

Morphometrics aid identification of non-native iguanas to improve conservation of native Saba Green Iguanas, *Iguana iguana* (Linnaeus, 1758)

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Abstract. The Lesser Antilles are part of the Caribbean biodiversity hotspot with relative high levels of diversity, also within the genus *Iguana*. However, these islands and their native *Iguana* populations are equally known for presence of invasive alien species, including non-native Green Iguanas. These threaten native iguanid populations through displacement and competitive hybridisation. The most recent island where the presence of non-native iguanas has been identified is Saba, Caribbean Netherlands. To aid rapid identification of non-native iguanas and potential future arrivals, we assessed the presence of morphometric and meristic differences between native Saba Green Iguanas and non-native Green Iguanas from neighbouring St. Martin. The latter is a shipping hub for the northern Lesser Antilles and the main source of non-native iguanas to surrounding islands as iguanas hitch rides in materials shipments. Our results show 13 morphometric size-dependent characters that significantly differ between both populations. Furthermore, we identified that Saba Green Iguanas have larger and fewer femoral pores compared to the non-native iguanas of St. Maarten. To more accurately identify non-native iguanas on Saba, we highlight that in addition to colouration, the relative size of the dorsal spines and the subtympenic plate, as well as the lengths of the head and snout are useful. These characters are often clearly visible and aid rapid in-situ assessments from a distance without the necessity to capture an individual. Given the currently poor biosecurity on Saba, and the upcoming increased volume of materials to be shipped to the island for construction of a new harbour, these additional diagnostic characters should prove useful in combatting the expected surge in incursions of non-native iguanas.

Keywords. Caribbean, Extinction, Green Iguana, Hybridisation, Lesser Antilles

Introduction

Invasive non-native species can pose a significant threat to species and ecosystems causing biodiversity loss and ecological disruption (e.g., Strayer, 2010; Vilá et al., 2011; Bellard et al., 2016), especially on islands (e.g., Reaser et al., 2007; Tershy et al., 2015), such as in the Caribbean biodiversity hotspot region (Gleditsch et al., 2022). This holds true for Caribbean iguanid populations, which are impacted by a range of non-native vertebrate species. These include direct harm or predation by rats, cats, dogs and mongoose, as well as

negative impacts by goats, sheep and donkeys through direct competition for food, and habitat and nest site degradation (Iverson, 1978; Diaz, 1984; Mitchell et al., 2002; Alberts, 2004; Anderson et al., 2010; Wilson et al., 2016). However, also closely related taxa can be a severe threat (e.g., Moss et al., 2018), in particular non-native Green Iguanas which are negatively impacting native *Iguana* populations across the Lesser Antilles because of hybridisation.

Native *Iguana* populations within the Lesser Antilles constitute either *Iguana delicatissima* Laurenti, 1768 or populations that are part of the *Iguana iguana* (Linnaeus, 1758) species complex; Saba, Montserrat, St. Lucia, St. Vincent and the Grenadines and Grenada (ITWG, 2016). However, non-native Green Iguanas have been present within this region since at least the 1860's (Vuillaume et al., 2015), when iguanas from French Guyana were introduced to Les Saintes, part of the Guadeloupe Archipelago. Since then, additional introductions of Green Iguanas from varying geographic origins have been recorded on numerous islands (e.g., Censky et al., 1998; Morton, 2008; Breuil et al., 2019; van den Burg et al., 2020, 2025a; Pauwels and

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Courtoy, 2024), with Montserrat being the only main island from where non-native incursions appear absent (van den Burg et al., 2023). The negative impact of these non-native iguanas on native iguana populations first became evident between 1995–2000 (Day and Thorpe, 1996; Breuil, 2000; Day et al., 2000), through the notion of replacement and preliminary data on hybridisation between non-native Green Iguanas and native *I. delicatissima*. Concerns about hybridisation between non-native Green Iguanas and native insular populations of the *I. iguana* complex were expressed later (Morton and Krauss, 2011; Breuil et al., 2019; van den Burg et al., 2025a).

Rapid identification of non-native species is crucial for their effective management. However, such efforts are challenged when closely related and morphologically similar native and non-native species hybridise and produce fertile offspring that can resemble either parental species (Holsbeek et al., 2008; Haynes et al., 2012). Considering non-native Green Iguanas and *I. delicatissima* and non-native *Iguana* in the Lesser Antilles, Breuil (2013) addressed morphological characters that could distinguish between these iguanas (Breuil, 2013), and Vuillaume et al. (2015) showed the presence of wide-spread introgression between *I. delicatissima* and non-native Green Iguanas. Recently, morphometric characters were identified to discriminate between *I. delicatissima* and non-native Green Iguanas (van den Burg et al., 2024). Compared to *I. delicatissima*, less attention has been given towards the morphological differentiation between native Lesser Antilles populations of *I. iguana* and non-native *I. iguana* and their hybrids (but see Morton and Krauss 2011; Breuil et al. 2019; and van den Burg et al. 2023).

Contrary to *I. delicatissima*, the threat of hybridisation with non-native Green Iguanas for the Saba Green Iguana was only identified in 2021 when non-native iguanas were seen on Saba (van den Burg and Debrot, 2022; van den Burg et al., 2025a). The Saba Green Iguana population is native to Saba and belongs to the *I. iguana* species complex (Stephen et al., 2013; ITWG, 2016). Although the Saba population has been proposed to belong to another taxon, *Iguana melanoderma* Breuil et al., 2020, here we consider the Saba Green Iguana population as part of *Iguana iguana iguana* following ITWG (2022). This on-island threat has initiated eradication efforts through which at least 20 non-native iguanas have been removed as of March 2025. However, as efforts have been sporadic, an island-wide assessment for non-native iguanas and their distribution

is overdue. Such efforts would be aided using diagnostic morphometric data to more effectively identify non-native iguanas. Although a few non-native iguanas have already been morphologically compared to native Saba Green Iguanas, that dataset was preliminary with < 10 non-native iguanas (van den Burg et al., 2023). Therefore, we provide a more substantial morphometric dataset and comparison between native Saba Green Iguanas, and non-native Green Iguanas from neighbouring St. Maarten, from where these originate (Debrot et al., 2022; van den Burg et al., 2023, 2025b).

Methods and Materials

We performed fieldwork on Saba (2021–2024) and St. Maarten (March 2024) where we captured iguanas using a noose and rope or by hand. We used visual characters to determine sex; presence of large femoral pores and hemipenes for males. Native iguanas on Saba were identified through colouration and genetic data (van den Burg et al., 2023, 2025a). Thereafter we collected morphometric data on 18 characteristics explained below, following van den Burg et al. (2023, 2024). We measured snout-vent length (SVL) and tail length using a stick measure placed on a flat surface, and placed the iguana ventrally on top of that. Other measures were taken using a digital calliper to the nearest 0.01 mm; lengths of the upper and lower front leg, upper and lower hindleg, the 4th toe, head, snout, mouth, eye, and mid-body spine. Also head width and depth, tympanum height and width, and the height and width of the subtympenic plate were measured. Measurements were collected from the right side of an iguana's body by the first author. Thereafter, and prior to release at the capture location, we took photographs of the 4th toe on the hind claw, the femoral pores, and all sides of the head. From these photographs we subsequently collected data on the number of femoral pores and digital scales on the 4th toe.

For analysis, we first individually assessed normality and equality of variance for all length characteristics, which showed SVL-dependent characters lack allometry. For iguanas with ≥ 20 cm SVL (representing late subadults and older life stages), we then assessed the SVL-dependence per island population through linear regressions. Subsequently, we used ANCOVA tests with SVL as a covariate, to assess differences across these characteristics in SVL-dependence between sexes on each island, as well as between the Saba Green Iguana and St. Maarten Green Iguana populations. We then combinedly assessed all length characteristics through

a multi-variate Principal Component Analysis (PCA). Another two comparisons of differences in the number of digital scales and number of femorals between the Saba Green Iguana and St. Maarten Green Iguana populations were performed using Wilcoxon ranked-sum tests. Finally, we used the HY-FDR methodology to correct *p*-values given the large number of statistical tests (Benjamini and Yekutieli, 2006; White et al., 2019). All statistical analyses were done using R and the RStudio environment (RStudio Team, 2022; R Core Team, 2023).

Results

On Saba and St. Maarten, we captured 59 (23 females and 36 males) and 51 (23 females and 28 males) iguanas of ≥ 20 cm SVL, respectively. Except for length of the 4th toe and mid-body spine length for the Saba Green Iguana population ($R^2 = 0.59$), all size-dependent characters were correlated with SVL with R^2 values greater than 0.69. ANCOVA results showed 13 and 12

characters to significantly differ between sexes of native Saba Green Iguanas and non-native St. Maarten Green Iguanas, respectively. In addition, 13 SVL-dependent characters that significantly differed between both populations (Table 1; Fig. 1A–G). For both meristic characters, results of Wilcoxon ranked-sum tests for differences between sex and populations for the number of digital scales were insignificant, though significant for the number of femoral pores (Fig. 1H).

PCA clustering indicates Saba Green Iguanas and non-native Green Iguanas from St. Maarten partially overlap in morphospace for variation across 17 length dependent characters (Fig. 2). The first three principal component axes (or dimensions) explain 40.38%, 20.98%, and 10.55% of variance, respectively. The first principal component axis discriminates mostly based on sex with the highest contribution from upper front- and hindleg length and head length. The second principal component axis discriminates between both populations, with highest contributions from snout length and height and width of the subtympanic plate.

Table 1. Statistical results of morphometric analyses for Saba Green Iguanas and non-native Green Iguanas from St. Maarten. Columns show R^2 values of snout-vent length (SVL) regressions, and results of ANCOVA tests for differences between SVL-corrected residuals between sexes, per island. Asterisks indicate significant ANCOVA results for $P < 0.05$. Significant results of comparisons of variables between islands are denoted by means of “a” in the Variable column.

Variable	Saba Green Iguana				Green iguanas (St. Maarten)			
	R^2	<i>F</i>	<i>df</i>	<i>Adj. P</i>	R^2	<i>F</i>	<i>df</i>	<i>Adj. P</i>
Upper frontleg length	0.84	7.011	56	1.70 x -02*	0.92	14.901	48	1.28 x -03*
Lower frontleg length ^a	0.92	16.854	56	7.54 x -04*	0.94	14.398	48	1.41 x -03*
Upper hindleg length	0.88	3.286	56	8.79 x -02	0.92	15.928	48	9.52 x -04*
Lower hindleg length ^a	0.89	16.396	56	7.77 x -04*	0.91	29.354	48	1.63 x -05*
Length of 4th toe	0.59	9.343	55	1.51 x -02*	0.82	4.515	47	5.10 x -02
Head width	0.87	2.905	56	1.07 x -01	0.89	0.003	48	9.53 x -01
Head length ^a	0.88	20.240	56	2.37 x -04*	0.92	35.323	48	3.47 x -06*
Snout length ^a	0.90	6.409	56	1.98 x -02*	0.92	5.107	48	3.81 x -02*
Eye length ^a	0.78	1.940	55	1.85 x -01	0.76	0.059	48	8.34 x -01
Mouth length ^a	0.89	6.825	56	1.77 x -02*	0.94	13.256	48	2.05 x -03*
Head depth ^a	0.79	12.678	56	2.16 x -03*	0.91	0.952	48	3.55 x -01
Tympanum height ^a	0.69	11.621	56	2.43 x -03*	0.78	7.696	48	1.36 x -02*
Tympanum width ^a	0.69	8.413	56	8.95 x -03*	0.74	3.503	48	8.14 x -02
Height subtympanic plate ^a	0.71	8.410	55	8.95 x -03*	0.80	9.113	48	8.00 x -03*
Width subtympanic plate ^a	0.75	9.563	55	6.38 x -03*	0.75	11.151	48	4.53 x -03*
Mid-body spine length ^a	0.59	44.169	56	4.52 x -07*	0.71	31.362	48	1.73 x -06*
Tail length ^a	0.92	3.867	20	7.93 x -02	0.84	14.600	19	2.43 x -03*

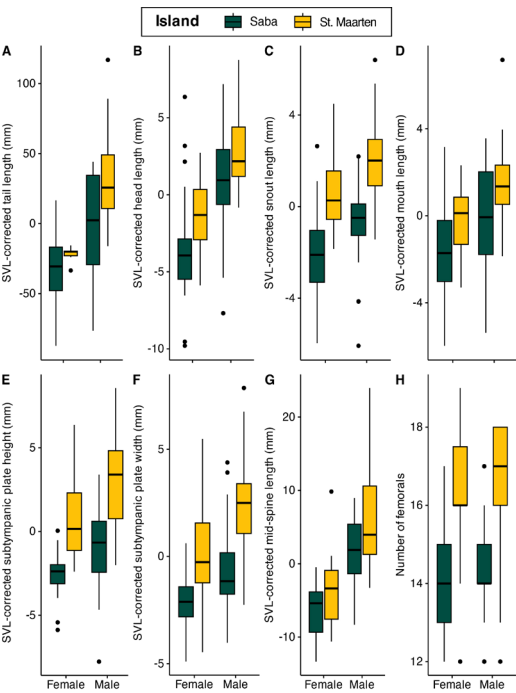


Figure 1. Variation in seven length-dependent characters (A–G) and the number of femorals (H) that significantly differed between male and female iguanas of ≥ 20 cm snout-vent length from Saba and St. Maarten; (A) tail length, (B) head length, (C) snout length, (D) mouth length, (E) height of subtympanic plate, (F) width of subtympanic plate, (G) mid-body spine length, and (H) number of femoral pores.

Discussion

Here we assessed differences in morphometric characters between the native Saba Green Iguana population of Saba and the non-native Green Iguana population on St. Maarten, from where repeated incursions to neighbouring islands have taken place (Questel, 2008; Debrot et al., 2022; van den Burg et al., 2023). Our comparison highlights 14 characters (13 morphometric, 1 meristic) that differ between Saba Green Iguanas and non-native Green Iguanas from St. Maarten. Local stakeholders are especially aided by the identification of characters that can be assessed without the necessity to capture an individual iguana. Among the morphometric characters that significantly differ between native and non-native iguanas, we find at least five morphometric characters that are often clearly visible and can have in-situ usage for detection of non-native iguanas on Saba; the size of the subtympanic plate (height and width) and dorsal spines, and length of

the head and snout.

This study builds on our earlier assessment of morphometric characters within the Saba Green Iguana population, for which we now increased the sample size by $\sim 50\%$. Dimorphic differences for Saba Green Iguanas were mostly identical to the 2023 dataset ($df = 39$). Several characters (upper front leg, tympanum width, and subtympanic plate height) are found to be dimorphically significantly different in our study ($df = 55\text{--}56$; Table 1), whilst these had relatively low but insignificant p -values (0.06–0.09) in the 2023 study (van den Burg et al., 2023). Contrarily, and compared to van den Burg et al. (2023), we found that head width lacked significant dimorphic difference. Van den Burg et al. (2023) also compared morphometrics between native Saba Green Iguanas and non-native Green Iguanas present on Saba, which highlighted 11 SVL-dependent characters significantly differed between those groups. Importantly, the non-native sample size has been increased by $> 700\%$ compared to van den Burg et al. (2023). In this expanded assessment we identify 13 morphometric characters that significantly differed between native and non-native individuals, of which two characters were and three characters were not significant in the 2023 assessment. As tails are often damaged and miss the original tip (and therefore length), our more-limited 2023 assessment lacked the sample size needed to assess the differentiating value of this characteristic. Our results indicate a lack

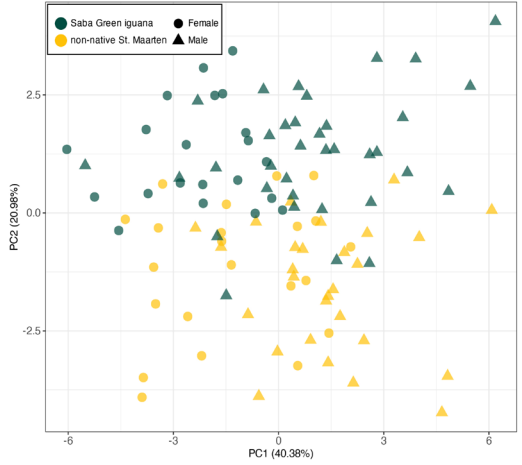


Figure 2. Principal component morphospace plot for all snout-vent length dependent variables, except tail length. Representing data from 56 native Saba Green Iguanas, and 50 non-native Green Iguanas from St. Maarten.

of relative difference in tail length between male and female Saba Green Iguanas, though with a low p -value which is contrary to the case for non-native iguanas (Table 1). However, our assessment highlights that non-native Green Iguanas have longer tails compared to Saba Green Iguanas of identical size, indicating that non-native iguanas can attain a larger overall size, a known dominance feature for iguanas (Dugan, 1982). On Saba, non-native males (max. SVL 44.0 cm, 150.3 cm total size) can attain similar or larger SVL compared to native Saba Green Iguana (max. SVL 43.9 cm, with stubbed tail). This difference in total size was recently also identified between *Iguana delicatissima* and non-native Green Iguanas (van den Burg et al., 2024), and could be one underlying cause driving displacements of native iguanas across the Lesser Antilles (Knapp et al., 2014; Vuillaume et al., 2015; van den Burg et al., 2018, 2023).

On Saba, colouration can provide another clue about the origin of individual iguanas. The native population is known to be melanistic (Breuil et al., 2020), although only about 10% of individuals are completely melanistic (van den Burg et al., 2025a). The degree of melanism on the lateral side of the head, namely a patch of scales between the eye and the tympanum, appears most important to differentiate native Saba Green Iguanas from non-native iguanas. However, non-native iguanas can have very dark colouration as well, with hybrids likely forming a mix of phenotypes. Further study is needed to assess colouration for genotyped hybrids and whether the lateral melanistic spot on the head remains diagnostic to native iguanas in the case of hybrids.

Green Iguanas use femoral glands to secrete lipids and proteins that are used in chemical signalling; characteristics of which can differ between populations (Alberts et al., 1992, 1993; Alberts and Werner, 1993). Reporting on data from Saba, Gerber (1999) provided data on length, weight and melanism, as well as a note that both sexes had developed secreting femorals and these were especially large in males. Our results show that Saba Green Iguanas have significantly fewer femorals compared to non-native Green Iguanas from St. Maarten, which are present at the same relative position on the ventral side of the upper hindlegs. Contrarily, van den Burg et al. (2024) found that this non-native population had fewer femorals compared to the St. Eustatius *I. delicatissima* population. Since femorals are present at the same location on the ventral upper hindleg, Saba Green Iguanas thus have fewer and larger femorals (pers. observ., M.P. van den Burg)

compared to both other studied populations. Although we did not measure the size of individual pores, and despite having fewer pores, the size difference suggests Saba Green Iguanas might release more secretion at a given time compared to non-native Green Iguanas. Whether closely related populations on Montserrat and coastal and mainland areas in northern Venezuela have similarly fewer femoral pores is unknown. In addition, subsequent research should focus on identifying the chemical signature of Saba Green Iguanas in a comparative study to other populations within the *Iguana iguana* species complex (Stephen et al., 2013), similar to Colosimo et al. (2020).

As native iguanid populations across the Lesser Antilles are threatened by non-native Green Iguanas (Knapp et al. 2020), morphological assessments to improve their in-situ identification are urgently needed. On Saba, over 20 non-native iguanas have already been removed (see van den Burg et al., 2025b), but others are known to be present, and an island-wide removal campaign is overdue. Stakeholders on Saba are encouraged to pay particular attention to the following morphometric characters, additionally to colouration: the size of the subtympenic plate and dorsal spines, and length of the head and snout. Apart from the currently present non-native/hybrid iguanas on Saba, biosecurity remains unimproved, meaning that additional incursions cannot be ruled out. Especially concerning are the high volumes of materials that will be imported for the construction of the Black Rock harbour (van den Burg et al., 2025c). Local and national policy officers should ensure the inclusion of strict biosecurity measures surrounding this large construction project and this work will aid in the rapid detection of non-native iguanas for removal.

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