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Nest site characteristics of the Critically Endangered Bahama Oriole (*Icterus northropi*)

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Abstract The Bahama Oriole (*Icterus northropi*) is a Critically Endangered species restricted to Andros in The Bahamas. Previous research suggested that the Bahama Oriole nested almost exclusively in coconut palms (*Cocos nucifera*) in developed habitats. In 2016, however, the Bahama Oriole was documented nesting in remote pine forests for the first time. Our goals were to document where orioles nest in pine forests and to characterize nest site vegetation to determine if orioles show a preference for specific habitat characteristics. Here, we document 12 pine forest nests: six nests in understory Key thatch palms (*Leucothrinax morrisii*) and six nests in Caribbean pines (*Pinus caribaea*). For each nest tree, we measured the tree height, tree diameter, and nest height. We also took measurements of habitat characteristics in 10-m and 100-m radius plots around the nest and compared these measurements to control plots. Orioles nested in a range of pine forest habitats. However, on average, Bahama Orioles nested in pine forests with more tall thatch palms (> 2 m tall) in the understory compared to control plots. They also tended to nest in the tallest thatch palms in the understory. The findings from this study further support the importance of protecting Bahamian pine forests on Andros.

Keywords Bahama Oriole, endangered species, *Icterus northropi*, nesting habitat, The Bahamas

Resumen Características del sitio de nidificación de *Icterus northropi*, especie En Peligro Crítico • *Icterus northropi* es una especie En Peligro Crítico restringida a Andros en las Bahamas. Investigaciones previas sugirieron que dicha especie nidificaba, casi de manera exclusiva, en cocoteros (*Cocos nucifera*) en entornos urbanizados. Sin embargo, en 2016 se documentó por primera vez que esta especie nidifica en pinares remotos. Nuestros objetivos fueron detectar los sitios de nidificación de estas aves en los pinares y caracterizar la vegetación circundante para determinar si esta especie muestra una preferencia por características específicas del hábitat. Documentamos 12 nidos en pinares: seis en el sotobosque de palmeras (*Leucothrinax morrisii*) y seis en en pinos (*Pinus caribaea*). Para cada árbol con nido medimos la altura del árbol, su diámetro y la altura del nido. También tomamos medidas de las características del hábitat en parcelas de 10 y 100 m de radio alrededor del nido y comparamos estas mediciones con parcelas de control. Las aves observadas nidificaron en una variedad de hábitats en los pinares. Sin embargo, en promedio, los individuos de esta especie anidaron en pinares con un sotobosque de palmeras más altas (más de 2 m de altura) comparadas con las de las parcelas de control. También tendieron a nidificar en las palmeras más altas del sotobosque. Los resultados de este estudio reafirman la importancia de proteger los pinares de las Bahamas en Andros.

Palabras clave Bahamas, especie amenazada, hábitat de nidificación, *Icterus northropi*

Résumé Caractéristiques des sites de nidification de l'Oriole des Bahamas (*Icterus northropi*), une espèce en danger critique d'extinction • L'Oriole des Bahamas (*Icterus northropi*) est une espèce en danger critique d'extinction, présente uniquement sur Andros aux Bahamas. Des recherches antérieures indiquaient qu'il nichait presque exclusivement dans les cocotiers (*Cocos nucifera*) des habitats anthropisés. En 2016, la nidification de l'espèce a cependant été observée pour la première fois dans des forêts de pins reculées. Notre objectif était de recueillir des informations sur les sites de nidification de l'Oriole des Bahamas dans ces pinèdes et d'en caractériser la végétation pour déterminer si cet oiseau montre une préférence pour certaines caractéristiques de l'habitat. Nous documentons ici 12 nids dans des forêts de pins: six dans le sous-étage de palmiers (*Leucothrinax morrisii*) et six dans les pins des Caraïbes (*Pinus caribaea*). Pour chaque arbre abritant un nid, nous avons mesuré la hauteur et le diamètre de l'arbre ainsi que la hauteur du nid. Nous avons également mesuré des caractéristiques de l'habitat dans des rayons de 10 m et de 100 m autour du nid et nous avons comparé ces mesures à celles des parcelles témoins. Les orioles nichaient dans divers habitats de pinèdes. Cependant, ils nichaient en moyenne dans des pinèdes présentant un sous-étage de palmiers plus élevé que dans les parcelles témoins (> 2 m de haut). Ils avaient aussi tendance à nicher dans les plus hauts palmiers du sous-étage. Les résultats de cette étude confirment encore l'importance de protéger les forêts de pins d'Andros aux Bahamas.

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Mots clés Bahamas, espèce en danger, habitat de nidification, *Icterus northropi*, Oriole des Bahamas

The Bahama Oriole (*Icterus northropi*) is a Critically Endangered species endemic to the Andros island complex in The Bahamas (Price *et al.* 2011). The Bahama Oriole was previously considered a subspecies of the Greater Antillean Oriole, which also included three other Caribbean oriole species: the Cuban Oriole (*I. melanopsis*), the Hispaniolan Oriole (*I. dominicensis*), and the Puerto Rican Oriole (*I. portoricensis*) (Chesser *et al.* 2010). In 2010, these species were all elevated to full species status based on differences in morphology, vocalization, and DNA (Omland *et al.* 1999, Garrido *et al.* 2005, Sturge *et al.* 2009, Chesser *et al.* 2010). The recognition of the Bahama Oriole as a distinct species brought new challenges for its conservation and a need for more in-depth research on its threats and habitat use.

The Bahama Oriole faces many potential threats as a species. Like other island endemics, it is threatened by invasive predators, including rats and feral cats, as well as native and non-native snakes (BirdLife International 2020). Baltz (1995) first documented the arrival of the Shiny Cowbird (*Molothrus bonariensis*) on Andros, which heavily parasitizes Bahama Oriole nests, perhaps especially in developed habitats (Price 2011). Finally, these orioles are threatened by habitat loss. The global range of the Bahama Oriole previously included Andros and Abaco; however, these orioles were extirpated from Abaco in the 1990s due to unknown causes (Price *et al.* 2011). In developed areas on Andros, many coconut palms (*Cocos nucifera*), an important nest tree for Bahama Orioles along the settled east coast, have been killed by lethal yellowing disease (Price *et al.* 2015). Logging and residential development have caused the orioles to lose native pine forest habitat as well (Price and Hayes 2017).

The number one priority conservation action proposed by the International Union for Conservation of Nature (IUCN) and BirdLife International for this species is to study the habitat use of the oriole throughout the year (BirdLife International 2020). Several studies have already begun to address this conservation action. Soon after the species was split, Price *et al.* (2011) conducted a population survey across three habitat types (coppice, pine forest, and developed areas). Assuming 50–90% detectability (Lloyd and Slater 2011 cited in Price *et al.* 2011), they estimated a population size of 141–254 individuals, with orioles predominately found in developed areas. Price *et al.* (2011) found nests only in palms: coconut palms ($n = 40$), sabal palms (*Sabal palmetto*; $n = 2$), and Key thatch palms (*Leucothrinax morrisii*; $n = 3$). Whereas Key thatch and sabal palms are native to Andros, the coconut palm is introduced and found almost exclusively in developed areas. This prior work, along with Baltz (1996), suggested that the orioles are highly synanthropic and prefer anthropogenic habitats.

However, orioles have been observed using other habitat types. Adult orioles have been seen foraging in coppice (broadleaf forest) and pine forests (Price *et al.* 2011). Furthermore, the decline in coconut palms due to lethal yellowing disease may make other nesting resources more important for this species (Price *et al.* 2015). In 2016, Stonko *et al.* (2018) documented Bahama Orioles nesting in native understory palms (*Leucothrinax morrisii*) and Caribbean pines (*Pinus caribaea var. bahamensis*) in the remote pine forests of Andros for the first time. They recorded 5–10 pairs of orioles that had breeding territories in the pine forest, which comprises the majority of dry land area on North Andros (unpubl. data; Fig. 1). This discovery demonstrated that Bahama Orioles can utilize other breeding habitats, including areas deep in the pine forest far from human settlements, meaning they are not as heavily dependent upon anthropogenic settlements or using coconut palms for nesting as previously thought (Stonko *et al.* 2018).

In 2017 and 2018, our team found several more nests in pine forests. Here, we characterize Bahama Oriole nesting sites for these nests found between 2016–2018. Our goals were to (1) characterize Bahama Oriole pine forest nest sites, and (2) determine if there are any nest site characteristics that differ significantly from surrounding areas in the pine forest. Importantly, no other Caribbean oriole species are known to nest in pine trees or in open pine forest (Jaramillo and Burke 1999). Therefore, no previous studies can be used to predict aspects of the pine forest that may be important for Bahama Orioles. Previous nest-site selection research on the Bahama Oriole conducted in developed areas found that orioles selected nest trees that were significantly taller, had more bare ground underneath, and had more palm trees near the nesting tree compared to randomly selected palm trees (Price *et al.* 2011). More recent research discovered these orioles nesting in the pine forest, specifically in Caribbean pines and Key thatch palms (Stonko *et al.* 2018). In addition, we needed to take into account that forest fires might

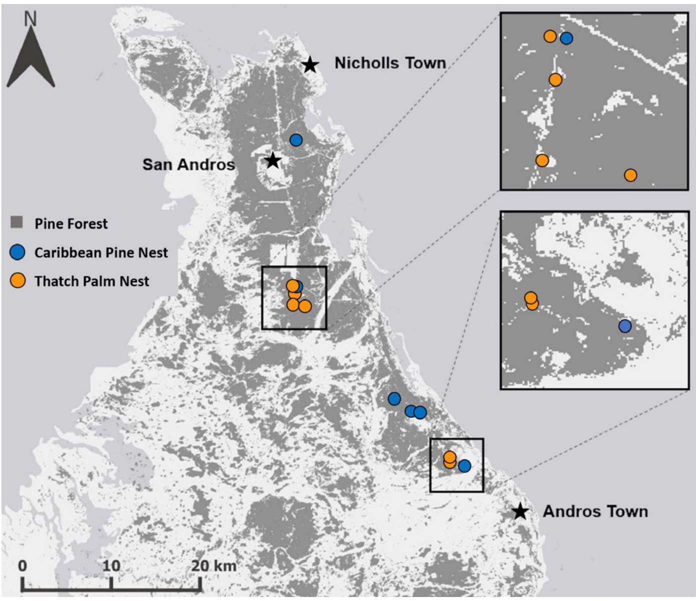

Fig. 1. Distribution of 12 Bahama Oriole nests in pine forests measured between 2016–2018 on the North Andros study site. The extent of pine forest is highlighted in dark gray.

influence nest-tree selection because they commonly occur in the Bahamian pine forest (Myers *et al.* 2004). Although no studies have examined the specific impact of wildfires on Bahama Orioles, Artman and Downhower (2003) studied Wood Thrush (*Hylocichla mustelina*) nest-site selection in relation to prescribed burning. They analyzed habitat characteristics such as ground cover, understory, tree height, and nest height and found that the Wood Thrush placed nests higher off the ground and in taller, larger trees in burned areas compared to unburned areas (Artman and Downhower 2003). Based on information gathered from these prior studies, we hypothesized that the following factors could influence nest-site selection: (1) number of pines (pine density), (2) number of short thatch palms, (3) number of tall thatch palms, (4) understory height, and (5) burn history. By characterizing Bahama Oriole nesting habitat, our study contributes to the number one priority conservation action proposed by the IUCN for this species (BirdLife International 2020). Our findings can be used to assist the Bahamas National Trust in managing national parks and developing overall strategies to conserve the Bahama Oriole.

Methods

Study Area

Andros is an island complex consisting of three main islands totaling ~6,000 km^2: North Andros, Mangrove Cay, and South Andros. Andros has several major habitat types: pine forest, coppice, developed habitats, and extensive wetlands. Our study focused on the pine forests in North Andros (Fig. 1), which were logged heavily in the mid-1900s (Henry 1974, Price and Hayes 2017). The pine forest vegetation includes Caribbean pines and an understory of Key thatch palms, poisonwood (*Metopium toxiferum*), ferns, and other broadleaf shrubs (Stonko *et al.* 2018).

We detected and measured nests from May to June in 2016, 2017, and 2018, during the Bahama Oriole breeding season. We located nests opportunistically during extensive point count surveys and habitat mapping studies. Whenever we saw orioles carrying nesting material or food, we attempted to follow them to the nest sites. Once we located nests, we marked the general location with flagging tape and recorded GPS coordinates. We created a map of nest site locations (Fig. 1) using QGIS version 3.10.6 (Open Source Geospatial Foundation, 9450 SW Gemini Drive, Beaverton, OR, USA) with Esri basemap (Esri, Redlands, CA, USA). Typically, on the same day that we located a nest tree, we also recorded nest-site measurements. Of the 12 nests found, only one was inactive.

We used methods similar to Price *et al.* (2011) to assess the nesting habitat of the Bahama Oriole at three spatial scales. First, we measured details of the nest tree itself ("micro scale"). Second, we assessed the proximal habitat within 10 m of the nest tree ("meso scale"). Finally, we assessed habitat characteristics within 100 m of the nest tree ("macro scale"). We chose the micro and meso scales to focus on the specifics of where exactly the nest was placed, and the macro scale to understand the features of the surrounding territory. Although we have not rigorously quantified the exact size of typical Bahama Oriole territories, these scales agree with preliminary data from radio tracking and typical territory sizes for other orioles breeding in forested habitats (e.g., Ligi and Omland 2007, Campbell *et al.* 2016). Furthermore, these scales also help detect the spatial area that orioles consider when selecting nest sites.

Micro Scale (nest tree)

We calculated the height of the nest tree and the height of the nest using a laser rangefinder and a clinometer. We measured the diameter of the trunk using a diameter at breast height (DBH) tape. If the nest was in a palm tree, we noted whether the nest was in a live or dead frond. We also took a panoramic picture of the site for visual validation. In order to compare the nest tree to nearby possible nest trees, we measured the height of the three closest pine trees and the three closest thatch palms to each nest. We focused on pines and thatch palms because Stonko *et al.* (2018) previously found orioles nesting in these two pine forest species.

Meso Scale (10-m radius)

We characterized habitat surrounding the nest by estimating: (1) the number of pines with DBH > 10 cm, (2) the number of thatch palms < 2 m tall, and (3) the number of thatch palms > 2 m tall. We used two height categories for the palms because we suspected that orioles might be more likely to nest in thatch palms with a stem > 2 m tall, as these fronds are less accessible to terrestrial predators. For each of these estimates, we used six abundance categories: 0, 1–4, 5–10, 11–20, 21–50, and 51–100.

Next, we collected information on the pine forest understory. For each nest tree, we estimated the average pine understory height into five possible categories: 0–1 m, 1–2 m, 2–4 m, and 4–10 m. Since fires commonly occur in this habitat, we estimated the burn history of the habitat based on visual indicators, particularly the amount of understory regrowth and trunk scorching (Artman and Downhower 2003). We characterized each site as either < 6 months, 6–18 months, or > 18 months since the last burn. We used our knowledge of stand recovery from other known fires across the island over the last four years to confirm these categories.

Macro Scale (100-m radius)

We estimated the number of thatch palms and pines into the same categories that we used for the meso scale. We also categorized average pine understory and burn history using the same categories previously stated for the meso scale.

Control Points

We paired each nest plot with two randomly selected meso scale control points (50 m from the nest) and two randomly selected macro scale control points (500 m from the nest). We selected these distances for meso scale and macro scale control points to measure variables well inside and generally outside of each oriole pair's likely breeding territory, respectively. We randomly selected control points by assigning the four cardinal directions (north, south, east, and west) the numbers 1–4, respectively, and then choosing two random numbers between 1–4. For the two meso control points, we walked 50 m away from the nest tree in the selected cardinal directions and recorded the same parameters as we measured for the meso scale nest site (within a 10-m radius). For the two macro control points, we walked 500 m from the nest tree in the selected cardinal directions and recorded the same parameters as we did for the macro scale nest site measurements (within a 100-m radius). If a cardinal direction had habitat that could not be traversed (e.g., if there was a pond or creek), we randomly chose an alternate cardinal direction.

Statistical Analysis

We collected data as discretized categories to facilitate data collection on many aspects of the nesting sites. The lack of prior knowledge of relevant habitat characteristics in the native pine forest impelled us to measure a large number of habitat variables. Since our measurements varied by over two orders of magnitude, estimating categories for discretized data allowed us to efficiently measure many variables while still capturing the overall variation in the habitats. For calculations involving the numbers of pine trees and thatch palms, we denoted the six abundance categories (0, 1–4, 5–10, 11–20, 21–50, and 51–100) as 0–5, respectively. For the average pine understory, we denoted the height categories (0–1 m, 1–2 m, 2–4 m, and 4–10 m) as 0–3, respectively. Finally, we denoted the burn categories as 1–3 for < 6 months, 6–18 months, or > 18 months since last burn, respectively. We averaged the two meso control points together and the two macro control points together before further testing. We used the Wilcoxon signed rank test (α = 0.05) to compare the control habitat variables to the nest habitat variables for each aspect of the meso scale and macro scale measurements. As our data were not normally distributed, we used a non-parametric method, similar to a paired t-test. Since our hypotheses were two-tailed, the test statistic (W) was the smaller of the rank sums either positive or negative (Wilcoxon *et al.* 1970). We corrected for multiple comparisons using the Bonferroni correction, as we measured many aspects of the nesting habitat. The Bonferroni correction adjusts probability (*p*) values because of the increased risk of type I error when conducting multiple statistical tests (e.g., McDonald 2014). We conducted all analyses using R (R Core Team 2018). Values are mean ± standard deviation (SD) unless noted otherwise.

Results

We collected data for all 12 Bahama Oriole nests found in the pine forest between 2016–2018. Generally, the pine forest habitat that the orioles nested in had scattered pines 15–25 m tall with an open understory frequently scattered with thatch palms (Fig. 2). Over the three years, we found a total of six nests in Caribbean pines and six nests in Key thatch palms. In 2016, we found three nests, two in Key thatch palms and one in a pine tree. In 2017, we found one nest in a thatch palm and three nests in pines. Finally, in 2018, we found three nests in thatch palms and two in pine trees.

Fig. 2. Photographs of two Bahama Oriole nest trees in pine forest. (a) Nest in Key thatch palm; the active nest was found hanging in a dead frond. The yellow arrow is pointing to the general location of the nest. (b) Nest in Caribbean pine; the researcher, Lehron E. Rolle, is pointing to the general nest location in a clump of pine needles. Photographs by Kevin E. Omland.

Micro Scale (nest tree)

Nests in pines were 2.6 times higher than nests in thatch palms, which was expected as most of the pines were much taller than the understory palms (Table 1). Nest tree heights ranged from 12.9 m to 23.6 m for pines compared to 4.5 m to 9.2 m for thatch palms (Fig. 3). Nests in thatch palms were generally 1–2 m below the top of the palm, concealed on the underside of either live or dead fronds. Orioles placed three of these nests in dead palm fronds hanging down from the tree and placed three of these nests in living, upright or horizonal palm fronds. Nests in pines were 1–4 m below the top of the nest tree. Pine nests hung under branches in clumps of needles so that they were generally difficult to spot without binoculars and visual confirmation of orioles going to and from the nest with materials or food. There were no tall thatch palms (> 2 m tall) within 10 m of four of the pine nest trees (Fig. 3), and in the case of three of these nests, there were no thatch palms within 100 m of the nest (unpubl. data).

Table 1. Micro scale characteristics of nest trees for 12 Bahama Oriole nests found in pine forest habitat. SD = Standard deviation. DBH = Diameter at breast height.

Nest Tree Species	Number of Nest Trees	Mean Tree Height (m) ± SD	Mean DBH (cm) ± SD	Mean Nest Height (m) ± SD
Leucothrinax morrisii	6	6.8 ± 2.0	14.0 ± 2.0	5.1 ± 1.5
Pinus caribaea var. bahamensis	6	17.9 ± 4.4	23.2 ± 7.1	16.0 ± 4.7

When nesting in thatch palms, Bahama Orioles chose significantly taller palms compared to the average of surrounding thatch palms within the plot ($n = 6$, W = 0, $p = 0.03$). When nesting in Caribbean pines, Bahama Orioles did not prefer the tallest pines in the plot, as there was only one case where the nest pine tree was taller than the average control pine trees (Fig. 3). There was no statistically significant difference between pine nest tree heights and control pine heights ($n = 6$, W = 6, $p = 0.4$).

Meso Scale (10-m radius)

On average, oriole nest plots had slightly fewer small thatch palms (< 2 m tall) and slightly fewer pine trees compared to the control plots. However, these differences were not significant after Bonferroni correction (Table 2). There was not a significant difference between the nest site and the controls for understory height before or after Bonferroni correction. After removing observations with paired differences equal to zero, sample sizes for tall Key thatch palms (> 2 m tall) and burn history were too small to formally test for statistical significance at our specified alpha. However, since all of the removed comparisons were locations where the nest site and control site had identical measures, this suggests that numbers of tall Key thatch palms and burn history were very similar between the site types (Table 2).

Macro Scale (100-m radius)

Orioles generally nested in areas that had significantly more tall thatch palms than other areas in the pine forest (Table 2). When we compared the macro scale nest sites to the macro scale controls, we found a significant difference in the number of thatch palms > 2 m tall after Bonferroni correction ($n = 10$, W = −1, $p^B = 0.035$). Orioles did not show a tendency to select nest sites at the macro scale that differed significantly in the number of small Key thatch palms compared to control sites. After removing observations with paired differences equal to zero, sample sizes for number of pines, understory height, and burn history were too small to formally test for statistical significance at our specified alpha, but these variables show no evidence of difference between nest sites and controls (Table 2).

Discussion

We found Bahama Oriole nests in typical pine forests throughout North Andros. Although Bahama Orioles are known to nest in anthropogenic habitats, such as residential areas, our findings confirm that they also frequently nest in native Bahamian pine forest (Stonko *et al.* 2018). Half of the nests we found were in Key thatch palms and half were in Caribbean pines. Previous work on this species conducted by Price *et al.* (2011) stated that the orioles are dependent upon anthropogenic habitats and nested mostly in coconut palms. However, the authors also suggested that before human settlement and the introduction of the coconut palm, the orioles likely nested in endemic palms, such as the Key thatch palms found both in their study and in ours. We were surprised to find orioles nesting in pines so frequently, as all other Caribbean orioles nest predominantly in palms (Jaramillo and Burke 1999). Our findings, combined with previous documentation of pine forest nesting in the Bahama Oriole (Stonko *et al.* 2018) as well as evidence from a recent population survey documenting that most of the Bahama Oriole population seems to

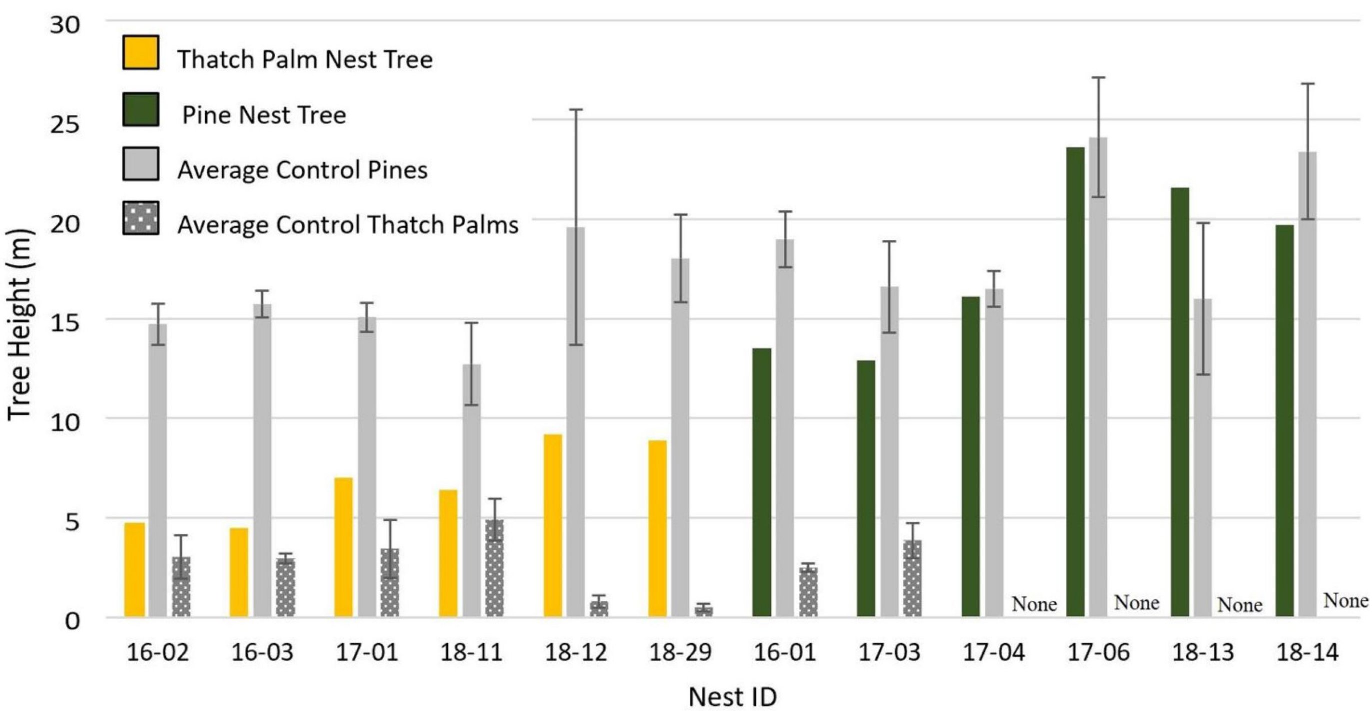

Fig. 3. Comparison of Bahama Oriole nest tree height to the average height of the three closest Key thatch palms and the three closest Caribbean pines. Four pine trees did not have thatch palms within a 10-m radius, which is indicated by the word none on the chart. Standard deviation is shown for average control thatch palm height (stippled) and average control pine height (open). The first two digits of the nest ID signify the year found and the last two digits indicate nest number. Note: some nest numbers are greater than the number of nests used in this study because some nests were in developed areas and wetlands, which were not the focus of this study.

Table 2. Comparison of Bahama Oriole paired nesting and control sites (*n* = 12 pairs) across two spatial scales. *n* = sites with paired differences > 0; W = Wilcoxon signed-rank test statistic; *p* = raw *p*-value; p^B = Bonferroni-corrected *p*-value. After removing observations with paired differences = 0, sample sizes for some variables were too small to test for statistical significance at our specified alpha of 0.05 (denoted by +). After Bonferroni correction, the only comparison that was significant was the number of tall thatch palms at the macro scale (shown in bold).

Variable	Mean ± SD	*n*	W	*p*	p^B
Meso Scale (10-m radius)					
Number of Caribbean pines					
Nest site	2.33 ± 0.78	9.00	6.50	0.06	0.30
Control site	2.83 ± 0.75				
Number of Key thatch < 2 m					
Nest site	1.00 ± 0.85	7.00	0.00	0.02	0.10
Control site	1.38 ± 1.03				
Number of Key thatch > 2 m					
Nest site	0.75 ± 0.87	5.00	7.50	1.00+	1.00+
Control site	0.75 ± 0.81				
Understory height (m)					
Nest site	1.25 ± 1.14	8.00	15.50	0.78	1.00
Control site	1.33 ± 0.89				
Burn history					
Nest site	2.00 ± 0.95	3.00	0.00	0.17+	0.85+
Control site	2.21 ± 0.89				
Macro Scale (100-m radius)					
Number of Caribbean pines					
Nest site	4.83 ± 0.39	4.00	−1.00	0.20+	1.00+
Control site	4.29 ± 1.29				
Number of Key thatch < 2 m					
Nest site	2.50 ± 2.28	7.00	−12.00	0.80	1.00
Control site	2.30 ± 2.16				
Number of Key thatch > 2 m					
Nest site	**2.40 ± 1.83**	**10.00**	**−1.00**	**0.007**	**0.035**
Control site	**1.00 ± 1.21**				
Understory height (m)					
Nest site	1.75 ± 0.87	5.00	−3.00	0.27+	1.00+
Control site	1.58 ± 0.82				
Burn history					
Nest site	2.08 ± 0.90	5.00	5.50	0.68+	1.00+
Control site	2.17 ± 0.91				

reside in the vast pine forests of Andros (Rowley *et al.* in review), suggest that most Bahama Orioles likely nest in pine trees and understory thatch palms.

When orioles nested in thatch palms, the nests were well concealed in both living fronds and hanging dead fronds (Fig. 2; also see Stonko *et al.* 2018, their Fig. 2). In this study, the orioles nested in thatch palms that were significantly taller than nearby thatch palms. This finding is consistent with Price *et al.* (2011), who found that when Bahama Orioles use anthropogenic areas during the breeding season, they select nest sites in the tallest available palm trees. Note, Price *et al.* (2011) also found orioles nesting in Key thatch palms, but predominately found them nesting in coconut palms. In our study, there were no coconut palms within 100 m of any of the pine forest nests we measured; in fact, none were visible from the nest trees at all. It is possible that orioles choose to nest in taller trees in order to avoid nest predators such as cats, rats, or snakes (Vanderwerf 2012, reviewed by Colombelli-Négrel and Kleindorfer 2009). Other than height, we are unsure whether any other specific characteristics of these palms are crucial for nest tree selection. Future studies should validate our findings and look for additional aspects of the thatch palms that could be important for nesting or foraging.

When orioles nested in pine trees, they did not choose the tallest pine in the area, possibly because the pine trees are tall enough that these orioles do not face much threat from ground predators. Nevertheless, the orioles nested near the top of the nest tree, generally above rather than below the canopy. Rigorous nest and fledging success monitoring were beyond the scope of the present study; however, we did observe successful fledging from several Caribbean pine nests and Key thatch palm nests (pers. obs.).

Our data indicate that, at the broad macro scale, the orioles frequently chose to nest in areas with more tall thatch palms (> 2 m tall), regardless of whether or not their nest tree was in a Key thatch palm or Caribbean pine. Tall thatch palms may be important foraging areas and, as mentioned, are likely important for nesting orioles to avoid ground predators (KEO pers. obs.). These results suggest that there are specific habitat characteristics that influence Bahama Oriole nest-site selection. However, other aspects of the nest site, including number of pines, number of small thatch palms (< 2 m tall), burn history, and understory height, did not differ significantly between the nest sites and their respective controls at either the meso or the macro scale. We did not find any significant preference for an abundance of thatch palms at the meso scale, likely because there were generally few dense clumps of tall thatch palms at this scale. Rather, the orioles chose areas of forest with many tall thatch palms dispersed over a wider area of the forest; having a larger number of tall thatch palms over a larger portion of the territory could be important for both nesting and foraging (KEO pers. obs.).

Furthermore, the Bahama Oriole did not show a preference for tree species when building their nests, as they used both Caribbean pines and Key thatch palm in the pine forest equally. Consistent with Price *et al.* (2011) and Stonko *et al.* (2018), we also observed orioles nesting in coconut palms, native Florida silver palms (*Coccothrinax argentata*), native sabal palms (*Sabal palmetto*), and even banana trees (*Musa sp.*) on other parts of the island, in both developed areas and wetlands (unpubl. data). Since this study was focused on the pine forest habitat, we did not record or analyze detailed data on nests in these other locations. However, for half of the pairs that nested in pine trees, there were no tall thatch palms near the nest, hinting that orioles may prefer to nest in thatch palms if they are available in the pine forest.

Since the majority of the Bahama Oriole population likely breeds in native pine forest (Stonko *et al.* 2018, Rowley *et al.* in review), it was crucial for our study to focus on quantifying nest characteristics in the pine forest. Importantly, we found nests in several different types of pine forest including dense stands, mixed pine-coppice habitat, and open pine forest. Because Bahama Orioles had only recently been discovered nesting in pine forest, there was no prior expectation as to which aspects of the pine forest might be important for nesting sites. Many of the variables we measured, especially those relating to the understory and the general pine overstory, did not explain nest-site selection among our sample. Finding more nests to increase the sample size is necessary to confirm if these features are important for oriole nesting requirements or other needs related to foraging and shelter.

This study is a first step towards characterizing Bahama Oriole nest-site selection in the native pine forest. We provide further evidence that many orioles use native pine forest as breeding habitat, as originally documented in Stonko *et al.* (2018). Our data suggest that areas in the pine forest with tall Key thatch palms are an important breeding habitat for the Critically Endangered Bahama Oriole. Future research will seek to validate these findings and determine which aspects of pine forests are most crucial to the oriole population. For example, quantifying fire frequency and intensity would be important because fires regularly burn the understory of these pine forests, which likely influences understory vegetation diversity and density. Note that without fires, the pine forest is gradually replaced by broadleaf forest (Myers *et al.* 2004, Currie *et al.* 2005). Further, forest fires burn many of the hanging dead palm fronds, which our observations, along with Price *et al.* (2011), suggest may be important nest sites for Bahama Orioles. Also, in some cases, hot fires kill thatch palms, which could decrease nest site availability. Thus, careful management of anthropogenic sources of fire and monitoring possible increases in fire frequency and intensity due to climate change (Dale *et al.* 2001) are necessary for nesting habitat protection. Key thatch palms were clustered intermittently across our North Andros study site. Generally, palms in pine forest seem to be associated with a higher water table (Henry 1974, Correll 1979, Myers *et al.* 2004, Currie *et al.* 2005). However, more information on thatch palm abundance, distribution, and fire response in Caribbean pine forest is required to better understand their role in oriole nest-site selection. The spatial scales in this study were based on our best understanding of oriole breeding territory sizes (Ligi and Omland 2007, Price *et al.* 2011, Campbell *et al.* 2016); however, further research is needed to provide more exact measurements of Bahama Oriole movements and territory size to inform additional surveys of nest-site selection and breeding behavior.

We have now initiated studies using radio telemetry and other tracking technology to facilitate finding more nests and delineating the extent of oriole breeding territories across Andros. If the findings in this study are further validated, then land managers should look for areas with abundant tall thatch palms already in national parks that need further protection as well as any additional habitat with these characteristics that could be preserved. In addition, researchers and land managers should investigate possible management practices that would increase the number and height of thatch palms in the pine understory.

Conclusions

Since pine forests are the most extensive terrestrial habitat on Andros, it is likely that the majority of the Bahama Oriole population is dependent upon pine forest for nesting. The findings from this study add further support for the importance of protecting Bahamian pine forests. The Bahamas National Trust manages Blue Holes National Park (~160 km^2) and West Side National Park (~6,000 km^2), which both contain pine forest habitat (Bahamas National Trust 2018). Given the importance of Caribbean pine forest for breeding (Lloyd and Slater 2011) and migrant songbirds (Wunderle and Waide 1993), as well as its newfound role in the Critically Endangered and endemic Bahama Oriole's breeding biology (Stonko *et al.* 2018), it is crucial to conserve pine forest ecosystems. Since orioles can utilize a variety of different pine forest habitats, there are many locations of pine forest that may be suitable. However, large areas with tall thatch palms in the understory may be the most useful habitat to preserve. Furthermore, we recommend that the residents plant more native palms such as Key thatch palms and sabal palms for orioles nesting in developed areas.

We now know that Bahama Orioles are found throughout much of the pine forests of North Andros. Previous population estimates that focused mostly on developed residential areas are clearly major underestimates. In combination, our findings suggest a brighter short-term outlook for the Bahama Oriole. The orioles extensively utilize the most abundant terrestrial habitat on the island, they use different parts of the pine forest, and they nest in several different tree species.

However, there are still many aspects of Bahama Oriole ecology and behavior that remain unclear. For example, we do not know whether orioles maintain year-round territories or whether or not they use the same parts of the pine forest during the non-breeding season. We also do not know which predators may have the biggest impact on nests or adults. More broadly, climate change is likely to affect fire regimes as well as the intensity, frequency, and tracks of hurricanes. Saltwater inundation due to storm surge quickly kills all pine trees. Sea level rise will reduce total island area and may increase the distance between the different islands of Andros. Thus, the impact of each of these changes on the orioles and other native songbirds needs to be investigated, and future research should address each of these threats to the Bahama Oriole. Nevertheless, conserving substantial tracts of native Bahamian pine forest will be an important first step towards the long-term survival of this species as well as many other native species.

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Title Page Illustration

Adult and yearling Bahama Oriole (*Icterus northropi*) amongst the Caribbean pines (*Pinus caribaea*). Painted in watercolor by Katherine Thompson, UMBC, in June 2020.

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