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Documentation of female song in a newly recognized species, the Puerto Rican Oriole (*Icterus portoricensis*)

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Abstract Evolutionary biologists often assume that male competition for females is the root of the evolution of elaborate coloration and song. However, recent findings show that in the ancestral history of songbirds, it is likely that song occurred in both males and females. Surprisingly, no data exist on female song for many species of birds. We investigated whether the Puerto Rican Oriole (*Icterus portoricensis*), a tropical songbird, exhibits both male and female song. For this project we marked individuals with sex-specific color bands and confirmed sex using genetic sexing. We repeatedly recorded both male and female orioles singing. Furthermore, female Puerto Rican Oriole song appears to be similar to male song, with no obvious differences in structure. Our study provides further evidence of the ubiquity of female song in tropical songbirds. Finally, our findings provide support that female song is ancestral in the Caribbean oriole clade, and that song dimorphism in temperate breeding species is a result of a loss of female song.

Keywords female song, female vocalizations, *Icterus portoricensis*, Puerto Rican Oriole, tropical songbirds

Resumen Documentación del canto de la hembra de en un especie recientemente reconocida, la Calandria Puertorriqueña (*Icterus portoricensis*)—Biólogos evolutivos a menudo asumen que la competencia masculina para las mujeres es la raíz de la evolución de la coloración y canción. Sin embargo, recientes hallazgos muestran que los machos y las hembras ancestrales de todos los pájaros cantores probablemente cantaban; pero existen pocos datos sobre el canto de las hembras de muchas especies de aves. Nosotros investigamos el actuada canta de los hembras y los machos el pájaro, la Calandria Puertorriqueña (*Icterus portoricensis*). Para este proyecto, marcamos individuos de diferentes sexos con bandas de color específicas y confirmamos el sexo usando métodos genéticos. Adicionalmente; grabamos las canciones de ambos sexos de las Calandrias Puertorriqueñas. Somos los primeros en documentar canción de ambos sexos en esta especie. Por otra parte, la canción de la Calandria Puertorriqueña aparece ser similar a la canción de los machos, sin diferencias evidentes en la estructura de la canción. Nuestro estudio ofrece evidencia adicional de la omnipresencia de la canción femenina en las aves canoras tropicales. Por último, nuestros resultados respaldan la idea de que la canción femenina es ancestral en la clade de las calandrias caribes, y que el dimorfismo en la canción de especies de aves templadas es un resultado de la pérdida de la canción femenina.

Palabras clave aves canoras tropicales, Calandria Puertorriqueña, canto de hembras, *Icterus portoricensis*, vocalizaciones de hembras

Résumé Information sur le chant des femelles d'une espèce nouvellement reconnue, l'Oriole de Porto Rico (*Icterus portoricensis*)—Les biologistes évolutionnistes supposent souvent que la compétition entre mâles pour les femelles est à l'origine de l'évolution vers une coloration et un chant élaborés. Toutefois, des résultats récents montrent que, dans l'histoire ancestrale des oiseaux chanteurs, il est probable que le chant ait été présent à la fois par chez les mâles et chez les femelles. Étonnamment, aucune donnée n'existe sur le chant des femelles pour de nombreuses espèces d'oiseaux. Nous avons étudié si l'Oriole de Porto Rico (*Icterus portoricensis*), un oiseau chanteur tropical, présentait à la fois un chant mâle et un chant femelle. Pour ce projet, nous avons marqué les individus avec des bagues de couleurs différentes selon le sexe et confirmé le sexe par des analyses génétiques. Nous avons enregistré à plusieurs reprises des mâles et des femelles en train de chanter. En outre, le chant des femelles d't semble être similaire à celui des mâles, sans différence évidente dans la structure. Notre étude fournit une preuve supplémentaire de l'omniprésence du chant des femelles chez les oiseaux chanteurs tropicaux. Enfin, nos résultats soutiennent l'hypothèse affirmant que le chant des femelles est ancestral dans le clade des orioles des Caraïbes, et que le dimorphisme du chant chez les espèces nichant dans les régions tempérées est le résultat d'une disparition de chant chez les femelles.

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Mots clés chant des femelles, *Icterus portoricensis*, oiseaux chanteurs tropicaux, Oriole de Porto Rico, vocalisation des femelles

There are an estimated 5,000 species of songbirds (oscine passerines; Gill and Donsker 2015), which use song for a variety of behavioral functions, especially mate attraction and territory defense. Historically, bird song has been defined as "long, complex, vocalizations produced by males in the breeding season" (Catchpole and Slater 2008:8). However, females of many species also produce these same long, complex vocalizations. Female song is especially common in the tropics, whereas the majority of bird vocalization research is conducted in temperate regions (Slater and Mann 2004). This geographic bias means that many temperate-zone researchers do not encounter female song on a daily basis. This is likely the main reason that earlier researchers excluded females from their definition of bird song. Biased definitions are also impacted by sexual monomorphism, which is common in the tropics (Friedman *et al.* 2009). For a sexually monomorphic songbird species, a singing female will be visually indistinguishable from a singing male. This obstacle to identifying female song combined with a lower number of tropical song studies thus leads to temperate-zone biased definitions of bird song (Slater and Mann 2004).

Despite this bias, the evolution of female song has been receiving increasing attention in recent years (e.g., Whittingham *et al.* 1997, Langmore 1998, Price *et al.* 2008). As a result, researchers have a better understanding how this trait has evolved. Historically, ornithologists have assumed that elaborate traits such as coloration and complex song evolve through male competition for females (Beecher and Brenowitz 2005, Byers and Kroodsma 2009). Similarly, it is assumed that males gain elaborate or complex song when it increases mating success (e.g., Catchpole and Slater 2008), which implies a character state change from absence to presence of song (Fig. 1a). However, recent research has shown that both the males and the females of the common ancestor to all songbirds sang (Odom *et al.* 2014). This finding implies that the males of lineages with only male song have likely retained that trait whereas females have lost the trait (Fig. 1b). Generally, the loss of female song is correlated with the transition to temperate breeding from tropical residence (Price *et al.* 2009). Thus, when the lineages shift from tropical to temperate breeding, often there is a corresponding shift from both male and female song to just male song. This seems to be the case in New World orioles (genus *Icterus*; Price *et al.* 2009).

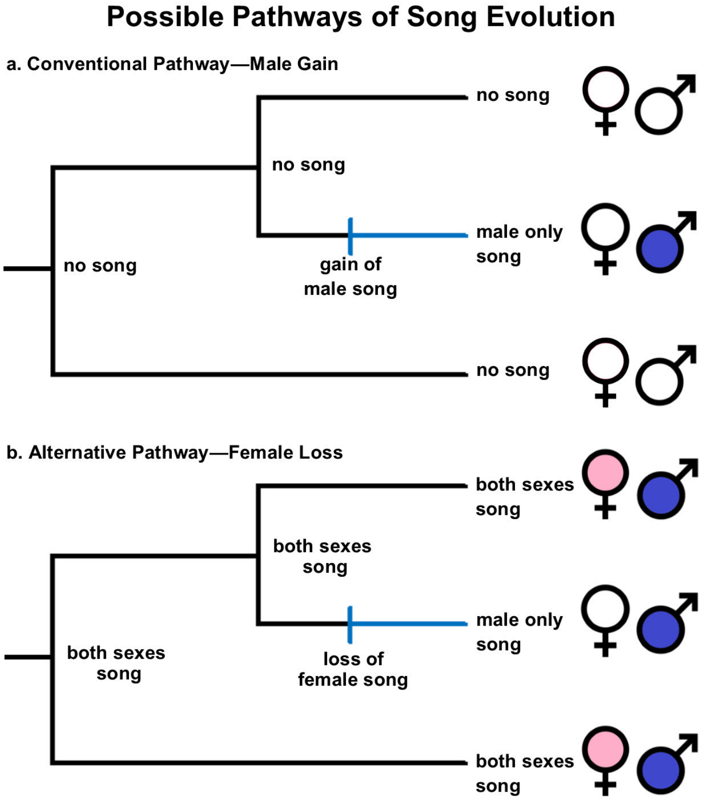

Fig. 1. (a) Conventional Pathway—Male Gain. The common ancestor of this clade lacked complex song. The slash represents a character state change from no bird song to male only bird song as if males gained song, for example, due to female choice. (b) Alternative Pathway—Female Loss. The common ancestor in this scenario had complex song in both sexes. The slash represents a character state change from both male and female song to male only song as if females lost their ability to sing.

However, in order to further evaluate this hypothesis, it is necessary to collect song data from additional tropical oriole species. Whereas there are sufficient data on song presence for most temperate oriole species, there are limited data for oriole species that are resident in the tropics, especially the Caribbean oriole clade. This deficiency is likely due to the various challenges facing tropical research, such as taxonomic lumping. For example, the Puerto Rican Oriole (*Icterus portoricensis*) was previously lumped with three other Caribbean oriole species, Bahama Oriole (*I. northropi*), Cuban Oriole (*I. melanopsis*), and Hispaniolan Oriole (*I. dominicensis*), as one of four subspecies of *I. dominicensis* (Greater Antillean Oriole, broad sense). Genetic analysis showed that this group of taxa is paraphyletic, and deeply diverged based on mitochondrial DNA (Sturge *et al.* 2009). Furthermore, these taxa all have distinct song (Garrido *et al.* 2005) and plumage patterns (Omland and Lanyon 2000, Price and Hayes 2009). In 2010, the American Ornithologists' Union declared the four subspecies as full species (Chesser *et al.* 2010).

With the recognition of these four orioles as distinct species, there is a gap in many types of data including female vocalizations for this Caribbean clade of orioles. Furthermore, in order to determine the ancestral character state of the Caribbean oriole clade, it is necessary to determine if female song is present in Puerto Rican Orioles. This information will allow us to reconstruct the history of the female song trait in the Caribbean oriole clade.

The goals of this project were to 1) determine if female Puerto Rican Orioles sing, 2) if they do sing, determine when and how often females and males sing, 3) compare the acoustic features of female and male song, and 4) reconstruct the phylogenetic distribution of female song across the Caribbean oriole clade.

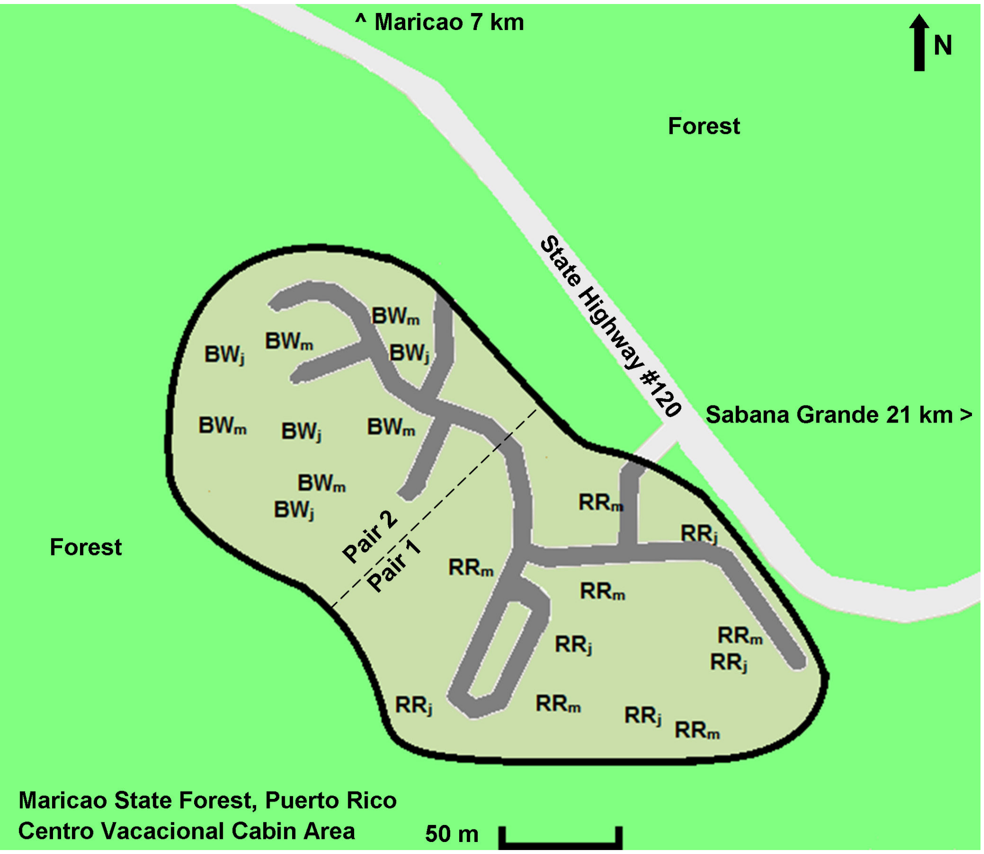

Fig. 2. Map of Maricao Study Site. Confirmed sightings of two pairs of Puerto Rican Orioles are marked by the band combinations: RR = female of pair one and BW = male of pair two. Subscript letters indicate the month of the sighting (j = January and m = March). The black line marks the outline of the cabin area study site while state highway 120 is in light gray and roads to the cabins are in dark gray. The dashed line represents a rough territory boundary.

Methods

In March of 2013, we surveyed four forest locations on the island of Puerto Rico in search of territorial pairs of Puerto Rican Orioles. After locating two non-overlapping territorial pairs within Maricao State Forest, we observed the pairs for 8 days in June 2013, 9 days in January 2014, and banded the female of pair one. We then returned for an additional 10 days in March 2014, banded the male of pair two, and carried out additional observations. We banded both with unique sex-specific color combinations of leg bands and collected feather samples for molecular sexing.

We used a combination of mist nets and playback recordings of local Puerto Rican Orioles in order to capture individuals within the study population. Playback recordings consisted of song and calls of an unknown Puerto Rican Oriole. Additionally, one playback recording contained chatter from a pair of Puerto Rican Orioles from a nearby state forest, Bosque Estatal Susua.

We provisionally determined sex based on size dimorphism (Garrido *et al.* 2005) and later confirmed our sex assignment using standardized molecular sexing techniques (Griffiths *et al.* 1998) with the addition of 0.5 µL BSA per sample. We used a 2% agarose gel at 80 V for 1 hr to visualize band separation. The PCR cycling profile was as follows: 94°C for 7 min; 45 cycles of 92°C for 1 min, 50°C for 1 min (annealing), 72°C for 1 min.

We observed the orioles during the pre-breeding season (11–23 January 2014) and the breeding season (4–14 June 2013 and 14–23 March 2014). We recorded and observed the songs of known-sex Puerto Rican Orioles during the breeding season, as well as the songs of unknown-sex individuals during the pre-breeding season. All individuals that we recorded were in mated pairs. Songs were recorded using a shotgun microphone and a Marantz PMD 661 digital recorder and then visualized using Raven (Bioacoustics Research Program 2006).

We collected known female song data for the orioles within the Caribbean oriole clade from published data (Jaramillo and Burke 1999, Lee 2011, Odom *et al.* 2015) and carried out maximum parsimony ancestral state reconstruction in Mesquite (Maddison and Maddison 2011). We used the phylogenetic tree produced by Sturge *et al.* (2009) and included three outgroup species: Orchard Oriole (*Icterus spurius*), Venezuelan Troupial (*I. icterus*), and Streak-backed Oriole (*I. pustulatus*).

Results

We observed two territorial pairs of Puerto Rican Orioles around the cabin area in the Maricao State Forest study site (Fig. 2). The male and female of the pairs were together (within 5 m) the majority of the time in which we observed them during both the pre-breeding and breeding seasons (Fig. 2).

The breeding season begins in mid-February with nest building and clutch initiation, and it generally continues from March through July. During the pre-breeding season in January, there was no obvious nesting behavior. However, the banded female of pair one and her mate were always observed in a restricted area within the study site (Fig. 2), displayed consistent territorial behavior, and responded to playbacks in both January and March.

We successfully recorded the songs of one female and two male Puerto Rican Orioles during the early stages of the breeding season in March (during nest building and egg laying). On three occasions we recorded female song (Fig. 3); on two additional occasions we observed the banded female singing, without recording her. We observed and recorded male song numerous times during the breeding season (Figs. 4 and 5). We did not witness any duetting behavior during our study according to the Thorpe *et al.* (1972) definition of duets: synchronous or alternating song between a mated male and female.

For both males and females, each recorded song had 6–8 notes (Figs. 3–5). The song frequencies of both the male and female songs ranged from approximately 1.5 to 6.0 kHz and the duration of each song ranged from 1.5 s to 3.0 s. The majority of songs sung by Puerto Rican Orioles were heard before sunrise: 0515 to 0630 in March. The orioles consistently sang through the first hour of the morning and then the rate of song steadily decreased. Song was occasionally heard throughout the day with a

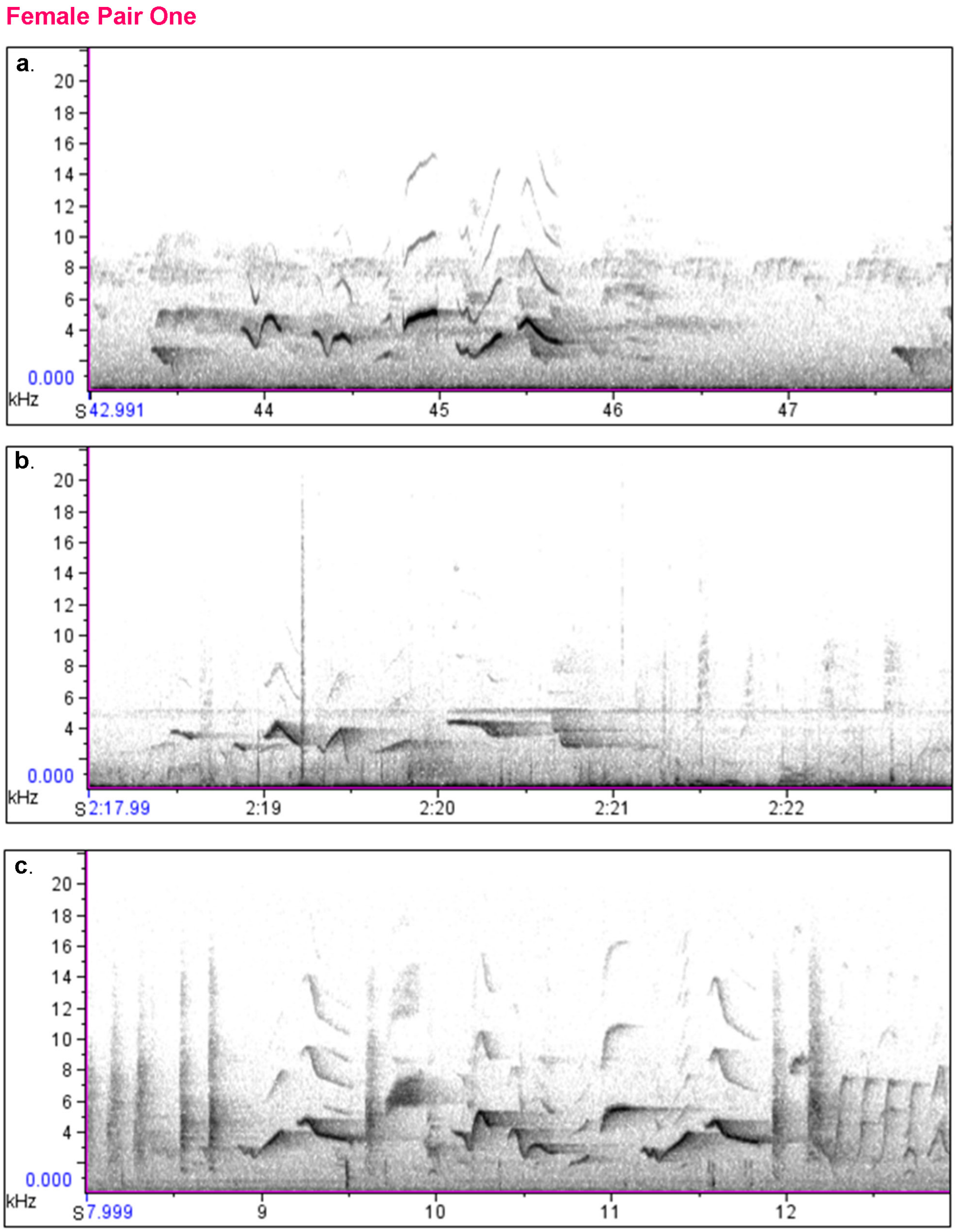

Fig. 3. Female Song, Pair One. Three recordings of female Puerto Rican Oriole song by the banded female of pair one in March 2014. All spectrograms produced in Raven with the same time and frequency scale.

slight increase around dusk.

Both pairs of Puerto Rican Orioles in this population were nesting during the time of our study in March 2013 and March 2014. Both the male and the female of both pairs were seen repeatedly around the nest. Orioles utilized three native types of palm trees for nesting within Maricao State Forest: the sierra palm (*Prestoea acuminata*), the Puerto Rico palmetto (*Sabal causiarum*), and most often, the royal palm (*Roystonea borinquena*). Exotic ornamental palm species like the Fiji fan palm (*Pritchardia pacifica*) and the spindle palm (*Hyophorbe verschaffeltii*) were also used for nesting around the cabin recreation area. In addition, we also observed Shiny Cowbirds (*Molothrus bonariensis*) near and around the nests; these are known nest parasites of Puerto Rican Orioles (Jaramillo and Burke 1999).

The results of ancestral state reconstruction indicate the common ancestor of the Caribbean oriole clade exhibited both male and female song (Fig. 6). Our reconstruction incorporates female song data for four of nine species within the Caribbean oriole clade; the other five species do not have published female song data (Fig. 6). All four species which we have data for exhibit both female and male song: the Bahama Oriole (Lee 2011), the Puerto Rican Oriole (this study), the Montserrat Oriole (*Icterus oberi*; Oppel *et al.* 2012, Fraga *et al.* 2016), and the Moriche Oriole (*I. cayanensis chrysocephalus*; Jaramillo and Burke 1999).

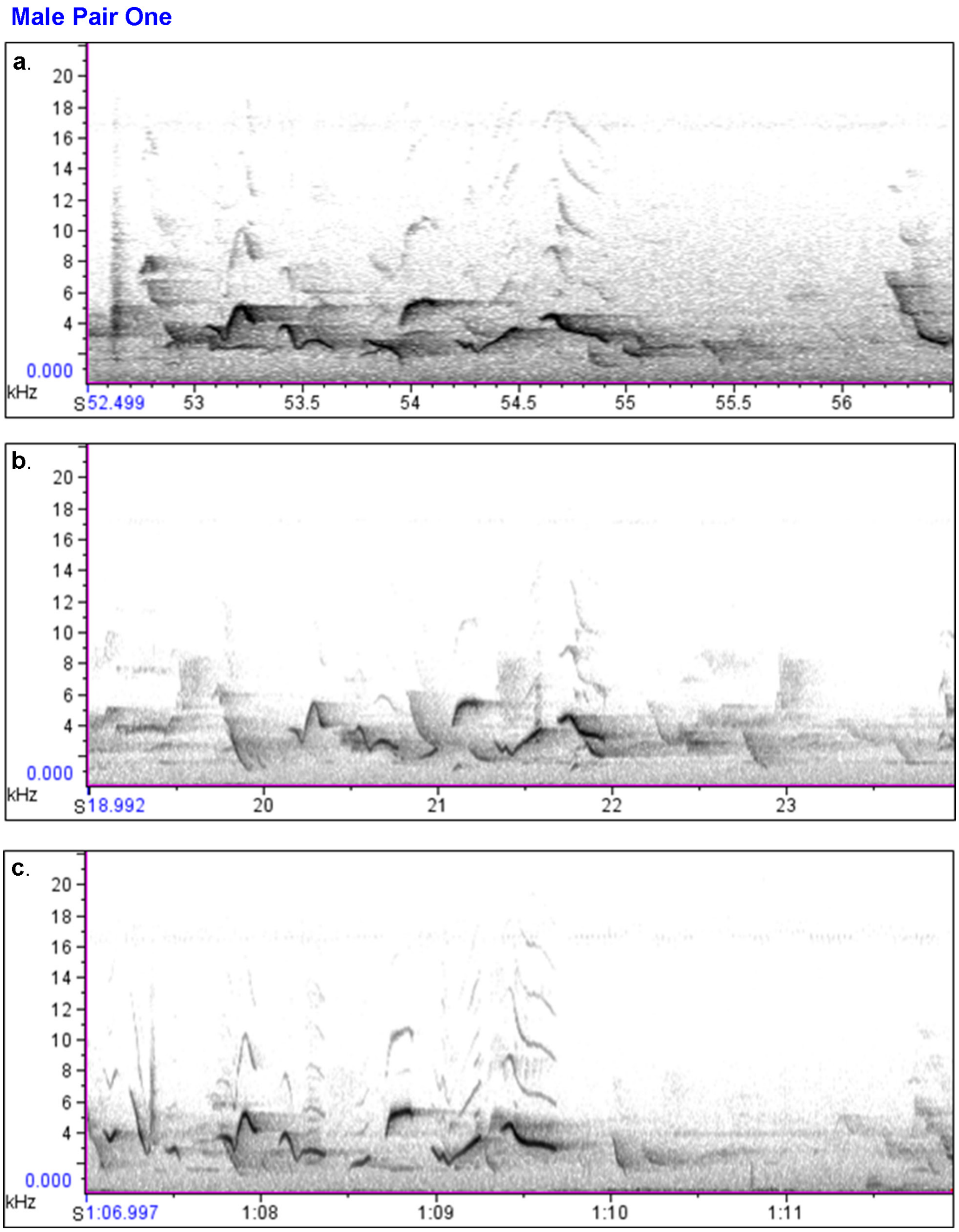

Fig. 4. Male Song, Pair One. Three recordings of male Puerto Rican Oriole song by the male from pair one in March 2014. All spectrograms produced in Raven with the same time and frequency scale.

Discussion

We observed and recorded female Puerto Rican Oriole song for the first time. Before this study, female Puerto Rican Oriole song had not been identified or recorded; in fact, many experts in Puerto Rico believed that only males sang. Furthermore, all previous recordings of Puerto Rican Oriole song were from unknown-sex individuals. Thus, our recordings are also the first confirmed male recordings of this island endemic.

We observed more male songs than female songs. This leads us to believe that male song is more common than female song. However, our data suggest that male and female Puerto Rican Orioles sing similar songs. The song is comprised of a series of melodic whistles, whereas the calls and chatter are less musical. This information is consistent with previous characterization of Puerto Rican Oriole song (Price *et al.* 2007). Future comparisons of many male and female individuals can test for quantitative similarities and differences between the sexes.

The Puerto Rican Oriole is the first tropical oriole that our group explicitly set out to study and determine whether or not it has female song. Nearly all tropical orioles with well-documented singing behavior have female song (Price *et al.* 2009). However, the singing behavior of most tropical oriole species is not well-documented.

Our new female song results, incorporated with the phylo-

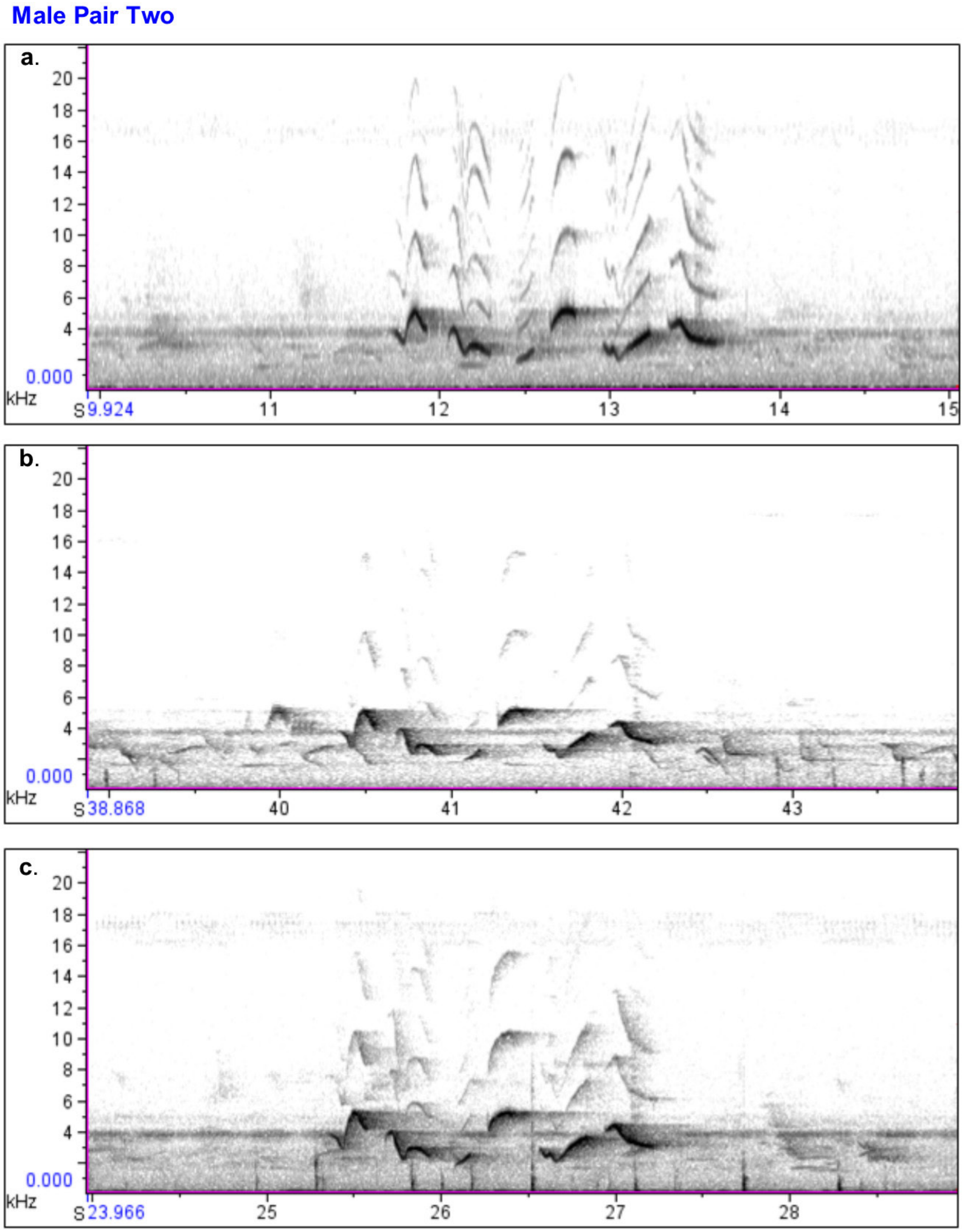

Fig. 5. Male Song, Pair Two. Three recordings of male Puerto Rican Oriole song by the banded male from pair two in March 2014. All spectrograms produced in Raven with the same time and frequency scale.

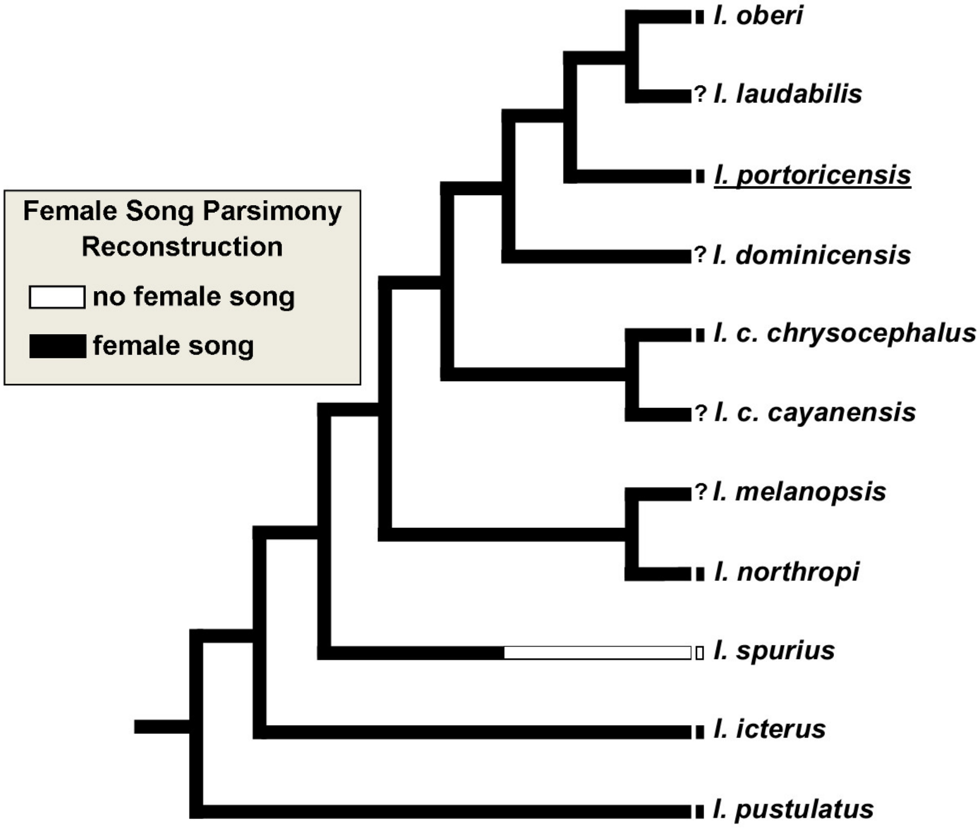

Fig. 6. Ancestral state reconstruction of the Caribbean oriole clade completed in Mesquite. Each species is scored as either having both female and male song, having male but no female song, or unscored due to missing data ("?"). *Icterus icterus* and *I. pustulatus* are included as outgroup representatives of the two other main oriole clades (most of which also have female song; Odom *et al.* 2015). Phylogeny is based on Sturge *et al.* (2009). *I. cayanensis chrysocephalus* and *I. cayanensis cayanensis* are abbreviated as *I. c. chrysocephalus* and *I. c. cayanensis*, respectively. Two species within the Caribbean oriole clade (*I. bonana* and *I. auricapillus*; female song presence unknown) are not included in the figure.

genetic reconstruction of the Caribbean oriole clade (Fig. 6), provide further evidence that the common ancestor of the Caribbean oriole clade likely had female song. Since these tropical Caribbean species produce both male and female song, they have retained the ancestral state of the common ancestor for the clade. These birds also exhibit tropical residence, thus providing further support for previous findings that female bird song correlates with tropical residence (Price *et al.* 2009). In addition, one of the outgroup species, the Orchard Oriole, lost female song in correlation with a move to temperate residence and breeding (Price *et al.* 2009).

Many studies show that female song correlates with tropical residence (Langmore 1998, Price 2009). Differences in life history traits between temperate and tropical regions could drive the correlation between female song and tropical latitudes. In the tropics, there are longer breeding seasons due to decreased or no seasonal shifts, which facilitates year-round territory holding. We repeatedly observed and recorded territorial behavior of two pairs of Puerto Rican Orioles at the Maricao study site. Pairs consistently moved together through the study site, responded to playbacks, and maintained stable territories both in the breeding and non-breeding seasons (Fig. 2). This tropical lifestyle likely increases the opportunity for female-female competition and joint territory defense and increases risk for the breaking of monogamous or long-term pair bonds (Morton 1996, Langmore 1998, Stutchbury and Morton 2001, Odom *et al.* 2014).

In contrast, temperate female songbirds arrive on their breeding grounds, quickly find a mate, build a nest, and raise their young. Generally, the female is less likely to participate in territory defense, thus song is likely less important to them. Female song in the tropics is likely to function in territory defense, which could explain its apparently greater prevalence in the tropics (Cooney and Cockburn 1995). Documentation of female song throughout the year in tropical areas would provide further evidence for the importance of female song in territory defense (Odom *et al.* 2014).

Further studies should focus on determining the rate and specific function of female song in the Puerto Rican Oriole and other species within the Caribbean oriole clade. Analyses of vocalizations throughout the annual cycle will be useful in determining the extent and role of song by the two sexes during the breeding and non-breeding seasons. Ideally, studies of several of these taxa should evaluate the full range of hypothesized functions of female song, ranging from mate attraction during the breeding season to competition for resources during the non-breeding season (e.g., Langmore 1998). Furthermore, we lack good female song data for many other tropical icterids (Odom *et al.* 2015). In fact, even basic information on the presence or absence of female song is lacking for the majority of songbird species (Odom *et al.* 2014). Ornithologists and birders across the Caribbean should be alert for and should attempt to observe and record additional examples of female bird song.

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