SEX-ROLE REVERSAL IN SONG? FEMALES SING MORE FREQUENTLY THAN MALES IN THE STREAK-BACKED ORIOLE

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Abstract.   Birds in which both sexes produce complex song are more common in the tropics than in the temperate north, where typically only males sing. Yet surprisingly little is known about female song characteristics in most tropical species. Here we present a comparison of female and male singing behaviors in the Streak-backed Oriole (*Icterus pustulatus*), a tropical songbird in which both sexes perform solo songs. Females sing much more frequently than males and produce songs with similar acoustic complexity. Rates of singing by both sexes were higher during breeding than postbreeding while the rates of most other vocalizations did not change, suggesting that song plays an important role in breeding. To our knowledge, this is the first reported species in which females regularly sing at higher rates than males; however, few studies have examined female song in other sexually monomorphic or weakly dimorphic species, so such patterns might not be unique.

Key words: Bird song, female song, Icterus pustulatus*, tropical songbird, sexual selection, vocal behavior.*

¿Inversión del Rol Sexual del Canto? Hembras Cantan con Mayor Frecuencia que Machos en *Icterus pustulatus*

Resumen.   En aves tropicales es más común que ambos sexos produzcan cantos complejos que en aves de zonas templadas, en donde típicamente el macho es el que canta. Por lo que es sorprendente que se conozca tan poco de las características del canto de las especies tropicales. Con nuestro estudio reportamos una comparación entre sexos de la conducta del canto en *Icterus pustulatus*, ambos sexos de esta ave canora tropical cantan. Las hembras cantaron con mayor frecuencia que los machos y produjeron cantos con complejidad acústica similar. Las tasas de canto de ambos sexos fueron mayores durante el periodo reproductivo que el post-reproductivo, mientras que las tasas de otras vocalizaciones no cambiaron, lo que sugiere que el canto juega un papel importante en la reproducción. Hasta donde sabemos este es la primera especie en donde se reporta que las hembras cantan regularmente con mayor tasa que los machos; sin embargo, pocos estudios han examinado el canto de las hembras en especies sexualmente monomórficas o poco dimórficas, por lo que este patrón puede no ser único.

Bird song is generally thought to be restricted to male songbirds. Indeed, song has been defined by some authors as being produced primarily by males during the breeding season (Catchpole and Slater 1995). This view may be largely attributed to the fact that the majority of research effort on bird song has been directed toward temperate passerines in which typically only males sing (Marler and Slabbekoorn 2004). Female song is uncommon in the temperate north (Riebel 2003), and in species in which it does occur, females usually sing less frequently than males and often with less complexity (Beletsky 1982, Arcese et al. 1988, Langmore et al. 1996, Langmore 2000, Vondrasek 2006, Garamszegi et al. 2007).

Evidence is accumulating, however, that species in which both sexes regularly produce complex song are relatively common in the tropics (Morton 1996, Langmore 1998, Stutchbury and Morton 2001, Riebel 2003, Collins 2004, Slater and Mann 2004). Females of many tropical species even coordinate their vocalizations with males to perform complicated duets (Farabaugh 1982, Langmore 1998, Hall 2004). Female bird song could be the rule rather than the exception in tropical environments (Morton 1996), yet surprisingly little is known about the prevalence or function of these vocalizations in tropical taxa (Kroodsma et al. 1996).

Most research to date on tropical female song has focused on duetting species rather than species in which females produce complex vocalizations individually as solo songs (Slater and Mann 2004). This bias is at least partly explained by the fact that the complex coordination between males and females to create synchronized duets is seen as such a remarkable phenomenon (Levin 1996, Mennill and Vehrencamp 2005, Hall and Magrath 2007). But it is also likely that female solo song in the tropics has been widely underreported, since many tropical species are sexually monomorphic with year-round territorial defense by both sexes, so female singers are probably frequently mistaken for males.

Here we present the first detailed description of singing behavior in the Streak-backed Oriole (*Icterus pustulatus*), a socially monogamous tropical songbird in which pairs maintain year-round

territories, nest-building and incubation are performed exclusively by females, and both sexes are known to sing (Jaramillo and Burke 1999, Howell and Webb 2000). Streak-backed Orioles occur from northern Mexico to Costa Rica and vary in physical appearance across this range (Jaramillo and Burke 1999). Northern forms are sexually dichromatic, with males more colorful than females, whereas southern forms are monomorphic, with males and females that are similar in appearance. Our study focused on a color-banded population of Streak-backed Orioles in the middle of this range in the state of Morelos, Mexico. Females and males of this subspecies (*I. p. pustulatus*) are only moderately dichromatic, with the most colorful females nearly indistinguishable from males.

Our primary objective in this study was to compare the singing behaviors of males and females to determine whether their songs differ in rates of delivery or in vocal complexity. We report natural singing rates as well as rates of other vocalizations in this species, and we compare a variety of song features between the sexes. We also compare vocal behaviors between the breeding and postbreeding seasons to examine how they change over time. This analysis provides one of the few descriptions of singing behavior in a species with frequent female solo song and represents a first step toward understanding the functional significance of female song in this little-studied songbird.

METHODS

We recorded the vocalizations of male and female Streak-backed Orioles during two distinct phases of their annual cycle: from 11 May to 1 June 2006 during the breeding season when birds were establishing territories, building nests and initiating clutches; and again from 4 to 28 August 2006 during the postbreeding season after young had fledged. We also observed behaviors of these birds during the period between these two seasons as part of a larger study in which we collected detailed records on nesting success and other breeding activities. Most males and females recorded in this study were in mated pairs (91% of birds recorded in the breeding season and 100% of those in the postbreeding season were in known pairs), and all were recorded within a 700×400 m area of tropical deciduous forest and pastureland near the Sierra de Huautla Biosphere Reserve, Morelos, Mexico (18°26′N, 99°00′W). We captured most individuals in this population (>200 birds total), banded them with unique combinations of colored leg bands, and collected blood samples for molecular sexing. Sex was determined based on coloration of tail plumage of adults (Jaramillo and Burke 1999) or standardized molecular sexing techniques (Griffiths et al. 1998; with modified primers available from KEO). Genetic analyses agreed 100% with sexing based on plumage ($n = 80$).

VOCALIZATION RATES

During each season (breeding and postbreeding), we followed individual color-banded birds during peak activity in the morning (a 4-hr period beginning at sunrise) and recorded each individual's vocalizations for up to 10 min at a time, or until the bird was lost from view (mean ± SE recording bout was 8.3 ± 0.2 min). All recordings were made using an omnidirectional microphone (model ME62 with K6 power supply; Sennheiser Electronic Corporation, Wennebostel, Germany) in a parabolic dish (Telinga Microphones, Tobo, Sweden) connected to a solid state digital recorder (model PMD670; Marantz, Sagamihara, Japan). Male and female orioles were followed on alternate days (i.e., males on one day, females on the next) over a total of 20 days during each season, so that we obtained 10 recording days for each sex

spanning the same phase of the breeding cycle. We recorded each bird on multiple days for no more than 10 min each day, with the goal of obtaining a maximum of 30 min of recordings from each bird each season (mean ± SE recording time per individual was 22.0 ± 2.1 min for females and 18.6 ± 2.2 min for males). We recorded 23 males and 24 females during the breeding season and 13 males and 12 females during the postbreeding season, with 7 males and 7 females recorded during both seasons (i.e., 58 total individuals recorded).

Digital recordings were made at a sampling rate of 48 kHz, and spectrograms were generated using either Raven 1.2.1 or Raven Lite 1.0 (Cornell Lab of Ornithology, Ithaca, New York; frequency resolution = 135 Hz, time resolution = 10.7 msec). Streak-backed Orioles produce a variety of different types of sounds in addition to those generally considered songs (Hardy et al. 1998, Jaramillo and Burke 1999). Thus, we divided all vocalizations into four categories based on consistent acoustic patterns in spectrograms (Fig. 1). (1) Songs were defined as any vocalizations that included multiple whistled notes and were preceded and followed by intervals greater than 0.5 sec. These vocalizations were relatively stereotyped and resembled the complex whistled songs of many other oriole species (Hardy et al. 1998, Price et al. 2007). (2) Chits were single whistled notes preceded and followed by >0.5 sec intervals. These notes were similar in structure to the individual syllables included in songs, but they were clearly distinguished by being produced singly rather than as components of a song type. (3) Chatters consisted of harsh, short (<50 msec), broadband sounds given in rapid succession. (4) Whines were longer (>200 msec), harmonically rich calls, typically produced singly and at relatively low amplitudes. Calls with characteristics very similar to our chits, chatters, and whines have been described for various other oriole species (Miller 1931, Beletsky 1982, Hardy et al. 1998, Jaramillo and
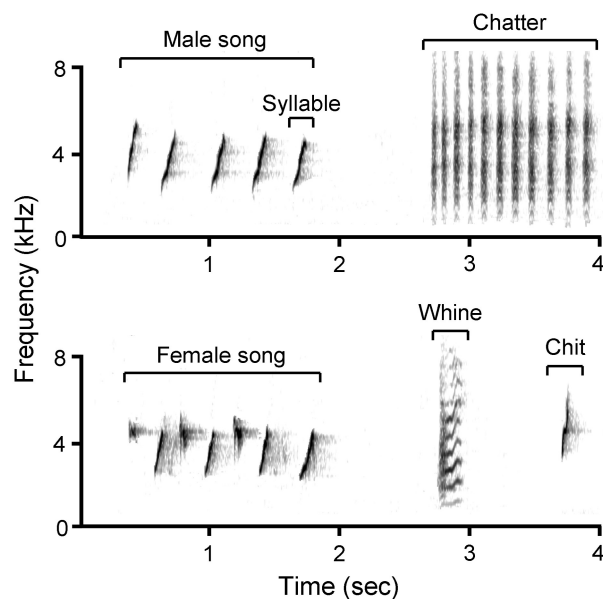

FIGURE 1. Spectrograms showing representative samples of Streak-backed Oriole vocalizations, recorded in Sierra de Huautla, Morelos, Mexico in 2006. Top: song by a male with an example of a syllable indicated, and a chatter. Bottom: song by a female, a whine, and a chit. Both sexes were observed producing all four types of vocalization.

Burke 1999, Howell and Webb 2000). All four types of vocalization were produced by both sexes, were similar in general acoustic pattern across individuals, and were easily distinguished from each other in spectrograms.

SONG STRUCTURE

To compare the songs of males and females, we measured the acoustic features of up to 10 randomly selected examples of song from each recorded individual. Many individuals were represented by fewer than 10 examples (mean ± SE: 7.0 ± 0.6 songs per female and 4.7 ± 0.8 songs per male) because they produced fewer than 10 clear songs in our recordings, and we did not include recorded vocalizations that were distorted or not clearly distinguishable from background sounds. We used these replicate measurements to calculate mean song features for each individual bird ($n = 31$ females and 18 males).

For each song, we measured the song duration, frequency range, number of syllables, number of syllable types, and syllable diversity (described below), using the time and frequency cursors in Raven 1.2.1. Song duration was measured as the interval from the beginning of the first syllable to the end of the last, and frequency range was the difference between the highest and lowest frequencies of whistled syllables that were clearly detectable above background noise. We counted the number of individual syllables, defined as continuous sounds in onscreen spectrograms (Fig. 1), and the number of syllable types, defined as sounds with identical or nearly identical acoustic measurements (Price et al. 2007). Syllables classified as the same type were very similar and clearly different from other types. Syllable diversity was calculated as the number of syllable types divided by the total number of syllables in each song.

STATISTICAL ANALYSES

We compared median vocalization rates and song feature measurements between the sexes and between seasons using two-tailed Mann-Whitney U-tests. We measured the rates of songs, chits, chatters, and whines produced per minute by each individual across multiple recordings, then used these mean values in our statistical comparisons, with individual birds as our data points. Likewise, to analyze song features, we used measurements of up to 10 clearly recorded song exemplars to calculate measurements of each song feature for each individual. Using mean values from recordings made on multiple days and locations was intended to minimize the effects of social context and different sound recording environments on our measurements of individual birds.

Because birds sang relatively rarely during the postbreeding season (see below), we were able to obtain fewer recordings of song suitable for measuring song features during the postbreeding recording period in August (four male songs and 32 female songs) in comparison to during the breeding season in May (80 male songs and 186 female songs). Therefore, we combined our recordings from both seasons to compare the song features of males ($n = 18$ individuals) and females ($n = 31$ individuals). Song features did not differ statistically between seasons (Mann-Whitney U-tests; $P > 0.10$ for all comparisons). All statistical tests had significance set at $P = 0.05$ and were conducted using SPSS Version 11.0 (SPSS Inc., Chicago, Illinois). Results are presented as means ± SE.

RESULTS

Females produced songs significantly more often than did males, both during the breeding season ($U_{24,23} = 71.5$, $P < 0.001$; Fig. 2A) and the postbreeding season ($U_{12,13} = 42.0$, $P = 0.02$; Fig. 2B). Females sang nearly four times more often than males in the

breeding season (0.78 ± 0.11 versus 0.22 ± 0.05 songs per min, respectively) and over six times more often after the breeding season had ended (0.12 ± 0.04 versus 0.02 ± 0.01 songs per min, respectively). Females also produced chatters more frequently than males during the breeding season (Fig. 2A, 0.86 ± 0.10 versus 0.64 ± 0.13 chatters per min, respectively; $U_{24,23} = 174.5$, $P = 0.04$), but these rates did not differ between the sexes later in the year (Fig. 2B, 1.14 ± 0.35 versus 0.79 ± 0.23 chatters per min, respectively; $U_{12,13} = 72.0$, $P = 0.23$). Other vocalizations were not produced at significantly different rates by the sexes during either season ($P > 0.3$ for all comparisons).

Birds in our population began building nests in early May, and the majority of females were engaged in nest building during most of our first recording period. The first clutches were laid on 25 May, with other pairs laying within the subsequent two weeks. For both males and females, singing rates appeared to decline during May after nest building had begun (Fig. 3) and decreased significantly between the breeding and postbreeding seasons (males: $U_{23,13} = 54.0$, $P < 0.001$; females: $U_{24,12} = 74.0$, $P < 0.001$; Fig. 2A, 2B). This decrease was particularly dramatic in males, whose average song rates declined from >0.4 songs per min in mid-May (Fig. 3) to 0.02 songs per min in August. Only four songs from three males were recorded during the entire 20-day postbreeding recording period, whereas 103 total songs from 15 males (including poor recordings) were recorded over the same number of days during the breeding season. Furthermore, few male songs were heard during daily field observations in June following the first recording period (<10% of identified singers were male), indicating that the relatively low song rates by males continued throughout the breeding season.

Production of whines also decreased somewhat in both sexes between the breeding and postbreeding seasons (males: $U_{23,13} = 91.5$, $P = 0.06$; females: $U_{24,12} = 120$, $P = 0.006$; Fig. 2A, 2B).
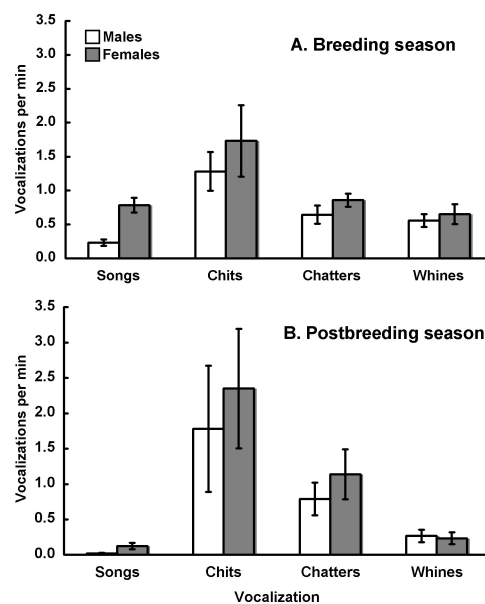

FIGURE 2.   Mean (± SE) vocalizations per min of male and female Streak-backed Orioles recorded during (A) the breeding season from 11 May–1 June 2006 ($n = 23$ males and 24 females) and (B) the postbreeding season from 4–28 August 2006 ($n = 13$ males and 12 females) in Morelos, Mexico.
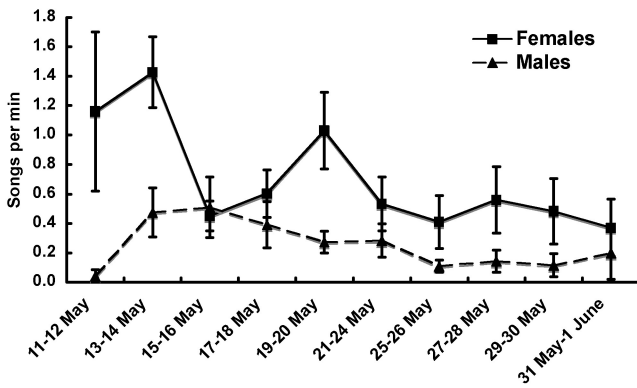
FIGURE 3.   Mean (± SE) song rates per min of male and female Streak-backed Orioles recorded over 20 days of observation during the 2006 breeding season in Morelos, Mexico. Males and females were recorded on alternate days (i.e., males on 11 May, females on 12 May, etc.), and days are paired in this figure to allow comparison between the sexes. Songs of four to eight individuals were recorded each day, and no recordings were made on 22 and 23 May due to weather.

Rates of chits and chatters, however, remained unchanged ($P > 0.6$ for all comparisons). Males and females often appeared to produce whines in response to the calls of their mates, suggesting that these acoustically complex vocalizations play a role in inter-sexual communication.

Male and female songs were similar in overall acoustic structure. We found no consistent differences between the sexes in any of the song components we measured ($U_{18,31} \leq 215, P \geq 0.18$ for all comparisons; Fig. 4). Both male songs and female songs were typically between 0.5 sec and 2.0 sec in duration and consisted of three to seven whistled syllables with frequencies between 2 and 6 kHz (Fig. 1). Songs usually included two or more syllable types and occasionally included notes similar to chatters and whines. Although we were unable to investigate the sizes of syllable type and song type repertoires in individuals, we did observe that songs produced by the same individual on different occasions sometimes differed, usually by the apparent addition or
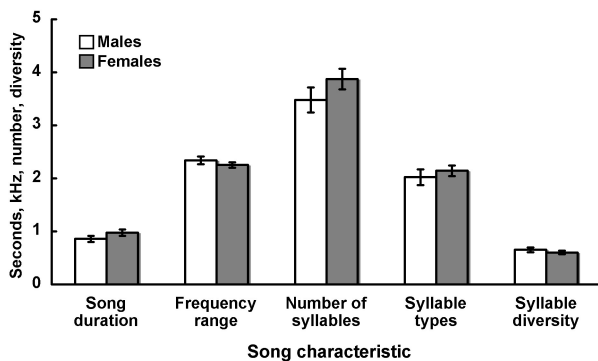

FIGURE 4.   Mean (± SE) measurements of song duration (sec), frequency range (kHz), number of syllables, number of syllable types, and syllable type diversity (syllable types divided by number of syllables) of songs recorded from male ($n = 18$) and female ($n = 31$) Streak-backed Orioles in Morelos, Mexico in 2006. No song measurements differed consistently between the sexes.

subtraction of syllables, suggesting that birds do not produce just one stereotyped song type each. Individuals occasionally produced songs following the songs of their mates or neighbors, but these vocalizations were never produced as parts of coordinated antiphonal duets as observed in some other tropical oriole species (Jaramillo and Burke 1999).

DISCUSSION

In their species account for Streak-backed Orioles, Jaramillo and Burke (1999) report that males of this species do not sing often and that female songs "are even more infrequent and less complex than the songs of males." In contrast to this description, our data provide strong evidence that the majority of songs in this species are produced by females and that female songs are at least as complex as those of males. Rates of most other types of vocalizations in our study did not differ between the sexes, suggesting that differences in singing rates were not due to differences in overall vocalizing rates or to bias in the way these vocal behaviors were measured. Furthermore, we found a similar difference between male and female song rates in another population of Streak-backed Orioles (I. pustulatus microstictus) in Sonora, Mexico (27°10′N, 108°55′W; JJP, unpubl.data), showing that this pattern is not unique to our study population. Thus, this species appears to provide a striking example of how female song can be overlooked in the field when males and females have similar plumage. More studies of color-banded individuals of known sex are clearly needed to improve our understanding of song in tropical songbirds.

Female solo song is also reported to occur in other members of the genus *Icterus* (Jaramillo and Burke 1999, Howell and Webb 2000), though most observations to date have been anecdotal, and vocal behaviors have been analyzed systematically in only a few mostly northern species. In the Baltimore Oriole (I. galbula), the only other oriole in which female song has been studied directly, females produce songs that resemble male songs in their frequency characteristics and duration, but females sing rarely in comparison to males (Beletsky 1982). Female Orchard Orioles (I. spurius) and Hooded Orioles (I. cucullatus) also sing relatively rarely in comparison to males (Scharf and Kren 1996, Pleasants and Albano 2002; JJP, pers. obs.), and female song in Hooded Orioles is reported to be less elaborate than the song of males. In Audubon's Oriole (I. graduacauda), a tropical resident species, females appear to sing as frequently as males, and mated pairs often appear to counter-sing with each other (Flood 1990). Interestingly, in the Bullock's Oriole (I. bullockii), the sister taxon to the Streak-backed Oriole (Omland et al. 1999), observations by Miller (1931) suggest that females sing more often than males during certain times of the year. Further study of that species is certainly warranted to investigate this possibility.

Birds in which both sexes sing are relatively common in the tropics (Morton 1996, Langmore 1998, Stutchbury and Morton 2001, Slater and Mann 2004); however, to our knowledge, our study provides the first evidence of a species in which females regularly sing more frequently than males. As in other previously studied oriole species (Skutch 1996, Jaramillo and Burke 1999), singing in Streak-backed Orioles appears to decline after the beginning of nest construction, indicating that song may play an important role in territorial interactions and pair bond establishment prior to the nesting period (Whittingham et al. 1997). Production of whines also decreased somewhat in both sexes after the breeding season, suggesting that these calls may play a role during breeding as well.

Why females sing so much more often than males in Streak-backed Orioles is unclear. In most passerines, males are the more competitive sex, and male songs are thought to have evolved through sexual selection for defense against male rivals and for attracting mates (Catchpole and Slater 1995, Collins 2004). When females sing, either solo or in duets with males, it is often thought to occur primarily for the same reasons (Langmore 1998, 2000, Hall 2004). For example, evidence from a variety of species suggests that female songs function to deter same-sex competitors for territories or mates (Beletsky 1983, Arcese et al. 1988, Cooney and Cockburn 1995, Levin 1996). Female solo song may also function in mate attraction (Langmore et al. 1996, Morton 1996, Eens and Pinxten 1998) or to maintain intrapair contact and coordinate breeding activities (Halkin 1997, Whittingham et al. 1997, Slater and Mann 2004). None of these hypotheses, however, adequately explains why females would sing more frequently than males, as occurs in Streak-backed Orioles.

Female Streak-backed Orioles also produce chatters more often than do males during the breeding season, and these vocalizations are presumed to have an agonistic function in many oriole species (Beletsky 1982, Flood 1990, Scharf and Kren 1996, Jaramillo and Burke 1999, Pleasants and Albano 2002). Female song might have a similar function, perhaps in defending the nest site or other forms of resource defense. Studies in a variety of other species suggest that female signaling is more likely to evolve in the context of such resource competition than for mate attraction (LeBas 2006). Both male and female Streak-backed Orioles regularly leave the territory to forage, and off-territory behavior seemed particularly common in our population during the early breeding season when song rates were at their peak. Perhaps females need to sing at higher rates because males spend more time than females away from their territories during this period, leaving females to defend areas on their own (Cooney and Cockburn 1995, Heinsohn et al. 2005). Future studies should examine the social contexts of male and female song as well as how much time each sex spends near the nest during the breeding season to investigate these possibilities.

Streak-backed Orioles are a moderately sexually dichromatic, socially monogamous species (Jaramillo and Burke 1999, Howell and Webb 2000). Females alone build the nests and incubate eggs, and both sexes feed the young. Thus, at least superficially, this species does not appear to be one in which the standard mating roles are reversed. However, observed breeding behaviors do not always reflect actual reproductive patterns (Birkhead and Møller 1992), and the selection pressures acting on female signals are not necessarily the same as those acting on males (Langmore 1998, LeBas 2006, Murphy 2007). Future studies should use molecular analyses to determine mating patterns and reproductive success of individuals. Studies should also investigate the function of female song in this species through detailed playback experiments. Communication systems in which songs are performed mostly by females are unusual in songbirds. However, considering how few previous studies have examined female song in tropical monomorphic or weakly dimorphic species, such patterns might not be unique.

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