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Description of the nesting sites of the critically endangered Jamaican iguana *Cyclura collei*

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ABSTRACT - The Jamaican iguana, *Cyclura collei*, is one of the world's rarest iguanas. It is restricted to the dry forest of the Hellshire Hills, where the availability of suitable soil for nesting limits population growth. Once a year, Jamaican iguanas move from the surrounding forest to two main nesting sites, the Upper Nesting Site (UNS) and the Lower Nesting Site (LNS), to excavate nests and deposit their eggs. There is little information on the soil condition at these two sites. Due to population growth, resulting from intensive conservation efforts, the availability of nesting sites is now limited. Consequently, qualitative and quantitative information is needed to improve existing sites and inform the creation of additional nesting sites. Here we investigate soil depth, nest openness, soil compaction and other soil characteristics at the Jamaican iguana's two main nesting sites and, from our observation, make recommendations for creating and/or improving nesting sites.

INTRODUCTION

The Jamaican iguana, *Cyclura collei* Gray 1845, is from a genus commonly known as the rock iguanas. It is among the 11 species of threatened rock iguanas found in the Caribbean (Buckley et al., 2016; IUCN, 2021) and is ranked as one of the world's rarest (Alberts, 1999). It was once common in southern Jamaica and the Goat Islands (Vogel & Kerr, 1992; Woodley, 1980, 1968). After the introduction of invasive predator species, the population declined and was thought to be extinct. However, it is now found only in a small, remote area in the Hellshire Hills (Vogel, 1994; Vogel & Kerr, 1992). Its population in 1991 was roughly estimated to be less than 100 mature individuals (Vogel et al., 1996).

The Jamaican iguana may nest in one of two ways depending on the nature of the substrate. When there is deep soil available, they will excavate tunnels that lead to an egg chamber (Vogel, 1994). Otherwise, they may nest in small rock crevices containing soil but with more or less no tunnel (Wilson, 2014). Few iguanas choose to nest in rock crevices compared to nesting in deep soil as there is limited soil to cover the eggs. When they nest in rock crevices, the females nest individually. Nests in rock crevices are more accessible to predators and are more heavily predated, mainly by the Indian mongoose, *Herpestes auropunctatus* (Wilson, 2014).

Nesting in deep soil is the primary form of nesting behaviour in the Jamaican iguana; however, such soils are rare in the limestone dominated Hellshire Hills and occur only in pockets. There are a few sites with deep soil that the iguanas nest in; however, there are two such sites they use yearly. These have been termed the Lower Nesting Site (LNS) and the Upper Nesting Site (UNS) (Vogel, 1994). Other sites have been used occasionally (van Veen & Wilson, 2017). Gravid females aggregate over a period of 3 months (June to August) at these two sites (Vogel, 1994) and, because nesting space is limited, there is often intense competition. Females are known to excavate existing nests containing clutches laid by other females and may protect their nests for up to 14 days by physical contact, fighting, and biting (Wilson et al., 2016; Vogel, 1994).

The success of the conservation programme has led to an increase in the number of nesting females from 8 in 1991 (Vogel, 1994) to 53 in 2013, which resulted in increased competition between females at the two nesting sites (Wilson, 2014). For continued success, the programme will need to create artificial nesting sites. There are also plans to reintroduce the Jamaican iguana to the Goat Islands (Island Conservation, 2008; NEPA, 2019); however, this area has changed since the time that the iguanas became extinct on the island in the 1940s. Such changes resulted from occupation by the American Military, charcoal burning and goat farming. One of the most pressing questions linked to this species continued recovery is whether additional suitable nesting sites exist or whether there is a need for supplemental nesting sites. Answering these questions will require detailed knowledge of Jamaican iguana nesting preferences and habits. Hence, the main objective of the current study was to describe the physical characteristics of the two main nesting sites. This information can be used to i) advise on the construction of new nesting sites, and ii) assess the suitability of potential nesting sites on the Goat Islands. In addition, as there is little information on the nesting preferences of other Cyclura species, this information may also contribute to their conservation.

MATERIALS & METHODS

We conducted fieldwork under the purview of the National Environmental and Planning Agency (NEPA) of Jamaica. Permission is only granted to studies with limited disturbance to the nesting sites because the Jamaican iguana is listed as Critically Endangered (IUCN, 2021). This study was carried out during the dry season from December 2018 to February 2019, over a 14-day period that is outside of the nesting season although the nesting season itself is also within the dry season.

Study site

The Hellshire Hills are located in southern Jamaica. The area consists of limestone hills, rocky substrate, no surface water and the soil is restricted to rock crevices and small depressions. The Hellshire Hills region (60 km^2) is also the largest remaining undisturbed dry limestone forest in Jamaica (Vogel, 1994) and has remained under-developed due to its inhospitable conditions. The vegetation types range from cactus scrub to dry evergreen thicket (Woodley, 1980). The patchy forest is also characterised by a thin canopy (IUCN, 2021). The location of both nesting sites was recorded using a Garmin eTrex 20 HikingGPS (Garmin Ltd., Schaffhausen, Switzerland). All measurements were taken in the middle of each site unless otherwise noted. The UNS is elliptical, while the LNS is roughly rectangular; the length and width of each were measured to calculate area.

Soil characteristics

Depth. We measured soil depth by hammering a 2 m metal rod into each nesting site until contact was made with the bedrock. Measurements were taken at the middle and two other random areas at each nesting site. When air pockets were encountered, the soil depth at the top and bottom of each pocket was measured.

Compaction (handheld penetrometer). To measure the soil compaction we used a handheld cone penetrometer (Eijkelkamp Soil & Water, Giesbeek, Netherlands). Due to soil dryness, the penetrometer was fitted with a 2 cm^2 cone. The soil compaction measurements were taken at 5 cm depth intervals until the probe could go no further. Most nesting occurs towards the centre of the sites. Thus, we took two samples in the middle and two other areas; these sample sites were at least 100 cm apart.Air pockets encountered while using the penetrometer were also recorded. We examined the relationship between soil depth and degree of soil compaction by plotting the data and estimating the correlation coefficient in RStudio by using the Rstatix package (Kassambara 2021).

Bulk density. We measured soil bulk density for only the upper 5 cm of soil, as going any deeper would have resulted in too much disturbance to the soil. One sample was taken in the centre of the nesting site, and the others at two random points. The sampling method used by Page-Dumroese et al. (1999)was adapted. A thin layer of soil was first cleared from the sample area and a metal coring cylinder, 50 mm in length and diameter, was then used to collect the samples (Page-Dumroese et al., 1999). The cylinder with soil was carefully removed and sealed with plastic caps. The samples were analysed by Soil Health, Plant Tissue and Water Laboratory, Agricultural Land Management Division, Ministry of Industry, Commerce, Agriculture and Fisheries.

Soil profile. We extracted soil cores using a 53 mm split tube sampler (Eijkelkamp Soil & Water, Giesbeek, Netherlands). These cores provided data on soil profile, organic matter, pH and soil type (based on particle size classes; sand (50–2000 µm), silt (2–49 µm) and clay (<2 µm). Prior to collecting the soil core sample, we drove a metal rod into the selected areas of the nesting site to ensure no rocks were present to damage or impede the auger. Cores were taken in two areas (middle and another random site) at each nesting site to a depth of 40 cm, as the likelihood of damage to the auger increased beyond this depth. Once the core was extracted, a photograph was taken of the soil profile. The samples were later analysed by the Soil Health, Plant Tissue and Water Laboratory, Agricultural Land Management Division, Ministry of Industry, Commerce, Agriculture and Fisheries.

Vegetation cover

The plants within the nesting sites, as well as within a 5 m perimeter around each nesting site, were identified directly in the field or photographed, and voucher specimens were taken for study at the herbarium at the Department of Life Sciences, University of the West Indies, Mona, Jamaica.

The fraction of the ground without tree cover (nest openness) was assessed using the CanopyApp (University of New Hampshire University, New Hampshire, USA) for the Android application installed on a Samsung S7 smartphone. The phone was held 0.5 m above the ground with the camera facing upward, and two pictures were taken in the middle of each nesting site and saved to the device for further analysis.

RESULTS

The LNS is the larger of the two sites, is rectangular, with an area of 47.5 m^2 (length 9.5 m x width 5.0 m); the UNS has an area of 28.0 m^2 (diameter = 6.0 m) (Fig. 1). The average soil depth (3 sample points) for both sites was 60 cm, the ranges being 41–77 cm and 46–76 cm for UNS and LNS, respectively. Soil depth decreased from the middle to the edge of the nesting sites, and the likelihood of encountering rocks increased. The general depth at the periphery of the nesting sites was < 20 cm.

The soil type at both nesting sites was silt loam, consisting of approximately 66 % silt, 26 % clay, and 4 % organic matter. The pH at the LNS was 7.6 and 6.7 at the UNS. The colour of the soil samples from the core is red, and it did not show any distinct soil horizons. Roots occurred mainly at the first 5 cm, and a few extended to depths of 10 cm. Iguana eggshells were found at various levels. Charcoal fragments were also observed in the soil at both nesting sites.

Using the cone penetrometer, we measured soil compaction to a depth of 25 cm. Compaction varied between 260 and 385 N/cm^2 in the UNS and 190 to 355 N/cm^2 in the LNS (Table 1). There was no significant correlation between soil compaction and soil depth in either the UNS ($R = -0.057$, $p > 0.05$) or the LNS ($R= 0.42$, $p > 0.05$).

The average bulk density for the first 5 cm was 1.2 g/cm^3 at the UNS and1.0 g/cm^3 at the LNS. We encountered four air

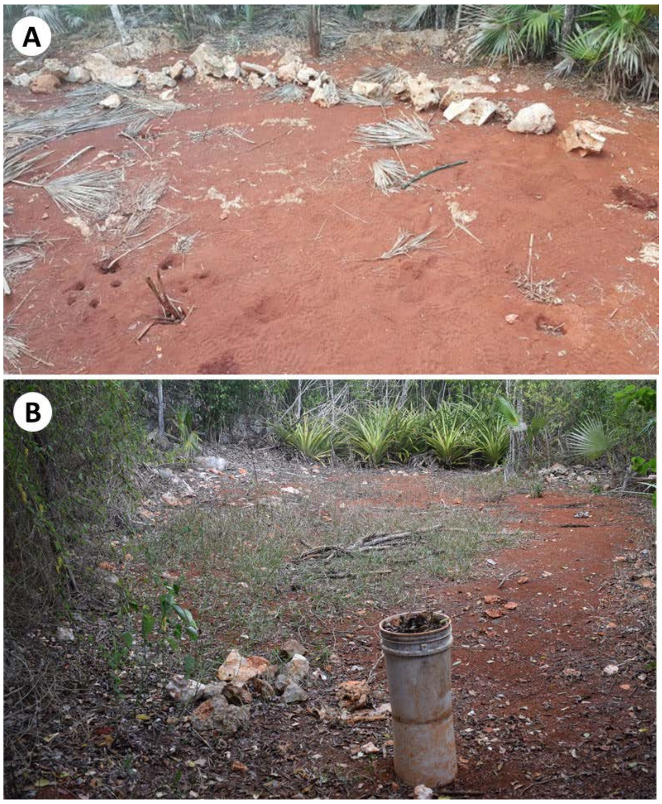

Figure 1. The two nesting sites of *Cyclura collie* - **A.** The upper nesting site where a ring of stones was used to create an enclosure to capture the hatchlings for the Jamaica iguana headstart programme, **B.** The bucket in the forefront of the lower nesting site is a part of a trap used to catch feral cats in the invasive alien species IAS management programme

Table 1. The soil compaction values, using the handheld penetrometer, at the two *Cyclura collei* nesting sites

Soil depth (cm)	Average soil compaction (N/cm2)	Shelter direction
	Upper Nesting Site	Lower Nesting Site
5	260	190
10	385	355
15	300	243
20	305	270
25	240	340

Table 2. Depth and diameter of air pockets at the two *Cyclura collei* nesting sites

	Depth at which air pockets were encountered (cm)	Diameter of air pocket (cm)
Lower Nesting Site	5	10
	10	20
	10	15
	25	5
Upper Nesting Site	5	35
	40	10

Table 3. Plant species found in a 5 m perimeter around the upper (UNS) and lower (LNS) *Cyclura collei* nesting sites

Family	Scientific Name	Plant form	UNS	LNS
Anacardiaceae	*Metopium brownei*	Tree	x	x
	Commocladia pinnatifolia	Shrub	x	x
Apocynaceae	*Plumeria obtuse*	Shrub	x	-
Arecaceae	*Thrinax parviflora*	Tree	x	x
	Coccothrinax sp.	Tree	x	-
Bignoniaceae	*Tabebuia riparia*	Tree	x	-
Bromeliaceae	*Bromelia pinguin*	Shrub	-	x
Burseraceae	*Bursera simaruba*	Tree	x	-
Capparaceae	*Capparis ferruginea*	Shrub	-	x
Euphorbiaceae	*Croton linearis Jacq.*	Shrub	-	x
Myrtaceae	*Eugenia maleolens Pers.*	Tree	x	-
Poaceae	Species 1	Grass	x	x
	Species 2	Grass	-	x
Polygonaceae	*Coccoloba jamaicensis Lindau*	Tree	x	-

pockets in the UNS and two air pockets in the LNS, these are presumed to be old nest cavities. The air pockets occurred in areas with soil depth >20 cm and occurred between 5–50 cm (Table 2). The diameters of the air pockets varied from 5–35 cm.

The dry forest was well developed at the periphery of the nest sites (Fig. 1), with trees growing up to 4 m; however, there was no distinct canopy or shrub layer. The substrate was primarily rocky and the trees grew from pockets of soil/ leaf litter. A total of 14 species of plants (7 trees, 2 grasses and 5 shrubs/herbs) were recorded at the periphery of the nesting sites: the UNS had 9 of these while the LNS had 8 (Table 3).

The vegetation within the nest sites consisted of grasses, shrubs, and a few stunted trees no more than 50 cm in height. Consequently, the sites were very open. The average nest openness value of the centre of the nesting site was LNS 95 % and UNS 94 %. The openness value decreased from the centre of the nesting site to the periphery due to the forest shading the area. At the LNS, there was a section overgrown by *Bromelia pinguin*; there was a canopy overhanging this section, and an accumulation of leaf litter was observed.

DISCUSSION

Soil depth is one of the factors that could determine the suitability of a site for nesting. The average soil depth was 60 cm for both nesting sites. The depth was greatest in the middle of both nesting sites and decreased towards the perimeters. The air pockets assumed to be old nest cavities occurred in areas with soil depth >20 cm and occurred between 5–50 cm. The older and bigger females generally occupy the central region, where more nest pockets are encountered while the younger females move closer to the edge (Jamaica iguana field team; Williams, pers. comm.). Further studies are needed to confirm if the central region is best for nesting.

The presence of rocks and roots may affect iguana nesting efforts by increasing the difficulty of digging, resulting in them abandoning their nest burrows (Morrison et al., 2009; Iverson et al., 2004). The number of rocks and roots decreases from the perimeter towards the middle for both nesting sites. In addition, no nest pockets were encountered in soil depth < 20 cm, which is the general depth at the periphery of the nesting sites. This suggests that nest construction is less successful in this area.

Soil cores from both nesting sites indicated the absence of the typical soil profile, i.e., topsoil (Horizon A) and subsoil (Horizon B) (Olson, 1984). This could be the result of the iguanas mixing the soil when digging test burrows throughout the site and also by actually building their nests. The volume of a hypothetical iguana nest (excluding the test digging test burrows) was calculated as 0.032 m^3 (Vogel, 1990; Hope Zoo, unpublished). Twenty-five iguanas will potentially excavate 0.80 m^3, representing approximately 3–4 % of the nesting sites annually. Consequently, the mixing of the soil by the iguanas contributes to the absence of a distinct soil profile.

Charcoal fragments found in the soil indicated previous use of the sites for charcoal kilns. The nesting sites are flat and have a large volume of soil, which are rare features in the Hellshire Hills, making them attractive to charcoal burners. The charcoal burners obtained hardwood from the forest and use areas similar to the nesting sites as they provide enough soil to cover the kilns. This activity contributes to the mixing of the soil. However, there have been no active charcoal kilns at these sites for the last 30 years, since the rediscovery of the iguana. Charcoal burning also has a negative impact on the iguana's habitat in terms of the loss of limited nesting sites and food resources (Wilson et al., 2004). In their study in the Hellshire Hills, Niñ et al. (2014) estimated that it would take approximately 45 years for regrowth in the clear-cut areas.

Soil compaction affects the suitability of the area for the iguana to nest and is generally affected by moisture, soil density, porosity and rock content of the soil (Kees, 2005). If the soil is too compacted, it increases the difficulty for an iguana to dig a tunnel; if the soil is too loose, the nest tunnel will collapse. Additionally, the area cannot be too compact if the hatchlings are to dig their way out of the nest cavity. Iverson et al. (2004) reported that iguanas took longer to dig their nest tunnels during drought conditions. The nest cavities occurred at compaction between 240 and 385 N/cm² (Table 1 and Table 2). The regular tunnelling by the iguana negates the trend of increasing compaction with depth seen in most soils. These values provide a guide for the construction of supplemental nests.

The soil compaction might partially explain the lack of trees in the nesting sites. Root growth begins to be inhibited at a compaction of approximately 150 N/cm² as measured using a handheld penetrometer (Kees, 2005), or a bulk density of 1.6 g/cm^3 for silt loam soil (Arshad et al., 2015). The average bulk density of the upper 5 cm of the nesting sites were 1.2 g/cm^3 at UNS and 1.0 g/cm^3 at LNS, well within the limit for normal plant growth. Using the penetrometer, we obtained values of 260 & 190 N/cm² in UNS and LNS for the first 5 cm; these are just at the limits of root penetration.

Below 10 cm, the soil density ranged between 240 and 385 N/cm² (Table 1); this compaction is much too high for root growth. This explains why most of the plants observed growing in the nesting sites include *Bromelia pinguin* and small shrubs whose roots do not penetrate much below 5 cm. In the soil cores, few roots were observed up to a depth of 10 cm. The absence of roots in the nesting sites is ideal as roots do retard tunnelling by the iguana (Vogel, 1993). The absence of trees in the nesting sites also creates an open area.

The nest sites had very little canopy cover (openness of 94–95 %). This is much more open than the surrounding dry forest, with an openness of about 65 % (data from a similar dry forest on Goat Island). Rock iguanas (*Cyclura cychlura inornata*) usually nest in open areas, which provide conditions for optimal incubation temperatures (Iverson et al., 2004). It was found that tunnel length in rock iguanas was inversely correlated with canopy cover, and nests tend to be shallower in shaded areas and deeper in open areas (Iverson et al., 2004). No soil temperature readings were taken during the present study; however, Grant and Lemm (1996) reported surface temperature as high as 54.4 °C and at 0.9 m below in the egg chamber temperature remained at 26–30 °C. The depth of 0.9 m exceeded measurements in this study. It appears that Grant and Lemm (1996) assessed the depth of the egg chamber by measuring the length of the tunnel. However, tunnels do not go straight down (i.e., iguanas always dig their tunnels at an angle ranging from 50–60° to the ground), and so the final depth would be less than 0.9 m.

We calculated the soil depth for an effective artificial iguana nesting site. We encountered the uppermost air pocket nests at 5 cm (Table 2). The only record of the diameter of an egg tunnel was from a large female in captivity at the Hope Zoo, which was 26 cm (Hope Zoo, unpublished). Combining these two measurements, the floor of that tunnel would be 31 cm below the surface. Making allowance for variations, we estimate that a minimum soil depth of about 40 cm is necessary for the establishment of an iguana nest site. Although this leaves little or no room for changes in tunnel depth in response to the temperature variations from year to year. The top of one tunnel was encountered at 40 cm, in which case the floor of that tunnel could be over 60 cm below the surface. Therefore, ideally, if any new nesting areas are to be constructed they should be at least be 60–70 cm deep. However, it should be noted that the deep nests recorded here could only be constructed at the centre of both nest sites and in any case may not represent the deepest that the iguanas will burrow; they were probably limited by the depth of soil in the nesting sites (77 and 76 cm).

In Vogel's (1994) study of the nesting habits of *Cyclura collei* it is stated that the nest has a straight tunnel 60 cm in length burrowed to a depth of 50 cm, followed by a second section at right angles to the first, at the same depth and 30 cm long leading to the egg chamber. Given that the tunnel penetrated 50 cm below the surface, and if the straight tunnel of 60 cm is considered the hypotenuse of a right-angle triangle, the horizontal distance tunnelled was thus 33 cm. Making allowance for variation in size of the females and other factors, it might be safe to recommend at least a doubling of this distance to 66 cm. If females are allowed to tunnel from any direction, the site might be considered a square of 66 cm, therefore, the recommended minimum surface area for a nesting site would be 0.44 m^2/individual; this will also accommodate egg chambers longer than 30 cm.

Recommendations for creating and/or improving nesting sites

i) In preparing potential nesting sites, obstacles to tunnelling should be removed. All plants, including the shallow root species such as *Bromelia pinguin*, should be removed as it is difficult for the iguanas or the hatchlings to tunnel through thick mats of roots. Large rocks and old tree stumps should also be removed.

ii) The trees overhanging the site should be cut or pruned, which would increase the amount of sunlight reaching the nesting site.

iii) The ideal nesting site should be of a depth >60 cm, and for determining the capacity of a site for usage by the iguana it may be assumed that each female would require at least 0.44 m^2 of nesting site surface.

iv) Soil added to the nesting area should be compacted to the levels found in this study. If clay-loam soils are being used, they should be compacted from approximately 190 N/cm^2 to 350 N/cm^2.

v) If other soils are used, there will be a need for further analysis. It should be noted that while these nests are constructed in clay-loam soils, this is not necessarily the only soil type or even the ideal soil type for nesting; they are the only soils available in the Hellshire Hills, but the iguana originally had a much wider distribution and may have used other soil types for nesting. However, as these are the only known major nesting sites for this species at present, we base our recommendations on their characteristics.

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