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Population estimate and conservation of the melanistic *Iguana iguana* population on Saba, Caribbean Netherlands

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Conservation management of natural populations is ideally based on the most accurate data of critical variables including demography, natural history and population size. Although Caribbean iguanids are highly threatened by a range of anthropogenic threats, the native melanistic *Iguana iguana* populations in the Lesser Antilles have received surprisingly little research attention. Here we assessed population size, distribution and degree of melanism for the melanistic iguanas of Saba, Caribbean Netherlands based on one month of fieldwork. Distance sampling (based on 117 separate surveys along 38 unique transects, totalling 48 survey hrs) estimated the island population size at 8233 ± 2205 (SD) iguanas. Female maximum snout-vent length (39.0 cm) of 56 captured iguanas was less than that of males (43.9 cm). Iguanas mainly occurred on the southern and eastern sides of the island, at mid-altitudes between 180 and 390 m (max 530 m), with highest densities being in residential and certain natural areas. Historically, iguanas have been reported from higher altitudes, where their presence was likely facilitated by former extensive forest clearing for agricultural reasons. Contrary to earlier statements claiming that 20% of adult males were fully melanistic, we found that only 1% of adult iguanas exhibited > 90% melanism, whereas 81% of males were less than 50% melanistic on the body. No relationship was found between the degree of melanism and elevation, which has been suggested by others. Probably, one main threat to the Saba green iguana population is the documented crossbreeding with non-native green iguanas. Beyond non-native iguanas, the long-term stability of the native population appears under pressure given the limited nesting sites and extremely low presence of juvenile and hatchling iguanas (2.4%). In particular, the island's feral cat and large goat population likely impact nest-site quality, nest success and hatchling survival.

Keywords: ecology, Iguanidae, Lesser Antilles, management, population assessment

INTRODUCTION

Effective conservation is ideally based on the most accurate data on critical variables including demography, natural history and population size (Mills, 2007). The lack of such basic data is especially acute for reptiles (Meiri & Chapple, 2016; Saha et al., 2018). A consequence of this absence of quantitative population data means over 80% of IUCN-assessed reptiles are categorised based solely on range criteria (Böhm et al., 2013; Saha et al., 2018). This is alarming, as population size has been identified as the most critical IUCN Red List metric (Traill et al., 2007; Frankham et al., 2014).

Insular endemic species have an elevated extinction risk given they have restricted distributions with small and 'closed' populations and are often ecologically 'naive' (Lomolino et al., 2017). Common threats include the introduction of new species, habitat destruction, exploitation (both for consumption and the frequently illegal trade) and stochastic mortality events like hurricanes or disease (Johnson & Winker, 2010; Medina et al., 2011; Meléndez-Vazquez et al., 2019; van den Burg et al., 2022a). In the West Indies, 80% of species extinctions have been attributed largely to biological invasions, and the region continues to be a hotspot of insular extinctions (Leclerc et al., 2018).

Within the context of extreme urgency for conservation action given a near absence of population data for the Saba green iguana *Iguana iguana*, this study's focus is on this island subpopulation of *I. iguana* that has been categorised as Critically Endangered following IUCN guidelines (van den Burg & Debrot, 2022). It has been proposed that the Saba native iguanas are part of a distinct species, *Iguana melanoderma* (Breuil et al., 2020). However, here we follow the taxonomic position of the Iguana Taxonomy Working Group (2022) and used in the IUCN assessment, which considers the Saba native iguanas to represent a subpopulation of *I. iguana*. Our decision is based predominantly on the fact that the dataset from Breuil et al. (2020) only represented a minor fraction of the range and diversity of the *I. iguana* species complex. Thus, statements on uniqueness are not substantiated.

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One main threat to this *I. iguana* population likely is the presence of non-native mainland iguanas on Saba (van den Burg et al., 2023), which are known to outcompete insular *Iguana* populations (e.g. Vuillaume et al., 2015; Knapp et al., 2021). During a one-month visit to Saba in 2021 (17 August–17 September) we conducted a preliminary assessment of population size and distribution across the island, examined melanism and morphology and collected other opportunistic data to provide a more quantitative baseline for this understudied iguana population.

MATERIALS & METHODS

Study area

Saba is a small Lesser Antillean island (13 km^2; 17.63° N, -63.23° W; Fig. 1) and home to ~2,000 people (Statistics Netherlands, 2021). Habitat types were recently mapped by de Freitas et al. (2016) and fall within the Caribbean dry forest biome (Portillo-Quintero & Sánchez-Azofeifa, 2010). The main geological characteristic of the island consists of an 870 m dormant volcano (Roobol & Smith, 2004) named Mount Scenery. The volcano causes uplift of air and adiabatic cooling, thereby creating a high presence of clouds and mist at elevations above 500–600 m. Below these rainforest-covered elevations, the natural vegetation is drier and less dense, representing xeric Caribbean forest and shrubland (Fig. 1). However, large areas of the valleys, several hills (e.g. Old Booby hill) and lower coastal areas are almost devoid of trees due to overgrazing by a large feral goat population that hinders forest recovery (de Freitas et al., 2016). Due to the overall steepness of the terrain, urbanisation has remained very limited in recent decades. Hence, aside from one coastal marine harbour, one airport and one coastal quarry area, urbanisation is largely limited to four small villages (The Bottom, St. John's, Windward Side and Zion's Hills) at elevations of roughly 300–500 m a.s.l. and most of the island (97%) remains free of anthropogenic infrastructure (Fig. 1). As permanent beaches are absent on Saba, soil for nesting by terrestrial breeders (like iguanas) is essentially limited to arid coastal scrub and forests, and these are highly affected by feral goats that reduce both soil presence and quality (de Freitas et al., 2016).

Population distribution and size

During our visit in 2021, we collected data on population density and distribution by means of transect-line surveys (Thomas et al., 2010). Iguanas are mostly territorial and largely site-bound with dominant males that defend their territories and a harem of several females (Rand et al., 1989; Rodda, 1992). Thus, animals do not migrate significantly on an annual basis, allowing a one-month population assessment to give a reliable assessment of population distribution, density and size, as long as sufficient area is covered in the various habitats. Based on knowledge of timing of reproduction in this population (Breuil et al., 2020; van den Burg, unpublished data), hatching takes place during June–July. Therefore, during our surveys we expected that the abundance of hatchlings would be relatively high compared to other seasons of the year and that female migration to nesting sites would be limited or absent.

During distance surveys (Thomas et al., 2010), a single observer surveyed 100 m transects for iguanas < 25 m on

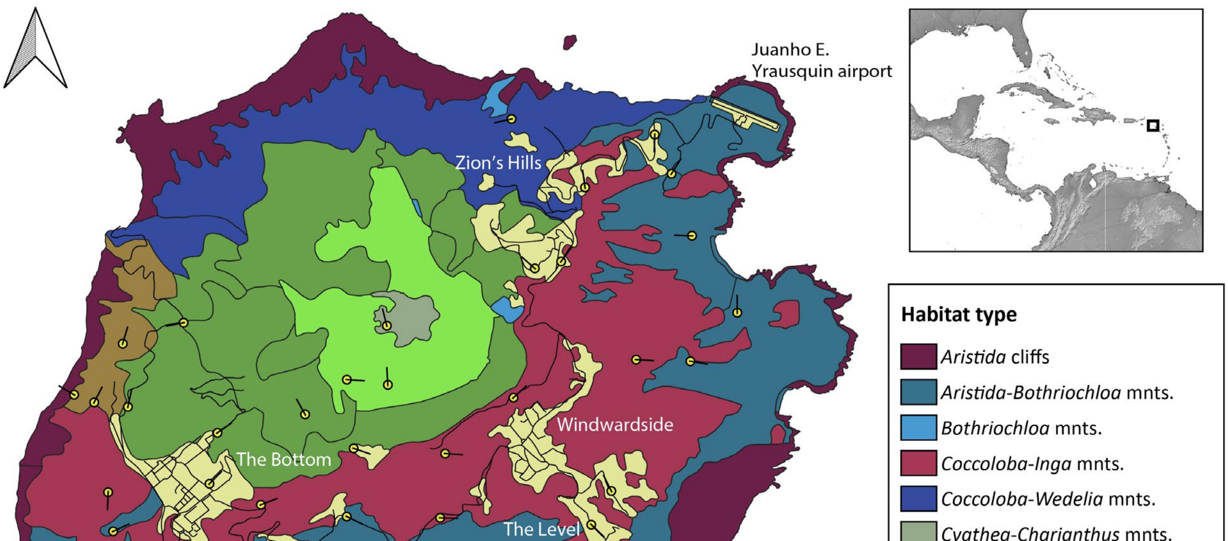

Figure 1. Distribution of transect lines across habitat map of Saba. Names indicate locations on Saba; towns, harbour and airport. Inset map shows location of Saba within Greater Caribbean region. Habitat types follow de Freitas et al., (2016).

Table 1. Data on survey transects and observed iguanas per vegetation type following de Freitas et al., (2016)

Vegetation type	Transect count	Iguana Sightings	
		Transect	Opportunistic
Aristida cliffs (C)	2	1	3
Aristida-Bothriochloa mnts. (M7)	11	99	172
Bothriochloa mnts. (M8)	0	0	0
Coccoloba-Inga mnts. (M6)	7	14	121
Coccoloba-Wedelia mnts. (M5)	1	0	1
Cyathea-Charianthus mnts. (M1)		1	0
Philodendron-Inga mnts. (M3)	4	9	9
Philodendron-Marcgravia mnts. (M2)	2	0	0
Swietenia mnts. (M4)	2	0	2
Urban areas (U)	8	54	172
Total	**38**	**177**	**480**

both sides of the transect. We used the vegetation type classifications and distributions described by de Freitas et al. (2016) to model the habitat-specific abundance of iguanas. We did not survey the vegetation type *Bothriochloa* mountains, as it is restricted to a very small and inaccessible area of the island (Fig. 1). Across the other vegetation types, 38 transects were roughly distributed according to their proportional surface coverage and the precise transect locations within each vegetation type were randomly assigned (Table 1). We surveyed the north-western side of the island to a lesser extent due to time limitations and limited trail access given ongoing goat-eradication efforts.

We surveyed each transect a minimum of three times, between 07.00 and 17.00 h based on observations of local diurnal activity patterns (Breuil et al., 2020). Generally, iguanas emerge from their refuges to bask as soon as the sun is out, although some animals can emerge later since the complex geography of Saba can leave areas shaded during the first hour of daylight. Generally, during the early hours (07.00–09.00 h) they sit on sun-exposed areas close to their rock lairs, while during late morning to midday hours they tend to move about in the vegetation to feed (van Marken Lichtenbelt & Albers, 1993). Finally, in the afternoon, animals tend to congregate on sun-exposed spots adjacent to their night-time lairs. Although the covariates time and day are included within the analyses, we performed the different surveys for each transect at different times and made sure we had roughly equal intervals between subsequent surveys per transect. The average time interval between subsequent surveys of the same transects was 7 days (SD ± 1.2; 2–12 day intervals). Upon detection, we estimated the perpendicular distance of the iguana from the centre of the transect, to the nearest metre.

Analysis of transect-derived distance data first entailed examining histograms of the raw data in the R package Rdistance (McDonald et al., 2019; R Core Team, 2022) to identify clumped detections or outlying observations at minimum or maximum distances in order to apply an appropriate level of truncation. We then applied a right truncation (w = 20 m) to the data (Buckland et al., 2001). Following truncation, detection function curves were fit to the data using the key function + adjustment terms and the Akaike Information Criteria (AIC) was used to select between competing models (Anderson et al., 2008). Then we examined the goodness-of-fit (GOF) of each model. Based on the most parsimonious model, we subsequently derived an estimate of iguana population size in each vegetation type and extrapolated the results across the entire island (13 km^2). We determined model precision using 95% confidence intervals (CI) and a coefficient of variation (CV), with a CV of 20–30% being chosen as the preferred measure of precision. Subsequently, we used multiple covariate distance sampling to model the detection curve as a function of distance and one or more of the following covariates: survey time (minutes), elevation (m), height (of iguana) above ground (m), and 'weather'. We discretised the covariate 'weather' for each transect as follows: 0 = no clouds; 1 = < 25% cloud cover; 2 = 25–75% cloud cover; 3 = 75–100% cloud cover. Low numbers of detections within given surveys made fitting of detection functions difficult and resulted in a low precision of estimates, especially when the data were separated into different vegetation types. Consequently, additionally to these estimates per habitat type, to obtain a single population estimate across the survey area we pooled distance data across all surveys and vegetation types, with the exception of the habitat types M1 and M2 which occur at highest elevation where iguanas are largely absent. Finally, after selecting the most parsimonious model we performed 1,000 iterations to obtain stratified bootstrapped estimates.

Size, melanism and morphology

Handling vertebrates on Saba is not regulated by any animal welfare regulations but all work was done under auspices of the local nature management authority, the Saba Conservation Foundation, and under a permit from the Island Council (#663/2021). Iguanas were caught by hand or using a traditional pole and noose, and released after data collection.

Breuil et al. (2020) identified two phenotypic characteristics as particularly important in differentiating the Saba green iguana from other (possible) species or subspecies of *I. iguana*. These are: a) the size ratio between the tympanum and subtympanic plate, and b) the high extent of melanism of the lateral spot, head and body. We set out to test the supposed diagnostic utility of these characteristics, and to test our hypothesis that melanism varies with elevation on Saba. First, we took lateral photographs of the entire body and head using either a 300 mm telephoto lens, a 35 mm macro lens, or a phone camera for captured animals. From these pictures we assessed the degree of melanism using one or two pictures that together showed a complete lateral view of each individual., We assumed that colouration was symmetrical on both sides of each animal. As melanism appears to increase with age (Breuil et al., 2020; this study), by eye we estimated the percentage of melanistic skin surface in larger adults (snout-vent length [SVL] > 25 cm), separately for the head and body. Life stage classes are considered based on SVL; adults ≥ 20 cm, subadults ≥ 15 | < 20 cm, juveniles ≥ 10 | < 15 cm, and hatchlings < 10 cm. We classified melanism (all black) according to four percentage categories: 1) 0–25, 2) > 25–50, 3) > 50–90, and 4) > 90–100%. These latter two categories were chosen as we especially wanted to categorise animals with (near) complete melanism. Additionally, we recorded whether the lateral spot on the head between the eye and tympanum was melanistic (Breuil et al., 2020). Secondly, for the ratio analysis, we measured three variables for each captured animal. Using a calliper, we measured the maximum height of the tympanum and of the subtympanic plate to the nearest hundredth of a mm. Using a wooden measuring stick we recorded the SVL to the nearest mm. We then assessed the relation between the tympanum-subtympanic plate ratio and SVL for size-dependence using linear regression.

Data handling and analyses were performed in Rstudio Version 1.2.5033 (Rstudio Team, 2019). Basemaps were created in QGIS 3.8.0-Zanzibar (QGIS.org, 2022) and finalised in Adobe Illustrator 25.3.1 (Adobe Inc., 2019).

Additional opportunistic data and observations

We further opportunistically recorded all iguana presence and GPS locations for animals detected outside assigned transects, and determined sex based on body ratios and overall appearance. To prevent double counts, we only recorded the maximum number of iguanas sighted in a single location. Iguanas display strong sexual phenotypic differentiation, for example in terms of dorsal-spine size and head width (Dugan, 1982; Rodda, 1992; van den Burg et al., 2023). As a consequence, subadult and adult iguanas can, if properly sighted, be reliably sexed from a distance without closely examining femoral pores or hemipenial eversion. Iguanas mapped opportunistically were not used in our distance sampling population assessment. While performing fieldwork, we also collected data on nest site presence, size, threats (e.g. presence of non-native predators), and road kills. Lastly, to generate additional insights into such aspects as habitat and land-use changes over time, we informally solicited information on the iguana population from local residents and the park management authority, the Saba Conservation Foundation. Finally, opportunistic nocturnal surveys for hatchling and juvenile iguanas were conducted using a high-grade head torch (> 800 lumens) for three survey hours over three nights (9 hrs total) divided among four areas (the harbour, southside of the Bottom, Windward Side, and Upper Zion's Hills; Fig. 1).

RESULTS

Population distribution and size

Overall, we performed 117 unique transect surveys totalling 48 survey hours across 38 transects. Respectively, 35 and three transects were surveyed three and four times. During these search efforts we made 177 iguana detections (Table 1), of which 87 were female, 51 were male and 39 were of undetermined sex. The latter concerned animals either not properly sighted or smaller animals in which sexual dimorphism was not yet reliably developed. Survey-counted iguanas included 168 adults, three subadults, two juveniles and four iguanas of unknown life stage. Among survey transects, most iguanas (n = 44) were encountered on transect #4, located halfway between the main road and coast along the Gilles Quarter trail within *Aristida-Bothriochloa* mountains vegetation. The majority (56%) of transect-counted iguanas were encountered within this habitat type, followed by urban areas (31%) (Table 1).

Encounter rates were estimated at an average of 23.16 ± SE 5.39 iguanas/100 m transect across the entire survey region. Based on GOF tests and minimisation of AIC, the uniform model without series expansion and the half-normal key function with cosine series expansion both

Table 2. Top five-ranked detection models using conventional (CDS) and multiple-covariate (MCDS) distance sampling for iguana line transect surveys on Saba, Caribbean Netherlands, in August –September 2021. Distance data right truncated at w = 25 m. Superscripts concern: 1) UN = uniform; HN = half-normal key function; HR = hazard-rate; 2) COS = cosine; SP = simple polynomial series expansion; 3) Time = survey time; Elev = elevation (m), Weather = 0, no clouds; 1, < 25% cloud cover; 3, 25–75% cloud cover; 4, 75–100% cloud cover; Height = height of iguana above ground (m); 4) Number of parameters; 5) Goodness-of-fit.

Method	Key[1]	Series[2]	Covariate[3]	AIC	ΔAIC	k[4]	GOF[5]
CDS	UN	-	-	523.66	0	1	0.19
	HN	-		525.49	1.83	1	0.21
	HN	COS		525.49	1.83	1	0.21
	HR	-		526.04	2.38	2	0.28
	HR	SP		526.04	2.38	2	0.28
MCDS	HR	-	Time	520.67	0	3	0.18
	HR	-	Elev + Time	521.18	0.51	4	0.09
	HN	-	Time	522.00	1.33	3	0.22
	HN	-	Time + Weather	522.04	1.37	4	0.22
	HR	-	Elev + Time + Weather + Height	522.72	2.05	6	0.06

Table 3. Stratified bootstrapped estimates of total abundance (left) and density/km^2 (right) per habitat for the conventional distance sampling model

	Abundance					Density (iguanas per km^2)				
	Mean	**SD**	**LCL**	**UCL**	**CV**	**Mean**	**SD**	**LCL**	**UCL**	**CV**
C	2053.16	1639.99	0	5013.24	1.00	156.73	125.19	0	382.69	1.00
M1	0	0	0	0	0	0	0	0	0	0
M2	0	0	0	0	0	0	0	0	0	0
M3	9523.83	6862.57	0	26425.19	0.72	727.01	523.86	0	2017.19	0.72
M4	0	0	0	0	0	0	0	0	0	0
M5	0	0	0	0	0	0	0	0	0	0
M6	6501.53	4311.34	878.01	16434.47	0.61	496.30	329.11	67.03	1254.54	0.61
M7	10592.53	3326.75	4686.66	17826.74	0.36	808.59	253.95	357.76	1360.82	0.36
Urban	19922.09	8015.76	5442.66	36233.81	0.36	1520.77	611.89	415.47	2765.94	0.36
Total	**8233.48**	**2204.86**	**4554.74**	**12997.69**	**0.25**	**628.51**	**168.31**	**347.69**	**992.19**	**0.25**

provided adequate fits to the distance data (ΔAIC < 2; Table 2). Models that included the covariates survey time, elevation + time, and time + weather also received support from the distance data (ΔAIC < 2; Table 2). However, we decided to retain the model without covariates (half-normal with cosine series expansion) based on the best GOF and lowest CV. Stratified bootstrapped estimates for this model provided a mean density across the entire survey region of 628.51 ± 168.31 SD iguanas per km^2 (Table 3). Lastly, bootstrapped abundance estimates suggest a total island iguana population of 8,233 ± 2,205 SD animals (adults and subadults).

Size, melanism and morphology

A total of 474 adult iguanas were photographed across Saba (Fig. 2). Of these, 56 were first opportunistically caught by hand using a stick and lasso (n = 54) or by using cage traps baited with fruit (n = 2). Two additional animals were collected as road kills. Snout-vent length of the 56 captured iguanas (50 adults and six hatchlings) ranged from 9.1 to 43.9 cm, with the female maximum SVL (39.0 cm) lower than that of male iguanas (43.9 cm).

Body positioning of the 474 photographed iguanas did not allow us to characterise 139, 162 and 179 individuals, respectively, for the lateral spot, head and body melanism. For head melanism, 79% of 309 characterised iguanas demonstrated over 50% melanism, whereas for body melanism 81% of 295 characterised iguanas demonstrated less than 50% melanism (Fig. 3). Figure 4 shows a male and female Saba green iguana both with > 90% head melanism, and < 50% and > 90% body melanism, respectively. As data was not normally distributed, Bonferroni-corrected pairwise Wilcox tests indicated there were no significant ($p < 0.05$) differences in elevational distribution of the degree of melanism of iguanas for either head or body melanism (Fig. 3). Visual assessment of melanism % on a map did not indicate any geographic clustering among melanism groups. Only five individuals lacked the facial black spot (1.5%); these animals were classified as likely non-native given their overall lack of melanism, raised nasal scales and divergent colouration of body, head and eyes.

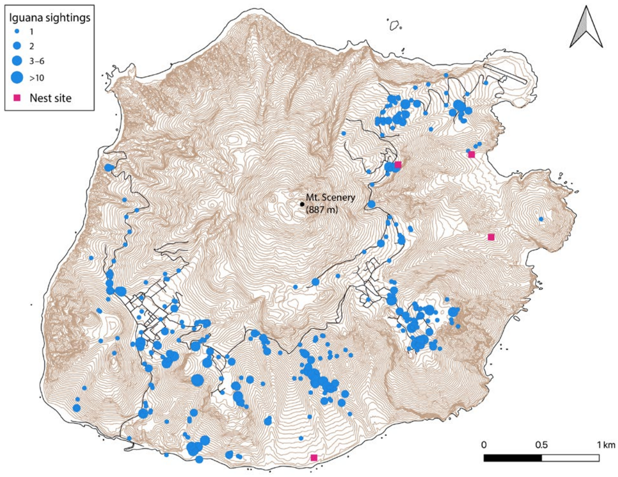

Figure 2. Distribution of sighted iguanas and nest sites across Saba. Data represent both opportunistic sightings and those observed during surveys, n = 657. Contour lines at 10-metre intervals.

We were able to calculate the ratio between the height of the subtympanic plate and the tympanum for 44 adults (> 20 cm SVL). This ratio ranged from 1.03 to 1.84, with two outliers on either extreme (0.92 and 2.22); the ratio was SVL-dependent. This regression line yielded an R^2 = 0.24 with formula $y = 0.711 + 0.0021x$.

Additional opportunistic data and observations

Opportunistic sightings recorded outside transects totalled 480 iguanas, including 453 adults, 13 subadults, five juveniles, eight hatchlings and one of unknown life stage (Fig. 2). Of these, 181 were females, 138 males, and the sex of 161 iguanas was unknown. All except one of the eight hatchlings encountered were observed during opportunistic nocturnal surveys. In contrast, we observed only a single non-hatchling iguana after sunset, as adults appeared to return to their rock lairs at night while juveniles remained detectable in the vegetation. Opportunistic iguana sightings were mostly from urban areas and the *Aristida-Bothriochloa* mountains. vegetation type (each

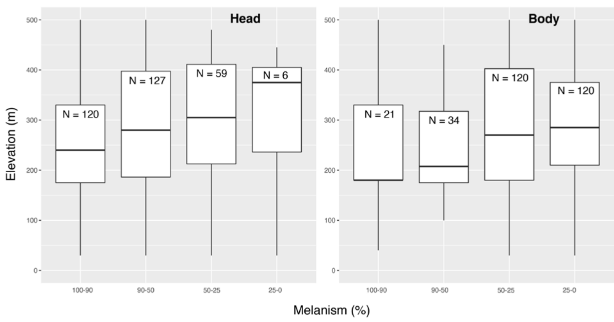

Figure 3. Elevational occurrence of melanism presence in iguanas on Saba, separated by head and body melanism

Figure 4. Photo of a male (left) and female (right) adult Saba green iguana on Saba. Both individuals were assigned > 90% head melanism, and body melanism < 50% and > 90% for the male and female, respectively

n = 172; Table 1). Considering all observations (n = 657), elevational limits of iguanas ranged from 5 to 530 m above sea level, with half of all sightings recorded on elevations between 180–390 m. Juveniles and hatchlings represented 2.4% of all iguanas observed on Saba.

We were also able to locate and map four communal nesting sites (Fig. 2). A commonality was their location in relatively barren, afternoon sun-exposed, soil-dominated areas with good drainage. From 2 to 15 emergence holes were encountered at each site (Fig. 2).

DISCUSSION

With only few remaining native Iguana populations in the Lesser Antilles, understanding their population sizes, distribution, natural history and threats is important. Here, we provide a first baseline population assessment of the melanistic *I. iguana* population of Saba, Caribbean Netherlands. This work provides a robust baseline for continued research and highlights essential conservation and research priorities.

Population distribution and size

Without further knowledge regarding other factors, such as the critical availability of genetic diversity in the population, the minimum viable population size for long-term survival of a population is more generally set at 5,000 individuals, even though this figure may differ considerably between taxa and is very difficult to accurately estimate (Flather et al., 2011). We provide a rough estimate of the population on Saba as 8,233 ± 2,205 SD individuals. This contrasts sharply with the neighbouring St. Eustatius *I. delicatissima* population of ~500 individuals, for which a costly captive propagation was proposed (Debrot et al., 2013). Our results suggest that on Saba such a measure might not be necessary. Thus not only do our findings provide a robust baseline for continued monitoring of population size and age structure, but they can be of practical value in determining conservation priorities as well.

Our population size estimate is in sharp contrast with the preliminary low population size estimates presented by Powell (2006) and Breuil et al. (2020), with the latter estimating a population size of 400 individuals for the Saba and Montserrat populations combined. While performing fieldwork on Saba in 2012 previous authors found iguanas to be fairly abundant (Debrot & Boman, 2013) and our count of unique individuals based on our coverage of a small portion of the island already far exceeded Breuil et al.'s (2020) estimate. So, while our average estimate of ~8,000 animals is certainly far from precise, when extrapolating these data to the whole island the population size clearly must be much higher than that estimated by Breuil et al. (2020).

Our population estimate is preliminary and based on a limited dataset collected within a short timeframe outside of the reproductive season. Although we believe the true population size lies in the lower part of our estimated range, given the high variability of within-habitat population estimates (e.g. de Infante Anton et al., 2013), high CVs and seeming absence of iguanas in some areas from habitats with high abundance estimates (Table 3), we present the first quantitative population size estimate for the Saba green iguana population. For future comparisons, it is important to note that our data collection occurred four years after the 2017 hurricane season, which was the strongest-recorded Atlantic hurricane season on record and heavily affected species and populations, such as both forests and the Red-bellied racer *Alsophis rufiventris* population on Saba (Eppinga & Pucko, 2018; Shultz et al., 2018; Madden & Mielke, 2021). Also the neighbouring iguana population on St. Eustatius (van den Burg et al., 2022a) was strongly affected by the 2017 hurricane season, with the population showing little-to-no sign of recovery as of late 2019. Therefore, our data from the Saba iguana population, which is larger than the St. Eustatius population, could represent those of a recovering population.

Despite the rather large apparent population size, our dataset includes a low number of observed non-adult iguanas and only few hatchlings were spotted during nocturnal surveys. Notably, we performed our fieldwork during a period of high expected hatchling occurrence, given that the hatching season is (most likely in June; pers. observations authors). Hence, we suspect that the low abundance of hatchlings follows from the very limited availability of suitable nesting sites, which likely are strongly and negatively impacted by the large feral goat population (Lotz et al., 2020). However, whether and to what extent hatchlings on Saba sleep in burrows (and would not have been observed during nocturnal surveys) is unknown. Given the additional stressors of an island-wide feral cat population that increased between 2000–2010 (Debrot et al., 2014), iguana nesting and recruitment might be further restricted on Saba.

Concerning distribution, Lazell (1973) indicated that iguanas were common across Saba, including at high elevations around the summit of Mt. Scenery. This is apparently no longer the case. Although Breuil et al. (2020) observed iguanas at a maximum elevation of 500 m at The Level and suggested that a population of iguanas could not be present due to high moisture and cloud presence at similar heights (400–500 m) on Mt. Scenery, our findings of iguanas throughout the island of Saba but only to a maximum elevation of ~550 m suggest that iguanas occur in a smaller area than that observed by Lazell (1973) but wider than presented by Breuil et al. (2020).

The majority of iguana detections were at elevations of 180–390 m, where habitat types M6, M7, as well as urban areas are most abundant (de Freitas et al., 2016). Although we were unable to visit the north-western region (windward side of the island) as mentioned above, interviews with the Saba Conservation Foundation and numerous residents indicated that iguanas do occur in that area, although likely at low densities. We thus argue that, according to IUCN mapping guidelines (IUCN, 2021), the species is present across the island (Figs. 2 & 3), except at elevations higher than 550 m.

During the limited time that we conducted surveys, we did not detect iguanas in vegetation types M1 (*Cyathea-Charianthus* mountains), M2 (*Philodendron-Marcgravia* mountains), M4 (*Swietenia* mountains) or M5 (*Coccoloba-Wedelia* mountains). Iguanas might not occur in vegetation types M1 or M2, with elevations > 550 m and lower temperatures may not be favoured. However, dense vegetation in these areas likely makes detection more difficult than in habitats at lower elevations, and we recommend that any future comparative assessments include these vegetation types. No iguanas were detected in vegetation type M4 during fieldwork; however, they are considered to occur there in low densities based on opportunistic sightings. Similarly, no iguanas were detected in M5; however, access to the area was severely restricted due to ongoing goat removal actions and thus little can be said about their possible occurrence there. Iguanas were detected in vegetation types C (*Aristida* cliffs), M3 (*Philodendron-Inga* mountains), M6 (*Coccoloba-Inga* mountains), M7 (*Aristida-Bothriochloa* mountains), as well as in urban areas, suggesting that they can persist in fragmented and degraded habitats and among humans, despite the associated risks of mortality such as vehicles, fences, cats and dogs (Smith et al., 2007; Knapp et al., 2016; van den Burg et al., 2018a). Actual exploitation of iguanas for consumption is likely no major risk as locals, with minor exceptions, do not eat iguanas. Some guest labourers from regional islands (e.g. Haiti, Dominican Republic) do occasionally consume iguanas (Saba Conservation Foundation, pers. communication). A recommended social study on this topic would provide actual data on the occurrence of iguana consumption and insights on the extent of this threat.

Size, melanism, and morphology

Although Breuil et al. (2020) described *I. melanoderma* with melanism as the most distinct characteristic, its extent per individual differs and increases with age, but a black spot between the eye and tympanum is present from a very early age. Lazell (1973) estimated that ~20 % of adult males were completely melanistic. Here we provide additional data on melanism in the Saba population, which is regarded as more melanistic than the population on Montserrat (Breuil et al., 2020). These data demonstrate that melanism is most clearly represented on the head, with 79% of all photographed and characterised adults (n = 312) showing > 50% head melanism. Contrarily, melanism is much more limited on the body as 81% of all photographed and characterised adults for this feature (n = 295) showed less than 50% melanism. Among adult male iguanas (n = 100), 2% had > 90% body melanism and 1% had both > 90% body and head melanism, whereas 9% of adult females (n = 135) had > 90% body and head melanism. Although numerous adults appear to have body melanism, the scales often are actually dark brown but might also be dark reddish. The characteristic black facial area as assigned to *I. melanoderma* by Breuil et al. (2020) was absent in five individuals on Saba, all of which also showed a divergent head and body colouration. Previously, we assessed the geographic origin of four of these iguanas from Saba using microsatellite data (van den Burg et al., 2021) and demonstrated their non-native origin (van den Burg et al., 2023).

Using open-source images on the internet, Breuil et al. (2020) proposed that non-native iguanas are likely present on Isla Margarita (Venezuela). Our assessment suggests that not all iguanas meeting the 'black spot' criterion for *I. melanoderma* are unequivocally melanistic, and considerable variation is present. Hence, given this seemingly inherent variability without any genetic data, we suggest that determining the presence of non-native iguanas becomes more complicated than what can be done based solely on photographs. Complicating the matter further, the phenotypic variability of iguana populations in the geographical source region for Saba and Montserrat (insular and continental Venezuela; Stephen et al., 2013) may be inherently variable, resulting from periods of isolation and connectivity due to sea level changes during the ice-ages (Mayle et al., 2009). This means that an integrative assessment is critical to detect and remove non-native iguanas (van den Burg et al., 2023) before they can threaten the genetic integrity of native island subpopulations.

Melanism can provide an adaptive advantage to ectotherms in cooler climates, as well as provide UV protection at high elevations (Clusella Trullas et al., 2007; Reguera et al., 2014). Our data, however, do not support such explanatory mechanisms for the melanistic Saba population given the absence of a trend between percent melanism and elevation (Fig. 3). We thus propose that the most parsimonious reason these iguanas exhibit melanism is that the population originated from melanistic iguanas from the northern region (mainland or islands) of Venezuela, as suggested by genetic data (Stephen et al., 2013) and as based on the findings by Breuil et al. (2020).

Breuil et al. (2020) stated that the ratio between the height of the subtympanic plate to the tympanum in *I. melanoderma* reaches 2–2.5 in large adults. However, the authors provided no mention of sample size or measurement methodology, nor was the definition of a 'large adult' provided. Here, we assessed this ratio in 44 adults and found that only a single male (35 cm SVL) had a ratio higher than 1.84 (2.22). Considering the retrieved ratio-SVL regression, a 'subtympanic plate to tympanum' ratio of two is expected for iguanas with a SVL of 61.4 cm. Although Breuil et al. (2020) might have captured larger iguanas than those present in our dataset, maximum SVL for *I. iguana* across its range are ~45–58 cm SVL (Fitch & Henderson, 1977; Dugan, 1982; McCranie et al., 2005). Breuil (2013) proposed a set of useful morphological characters to differentiate *I. delicatissima* and *I. iguana*, their hybrids, and several insular *I. iguana* populations. These were proposed as "determinable from photographs", including the 'subtympanic plate to tympanum' ratio. Although photographs have been used for morphological purposes by other authors (Stevens et al., 2007; Lehtinen et al., 2020) as well as for distribution studies in *I. iguana* (van den Burg et al., 2020; Mo & Mo, 2022), we question their use for non-meristic, size-related characteristics. Namely, for an accurate comparison of two measures within a single 2D-photograph, these measures must lie within the same 2D-field relative to the camera sensor. However, especially (large dominant) adults have swollen lower jaws that 'push' the subtympanic plate out towards the observer, effectively exaggerating its size compared to the tympanum. Therefore, while the use of 2D photographs may be useful for preliminary assessments, we highly recommend the use of actual measurements on captured animals as in this study.

Clutch sizes and nest sites

Clutch size within *Iguana*, as for most reptilians, is SVL-dependent but differs per population, seemingly due to climate and food availability (Novosolov et al., 2013). For example, iguanas in Central America lay much larger clutches than iguanas on the arid islands of Aruba, Bonaire and Curacao (van Marken Lichtenbelt & Albers, 1993), and *I. delicatissima* x *I. iguana* hybrids lay larger clutches than pure *I. delicatissima* (van Wagensveld & van den Burg, 2018). For the melanistic populations on Saba and Montserrat, only Blankenship (1990) provided information on clutch size (15–30 eggs) but without an indication of the sample size. We dissected a single road-killed gravid female (32.5 cm SVL) that had 29 well-developed eggs. As larger females are present on Saba, maximum clutch size within this population is likely > 30. Successful nesting and recruitment are essential for population size maintenance and long-term survival (Bock et al., 2016; Warret Rodrigues et al., 2021). As we identified only four communal nesting sites, we suggest that these appear to be limited on rocky, volcanic Saba, and might be particularly negatively affected by the large feral goat population, a species known to aggregate on and destroy iguana nesting sites (Diaz, 1984; Alberts, 2004). As all communal nesting sites were located in sparsely vegetated areas of shallow-sloping surface topography (Fig. 2), these data provide useful insights for high-priority follow-up studies as to which areas may harbour additional nesting sites.

Conservation

Long-term conservation of the Saba green iguana population is challenged by several factors that impact other iguanid species as well. Firstly, the presence of several non-native iguanas on Saba should be considered as especially alarming due to the risk of competition and crossbreeding with native iguanas (van den Burg et al., 2023). Rapid action is being undertaken to map the distribution of non-native iguanas and plan their subsequent removal. Secondly, the upcoming construction and increased import of construction materials for a new harbour on the island will likely affect the local iguana population, since cargo imports are known to cause the introduction of non-native iguanas (van den Burg et al., 2018b; 2020; Breuil et al., 2019). Additionally, iguanas were not thoroughly included in the environmental impact assessment for the planned harbour, and therefore it is unknown whether the proposed location holds iguana nesting sites. Thirdly, Debrot et al. (2014) demonstrated the presence of iguana bones in the faeces of feral cats on Saba; hatchling and juvenile iguanas are especially vulnerable to cat predation (Iverson, 1978; Mitchell et al., 2002; Wilson et al., 2004; van den Burg et al., 2018a). Lastly, the suggested illegal trade in iguanas from Saba (Noseworthy, 2017; van den Burg & Weissgold, 2020) has recently been confirmed (Mitchell et al., 2022), highlighting the need for a temporary trade ban until legislation and enforcement is improved (van den Burg et al., 2022b). Additional data to more fully assess these actual and potential threat factors are hence urgently needed for improved conservation insights and more effective management decisions.

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Author Contributions

MPB and AOD conceived the ideas, designed the methodology and acquired the funding; MPB collected the data; HM led the data analyses, MPB co-led data analyses; MPB led to the writing of the manuscript, AOD and HM co-led writing of the manuscript. All authors contributed critically to the drafts and gave the final approval for publication.

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