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Vocalization Behavior of the Endangered Bahama Oriole (Icterus northropi): Ontogenetic, Sexual, Temporal, Duetting Pair, and Geographic Variation

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

Vocalization Behavior of the Endangered Bahama Oriole (*Icterus northropi*): Ontogenetic, Sexual, Temporal, Duetting Pair, and Geographic Variation

by

Valerie A. Lee

A Thesis submitted in partial satisfaction of
the requirements for the degree of
Master of Science in Biology

March 2011

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

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ABBREVIATIONS

ANOVA	Analyses of variance
ASY	After-second-year bird or adult
DFA	Discriminant function analyses
Hz	Hertz, frequency
IUCN	International Union for Conservation of Nature
MC	Mangrove Cay
NA	North Andros
SA	South Andros
Sec	Seconds
SPCC	Spectrographic Cross-correlation
SY	Second-year bird or juvenile

ABSTRACT OF THE THESIS

Vocalization Behavior of the Endangered Bahama Oriole (*Icterus northropi*): Ontogenetic, Sexual, Temporal, Duetting Pair, and Geographic Variation

by

Valerie A. Lee

Master of Science, Graduate Program in Biology

Loma Linda University, March 2011

Dr. William K. Hayes, Chairperson

Many birds communicate via a diverse set of vocalizations, but the contexts, roles, and structure of their varied songs and calls may change with age, differ between sexes, and vary temporally and geographically. In New World orioles, most tropical species exhibit the ancestral states of sexual monochromatism (both sexes have similar plumage) and monovocalism (both sexes sing and often duet together), whereas migratory temperate species tend toward dichromatism (males brightly colored and females drab) and divocalism (males sing almost exclusively). In this study, I examined the vocalizations of the Bahama Oriole, a non-migratory, monochromatic species, to learn where it fits within this generalized dichotomy; to document sources of variation in vocalization rates and spectrographic structure; and to improve survey design for this critically endangered species. Accordingly, this study describes the primary vocalizations of the Bahama Oriole, and examines how vocalizations vary with age, between sexes, at different times of day, during the breeding season, and among the three remaining island metapopulations on Andros, The Bahamas.

Hatchlings and fledglings produced vocalizations that were higher pitched than those of adults. Adults possessed a large repertoire, including five main vocalization types that were delivered independently or in combination. Second-year and after-second-year-plumaged adults produced spectrographically similar vocalizations at similar rates. Although adult males and females could not be reliably distinguished in the field, both individuals of pairs were often heard giving the full range of vocalizations and frequently duetted together, particularly during the pre-incubation period. Antiphonal duets involved mated pairs, were limited to songs and whistle calls, and exhibited similar within-individual and between-individual variation in the spectrographic and temporal features of duets. Thus, the Bahama Oriole more closely resembles tropical oriole species (monovocal) than temperate species (divocal) in its vocalization behaviors. Adults vocalized at similar rates throughout the day prior to incubation, suggesting that surveys can be conducted at virtually any time of day during this period. Singing and most call types waned after chicks hatched, but whines increased dramatically as adults engaged in caring for their offspring. Minor but significant clinal variation in singing existed among the three metapopulations, suggesting possible cultural drift.

CHAPTER ONE

GENERAL INTRODUCTION

The study of bird vocalizations can broadly inform our understanding of evolution, ecology, behavior, and conservation. Bird song serves many purposes, including species and individual recognition, mate attraction and pair bonding, territory establishment, aggression, alarm, and spacing (Langmore 1998, Marler and Slabbekoorn 2004, Rogers et al. 2006, Topp and Mennill 2007, Hall and Peters 2008). Many birds communicate via a diverse set of vocalizations, but the contexts, roles, and structure of their songs and calls may change with age, differ between the sexes, and vary temporally and geographically.

New World orioles (genus *Icterus*) represent an excellent group to evaluate variation in vocalizations. The molecular phylogeny of this species-rich group is well understood (Omland et al. 1999, Sturge et al. 2009). From this phylogeny, reconstruction of the evolution of plumage and song suggests that both traits are highly labile, with repeated convergence in individual elements and in overall patterns across the clade (Price et al. 2007). Both monochromatic and dichromatic species occur in this group (Hofmann et al. 2008a,b, Friedman et al. 2009), and sexual differences in singing are well documented among species, suggesting that varying levels of sexual and natural selection have contributed to the structure and roles of vocalizations in this group (Price et al. 2007, 2009).

Ontogeny of Vocalizations

Song development has both innate and learned properties (Slater 2003), as many species learn to vocalize at an early age from their parents and neighbors, developing dialects and personal signatures (Nowicki and Searcy 2005). Unfortunately, there is limited information on the extent to which genes, environment, or both affect song development in orioles (Rising and Flood 1998, Rising and Williams 1999, Pleasants and Albano 2001, Flood 2002, Flood et al. 2002, Brush and Pleasants 2005, Scharf and Kren 2010). Many song characters are relatively invariant within oriole taxa compared to between taxa, suggesting a strong genetic component (Price et al. 2007). However, learning may still be important to song development. Songs of hybrid Baltimore (*Icterus galbula*) and Bullock's Orioles (*I. bullockii*) in Colorado, for example, are not intermediate, but strongly resemble those of the Baltimore Oriole, suggesting they were learned from a (Baltimore) parent rather than genetically encoded (Edinger 1985). Portions of the songs of second-year (SY) Orchard Oriole (*I. spurius*) males differ from those of after-second-year (ASY) males (Scharf and Kren 2010), further suggesting a learning component to oriole song development.

There is little early life history information available for most North American orioles. Information regarding the behavior and vocalizations of hatchlings, for example, is difficult to obtain due to the relative inaccessibility of oriole nests, which are tightly woven, pendulous, basket-like structures made of grass and twigs, and generally suspended from the smaller branches high in trees (Rising and Williams 1999, Pleasants and Albano 2001, Flood 2002, Flood et al. 2002, Brush and Pleasants 2005, Scharf and Kren 2010). The most detailed information on the vocalizations of young is from the

Baltimore Oriole (Rising and Flood 1998). Young are relatively quiet during the first week in the nest and vocalizations become louder as the hatchlings age. During the second week, they can be heard when parents approach the nest. Their calls have been described variously as teé-dee-dee, teé-dee-dee, or dee-dee-dee-dee, dee-dee-dee-dee (Bent 1958, Baumgartner and Baumgartner 1992). Just before fledging, young vocalize regularly, even between feeding visits by parents. After leaving the nest, fledglings are very noisy, uttering he-he-häe or heck-heck-he calls interspersed with low twittering (Bendire 1895). Nestlings of the Altamira Oriole (*I. gularis*), by comparison, were described as producing low-pitched begging calls (Brush and Pleasants 2005).

Oriole nests are frequently victimized by cowbirds, which are avian host parasites. Even less than orioles is known about the behavior and vocalizations of cowbird hatchlings and fledglings (Lowther 1993, Lowther and Post 1999, Ellison and Lowther 2009). In most oriole species, young fledge about two weeks after hatching, usually at the same time or within a two- or three-day window (Rising and Flood 1998, Rising and Williams 1999, Pleasants and Albano 2001, Flood 2002, Flood et al. 2002, Brush and Pleasants 2005, Scharf and Kren 2010). Cowbird young presumably fledge at the same time as the oriole young. Bronzed Cowbirds (*Molothrus aeneus*), Brown-headed Cowbirds *(Molothrus ater)*, and Shiny Cowbirds (*Molothrus bonariensis*), fledge at 10–12 8–13, and 12–15 days, respectively (Lowther 1993, Lowther and Post 1999, Ellison and Lowther 2009).

Sexual Differences in Vocalizations

Among songbirds, males have traditionally been viewed as the only sex that sings. Although female song is rare in temperate migratory songbirds and typically less complex than male song, females of many tropical non-migratory species are now known to sing complex songs (e.g., Kellner and Ritchison 1988, Gilbert and Carroll 1999, Ogden et al. 2003, Pavlova et al. 2007), often duetting with and sometimes even singing more frequently than males (Morton 1996, Price et al. 2008). This geographic difference (temporal versus tropics) is apparent in orioles (Price et al. 2008). Phylogenetic reconstruction of female song in New World blackbirds (*Icteridae*) suggests that male-biased song production does not result from sexual selection for complex song in males, but from selection against such songs in females (Price et al. 2009). One study suggests that female song may be the rule rather than the exception in tropical environments (Price et al. 2008). This may relate to the fact that temperate species are often dichromatic, whereas tropical species tend to be weakly dichromatic or monochromatic (Brush and Pleasants 2005). In these tropical environments, evidence suggests that females sing primarily for the same reasons as males do in temperate species (Langmore 1998, 2000, Hall 2004).

A similar reconstruction of plumage suggests that losses in female color, not elaboration of male color, has promoted the evolution of dichromatism in orioles (Hofmann et al. 2008a, Friedman et al. 2009). Thus, the traditional explanation for the evolution of sexual dimorphism, that sexual selection leads to increased male elaboration and natural selection opposes this elaboration in females (Darwin 1871, Andersson 1994), may need broad reexamination.

Temporal Variation in Vocalizations

Seasonal variation of vocalizations occurs in birds. In many songbirds, the function of male song differs upon whether or not it is sung within the context of breeding. For some species, song during the breeding season helps with mate attraction and territorial defense. (e.g., Catchpole 1973, Eens, et al. 1994, Catchpole and Slater 1995). Many birds sing little, if at all, outside the breeding season (Ball 1999).

Seasonal variation of song occurs in many oriole species, with males producing song during the breeding season in some species (Brush and Pleasants 2005), and some birds singing in all seasons though less during cold weather (Rising and Flood 1998, Flood and Brush 2002). Females of Bullock's Orioles sing early in the nesting period and before and during nest-building, possibly even singing more than males during these time periods (Miller 1931).

Not much is known about the daily time budget of most New World oriole species (Pleasants and Albano 2001, Flood et al. 2002, Brush and Pleasants 2005). Males of the Baltimore Oriole sing throughout the day, but song frequency is highest in the morning (Rising and Flood 1998). Scott's Oriole males (*I. parisorum*) reportedly sing throughout the day, even during the hottest midday period (Flood 2002). In terms of activity, Bullock's Orioles are most active in morning and evening (Rising and Williams 1999), and Orchard Orioles forage from dawn until noon (Scharf and Kren 2010).

Because population surveys often rely on detection via vocalizations, knowledge about temporal variation in singing can be useful for designing optimal survey strategies. The timing of surveys should, ideally, coincide with seasonal and daily periods of peak singing.

Geographic Variation

Clarifying geographic variation in birds is important for defining species limits. Bird songs and calls reflect population differences, and variation can promote speciation through the formation of isolating barriers to gene flow (Slabbekoorn and Smith 2002, Alstrom and Ranft 2003, Seddon 2005, Grant and Grant 2006, Brambilla et al. 2008). This idea is especially evident in Darwin’s finches, 14 species of which occur on the Galapagos Archipelago. Some of these species vary vocally while others vary morphologically in beak size (Grant and Grant 2006). Although not common, geographic variation does occur within several species of New World orioles. Differences between populations of Audubon’s Oriole in Texas and Mexico, for example, were described by Flood (1990). Determining geographic variation in small populations is important in maintaining maximum diversity.

Duetting

Although males sing primarily or exclusively in many north temperate bird species, there are many species in other parts of the world in which both sexes sing (Catchpole and Slater 1995, Hall 2009). Sometimes, paired birds coordinate their songs by overlapping or alternating notes to produce joint acoustic displays called duets (Farabaugh 1982, Langmore 1998). Duetting species are phylogenetically diverse, and their duets vary in temporal precision, complexity, and degree of sex specificity (Wickler and Seibt 1982, Hall 2000).

The purpose of duets between bird pairs remains controversial. Theories suggest birds duet because of sexual conflict over mating (Rogers et al. 2006), cooperative displays functioning in joint territory defense and/or coordination of breeding activities (Topp and Mennill 2007, Hall and Peters 2008), or a combination of these and other hypotheses (Langmore 1998). Duets have been linked to pair bonding in several species of New World orioles, including the Audubon's Oriole (*I. graduacauda*), Baltimore Oriole, and Scott's Oriole (Rising and Flood 1998, Flood 2002, Flood et al. 2002).

Conservation Relevance

Recent elevation of the Bahama Oriole (*I. northropi*; see Fig. 1-1) to species status (Chesser et. al 2010) has dramatically elevated its conservation status (Hayes 2006, Price and Hayes 2009). Prior to 2010, oriole populations in the Bahamas (*I. northropi*), Cuba (*I. melanopsis*), Hispaniola (*I. dominicensis*), and Puerto Rico (*I. portoricensis*) were regarded as subspecies within a single species, the Greater Antillean Oriole (*I. dominicensis*; Jaramillo and Burke 1999). Substantial genetic separation (Omland et al. 1999), diagnosable plumage differences (Omland et al. 1999, Price and Hayes 2009), and other attributes, including vocalizations (Garrido et al. 2005), supported the elevation of each population to allospecies. The Bahama Oriole is the most endangered of these taxa, and has suffered recent range contraction. The population on Abaco became extirpated in the early 1990s (White 1998), so the only remaining populations are now confined solely to Andros. Baltz (1997) estimated that only 150-300 individuals remain, with most of the population concentrated among the residential areas on the eastern coast. More recent surveys estimated 90-162, 24-44, and 27-48 individuals remaining on North Andros, Mangrove Cay, and South Andros, respectively (Price et al. under review). Thus, the Bahama Oriole is one of the rarest bird species in the world.

Island taxa are particularly vulnerable to extinction. Their relatively small distributions and population sizes render them more vulnerable to disturbance and stochastic processes (Şekercioğlu et al. 2004, Blackburn et al. 2008, Karels et al. 2008, Trevino et al. 2008, Boyer 2010). Eruptions of the Soufriere Hills volcano in Montserrat, for example, destroyed more than half of the Montserrat Oriole's (*I. oberi*) range (Hilton et al. 2003). It is a paradigm of conservation biology that species with the smallest ranges are most vulnerable to the occurrence of rare catastrophic events (Caughley and Gunn 1995).

The Bahama Oriole is threatened by the recent arrival of a pernicious brood parasite, the Shiny Cowbird (*M. bonariensis*; Baltz 1995), and continuing devastation of its favored nesting habitat, Coconut Palm (*Cocos nucifera*), by lethal yellowing disease (Curie et al. 2005, pers. obs., Price et al. under review). Clearly, we need a better understanding of the bird's natural history if we are to develop adequate management plans for saving the species from extinction.

Objectives and Significance of Study

The general objective of this thesis is to characterize the range of vocalizations of the Bahama Oriole and the behaviors associated with them. Other than the song, little is known about the vocalizations of the Bahama Oriole. White (1998) stated that the song is a rising whistle followed by two quick notes, with the triad repeated and the song then ending with a whistle. Referring to Maynard (1915), White described the triad as *Poor Willy*, with the complete song being *Poor Willy, poor Willy, poor.*" Jaramillo and Burke (1999) described the song as eight or nine sweet whistles. Garrido et al. (2005) showed

Figure 1-1. An adult Bahama Oriole, *Icterus northropi* (photo courtesy of Stephen J. Myers, 2009).

that the vocalizations of the allopatric populations of Greater Antillean Orioles differed to a greater extant than their morphology. They found little within-population variation in song among the island forms, and the two subspecies most similar in morphology (Cuban Oriole and Hispaniolan Oriole; Jamarillo and Burke 1999, Omland and Lanyon 2000*)* differed the most in vocalizations. Bahama oriole songs (recorded from North Andros) showed the greatest frequency range of this oriole group, with lowest and highest frequencies averaging 1951 Hz (range 1225–1942) and 5467 Hz (range 4541-5745). Their songs also had a mean duration of 2.4 sec (range 1.2–2.9) and an average of 9 (range of 6–11) emphatic whistled elements.

More specifically, I seek to accomplish the following objectives in this thesis. First, I characterize the vocal repertoire of the species, including the vocalizations of nestlings through adulthood, and the duetting of adults. Second, I examine age-related, temporal, and geographic variation in the rates of production of each of the major vocalization types. Third, I compare the structure of songs between the two age classes of adults, and among the three different island populations. Fourth, I compare within-individual, within-pair, and between-pair variation in the duetting vocalizations of adults. Finally, although the species is monochromatic (Garrido et al. 2005) and sexes cannot be distinguished in the field, I infer the similarity of vocalizations between sexes based on several lines of reasoning.

To accomplish these objectives, Chapter 2 describes the different vocalizations of young and adult orioles, and the factors that contribute to variation in vocalization rates and spectrographic structure. Chapter 3 focuses exclusively on the duetting vocalizations of male-female pairs.

My findings shed light on the extent of song learning and sexual divocalism in this sexually monochromatic taxon. The results also add to our understanding of the evolution and ontogenetic development of vocalizations within orioles, and they provide insights on the functions of vocalizations in the different age and sex classes. These results can be used to improve the design of survey protocols. Finally, this study provides much-needed basic natural history information that can help inform development of a management plan for this endangered species.

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CHAPTER TWO

VOCALIZATION BEHAVIOR OF THE CRITICALLY ENDANGERED BAHAMA ORIOLE (*ICTERUS NORTHROPI*): ONTOGENETIC, SEXUAL, TEMPORAL, AND GEOGRAPHIC VARIATION

Valerie A. Lee, Melissa R. Price, and William K. Hayes

Abstract

Many birds communicate via a diverse set of vocalizations, but the contexts, roles, and structure of their varied songs and calls may change with age, differ between sexes, and vary temporally and geographically. In New World orioles, most tropical species exhibit the ancestral states of sexual monochromatism (both sexes have similar plumage) and monovocalism (both sexes sing and often duet together), whereas migratory temperate species tend toward dichromatism (males brightly colored and females drab) and divocalism (males sing almost exclusively). In this study, we examined the vocalizations of the Bahama Oriole, a non-migratory, monochromatic species, to learn where it fits within this generalized dichotomy; to document sources of variation in vocalization rates and spectrographic structure; and to improve survey design for this critically endangered species. Hatchlings and fledglings produced vocalizations that were higher pitched than those of adults. Adults possessed a large repertoire, including five main vocalization types that were delivered independently or in combination. Second-year and after-second-year-plumaged adults produced spectrographically similar vocalizations at similar rates. Although adult males and females could not be reliably distinguished in the field, both individuals of pairs were often heard giving the full range of vocalizations and frequently duetted together, particularly during the pre-incubation period. This finding suggests that the Bahama Oriole more closely resembles tropical oriole species (monovocal) than temperate species (divocal) in its vocalization behaviors. Adults vocalized at similar rates throughout the day prior to incubation, suggesting that surveys can be conducted at virtually any time of day during this period. Singing and most call types waned after chicks hatched, but whines increased dramatically as adults engaged in caring for their offspring. Minor but significant clinal variation in singing existed among the three metapopulations, suggesting possible cultural drift.

Introduction

The study of bird vocalizations can broadly inform our understanding of evolution, ecology, behavior, and conservation. Bird song serves many purposes, including species and individual recognition, mate attraction and pair bonding, territory establishment, aggression, alarm, and spacing (Langmore 1998, Marler and Slabbekoorn 2004, Rogers et al. 2006, Topp and Mennill 2007, Hall and Peters 2008).

Many birds communicate via a diverse set of vocalizations, but the contexts, roles, and structure of their varied songs and calls may change with age, differ between sexes, and vary temporally and geographically. Song development has both innate and learned properties (Slater 2003), as many species learn to vocalize at an early age from their parents and neighbors, developing dialects and personal signatures that can change with age (White and Mooney 1999, Nowicki and Searcy 2005). Adults generally sing most frequently during the breeding season, when song plays a critical role in mate attraction and territorial defense (e.g., Catchpole 1973, Eens et al. 1994, Catchpole and Slater 1995, Ball 1999). Rates of song production typically vary during different stages of the breeding cycle (Catchpole and Slater 1995), and may reflect the different roles of vocalizations in males and females (Topp and Mennill 2008). Song output generally peaks during the dawn chorus (Catchpole and Slater 1995), but daily vocalization patterns can vary during the reproductive cycle (Amrhein et al. 2004). Geographic variation in vocalizations can arise through either natural selection (e.g., via habitat structure or as a byproduct of morphological adaptation; Morton 1975, Ryan and Brenowitz 1985, Slabbekoorn and Smith 2002, Seddon 2005) or by founder effects and drift (e.g., via culture; Podos and Warren 2007). Geographic variation can also promote speciation through the formation of isolating barriers to gene flow (Slabbekoorn and Smith 2002, Alstrom and Ranft 2003, Seddon 2005, Grant and Grant 2006, Brambilla et al. 2008).

Because of a well-established phylogeny for orioles (genus *Icterus*; Omland et al. 1999), historical reconstructions of character states have shed surprising light on the influence of natural and sexual selection on the evolution of complex phenotypic characters in this New World group. Most tropical species, for example, exhibit the ancestral states of sexual monochromatism (both sexes have similar plumage) and monovocalism (both sexes sing and often duet together), whereas migratory temperate species tend toward dichromatism (males brightly colored and females drab) and divocalism (males sing almost exclusively; Price et al. 2007, 2008, 2009, Friedman et al. 2009). This unexpected pattern suggests that dichromatism and divocalism in this group originated from natural selection favoring duller coloration and reduced vocalizations by females, rather than sexual selection favoring bright plumage and song in males. Similar character state reconstructions are needed to further refine our understanding of the factors that shape complex phenotypic characters such as bird vocalizations. These analyses, however, require detailed information from a broad range of species, including those that have received relatively little attention.

Other than the song (Maynard 1915, White 1998, Jamamillo and Burke 1999, Garrido et al. 2005), little is known about the vocalizations of the Bahama Oriole (*Icterus northropi*). Recent elevation of this taxon to species status (Chesser et. al. 2010) reflects the general neglect of this taxon by researchers, and has dramatically elevated its conservation status (Hayes 2006, Price and Hayes 2009). Recent surveys estimated fewer than 300 individuals remaining on the three major islands known collectively as Andros in the Bahamas (Price et al. under review), prompting Birdlife International to recognize it as a critically endangered species. Although sister species in the Greater Antilles may nest throughout the year (Garrido et al. 2005), the Bahama Oriole appears to have a well-defined breeding season (Price et al. under review) more typical of temperate species. Adults are monochromatic (Garrido et al. 2005), but it remains unknown whether both sexes sing similarly or frequently.

Our primary objectives in this study were: 1) to characterize the vocal repertoire of the Bahama Oriole, including the vocalizations of nestlings, fledglings, and two adult age classes; 2) to examine age-related, sexual, temporal, and geographic variation in the production rates of each major adult vocalization type; and 3) to compare the spectrographic structure of songs between the two age classes of adults and among the three island metapopulations. We predicted that, like other oriole species, the Bahama Oriole would have a rich repertoire of vocalizations. Because the species is monochromatic, we also predicted that it would exhibit behaviors more typical of "tropical" oriole species, with females singing frequently and even duetting with males (i.e, monovocalism). A better understanding of this bird's vocal repertoire and behavior can advance our understanding of the evolution and development of song, improve our ability to conduct surveys and monitor populations, and supplement the body of natural history knowledge that is required for developing a sound management plan.

Methods

Study Area

The study encompassed the three major islands collectively referred to as Andros, The Bahamas: North Andros (NA, 3600 km^2), Mangrove Cay (MC, 200 km^2), and South Andros (SA, 800 km^2; Fig. 2-1). These islands, separated by relatively narrow channels approximately 1-5 km wide, are dominated on the eastern portion by extensive Caribbean Pine (*Pinus caribaea*) forest interspersed with patches of coppice. Mangrove, associated with vast tidal wetlands and accessible only by boat, dominates the western half of the islands. Because the orioles are largely absent from the pine forests and mangroves, we focused our work in the vicinity of townships scattered along a single highway running north to south along the east coast of each island. Orioles are concentrated in these townships, where they preferentially nest in the tallest palm trees available—usually

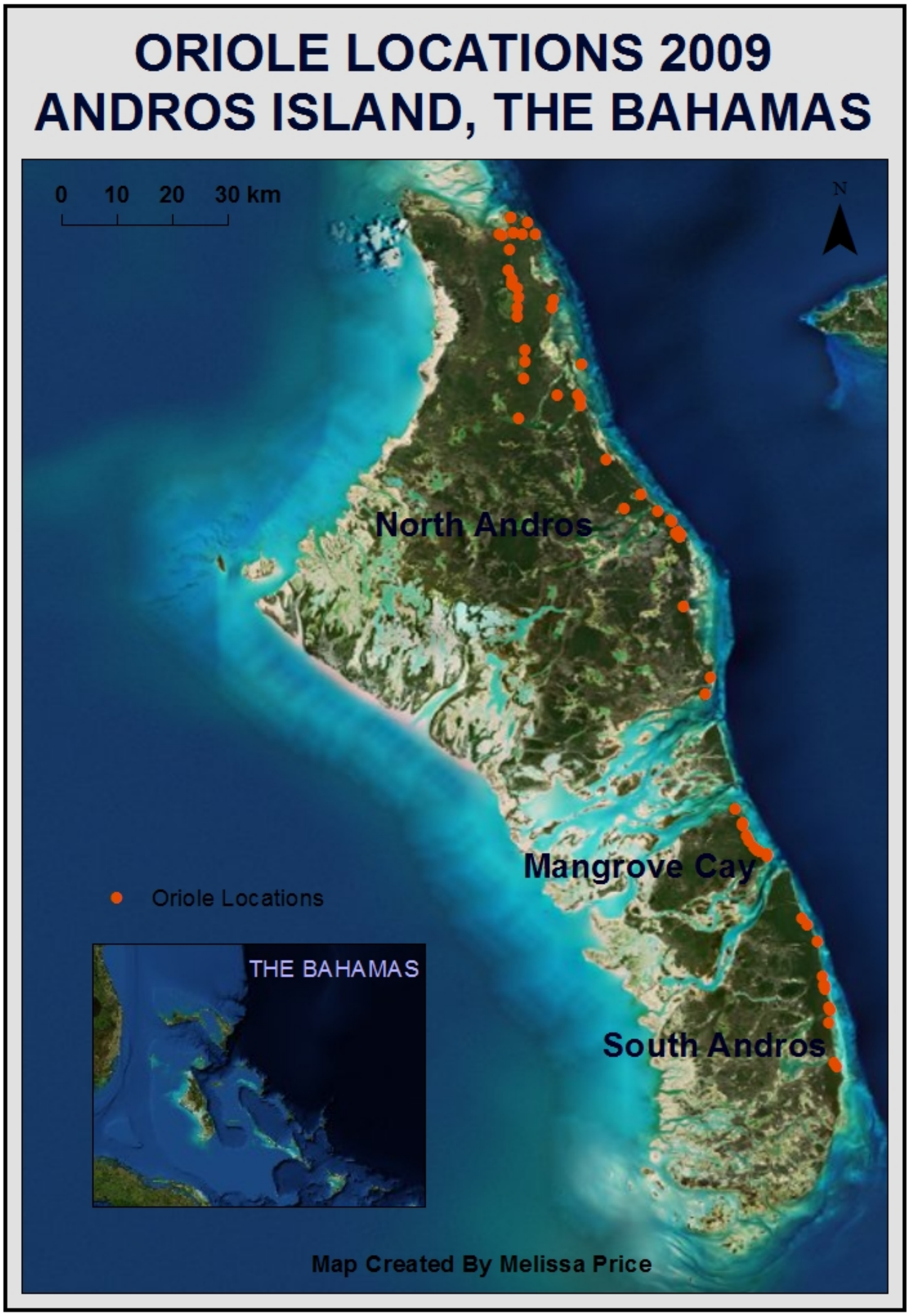

Figure 2-1. Map of the study area, Andros Island, the Bahamas.

introduced Coconut Palm (*Cocos nucifera*; Baltz 1997, Price et al. under review). Agricultural plots and imported ornamental and fruit trees further entice orioles and other birds to the townships (Baltz 1993; 1997).

Field Work

We recorded vocalizations and conducted ethological observations during the early breeding season of 2009 on SA (28 hr, 30 March–1 April), MC (14 hr, 2–3 April), and NA (336 hr, 4 April–4 June). We procured recordings at 48 kHz using an Audio-Technica AT815b Shotgun Microphone (Audio-Technica Corp., Tokyo, Japan) and a Marantz PMD660 Portable Solid State Recorder (Marantz, Kanagawa, Japan). We used time sampling to study individual birds and pairs at different times of the day and on multiple days spanning the reproductive cycle. Recording generally began as birds were heard and ended when they stopped vocalizing or flew away. Data on the time, location, habitat, and behaviors associated with vocalizing were recorded, along with age of the bird based on plumage (see below), and any intra- or interspecific interactions. Nest sounds were recorded up to 35 min while the parents fed hatchlings or fledglings. We obtained a total of 272 sound files ranging from a few seconds up to 35 min in duration. Of these, 175 were of suitable quality for analysis.

We distinguished two age classes of adults: those in juvenal, or second-year (SY) plumage, and those in full adult, or after-second-year (ASY) plumage (Jaramillo and Burke, 1999). Most SY birds represented by recordings were paired with either an ASY or another SY individual at an active nest, and therefore were breeding adults. Because the species is sexually monochromatic (Garrido et al. 2005), at least with respect to human vision (see Eaton 2005), we captured birds by mist net during the first 6 weeks of the study to place color leg bands for field identification and to collect blood and feather samples for molecular sex determination (see next section). Birds were considered to be duetting if they were alternately vocalizing in close proximity (within 50 m of each other). We assumed from the behavioral interactions that duetting pairs were comprised of a male and female if the pairs were foraging together, constructing a nest, and/or defending a nest area without antagonistic interactions.

Molecular Sex Determination

We collected blood and feather samples with required permits from seven adult birds captured by mist net using song playback at five scattered locations on North Andros. We pulled two tail feathers from each bird and obtained blood by pricking the brachial vein 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), and placed on ice. After transportation to the laboratory, samples were stored at -20°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 followed after sampling, with no casualties observed.

We extracted DNA from blood and feathers following the protocol of Fetzner and Crandall (2003) with minor modifications. Feather shafts were minced and subjected to protein digestion prior to DNA extraction by adding 500 µL cell lysis buffer and 5 µL protinase K, and then placing the mixture in a 55°C water bath for 24 hours. We amplified DNA sequences from the genomic DNA samples using two sets of primers for sex determination (Griffiths et al. 1998: P2, P8; Fridolfsson and Elegren 1999: 2550F, 2718R). The 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. A single band indicated a sample was male, and two bands indicated a female.

Vocalization Analyses

We produced oscillograms and spectrograms of individual vocalizations with Raven 1.2.1 for Windows™ (Cornell Lab of Ornithology, Ithaca, New York, USA), following methods and terminology of Reynolds et al. (2010) and McKay et al. (2010). Vocalization types were categorized in part following the terminology of Rising and Flood (1998) for hatchlings and fledglings, and Price et al. (2007, 2008) for adults. We supplied our own names for vocalizations lacking descriptions in the literature, especially for hatchling and fledgling calls. We considered a song or call to be a single syllable or group of syllables preceded and followed by 0.5-sec intervals of silence (Price et al. 2007, 2008).

For each recording of suitable quality, all vocalizations from adults were counted to compute vocalization rates. Vocalization rates were compared between the two age classes (SY and ASY), among three times of the day (morning, 0600-1059 hr; mid-day, 1100-1559 hr; evening, 1600-2000 hr), between two reproductive periods (before versus after incubation), and among the three island metapopulations (NA, MC, SA). In some cases, more than one bird was vocalizing during a recording (i.e., a neighbor or mate), and individuals could not be distinguished from the spectrographic record; thus, the rates we computed may be upwardly biased.

We analyzed the spectrographic structure of the first clear song and one or more of the other call types from each bird or pair. We obtained the following measurements: minimum and maximum frequency and frequency range (Hz); duration of vocalization (sec); and number of syllables. Harmonics were not included in the analyses. A faint grace note (McCallum 2010) or a chit sometimes preceded the first loud syllable of songs and calls, and these were counted as syllables. To avoid pseudoreplication, spectrographic characters obtained from more than one vocalization from an individual were averaged for statistical analysis.

Statistical Analyses

Statistical analyses were conducted using SPSS 13.0 for Windows^{TM} (SPSS Inc., Chicago, Illinois, USA), with alpha of 0.05. Mean values are reported with 1 S.E. due to disparate sample sizes. Vocalization rates were subjected to analyses of variance (ANOVAs; Mertler and Vannatta 2002) to test whether age, time of day, incubation stage, or geographic location (island) had an effect on the rates of the five primary vocalization types analyzed. Our sample size did not permit an omnibus analysis, so we conducted a separate analysis for each of these four sources of variance, but restricted the data sets to avoid bias from other sources of variance. Recordings that had human disturbance were excluded from these analyses. All variables met parametric assumptions after rank transformation. However, because all ANOVAs included a repeated-measures variable (vocalization type), and failed the assumption of sphericity (multivariate homoscedasticity), we applied Greenhouse-Geisser adjustments to the degrees-of-freedom (Mertler and Vannatta 2002). For each ANOVA, we also computed partial eta-squared (η^2) for effect sizes, with values of ~0.01 regarded as small, ~0.06 medium, and ≥0.14 large (Cohen 1988). These can be interpreted as the proportion of variance explained by each main effect or interaction. Effect sizes are independent of sample size, in contrast to statistical significance, and can be more readily compared among independent variables, data sets, and studies.

Spectral characteristics of the songs were compared between the two age groups by *t*-tests, and among the three island populations by one-way ANOVAs (Mertler and Vannatta 2002). For these comparisons, four of the five spectral characters (minimum and maximum frequencies, song duration, and number of syllables) were rank-transformed to meet parametric assumptions. We calculated Cohen's *d* as effect sizes for *t*-tests, with values of ~0.2 considered small, ~0.5 medium, and ≥0.14 large (Cohen 1988). We also conducted two discriminant function analyses (DFA; Mertler and Vannatta 2002) to further compare song structure between the two age classes and among the three island populations. The DFA models used all five characters (four of which were rank-transformed), and were constructed using SPSS defaults, with prior probabilities equal for all groups, and with leave-one-out classification (a jackknife procedure) to reduce bias that can be associated with small sample sizes (Lance et al. 2000).

Results

Molecular Sex Determination

All of the seven orioles (5 SY, 2 ASY) captured by mist net and banded were later determined to be males, suggesting they were more responsive to song playback in approaching the nets than females. Two sets of SY individuals, apparent bachelor males associating together, were captured at the periphery of mated pair territories. The fifth SY male was paired with an ASY female at a nest territory. The two ASY males were in areas with three adults present, and we were unable to determine pairing. Thus, only in one pair were we able to definitely assign vocalizations to a female. However, because both individuals of other unambiguous pairs frequently vocalized, we could still make inferences about the vocalization behavior of females.

Hatchling and Fledgling Vocalizations

Nestlings were silent or very quiet the first week after hatching (c.f., Rising and Flood 1998); thus, we obtained recordings only during the second week. Hatchlings were usually quiet until the parent bird arrived at the nest, usually accompanied by a *chit* call but occasionally after a *whistle* or song from the adult (see Adult Vocalizations, below). The hatchlings would then begin a noisy frenzy. We obtained recordings from seven nests, one of which we followed from late-incubation to fledging over an 18-d period. One nest harbored a Shiny Cowbird chick in addition to two oriole hatchlings. Early begging calls, possibly corresponding to the written description of the *dee-dee-dee-dee* of the Baltimore Oriole (Rising and Flood 1998), were recorded in three nests 5–6 d before fledging. These serial *peep* calls (Fig. 2-2) were relatively lengthy (0.2 sec) and high pitched (8000-9000 Hz). We detected three additional call types 2 d before fledging, but all were from the nest that had a cowbird chick. The *chit*-like (ca. 0.05 sec, 5000-12000 Hz) and *whine*-like (ca. 0.05 sec, 6000-8000 Hz) calls (Fig. 2-2) were similar to the corresponding adult oriole calls (Fig. 2-3), but with higher minimum frequencies and larger frequency ranges. The lengthy, high-pitched *squeal* call (Fig. 2-2) resembled the hatchling call of a Brown-headed Cowbird (Pagnucco et al. 2008), and was likely produced by the Shiny Cowbird chick. Late begging calls, possibly corresponding to the *he-he-häe* of the Baltimore Oriole (Rising and Flood 1998), were recorded in three nests within 2 d of fledging. These rapidly repeated, harmonically rich *chu* calls (Fig. 2-2) were much briefer and of lower frequency (ca. 0.03 sec, 6000-11000 Hz) than the early begging calls, and lacked a clearly distinguishable fundamental frequency.

Recently-fledged young also gave *chu* calls, but lower-pitched (ca. 0.08 sec, 4000-7000 Hz) *twitter* calls (Fig. 2-2) became the most frequent vocalization heard on most recordings of fledglings. The *twitter* call may have been a lower-pitched version of the *chit*-like hatchling call. We also detected several relatively high-pitched, modulated *seet* calls (ca. 0.09 sec, 7000-9000 Hz; Fig. 2-2), and brief, whistle-like, low-frequency *chee* calls (ca. 0.16 sec, Hz 3000-6000 Hz; Fig. 2-2).

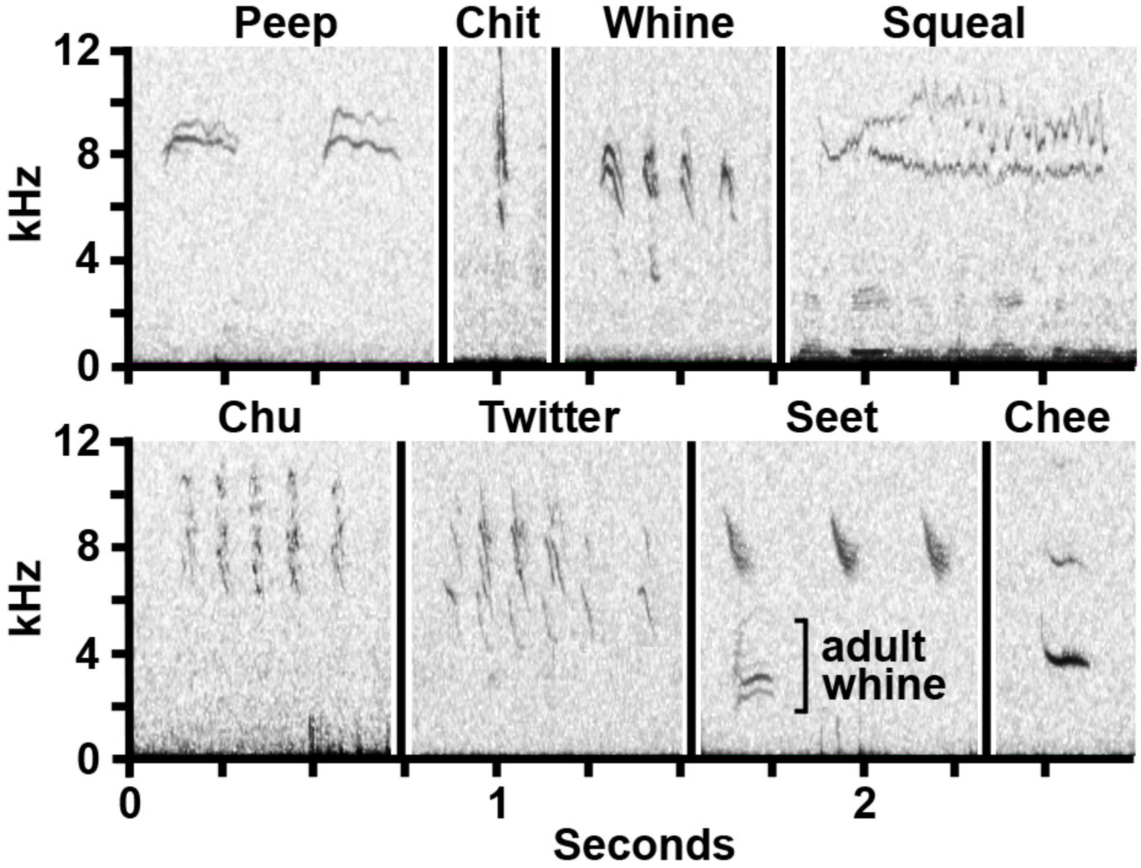

Figure 2-2. Representative spectrograms of hatchling (*peep*, *chit*, *whine*, and *chu*) and fledgling (*chu*, *twitter*, *seet*, *chee*) vocalizations of the Bahama Oriole (*Icterus northropi)*. The *squeal* call probably originated from a Shiny Cowbird (*Molothrus bonariensis*) chick.

Adult Vocalizations

We identified five major vocalizations based on consistent acoustic patterns in spectrograms. These included songs (defined as three or more whistled notes; Price et al. 2007), *whistles*, *chits*, *whines*, and *squawks*, as portrayed in Fig. 2-3. Although songs and calls appeared to be similar among the three islands, geographic variation was compared statistically only for songs (see Geographic Variation). Two vocalization types were sometimes combined in rapid succession (Fig. 2-3), illustrating continuity in the oriole's repertoire. Songs and calls similar to *whistles*, *chits*, and *whines* have been described for various oriole species (Miller 1931, Beletsky 1982a, Hardy et al. 1998, Jaramillo and Burke 1999, and Howell and Webb 2000). However, the *chatter* call present in many oriole species was apparently absent from the Bahama Oriole's vocabulary, and the *squawk* call may be unique.

Songs were highly varied in structure, but were nevertheless relatively stereotyped and resembled the complex whistled songs of many other oriole species (Hardy et al. 1998, Price et. al. 2007). Songs were comprised of 3–24 syllables, averaging (± 1 S.E.) 6.7 ± 0.509 whistled notes and 1.82 ± 0.357 sec total duration, with fundamental frequencies of 1397-5628 Hz ($N = 35$ songs from 35 individuals). *Whistle* calls involved single or double notes, averaging 0.51 ± 0.058 sec total duration, with fundamental frequencies of 2122-5405 Hz ($N = 40$ whistles from 20 individuals). Songs and individual *whistles* were sometimes combined with *chits* or *whines* (Fig. 2-3), but usually were given independently.

Chits were much briefer than whistles, with a mean duration of 0.04 ± 0.003 sec (Fig. 2-3), and a large fundamental frequency range of 1749-8045 Hz. They appeared to be more distinct from *whistle* notes than those of the Streak-backed Oriole (*I. pustulatus*; Price et al. 2008). *Chits* were usually solo or double, and could be inserted anywhere within a song. Multiple-syllable *chits* and other *chit* combinations (*chit-whines* and *chit-whistles/songs*) were most often issued by stressed (louder and more aggressive) birds.

Whine calls were lengthier than *chits* (averaging 0.12 ± 0.006 sec) and harmonically rich (Fig. 2-3). They were typically produced singly or doubly at relatively low amplitudes (1166-3992 Hz). *Whines* were sometimes produced in rapid succession similar to the *chatter* of other species, usually when agitated (e.g., during banding or examination of nests). *Whines* were sometimes combined with a *whistle*, *chit*, or even a song.

A harsh *squawk* call (Fig. 2-3) with no distinguishable fundamental frequency was rarely recorded. The duration was longer (mean of 0.33 ± 0.017 sec) and the minimum frequency lower (mean of 699 Hz) than syllables of other vocalization types, with a broad frequency range (646-9969 Hz). *Squawks* were noted at least three times and recorded twice, once after an adult Shiny Cowbird called, and once upon our close approach to parents feeding a newly-fledged baby. The Shiny Cowbird call that elicited the first recorded oriole *squawk* resembled a combination of the oriole's *whine* and *squawk*. It was a harmonically-rich, harsh call, and of the six calls measured, had an average duration of 0.05 sec (range 0.04-0.06 sec) and a fundamental frequency range of 587-9269 Hz.

Analyses in the following sections examine only adult vocalizations. For vocalization rates (vocalizations/min), we categorized vocalizations as songs, *whistles*,

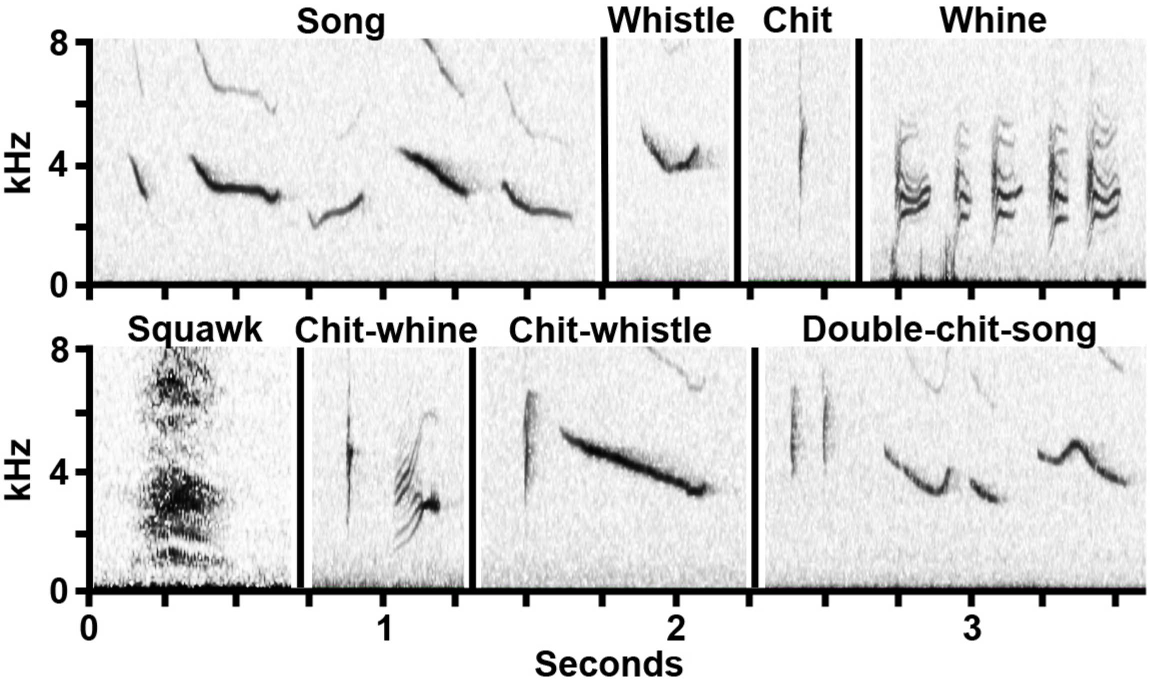

Figure 2-3. Representative spectrograms of the five main vocalizations of the adult Bahama Oriole (*Icterus northropi*), including song, *whistle*, *chit*, *whine*, and *squawk*. Three additional combination vocalizations are also portrayed: chit-whine, chit-whistle, and double-chit-song.

chits, *whines*, and others (the latter including *squawks* and vocalizations that combined two vocalization types).

Age Variation

To avoid confounding with temporal and geographic variation, we restricted analysis of age variation (SY versus ASY birds) in vocalization rates to the pre-incubation period on NA, resulting in a sample of 6 SY and 9 ASY individuals. We computed average vocalization rates for each individual across the three times of day (after learning there was no time-of-day variation; see next section), and subjected these (after rank-transformation) to a 2 × 5 (age × vocalization type) mixed ANOVA, with age treated as a between-subjects factor and vocalization type as a within-subjects factor. The main effect of bird age was not significant ($F_{1,13} = 0.48$, $P = 0.50$, partial $\eta^2 = 0.04$), indicating that age of the bird did not affect vocalization rates (Fig. 2-4). There was a significant difference, however, among vocalization types ($F_{2.1,26.8} = 6.24$, $P = 0.006$, partial $\eta^2 = 0.32$), with birds giving *chits* most frequently, followed by songs, *whistles*, other vocalizations, and *whines* (Fig. 2-4). There was no interaction between age and vocalization types ($F_{2.1,26.8} = 0.98$, $P = 0.39$, partial $\eta^2 = 0.07$).

We compared the song structure of SY and ASY adults using four confirmed SY adults (two single birds, one in SY/SY pair, one in SY-ASY pair) and 20 confirmed ASY adults. Songs from eleven adults of unknown age (eight in SY/ASY pairs, three not seen well enough to confirm age) were excluded from this analysis. Independent *t*-tests showed no significant differences between SY and ASY adults in the spectral characteristics of songs (all *P*-values > 0.12), including minimum frequency (mean ± 1

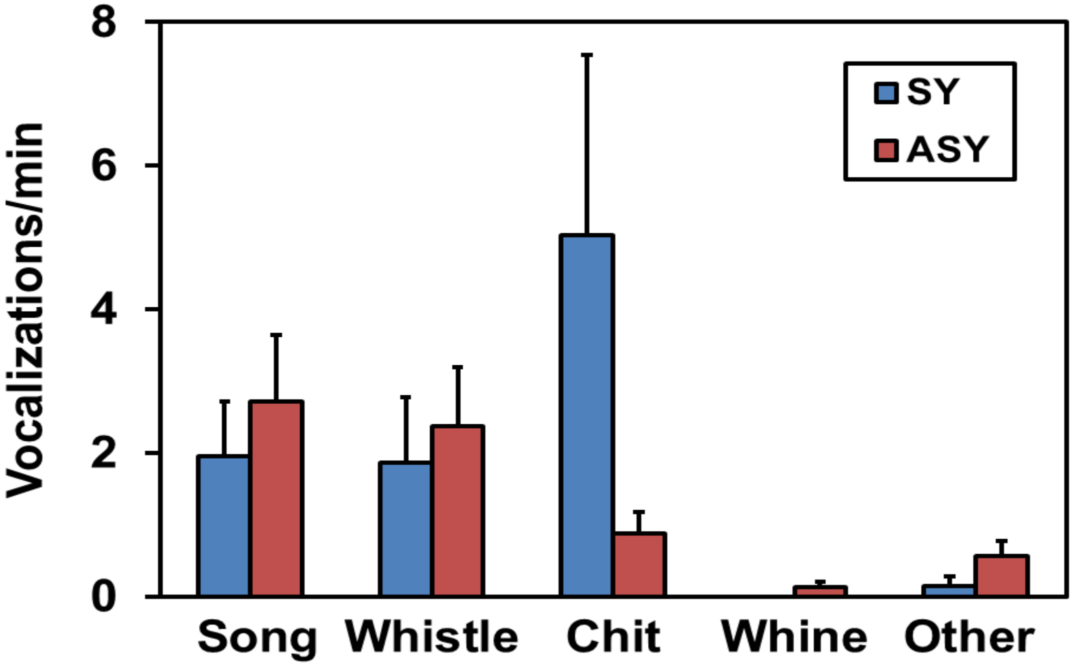

Figure 2-4. Vocalization rates of two adult age classes of the Bahama Oriole (*Icterus northropi*). No age differences existed. SY = second-year plumage (*N* = 6); ASY = after-second-year plumage (*N* = 9).

SE = 2202 ± 318 Hz and 2053 ± 71 Hz, respectively; Cohen's *d* = 0.12), maximum frequency (4953 ± 198 Hz and 4660 ± 82 Hz; *d* = 0.88), frequency range (2750 ± 256 Hz and 2607 ± 99 Hz; *d* = 0.32), number of syllables (5.0 ± 0.9 and 7.1 ± 0.8; *d* = 0.65), and song duration (1.38 ± 0.28 sec and 1.87 ± 0.22 sec; *d* = 0.46). However, the moderate to large effect sizes (Cohen's *d* values of ~0.5 and ≥0.8, respectively) suggested that the small sample of SY adults obscured possible age-related differences, with SY males producing comparatively brief songs with fewer syllables and higher frequencies. Even so, the DFA model still failed to distinguish songs of the two age classes in multivariate space (Wilks $\Lambda = 0.80$, $\chi^2 = 4.44$, $df = 5$, $P = 0.49$), with only 66.7% of the songs assigned correctly, and only 58.3% with cross-validation.

Differences Between Sexes

Both individuals of unambiguous pairs were often heard giving the full range of vocalizations, including songs, *whistles*, *chits*, and *whines*, particularly during the pre-incubation period. The two individuals often duetted as well, with antiphonal examples illustrated in Fig. 2-5. Unambiguous duets appeared to consist exclusively of songs, *whistles*, or a combination of these two vocalizations. Because we could not reliably distinguish males and females, we could not directly compare production rates or the spectrographic features of the non-duetting vocalizations of males and females.

Duetting occurred with certainty only early in the breeding season. During weeks 1 and 2 of our research, for example, duetting accounted for 89% and 43% of recordings, respectively. During weeks 5 and 7, there were no cases of observed duetting. Recordings were ambiguous enough during other weeks that we could not rule out duetting. There

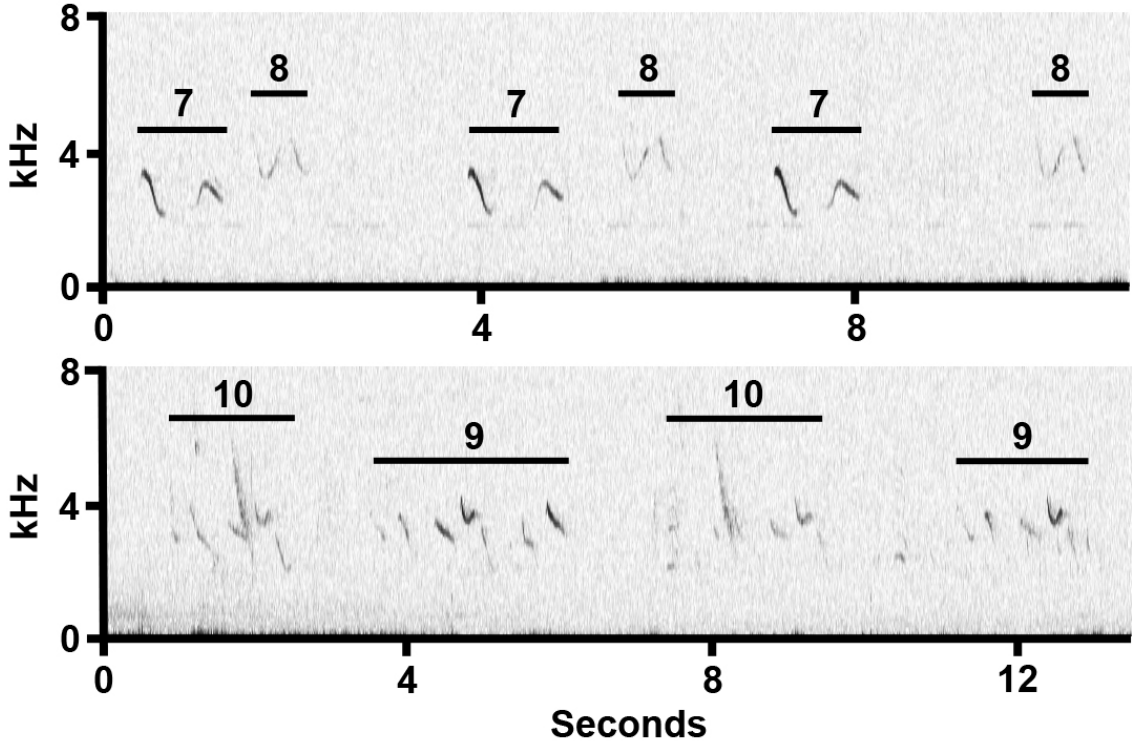

Figure 2-5. Representative spectrograms from duetting male-female pairs of Bahama Orioles (*Icterus northropi*). Song bouts of individual birds are identified by number (pairs 7-8 above, 9-10 below).

was an obvious shift from duets to solo songs as the breeding season progressed. During nest construction, one bird (probably the male) generally sang more often, while the other (probably the female; c.f., Rising and Flood 1998, Brush and Pleasants 2005, Price et al. 2008) was engaged in nest building and sang less often. The nest builder occasionally replied with a song or *whistle*, but more often used *chits* to maintain vocal contact with its mate. We may have detected duetting during the post-incubation period on NA, but this was in an area with a relatively high density of orioles, and we were less confident of distinguishing between duetting partners and counter-singing individuals.

Time-of-Day Variation

For time-of-day variation in vocalization rates, we used birds of both age groups and from all islands, but restricted analysis to the pre-incubation period. Relatively few birds were recorded at all three times of the day, so we compared different birds singing at each time period, and therefore treated time of day as a between-subjects factor. For birds with data for more than one time period, we used data only for the time period with the smallest sample size (either mid-day or evening), resulting in a final data set of 16, 11, and 13 birds for the morning, mid-day, and evening time periods, respectively. A 3 × 5 (time of day × vocalization type) mixed ANOVA indicated that birds vocalized at similar rates throughout the day ($F_{2,37} = 0.46$, $P = 0.64$, partial $\eta^2 = 0.02$; Fig. 2-6).

Again, there was a significant difference among vocalization types ($F_{2.9,107.7} = 13.68$, $P < 0.001$, partial $\eta^2 = 0.27$), with *whistles* and songs given most frequently, followed by *chits*, *whines*, and other vocalizations (Fig. 2-6). There was no interaction between time of day and vocalization type ($F_{5.8,107.7} = 0.92$, $P = 0.48$, partial $\eta^2 = 0.05$).

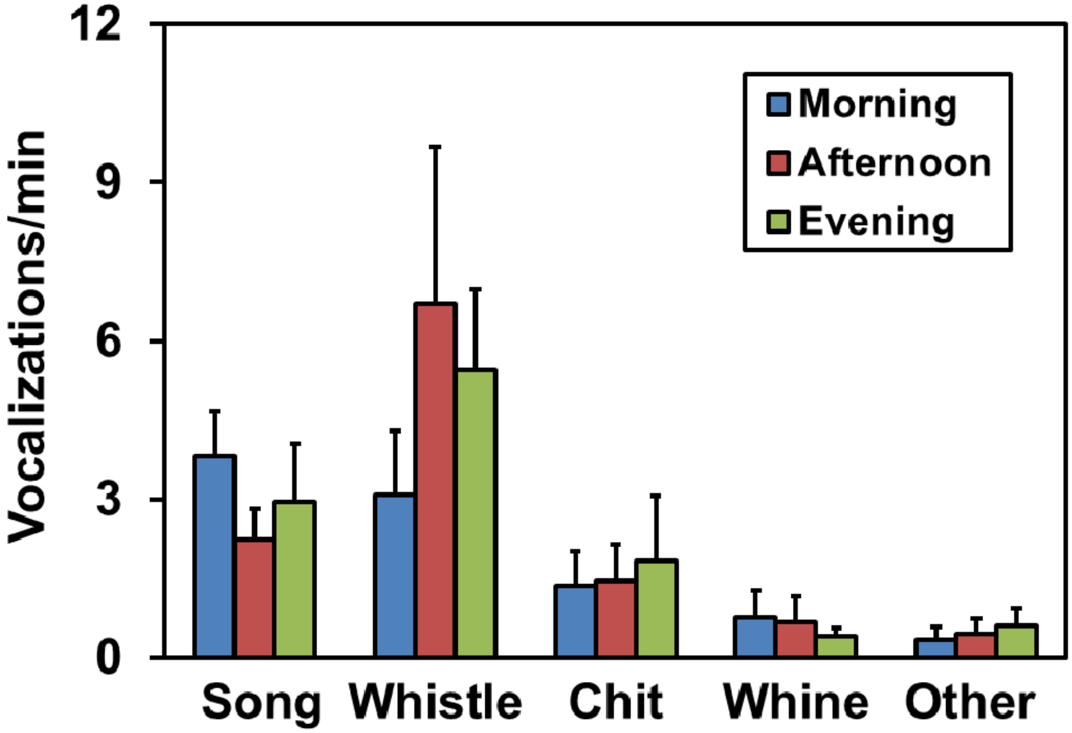

Figure 2-6. Vocalization rates of the Bahama Oriole (*Icterus northropi*) at different times of the day (N = 16, 11, and 13 for morning, mid-day, and evening, respectively). Vocalization rates were similar throughout the day.

Incubation Period Variation

For vocalization rates during the incubation period, we restricted analysis to NA, which was the only island we obtained recordings from both pre-incubation and post-incubation periods. Because we recorded only one bird singing during the two weeks of incubation (birds sang much less during this time), we compared only the pre-incubation versus post-incubation periods. Because of the larger sample available with between-subjects compared to within-subjects data, we compared 21 individuals during pre-incubation with seven different individuals during post-incubation (i.e., incubation period was a between-subjects factor). This analysis included both SY and ASY birds, and used mean values pooled across the three times of day. The 2 × 5 (incubation period × vocalization type) mixed ANOVA revealed a significant interaction between incubation period and vocalization type ($F_{2.9,74.3} = 3.71$, $P = 0.017$, partial $\eta^2 = 0.13$; Fig. 2-7), suggesting that relative rates of the different vocalization types changed after incubation. Production of songs, *whistles*, and *chits* decreased by 73.2% (2.54 to 0.68/min), 69.7% (1.78 to 0.54/min), and 60.3% (2.72 to 1.08/min), respectively, whereas *whines* increased by 827.1% (0.48 to 3.97/min) after incubation (Fig. 2-7).

Geographic Variation

For geographic variation, vocalization rates were confounded with incubation, age, and time of day. We therefore restricted analysis to the pre-incubation period and ASY birds, resulting in $N = 9$, 8, and 7 birds, from NA, MC, and SA, respectively. Since there was no time of day bias (as described in a previous section), we computed the average vocalization rate across the three time periods and conducted a 3 × 5

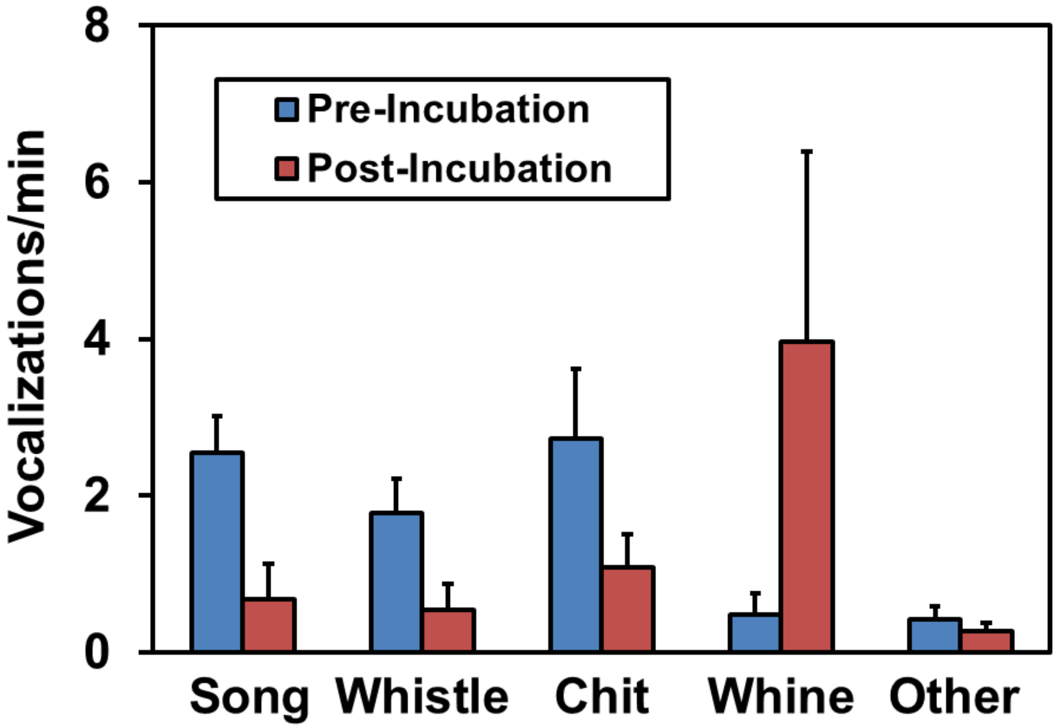

Figure 2-7. Vocalization rates of the Bahama Oriole (*Icterus northropi*) before (N = 21) and after (N = 7) the incubation period. The significant interaction suggests that songs, *whistles*, and *chits* decreased after incubation, whereas *whines* increased.

(island × vocalization type) mixed ANOVA, with island metapopulation treated as a between-subjects factor and vocalization type as a within-subjects factor. The main effect of island on vocalization rate was not significant ($F_{2,21} = 1.54$, $P = 0.24$, partial $\eta^2 = 0.13$), indicating that the birds on each island vocalized at similar rates (Fig. 2-8), though the relatively large effect size suggested that differences might exist. Again, vocalization type was significant ($F_{2.6,54.4} = 10.25$, $P < 0.001$, partial $\eta^2 = 0.33$), and there was no interaction between island and vocalization rate ($F_{5.2,54.4} = 1.17$, $P = 0.34$, partial $\eta^2 = 0.10$).

We analyzed geographic variation in song structure using songs from 23, 7, and 5 individuals from NA, MC, and SA, respectively. One-way ANOVA results for the spectral characteristics of songs showed that location had no significant effect on the maximum frequency, song duration, or number of syllables (Table 2-1); however, differences existed among the islands in lowest frequency ($P = 0.019$), frequency range ($P = 0.002$), and probably highest frequency ($P = 0.074$; note large effect size), with the lowest frequency increasing from north to south, higest frequency decreasing from north to south, and the frequency range decreasing from north to south. Multiple comparisons suggested that adjacent islands were similar, with population differences significant only for the two islands farthest apart (NA and SA; Table 2-1). These results suggest significant clinal variation in song structure; however, all song characters overlapped substantially among populations, indicating the absence of diagnosability among the three island metapopulations.

The DFA model for song spectrographic characters proved significant (Wilks $\Lambda = 0.497$, $\chi^2 = 20.97$, $df = 10$, $P = 0.021$), confirming that the three populations could be

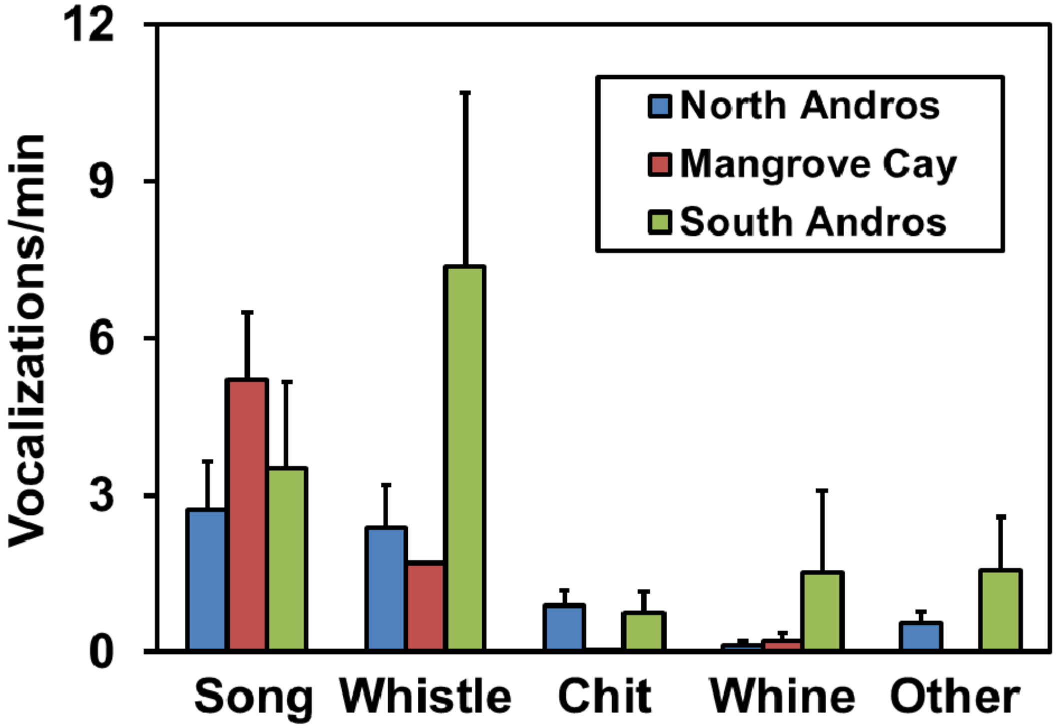

Figure 2-8. Vocalizations rates of the Bahama Oriole (*Icterus northropi*) in three island populations. No differences existed among the populations. *N* = 9, 8, and 7 for North Andros, Mangrove Cay, and South Andros, respectively.

Table 2-1. Spectral characters (mean ± 1 S.E., range) of songs from the three populations of Bahama Oriole (*Icterus northropi*).

Spectral Characters	**North Andros** **(*n* = 23)**	**Mangrove Cay** **(*n* = 7)**	**South Andros** **(*n* = 5)**	***F***	***P***	η^2
Lowest freq (Hz)	$1972^{a} \pm 63$ (1397-3003)	$1987^{ab} \pm 65$ (1828-2311)	$2400^{b} \pm 203$ (2059-3100)	4.53	0.019	0.22
Highest freq (Hz)	4865 ± 79 (4341-5515)	4627 ± 188 (3977-5628)	4481 ± 97 (4201-4700)	2.83	0.074	0.15
Delta freq (Hz)	$2893^{a} \pm 95$ (2219-4061)	$2641^{ab} \pm 148$ (2055-3317)	$2082^{b} \pm 130$ (1599-2369)	7.59	0.002	0.32
Syllables	7.0 ± 0.7 (3-18)	7.0 ± 1.0 (3-12)	5.4 ± 0.7 (4-8)	0.697	0.506	0.04
Duration (sec)	1.93 ± 0.19 (0.866-4.86)	1.60 ± 0.20 (0.630-2.29)	1.67 ± 0.21 (1.16-2.26)	0.259	0.773	0.02

n = number of individuals, with one representative song analyzed from each bird.

Statistical significance (*P*-values): one-way ANOVA, with similar mean values sharing the same superscript and those that differ having unique superscripts (Tukey's multiple comparisons).

Practical significance (effect size): eta-squared (η^2).

differentiated better than by chance in multivariate space. Birds from NA were correctly assigned for 60.9% of the cases, MC 57.1%, and SA 80% (compared to an expected probability of 33.3% for each). With cross-validation, the values were similar at 56.5%, 57.1%, and 80%, respectively. Function 1, comprised primarily of frequency range (negatively associated) and lowest frequency (positively associated), captured 71.4% of the variance (canonical $r^2 = 0.62$), and best separated the SA population from the other two populations. Function 2, comprised primarily of highest frequency (positively associated), captured 28.6% of the variance (canonical $r^2 = 0.44$), and also separated the SA population from the other two populations.

Discussion

Similar to other oriole species (Hardy et al. 1998, Jaramillo and Burke 1999), the Bahama Oriole possesses a substantial vocal repertoire, which includes a variety of different types of sounds in addition to those generally considered its songs. Our analyses fill a gap in our understanding of the phylogenetic influences upon oriole vocalizations, and suggest that this seasonal-breeding monochromatic species exhibits monovocalism typical of tropical oriole species.

By recording the vocalizations of hatchlings, fledglings, and adult birds, we were able to document some of the stages in the ontogenetic development of vocalizations. Bahama Oriole hatchlings produced high-pitched calls similar to those described for Baltimore Oriole (Rising and Flood 1998) and Scott's Oriole (Flood 2002), but unlike the description of the low-pitched begging calls of Altamira Oriole hatchlings (Brush and Pleasants 2005). We observed a transition from higher-pitched hatchling calls to the lower-pitched fledgling calls that more closely resembled those of adults. However, we missed a key stage of further song development that presumably took place later in the summer and likely continued into the second year. Adults produced five main vocalization types (songs and four call types) that were delivered independently or in combination. We were surprised that the *chatter* which occurs in many oriole species (Jaramillo and Burke 1999) was apparently absent in this species.

Some theories propose that the evolution of begging calls is part of a parent/offspring conflict wherein offspring exaggerate their begging to outcompete nest mates and increase their fitness, even at the expense of their parents (Trivers 1974, Leech and Leonard 1997). Host-parasite nestlings often exaggerate their vocalizations to increase and monopolize parental feedings, causing host nestlings in turn to exaggerate their own vocalizations (Pagnucco et al. 2008). More research may shed light on how host parasitism by Shiny Cowbirds influences Bahama Oriole hatchling vocalizations, parental provisioning, and associated fitness costs. Because cowbirds on Andros represent a research range expansion, interactions between orioles and cowbirds are presumably at an early stage of coevolution.

Although songs of SY and ASY males differ in several oriole species (Clawson, 1980), we found no comparable differences in the rates of various vocalization types or in the structure of the song. Some vocalizing SY individuals were bachelor males on the periphery of nesting pair territories, but others were pair-bonded and engaged in breeding. Although most vocalizing SY birds paired with ASY birds might have been female (assuming all available females, but not necessarily all males, were paired), the SY individuals were represented by both sexes. One breeding pair was comprised of two

SY individuals, and genetic analysis confirmed another SY male paired with an ASY bird on a breeding territory. Thus, if vocalizations are important for mate choice, the SY individuals appeared to be competent. Some evidence suggests that oriole males learn their songs and adjust singing to that of neighbors after territories become established (Edinger, 1985).

Because the Bahama Oriole is monochromatic (Garrido et al. 2005), we were unable to distinguish reliably between males and females, and therefore could not compare directly the vocalizations of the two sexes. Nevertheless, we heard both individuals of unambiguous pairs producing the full range of vocalizations, especially prior to incubation. Furthermore, both individuals often duetted antiphonally, especially prior to incubation. Spectrographic cross-correlation analyses of variation within and between individuals of duetting pairs further suggest that females produce *whistles* and songs very similar to those of males (see Chapter 3). Nevertheless, females appeared to sing less often than males once nest-building commenced. We conclude that the non-migratory, monochromatic Bahama Oriole more closely resembles tropical oriole species (monovocal) than temperate species (divocal) in its vocalization behaviors.

Not much is known about the daily time budget of most New World oriole species (Pleasants and Albano 2001, Flood et al. 2002, Brush and Pleasants 2005). Some species are thought to be most active during the morning and evening (Rising and Williams 1999, Price et al. 2008, Scharf and Kren 2010). Thus, male Baltimore Orioles sing throughout the day, but with highest rates in the morning (Beletzky 1982a, Rising and Flood 1998). Males of the Scott's Oriole (*I. parisorum*; Flood 2002) and Audubon's Oriole (Flood et al. 2002) also sing throughout the day, but the latter reportedly sing with similar rates throughout the day (Flood et al., 2002). Our finding that the Bahama Oriole vocalizes at similar rates throughout the day suggests that surveys can be conducted essentially any time of the day. However, it is best to locate orioles early in the breeding season, prior to incubation, when their rates of singing and most other call rates are higher. Songs and *whistle* calls generally carry best and make it easiest to locate birds.

Orioles sing most frequently during the breeding season, but a number of species continue to sing sporadically throughout the year (Rising and Flood 1998, Flood 2002, Flood and Brush 2002). As in other oriole species (Skutch 1996, Jaramillo and Burke 1999, Price et al. 2008), vocalizations of the Bahama Oriole declined after nest construction and especially during incubation, but picked up somewhat after chicks hatched. However, *whine* call production increased dramatically after incubation ended, when adults became engaged in caring for their offspring. Whereas song may play an important role in territorial interactions and pair bond establishment prior to the nesting period (Whittingham et al. 1997, Price et al. 2008), *whine* calls are thought to function largely in inter-sexual communication (Price et al. 2008), and may serve functions similar to that of the *chatter* call present in other orioles but absent in this species (Rising and Flood 1998). High detections of *whines* during surveys could be indicative of fledging success, and therefore may be an indicator of breeding phenology. *Whines* were also the most frequent vocalizations given when we banded the young.

Vocalization rates of the Bahama Oriole did not vary substantially among the three islands, but the large effect size suggested that differences may exist. Such differences might be expected from variation in local density. Because an outbreak of lethal yellowing has decimated Coconut Palms—the oriole's favored nesting habitat—on

NA, local oriole density was greater on MC and SA (Price et al. under review). Analyses of spectral characters suggest that geographic variation exists in the structure of songs, with lowest frequency increasing and highest frequency decreasing from north to south, and delta frequency also decreasing from north to south. The DFA outcomes strongly supported this conclusion. Geographic variation in song remains largely unstudied in orioles. Although Bahama Orioles likely move between adjacent islands (Melissa Price, unpubl. data), clinal variation in song structure suggests that drift, perhaps driven culturally, maintains a degree of vocal distinctiveness among the metapopulations. Vocal diagnosability can be informative for taxonomic purposes (e.g., McKay et al., 2010), but the oriole metapopulations were not diagnosable, as expected. Conservation efforts should seek to maximize all forms of diversity, including cultural diversity (Whitehead et al. 2004, Ryan 2006); thus, the present study underscores the need to maintain healthy oriole populations on all three islands, and to maintain cultural diversity if a translocation program is implemented to increase the number of populations.

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CHAPTER THREE

DUETTING BEHAVIOR AND VOCALIZATIONS OF THE CRITICALLY ENDANGERED BAHAMA ORIOLE (*Icterus northropi*)

William K. Hayes, Valerie A. Lee, and M. Bryant J. Reynolds

Abstract

Although hypotheses have been advanced to explain the prevalence of female song in non-migratory tropical oriole species, it remains unclear why males and females of some oriole species engage in antiphonal song duetting and others do not. Understanding the evolution of duetting in this group is hampered from a lack of detailed studies of the vocalization behavior of many species. To address this information gap, we used spectrographic cross-correlation to compare the vocalizations of duetting male and female Bahama Orioles (*Icterus northropi*). Because the species is monochromatic, and we therefore could not reliably distinguish the sexes in the field, we inferred similarity between the sexes by comparing the pattern and structure of vocalizations of duetting individuals. Duets in this species consisted of either songs or *whistle* calls. Through spectrographic cross-correlation, we showed that within-pair cross-correlations of duetting vocalizations (mean ± SD = 0.39 ± 0.13) were similar to within-individual cross-correlations (0.46 ± 0.8). If female songs and *whistles* differed substantially from those of males, we would have expected a greater difference between individuals of a pair.

Other spectrographic characters, including lowest fundamental frequency, highest fundamental frequency, number of syllables, and bout duration were also remarkably similar between duetting individuals. We conclude that male and female song and *whistle* vocalizations are similar in this species.

Introduction

Among songbirds, males at one time were viewed as the only sex that sings. Although female song is rare in temperate migratory songbirds and typically less complex than male song, females of many tropical species are now known to sing complex songs (e.g., Kellner and Ritchison 1988, Gilbert and Carroll 1999, Ogden et al. 2003, Pavlova et al. 2007), often duetting with, and sometimes even singing more frequently than, males (Morton 1996, Price et al. 2008). This geographic difference (temporal versus tropics) is apparent in orioles (Price et al. 2008). Phylogenetic reconstruction of female song in New World blackbirds (*Icteridae*) suggests that male-biased song production results from selection against singing in females rather than sexual selection for complex song in males (Price et al. 2009). Female song tends to be more common in monogamous, sedentary icterids that live in the tropics, where territorial pairs are able to maintain year-round relationships (Price 2009).

Duetting occurs when paired birds coordinate their songs so that their phrases alternate or overlap producing joint acoustic displays (Farabaugh 1982, Langmore 1998, Hall 2009). Duetting species are phylogenetically diverse, and their duets vary in temporal precision, complexity, and degree of sex specificity (Wickler and Seibt 1982, Hall 2000). The purpose of duets between bird pairs remains controversial. Theories suggest birds duet because of sexual conflict over mating (Rogers et al. 2006), cooperative displays functioning in joint territory defense and/or coordination of breeding activities (Topp and Mennill 2007, Hall and Peters 2008), or a combination of these and other hypotheses (Langmore 1998). Year-round territoriality may also be an important factor in the evolution of coordinated male-female duets (Hall 2004, Benedict 2008).

A number of oriole species have been documented to engage in antiphonal duetting. Among those that reportedly duet are species in which female song appears to be prominent (e.g., *Icterus chrysocephalus*, *I. croconotus*, *I. graduacauda*, *I. mesomelas*; Jaramillo and Burke 1999; Price et al. 2009) and those in which females seldom sing (e.g., *I. galbula*, *I. parisorum*; Rising and Flood 1998, Flood 2002). Duetting was absent in one tropical species in which females sing more than males (*I. pustulatus*; Price et al. 2008). Unfortunately, many oriole species have lacked sufficient study to document whether they duet. Thus, more studies are needed to help us better understand why some species duet and others do not.

In Chapter 2, I documented duetting in the Bahama Oriole (*I. northropi*), a non-migratory monochromatic species that appears to exhibit monovocalism. The duets recorded consisted only of songs and *whistle* calls. However, the degree of similarity of vocalizations between male and female duet participants remains unclear. Thus, the purpose of this study was to determine the degree of similarity in the duetting vocalizations of male and female Bahama Orioles. Because this species is monochromatic (Garrido et al. 2005), and we were unable to reliably distinguish the sexes while in the field, we sought to infer similarity by comparing the pattern and structure of vocalizations of the duetting male-female pairs. We also employed spectrographic cross-correlation to examine within-individual, within-pair, and between-pair variation in the spectrographic characters.

Methods

Field Recording

We recorded vocalizations and conducted ethological observations during the early breeding season of 2009 on the three islands known collectively as Andros: South Andros (28 hr, 30 March–1 April), Mangrove Cay (14 hr, 2–3 April), and North Andros (336 hr, 4 April–4 June) (see Chapter 2).

Time sampling was used to study each pair at different times of the day at the beginning of the breeding season. Recordings were obtained at 48 kHz using an Audio-Technica AT815b Shotgun Microphone (Audio-Technica Corp., Tokyo, Japan) and a Marantz PMD660 Portable Solid State Recorder (Marantz, Kanagawa, Japan). Duets were recorded when we determined there were two birds singing and ended when they stopped singing or flew away. Other data on the time, location, habitat, and behaviors associated with singing were recorded (see Chapter 2). Because the species is sexually monochromatic (Garrido et al. 2005), at least with respect to human vision (see Eaton 2005), we were unable to determine the sex of duetting pairs. However, we were able to distinguish between second-year (SY) and after-second-year (ASY) adults, with many SY individuals forming reproductive pairs (see Chapter 2, c.f. Price et al. submitted).

Birds were considered to be duetting if they were alternately vocalizing in close proximity (within 50 m apart). We assumed from the behavioral interactions that duetting pairs were comprised of a male and female if the pairs were foraging together, constructing a nest, or defending a nest area without antagonistic interactions.

Vocalization Analyses

We used spectrographic cross-correlation (SPCC; Clark et al. 1987, Cortopassi et al 2006, Moravec et al. 2006, Coleman et al. 2007) to compare the structural similarity of duetting vocalizations (1) within individuals, (2) between individuals within pairs, and (3) between individuals of different pairs. We used the batch correlator in Raven 1.4RC software (Cornell Lab of Ornithology, Ithaca, New York, USA) to produce a triangular half-matrix of peak correlation values for vocal pairings. All duetting vocalizations that were clear of background noise were used for cross-correlation comparison within individuals and between individuals within pairs. A single randomly-selected vocalization was used to compare individuals with those of different pairs. All tracks were opened with the default Hann window, bandpass filtered between 1000 and 7000 Hz, and clipped below 40 db to remove background noise. Tracks were normalized to compare the songs in two dimensions and to ignore the magnitude. Linear power values were used with no demeaning. We also obtained the following measurements of each vocalization: minimum and maximum frequency and frequency range (Hz); duration of vocalization (sec); and number of syllables. Harmonics were not included in the analyses. Additionally, songs were classified by visual examination of spectrograms into syllable types, but these data required reassessment, and therefore are omitted from this thesis.

Statistical Analyses

Statistical analyses were conducted using SPSS 13.0 for Windows^{TM} (SPSS Inc., Chicago, Illinois, USA), with alpha of 0.05. We used a repeated-measures one-way analysis of variance (ANOVA; Mertler and Vannatta 2002) to compare mean SPCC-derived values for within-individual, within-pair, and between-pair groups. We also computed partial eta-squared (η^2) for effect sizes, with values of ~0.01 regarded as small, ~0.06 medium, and ≥0.14 large (Cohen, 1988). These values can be loosely interpreted as the proportion of variance explained by each main effect or interaction.

Results

We observed duetting with certainly only early in the breeding season, and therefore our recordings were limited to the pre-incubation period. We may have detected duetting during the post-incubation period on North Andros, but this was in an area with a relatively high density of orioles, and we were less confident of distinguishing duetting partners from countersinging individuals on different territories. During nest construction, only one bird (probably the male) was generally observed singing, while the other (probably the female; c.f., Rising and Flood 1998, Brush and Pleasants 2005, Price et al. 2008) was engaged in nest construction. The nest builder sometimes replied with a song or *whistle*, but more often used *chits* to maintain vocal contact with its mate. Both individuals of a pair were often heard giving the full range of vocalizations, including songs, *whistles*, *chits*, and *whines* (Chapter 2). However, unambiguous duets appeared to consist exclusively of songs, *whistles*, or a combination of these two vocalizations. Representative duets are illustrated in Fig. 3-1.

Although duetting was observed on North Andros, many of these pairs were spaced farther apart and the spectrograms lacked sufficient clarity to identify duetting partners. We obtained sufficiently clear recordings from six duetting pairs: three from Mangrove Cay, and three from South Andros. Spectrographic cross-correlations were made of all vocalizations within individuals (4–45 vocal bouts compared per individual; $N = 11$ individuals; one bird provided only a single vocalization, and was excluded), between individuals within pairs (5–45 bouts per pair; $N = 6$ pairs), and between individuals of different pairs (11 bouts per comparison, one randomly selected bout from each individual compared to a randomly selected bout from each other individual; $N = 12$ individuals). Mean values from each of the multiple correlations obtained per individual were then computed for each individual (Table 3-1). A one-way ANOVA of rank-transformed data revealed that vocalization similarity differed substantially among the three groups ($F_{2,20} = 18.26$, $P < 0.001$, $\eta^2 = 0.65$). Bonferroni multiple comparisons suggested that within-individual and within-pair variance were similar (though a Cohen's *d* of 0.63 suggested a moderate effect), and both were less than between-pair variance (Table 3-1).

The pattern of vocalizations appeared to be well synchronized in some pairs, with sequentially alternating bouts (pairs 7-8 and 9-10), and less well structured in others (Fig. 3-1, Table 3-1). The rate of vocalizations was highly variable (1.1-35.8 vocalizations/min), with both individuals vocalizing at similar rates in some pairs (pairs

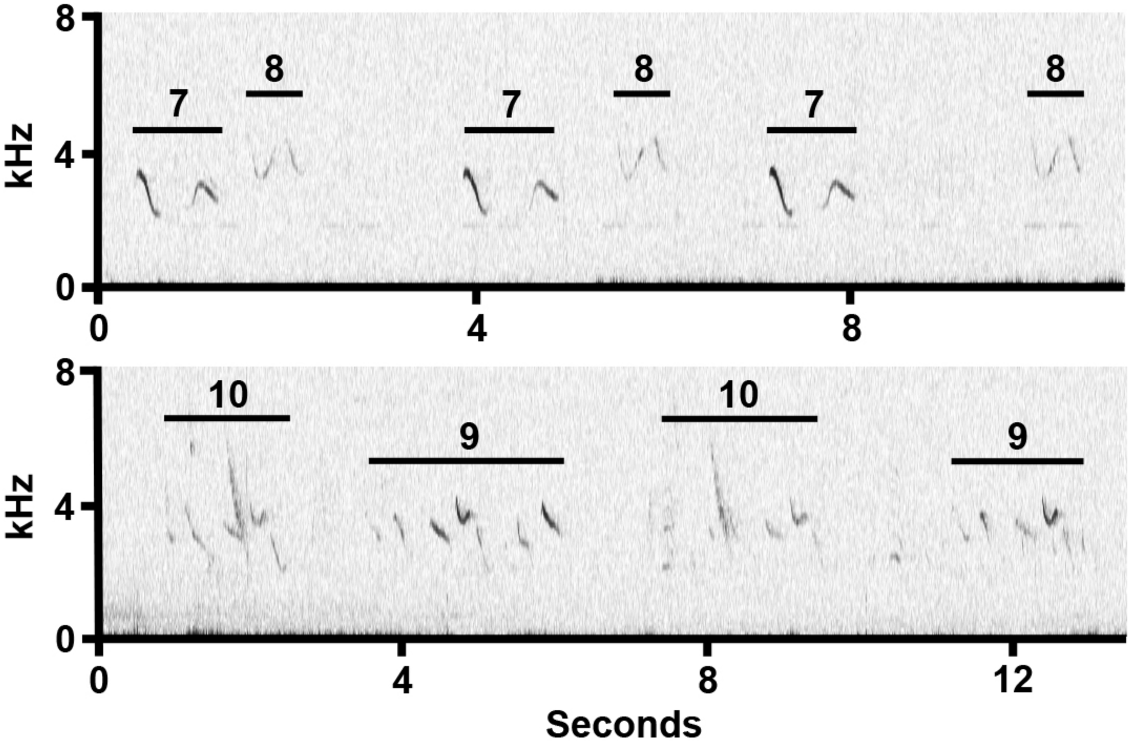

Figure 3-1. Representative spectrograms from duetting male-female pairs of Bahama Orioles (*Icterus northropi*). Song bouts of individual birds are identified by number (pairs 7-8 above, 9-10 below).

Table 3-1. Vocalization patterns, rates, and mean spectrographic cross-correlation values of duetting pairs of Bahama Orioles (*Icterus northropi*). $N = 12$ individuals in six pairs.

Duetting pair	Duet pattern	Rate (per min)	Cross-correlations		
			Within-individual	Within-pair	Between-pair
1(a)	Abaaabaaabbbbb	9.09	0.64	0.36	0.25
2(b)		9.09	0.38	0.36	0.26
7(a)	bababababababababbbababababababbabababaubaabuabauauu-	15.5	0.38	0.31	0.24
8(b)	aaaaabaababababbaabababuuabaabauuuabuabbabababababab	14.15	0.34	0.31	0.32
9(a)	bababababababaabababababababa	11.4	0.44	0.46	0.29
10(b)		10.6	0.44	0.46	0.35
24(a)	aaaaababaaaaabaabaabbbbbbbbbbbb	31.5	0.65	0.34	0.27
25(b)		35.8	0.32	0.34	0.29
30(a)	aaaaaaaaabaabaaaaaaaabaabaaaaaaaaababaaaaaaaaaa	15.2	0.55	0.34	0.36
31(b)		2.4	0.30	0.34	0.23
36(a)	Aaab	1.1	0.64	0.54	0.31
37(b)		0.4	–	0.54	0.33
Mean		13.0	0.46^{a}	0.39^{a}	0.29^{b}
1 SD		11.0	0.13	0.08	0.04
95% CI		6.0–20.0	0.37–0.55	0.34–0.45	0.27–0.33

Duetting birds 1–10 (3 pairs) from South Andros; birds 24–37 (3 pairs) from Mangrove Cay. Pairs 7-9 included vocalizations from an additional unidentified bird (u), as indicated in the pattern. Bird 37 uttered just one vocalization; hence, no within-individual cross-spectrographic correlation could be computed.

Statistical significance comparing the three mean values: one-way ANOVA of rank-transformed data ($F_{2,20} = 18.26$, $P < 0.001$, $\eta^2 = 0.65$), with similar mean values sharing the same superscript and those that differ having unique superscripts (Bonferroni multiple comparisons).

1-2, 7-8, 9-10, 24-25), and dissimilar rates in other pairs (pair 30-31; pair 36-37 was of insufficient duration to generalize; Table 3-1).

Within-pair similarities in the spectrographic characters of individual vocalization bouts can be better appreciated in Table 3-2. Minimum and maximum frequencies, mean number of syllables, and mean duration of vocalization bouts were consistently more similar between individuals of a pair than between pairs.

Discussion

Because the Bahama Oriole is sexually monochromatic, we were unable to distinguish between the sexes in the field, and therefore could not directly compare the vocalizations of males and females. However, we can infer that the diversity and structure of songs and *whistle* calls are similar for the two sexes. Both birds in a pair were often observed vocalizing the same repertoire of sounds. Within-pair cross-correlations of duetting vocalizations (mean ± SD = 0.39 ± 0.13) were surprisingly similar to within-individual cross-correlations (0.46 ± 0.8). If female songs and *whistles* differed substantially from those of males, we would have expected a much greater difference difference between individuals of a pair. Spectrographic characters, including lowest fundamental frequency, highest fundamental frequency, number of syllables, and bout duration were also remarkably similar between duetting individuals (Table 3.2).

Table 3-2. Within-individual variation in spectrographic characters of vocalization bouts during duetting by Bahama Oriole (*Icterus northropi*) pairs. N = 12 individuals in six pairs.

Duetting birds (pair)	Bouts (N)	Minimum frequency (Hz)	Maximum frequency (Hz)	Number of syllables			Bout duration (sec)		
				Mean	SD	CV	Mean	SD	CV
1	7	2699	5487	1.0	0.0	0.00	0.53	0.05	9.00
2	7	2856	4556	1.0	0.0	0.00	0.52	0.17	32.86
7	46	983	9965	1.8	0.4	21.90	0.66	0.23	35.12
8	42	1509	8316	1.9	0.5	28.91	0.60	0.25	41.63
9	14	951	6211	4.6	0.9	18.86	1.59	0.26	16.55
10	13	996	6793	4.6	1.2	26.23	1.63	0.41	25.32
24	15	580	6526	7.8	0.7	8.80	1.76	0.14	8.00
25	17	363	7831	4.4	2.3	52.56	1.48	0.78	52.76
30	38	697	8748	3.1	0.5	15.56	0.65	0.11	17.65
31	6	697	9368	2.3	0.5	22.59	0.66	0.12	18.52
36	3	1096	5250	8.0	1.5	19.09	2.48	0.54	21.84
37	1	1798	4826	9.0	–	–	2.56	–	–
Mean		1269	6990	4.1			1.26		
1 SD		806	1829	2.8			0.76		
95% CI		757–1781	5827–8152	2.3–5.9			0.78–1.74		

Our somewhat limited evidence suggests that duetting in the Bahama Oriole may function primarily in pair bonding. We observed duetting with certainty only early in the breeding season, prior to incubation. Nest-building and subsequent nest-focused activities appeared to preclude duetting. Further study is required to learn whether duetting resumes after incubation and is exhibited at other times of the year. Although we cannot compare the song rates of males and females, we believe that females sing quite frequently, and therefore this species fits the general trend of monovocalism in tropical oriole species.

Spectrographic cross-correlation is ideally suited for analyzing variation in vocalizations at different levels. The relatively low correlation values we measured within individuals (mean of 0.30) underscores the substantial variation in the number, duration, intervals, and frequencies of *whistle* syllables issued independently by orioles or linked together to form a song. Comparable SPCC analyses are not available for other oriole species; however, other bird species show much less within-individual variation in their songs, as indicated by much higher correlation values (e.g., Shieh and Liang 2007, Lein 2008). In spite of its advantages for objectively characterizing similarities, SPCC cannot inform what particular characters vary between vocalizations, and it is especially sensitive to varying intervals between syllables. Thus, multivariate analyses of individual spectrographic characters remain essential for studies of vocal variation. Nevertheless, SPCC analyses offer considerable promise for obtaining a broader understanding of the sources of vocal variation among orioles and other groups, including founder effects for island populations (Shieh and Liang 2007).

Although hypotheses have been advanced to explain the prevalence of female song in non-migratory tropical oriole species (Price 2009, Price et al. 2009), it remains unclear why some oriole species duet and others do not. Within orioles and blackbirds, duetting and frequent female singing are thought to be associated (Price et al. 2009), but duetting has been described in several species in which females seldom sing (e.g., *I. galbula*, *I. parisorum*; Rising and Flood 1998, Flood 2002), and it does not occur in one species with frequent female singing (*I. pustulatus*; Price et al. 2008). Understanding the evolution of duetting in this group is hampered from a lack of detailed studies of the vocalization behavior of many species. Our study helps to fill this gap.

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APPENDIX

VOCALIZATION TYPE SPECTRAL CHARACTERISTICS

Spectral characters of the five vocalization types for the three populations of the Bahama Oriole (*Icterus northropi*).

Characters	All Islands	North Andros	Mangrove Cay	South Andros
Whistle	***n* = 20 (40,40)**	***n* = 10 (23,23)**	***n* = 4 (5,5)**	***n* = 6 (12,12)**
Lowest freq (Hz)	3025 ± 69 (2122-3710)	3088 ± 96 (2634-3710)	3070 ± 88 (2882-3255)	2891 ± 156 (2122-3144)
Duration (sec)	0.508 ± 0.058 (0.260-1.42)	0.530 ± 0.110 (0.260-1.42)	0.393 ± 0.041 (0.295-0.498)	0.549 ± 0.053 (0.307-0.679)
Song	***n* = 35 (35,35)**	***n* = 23 (23,23)**	***n* = 7 (7,7)**	***n* = 5 (5,5)**
Lowest freq (Hz)	2036 ± 56 (1397-3100)	1972 ± 63 (1397-3003)	1987 ± 65 (1828-2311)	2400 ± 203 (2059-3100)
Duration (sec)	1.82 ± 0.357 (0.630-4.86)	1.93 ± 0.191 (0.866-4.86))	1.60 ± 0.198 (0.630-2.29)	1.67 ± 0.209 (1.16-2.26)
Chit	***n* = 23 (140,104)**	***n* = 19 (129,97)**	***n* = 1 (1,1)**	***n* = 3 (10,6)**
Lowest freq (Hz)	2636 ± 109 (1749-3928)	2579 ± 125 (1749-3928)	2676	2982 ± 195 (2698-3356)
Duration (sec)	0.040 ± 0.003 (0.026-0.080)	0.039 ± 0.003 (0.026-0.063)	0.080	0.031 ± 0.002 (0.029-0.035)
Whine	***n* = 19 (77,45)**	***n* = 15 (68,41)**	***n* = 1 (2,1)**	***n* = 3 (7,3)**
Lowest freq (Hz)	1898 ± 102 (1166-3065)	1872 ± 87 (1166-2288)	1684	2101 ± 548 (1166-3065)
Duration (sec)	0.121 ± 0.006 (0.074-0.179)	0.128 ± 0.006 (0.093-0.179)	0.147	0.081 ± 0.004 (0.074-0.086)
Squawk	***n* = 2 (8,7)**	***n* = 2 (8,7)**		
Lowest freq (Hz)	692 ± 46 (646-739)	692 ± 46 (646-739)	-----	-----
Duration (sec)	0.327 ± 0.017 (0.311-0.344)	0.327 ± 0.017 (0.311-0.344)	-----	-----

n = number of individuals and, within parentheses, total number of vocalizations analyzed (for duration and frequency, respectively).
Mean ± 1 S.E. computed from individuals; within parentheses, minimum, maximum, or range for all vocalizations analyzed.