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Behavioral Ecology, Taxonomy, and Conservation Genetics of the Bahama Oriole (Icterus northropi)

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LOMA LINDA UNIVERSITY
School of Science and Technology
in conjunction with the
Faculty of Graduate Studies

Behavioral Ecology, Taxonomy, and Conservation Genetics of the Bahama Oriole (*Icterus northropi*)

by

Melissa R. Price

A Dissertation submitted in partial satisfaction of
the requirements for the degree of
Doctor of Philosophy in Biology

June 2011

Each person whose signature appears below certifies that this dissertation in his/her opinion is adequate, in scope and quality, as a dissertation for the degree Doctor of Philosophy.

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ABSTRACT OF THE DISSERTATION

Behavioral Ecology, Taxonomy, and Conservation Genetics of the Bahama Oriole (*Icterus northropi*)

by

Melissa R. Price

Doctor of Philosophy, Graduate Program in Biology
Loma Linda University, June 2011
Dr. William K. Hayes, Chairperson

In this dissertation, I examined the Bahama Oriole (*Icterus northropi*) at multiple scales, with the aim of developing a sound management plan for this critically endangered bird. In the first of five studies, I measured plumage variation among four allopatric populations of the former *Icterus dominicensis* complex in the Caribbean. Diagnosable plumage differences among populations contributed to the subsequent elevation of each of these populations (including *northropi*) to species status. In the second study, I examined molecular variation in subpopulations of *I. northropi* on North Andros, Mangrove Cay, and South Andros, The Bahamas. I identified several patterns of genetic variation that will inform conservation planning. The third study explored the population status and breeding ecology of the Bahama Oriole. My estimates of 141–254 individuals remaining globally contributed to an IUCN Red List designation as "critically endangered." Orioles selected nesting trees that were significantly taller, less likely to have shrubs underneath, farther from cover, and with more palm trees nearby than randomly available palm trees. Lethal yellowing disease devastated coconut palms regionally on North Andros during the course of our study, but palms on South Andros and Mangrove Cay, where oriole density was higher, remained healthy. In the fourth study, I assessed the Bahama Oriole's community-level relationships, including the relative densities of other avian species in three habitats (pine forest, coppice, and anthropogenic habitat), foraging strategies, and inter- and intraspecific social interactions. My findings indicate coppice is vitally important to resident, migrating, and wintering birds. Collectively, these studies identify key conservation priorities to save this critically endangered bird. In my final study, a literature review, I explored the ecological consequences of extinction in a well-studied insular model: the Hawaiian Islands avifauna. Five of six islands have significantly different trophic guild structure now than they did prior to the arrival of humans, due to a combination of extinction events and introduced bird species. Very few extinct bird species have been replaced by equivalent ecological substitutes in the present day avifauna, leading to coextinctions of dependent species. This research highlights the importance of preventing extinctions in the remaining global avifauna.

CHAPTER ONE

INTRODUCTION

In this dissertation, I assess multiple factors that may contribute to conservation efforts of the Bahama Oriole (*Icterus northropi*), a critically endangered island endemic. In this chapter, I begin by reviewing the commonly understood threats to island endemics, the Bahama Oriole's conservation needs, and the importance of species conservation in general.

The Special Case of Island Endemics

Oceanic islands present opportunities to test and implement management solutions in defined areas at high risk for species loss (Paulay, 1994; Şekercioğlu et al., 2004). Multiple studies have shown a higher extinction rate for island species, compared with mainland species, due to restricted ranges, habitat destruction, and vulnerability to the introduction of novel predators and diseases, among other factors (Johnson and Stattersfield, 1990; Pimm, 1991; Blackburn et al., 2004; Whittaker and Fernandez–Palacios, 2007). Since 1600, 97 out of 108 documented bird extinctions have been island endemics (Johnson and Stattersfield, 1990). Endemism richness of plants and vertebrates on islands exceeds that of continents by a factor of nearly ten (Kier et al., 2009), a statistic of considerable concern since island species continue to face a higher threat from human impact than those on the mainland (Kier et al., 2009).

Extinction rates in the Caribbean islands, a formally recognized biodiversity hotspot (Myers et al., 2000), have increased over the last several thousand years due to climatic changes and human influence (Woods and Sergile, 2001; Steadman, 2006; Ricklefs and Bermingham, 2008). Three-quarters of West Indian parrots and macaws, 10 of 12 avian insectivores, and 27 bats, for example, have become extinct, while many more taxa are now threatened (Woods and Sergile, 2001). Efforts to protect, manage, and preserve the remaining taxa are often hindered by limited knowledge of natural history, lack of financial and educational resources, and a diversity of independently governing bodies (Ricklefs and Bermingham, 2008). Basic research identifying high-quality habitats for all life history stages is needed to implement effective management solutions for many of the remaining endangered species (Donovan et al., 2002).

A Critically Endangered Island Endemic: The Bahama Oriole (*Icterus northropi*)

As one of the few endemic birds to The Bahamas, the Bahama Oriole (*Icterus northropi*), recently given species status (American Ornithologists' Union, 2010), is also one of the world's rarest. After disappearing from Abaco Island, The Bahamas, in the early 1980s (A. W. White, pers. comm.), the oriole remains today only on Andros. Baltz (1997) suggested that fewer than 300 individuals persist, with populations largely confined to townships and agricultural areas along the coast where introduced coconut palm (*Cocos nucifera*) abounds (Allen, 1890; Baltz, 1997). This number may be unsustainable given recent devastation of the oriole's favored coconut palm nesting habitat by lethal yellowing disease (Currie et al., 2005), loss of coppice (dry broadleaf forest) to farming and coastal development (Wunderle and Waide, 1993), and the recent arrival of the Shiny Cowbird (*Molothrus bonariensis*; Baltz, 1995, 1996), a brood parasite that favors this host (Wiley, 1985).

Conservation Taxonomy

Until 2010, four island subspecies of the Greater Antillean Oriole (*Icterus dominicensis*) were recognized from The Bahamas (*I. d. northropi*), Cuba (*I. d. melanopsis*), Hispaniola (*I. d. dominicensis*), and Puerto Rico (*I. d. portoricensis*). Using mitochondrial cytochrome *b* and ND2 markers, Omland et al. (1999) found a substantial genetic distance (>5%) separating *I. d. portoricensis* from both *I. d. northropi* and *I. d. melanopsis*. However, *I. d. northropi* and *I. d. melanopsis* differed by only 0.9%, which was more typical of subspecies within the genus. Unfortunately, because only cytochrome *b* could be sequenced from *I. d. dominicensis*, the genetic relationships among the group remained unclear.

Omland and Lanyon (2000) subsequently mapped plumage characters on their genetic tree, showing *I. d. dominicensis* close to *I. d. portoricensis* and distinct from the sister taxa *I. d. northropi* and *I. d. melanopsis*, presumably on the basis of cytochrome *b* data. They indicated a substantial number of plumage characters separating males of each of the four taxa. *Icterus d. northropi*, for example, was separated from *I. d. melanopsis*, *I. d. dominicensis*, and *I. d. portoricensis* by six, five, and seven characters, respectively. Although these plumage characters could be inferred as diagnosable, the authors did not indicate sample sizes or possible within-taxon variation in their plumage assessments. Additional differences in adult morphology, juvenal plumage, and vocalizations prompted Garrido et al. (2005) to elevate each of the island groups to full allospecies status. However, the studies by Omland and Lanyon (2000) and by Garrido et al. (2005) failed to establish 100% reciprocal diagnosability of the four taxa, a species criterion frequently relied on by ornithologists (Helbig et al., 2002; de Queiroz, 2005). In chapter 2, by demonstrating 100% reciprocal diagnosability using plumage characters of the four *I. dominicensis* taxa, I provided additional evidence that *I. d. northropi* warranted full species status and, subsequently, a higher conservation priority.

Conservation of Genetic Diversity

The Bahama Oriole is a year-round resident on Andros, The Bahamas, a land mass riddled with waterways that effectively divide it into multiple islands. The largest three islands, and the only ones with significant human development, include North Andros, Mangrove Cay, and South Andros. These islands are separated by channels that range in width from 1–5 km, which previous population assessments assumed to be isolating barriers (Baltz, 1997). Considering the exceptional flight capabilities of migratory oriole species (Jaramillo and Burke, 1999), movement of orioles among the three islands seems highly likely.

The level of inter-subpopulation movement can be inferred by quantifying and mapping haplotype diversity among the North Andros, Mangrove Cay, and South Andros subpopulations. Patterns of genetic variation can help us identify whether these groups should be managed as one or multiple conservation units.

In chapter 3, I assessed genetic variation in the remaining Andros population for three purposes: (1) to discern genetic structuring of the subpopulations on North Andros

Island, Mangrove Cay, and South Andros Island, (2) to establish possible historical genetic patterns of geographical variation, or demographic history, of the subpopulations, and relate these to current conservation concerns, and, and (3) to inform planning for possible translocation of the Bahama Oriole to Abaco Island, where it formerly occurred. Translocation of individuals to other areas can increase the species' effective population size and decrease the probability of extinction through stochastic effects (e.g., hurricanes; Fleischer, 2007) Our study suggests translocation of Bahama Orioles from Andros to Abaco Island, where they formerly occurred, should include individuals from North Andros, Mangrove Cay, and South Andros to maintain genetic diversity in the translocated population.

Population Ecology

In the study presented in chapter 4, I sought to accomplish three major objectives. First, I ascertained relative population density of the Bahama Oriole in each of three primary habitats, and estimated global population size. Second, I studied the oriole's breeding ecology, with emphases on nest attributes, nest site selection at three scales (micro–, meso–, and macrohabitat), and the provisioning of nestlings. Third, I assessed the potential impacts of Shiny Cowbirds and lethal yellowing on reproductive success and local population density of the oriole. Collectively, the findings provide important information for developing a sound management plan for this critically endangered species

Previous population surveys estimated 50–100 Bahama Orioles on North Andros, and 100–200 on South Andros (Baltz, 1997, unpublished). Baltz considered these estimates very liberal, although he surveyed only residential areas on North Andros, and based his South Andros estimates on personal communication with Tony White. As a full species, these numbers suggested *I. northropi* was critically endangered, based on the IUCN Red List Criterion of an estimated population of <250 mature individuals, and the recent disappearance of the oriole from Abaco Island (A. W. White, pers. comm.). A current evaluation of the population was needed to ascertain whether the numbers were indeed declining, and to provide estimates for Mangrove Cay, which previously had not been surveyed.

In this chapter, I report the results of two sets of surveys. In 2005, we assessed relative population density of the Bahama Oriole and Shiny Cowbird in the three habitats where orioles had previously been observed: Caribbean pine (*Pinus caribaea*) forest, coppice (dry broadleaf forest), and anthropogenic habitat. Orioles were most common in coppice and anthropogenic habitat, but Shiny Cowbirds were most common in anthropogenic habitat, where orioles breed. In 2009 we conducted thorough searches of breeding habitat on North Andros, Mangrove Cay and South Andros, and obtained estimates of 90–162, 24–44, and 27–48 orioles, respectively, remaining on each island.

Knowledge of basic natural history is necessary to conduct effective monitoring at meaningful spatial scales (Donovan et al., 2002), yet this information was scarce for *Icterus* when I began my research (Garrido et al., 2005). In this study, I discovered that orioles mostly used anthropogenic habitat (residential and agricultural land) during the breeding season, although home ranges included nearby pine forest and coppice. The majority (87%) of 46 nests observed were constructed in nonnative coconut palm (*Cocos nucifera*), with native *Sabal palmetto* and *Thrinax morrisii,* and an introduced *Brassaia* *actinophylla* also used. Trees selected by orioles for nesting were significantly taller, less likely to have shrubs underneath, farther from cover, and had more palm trees nearby than randomly available palm trees in the area. The juxtaposition of anthropogenic habitat to suitable native habitats appeared to be more important than any single factor in meeting the Bahama Oriole's life history needs, especially for breeding adults and fledging chicks.

I also assessed two major threats to the oriole's breeding success: the Shiny Cowbird (*Molothrus bonariensis*), a brood parasite that became established in the 1990s without subsequent population increases, and lethal yellowing disease, which attacks the oriole's preferred nesting tree, the coconut palm. Three of eight nests with known contents were parasitized by Shiny Cowbirds. My surveys of palm health showed that lethal yellowing disease has devastated coconut palms and reduced local breeding oriole density on North Andros, but palms on Mangrove Cay and South Andros remain healthy, and local oriole densities are higher on these islands.

Community Relationships

The Bahama Oriole (*Icterus northropi*) faced many habitat changes over the past centuries, as logging and human development removed native breeding and foraging habitats (Currie et al., 2005) and provided new opportunities in the form of novel, introduced plant species (Nickrent et al., 2008). Resource subsidies in human-disturbed areas, such as cultivated plants or discarded food items, may have increased or stabilized avian productivity in some species (Faeth et al., 2005), although other bird species may have avoided these disturbed habitats or declined following habitat disturbance (Miller et al., 2007; Norris et al., 2009). Even birds that regularly use anthropogenic habitats can be negatively affected by forest loss, as multiple habitat types may be needed to sustain viable populations (Cohen and Lindell, 2005).

In chapter 5, I evaluated foraging strategies, habitat distribution, and species composition in Caribbean pine forest, coppice, and anthropogenic habitat on Andros Island. As interspecific and intraspecific interactions can influence habitat distribution and foraging strategies (Mac Nally and Timewell, 2005; Shochat et al., 2010), I also identified interactions between Bahama Orioles and other birds when observed. I found that the oriole may be benefitting from some aspects of human disturbance, including resource subsidies and the planting of coconut palms; however, I also found that coppice and pine forest represent important foraging grounds for young orioles, as well as other migrating and overwintering species. The Bahama Oriole benefits from anthropogenic habitat, but also depends on other natural habitats throughout its life history, and will benefit especially from careful management of coppice, which is currently at high risk of rapid loss due to agricultural development on South Andros (Lloyd and Slater, 2010; Thurston, 2010), and pine forest, which has become homogenized due to poor management following deforestation.

Ecological Replacement of Extinct Species

The Bahama Oriole, although it may never have existed in large numbers, occupies an important ecological role as an insectivore, reducing and selecting the insect population, as a nectarivore, pollinating plants, and as a frugivore, dispersing seeds. If management efforts fail and the oriole becomes extinct, what is the likelihood that an

ecological equivalent would provide a substitute for these roles? I examined this question by comparing the historic and present-day avifaunas of the Hawaiian Islands. The arrival of the Polynesians and subsequent waves of settlers to the Hawaiian Islands resulted in high numbers of avian extinctions, leaving ecological voids which may or may not have been filled by other species. Concurrently, a high number of species introductions may have provided ecological equivalents to fill these voids. In this literature review, I compared the trophic guild composition of the historic Hawaiian avian community with that of the present avian community. I also conducted literature searches for known, specific cases of ecological substitutions for extinct Hawaiian bird species.

Avian trophic guild composition has changed significantly since the arrival of Polynesians for all islands except Kauai. On all islands, distribution of birds among guilds has changed; for example, greater than 40% of Hawaii's current avian species are granivorous, vastly outnumbering each of the other trophic groups. Ecological substitutes have been suggested for eleven extinct Hawaiian bird species, in some cases reducing coextinctions of dependent plant species; however, the lack of ecological equivalents for many extinct species resulted in cascading coextinctions. The results of this study highlight the importance of species conservation and the prevention of extinctions whenever it is within our power to do so. Based on the statistics in this study, if the Bahama Oriole declines to extinction, its ecological roles in insect reduction and selection, flower pollination, and seed dispersal, are unlikely to be fulfilled by a substitute species.

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CHAPTER TWO

CONSERVATION TAXONOMY OF THE GREATER ANTILLEAN ORIOLE (*ICTERUS DOMINICENSIS*): DIAGNOSABLE PLUMAGE VARIATION AMONG ALLOPATRIC POPULATIONS SUPPORTS SPECIES STATUS[1]

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[1] Price, M. R., and Hayes, W. K. (2009) Conservation taxonomy of the Greater Antillean Oriole (*Icterus dominicensis*): diagnosable plumage variation among allopatric populations supports species status. Caribbean Ornithology 22, 19–25.

Abstract

Allopatric populations, such as those present on islands, pose special challenges to identifying taxonomic boundaries, which can be practically addressed using diagnostic criteria. To assess the taxonomic and, hence, conservation status of the four island populations of the Greater Antillean Oriole (*Icterus dominicensis*), we examined 156 male specimens of *I. dominicensis* for six discrete and three continuous plumage characters. The four island populations proved to be 100% diagnosable. *Icterus d. northropi* differed from all other taxa by having the greatest extent of yellow on the venter (non-overlapping with other taxa). *Icterus d. portoricensis* was distinguished from all other taxa by the presence of a black upper rump (yellow in other taxa) and the least extent of yellow on the rump (non-overlapping with other taxa). *Icterus d. melanopsis* and *I. d. dominicensis* were fully discriminated from *I. d. northropi* and *I. d. portoricensis* by the aforementioned characters and from each other by upper-tail covert color (black and ≥50% yellow, respectively). Our findings support recent studies suggesting that the four island groups represent distinct allospecies consistent with interpretations of both the phylogenetic and evolutionary species concepts. With elevation to full species, conservation priorities need to be revisited, particularly for the critically endangered Bahamas taxon (*I. d. northropi*).

Introduction

Prior to the emergence of molecular techniques, morphology, song, and plumage characters played the most important roles in designating avian taxa (Coyne, 1994; Peterson, 1998). Today, in spite of increased emphasis on molecular systematics and the phylogenetic species concept, morphology and plumage characters are still viewed as valuable for defining species limits (Helbig et al., 2002; Wiens, 2004). Research has shown that sexually selected traits, such as bird plumage characters, are likely to evolve quickly (Omland and Lanyon, 2000), making them useful for delineating young taxa.

The taxonomic status of the Greater Antillean Oriole (*Icterus dominicensis*) has long been disputed. Four island subspecies are currently recognized from The Bahamas (*I. d. northropi*), Cuba (*I. d. melanopsis*), Hispaniola (*I. d. dominicensis*), and Puerto Rico (*I. d. portoricensis*). In the past, these populations were either lumped with (Hellmayr, 1935) or separated from (Phillips and Dickerman, 1965) populations of the similarly plumaged Black-cowled Oriole (*I. prosthemelas*) of Central America (see Garrido et al., 2005 for history of taxonomy). Recent molecular and plumage analyses confirmed the substantial genetic distance between *I. dominicensis* and *I. prosthemelas*, which suggested that plumage similarities arose through convergent evolution (Omland et al., 1999; Omland and Lanyon, 2000).

Using mitochondrial cytochrome *b* and ND2 markers, Omland et al. (1999) found a substantial genetic distance (>5%) separating *I. d. portoricensis* from both *I. d. northropi* and *I. d. melanopsis*. However, *I. d. northropi* and *I. d. melanopsis* differed by only 0.7%, which was more typical of subspecies within the genus (but see Baker et al., 2003; Kondo et al., 2004; Cortes-Rodríguez et al., 2008). Unfortunately, because only cytochrome *b* could be sequenced from *I. d. dominicensis*, the genetic relationships among the group remained unclear. Omland and Lanyon (2000) subsequently mapped plumage characters on their genetic tree, showing *I. d. dominicensis* close to *I. d. portoricensis* and distinct from the sister taxa *I. d. northropi* and *I. d. melanopsis*. These relationships were later confirmed by Sturge et al. (2009) using both cytochrome *b* and ND2 markers. Omland and Lanyon (2000) indicated a substantial number of plumage characters separating males of each of the four taxa. *Icterus d. northropi*, for example, was separated from *I. d. melanopsis*, *I. d. dominicensis*, and *I. d. portoricensis* by six, five, and seven characters, respectively. Although these plumage characters could be inferred as diagnosable, the authors did not indicate sample sizes or possible within-taxon variation in their plumage assessments. Additional differences in adult morphology, juvenal plumage, and vocalizations prompted Garrido et al. (2005) to elevate each of the island groups to full allospecies status. On the basis of mitochondrial DNA differences, Sturge et al. (2009) later echoed this call. Support for elevating these taxa to full species could be strengthened by demonstrating 100% reciprocal diagnosability of the four taxa, a species criterion frequently relied on by ornithologists (Helbig et al., 2002; de Queiroz, 2005). The studies by Omland and Lanyon (2000) and by Garrido et al. (2005) did not establish reciprocal diagnosability.

Taxonomic decisions often have profound ramifications for conservation (e.g., McNeely, 2002; Dubois, 2003; Mace, 2004), which may be especially important for insular populations (Hayes, 2006; Phillimore and Owens, 2006). Among the four oriole subspecies, the Bahamas population appears to be at high risk of extinction. Although it formerly occurred on Abaco, the population there apparently became extirpated in the

1980s (White, 1998. pers. comm..). Today, it persists only on Andros, where the population was liberally estimated to comprise 150–300 individuals (Baltz, 1997). Elevation of each of the four subspecies to full species status would change their conservation priority, particularly for the Bahamas form (Hayes, 2006). Although taxonomy should inform conservation, as we seek to do here, conservation priorities should never influence taxonomic decisions (Bowen and Karl, 1999).

In this study, we evaluated the taxonomic status of the four West Indies populations of *I. dominicensis* for conservation purposes. We analyzed plumage variation to determine whether reciprocal diagnosability exists among the allopatric populations.

Methods

We examined 156 male specimens of *I. dominicensis* from six museums to evaluate six plumage characters that reportedly vary among this group (Omland and Lanyon, 2000). Five of these discrete characters were based on color of the feather tract being either black or yellow. These included the upper rump (dorsum, but distinct from the lower rump, which was yellow in all island forms; c.f. Omland and Lanyon, 2000), flank (venter, at point of leg attachment), belly (venter, 1 cm anterior to leg attachments), upper-tail coverts (longest two terminal-most feathers), and under-tail coverts (longest two terminal-most feathers). For tail coverts, both black and yellow were often present and we recorded the color of highest proportion; however, in some cases, the terminal-most coverts were either missing or equally black and yellow, and recorded as such (i.e., we recorded three character states). For the sixth discrete character, tips of the outermost retrices were examined against a black background and identified as either black or white.

We also collected mensural data for three continuous characters using digital calipers (to nearest 0.1 mm). Using straight-line measurements not following the contour of the body, we recorded black on the venter (continuous area of black along midsagittal line from throat to belly, excluding black and yellow mottling at the transition between black anteriorly and yellow posteriorly), yellow on the venter (continuous area of yellow along midsagittal line from belly to undertail coverts, including mottling), and yellow on the rump (continuous area of yellow along midsagittal line from rump to, and including, the upper-tail coverts). Because black and yellow on the venter covaried, we calculated and considered only the proportion of the venter that was yellow (i.e., yellow divided by the sum of black and yellow).

Because we were looking for diagnosable characters, we report only species-descriptive data. Some specimens exhibited minor damage, resulting in sample sizes varying slightly among the characters assessed.

Results

When plumage color and mensural data were considered together, the four island populations proved to be 100% diagnosable (Table 2.1). *Icterus d. northropi* differed from all other taxa by having the greatest extent of yellow on the venter (non-overlapping with other taxa). *Icterus d. portoricensis* was distinguished from all other taxa by the presence of a black upper rump (yellow in other taxa) and the least extent of yellow on the rump (non-overlapping with other taxa). *Icterus d. melanopsis* and *I. d. dominicensis* were fully discriminated from *I. d. northropi* and *I. d. portoricensis* by the aforementioned characters and from each other by upper-tail covert color (black and ≥50% yellow, respectively).

Table 2.1. Plumage colors and measurements from adult male study skins of Greater Antillean Orioles (*Icterus dominicensis*).

Character	***I. d. northropi*** **(Bahamas)** *N* = 9	***I. d. melanopsis*** **(Cuba)** *N* =47–49	***I. d. dominicensis*** **(Hispaniola)** *N* = 51–52	***I. d. portoricensis*** **(Puerto Rico)** *N* = 45–46
Upper rump color	B = 0% Y = 100%	B = 0% Y = 100%	B = 0% Y = 100%	**B = 100% Y = 0%**
Flank color	B = 0% Y = 100%	B = 100% Y = 0%	B = 29% Y = 71%	B = 100% Y = 0%
Belly color	B = 0% Y = 100%	B = 100% Y = 0%	B = 100% Y = 0%	B = 98% Y = 2%
Upper-tail coverts color	B = 38% Y = 50% B/Y = 12%	**B = 100% Y = 0%**	**B = 0% Y = 98%** **B/Y = 2%**	B = 100% Y = 0%
Under-tail coverts color	B = 0% Y = 100%	B = 100% Y = 0%	B = 32% Y = 64% B/Y = 4%	B = 93% Y = 2% B/Y = 5%
White tips to retrices	B = 0% W = 100%	B = 92% W = 8%	B = 78% W = 22%	B = 89% W = 11%
Yellow on venter (%)	**56.8 – 64.3**	6.7 – 37.3	17.8 – 48.8	19.6 – 44.3
Yellow on rump (mm)	39.4 – 51.2	29.4 – 51.6	32.2 – 55.2	**12.4 – 28.6**

For discrete color characters (B = black, Y = yellow, B/Y = equally black and yellow, W = white), proportion of specimens having each color is indicated. For mensural characters (yellow on venter and rump), low and high values are indicated. Diagnosably relevant characters are indicated in bold. Because of minor damage to some specimens, sample sizes varied slightly among the characters assessed.

Pairwise comparisons indicated that populations were diagnosable by up to three functionally independent characters (Table 2.2). We considered two sets of characters to be functionally related: belly color and extent of yellow on the venter, and upper rump color and extent of yellow on the rump. Populations from geographically distant islands were sometimes distinguished by fewer diagnostic characters than those from adjacent islands. Thus, *I. d. northropi* was more similar to *I. d. dominicensis* than adjacent *I. d.*

Table 2.2. Plumage characters providing pairwise diagnosis among the four Greater Antillean Oriole (*Icterus dominicensis*) populations.

Populations	*I. d. melanopsis*	*I. d. dominicensis*	*I. d. portoricensis*
I. d. northropi	**3 independent characters:** Flank color Belly color* Under-tail coverts color Yellow on venter (extent)*	**1 independent character:** Belly color* Yellow on venter (extent)*	**3 independent characters:** Upper rump color* Flank color Yellow on venter (extent) Yellow on rump (extent)*
I. d. melanopsis		**1 independent character:** Upper-tail coverts color	**1 independent character:** Upper rump color* Yellow on rump (extent)*
I. d. dominicensis			**2 independent characters:** Upper rump color* Upper-tail coverts color Yellow on rump (extent)*

Within each comparison (cell), asterisks indicate functionally related characters.

melanopsis, and *I. d. portoricensis* was more similar to *I. d. melanopsis* than adjacent *I. d. dominicensis*.

Several characters were variable within a single population, including flank color in *I. d. dominicensis*, upper-tail coverts color in *I. d. northropi*, and undertail-coverts color in *I. d. dominicensis* and *I. d. portoricensis*. All *I. d. northropi* had white tips (sometimes faint) to the outer rectrices, as described by Omland and Lanyon (2000), but so did several or more individuals from each of the other populations.

Discussion

Our findings of diagnosable plumage characters support the conclusion of Garrido et al. (2005) and Sturge et al. (2009) that the four island groups represent distinct allospecies, consistent with interpretations of both the phylogenetic and evolutionary species concepts (Cracraft, 1983; Mayden, 1997; de Queiroz, 2005). In delineating full species for allopatric taxa, Helbig et al. (2002) recommended 100% reciprocal diagnosability based on one or more functionally independent characters and level of divergence equivalent to closely related sympatric species. As we show here, the allopatric populations of *I. dominicensis* meet the conservative criteria of Helbig et al. (2002).

In our pairwise comparisons, populations were diagnosable from each other based on one to three plumage characters, but the number of diagnosable characters did not correspond to geographic proximity. *Icterus d. northropi*, for example, was readily diagnosed from both *I. d. melanopsis* (the nearest population) and *I. d. portoricensis* by three characters, but differed from *I. d. dominicensis* by only one character. However, molecular, morphological, vocalization, and additional plumage characters, including those of juveniles, provide strong support for *I. d. northropi* and *I. d. melanopsis* being sister taxa well separated from *I. d. dominicensis* and *I. d. portoricensis* (Omland et al., 1999; Omland and Lanyon, 2000; Garrido et al., 2005; Sturge et al., 2009). *Icterus d. melanopsis* and *I. d. dominicensis* also differ the most in vocalizations (Jaramillo and Burke, 1999; Garrido et al., 2005). Thus, plumage similarity between *I. d. northropi* and *I. d. dominicensis* likely arose through convergence (Omland and Lanyon, 2000). *Icterus d. portoricensis* was also readily diagnosed from *I. d. northropi* and *I. d. dominicensis* (the nearest population) by three and two characters, respectively, but differed from *melanopsis* in only one character. However, *I. d. portoricensis* may be the most distinct among this group, as it appears more closely related to the Lesser Antilles oriole taxa, *I.*

oberi and *I. laudabilis*, in molecular and other plumage characters (Omland et al., 1999; Omland and Lanyon, 2000). Although Omland and Lanyon (2000) treated white tips on the retrices as fixed, present only in *I. d. northropi*, we observed them on some specimens of all taxa.

Based on comparative data reported by Omland and Lanyon (2000), plumage differences among the allopatric *I. dominicensis* populations were comparable to those of sympatric oriole species. Of three sympatric species that readily nest alongside each other in Central America (Howell and Webb, 1995), the Altamira Oriole (*I. gularis*) differed from the Spot-breasted Oriole (*I. pectoralis*) in four characters and from the Streak-backed Oriole (*I. pustulatus*) in six characters. Sympatric Baltimore (*I. galbula*) and Orchard (*I. spurius*) Orioles in eastern North America also differed in four characters. By comparison, *I. d. northropi* differed from *I. d. melanopsis*, *I. d. dominicensis*, and *I. d. portoricensis* in six, five, and seven characters, respectively. The latter three taxa were less well differentiated, with one to three characters separating them.

The substantial plumage differences between *I. d. northropi* and *I. d. melanopsis* have evolved in spite of the molecular similarity and relatively recent separation of these taxa (0.7% sequence divergence for cytochrome *b* plus ND2; Omland et al., 1999; Sturge et al., 2009). Both natural and sexual selection have been proposed as drivers for rapid plumage evolution, with sexual selection believed to operate more rapidly (e.g., Warren et al., 2005; Mila et al., 2007). Rapid plumage evolution in orioles can occur in the absence of sexual selection, either by genetic drift within small populations resulting in rapid fixation of alleles (Kondo et al., 2008) or by natural selection, although sexual selection is thought to be the most likely cause of rapid plumage evolution in orioles

(Omland and Lanyon, 2000; Baker et al., 2003; Kondo et al., 2004, 2008; Hofmann et al., 2008a,b). Although all *I. domincensis* taxa are sexually monochromatic, at least with respect to human vision (Garrido et al., 2005; c.f. Eaton, 2005), sexual selection can still act on plumage characters of monochromatic species (Amundsen and Pärn, 2006).

Because conservation priority setting depends heavily on systematics, our findings have added importance. Our interest in the taxonomy of this group arose from concerns about the conservation status of the Bahamas population (Hayes, 2006). Population estimates have given a "liberal" estimate of 50–100 *I. d. northropi* on North Andros, and 100–200 on South Andros (Baltz, 1997). If these estimates are accurate, the Bahama Oriole, as a full species, should qualify as critically endangered, based on the IUCN Red List Criterion of an estimated population of <250 mature individuals. Although the Bahama Oriole formerly occurred on Abaco, it disappeared in the early 1990s for unknown reasons (White, 1998). It may be in decline on Andros as well, as only one oriole in juvenal plumage was observed in the 1997 survey by Baltz (1997). Threats to this population include: recent arrival of the Shiny Cowbird (*Molothrus bonariensis*; Baltz, 1995), a brood parasite that heavily parasitizes *I. dominicensis* (Wiley, 1985, 1988); lethal yellowing disease (Ogle and Harries, 2005) in its primary breeding habitat, the introduced coconut palm (*Cocos nuciferus*; Currie et al., 2005, M. R. Price et al. unpubl. data); introduced animals, plants, and exotic diseases; habitat change associated with global warming and rising sea levels; and continued human development accompanied by possible renewed logging of the Caribbean pine (*Pinus caribaea*) forest (Smith and Vankat, 1992). The other taxa face similar threats, and would also benefit from the conservation priority they would receive as a result of elevation to species status (Garrido et al., 2005). As the rarest bird species in The Bahamas (Hayes, 2006), the Bahama Oriole could join the Bahama Parrot as an avian flagship species (Reynolds and Hayes, 2009), stimulating much-needed conservation activities on Andros.

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Appendix

Male specimens ($N = 156$) examined from the following museums: Carnegie Museum of Natural History (CMNH); Field Museum of Natural History (FMNH); Louisiana State Museum of Zoology (LSUMZ); United States National Museum of Natural History (USNM).

Icterus dominicensis northropi.—Abaco, The Bahamas (2): CMNH 130996; FMNH 29818. Andros, The Bahamas (7): CMNH 30962, 30976; LSUMZ 146653, 146654, 146657, 146658; USNM 257099.
Icterus dominicensis dominicensis.—Hispaniola (52): CMNH 91567, 91328; FMNH 1084, 1086, 1087, 1090, 1095, 1088, 1100, 1103, 1105, 1112, 1120, 1122, 1125, 29732, 29735, 29741, 29742, 29747, 29748, 29750, 29752, 29809, 29745, 29746, 29753; USNM 249421, 249544, 249545, 249546, 249547, 249548, 250448, 250449, 250453, 250573, 251580, 251581, 251583, 252842, 252890, 252891, 264790, 264792, 280459, 280460, 305585, 327892, 573657.
Icterus dominicensis melanopsis.–Cuba (31): CMNH 138759; FMNH 29807, 72054, 111981, 375109, 375112, 375113, 375116, 375117, 375122; USNM 171277, 171448, 171449, 171451, 171452, 171453, 172642, 172647, 177467, 177834, 177866, 200391, 310429, 316264, 355986, 395830, 395831, 395836, 396651, 454581, 454583. Isle of Pines (15): CMNH 39460, 39531, 39548, 39549, 39550, 39774, 39779, 39871, 39903, 39940; USNM 172816, 172819, 324041, 324042, 324043. Unknown location (3): FMNH 29810, 308980; USNM 31989.
Icterus dominicensis portoricensis.—Puerto Rico (46): CMNH 38843, 38844, 39078, 39097, 39118, 39157, 39227, 39252, 39326; FMNH 29686, 29687, 29692, 29695, 29696, 29697, 29700, 29701, 29708, 29712, 29714, 29715, 29716, 29717, 29724, 29727; USNM 17154, 168974, 169058, 169061, 171544, 231637, 231639, 231642, 231645, 231646, 231650, 231651, 231653, 238221, 238222, 238224, 238385, 238386, 355970, 355976, 355981.

CHAPTER THREE

GEOGRAPHIC VARIATION AND GENETIC STRUCTURE IN THE CRITICALLY ENDANGERED BAHAMA ORIOLE (*ICTERUS NORTHROPI*): THE IMPORTANCE OF SAMPLING MULTIPLE GENES AND GEOGRAPHIC REGIONS

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Abstract

We examined 1858 base pairs of mitochondrial DNA sequenced from four gene regions in 14 Bahama Orioles (*Icterus northropi*), a critically endangered island endemic with a declining population of less than 300 individuals. We sought to: (1) discern genetic structuring of and movements between the remaining subpopulations; (2) to establish possible historical genetic patterns of geographical variation, or demographic history, of the subpopulations, and relate these to current conservation concerns; and (3) to inform planning for possible translocation of the Bahama Oriole to Abaco Island, where it formerly occurred. Four unique haplotypes were identified, with only one shared between populations. Nucleotide and haplotype diversity were higher for North Andros than for South Andros and Mangrove Cay. Analysis of molecular variance yielded a Wright's fixation index (F_{st}) of 0.60 ($P_{\mathrm{Fst}} = 0.016$), with 40.2% of the molecular variation explained by within–population differences and 59.8% by among–population differences. Results of Fu's *Fs* and Tajima's *D* tests of neutrality indicate the populations are not significantly expanding; however, geographic differences between diversity values, and the unimodal shape of the mismatch distribution in the southern population, may indicate expansion from north to south. Our study suggests the remaining subpopulations of Bahama Oriole represent at least two management units, and translocation of Bahama Orioles from Andros to Abaco Island, where they formerly occurred, should include individuals from North Andros, Mangrove Cay, and South Andros to maximize genetic diversity in the translocated population.

Introduction

The critically endangered Bahama Oriole (*Icterus northropi*), recently elevated to species status (American Ornithologists' Union, 2010), has a declining population of fewer than 300 individuals (Price et al. under review). Historically known from only two major islands in the Bahamas, the species became extirpated from Abaco in the 1980s (Baltz, 1997; AW White, 1998, pers. comm.). Two potential threats now jeopardize the last remaining population on Andros: the recent appearance of lethal yellowing, a phytoplasma which has devastated oriole breeding habitat (Price et al., under review); and the recent natural arrival of the Shiny Cowbird (*Molothrus bonariensis*), a brood parasite that targets *Icterus* (Baltz, 1995, 1996; Wiley, 1985). In addition to these threats, coppice habitat (native dry broadleaf forest), which appears to be crucial to year-round survival of the oriole (Currie et al., 2005; Price et al., under review), continues to be destroyed for agricultural and other anthropocentric purposes (Thurston, 2010; Wunderle and Waide, 1993).

The Bahama Oriole is a year-round resident on Andros, a land mass riddled with waterways that effectively divide it into multiple islands. The largest three islands, and the only ones with significant human development, include North Andros (NA), Mangrove Cay (MC), and South Andros (SA). These islands are separated by channels that range in width from 1–5 km, which previous oriole population assessments assumed to be isolating barriers (Baltz, 1997). Approximately 20 km, including two 5 km-wide channels and a small cay, separate the southern tip of NA from the northern tip of MC. Mangrove Cay and SA are separated by a mere 1–3 km-wide channel. Considering the exceptional flight capabilities of migratory oriole species (Jaramillo and Burke, 1999), movement of orioles among the three islands seems highly likely.

We assessed genetic variation in the Bahama Oriole for three purposes: (1) to discern genetic structuring of the two potential subpopulations (NA and MC/SA); (2) to establish possible historical genetic patterns of geographical variation, or demographic history, of the subpopulations, and relate these to current conservation concerns; and (3) to inform planning for possible translocation of the Bahama Oriole to Abaco, where it formerly occurred, or to other islands (e.g., New Providence). Translocation of individuals to other areas can increase the species' effective population size and decrease the probability of extinction through stochastic effects (e.g., hurricanes; Fleischer, 2007). The population on MC and SA is roughly half the size of the NA population, but has a higher population density (Price et al, under review). If genetic variation is minimal and structure lacking, birds can be captured from areas of greatest oriole density to decrease negative impacts on breeding selection in the remaining individuals. If, however, significant genetic structure exists, birds having each available haplotype can be selected to provide the greatest genetic variation in the translocated population.

Methods

Sample Collection

We collected blood and feather samples in accordance with all required permits and an IACUC protocol from 16 live birds captured at 11 locations throughout the Bahama Oriole's distribution on NA (*N* = 11), MC (*N* = 1), and SA (*N* = 4) during the years 2009–2010 (Table 3.1). Birds were captured by mist net using song playback (*N* =

12), or as nestlings briefly removed from the nest (*N* = 4). Captured birds were measured, sampled, banded using standard issue aluminum USGS identification bands, and immediately released. Two tail feathers were pulled from adult birds, and blood samples were obtained by pricking the brachial vein (Arctander, 1988) and collecting pooling blood with a capillary tube. Blood was immediately mixed with lysis buffer (100 mM Tris pH 8.0, 100 mM EDTA, 10 mM NaCl, 0.5% SDS; Longmire et al., 1988), and placed on ice. After transportation to the laboratory, samples were stored at - 0 °C. Blood volumes collected from each individual (0.1–0.2 mL) were well below the recommended limit of <1% of the body weight for a 30–35 g bird (Gaunt and Oring, 1997). Individuals were tracked after sampling, and no casualties were reported.

Table 3.1. *Icterus northropi* samples used for genetic analysis and their haplotypes.

Island	Year	Haplotype	Band number
North Andros	2009	B	120239501
			120239502
		B	120239503
		B	120239504
		B	120239505
		A	120239506
		A	120239507
			120239509
		B	120239510
			120239511
		D	120239512
Mangrove Cay	2010	A	120239517
South Andros	2010	A	120239524
		C	120239526
		A	120239527
		A	120239528

Since two pairs of samples were from siblings pulled from two nests, and were subsequently found to share the same haplotypes, one sibling from each pair was excluded from further analysis. An additional individual was excluded due to an inability to sequence ATP 6/8.

DNA Isolation

DNA extractions were based on the protocol of Fetzner and Crandall (2003) with minor modifications. Two μL of blood were diluted in 300 μL of cell lysis buffer, and 1.5 μL of RNAase A was added. Samples were placed in a 37°C water bath for 15 minutes. After returning to room temperature, 100 μL ammonium acetate was added, and samples were vortexed and centrifuged. The supernatant was poured into new tubes with 500 μL isopropanol, washed several times with 300 μL ice cold ethanol, then air dried to remove alcohol. Finally, samples were reconstituted with 30 μL TE buffer (10 mM Tris–HCl, pH 8.0, 1 mM EDTA). Similar protocols were followed for feather DNA extractions, with a few additional initial steps. Feather shafts were minced and added to 500 μL cell lysis buffer and 5 μL protinase K, then placed in a 55°C water bath for 24 hours. Following protein digestion, the above protocols for blood DNA extraction were followed.

We amplified mitochondrial DNA (mtDNA) sequences from the genomic DNA samples using standard polymerase chain reaction (PCR) methods, as detailed below. Four mtDNA gene regions were amplified: ATP synthase subunits 6 and 8 (ATP6/8); cytochrome *b* (cyt*b*); and NADH dehydrogenase subunit 2 (ND2), using primers in Table 3.2. We chose these primers because they evolve at different but relatively high rates, are as much as 6000 kb away from each other, and the use of multiple primers allowed comparison of genetic variation between the Bahama Oriole and other species (Omland et al., 1999). PCR reactions of 50 μL were prepared according to manufacturer's instructions by mixing 25 μL Maxima Hot Start PCR Master Mix (Thermo Scientific), 2 μL whole genomic reconstituted DNA, 1 μL each of up and down primers, and 21 μL nuclease-free water. PCR conditions were as follows: initial denaturation at 95°C for 4 min, followed by 60 cycles of denaturation at 95°C for 30 sec, annealing at 50°C for 30 sec, and extension at 72°C for 1 min, with a final extension at 72°C for 15 min. PCR products were separated in non-denaturing 1.5% agarose gels, then stained with 0.05% ethidium bromide (EtBr), and visualized using an UV imager. After confirmation of the presence of DNA, PCR products were sequenced by Macrogen (Rockville, MD).

Table 3.2. Mitochondrial DNA PCR primers used to assess genetic variation in *Icterus northropi*.

mtDNA gene[a]	Primer sequence	Reference	bp
ATP6/8	5'AAAGCRTYRGCCTTTTAAGC 5'GTTAGTGGTCAKGGGCTTGGR	L8331 CO 3.2 H936 (Perdices and Doadrio 2001)	860
Cyt*b*	5'TCAAACATCTCAACCTGATGA 5'GGCAAATAGGAAGTATCATTC	(Pook et al. 2000)	667
ND2	5'TATCGGGCCCATACCCCGAAA 5'CCTTGAAGCACTTCTGGGAAT	L5215 H57761 (Hackett et al. 1996)	331

[a] ATP6/8 = ATP synthase, subunits 6 and 8, Cyt*b* = cytochrome *b*, ND2 = NADH dehydrogenase, subunit 2

Statistical Analysis

Multiple alignments for each gene region were performed in CLUSTALX version 2.1 (Larkin et al., 2007), and haplotypes were determined using Dnasp 5.10 (Librado and Rozas, 2009). Since two pairs of samples were from siblings pulled from two nests on North Andros, and were subsequently found to share the same haplotypes, one sibling from each pair was excluded from further analysis. We were also unable to sequence ATP 6/8 for an additional individual from North Andros, excluding it from some analyses. To quantify levels of genetic variation in the Bahama Oriole, haplotype variability was calculated as the number of haplotypes (*N*), haplotype diversity (*h*), and nucleotide diversity (π; Nei 1987, Eq. 8.4 and 10.6, respectively) using ARLEQUIN 3.5 (Excoffier and Lischer, 2009). We explored relationships between individuals by constructing haplotype networks using the method of statistical parsimony implemented in TCS 1.21 (Clement et al., 2000). This network method (Templeton et al., 1992) allows for the non-bifurcating genealogical relationships often found in mitochondrial DNA at population-level studies (Crandall and Templeton, 1996). Analysis of molecular variance (AMOVA; Excoffier et al., 1992), performed with ARLEQUIN, was used to estimate F_{st}-statistics, which synthesize information on nucleotide differences between haplotypes both within and among populations. Wright's fixation index (F_{st}) ranges from 0 to 1, with values less than 0.01 indicating little divergence among populations, and values above 0.1 indicating great divergence among populations.

Tajima's (1989) test of neutrality and Fu's test for selective neutrality (1997) were performed using ARLEQUIN with 1000 randomizations to test for departures from neutrality in the population. Significantly large negative *D* and *Fs* values can be interpreted as evidence of population expansion, and an excess of new mutations relative to equilibrium expectations on the basis of the number of segregating sites (Tajima's *D*) or number of observed alleles (Fu's *Fs*). The direction of population expansion can be inferred from nucleotide diversity (π), assuming smaller nucleotide diversity values in populations with recent colonization (Zink et al., 2001). Mismatch distribution of pairwise differences was computed with ARLEQUIN to examine the demographic history of the two populations. For this analysis, the null hypothesis of an expanding population (Rogers, 1995; Rogers and Harpending, 1992) produces a unimodal distribution, and a ragged or multimodal distribution indicates a population in stable equilibrium. As part of this analysis, we calculated the raggedness index, which yields values smaller than 0.04 for an expanding population and larger values for stable populations (Harpending, 1994). Values are reported as mean ± SD.

Results

Patterns of Sequence Variation

Sequences for ATP6/8, cyt*b*, and ND2 matched previously published sequences for *Icterus northropi* (Genbank accession numbers, respectively: AF109419.1, Lovette et al., 2003; AF099287, Omland et al., 1999; AF099325, Omland et al., 1999). This indicates the DNA fragments amplified in the present study (GenBank accession numbers JN020589–JN020630) likely represented the intended mitochondrial targets rather than nuclear homologues.

We amplified 162 bp from ATP6, 698 bp from ATP8, 667 bp from cyt*b*, and 331 bp from ND2, for a total of 1858 bp. Of these, 1852 (99.7%) characters were constant, and 6 (0.3%) characters were variable and phylogenetically informative. Variation within the combined four gene regions included 5 transitions and 1 transversion, consistent with the expectation that transitions outnumber transversions. Four unique haplotypes were identified among the 13 individuals sequenced for all four gene regions. The most common haplotype (A, *N* = 6) was found in both subpopulations, and the second most common haplotype (B, *N* = 5) was found only on NA (Fig 3.1). Two haplotypes existed in only one individual each. A total of three haplotypes occurred on NA, and two

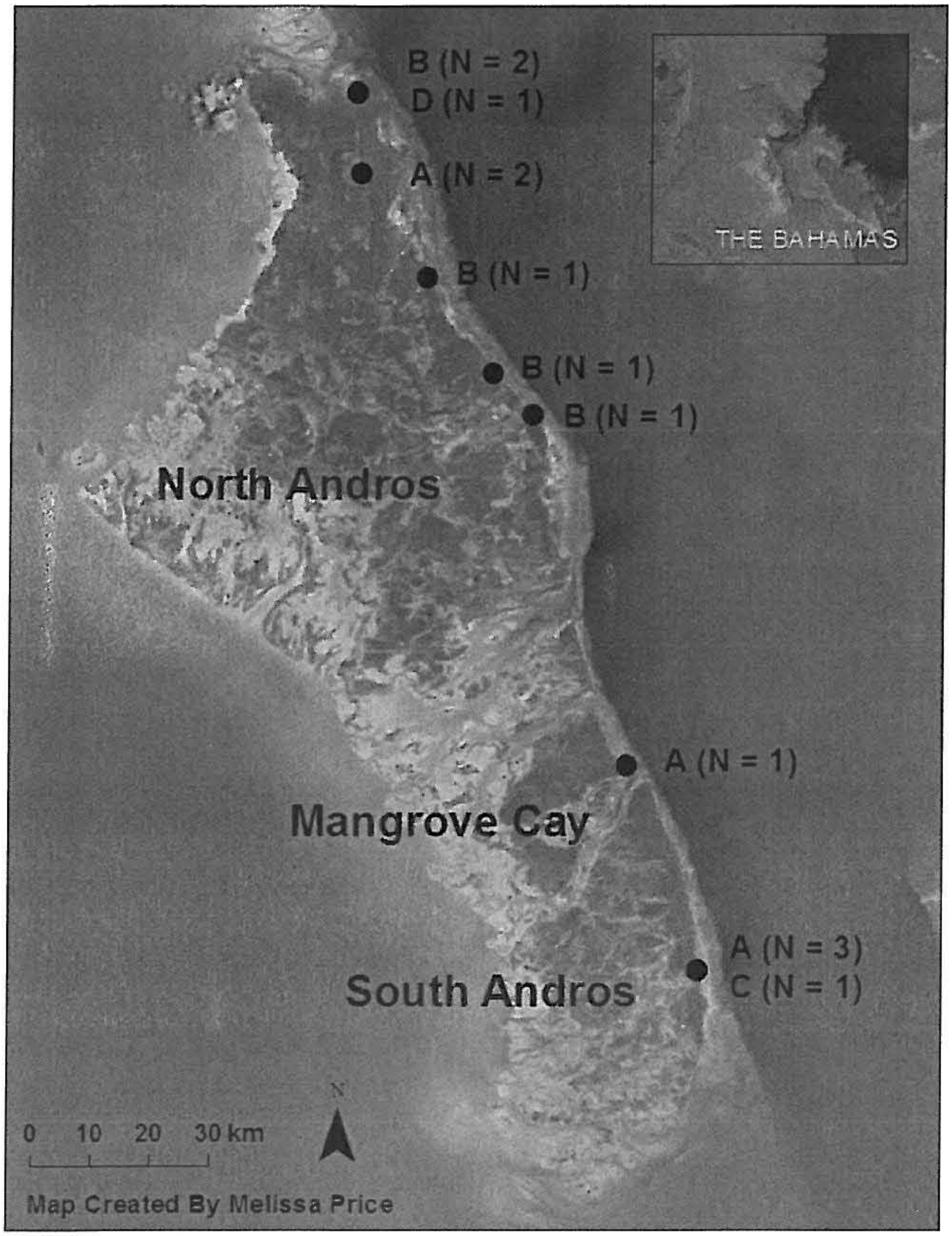

Fig 3.1 Bahama Oriole haplotype distribution among sampled localities on Andros, The Bahamas.

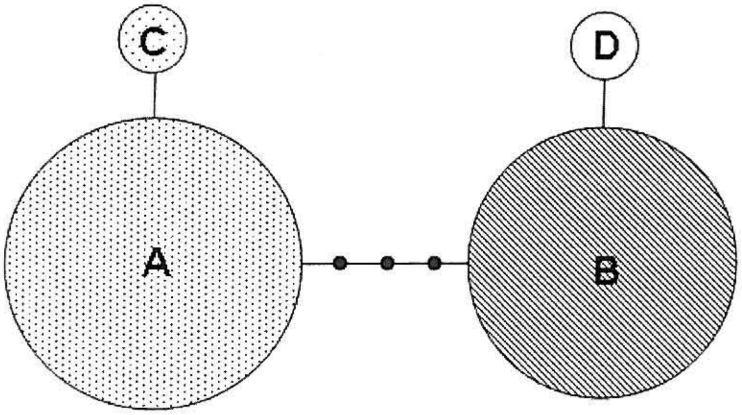

Fig 3.2 Haplotype network for 4 gene regions, combined, in the Bahama Oriole, constructed using the method of statistical parsimony implemented in TCS 1.21 (Clement et al., 2000).

on MC/SA. Haplotype network construction resulted in a single network for the two subpopulations (Fig 3.2).

The AMOVA for combined sequences (Table 3.3) yielded a Wright's fixation index (F_{st}) of 0.60 ($P_{\mathrm{Fst}} = 0.016$), with 40.2% of the molecular variation explained by within-population differences and 59.8% by among-population differences. Nucleotide and haplotype diversity (Table 3.4) were higher for NA (combined sequences: $\pi = 0.33$; $h = 0.61$) than for SA/MC ($\pi = 0.067$; $h = 0.40$).

Table 3.3. Analysis of molecular variance based on four mtDNA gene regions (ATP synthase subunits 6 and 8, cytochrome *b*, NADH dehydrogenase subunit 2) for the two remaining subpopulations of Bahama Oriole.

Source of variation	df	Sum of Squares	Variance	% of variation	F_{st}	P
Among populations						
ATP 6	1	0.048	– 0.005	– 6.9	–0.07	1.00
ATP 8	1	5.192	0.777	65.5	0.66	0.019
Cyt*b*	1	0.129	0.010	12.6	0.13	0.35
ND2	1	1.944	0.282	68.5	0.69	0.020
Combined sequences	1	7.094	1.039	59.8	0.60	0.016
Among individuals						
ATP 6	11	0.875	0.080	106.9		
ATP 8	11	4.500	0.409	34.5		
Cyt*b*	12	0.800	0.067	87.4		
ND2	12	1.556	0.130	31.5		
Combined sequences	11	7.675	0.698	40.2		
Total						
ATP 6	12	0.923	0.074			
ATP 8	12	15.857	1.501			
Cyt*b*	13	0.929	0.076			
ND2	13	3.500	0.412			
Combined sequences	12	14.769	1.737			

Demographic History

Positive values for both Tajima's D ($D = 1.01$, $P = 0.75$) and Fu's Fs ($Fs = 1.61$, $P = 0.89$), indicated a lack of evidence for recent population expansion (Table 3.4). The NA subpopulation exhibited a multimodal mismatch distribution (Fig 3.3a), and MC/SA exhibited a unimodal mismatch distribution (Fig 3.3b), although the latter was based on only two pairwise differences. Raggedness values for both ($r_{\mathrm{NA}} = 0.292$; $r_{\mathrm{SA/MC}} = 0.200$) were consistent with the model of a stable population; however, neither differed significantly from the distribution expected under a recent population expansion ($P_{\mathrm{NA}} = 0.97$; $P_{\mathrm{SA/MC}} = 0.93$).

Table 3.4. Comparison of nucleotide (π) and haplotype (*h*) diversity estimates, and results of Fu's *Fs* and Tajima's *D* tests of neutrality, between 4 mitochondrial genes (cytochrome *b*, NADH dehydrogenase subunit 2, ATP synthase subunits 6 and 8) for two subpopulations of Bahama Oriole (North Andros and Mangrove Cay/South Andros).

Geographic Region and Gene	*N*	No. base pairs	No. haplo–types	π	*h*	*Fs*	*D*
North Andros							
ATP 6	8	162	2	0.25	0.25	-0.18	-1.05
ATP 8	8	698	2	0.43	0.43	2.47	0.46
Cyt*b*	9	667	1	0	0	–	–
ND2	9	331	2	0.39	0.39	0.48	0.16
Combined	8	1858	3	0.33	0.61	1.53	0.08
Mangrove Cay & South Andros							
ATP 6	5	162	1	0	0	–	–
ATP 8	5	698	1	0	0	–	–
Cyt*b*	5	667	2	0.40	0.40	0.090	-0.82
ND2	5	331	1	0	0	–	–
Combined	5	1858	2	0.067	0.40	0.09	-0.82
Total Population							
ATP 6	13	162	2	0.15	0.15	-0.54	-1.15
ATP 8	13	698	2	0.54	0.54	3.79	2.12
Cyt*b*	14	667	2	0.14	0.14	-0.59	-1.15
ND2	14	331	2	0.54	0.54	1.29	1.51
Combined	13	1858	4	0.41	0.68	1.61	1.01

Nucleotide (π) and haplotype (*h*) diversity are reported as means; *N* = number of individuals. None of the tests of neutrality (Fu's *Fs* and Tajima's *D*) resulted in significant *P* values.

Comparison of Gene Regions

A comparison of the four gene regions can be found in Table 3.4. Three of four gene regions, totaling 1191, lacked any variation in the MC/SA subpopulation, and the fourth gene region (667 bp) lacked variation in the NA subpopulation. Cytochrome *b* had the highest nucleotide diversity of the four gene regions examined for MC/SA, and ATP8 had the highest nucleotide diversity of the NA gene regions. Each of the four gene regions resolved 2 haplotypes, but haplotypes were not distributed in the same way. Haplotype networks either grouped most samples together (ATP6, Fig 3.3a; cyt*b*, Fig 3.3c), or separated samples into 2 haplotypes correlated largely with geographic location (ATP8, Fig 3.3b; ND2, Fig 3.3d). Although Tajima's *D* and Fu's *Fs* were negative for some gene regions, all gene regions consistently showed a lack of significance for population expansion.

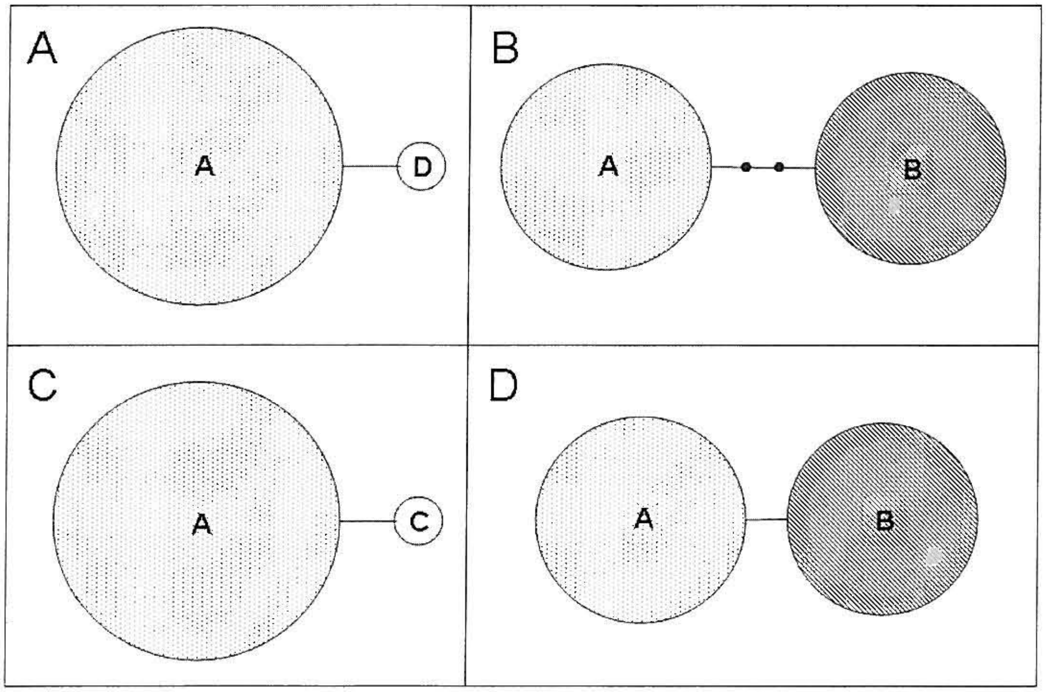

Figure 3.3A–3.3D. Haplotype networks for *Icterus northropi* from North Andros (NA, $N = 8$), Mangrove Cay (MC, $N = 1$), and South Andros (SA, $N = 4$). 3.3A. ATP6: all but one sample (from NA) grouped together. 3.3B. ATP 8: haplotype B includes only NA samples, haplotype A includes two samples from NA and all MC and SA samples. 3.3C. *cytb*: all but one sample (from SA) grouped together. 3.3D. ND2: haplotype B included only NA samples; haplotype A included two samples from NA and all MC and SA samples.

Discussion

The recent range contraction of the Bahama Oriole for unknown reasons (A. W. White, pers. comm.) raises concern about the remaining population of fewer than 300 individuals. Overall heterozygosity is often positively associated with fitness (Hedrick, 1998; Mitton, 1998), as decreased mate choice and increased inbreeding often result in a loss of genetic variation, and a decrease in fitness (Grant et al., 2001). Our results suggest the remaining subpopulations of the Bahama Oriole are genetically robust compared with other bird species (Table 3.5). This may change if the oriole population continues to decline due to parasitism by the Shiny Cowbird, devastation of the oriole's favored breeding habitat by lethal yellowing disease, or continued habitat destruction.

Population Differences and Gene Flow

We found some evidence for genetic differences between Bahama Orioles from NA and those from MC/SA. Only one haplotype was shared between islands, with two individuals on NA sharing a haplotype otherwise found only on MC/SA. A majority of the diversity was between subpopulations (59.8%), with 40.2% of the genetic variation explained by differences among individuals. The calculated F_{st} value (0.60; $P_{\mathrm{Fst}} = 0.016$) for the two Andros subpopulations indicates significant genetic divergence between localities. The high degree of genetic differentiation found in this species is typical of other sedentary, or non-migratory, species (Hackett, 1996).

Table 3.5. Comparison of genetic variability in orioles and other birds.

Species	Primer(s)	No. bp	*N*	No. variable sites	No. haplo-types	Nucleotide Diversity (π)	Source
Bahama Oriole[a]	ATP6/8, Cyt*b*, ND2 combined	1858	13	6	4	0.41	This Study
Nihoa Millerbird[a]	ATP6/8, CR, Cyt*b*, ND2 combined	2624	15	1	2	0.00005	Fleischer et al. 2007
Laysan Millerbird[b]	ATP6/8, CR, Cyt*b*, ND2 combined	255	5	2	3	0.0023	Fleischer et al. 2007
White–headed Woodpecker	ATP6 and Cyt*b* combined	1777	78	17	25	0.002	Alexander and Burns 2006
Ancient Murrelets	CR and Cyt*b* combined	1132	58	20	20	0.41	Pearce et al. 2002
California Thrasher	ATP 6/8 and Cyt*b* combined	2086	64	49	37	0.0025	Sgariglia and Burns 2003
Streak–backed Oriole	CR	344	102	13	16	0.0041	Cortes–Rodriguez et al. 2008
Tree Swallow	ND2	966	155	44	43	0.27	Stenzler et al. 2009
Curve–billed Thrasher	CR, Cyt*b*, ND2 combined	1115	66	67	48	0.011	Zink and Blackwell–Rago 2000
Savanna Sparrow	ND2, ND3	1440	112	–	57	0.013	Zink et al. 2005

[a] Designates an endangered taxon

[b] Designates an extinct taxon

Demographic History

Several parameters suggest the Bahama Oriole population is largely in equilibrium between mutation and genetic drift, with some geographic movement. Tajima's *D* did not differ significantly from zero, and the mismatch distribution for North Andros was ragged (Fig 3.4a). Results of Fu's *Fs* test also indicate the population is not significantly expanding; however, the geographic difference between diversity values, and the unimodal distribution of the mismatch distribution on MC/SA (Fig 3.4b) may indicate expansion from NA (higher diversity values), to MC/SA (lower diversity values).

Comparison of Gene Regions

The examination of multiple gene regions offers several benefits in population-level studies, primarily because it provides the greatest possible explanatory power when examining relationships (Nixon and Carpenter, 1996). Corroboration between data sets increases their significance, and disagreement can provide important insights into evolutionary processes (Myamoto and Fitch, 1995; Wiens, 1998). The use of four gene regions allowed us to identify diversity and relationships that a single gene assessment would have overlooked. Three of four gene regions had no genetic variation in the MC/SA subpopulation, and the remaining gene region lacked genetic variation on NA. Although nucleotide diversity for the combined regions was low for MC/SA, we would have failed to identify any existing diversity without examining cyt*b*. Haplotype networks either grouped most samples together, or separated samples into 2 haplotypes largely correlated with geographic location. The corroboration of haplotype networks for ND2, which evolves at a relatively fast rate, and ATP8, a comparatively conserved gene region,

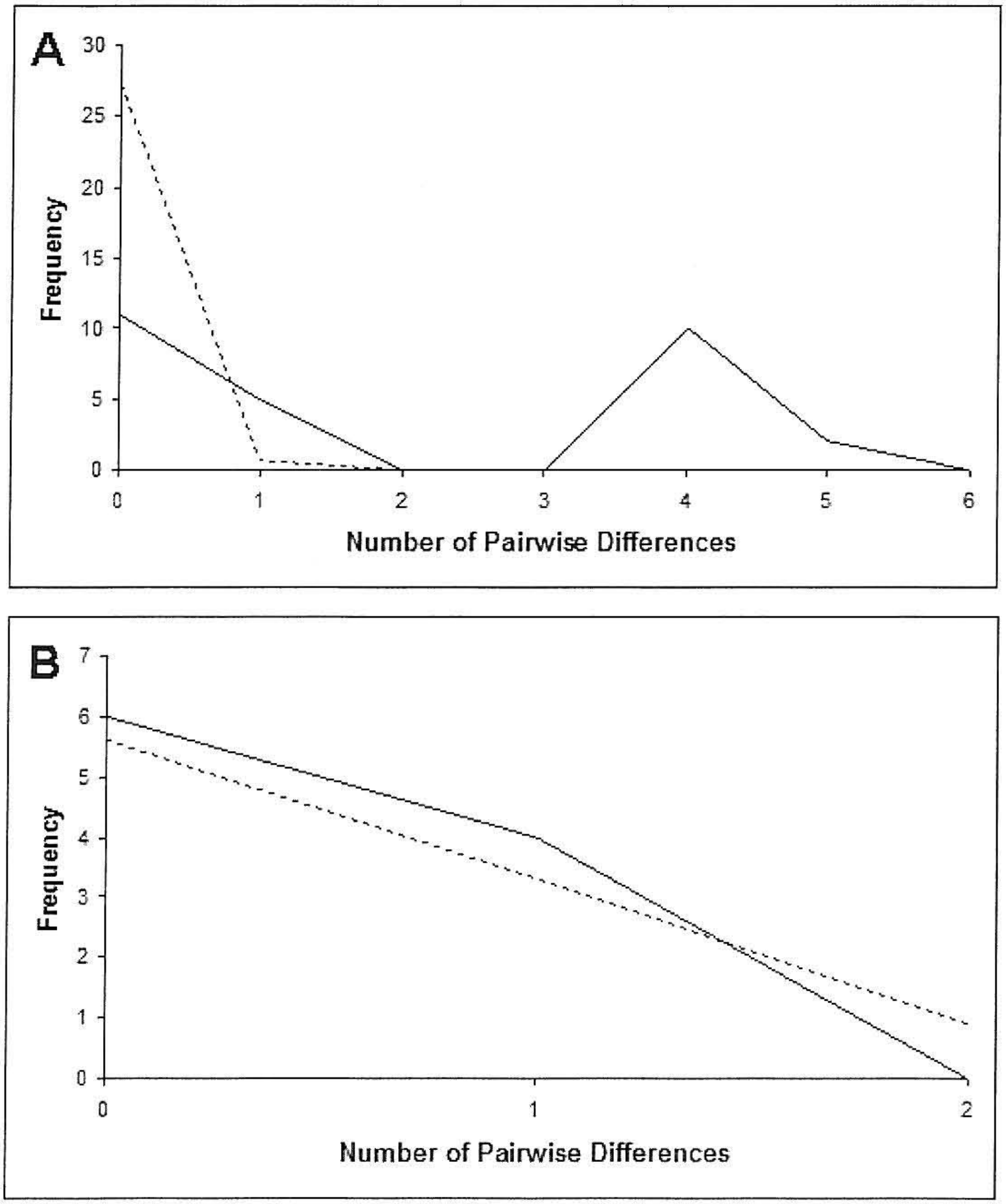

Fig 3.4A, 3.4B. Mismatch distribution for the North Andros (3.4A) and South Andros/Mangrove Cay (3.4B) subpopulations of the Bahama Oriole. Dashed lines show expected values; solid lines show observed values.

strengthens the case for managing these subpopulations as two management units, as does the extremely low diversity found in three gene regions for MC/SA. Further studies should include one or more nuclear genes for comparison.

Conservation Implications

Our results suggest that geographic distance, enhanced by water barriers, may be hindering gene flow, resulting in genetic differences within the remaining Bahama Orioles. Cultural differences, such as vocalization dialects, may further reduce gene flow, increasing genetic differentiation between subpopulations (MacDougall–Shackleton and MacDougall–Shackleton, 2001). Lee et al. (unpublished data) found evidence for clinal vocalization differences among subpopulations on NA, MC, and SA. Minimum frequency increased and frequency range decreased from north to south, suggesting significant geographic variation in song structure; however, all other song characters overlapped substantially among subpopulations, resulting in the absence of diagnosability among the subpopulations.

Only one haplotype was shared between the two subpopulations sampled, indicating minimal gene flow across the water channels separating NA from MC and SA and relatively sedentary subpopulations. These results suggest the small number of orioles known to nest on the west coast (Allen 1890; Price et al., under review), which we were unable to sample, and the extirpated population on Abaco, may represent additional haplotypes if gene flow has been restricted, allowing for genetic drift.

The SA/MC subpopulation has substantially lower nucleotide diversity than the NA subpopulation, which may indicate decreased fitness (Grant et al., 2001). Continued monitoring of the SA/MC subpopulation is desirable to determine levels of inbreeding and reproductive success, particularly during the severe habitat destruction currently underway on SA (Thurston, 2010). If SA/MC numbers continue to decline, translocation of individuals from NA to MC and SA should be considered to increase heterozygosity, fitness, and population stability.

Translocated individuals may have increased mortality risk, delayed breeding, and decreased clutch size (Kaler et al., 2010). Nevertheless, translocation can be an effective management tool to restore or supplement populations if individuals are carefully chosen, release areas are selected properly, and effective habitat management is practiced (Letty et al., 2007). Our study suggests translocation of Bahama Orioles from Andros to Abaco Island, where they formerly occurred, should include individuals from NA, MC, and SA to maintain genetic diversity in the translocated population. Molecular testing should be performed prior to selection to identify individuals of multiple haplotypes for transfer.

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CHAPTER FOUR

POPULATION STATUS, HABITAT DEPENDENCE, AND REPRODUCTIVE ECOLOGY OF THE BAHAMA ORIOLE (*ICTERUS NORTHROPI*): MANAGING A CRITICALLY ENDANGERED SYNANTHROPIC SPECIES

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Abstract

Recent elevation of the critically endangered Bahama Oriole (*Icterus northropi*) to species status prompted us to evaluate its population status, habitat use, and breeding ecology. From surveys, we estimated that 90–162, 24–44, and 27–48 individuals remain on North Andros Island, Mangrove Cay, and South Andros Island, The Bahamas, respectively. Orioles mostly used anthropogenic habitat (residential and agricultural land) during the breeding season, although home ranges included nearby pine forest and coppice (dry broadleaf forest). The majority (87%) of 46 nests observed were constructed in nonnative coconut palm (*Cocos nucifera*), with native *Sabal palmetto* and *Thrinax morrisii,* and an introduced *Brassaia actinophylla* also used. Trees selected by orioles for nesting were significantly taller, less likely to have shrubs underneath, farther from cover, and had more palm trees nearby than randomly available palm trees in the area. Three of eight nests with known contents were parasitized by Shiny Cowbirds (*Molothrus bonariensis*), a brood parasite that became established in the 1990s without subsequent population increases. Lethal yellowing disease recently devastated coconut palms and reduced local breeding oriole density on North Andros, but palms on Mangrove Cay and South Andros remain healthy. The juxtaposition of anthropogenic habitat to suitable native habitats may be more important than any single factor in meeting the Bahama Oriole's life history needs, especially for breeding adults and fledging chicks. Conservation of coppice habitat, at high risk for agricultural and residential development, is crucial for survival of this critically endangered synanthropic species.

Introduction

Synanthropic species cohabit with humans and benefit from anthropogenic landscapes. Thus, paradoxical examples of highly endangered synanthropic species are exceptionally scarce, with only one species heretofore recognized among birds—the critically endangered Sociable Lapwing (*Vanellus gregarius*; Kamp, 2009). Saving synanthropic species seems intuitively straightforward; however, they can present unique challenges for conservation management because of potentially rapid cultural and evolutionary changes associated with landscape modification (Johnston, 2001; Boardman, 2006), other anthropogenic threats that counter the benefits of synanthropy (e.g., pesticide use, vehicle and window collisions, introduced predators), and partial continued dependence on natural habitats. Here, we present the highly unusual case of a critically endangered synanthropic species whose conservation is further complicated because it is an island endemic.

Oceanic islands present opportunities to test and implement management solutions in defined areas at high risk for species loss (Paulay, 1994; Şekercioğlu et al., 2004). Extinction rates in the Caribbean islands, a biodiversity hotspot (Myers et al., 2000), have increased over the last several thousand years due to climatic changes and human influence (Woods and Sergile, 2001; Steadman, 2006; Ricklefs and Bermingham, 2008). Three-quarters of West Indian parrots and macaws, 10 of 12 avian insectivores, and 27 bats, for example, have become extinct, while many more taxa are now threatened (Woods and Sergile, 2001). Efforts to protect, manage, and preserve the remaining taxa are often hindered by limited knowledge of natural history, lack of financial and educational resources, and a diversity of independently governing bodies (Ricklefs and

Bermingham, 2008). Basic research identifying high-quality habitats for all life history stages is needed to implement effective management solutions for many of the remaining endangered species (Donovan et al., 2002).

As one of the few endemic birds to The Bahamas, the Bahama Oriole (*Icterus northropi*), recently given species status (American Ornithologists' Union, 2010), is also one of the world's rarest. After disappearing from Abaco Island, The Bahamas, in the 1990s, the oriole remains today only on Andros. Baltz (1997) suggested that fewer than 300 individuals persist, with populations largely confined to townships and agricultural areas along the coast where introduced coconut palm (*Cocos nucifera*) abounds (Allen, 1890; Baltz, 1997). This number, if confirmed, may be unsustainable given recent devastation of the oriole's favored coconut palm nesting habitat by lethal yellowing disease (Currie et al., 2005), loss of coppice (dry broadleaf forest) to farming and coastal development (Wunderle and Waide, 1993), and recent arrival of the Shiny Cowbird (*Molothrus bonariensis*; Baltz, 1995, 1996), a brood parasite that favors this host (Wiley, 1985). Baltz (1997), Jaramillo and Burke (1999), and Garrido et al. (2005) summarized the scant information available on reproduction.

In this study, we sought to accomplish three major objectives. First, we ascertained relative population density of the Bahama Oriole in each of three primary habitats, and estimated global population size. Second, we studied the oriole's breeding ecology, with emphases on nest attributes, nest site selection at three scales (micro-, meso-, and macrohabitat), and the provisioning of nestlings. Third, we assessed the potential impacts of Shiny Cowbirds and lethal yellowing on reproductive success and local population density of the oriole. Collectively, the findings provide important information for developing a sound management plan for this critically endangered synanthropic species.

Methods

Study Area

The three major islands collectively referred to as Andros, The Bahamas, include North Andros (NA, 3600 km^2), Mangrove Cay (MC, 200 km^2), South Andros (SA, 800 km^2), and a number of small cays. These islands, separated by channels 1–5 km wide, are dominated on the eastern portion by extensive Caribbean pine (*Pinus caribaea*) forest, interspersed with patches of coppice at higher elevations. Mangrove, associated with vast tidal wetlands, dominates the western half of the islands. The pine forest was heavily logged in the mid-1900's (Myers et al., 2004), and degraded logging roads provide the only ground access to the interior. Pine trees in the secondary forest are slender and closely spaced, with an understory of poisonwood and palmetto, fern, or shrub (Currie et al., 2005). Townships are spread along a single highway running north to south along the east coasts of NA, SA and MC.

Population Surveys and Observational Effort

To evaluate population density in the three primary habitats, we conducted line transects between 5–18 July 2005 (late in the oriole breeding season) on NA following methods similar to Hayes et al. (2004). We walked individually or paired at approximately 1 km/hr, surveying 33 transects totaling 19.5 km, with 9.8 km in coppice, 2.4 km in pine forest, and 7.3 km in anthropogenic habitat. We recorded all birds sighted or heard to compare relative and habitat-specific abundance of orioles and cowbirds.

We obtained additional population data earlier in the breeding season while studying oriole reproduction and foraging on NA from 17 June–13 July 2007; on NA, MC, and SA from 29 March–30 May 2009; and on MC and SA from 18 April–8 May 2010. Traveling at a slow pace, we searched for orioles in coppice, pine forest, and anthropogenic habitat. This method was effective, as the birds are large, colorful, and usually sing from exposed perches (Baltz, 1997). Nests were easily located on the underside of palm fronds. Because the orioles were most common in and adjacent to anthropogenic habitat, we focused our efforts there and surveyed roughly 90% of all townships on NA, 95% on MC, and 95% on SA. We computed the approximate area for each township surveyed using ArcGIS (ESRI, Redlands, CA, USA) and calculated oriole density (total birds discovered per unit area) for each township.

Total field time devoted to searching for and observing orioles was approximately 770 hours (72, 158, and 336 hr on NA in 2005, 2007, and 2009, respectively; 14, 81 hr MC 2009, 2010, respectively; 28, 81 hr SA 2009, 2010, respectively). Total time in direct observation of orioles was approximately 243 hr (100 hr NA, 65 hr MC, 78 hr SA).

Ethological Observations

We conducted continuous observations of breeding oriole pairs up to 2 hr, every 1–4 d. We noted time, habitat, behavior, and age of bird as hatch-year (HY), second-year (SY), or after-second-year (ASY) plumage (Jaramillo and Burke, 1999). As the Bahama Oriole is monomorphic and monochromatic (Garrido et al., 2005), sex could not be determined visually. We determined clutch size of accessible nests using a hand-built pole-mounted infrared video camera when adults were absent, or by observing chicks directly. We also observed adult provisioning of nestlings to quantify intervals between visits, duration of visits, and food items delivered to offspring.

Nest-Site Selection

We used a paired design to compare nest-site and corresponding randomly-located palm locations within 100 m of the nest tree to identify possible nest-site selection factors (Beck and George, 2000). Only palms were evaluated because the orioles nested almost exclusively in palm trees. For each nest-site, we measured microhabitat- (nest tree), mesohabitat- (0.04-ha circular plots), and macrohabitat- (beyond mesohabitat) scale attributes. These three sets of attributes were used to identify the spatial scale at which birds potentially select nesting locations. We measured the same attributes of four randomly-selected palms within 100 m of the nest tree by generating four random directions and distances between 25–100 m, and choosing the individual palm tree (>2 m height) nearest each randomly-generated location. Mean values of the four randomly-selected palms were compared to nest-site values. If multiple nests were present in the same territory, mean values were used to avoid pseudoreplication. Nest height, frond layer in which the nest was located, and compass direction of the nest relative to the trunk were also noted.

Microhabitat-Scale (Tree) Attributes

At each nest-site and randomly-generated location, we recorded the tree species, height, diameter-at-breast-height (dbh), and distance to nearest cover > 1 m in height. Height was determined by measuring from the trunk base to the first frond attachment point (or to the top of the trunk for dead palms), which meant nest height was sometimes greater than tree height. We evaluated health of the tree using a scale inversely corresponding to the stages of lethal yellowing, with 0 = no fronds remaining on trunk, 1 = all fronds yellow or brown, 2 = greater than 50% fronds yellow, 3 = less than 50% fronds yellow, and 4 = no evidence of lethal yellowing.

Mesohabitat Attributes

Within 0.04-ha circular plots (11.4 m radius from palm at center), we recorded species, health using the aforementioned scale, and height of each palm tree > 1 m in height. Percent cover of shrub, bare ground, and litter were estimated within the plot.

Macrohabitat Attributes

From the center of each plot, we measured distance to the nearest road (as a proxy for human disturbance), distance to nearest pine forest, and distance to nearest coppice.

Potential Impacts of Cowbirds and Lethal Yellowing

We determined incidence of Shiny Cowbird brood parasitism via direct observation of accessible nests. We evaluated palm health using the aforementioned scale by conducting line transects of palms having a height > 1 m. As coconut and other non-native palms are primarily present in areas where people have planted them, surveys were restricted to townships and agricultural fields. Palm health was evaluated at limited locations on NA in 2005 and 2007, and more extensively on NA, MC, and SA in 2009.

Statistical Analyses

We used both parametric (*t*-tests, Pearson's correlation, logistic regression, analysis of variance [ANOVA] with Tukey's HSD post-hoc comparisons) and non-parametric (Chi-square, Friedman's ANOVA) tests, depending on the nature of the dependent measure and whether assumptions were met (Zar, 1996; Mertler and Vannatta, 2004). We did not arcsin-transform percentage data, because doing so did not improve normality. We also computed effect sizes, which are independent of sample size (in contrast to statistical significance), and more readily compared among different data sets and studies. These included: Cohen's *d* using pooled standard deviation for pairwise comparisons (~0.5 considered moderate and ≥0.8 large); Phi (φ) for 2×2 and Cramer's *V* for larger contingency tables (~0.3 deemed moderate and ≥0.5 large); coefficients of determination (r^2) and Nagelkerke R^2 for correlations and logistic regression model fit, respectively (~0.09 considered moderate and ≥0.25 large); and log-odds ratios for logistic regression (with deviation from 1.0 indicating proportion of variance explained; Cohen, 1988; Mertler and Vannatta, 2004). The terms "moderate" and "large" are used loosely. We employed Rayleigh's test of uniformity and a Watson-Williams test for circular data (Zar, 1996).

Statistical analyses were conducted using SPSS 17.0 (SPSS Inc., Chicago, IL, USA) for most data, employing standard defaults for full logistic regression models, and alpha = 0.05. We analyzed circular data using R 2.12.1 with the package Circular (Lund and Agostinelli, 2011). Following Nakagawa (2004), we chose not to adjust alpha for multiple tests. Values are presented as mean ± 1 SE.

Results

Population Densities and Estimates

Distance transects late in the breeding season of 2007 revealed that Bahama Orioles on NA were most numerous in coppice (5.6/km ± 4.4), followed by anthropogenic habitat (1.2/km ± 0.6). Although orioles were not detected in pine forest, they were occasionally observed in this habitat during subsequent work. Shiny Cowbirds were scarce in anthropogenic habitat (0.3/km ± 0.2) and pine forest (0.2/km ± 0.2), and absent from coppice. The comparatively low cowbird density (ratio of 0.17 per oriole) was confirmed by informal observations in subsequent years. Transects with zero counts limited the statistical power of comparisons; thus, we could not identify possible habitat preferences of either species.

During more extensive field work early in the breeding season of 2009, we observed 81 orioles on NA (48 ASY, 21 SY, 12 unknown; 29 observed pairs), 22 on MC (19 ASY, 3 SY; 10 observed pairs), and 24 on SA (19 ASY, 3 SY, 2 unknown; 8 observed pairs). Surveys in Caribbean pine forest habitats on Grand Bahama by Lloyd and Slater (in press) resulted in 50–90% detectability for most bird species during single transects. Our surveys in 2009, focused on orioles, were much more comprehensive than those of Lloyd and Slater, likely resulting in detectability at the higher end of this range. Based on 50–90% detectability, we estimated that 90–162, 24–44, and 27–48 Bahama

Orioles remain on NA, MC, and SA, respectively. In sum, we estimated the global population of this taxon at 141–254 individuals (but see Discussion).

Breeding and Nesting

We observed orioles pairing and duetting together as early as 30 March (2009), initiating incubation on 15 April (2009), and feeding chicks as late as 8 August (2010, Cindy Rimstad, pers. comm.). From bouts of continuous observations of three focal pairs, only one individual per pair, assumed to be female as in other oriole species (Rising and Flood, 1998; Rising and Williams, 1999; but see Jarmillo and Burke, 1999), constructed the nest over approximately one week. The mate attended her movements, often singing on a perch nearby during this time. Nests were discovered only in residential and agricultural habitats where coconut palms were present, despite searches elsewhere. On NA, a significantly higher proportion of oriole pairs included a SY mate (50% of 18) compared to pairs on MC and SA (7% of 15, pooled; $\chi^2_2 = 7.27$, $P = 0.007$, $\varphi = 0.47$).

In 2009, we discovered 37 nests built by 24 pairs on NA (1–4 nests/pair, mean = 1.5). In 2010, we found eight nests built by six pairs on MC and one nest on SA (1–2 nests/pair, mean = 1.3). At six sites, the same tree was used for multiple nests built in the same year by the same pair. Nearest-neighbor distances between nests (excluding distances between nests within the same territory) ranged from 75–11436 m (1297 ± 552; $N = 24$) on NA to 265–3591 m (2003 ± 477; $N = 6$) on MC, with no significant difference between islands ($t_1 = 0.71$, $P = 0.49$, Cohen's $d = 0.33$). Mean nest height was 6.0 ± 0.4 m (range 1.8–12.9 m) in trees having a mean height of 6.1 ± 0.5 m (range 2.0–13.7 m) and a mean health of 3.6 ± 0.1 (range 3.0–4.0). Nest orientation data for 2009

(NA) and 2010 (MC, SA) did not differ significantly (Watson-Williams test), and therefore were combined. Nests were built with directional preference relative to the trunk ($z = 0.28$; $P = 0.040$; $N = 41$), and were most often found in the northwest quadrant (leeward side) of the palm tree (mean orientation = 307°). Nests were more often built in the lowest layer of palm fronds (96%) than in higher layers (4%; $\chi^2_2 = 78.4$, $P < 0.001$, $N = 45$). Because coconut fronds remain on the tree only 2.5 yr, and the lowest fronds are oldest (Child, 1974), nests built in the lowest frond layer are probably unavailable for reuse in successive years. However, fronds are retained in *Thrinax* and *Sabal* in the absence of fire (pers. obs.), so nests may accumulate in these tree species from year to year. Oriole nests discovered in endemic *Thrinax morissi* and *Sabal palmetto* ($N = 5$) were built in the retained dead layers of thatch under the crown of the palm. One *T. morissi* contained three nests, two built in 2009, and one reportedly from the prior year (Prescott Smith, pers. comm.)

Nest-Site Selection

We relied on binary logistic regression models to identify which scale (micro, meso, macro) was most successful in discriminating nest trees from random trees. Because of sample size limitations, we used univariate analyses (*t*-tests and corresponding effect sizes; Table 4.1) to identify three factors at each scale (macro, meso, micro) that explained the most variance, and then used these in the full binary logistic regression models. None of the predictors within a given model covaried (as determined by tolerance levels).

Table 4.1. Potential nest-site selection by Bahama Orioles (*Icterus northropi*), with comparisons of nest trees versus random trees ($\bar{\chi}$ ± 1 SE) at micro-, meso-, and macrohabitat levels via paired *t*-tests (for quantitative variables) and Chi-square tests (for categorical variables).

Nest-site scale	**Nest**	**Random**	**Test statistic**	***P***	**Effect size**
	$\bar{\chi}$ ± SE	**$\bar{\chi}$ ± SE**			
Microhabitat variables	($N = 31$)	($N = 31$)			
Tree height (m)	6.1 ± 0.5	4.9 ± 0.3	$t_{30} = 2.83$	0.008	$d = 0.56$
Tree health (0–4)	2.6 ± 0.1	2.5 ± 0.1	$t_{30} = 1.56$	0.13	$d = 0.28$
Tree dbh (cm)	25.5 ± 0.7	25.5 ± 0.5	$t_{23} = 0.017$	0.99	$d = 0.00$
Distance from tree to cover (m)	6.9 ± 0.7	5.3 ± 0.4	$t_{30} = 2.46$	0.02	$d = 0.53$
Tree species (number)					
Cocos nucifera	40 (87.0%)	194 (91.5%)			
Sabal palmetto	2 (4.3%)	6 (2.8%)	$\chi^2_3 = 1.05$	0.79	$V = 0.06$
Thrinax morrisii	3 (6.5%)	8 (3.8%)			
Brassaia actinophylla	1 (2.2%)	4 (1.9%)			
Mesohabitat variables	($N = 20$–31)	($N = 20$–31)			
Litter (%)	6.9 ± 2.8	10.5 ± 2.7	$t_{30} = 1.17$	0.25	$d = 0.24$
Bare (%)	83.9 ± 3.8	71.6 ± 3.6	$t_{30} = 2.44$	0.021	$d = 0.61$
Shrub (%)	8.3 ± 1.9	18.0 ± 2.3	$t_{30} = 3.34$	0.002	$d = 0.86$
Palms in meso-plot (#)	1.3 ± 0.2	1.0 ± 0.1	$t_{30} = 1.93$	0.064	$d = 0.28$
Height of palms in meso-plot (m)	5.5 ± 0.5	4.2 ± 0.4	$t_{30} = 2.98$	0.007	$d = 0.71$
Health of palms in meso-plot (1–5)	3.4 ± 0.2	3.4 ± 0.1	$t_{30} = 0.29$	0.78	$d = 0.10$
Macrohabitat variables	($N = 23$–31)	($N = 23$–31)			
Distance to road (m)	14.2 ± 3.0	16.6 ± 2.5	$t_{30} = 1.18$	0.25	$d = 0.16$
Distance to coppice (m)	48.8 ± 9.3	51.6 ± 9.7	$t_{30} = 0.38$	0.71	$d = 0.02$
Distance to pine forest (m)	183.9 ± 33.6	184.7 ± 34.2	$t_{23} = 0.18$	0.85	$d = 0.00$

Microhabitat-Scale Model

The majority of 46 nests observed were constructed in coconut palms (87%), with native *S. palmetto* (4%) and *T. morisii* (7%) palms and an introduced *Brassaia actinophylla* tree (2%) also used. The proportion of tree species used did not differ significantly from availability (Table 4.1). *T*-tests revealed that nest trees were significantly taller ($P = 0.008$) and farther from nearest cover ($P = 0.020$) than random trees, but were similar in girth (dbh) and health (Table 4.1). The logistic regression model, including the variables tree height, health, and distance to cover, significantly distinguished between nest trees and random trees ($P = 0.009$; Table 4.2). The model predicted nest (58.1%) and random (68.8%) trees with weak to moderate success (63.5% overall). Tree height ($P = 0.031$) and distance to cover ($P = 0.033$) remained significant, with log-odds ratios (exp[B] values, Table 4.2) indicating a 27.6% increase in probability of tree use for nesting with each 1 m increase in height, and a 17.4% increase with each 1 m increase in distance to cover.

Mesohabitat-Scale Model

Of the six mesohabitat-scale variables (Table 4.1), palm tree height ($P = 0.007$) and proportion of bare ground ($P = 0.020$) in nest meso-plots were significantly higher than random meso-plots, whereas proportion of ground covered by shrubs was significantly less ($P = 0.002$). The logistic regression model using three predictors (palm tree height, percent ground cover in shrubs, and number of palms; proportion of bare ground was omitted due to reciprocality with ground cover) provided strong discrimination between nest and random meso-plots ($P < 0.001$; Table 4.2), and predicted nest (71.4%) and random (80.8%) meso-plots with high success (76.6% overall). All three variables were significant, with log-odds ratios indicating a 46.1% increase in probability of nesting with each 1 m increase in average height of palms, a 73.9% increase with each additional palm in the plot, and a 10.4% decrease with each 1% increase in shrubs.

Table 4.2. Results of logistic regression models for three scales of potential Bahama Oriole nest site selection, comparing nest sites (coded as zero) paired with random sites (coded as one).

Predictors	**B**	**SE**	**Wald**	***P***	**Exp(B)**
Microhabitat model ($N = 31$)					
Height	-0.32	0.15	4.67	0.031	0.72
Health	0.70	0.65	1.16	0.28	2.01
Distance to cover	-0.19	0.09	4.55	0.033	0.83
Mesohabitat model ($N = 21$)					
Shrub ground cover (%)	0.10	0.04	5.45	0.020	1.10
Number of meso-plot palms	-1.34	0.53	5.11	0.024	0.26
Height of meso-plot palms (m)	-0.62	0.25	6.39	0.011	0.54
Macrohabitat model ($N = 23$)					
Distance to road (m)	0.01	0.02	0.18	0.67	1.01
Distance to coppice (m)	0.00	0.01	0.01	0.92	1.00
Distance to pine forest (m)	0.00	0.00	0.01	0.91	1.00

Microhabitat: $\chi^2_3 = 11.50$; $P = 0.009$, -2 log likelihood = 75.22, Nagelkerke $R^2 = 0.22$, 63.5% predicted correctly.

Mesohabitat: $\chi^2_3 = 23.34$; $P < 0.001$, -2 log likelihood = 41.28, Nagelkerke $R^2 = 0.52$, 76.6% predicted correctly.

Macrohabitat: $\chi^2_3 = 0.19$; $P = 0.98$, -2 log likelihood = 64.94, Nagelkerke $R^2 = 0.01$, 59.6% predicted correctly.

Macrohabitat-Scale Model

None of the three macrohabitat variables differed significantly between nest and random sites (Table 4.1), as confirmed by logistic regression (Table 4.2), which yielded comparatively poor predictive success (nest trees, 56.5%; random trees, 62.5%; overall, 59.6%).

Incubation, Provisioning, Fledging, and Nest Defense

Incubation lasted 12–14 days in four nests observed. Only one bird, presumed to be female, appeared to incubate. Both parents, in contrast, participated in brooding and feeding offspring, sometimes conducting feedings simultaneously. Nests were covered, making it difficult to see food presented to chicks, but we observed parents deliver berries, an occasional *Anolis* lizard, and insects, with the latter most commonly delivered. Mean feeding interval decreased from 12.0 ± 2.5 min in the first 6 days after hatching to 10.7 ± 8.6 min for days 7–10, and to 7.8 ± 1.7 min for days 11–14 ($N = 5$, 6, and 5, respectively). Mean time at nest decreased from 3.5 ± 1.2 min, to 1.4 ± 0.6 min, and to 1.0 ± 0.3 min for the same time periods ($N = 5$, 6, and 5, respectively). Using only nests which had data for each age group, neither feeding interval (Friedman's ANOVA: $\chi^2_2 = 1.50$, $P = 0.47$, $N = 4$) nor parent time-at-nest (Friedman's ANOVA: $\chi^2_2 = 2.80$, $P = 0.25$, $N = 4$) differed significantly among the three age classes, but sample sizes were small. Both parents removed fecal sacs in their bills of older (>5 days) but not younger nestlings, and dropped them as they flew away from the nest; sacs of younger chicks may be eaten, as reported for related species (Flood et al., 2002). Both adults contributed to nest defense when we banded chicks.

In July, 2007, we observed a hatch-year (HY) bird assisting in feeding hatchlings and receiving feedings from an oriole in ASY plumage. This HY bird was able to fly to and from the nest, but often stayed in the nest for prolonged periods of time, perhaps assisting with brooding. Another ASY adult was in the area but we could not confirm pair status. Hatchlings approximately 4–6 days old could be heard peeping inside the nest.

Of the six nests observed closely enough to determine success, all fledged 2–4 oriole chicks (mean = 2.5) at 12–14 days after hatching, within a 24-hour period. In two fledging events witnessed, chicks flew to cover <10 m from the nest and were fed by parents for several hours before moving to nearby coppice, where they were observed being fed several days later.

Shiny Cowbird Brood Parasitism

Shiny Cowbirds parasitized two (28.6%) of seven active nests with known contents. One nest fledged one cowbird and two oriole chicks. A second nest undergoing incubation later in the season contained four cowbird eggs. Additionally, at least one abandoned nest contained a cowbird egg. Cowbirds may have contributed to other abandoned nest attempts, as 39% of 31 nest sites contained one or more abandoned nests in addition to the active nest. Cowbirds were observed cryptically watching within an oriole's territory ($N = 2$), flying into view during taped playback of the Bahama Oriole song ($N = 1$), and flying into the vicinity when orioles themselves gave calls ($N = 1$).

Lethal Yellowing Impact

Analysis of 2009 data revealed significant differences among islands in palm tree health (one-way ANOVA: $F_{2,1054} = 250.96$; $P < 0.001$; $\eta^2 = 0.32$). Tukey's HSD post hoc tests suggested the lethal yellowing outbreak began in, and may presently be confined to, NA, where scores for palm health (2.06 ± 0.09, $N = 365$) were significantly lower ($P < 0.001$) than on MC (3.59 ± 0.04, $N = 299$) and SA (3.67 ± 0.03, $N = 393$). Palm health was similar for MC and SA ($P = 0.91$). In Staniard Creek, NA, where the lethal yellowing outbreak appears to have originated (Fig 4.1), mean palm tree health decreased significantly from 1.54 ± 0.07 in 2005 ($N = 444$) to 0.06 ± 0.03 in 2007 ($N = 101$), and to 0.03 ± 0.03 in 2009 ($N = 66$; $F_{2,608} = 135.61$; $P < 0.001$; $\eta^2 = 0.21$), with 97% mortality.

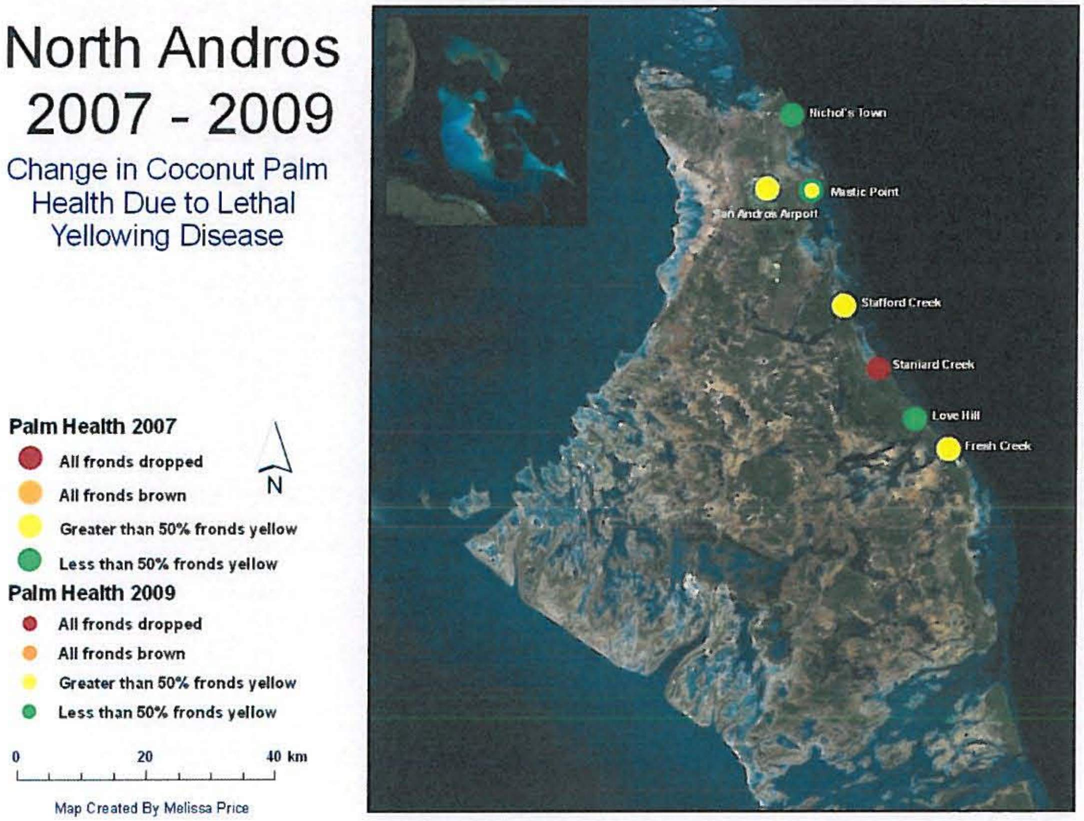

Figure 4.1. Changes in coconut palm health due to lethal yellowing disease, 2007–2009.

In 2009, no orioles were observed in Staniard Creek, where they were present in previous years. Healthier palm communities were associated with higher oriole density (Pearson's $r^2 = 0.38$, $P = 0.019$, $N = 14$ townships; Fig. 4.2). In 2009, mean individual oriole density in NA townships was 2.2 orioles/km^2, compared to 11.8/km^2 on MC and 6.7/km^2 on SA. Interestingly, the Atlantic Undersea Test and Evaluation Center

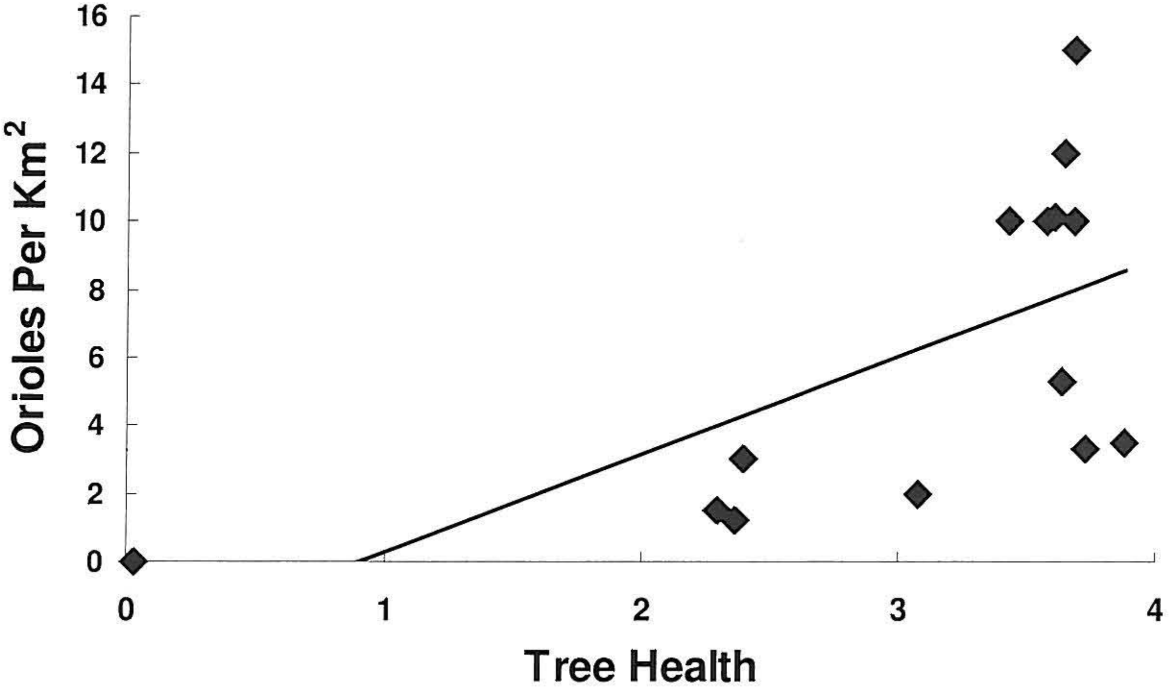

Figure 4.2. Bahama Oriole (*Icterus northropi*) density as a function of average palm tree health among 14 anthropogenic areas (townships and agricultural fields) on Andros Island, Bahamas ($r^2 = 0.38$, $P = 0.019$; data from 2009 surveys). Palm health during transects was scored on a scale from zero (no fronds remaining) to four (no sign of injury). Oriole density was greatly decreased in areas where lethal yellowing reduced the health of palm trees.

(AUTEC) on NA, with healthy palm trees due to regular maintenance by grounds crews and inoculation against lethal yellowing, had a density of 10.0 orioles per km^2, which was similar to the density on MC and SA.

Discussion

Island endemics often have contracted ranges and population sizes, leaving them vulnerable to changes associated with human arrival and influence, as well as stochastic events (Karels et al., 2008). Furthermore, small islands may lose species more quickly than large islands because of the greater scope of human influence per island area

(Steadman, 2006). These factors may have contributed to the loss in the early 1980's of the Bahama oriole from Abaco Island (White, 1998, pers. comm..), which is a smaller and more developed island than Andros. Our findings confirm that anthropogenic habitats benefit this synanthropic species, at least during the breeding season. However, development on these Bahamian islands frequently occurs at the expense of coastal coppice (Pericles A. Maillis, pers. comm.), which appears to be particularly crucial for the oriole. The loss of coppice may have contributed to extirpation of the Abaco population. Although the Bahama Oriole may never have existed in large numbers (Baltz, 1997), recent arrivals of the Shiny Cowbird and lethal yellowing disease pose novel threats to the small remaining population. Our results point to several solutions that may provide hope for this endangered bird.

Population Densities and Estimates

Our early breeding season surveys (2007-2010) corresponded with previous observations by Baltz (1996, 1997), who found orioles and cowbirds primarily in anthropogenic habitat. However, we frequently saw adults foraging in nearby pine and, especially, coppice habitats. Later in the breeding season, after most nestlings had fledged, we more often encountered orioles in coppice habitats, but sometimes in pine forest as well. During winter surveys, Currie et al. (2005) detected the orioles only in coppice and agricultural areas, and did not observe them in pine forest lacking a coppice understory. Collectively, these studies suggest that anthropogenic habitat, although beneficial for breeding, is not sufficient to sustain oriole populations. Natural habitat, especially coppice, appears to be important year-round for the oriole's survival.

Currie et al. (2005) did not detect Shiny Cowbirds in any of their winter surveys, so we are unable to compare winter and breeding habitat use for this species. Shiny Cowbirds were detected during the 1995 Christmas Bird Counts (CBC) on NA, but not before or since this count (National Audubon Society, 2010), which may indicate a migratory population (Baltz, 1995). However, since the arrival of the Shiny Cowbird in the Bahamas (Baltz, 1995), it has also been observed on Grand Bahama during the 2001, 2004, and 2009 CBCs, and on New Providence Island during the 2005 CBC. In spite of its spread, the species does not appear to be increasing substantially on Andros. Breeding season surveys by Baltz (1997) found ratios of 0.33 and 0.29 cowbirds to orioles in 1995 and 1997, respectively, compared to our observation of 0.17 cowbirds to orioles in 2005.

Our total population estimate for the Bahama Oriole (141–254) corroborates a previous estimate of approximately 300 individuals (Baltz, 1997), and suggests the taxon is critically endangered by IUCN criteria (<250 individuals globally, with decreasing numbers following extirpation on Abaco). Our surveys were confined to readily accessible habitat along the eastern portion of the islands, as were those of Baltz (1997). Abundance may be higher if some orioles are present in the pine forest interior, or on the less accessible western portion of the island (dominated by mangroves). Although rarely encountered in pine forest, scattered pairs may nest in the palm understory, or in patches of palms among the extensive mangrove flats. Orioles are still present near anthropogenic habitat on the west coast where Northrop observed them a century ago (Allen, 1890) in Red Bays (this study) and at Flamingo Cay Resort near Wide Opening (Cindy Rimstad, pers. comm.). Smaller cays, such as Big Wood Cay (40 km^2) just north of Mangrove Cay, may also be suitable for supporting a handful of pairs. The disparity in oriole density between NA, SA, and MC presumably reflects degradation of nesting habitat by lethal yellowing on NA or destruction of coppice for agricultural development, and presents some concern. Low density may lead to decreased mate choice, increased inbreeding, and decreased heterozygosity (Frankham et al., 2002).

Breeding

Prior to the arrival of humans and the coconut palm, the Bahama Oriole likely nested in endemic palms such as *T. morisii* and *S. palmetto*. In our study, oriole nests discovered in endemic palms were built in the dead layers of thatch under the crown of the palm, which accumulates in the absence of fires. Forest fires occurred less often prior to the arrival of humans (Myers et al., 2004), allowing endemic palms to grow taller, as preferred by the orioles in our study. Today, many forested areas burn every 1–3 years (Myers et al., 2004), which may limit palm availability in this habitat. Like others (Allen, 1890; Baltz, 1997), we were unable, despite searches, to find nests in the pine forest habitat we were able to access. However, pine forest deeper inland, further from human influence and spared from frequent fires, may support a palm understory that provides suitable oriole nesting habitat. Further research should explore this difficult-to-access terrain.

In 2009, 50% of 18 pairs on NA included at least one bird in second-year plumage. In two pairs on NA, both individuals were SY adults, indicating that at least some SY males are breeding. This was additionally confirmed with the observation of a SY male (sex identified through molecular sexing techniques; Price et al., unpubl. data) paired with an ASY adult. This proportion is within the normal range for breeding SY males among oriole species (6–55%; Rising and Flood, 1998; Rising and Williams, 1999; Flood, 2002; Brush and Pleasants, 2005). However, the higher proportion of oriole pairs that included a SY mate on NA compared to MC and SA suggests that the oriole density on NA is functionally low, promoting breeding by younger birds.

Our observations of reproduction augment the prior anecdotal reports of breeding phenology (March–August), nest tree preference (palms), clutch size (2–4), incubation duration and time to fledging (12–14 days each), and nestling diet (fruit, insects, lizards) of the Bahama Oriole and other Greater Antillean oriole species (Baltz, 1997; Rising and Flood, 1998; Jaramillo and Burke, 1999; Garrido et al., 2005). Although breeding may occur year-round in other Greater Antillean orioles, there is no evidence of this to date for the Bahama Oriole (Garrido et al., 2005). The preferred location of Bahama Oriole nests in the leeward (northwestern) side of trees is exhibited by some but not all populations of other oriole species (Schaefer, 1976; Rising and Flood, 1998).

Typical of other tropical birds (Russell et al., 2004), oriole family groups often remain together until the next breeding season. We observed family groups foraging together as late as April 2009 and May 2010. During the peak breeding season, from mid-May through early June, however, only paired or single birds were observed, suggesting that family groups do not remain together through the breeding season. An interesting derivative of delayed dispersal may be the occasional occurrence of a helper-at-the-nest when orioles double-brood. In July 2009, we observed a bird in HY plumage assisting in feeding chicks and receiving feedings from an oriole in ASY plumage. This HY bird was able to fly to and from the nest, but often stayed in the nest for prolonged periods of time, perhaps assisting with brooding. This is the first report to our knowledge of a helper-at-the-nest in any oriole species (Skutch, 1996; Nancy Flood, pers. comm.), and suggests double brooding, as occurs in some other oriole species (Jaramillo and Burke, 1999; Ligi and Omland, 2007).

Nest-Site Selection

Orioles nested in significantly taller trees than randomly available palm trees nearby, and preferred sites with less brush underneath and with taller palm trees within the meso-plot. These preferences likely explain the proclivity toward introduced palm trees, which attain greater heights than native palms. The greater heights of nest trees may provide some measure of protection from feral cats and rats. Preference for less brush near the tree could reflect selective pressure from biting insects and/or snake (*Epicrates striatus fowleri*) predators. Although the majority of nests were in coconut palms, proportional use of this species did not differ from palm species available within 100 m of the nest tree. However, the presence of coconut palms may be a selection factor at a larger scale (which we did not assess quantitatively), as we were unable to discover nests in areas lacking coconut palms.

Shiny Cowbird Brood Parasitism

Low density of the Bahama Oriole is of concern given the presence of Shiny Cowbirds in the oriole's preferred breeding habitat. While only two of seven active nests with known contents in our study were parasitized, Baltz (1996, 1997) found that 100% of four nests established later in the breeding season on North Andros were parasitized. At least one abandoned nest in our study was parasitized, and cowbird activity may have contributed to the high number of nest sites with one or more abandoned nests (39% of 31 nest sites). Intensive cowbird trapping programs have been successful in lowering parasitism rates on other islands, and may be considered for Andros (Baltz, 1997). However, the cowbird population on Andros does not appear to have increased substantially this past decade, so it may be premature to invest in such a program.

Lethal Yellowing

Palm viability was a major factor influencing local population density of orioles. Between 2005 and 2009, we noted a significant decline in coconut palm health on NA due to lethal yellowing, leading to local declines in breeding oriole density. Continuing palm losses on NA may increase competition for the remaining suitable nest sites or promote dispersal to new areas, potentially less favorable areas. A recent study showed that endemic *Thrinax* and *Coccothrinax* can host lethal yellowing without showing symptoms (Narvaez et al., 2006), providing a reservoir for future outbreaks and inhibiting efforts to combat the disease. Several resorts on NA have successfully inoculated their coconut palms against infection, and local efforts to plant disease-resistant cultivars are underway (pers. obs.). Palm trees on MC and SA appear to be disease-free at present, but remain vulnerable to spread of the phytoplasma from NA or introduction of a new phytoplasma.

Management Suggestions

Having lost access to 88.7% of their primary vegetation, the Caribbean's 148 remaining endemic bird species need careful planning and management if they are to continue providing crucial services such as seed dispersal, decomposition, and pollination to the ecosystems they are a part of (Şekercioğlu et al., 2004). Supporting 2.3% of the world's endemic plants and 2.9% of the world's endemic vertebrates in a proportionately small area (Şekercioğlu et al., 2004), management decisions in the Caribbean have important ramifications for global biodiversity. While the focus of conservation should rest on the protection of whole ecosystems, rather than piecemeal strategies for separate species (Myers et al., 2000), comprehensive species-focused studies must inform habitat management decisions.

Small endemic populations such as the Bahama Oriole may never have existed in large numbers (Baltz, 1997), but are nonetheless an important source of diversity. Recent studies have resulted in taxonomic elevation to species status for the Bahama Oriole, Cuban Oriole, Puerto Rican Oriole, and Hispaniolan Oriole (Garrido et al., 2005; Price and Hayes, 2009; Sturge et al., 2009; American Ornithologists' Union, 2010). With fewer than 300 individuals remaining, the Bahama Oriole may be the rarest bird species in the Bahamas and is facing the threat of extinction. Aggressive trapping programs to reduce the number of Shiny Cowbirds (Baltz, 1997), planting of disease-resistant palm cultivars, and conscientious management of coppice habitat may prevent the loss of this rare bird. Translocation of individuals to Abaco to reestablish the population recently lost there might prove more beneficial in the long term than intense cowbird removal.

The juxtaposition of residential and agricultural nesting areas to suitable native habitats for foraging may be more important than any single factor in meeting the Bahama Oriole's life history needs, especially for breeding adults and fledging chicks. We observed parents flying from nest sites in anthropogenic habitat to nearby coppice to forage, and chicks fledged to coppice. As winter surveys also noted oriole dependence on broadleaf habitat (Currie et al., 2005), coppice appears to be essential year-round to oriole survival. Pine forest has tended to increase with human occupation while coppice has decreased due to the effects of forest fires on ecological succession (Myers et al., 2004), resulting in limited patches of coppice interspersed throughout areas of anthropogenic habitat and pine forest. Coastal development has further exacerbated the loss of coppice (Wunderle and Waide, 1993), and continues unabated on Andros (Thurston, 2010). Coppice is also important for other resident, wintering, and migratory birds (Currie et al., 2005). Conservation efforts, therefore, should focus on preserving those areas of coppice that may be lost to future development, and pine forest should be managed so that succession to coppice is allowed to take place over time. Because of the oriole's current dependence on anthropogenic habitat, education of Bahamians will be especially important to preserve the species.

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CHAPTER FIVE

IMPACTS OF A TRANSITIONING LANDSCAPE ON THE BAHAMIAN AVIFAUNA AND A CRITICALLY ENDANGERED SPECIES

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Abstract

Dry tropical forest is one of the most endangered major tropical ecosystems globally, due to anthropogenic causes. In the Bahamas, pine forest has tended to increase with human occupation while coppice, or dry tropical broadleaf forest, has decreased due to the effects of forest fires on ecological succession. Furthermore, human development has removed native breeding and foraging habitats, but has also provided new opportunities in the form of novel, introduced plant species. I compared avian species composition among three major habitats on Andros Island, The Bahamas: Caribbean pine forest, coppice, or dry broadleaf forest, and anthropogenic habitat. I also evaluated habitat use, foraging strategies and social interactions of the Bahama Oriole, a critically endangered island endemic. Bird surveys in the different habitats indicated avian species richness was highest in coppice, and roughly equivalent in pine forest and anthropogenic habitat. Some coppice and pine forest species were never observed in agricultural or residential areas, and may be at risk if human disturbance of natural habitats increases, as is occurring at a rapid pace on South Andros. Of the foraging characters evaluated, only habitat type differed significantly between second-year and after-second-year adults. Although second-year adults foraged in all three habitats, after-second-year adults were only observed foraging in anthropogenic habitat. Additionally, second-year adults foraging in anthropogenic habitat were often paired with an after-second-year adult, possibly indicating divergent foraging strategies for younger birds. My findings concur with those of other studies indicating coppice is vitally important to resident, migrating, and wintering birds, including the critically endangered Bahama Oriole. Furthermore, given the importance of the wide swaths of Caribbean pine forest to wintering, migratory,

and permanent resident species, conservation plans should consider treatment of pine forests to increase heterogeneity.

Introduction

Dry tropical forest is one of the most endangered tropical ecosystems globally, due to anthropogenic causes (Janzen, 1988). In the Bahamas, pine forest has tended to increase with human occupation while coppice, or dry tropical broadleaf forest, has decreased due to the effects of forest fires on ecological succession (Myers et al., 2004). Andros Island, the largest land mass in the Bahamas, escaped much of the development associated with tourism that has devastated habitats on other Bahamian Islands, but was heavily logged in the mid-1900's (Myers et al, 2004).

Today, the landscape on Andros Island is composed of limited patches of coppice interspersed throughout areas of pine forest and anthropogenic habitat. Resource subsidies in anthropogenic habitat, such as cultivated plants or discarded food items, may have increased or stabilized avian productivity in some species, and has likely affected the abundance and distribution of species (Faeth et al., 2005). Other birds may have avoided these disturbed habitats, or may have declined over time following habitat disturbance, particularly in areas where much of the canopy was removed (e.g., >40%; Miller et al., 2007; Norris et al., 2009).

Even synanthropic bird species that regularly use anthropogenic habitats could have been negatively affected by forest loss, as multiple habitat types may be required to sustain viable populations in some species (Cohen and Lindell, 2005). The juxtaposition of multiple habitat types may be of particular importance to fledglings and young birds, which may leave breeding grounds for habitats nearby that presumably provide higher protection from predators and increased foraging opportunities (Cohen and Lindell, 2004; Price et al., under review). Juveniles are often less efficient foragers than adult birds (Heise and Moore, 2003), and may seek habitats with reduced competition.

The Bahama Oriole (*Icterus northropi*), a critically endangered island endemic found only on Andros Island, has contended with profound habitat changes since the arrival of humankind. While logging and human development removed native breeding and foraging habitats (Currie et al., 2005), humans provided new opportunities in the form of novel, introduced plant species (Nickrent et al., 2008). Coconut palms (*Cocos nucifera*), for example, were imported to the region by humans about 500 years ago (Child, 1974; Baudouin and Lebrun, 2009), and have become the oriole's favored nesting habitat (Allen, 1890; Baltz, 1996, 1997; Price et al. under review). Although partially a synanthropic species, the oriole may depend on other natural habitats to sustain various activities throughout a day or life cycle (Vega Rivera et al. 1998; Graham, 2001), and may benefit from foraging in multiple habitat types (Cohen and Lindell 2005).

In this study, I compared avian species composition among three major habitats on Andros Island, The Bahamas: Caribbean pine forest, coppice, or tropical dry broadleaf forest, and anthropogenic habitat. I also evaluated habitat use and foraging strategies of the Bahama Oriole. As interspecific and intraspecific interactions can influence habitat distribution and foraging strategies (Mac Nally and Timewell, 2005, Shochat et al., 2010), I identified interactions between Bahama Orioles and other birds when observed.

Methods

Study Area

Andros Island, The Bahamas, comprises a collection of small islands and cays riddled with waterways and bights up to 5 km wide. Andros is dominated on the eastern portion by extensive Caribbean pine forest, with coppice at higher elevations and in patches interspersed within the pine forest. Mangrove, associated with vast tidal wetlands and accessible only by boat, dominates the western half. The pine forest was heavily logged in the mid-1900's (Myers et al., 2004), and old logging roads provide the only ground access to the interior. Pine trees in the secondary forest are slender and closely spaced, with an understory of poisonwood (*Metopium toxiferum*) and palmetto, fern, or shrub (Currie et al., 2005). Townships and agricultural developments are spread along the eastern portion of the three major land masses: North Andros (3600 km^2), Mangrove Cay (200 km^2), and South Andros (800 km^2).

Population Surveys and Observational Effort

To evaluate population density and species composition, I conducted line transects between 5–18 July 2005 in coppice, pine forest, and anthropogenic habitat on North Andros, using methods similar to Emlen (1971) and Hayes et al. (2004). I walked individually or with an assistant at approximately 1 km/hr, surveying 33 transects totaling 19.5 km, with 9.8 km in coppice, 2.4 km in pine forest, and 7.3 km in anthropogenic habitat. I recorded all birds sighted or heard to compare relative and habitat-specific abundance of orioles with other species.

Foraging Behavior

I obtained foraging and social interaction data 17 June–13 July 2007 and 29 March–30 May 2009. Total time in direct observation of orioles was approximately 122 hr (100 hr North Andros, 7 hr Mangrove Cay, 15 hr South Andros), of which 20 hr included foraging behaviors or social interactions. To quantify foraging behaviors, I conducted continuous focal observations of an individual for up to 2 hr or until the bird flew out of sight. Independence of data was improved by recording the first behavior observed at 10-min intervals, or the first behavior after a location change > 10 m, whichever came first. For statistical analyses, only the first foraging behavior per bird per day was included in calculations. I recorded foraging variables per Remsen and Robinson (1990), including the age of the bird as second-year (SY) or after-second-year (ASY), habitat foraged in, location of the bird, the substrate fed upon, and the food identity. The foliage species was noted, and the location of the individual in the vegetation, both horizontally (by dividing the tree into visual thirds of inner, middle, outer) and vertically (using a clinometer), were recorded. Substrates foraged on were recorded as air, flowers, berries, leaves, twigs, ground, or bark. Foraging tactics were identified as perch gleaning (picking food from a nearby substrate while perched), hang gleaning (picking food from a substrate while hanging upside down), or air-gleaning (plucking insects from the air). The type of food eaten was noted if it could be identified.

Social Interactions

During focal observations, all intraspecific and interspecific interactions were noted, per Bowman et al. (1999), as an aerial chase, tree chase, lunge, or usurp. The species and sex (if they could be determined) of the birds were noted, as well as the outcome of the interaction.

Statistical Analyses

I used both parametric and non-parametric tests, depending on the nature of the dependent measure and whether or not assumptions were met. I also computed effect sizes, which are largely independent of sample size (in contrast to statistical significance) and more readily compared among different data sets and different studies. For pairwise comparisons (*t*-tests), I relied on Cohen's *d* using pooled standard deviation (Hojat and Xu, 2004), for which values of 0.1 are considered small, ~0.5 are loosely considered moderate and ≥ 0.8 large (Cohen, 1988). For tests of proportions (χ^2), I computed Phi (φ) for 2×2 and Cramer's V for larger contingency tables, with values of ~0.3 deemed moderate and ≥ 0.5 large (Cohen, 1988). Following Nakagawa (2004), I chose not to adjust alpha for multiple tests. All analyses were performed using SPSS 17.0 (2008), using alpha level 0.05. Values are presented as mean ± 1 SE.

Results

Population Densities and Estimates

Avian species richness was roughly equivalent in pine forest (24 species) and anthropogenic habitat (26 species), but higher in coppice (35 species; Table 5.1). Some species clearly associated with one or two habitats, whereas others were generalists; however, transects with zero counts limited statistical power and my ability to identify possible habitat preferences for a number of species, including the oriole ($P = 0.18$; $\chi^2 =$

3.44). Bahama Orioles were most numerous in coppice (5.6/km), followed by anthropogenic habitat (1.2/km). Although orioles were not detected in pine forest during these surveys, they were occasionally observed in this habitat during subsequent work.

The density of the Bahama Oriole can be compared to that of other species in Table 5.1, where some structuring of bird communities is evident. Thick-billed Vireo (*Vireo crassirostris*) was significantly associated with coppice. Cuban Emerald (*Chlorostilbon ricordii*), Eurasian Collared Dove (*Streptopelia decaocto*), Gray Kingbird (*Tyrannus dominensis*), Laughing Gull (*Leucophaeus atricilla*), Northern Mockingbird (*Mimus polyglottos*), Smooth-billed Ani (*Crotophaga ani*), and Turkey Vulture (*Cathartes aura*) were significantly more likely to be found in anthropogenic habitat. Black-faced Grassquit (*Tiaris bicolor*), Blue-gray Gnatcatcher (*Polioptila caerulea*), Greater Antillean Bullfinch (*Loxigilla violacea*), Pine Warbler (*Dendroica pinus*), and Western Spindalis (*Spindalis zena*) were significantly associated with pine forest. Bananaquit (*Coereba flaveola*) was significantly more likely to be found in pine forest and anthropogenic habitat.

Table 5.1. Relative density by habitat (individuals/km) of birds on North Andros, Bahamas, from 33 line transects during June and July of 2005, with Kruskal-Wallis ANOVA results.

Species	**Pine**	**Coppice**	**Residential**	χ^2_2	***P***
	$\bar{\chi}$ **± SE**	$\bar{\chi}$ **± SE**	$\bar{\chi}$ **± SE**		
American Kestrel (*Falco sparverius*)	0.0	0.0	0.9 ± 0.8	3.94	0.14
Bahama Mockingbird (*Mimus gundlachii*)	1.4 ± 0.8	4.4 ± 2.3	0.0	6.89	**0.032**
Bahama Oriole (*Icterus northropi*) **Critically Endangered**	0.0	5.6 ± 4.4	1.2 ± 0.6	3.44	0.18
Bahama Swallow (*Tachycineta cyaneoviridis*) **Endangered**	0.5 ± 0.4	2.0 ± 1.2	1.5 ± 1.1	0.92	0.63
Bahama Woodstar (*Calliphlox evelynae*)	0.0	0.2 ± 0.2	0.1 ± 0.1	1.74	0.42
Bahama Yellowthroat (*Geothlypis rostrata*)	0.2 ± 0.2	1.2 ± 0.6	0.0	6.83	**0.033**
Bananaquit (*Coereba flaveola*)	2.4 ± 0.8	1.1 ± 0.8	2.9 ± 0.9	4.24	0.12
Black-and-White Warbler[a] (*Mniotilta varia*)	0.0	0.2 ± 0.2	0.0	1.67	0.44
Black-faced Grassquit (*Tiaris bicolor*)	15.4 ± 4.6	5.5 ± 2.3	0.3 ± 0.2	13.05	**0.001**
Blue-gray Gnatcatcher (*Polioptila caerulea*)	10.2 ± 2.5	4.6 ± 2.4	1.1 ± 0.9	10.56	**0.005**
Black-whiskered Vireo (*Vireo altiloquus*)	8.3 ± 2.6	12.5 ± 4.2	2.5 ± 1.0	3.81	0.15
Common Ground Dove (*Columbina passerine*)	2.1 ±1.1	2.2 ± 1.0	5.4 ± 2.2	2.93	0.23
Greater Antillean Pewee (*Contopus caribaeus*)	0.6 ± 0.6	0.2 ± 0.1	0.0	2.97	0.23
Cuban Emerald (*Chlorostilbon ricordii*)	1.3 ± 1.1	5.3 ± 2.6	5.1 ± 1.4	6.48	**0.039**
Eurasian Collared Dove[b] (*Streptopelia decaocto*)	0.8 ± 0.6	1.5 ± 0.9	7.2 ± 3.7	5.59	0.06
Gray Kingbird (*Tyrannus dominensis*)	2.4 ±1.7	5.5 ± 4.5	5.0 ±1.7	6.00	0.050
Great Lizard Cuckoo (*Saurothera merlini*)	0.0	0.2 ± 0.1	0.3 ± 0.3	1.53	0.47
Greater Antillean Bullfinch (*Loxigilla violacea*)	6.0 ± 3.0	0.4 ± 0.4	0.0	8.20	**0.017**
Hairy Woodpecker (*Picoides villosus*)	4.2 ± 2.0	3.2 ± 1.6	0.1 ± 0.1	5.74	0.06

House Sparrow[b] (*Passer domesticus*)	0.0	1.7 ± 1.7	0.5 ± 0.5	0.81	0.67
Key West Quail Dove (*Geotrygon chrysie*)	0.0	0.8 ± 0.8	0.0	3.44	0.18
Killdeer (*Charadrius vociferous*)	0.0	0.0	1.1 ± 0.9	3.94	0.14
La Sagra's Flycatcher (*Myiarchus sagrae*)	0.8 ± 0.7	1.4 ± 0.7	0.0	4.09	0.13
Laughing Gull (*Leucophaeus atricilla*)	0.0	1.3 ± 1.1	3.0 ± 1.0	10.17	**0.006**
Loggerhead Kingbird (*Tyrannus caudifasciatus*)	0.0	0.0	0.0	0.00	1.00
Mangrove Cuckoo (*Coccyzus minor*)	0.0	1.1 ± 1.1	0.0	1.67	0.44
Northern Bobwhite[b] (*Colinus virginianus*) **Near Threatened**	2.3 ± 1.3	0.4 ± 0.3	0.0	4.35	0.11
Northern Mockingbird (*Mimus polyglottos*)	0.9 ± 0.7	2.2 ± 2.2	7.3 ± 1.8	15.34	**0.001**
Pine Warbler (*Dendroica pinus*)	2.6 ± 1.1	0.5 ± 0.4	0.0	6.88	**0.032**
Red-legged Thrush (*Turdus plumbeus*)	1.2 ± 0.6	1.9 ± 0.8	0.0	5.76	0.06
Red-winged Blackbird (*Agelaius phoeniceus*)	0.0	1.7 ± 1.7	0.1 ± 0.1	0.81	0.67
Rock Dove[b] (*Columba livia*)	0.2 ± 0.2	0.3 ± 0.3	2.2 ± 2.1	0.50	0.78
Shiny Cowbird (*Molothrus bonariensis*)	0.2 ± 0.2	0.0	0.3 ± 0.2	3.69	0.16
Smooth-billed Ani (*Crotophaga ani*)	0.0	0.7 ± 0.5	8.0 ± 6.3	8.08	**0.018**
Thick-billed Vireo (*Vireo crassirostris*)	0.3 ± 0.3	6.4 ± 1.7	2.5 ± 0.8	11.68	**0.003**
Turkey Vulture (*Cathartes aura*)	0.0	3.4 ± 2.4	5.4 ± 1.5	10.20	**0.006**
Western Spindalis (*Spindalis zena*)	7.0 ± 1.7	3.3 ± 1.3	0.3 ± 0.3	11.22	**0.004**
White-crowned Pigeon (*Patagioenas leucocephala*)	5.0 ± 2.5	5.5 ± 4.4	0.3 ± 0.2	4.46	0.11
Zenaida Dove (*Zenaida aurita*)	0.0	1.1 ± 1.1	0.0	1.67	0.44

[a] Non-resident migratory species

[b] Introduced species

Foraging

Foraging behaviors observed in 2007 and 2009, including habitat, perch, horizontal location, behavior, substrate, and food, were compared between SY and ASY adults using Chi-square for categorical data and *t*-tests for continuous data (Table 5.2). Data from 2007 and 2009 were combined due to statistical similarity. For habitat comparisons, categories were collapsed to "anthropogenic habitat" and "not anthropogenic habitat."

Of the foraging behaviors listed in Table 5.2, only habitat in which individuals foraged differed significantly between SY and ASY adults ($\chi^2_1 = 9.095$, $P = 0.003$).

Table 5.2. Comparison of foraging variables between SY and ASY Bahama Oriole adults, with Chi-square and *t*-test results.

Foraging Variable	**SY**	**ASY**	**Test statistic**	***P***	**Effect size**
Habitat					
Residential Palm	$N = 7$	$N = 12$	$\chi^2_1 = 9.10$	**0.003**	$\Phi = 0.58$
Not Residential Palm	$N = 8$	$N = 0$			
Height ($\bar{\chi}$ ± SE)	5.2 ± 0.4	4.9 ± 0.9	$t_{25} = -0.32$	0.75	$d = -0.19$
Horizontal location					
Inner	$N = 3$	$N = 5$			
Middle	$N = 9$	$N = 3$	$\chi^2_2 = 4.04$	0.13	$V = 0.40$
Outer	$N = 2$	$N = 4$			
Substrate					
Air	$N = 1$	$N = 0$			
Berries	$N = 0$	$N = 2$	$\chi^2_3 = 5.48$	0.14	$V = 0.45$
Flowers	$N = 3$	$N = 5$			
Leaves, twigs or bark	$N = 11$	$N = 5$			
Behavior					
Air-gleaning	$N = 1$	$N = 0$			
Hang-gleaning	$N = 1$	$N = 0$	$\chi^2_2 = 1.73$	0.42	$V = 0.25$
Perch-gleaning	$N = 13$	$N = 12$			
Food item					
Berries	$N = 1$	$N = 2$	$\chi^2_1 = 0.68$	0.41	$\Phi = 0.16$
Insects	14	10			

Only habitat type differed between SY and ASY adults.

Although SY adults (N =15) foraged in coppice, pine forest, and anthropogenic habitat, ASY adults (N =12) were only observed foraging in anthropogenic habitat. Those SY adults foraging in anthropogenic habitat were often paired with an ASY adult (six of seven individuals). Both age groups foraged in multiple floras, with no clear preference. Most food was obtained through perch-gleaning (93% of 27 observations), a simple and relatively inexpensive method in terms of energy (Vanderwerf, 1993), on leaves and twigs (60% of 27 observations) in the middle of a branch (46% of 27 observations). Both SY and ASY adults were observed air-gleaning and hang-gleaning, although not all of these observations were included in statistical analysis due to non-independence of data points. Birds were observed eating insects (89% of 27 observations) and berries (11%). Other food items included a Caribbean Hermit Crab (*Coenobita clypeata*), which a SY bird unsuccessfully attempted to ingest, and an endemic Brown Anole (*Norops sagrei*), which was fed to hatchlings. Although orioles foraged among flowers and may have ingested nectar, it is unknown whether their target was the nectar, or insects among the flowers.

Social Interactions

Intraspecific and interspecific interactions were rare, limiting statistical power for some tests (see Table 5.3). Habitat type in which interactions occurred was collapsed to "anthropogenic habitat" or "not anthropogenic habitat" for analysis. Interactions were significantly more likely to occur in anthropogenic habitat for ASY birds, and in other habitats for SY birds ($P = 0.039$; $\chi^2_1 = 4.3$). Older birds were more likely to "win" altercations than SY birds ($P = 0.029$; $\chi^2_1 = 4.8$); habitat type did not affect the outcome of an interaction ($P = 0.14$; $\chi^2_1 = 2.1$). The species that orioles interacted with ($P = 0.74$; $\chi^2_8 = 5.2$) and the height of the interaction ($P = 0.45$; $t_{13} = 0.17$) was similar for SY and ASY birds.

Table 5.3. Frequency of Bahama Oriole intraspecific and interspecific social interactions and their outcomes.

Variable	**SY**	**ASY**	***P***	**χ^2 or *t* (df)**	**Effect size**
Habitat					
Anthropogenic	$N = 1$	$N = 9$			
Coppice	$N = 2$	$N = 1$	**0.039**	2.3 (1)	$V = -0.53$
Pine Forest	$N = 1$	$N = 1$			
Outcome					
Oriole won	$N = 0$	$N = 7$	**0.029**	4.8 (1)	$\Phi = -0.56$
Oriole lost	$N = 4$	$N = 4$			
Species					
Bahama Oriole					
Northern Mockingbird	$N = 1$	$N = 2$			
La Sagra's Flycatcher	$N = 1$	$N = 3$			
Red-legged Thrush	$N = 0$	$N = 1$			
Red-tailed Hawk	$N = 1$	$N = 0$	0.74	5.2 (8)	$V = 0.59$
Shiny Cowbir	$N = 0$	$N = 1$			
House Sparrow	$N = 0$	$N = 1$			
Smooth-billed Ani	$N = 0$	$N = 1$			
Yellow-crowned Night-heron	$N = 0$	$N = 1$			
	$N = 1$	$N = 1$			
Height ($\bar{\chi}$ ± **SE**)	9.2 ± 2.3	8.8 ± 0.9	0.67	0.17 (13)	$d = 0.11$

Intraspecific and interspecific interactions were pooled for analyses; habitat type was collapsed to "anthropogenic" and "not anthropogenic" for analysis.

Intraspecific competitive interactions between orioles were rare. In 2009, at the Atlantic Undersea Test and Evaluation Center (AUTEC), where the highest density of orioles on NA was observed, two pairs of orioles with hatched chicks nested within 200 m of one another. One oriole from each pair engaged in an aerial chase at the presumed territory boundary. No physical contact was made, although the orioles sang from their respective territories for approximately 30 minutes following the encounter. On two other occasions, near the beginning of the nesting season, ASY adult oriole pairs were observed chasing SY adults, sometimes tussling with them to the ground.

Several interspecific interactions were observed. Orioles engaged a LaSagra's Flycatcher, a Smooth-billed Ani, a Red-legged Thrush, and a House Sparrow pair when these birds flew into an oriole nest tree (N = 1 observation per species). All were chased away except for the House Sparrow pair, which shared a nest tree with an oriole pair. When near a nest or fledglings, orioles chased a Shiny Cowbird away (N =1). When foraging on one occasion, the orioles did not interact with nearby cowbirds (N =1). Northern Mockingbirds with a nest nearby chased away Bahama Orioles that strayed too close (N =2).

I observed several cooperative efforts to chase away potential predators. On one occasion, an oriole and three unidentified passerines chased a Red-tailed Hawk from its perch in a Caribbean pine tree. On another occasion, one ASY and two SY orioles lunged at a Yellow-crowned Night Heron, a nest predator (Audubon, 1840), for over an hour. On two occasions, Gray Kingbirds whose territories overlapped with oriole territories chased away Turkey Vultures (*Cathartes aura*).

Discussion

Population Densities and Estimates

Pine forest, coppice, and anthropogenic habitats contained both habitat-specialists and habitat-generalists. As my surveys were conducted during the breeding season for many of the species surveyed, the habitat distributions may not represent a complete picture of the habitats important to long-term survival of both juveniles and adults. The Bahama Oriole appears to be somewhat of a habitat-generalist, but this becomes apparent only when considering both breeding and non-breeding periods. The oriole clearly associates with anthropogenic habitats during the breeding season, as it prefers to nest in the tallest palms available, which are now introduced species (Baltz, 1996, 1997; Price et al., under review). The oriole likely benefits also from other cultivated plants and ready access to adjacent coppice and pine forest foraging grounds. My survey results late in the breeding season, however, suggest that fledglings with their parents move into coppice habitat shortly after departure from nests. I also observed a high number of SY individuals foraging and interacting socially in coppice during the breeding season. Moreover, during winter surveys, Currie et al. (2005) detected the orioles only in coppice and agricultural areas, and did not observe them in pine forest lacking a coppice understory. Thus, these studies illustrate the contrasting needs of these birds for anthropogenic habitat, which is relied on heavily during nesting, and coppice, which appears to be important for fledglings, younger birds, and perhaps birds of all ages outside of the breeding season. Unfortunately, coppice is often cleared by humans for agriculture and residential development, and is currently undergoing rapid decimation on South Andros (Lloyd and Slater, 2010; Thurston, 2010).

A handful of species were significantly more likely to be found in human-disturbed anthropogenic habitat. These included the Cuban Emerald, European Collared Dove, Gray Kingbird, Laughing Gull, Northern Mockingbird, Smooth-billed Ani, and Turkey Vulture. Turkey Vultures, which frequent locations of trash disposal, clearly benefit from human-provided food resources. Other forms of resource subsidies include cultivated fields, imported plants, and fresh water (Faeth et al., 2005). Birds associating with human-disturbed habitats may also be attracted to the open spaces or edges created as land is cleared for development (Hawrot and Niemi, 1996). The frequent occurrence of Laughing Gulls in anthropogenic habitat may be due in large part because of the proximity of anthropogenic areas to coastal habitats. Some species were never observed in agricultural or residential areas, and may be at risk if human disturbance of coppice and pine forest increases. Among the resident species, the Bahama Mockingbird, Bahama Yellowthroat, Greater Antillean Pewee, Greater Antillean Bullfinch, Key West Quail Dove, La Sagra's Flycatcher, Mangrove Cuckoo, Northern Bobwhite, and Pine Warbler were never observed in anthropogenic habitat during this study, or during subsequent observations.

Foraging

Food availability and diet composition of the Bahama Oriole may change throughout the year, as one study found invertebrates to be the most common food delivered to hatchlings of the closely related Cuban Oriole (*Icterus melanopsis*), Hispaniolan Oriole (*Icterus dominicensis*), and Puerto Rican Oriole (*Icterus portoricensis*), while outside of the breeding season orioles were more likely to feed on fruit, flowers, and nectar (Garrido et al., 2005). Insects generally have higher densities in pine forest and coppice habitats, whereas fruit and nectar are more abundant in recently disturbed areas (Currie et al., 2005). I thus expected breeding orioles to forage in pine forest and coppice, whereas non-breeding orioles would forage in anthropogenic habitat with its high abundance of fruit, flowers and nectar.

My breeding season observations of the oriole's diet composition corresponded with previous studies of related orioles, and included fruit, nectar, arthropods, and occasional small vertebrates (Garrido et al., 2005). Contrary to expectations, however, my study found that lone SY orioles foraged only in coppice and pine forest, whereas ASY adults were observed foraging only in anthropogenic habitat. The oriole's proclivity for nesting in coconut palms (Price et al., under review), planted primarily in association with human development, may influence the foraging habits of ASY adults. Interestingly, SY orioles paired with an adult almost always foraged in anthropogenic habitat (six of seven observations). Lone juveniles may be forced out of the most desirable habitat due to despotism (Railsback et al., 2003), whereas juveniles paired with an adult, either for breeding or through delayed dispersal, benefit from association with an established territory.

Social Interactions

ASY orioles were significantly more likely to interact with other individuals in anthropogenic habitat and "win" altercations than were SY orioles. The ASY birds in anthropogenic habitat were often nesting or feeding young, and may have had more motivation to defend territories or offspring than SY individuals. Young birds may also lack the experience to outcompete other birds who challenge them, making it more likely for them to leave an area to avoid more serious altercations.

Intraspecific competitive interactions between orioles were rare on NA, probably due to the low density of the Bahama Oriole population. Competitive interactions between ASY adults were only observed in areas of better palm health and higher oriole density. Aggressive interactions between ASY and SY adults may have involved parents chasing away offspring from a previous brood prior to beginning a new breeding season, or the SY adults may have been young males encroaching on the territories of ASY adults. Long-term studies of individuals marked during their hatch year are needed to elucidate interactions within family groups and recruitment of juveniles.

Conservation Implications

My findings concur with other studies that indicate coppice is vitally important to resident, migrating, and wintering birds, including the critically endangered Bahama Oriole (Raffaele et al., 2003; Lloyd and Slater, 2010). My surveys found the highest number of avian species (35) in coppice, consistent with winter surveys on Andros by Currie et al. (2005) that detected the highest total number of species in coppice and shrubby field habitats (*N* =26–27). Young orioles often foraged in this habitat, and fledglings leaving nests in anthropogenic habitat fledged to coppice (Price et al. under review). As all species interact with one or more other species in food webs via competition, predation, parasitism, or mutualism, future studies should elucidate interactions within these habitats, as conservation efforts are unlikely to succeed unless these complex food web interactions and the ways human activities alter them are understood (Faeth et al., 2005).

Caribbean pine forests on Andros, logged heavily throughout the last century, have returned as homogenous stands with closely-spaced, slender trees (Currie et al., 2005). This has likely decreased species diversity in this habitat, compared with old-stand forests, as in one study even-aged pine forest stands 18–80 years old had the lowest abundance, richness, and diversity of birds, emphasizing the importance of snags, cavity trees, hardwoods, and large down woody material that were largely absent (Thill and Koerth, 2005). Hardwood forests treated to retain or increase large live trees, snags, and coarse woody debris have increased densities of many birds of conservation concern (Twedt and Somershoe, 2009). Given the importance of the wide swaths of Caribbean pine forest to wintering, migratory and permanent resident species, conservation plans should consider treatment of pine forests to increase heterogeneity.

Not all species will decline with human disturbance, and some may even benefit from resource subsidies and increases in open and edge habitats (Werner et al., 2007). For example, the Bahama Oriole uses anthropogenic habitat for breeding and foraging during the breeding season. However, this study also found coppice and pine forest to be important foraging grounds for young birds. The Bahama Oriole requires multiple habitats throughout its life history and will benefit from careful management of coppice, which is currently at high risk of rapid loss due to agricultural development on South Andros (Lloyd and Slater, 2010), and pine forest, which has become homogenized following deforestation.

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CHAPTER SIX

ECOLOGICAL SUBSTITUTION OF THE EXTINCT HAWAIIAN AVIFAUNA: QUANTIFYING THE REPLACEMENT OF LOST SERVICES

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Abstract

The Hawaiian Islands, Earth's most isolated archipelago, developed a diverse and unique biota prior to human arrival. The arrival of the Polynesians and subsequent waves of settlers resulted in high numbers of avian extinctions, leaving ecological voids which may or may not have been filled by other species. Concurrently, a high number of species introductions may have provided ecological equivalents to fill these voids. In this study, I compared the trophic guild composition of the historic Hawaiian avian community with that of the present avian community. I also conducted literature searches for known, specific cases of ecological substitutions for extinct Hawaiian bird species. Avian trophic guild composition has changed significantly since the arrival of Polynesians for all islands except Kauai. On all islands, distribution of birds among guilds has changed; for example, greater than 40% of Hawaii's current avian species are granivorous, vastly outnumbering each of the other trophic groups. Ecological substitutes have been suggested for eleven extinct Hawaiian bird species, in some cases reducing coextinctions of dependent plant species. Although additional cases of ecological substitution can be inferred by examining lists of extinct species and naturalized introductions, very few studies have examined ecological equivalence in Hawaiian communities. Because plant-animal mutualisms are integral to restoring native habitats, we must work to identify successfully naturalized ecological equivalents that are currently benefitting native plant communities.

Introduction

The Hawaiian Islands provide a unique opportunity to study evolution, ecological interactions, and island biology in Earth's most isolated archipelago (Pratt, 1994). This isolation produced a diverse and unique biota which evolved in the absence of many diseases and predators, resulting in enhanced vulnerability to novel threats (Cronk, 1997). Polynesians, and later, Europeans and others, introduced species and diseases that continue to have profound and lasting impacts on the islands' endemics (Tomich, 1986; van Riper et al., 1986). Humans also wrought extreme changes in habitat and vegetation as land was cleared for agriculture and development (Olson and James, 1982; Steadman, 1995). In the few areas where habitats remained intact, extinctions left ecological voids which may or may not have been filled by other species. The results of avian extinctions in the Hawaiian Islands, such as shifts in trophic guild composition and ecological substitution, potentially reveal how ecosystems may react to the loss of species and ecological services.

An ecological niche is the role a species plays in the ecosystem, defined in part by its resources and consumers (Elton, 1927). Ecological services such as pollination, seed dispersal, and nutrient cycling are associated with a species' niche and trophic guild. Frugivores and granivores disperse seeds, and nectarivores pollinate flowers (Loiselle and Blake, 2001). Herbivores maintain plant composition by selective foraging, and thereby drive the evolution of plants (Atkinson and Greenwood, 1989). Insectivores reduce and select insect populations, and like carnivores, may reduce herbivory in the process (Beard et al., 2003). Other ecological services may be indirectly related to trophic category, such as geochemical cycling of nitrogen and phosphorus through deposition of guano by seabirds (Croll et al., 2005), or the enhancement of multi-species foraging by hole-boring birds (Pejchar and Jeffrey, 2004; for a more complete list of ecosystem services provided by birds, see Şekercioğlu et al., 2004).

The loss of species and the ecological services they provide may result in cascading changes to the environment (Croll et al., 2005; Maron et al., 2006). On islands, where biotic communities are often simple rather than complex, and food chains are linear rather than webbed, there may be only a few or no species available to fill a role left by an extinction event (Roemer et al., 2009). Hawaiian bird extinctions removed most native folivores, granivores, frugivores, and predators of terrestrial vertebrates (James, 1990, 1995). These extinctions likely led to coextinctions if dependent species found no surrogate to provide necessary services such as pollination or seed dispersal (Olson and James, 1982, 1984; Chimera and Drake, 2010), a probable outcome with the loss of multiple species within the same genus or family, such as occurred in the Hawaiian Islands (Moir et al., 2010).

Following Hawaii's avian extinctions, remaining or newly introduced species may have altered their behavior, acting as ecological substitutes (Loiselle and Blake, 2001). The almost complete replacement of the native Hawaiian avifauna with non-native generalists provides an opportunity to explore the effectiveness of invasive species as surrogates in seed dispersal and other ecological processes (Pratt et al., 1987). If no suitable substitute was available, coextinction of dependents may have resulted, further reducing biodiversity. Such a loss could also reduce the availability of geochemical resources, as occurred in the Aleutian Islands when introduced foxes reduced the seabird population (Roemer et al., 2009), leading to a 60-fold decrease in guano deposition and transforming the plant community from grassland to maritime tundra (Croll et al., 2005; Maron et al., 2006).

The primary cause of extinctions at the local and metacommunity levels in most areas of the world is habitat alteration (Rosensweig, 2001). In the case of Hawaiian extinctions resulting from these altered habitats, the ecological services provided by extinct species may no longer be required, as the ecological niche formerly occupied by the extinct species may no longer exist (Şekercioğlu et al., 2004).

In this study, I compared the trophic guild composition of the historic Hawaiian avian community with that of the present avian community. Changes in trophic guild composition may indicate differences in ecosystem health (Dobiesz et al., 2010), such as a shift in primary productivity affecting food availability (Reed et al., 2006). I also conducted a literature search for known, specific cases of ecological substitutions for extinct Hawaiian bird species. I evaluated the results in the context of four possible outcomes for the ecological roles of extinct species: (1) introduced species acted as ecological substitutes, (2) endemic birds acted as ecological substitutes, (3) no suitable ecological substitute was available, resulting in coextinction of dependent organism(s), or (4) habitat alteration resulted in the loss of the ecological niche.

Methods

Trophic Guild Composition

Species lists of extant, extinct, and naturalized birds on the six main islands of Southeastern Hawaii (Kauai, Oahu, Molokai, Maui, Lanai, Hawaii) were composed using several sources (Pratt, 2009; Pyle and Pyle, 2009). Trophic guild for each species was identified using Birds of North America Online and Pyle and Pyle (2009) for available species. Related species or genera were used to predict trophic guild if no information was available for a particular Hawaiian species, such as those known only from the fossil record. If a species belonged to multiple guilds, the predominant trophic category was used for analysis.

Historic avian composition was derived by combining extinct and extant endemic bird species, and present day avian composition was derived by combining extant endemic and naturalized bird species. Historic and present day avian guild compositions were compared for each island using Chi-square. I computed Cramer's *V* for effect sizes, which are readily compared among different data sets and different studies. For these, values around 0.3 are deemed moderate and ≥0.5 large (Cohen, 1988). All analyses were performed using SPSS 17.0 (2008), using an alpha level of 0.05. Values are presented as mean ± 1 SE.

Ecological Substitution

Literature searches were conducted with key word searches using online databases, including BioOne, the Searchable Ornithological Research Archive, and Web of Science. Key words included variations of the following: ecological substitute, ecological role replacement, niche replacement, niche partitioning, and ecological analogues. Web of Science was also used to find articles referenced within discovered sources.

Results

Trophic Guild Composition

Avian trophic guild composition, summarized in Table 6.1, has changed significantly since the arrival of Polynesians for all islands except Kauai (Hawaii $P = 0.006$, $\chi^2 = 16.3$; Lanai $P = 0.008$, $\chi^2 = 15.5$; Maui $P = 0.045$, $\chi^2 = 11.3$; Molokai $P = 0.026$, $\chi^2 = 18.6$; Oahu $P = 0.043$, $\chi^2 = 11.5$). The effect size was moderate for Kauai (Cramer's $V = 0.30$), suggesting guild restructuring for this island as well. Some patterns are apparent for all six islands. Greater than 40% of Hawaii's current avian species are granivorous, vastly outnumbering each of the other trophic groups. Of the other trophic groups, only the number of insectivores has increased or held steady on all islands except Maui, where all trophic groups but granivores have been reduced.

Ecological Substitution

Ecological substitutes have been suggested for the ecological roles of eleven extinct Hawaiian bird species (Table 6.2). Japanese White-eye (*Zosterops japonica*), a very successful introduced species, has been proposed as an ecological substitute for the O'u (*Psittirostra psittacea*) and Kona Grosbeak (*Chloridops kona*; Cox, 1983), dispersing seeds of native plants. Moa-nalo, including *Thambetochen xanion* and *Thambetochen chauliodous*, may have been replaced by introduced mammalian herbivores as the primary grazers in their former habitats (Atkinson and Greenwood, 1989). The extinction of aggressive nectarivores, including the Bishop 'O'o (*Moho bishopi*), Black Mamo (*Drepanis funereal*), and Kioea (*Chaetoptila angustipluma*), left the Akohekohe (*Palmeria dolei*) behaviorally dominant (Carothers, 1986), and the primary pollinator of

Table 6.1. Trophic guild composition (*N* species, % of total species) for six Hawaiian islands compared between historic (endemic extant + endemic extinct) and present day (endemic extant + naturalized) avian species.

Guild	Historic *N* (%)	Present Day *N* (%)	χ^2 (df)	*P*	Cramer's V
Hawaii					
Carnivore	5 (16)	5 (9)			
Frugivore	4 (13)	4 (8)			
Granivore	4 (13)	29 (55)	16.3 (5)	0.006	0.44
Herbivore	5 (16)	3 (6)			
Insectivore	8 (26)	10 (19)			
Nectarivore	5 (16)	2 (4)			
Total species	31	53			
Kauai					
Carnivore	6 (19)	7 (14)			
Frugivore	4 (13)	2 (4)			
Granivore	6 (19)	20 (41)	7.3 (5)	0.20	0.30
Herbivore	6 (19)	5 (10)			
Insectivore	6 (19)	12 (25)			
Nectarivore	4 (13)	3 (6)			
Total species	32	49			
Lanai					
Carnivore	3 (27)	3 (13)			
Frugivore	2 (18)	0 (0)			
Granivore	0 (0)	13 (57)	15.5 (5)	0.008	0.68
Herbivore	1 (9)	2 (9)			
Insectivore	3 (27)	5 (22)			
Nectarivore	2 (18)	0 (0)			
Total species	11	23			
Maui					
Carnivore	7 (19)	4 (10)			
Frugivore	3 (8)	2 (5)			
Granivore	6 (17)	22 (52)	11.3 (5)	0.045	0.38
Herbivore	6 (17)	3 (7)			
Insectivore	9 (25)	8 (19)			
Nectarivore	5 (14)	3 (7)			
Total species	36	42			

Table 6.1. *Continued.*

Molokai					
Carnivore	10 (29)	4 (15)			
Frugivore	4 (12)	1 (4)			
Granivore	4 (12)	15 (58)	18.6 (5)	0.002	0.56
Herbivore	6 (18)	1 (4)			
Insectivore	5 (15)	5 (19)			
Nectarivore	5 (15)	0 (0)			
Total species	34	26			
Oahu					
Carnivore	10 (28)	4 (9)			
Frugivore	2 (6)	4 (9)			
Granivore	7 (19)	23 (50)	11.5 (5)	0.043	0.37
Herbivore	5 (14)	3 (7)			
Insectivore	9 (25)	10 (22)			
Nectarivore	3 (8)	2 (4)			
Total species	36	46			

Hawaii, Lanai, and Molokai now have a significantly different avian trophic guild composition than they did prior to the arrival of Polynesian settlers.

some plants. Introduced Ring-necked Pheasant (*Phasianus colchicus*) and Chukar (*Alectoris chukar*) have provided substitutes for several extinct higher elevation granivores (Cole et al., 1995), dispersing seeds. As Po'ouli (*Melamprosops phaesoma*) declined over the last century, the Maui Parrotbill (*Pseudonestor xanthophrys*) provided an ecological substitute (Pratt et al., 2001) reducing insects and dispersing fruit; however, this bird is also critically endangered, and may no longer be a viable long-term ecological replacement.

Table 6.2. Suggested ecological substitutes for extinct Hawaiian species.

Extinct or Declining Species	Ecological Substitute	Ecological Role	Reference
O'u (*Psittirostra psittacea*) Kona Grosbeak (*Chloridops kona*) Elepaio (*Chasiempis sandwichensis*) Iiwi (*Vestiaria coccinea*)	Japanese White-eye (*Zosterops japonica*)	seed dispersal	Cox 1983 Mountainspring and Scott 1985
Moa-nalo (*Thambetochen xanion*) (*Thambetochen chauliodous*)	Introduced mammals	herbivore; plant selection	Atkinson and Greenwood 1989
Bishop 'O'o (*Moho bishopi*) Black Mamo (*Drepanis funereal*) Kioea (*Chaetoptila angustipluma*)	Akohekohe (*Palmeria dolei*)	pollination	Carothers 1986
Great Nene (*Branta hylobadistes*) Moa-nalo (*Ptaiochen pau*)	Ring-necked Pheasant (*Phasianus colchicus*) Chukar (*Alectoris chukar*)	seed dispersal and selection	Cole et al. 1995
Po'ouli (*Melamprosops phaesoma*)	Maui Parrotbill (*Pseudonestor xanthophrys*)	insect reduction and seed dispersal	Pratt et al. 2001
Hawai'i 'O'o (*Moho nobilis*)	I'iwi (*Vestiaria coccinea*)	pollination	Smith et al. 1995

In some cases, endemic species expanded their niche as other species declined, although in other cases, introduced birds provided an ecological equivalent.

Discussion

Although extinctions decrease global biodiversity, local biodiversity may actually increase due to species introduced from other areas of the world (Vitousek et al., 1996).

For example, Hawaii's biodiversity increased with the introduction of new vertebrate groups or additions to existing groups, and now boasts at least 7 amphibians, 29 reptiles, and 20 terrestrial mammal species, where it previously had only one endemic mammal, a bat (Eldredge and Evenhuis, 2003). Consistent with this trend, in this study I found that the total number of resident avian species increased for five of the six islands we examined, despite the high number of extinctions; however, many island endemic species disappeared while introduced species dispersed and flourished on multiple islands, increasing homogeneity of species among islands.

Trophic Guild Composition

Significant changes have occurred in the avian community trophic guild structure since the arrival of humans, as the extinct Hawaiian avifauna has not been replaced by introduced species of equivalent trophic distribution. The number of introduced granivorous species is much higher than the number of extinct endemic granivorous species. This may be simply due to introduction effort (Cassey et al., 2005); more granivorous species may have been introduced than those of other trophic guilds. Anthropogenic food supplementation in the form of seed may also have helped granivores become the most successful guild among naturalized avian species. Another contributor to the success of granivores may be changes in plant community structure, as endemic flowering plant species (*N* = 896) are now outnumbered by naturalized invasive angiosperms (*N* = 1139; Eldredge and Evenhuis, 2003). This doubling of the number of flowering plant species, although not taking into account extinct endemics, indicates that plant community structure has undergone profound changes since human arrival. These changes, combined with other anthropogenic influences such as food supplementation, likely aided the naturalization of introduced birds, especially in lowland areas where most endemic bird species were excluded by introduced diseases, such as avian malaria, by the 1900's (Pratt, 1994).

Ecological Substitution

Introduced Species as Ecological Substitutes

More species of passerine birds have been intentionally introduced to the Hawaiian Islands than to any other place on Earth (Pratt, 1994). Introduced avian species have replaced many endemics in providing ecological services, especially below 1500 meters elevation, where there exists an almost entirely artificial terrestrial avifauna (Pratt, 1994). Introduced Chukars and Ring-necked Pheasants now occupy an ecological role in seed dispersal and selection formerly occupied by extinct or rare species in high-elevation Hawaiian shrubland (Cole et al., 1995). The Japanese White-eye, a very successful introduced generalist, is now the most abundant bird in the Hawaiian Islands, and is found at all elevations and in all habitats (Scott et al., 1986). It competes with, and has replaced in some areas, endemic Elepaio and Iiwi (Mountainspring and Scott, 1985), but is an important pollinator substitute for four species of Ieie (*Freycinetia arborea*; Cox, 1983). Because the extant endemic freshwater birds are all classified as Endangered Species with limited ranges (Pratt, 1994), naturalized resident and wintering water birds such as Pied-billed Grebes and Fulvous Whistling Ducks currently function as the primary avian freshwater herbivores, playing a role in selection and reduction of freshwater plants.

Although introduced species have, in some cases, preserved ecological functions, reducing the risk of cascading extinctions of dependent non-avian species (Brook et al., 2008), this naturalized avifauna is contributing in multiple ways to the further decline of Hawaii's remaining endemic flora and fauna. Introduced birds are resistant to the introduced diseases that exclude most endemic birds from lowland habitats, and provide a reservoir for these diseases, resulting in ongoing infections of endemic populations (Ralph et al., 1998; van Riper et al., 2002). Introduced birds also disperse seeds of non-native plants more often than native plants, promoting turnover of the remaining native flora (Chimera and Drake, 2010).

Non-avian introduced species also acted as substitutes for some extinct birds. The Moa-nalos, a group of large terrestrial herbivorous birds, grazed on the forest understory prior to the arrival of Polynesians (Atkinson and Greenwood, 1989). The grazing of introduced mammals has been suggested as a plausible ecological substitution, although the damage inflicted by ungulates makes them a poor ecological equivalent (Atkinson and Greenwood, 1989). An invasive ant, *Pheidole megacephala*, has reduced insect populations, a service insectivorous birds would have provided previously (Banko and Banko, 1976); however, some have suggested these ants likely also played an indirect, although important role in the reduction and extinction of insectivorous birds by reducing their food supply (Banko and Banko, 1976).

Endemic Birds as Ecological Substitutes

As Hawaii's avian species declined over the last few centuries, profound shifts in avian social structure likely occurred, allowing slight shifts in the ecological niches of remaining endemics. For example, the extinction of the aggressive Kioea (*Chaetoptila* sp.), Bishop's 'O'o (*Moho bishopi*), and Black Mamo (*Drepanis funereal*) left the less competitive 'Akohekohe behaviorally dominant (Perkins, 1903; Carothers, 1986), and the main pollinator for some plant species. The Maui Parrotbill broadened its niche to behaviorally replace the Po'ouli as a pollinator and disperser of seeds, as it declined, nearly to extinction (Pratt et al., 2001). The I'iwi replaced the 'O'o as a nectarivore, and thus a pollinator, on Ohia flowers (Smith et al., 1995). These shifts likely occurred in other endemic species as well, since smaller nectarivores, which were previously dominated by larger nectarivores (Carothers, 1986), were more likely to escape extinction (Boyer, 2008), and now enjoy reduced competition for nectar resources.

Effects Due to a Lack of Suitable Ecological Substitutes

Some ecological services previously provided by extinct Hawaiian birds remain unfulfilled, as there is no suitable ecological substitute. The Akiapolaau, a woodpecker-like keystone species, facilitates sap feeding for other organisms that are otherwise morphologically incapable of exploiting this energy-rich resource (Pejchar and Jeffrey, 2004). As this bird is susceptible to mosquito-borne avian disease below 1500 m elevation, and there is no suitable substitute, this ecological service is no longer provided at lower elevations. Unspecified effects on natural selection of plants and regeneration may have resulted from the extinction of the Moa-nalos, which have no direct ecological equivalent for plant selection (James, 1997). Extirpation of the Akepa (*Loxops coccineus*) and Hawaii Creeper (*Oreomystis mana*) from islands where they formerly occurred has likely resulted in a lack of mixed-species foraging flocks and the protective benefits they provided to members, as these are nucleating species on the islands where they still occur (Hart and Freed, 2003).

Coextinctions of non-avian species dependent on birds that became extinct were likely compounded by the loss of multiple species within the same family or genus, lessening the likelihood of a suitable surrogate (Moir et al., 2010). Following the loss of avian pollinators, 31 species of Campanulaceae plants became extinct in the last century (Cox and Elmqvist, 2000). The extinction of larger native avian frugivores resulted in dispersal failure of large-seeded native plants and, combined with high dispersal of non-native, smaller seeds by non-native birds, is resulting in forest homogenization, further endangering the remaining endemics (Chimera and Drake, 2010). Alarmingly, 50% of the remaining endemic plant species are at risk of extinction (Sakai et al., 2002). Extant plants with conspicuous flowers may be at risk of coextinction because of the continuing disappearance of specialist native birds that aid in the pollination of native plant species (Olson and James, 1982, 1984). Dry forest species with fleshy fruits also continue to be negatively impacted by the extinction and endangerment of endemic avian frugivores, most of which have no ecological substitute (Pau et al, 2009).

Habitat Alteration and the Loss of Ecological Niches

Species of birds restricted entirely to extinct or endangered habitats declined largely due to habitat loss, and the ecological niches they filled may not exist today. Most of Hawaii's habitats have been altered from what they were before the arrival of the Polynesians and Europeans. More than 75% of the recognized types of plant communities remaining in the coastal, lowland, and montane communities, and all of those in the subalpine zone are considered rare because of past disturbance and current vulnerability (Cuddihy and Stone, 1990). Most trees common before human arrival are now rare, restricted, or extinct, and many endemic plant species not found together today were previously juxtaposed (Burney et al., 2001). Early botanical surveys revealed that the drier lowland regions of the Hawaiian Islands once supported distinctive forest vegetation with many endemic species of plants that no longer exist (Olson and James, 1982).

Future Work

Because plant-animal mutualisms are integral to restoring native habitats (Kaiser-Bunbury et al., 2010), we must work to identify successfully naturalized ecological equivalents that are currently benefitting native plant communities. Conservation of endangered plant communities is currently hindered by a limited knowledge of germination factors (Perez et al., 2008), many of which may require processes previously provided by now-extinct birds. A recent study showed the importance of burial of seeds, removal of endocarp or operculum, and incubation at high temperatures for germinating seeds of some native plants (Perez et al., 2008), perhaps previously accomplished by frugivorous endemics. Introduced species may currently provide the only dispersal mechanisms for these and other native plants at lower elevations, where most endemic birds are excluded by disease (Foster and Robinson, 2007).

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CHAPTER SEVEN

DISSERTATION CONCLUSIONS AND MANAGEMENT PLAN

Having lost access to 88.7% of their primary vegetation, the Caribbean's 148 remaining endemic bird species need careful planning and management if they are to continue providing crucial services such as seed dispersal, decomposition, and pollination to the ecosystems they are a part of (Şekercioğlu et al., 2004). Supporting 2.3% of the world's endemic plants and 2.9% of the world's endemic vertebrates in a proportionately small area (Şekercioğlu et al., 2004), management decisions in the Caribbean have important ramifications for global biodiversity. While the focus of conservation should rest on the protection of whole ecosystems, rather than piecemeal strategies for separate species (Myers et al., 2000), comprehensive species-focused studies such as the ones contained in this dissertation must inform habitat management decisions.

Elevation to full species status has brought much-needed attention to the Bahama Oriole both locally, such as through the Bahamas National Trust, and globally, through Bird Life International. Based on the studies contained in this dissertation, I have outlined a management plan toward preventing the extinction of this critically endangered bird.

Translocation: A Prevention Measure

Translocation of individuals to other areas can increase the species' effective population size and decrease the probability of extinction through stochastic effects (e.g., hurricanes; Fleischer, 2007). The subpopulation on Mangrove Cay and South Andros is roughly half the size of the North Andros population, but has a higher population density. If genetic variation is minimal and structure lacking, birds can be captured from areas of greatest density to decrease negative impacts on breeding selection in the remaining individuals. If, however, significant genetic structure exists, birds having each available haplotype can be selected to provide the greatest genetic variation in the translocated population. Based on the multiple haplotypes distributed throughout the oriole's range, our study suggests translocation of Bahama Orioles from Andros to Abaco Island, where they formerly occurred, should include individuals from North Andros, Mangrove Cay, and South Andros to maintain genetic diversity in the translocated population.

Population Surveys

Several areas of Andros may contain breeding orioles, and should be surveyed to update population estimates. Big Wood Cay, located between North Andros and Mangrove Cay, has suitable palm habitat. Brief surveys conducted in 2010 did not reveal orioles, but further searches are needed. Several pairs have been observed on the west coast of North Andros, but only in areas with human development. Surveys of thatch palms on the west coast, away from human development, may reveal additional breeding pairs.

The Shiny Cowbird and Lethal Yellowing Disease

In spite of its spread, the Shiny Cowbird does not appear to be increasing in numbers on Andros Island. Continued monitoring of the parasitism rate of oriole nests, and correlations with oriole reproductive success, is necessary before more expensive and time-intensive actions, such as trapping and removal, are implemented.

Lethal yellowing appears to be confined to North Andros. Disease resistant cultivars of coconut palm should be planted as replacements for trees lost to lethal yellowing on North Andros. Although inoculation has proved effective in areas where it has been implemented, this is an expensive process, and impractical for most residential purposes. Continued monitoring of palms on Mangrove Cay and South Andros is necessary, and all palms imported to the islands should be screened for disease.

Habitat Management

Caribbean pine forests on Andros, logged heavily throughout the last century, have returned as homogenous stands with closely-spaced, slender trees (Currie et al., 2005). This has likely decreased species diversity in this habitat, compared with old-stand forests. Hardwood forests treated to retain or increase large live trees, snags, and coarse woody debris have increased densities of many birds of conservation concern (Twedt and Somershoe, 2009). Given the importance of the wide swaths of Caribbean pine forest to wintering, migratory and permanent resident species, conservation plans should consider treatment of pine forests to increase heterogeneity.

Coppice is vitally important to resident, migrating, and wintering birds, including the critically endangered Bahama Oriole (Raffaele et al., 2003, Lloyd and Slater, 2010). My surveys found the highest number of avian species (35) in coppice, consistent with winter surveys on Andros by Currie et al. (2005) that detected the highest total number of species in coppice and shrubby field habitats (N = 26–27). Young orioles often foraged in this habitat, and fledglings leaving nests in anthropogenic habitat fledged to coppice. The Bahama Oriole requires multiple habitats throughout its life history and will benefit from careful management of coppice, which is currently at high risk of rapid loss due to agricultural development on South Andros (Lloyd and Slater, 2010), and pine forest, which has become homogenized following deforestation.

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