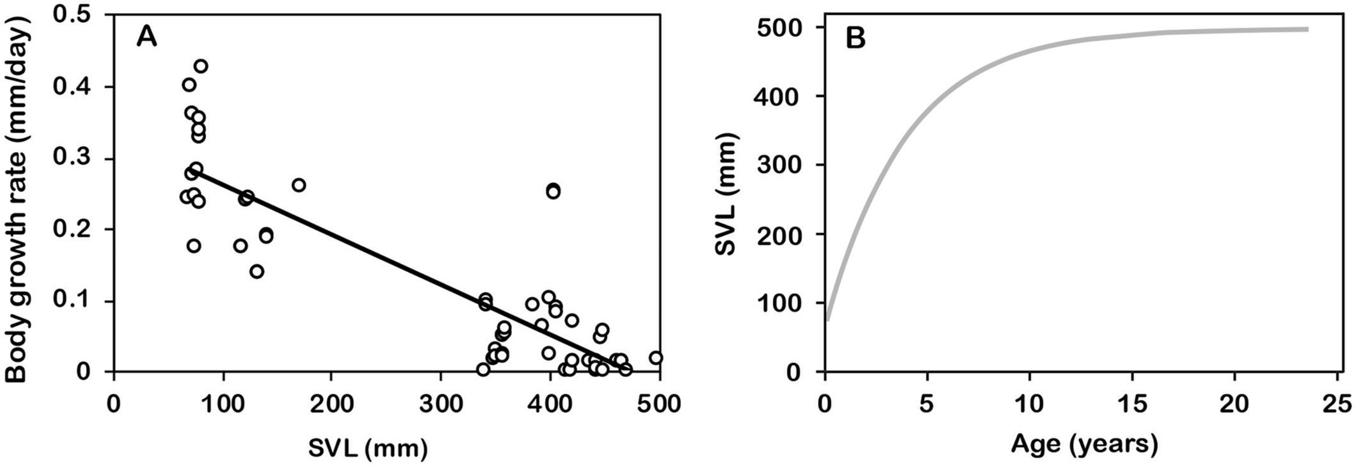

Figure 4. Body growth rate and growth curve estimated for Green Iguanas (*Iguana iguana*) at Club Miramar, Municipality of Barrancabermeja, Department of Santander, Colombia, pooling data from both sexes using the von Bertalanffy growth model. (A) Relationship between instantaneous growth rates and snout vent-length of individual iguanas showing the fitted line. (B) Growth curve relating snout-vent length (SVL) and age of individual iguanas, with the gray line depicting the estimated growth trajectory.

Table 1. Summary of parameter estimation for the models assessed for calculating the growth pattern for *Iguana iguana* at Club Miramar, Barrancabermeja, Colombia. Results are shown separately for females and males. Asymptotic body size (A_1 in mm) and characteristic growth parameter (r in mm day^{-1}) and their associated 95% support plane confidence intervals (CI) are shown. Models are presented in descending order according to AUC values.

Growth model	ΔAIC	A_1 (CI)	r (CI)
Females (n = 38)			
von Bertalanffy	0.00	403.7 (400–593)	0.0006 (0.0005–0.0009)
logistic-by-length	30.31	470.7 (378–440)	0.0029 (0.0022–0.0037)
logistic-by-weight	16.78	437.6 (381–444)	0.0045 (0.0027–0.0063)
Males (n = 40)			
von Bertalanffy	0.00	485.3 (446–537)	0.0007 (0.0006–0.0008)
logistic-by-length	41.43	443.9 (429–462)	0.0030 (0.0024–0.0037)
logistic-by-weight	24.76	445.5 (430–467)	0.0042 (0.0027–0.0057)

Table 2. Summary of parameter estimation for the models assessed for calculating the density (D = ind ha^{-1}) and its associated 95% confidence intervals (CI) of adult *Iguana iguana* at Club Miramar, Barrancabermeja, Colombia. Models are presented in descending order according to AUC values.

Detection function	Adjustment term	Covariate	AIC	Variance	$D_{(CI)}$
Half-normal	Cosine	Perch height	6398.72	0.12	$47.69_{(36.65–58.01)}$
Half-normal	Simple polynomial	Perch height	6408.22	0.11	$46.23_{(38.52–61.68)}$
Hazard-rate	Cosine	Perch height	6450.02	0.09	$45.54_{(38.42–53.27)}$
Hazard-rate	Simple polynomial	Perch height	6453.17	0.06	$45.79_{(37.15–56.42)}$
Hazard-rate	Cosine	—	6638.14	0.07	$44.59_{(38.26–47.47)}$
Hazard-rate	Simple polynomial	—	6639.87	0.11	$42.95_{(36.92–49.97)}$
Half-normal	Cosine	—	6641.60	0.08	$43.29_{(36.26–51.71)}$
Half-normal	Simple polynomial	—	6645.74	0.10	$41.84_{(33.82–51.75)}$

weight (ΔAICc weight = 0.15). Thus, ψ(infrastructure) was selected for modeling detectability based on three candidate models including detection variables (Appendix Table S3). From these, only the top model had substantial support in terms of AICc and weight scores (ΔAICc = 3.43, ΔAICc weight = 0.70): *p*(trees) ~ ψ(infrastructure). The MacKenzie and Bailey (2004) goodness-of-fit assessment of this model resulted in a good fit (p = 0.999) and low overdispersion ($\hat{c}$ = 0.61). Based on our final detection-corrected model *p*(trees) ~ ψ(infrastructure), occupancy decreased with increasing infrastructure (β = −1.56 ± 0.69 SE), while detection responded to tree cover with a peak at intermediate levels of coverage (β = 0.74 ± 0.18 SE; Fig. 5). The detection-corrected estimate of occupancy was 0.77.

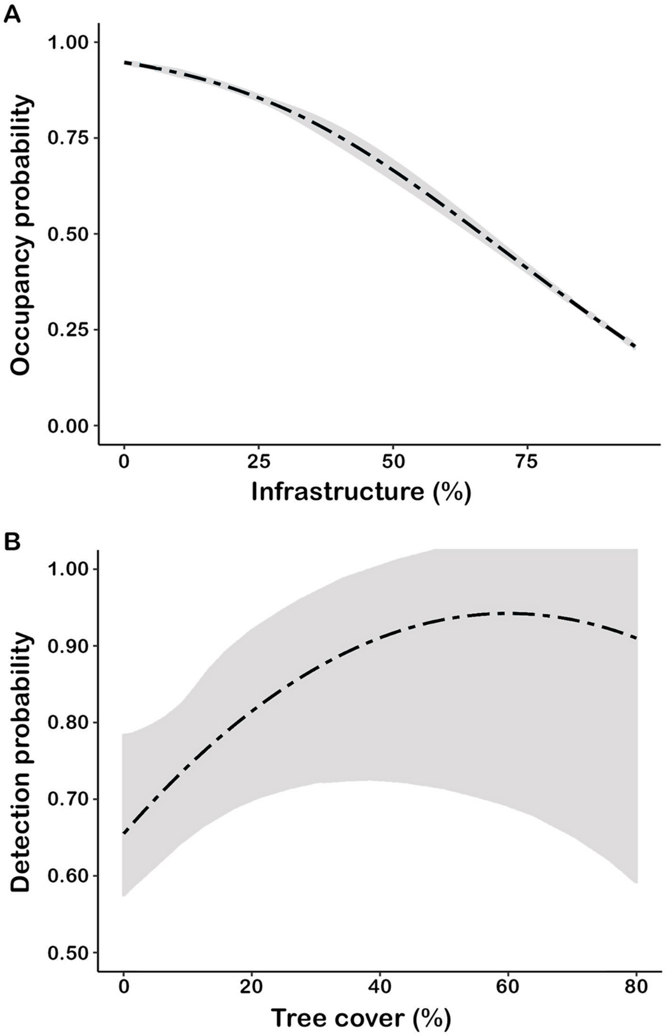

Figure 5. Occupancy and detection probabilities for Green Iguanas (*Iguana iguana*) at Club Miramar, Municipality of Barrancabermeja, Department of Santander, Colombia, were predicted using the final detection-corrected model. (A) Predicted occupancy decreases with increasing infrastructure, and (B) predicted detectability responds quadratically to tree cover. Shaded areas depict 95% confidence intervals.

Discussion

Human disturbance of natural habitats is known to affect the viability of native animal populations, especially for long-lived species such as those in the family Iguanidae (Romero and Wikelski 2002; Knapp 2004; Iverson et al. 2006). Wildlife populations inhabiting human-dominated landscapes often differ from those in natural areas in habitat selection, patterns of occurrence and mobility, and population dynamics (Rodewald and Gehrt 2014; Meza-Joya et al. 2019; Vanek et al. 2019). Herein we have shown that Green Iguanas at Club Miramar are successfully exploiting a novel environment as inferred from high population densities and individual growth rates, and the type of habitats they occupy in the studied location. We hypothesized that iguanas in this population would benefit from both direct and indirect benefits from humans, including food provisioning, reduction in overall predation risk, and protection against anthropogenic threats (e.g., hunting). Taken together, our data suggest that these urban iguanas in the studied area are under significantly different selection pressures than those in natural habitats and could be adapting to human-modified environments.

Skewed sex ratios in a population can reflect differential pressures on one sex arising from human-driven mortality or environmental pressures (Smith and Iverson 2016). The sex ratio in the studied population was approximately 1:1 at birth and adulthood, suggesting that both sexes are experiencing similar selective pressures (e.g., predation). Temporal deviations from this trend during the mating and nesting seasons are likely related to this species' polygynous mating system and nesting aggregation behavior. The sex ratio reported herein coincides with that from a Green Iguana population in an island uninhabited by humans in Panamá (Dugan 1982). In contrast, several studies have reported female-biased sex ratios (1:2–1:2.6) for populations inhabiting other natural areas (Rodda 1992; Muñoz et al. 2003; Campos and Desbiez 2013), but whether they represent a real demographic skew due to differential selective pressures between sexes or to sampling biases given the mating system and nesting behavior of this lizard is unclear. The opposite trend also has been reported and explained by female-biased human harvesting at nesting sites (Müller 1972). Whether the sex ratio in the studied population reflects a release from human-related pressures remains an open question.

The presence of individuals of all size classes throughout the year suggests a stable population (Campos and Desbiez 2013). Our density estimates (47.69 adults ha^{-1}) are far larger than those reported using the same method (1.2–13.7 adults ha^{-1}) for populations inhabiting natural areas in the Depresión Momposina in Colombia (Muñoz et al. 2003). This high density would be related to some benefits of urbanization, including abundant dietary resources and human trophic subsidies, leading to increased carrying capacities and abundances (e.g., Jessop et al. 2012). Likewise, predator and competitor release might allow Green Iguanas in the study area to exploit a greater fraction of the available resources, enabling them to reach higher population densities (see Novosolov et al. 2016). Nevertheless, the extent to which these results can be generalized across urban populations likely depends on the urban context. For instance, iguanas in highly urbanized parks in Barrancabermeja—where the proportion of paved surface is higher than 50%—seemingly occur at lower densities than those reported here (ER, pers. obs.), suggesting that the availability of specific landscape elements (e.g., tree cover) and resources (e.g., food and nesting areas) affect this lizard's numbers.

Growth rates in iguanids are largely modulated by environmental factors such as food availability (Müller 1968); thus, Green Iguanas from urban environments with greater access to food would grow faster than those from natural areas where resources are more limited. The estimated growth rate for young iguanas in the studied population (0.26 mm day^{-1}) was slightly higher than those reported for populations in natural habitats during similar survey periods: Belize City, Belize (0.22 mm day^{-1}; Henderson 1974), Barro Colorado Island, Panama (0.23 mm day^{-1}; Rand and Greene 1982), and Santa Marta, Colombia (0.25 mm day^{-1}; Harris 1982). Remarkably, young iguanas at Los Cocos, Natural Park Isla de Salamanca, Colombia, grow faster than any studied population (ca. 0.38 mm day^{-1}), and usually live in association with the park's infrastructure (e.g., buildings, facilities, and crocodile enclosures; Harris 1982). These interpopulational differences suggest that growth rates of young Green Iguanas from anthropized and urban environments are higher than those from natural areas, likely reflecting increased food availability, although research into the factors driving this change is warranted.

Contrary to our expectation, Green Iguanas at Club Miramar apparently reproduce twice per year, with the main breeding season during the driest months (December–February) and a minor season during a less intense dry season (June–August). This observation also is supported by the presence of gravid females between June and August 2015, shortly after our fieldwork was completed (H. Barbosa-Moyano, pers. comm.). However, additional data are needed to fully describe this second reproductive peak, as we did not observe mating behavior explaining the presence of gravid females during this second dry season, nor post-reproductive females or neonates in the subsequent months. Although this pattern was unexpected given that most populations of this species reproduces once per year (Harris 1982; Rand and Greene 1982; van Marken Lichtenbelt and Albers 1993), two breeding seasons have been suggested for some Green Iguana populations at Bocas del Toro in Panama and Paramaribo in Surinam (Rand and Greene 1982). Like our study area, these localities have bimodal annual rainfall patterns (Rand and Greene 1982), which could explain the presence of a second reproductive event during the year. Indeed, several studies have shown that rainfall regime is related to reproduction in Green Iguanas (Fitch and Henderson 1977; Rand and Greene 1982; Casas-Andreu and Valenzuela-Lopez 1984; Ferreira et al. 2002), with variations in breeding times probably associated with latitudinal variations in climatic variables (Rand and Greene 1982). Further studies are needed to fully document this second breeding season as mating and hatching were missed, probably due to sampling biases and the low proportion of gravid females recorded (≥ 20%).

Nest-site selection is an important form of parental care in squamates (Blouin-Demers et al. 2004; Ramos-Pallares et al. 2013), yet the determinants of nest placement are poorly understood for iguanids (Christian and Tracy 1982; Ryan 1982). Green Iguanas typically lay eggs during the driest part of the year, when climate conditions provide insolation and high nest temperatures during incubation (Wiewandt 1982). Neither temperatures of nests in partially shaded areas (28.0–31.3 °C) nor those directly exposed to the sun (29.8–32.1 °C) varied extensively. These temperatures are slightly higher than those from nests of this species in forested areas (26.8–27.3 °C) and exposed clearings (28.2–31.2 °C) at Barro Colorado Island, Panama (Bock et al. 1998), suggesting that iguana eggs are tolerant to higher incubation temperatures than previously reported. Interestingly, nests in open areas receiving more sunlight were not significantly warmer than those in partially shaded areas, suggesting that regardless of nest placement (partial shade or sun), the duration of the incubation periods could be similar. However, this observation must be taken with caution as incubation times for iguanas can vary depending on factors other than temperature, such as spawning time, nest depth, and humidity (Bock et al. 1998; Iverson et al. 2004; Morrison et al. 2009).

Our observation of communal nesting is consistent with studies portraying this strategy in iguanid lizards (Rand 1968; Christian and Tracy 1982; Wiewandt 1982; Rand and Dugan 1983). At first glance, iguanas could be selecting nesting sites constrained by the scarcity of nest space (Wiewandt 1982; Mora 1989), given the high density of females in the study area. However, this strategy also could be related to direct benefits for offspring (e.g., social grouping, reduced predation), as suggested for other communally nesting iguanas (Drummond and Burghardt 1982; Wiewandt 1982; Rand and Dugan 1983; Mora 1989). Energetic budgets are another key factor dictating reproductive decisions in iguanas (Rand and Rand 1978); therefore, by adopting this strategy female iguanas in this population would minimize investments in nest construction while avoiding costly competitive disputes, as they do not appear to defend their nests against conspecifics. The absence of nest-guarding behavior in wild Green Iguanas has been related previously to energetic constraints (Wiewandt 1982) and reductions in female predation risk (Rand and Dugan 1983). The fact that females at Club Miramar depart from the nesting area soon after laying suggests some mutual benefits of communal nesting such as cooperation among hatchlings (Rand and Dugan 1983) or that iguanas are forced to share the limited available nest space at the expense of conspecific intrusion and ovicide (Rand 1968; Rand and Rand 1978).

Natal dispersal was observed during the hatchling period when neonates emerged and rapidly moved away from the nesting sites in groups (5–20 individuals). In Green Iguanas, this behavior has been related to increasing survivorship, availability of resources, and landscape navigability (Burghardt et al. 1977; Drummond and Burghardt 1982; Burghardt and Rand 1985). The rapid dispersal of hatching groups outside the study area might explain the low recapture rate of neonates in this study (6%), as suggested for a population inhabiting a natural area at Slothia Island, Panama, for which the recapture rate was as low as 4% (Burghardt et al. 1977). Predation by native (e.g., herons, raptors, caimans) and alien animals (cats) could be another important factor explaining the low recapture rate of neonates at Club Miramar. Remarkably, newborns in this population generally settled down around dense ornamental shrubs surrounding the golf course, where shelter and food are abundant and where they can be easily overlooked; consequently, the low recapture rate might be a methodological artifact.

Green Iguana occupancy was influenced negatively by the percentage of human infrastructure, although some individuals used artificial surfaces for basking. In contrast to our expectations, we found models including only natural landscape elements (e.g., tree cover and distance to water) to be poor predictors of occupancy probability. This result suggests that contrary to populations in natural habitats where iguanas spend more of their lives high in the canopy (Bock 2014), iguanas in the studied population readily exploit grassy areas of the golf course for feeding and basking. This could be the result of two non-mutually exclusive factors affecting habitat selection by iguanas at Club Miramar. First, adult iguanas in this population could be benefitting from a reduction in overall predation risk (e.g., Eötvös et al. 2018) by spending more time foraging in open areas, where they have access to complementary trophic resources. Likewise, iguanas might perceive grassed areas as beneficial because of the combined effects of low predatory pressure and direct provision of food by humans (e.g., Oro et al. 2004; Jessop et al. 2012). On the other hand, we found tree cover to be a good predictor of detection probability rather than occupancy probability. This positive association might be the result of individuals selecting trees as critical refuges for avoiding predators at night, which in some cases also guarantees optimum sites for basking and feeding (Greene et al. 1978). As detection probability can be influenced by abundance (Royle and Nichols 2003), our results strongly suggest that the presence of specific landscape elements (i.e., tree cover) and aspects of urbanization (i.e., built-up area) can affect the occurrence of iguanas.

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Appendices

Table S1. Site and survey covariates used for modeling the occupancy (ψ) and detectability (*p*) of Green Iguanas (*Iguana iguana*) at Club Miramar, Municipality of Barrancabermeja, Department of Santander, Colombia. All variables are continuous. The first three variables were estimated based on aerial imagery from Google Earth Pro (https://www.google.com/earth) for each sampling site. Other variables were estimated during fieldwork.

Covariate	Code	Parameter	Description
Tree cover	trees	ψ, *p*	percent of each site covered by native or orchard trees
Infrastructure	infra	ψ, *p*	percent of each site covered by human infrastructure
Open areas	open	ψ, *p*	percent of each site covered by open (e.g., grassy) areas
Distance to water	water	ψ	distance (m) to the nearest body of water
Survey date	date	*p*	ordinal day of year of the survey period

Table S2. Model parameters used for calculating the monthly density (D = ind*ha^{-1}) and its associated 95% confidence intervals (CI) of adult Green Iguanas (*Iguana iguana*) at Club Miramar, Municipality of Barrancabermeja, Department of Santander, Colombia. Models are presented in descending order according to AIC values.

Month	Detection function	Adjustment term	Covariate	AIC	ΔAIC	Variance	D (95% IC)
January	Hazard-rate	Cosine	Perch height	671.2	0.00	0.29	74.87 (23.17–241.84)
	Half-normal	Cosine	Perch height	676.5	5.30	0.43	81.29 (25.36–260.52)
February	Hazard-rate	Cosine	Perch height	517.2	0.00	0.18	52.99 (30.44–92.25)
	Half-normal	Cosine	Perch height	519.1	1.90	0.17	47.04 (26.61–83.16)
March	Half-normal	Cosine	Perch height	616.2	0.00	0.20	48.95 (24.81–96.59)
	Hazard-rate	Cosine	Perch height	622.6	6.40	0.21	43.45 (21.71–86.94)
April	Half-normal	Cosine	Perch height	432.6	0.00	0.24	44.44 (26.51–92.23)
	Hazard-rate	Cosine	Perch height	436.7	4.10	0.23	42.06 (23.18–99.41)
May	Hazard-rate	Cosine	Perch height	488.9	0.00	0.13	39.94 (21.91–40.93)
	Half-normal	Cosine	Perch height	490.2	1.30	0.16	26.39 (19.31–36.05)
	Hazard-rate	Cosine	—	499.1	10.20	0.22	30.77 (19.98–47.39)
June	Hazard-rate	Cosine	Perch height	594.3	0.00	0.16	54.37 (33.71–87.69)
	Hazard-rate	Cosine	—	598.4	4.10	0.17	52.91 (33.35–83.94)
	Half-normal	Simple polynomial	—	601.9	7.70	0.17	48.31 (30.33–76.94)
July	Hazard-rate	Cosine	Perch height	539.1	0.00	0.26	45.85 (20.95–170.37)
	Half-normal	Cosine	Perch height	546.3	7.20	0.27	49.98 (23.71–185.66)
August	Half-normal	Cosine	Perch height	701.9	0.00	0.43	51.22 (9.41–278.71)
	Hazard-rate	Cosine	—	709.4	7.50	0.43	43.37 (8.12–231.62)
September	Hazard-rate	Cosine	—	452.4	0.00	0.25	38.36 (22.14–59.70)
	Hazard-rate	Cosine	Perch height	456.1	3.70	0.22	31.58 (25.52–39.08)
	Half-normal	Simple polynomial	—	447.3	8.10	0.11	26.89 (21.99–32.89)
October	Half-normal	Cosine	—	585.6	0.00	0.31	37.75 (12.38–62.18)
	Hazard-rate	Cosine	Perch height	590.3	4.70	0.29	29.09 (12.56–67.37)
	Half-normal	Cosine	Perch height	594.2	8.60	0.28	20.23 (8.58–47.00)
November	Half-normal	Cosine	Perch height	676.6	0.00	0.23	69.29 (30.85–155.59)
	Hazard-rate	Cosine	—	681.1	4.50	0.37	63.58 (32.07–126.05)
December	Hazard-rate	Cosine	Perch height	724.5	0.00	0.34	67.54 (17.79–256.35)
	Half-normal	Cosine	Perch height	731.5	7.00	0.35	75.39 (20.09–282.96)

Table S3. Modeling approach used to estimate occupancy (ψ) and detectability (p) for Green Iguanas (*Iguana iguana*) at Club Miramar, Municipality of Barrancabermeja, Department of Santander, Colombia. Detectability was modeled using the top-ranked occupancy model (M4). The top-ranked models are bolded. K = number of model parameters, ΔAICc = difference in Akaike's Information Criterion corrected for small sample size, AICcWt = model weight, Cum.Wt = cumulative model weight, LL = Log Likelihood. Covariates codes as in Table S2.

Model	Occupancy	K	AICc	ΔAICc	AICcWt	Cum.Wt	LL
M4	**infra**	**3**	**248.04**	**0.00**	**0.33**	**0.33**	**—120.16**
M5	water	3	249.55	1.51	0.18	0.51	—120.77
M13	open + infra	4	250.69	2.65	0.09	0.60	—119.81
M14	water + infra	4	250.91	2.87	0.08	0.68	—119.92
M9	trees + infra	4	251.12	3.08	0.07	0.75	—120.02
M10	trees + water	4	251.53	3.49	0.06	0.80	—120.23
M12	open + water + infra	4	252.03	3.99	0.04	0.85	—120.48
M3	open	3	252.68	4.64	0.03	0.93	—122.48
M1	null (no variables)	2	252.80	4.04	0.04	0.89	—123.64
M2	trees	3	253.02	4.98	0.03	0.95	—122.65
M8	trees + open	4	253.51	5.47	0.02	0.97	—121.22
M11	open + water + infra	5	254.37	6.33	0.01	0.99	—119.69
M7	trees + open + water	5	254.97	6.93	0.01	1.00	119.98
M6	trees + open + water + infra	6	258.60	10.56	0.00	1.00	—119.48
Model	**Detection**	**K**	**AICc**	**ΔAICc**	**AICcWt**	**Cum.Wt**	**LL**
M16	**trees**	**4**	**226.51**	**0.00**	**0.85**	**0.85**	**—107.72**
M17	date + trees	5	229.94	3.43	0.15	1.00	—107.47
M15	date	4	250.69	24.18	0.00	1.00	—119.81