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Authors: Christopher J. Clark, David Rankin, and Katherine Johnson

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## Female song in Costa's Hummingbird (*Calypte costae*)

Christopher J. Clark,<sup>1\*</sup> David Rankin,<sup>1</sup> and Katherine Johnson<sup>1</sup>

**ABSTRACT**—Bird song has been extensively studied in oscine passerines, but far less is known about song in hummingbirds, which are distantly related to passerines. Song is generally thought of as a male trait. Here we document song in 2 wild female Costa's Hummingbirds (*Calypte costae*) of 10 examined. Their vocalizations closely resembled male song and were produced, undirected, on territories just prior to the breeding season. Both birds were confirmed as female and not young males, which resemble females: one had an enlarged ovary, and the other laid eggs. Our results imply that at least some female hummingbirds may learn song as well as males and have similar song capacity as males. The function, if any, of female song was not immediately clear. Female song seemed rarer in this population than in males and thus easy to overlook. Presence of female song could also be an overlooked phenomenon in other hummingbird species. *Received 3 July 2017. Accepted 27 July 2018.*

**Key words:** female song, hummingbird, learning, Trochilidae, vocalization.

### Canto en las hembras del colibrí *Calypte costae*

**RESUMEN** (Spanish)—El canto de las aves ha sido estudiado extensivamente en las paserinas oscinas, pero se sabe mucho menos del canto de los colibríes, que están lejanamente emparentados de las paserinas. El canto se concibe generalmente como una cualidad de los machos. Aquí documentamos el canto de dos hembras silvestres del colibrí *Calypte costae* de un total de 10 examinadas.

<sup>1</sup>Department of Evolution, Ecology, and Organismal Biology, University of California, Riverside, CA, USA

\*Corresponding author: cclark@ucr.edu

Sus vocalizaciones se asemejan al canto de los machos y fueron producidos, sin dirección, en territorios justo antes del inicio de la estación reproductiva. Ambas aves fueron confirmadas como hembras y no machos juveniles, que se parecen a las hembras: una tenía un ovario agrandado y la otra puso huevos. Nuestros resultados implican que al menos algunas hembras de colibrí pueden aprender cantos tan bien como los machos y tienen capacidades de canto similares a las de éstos. La función, si existe, del canto en hembras no es inmediatamente clara. El canto de las hembras parece ser más raro en esta población que aquel de los machos y por ello fácil de ignorar. La presencia del canto en hembras podría ser un fenómeno que ha pasado desapercibido en otras especies de colibríes.

**Palabras clave:** Aprendizaje, canto en hembras, colibrí, Trochilidae, vocalización.

Hummingbirds and oscine passerines share a number of similarities in the biology of song. Because these 2 clades are distantly related (Prum et al. 2015), these similarities have apparently evolved convergently. We define song as a vocalization broadcast in an undirected fashion from a defended territory, whereas calls are either only directed at other individuals or are given in a variety of contexts rather than in a primarily territorial context. Although this definition would pose problems for some vocalizations made by members of other bird clades, it isolates songs as a distinct type of vocalization in the “bee” hum-

mingbirds (Mellisugini; Clark et al. 2018). Song is socially learned from conspecifics in hummingbirds (Baptista and Schuchmann 1990, Araya-Salas and Wright 2013), just as it is in oscines. Singing is usually associated with breeding territoriality and, in temperate oscines, is often thought of as performed by males but not females. However, this belief could be caused by ascertainment bias, in which female song is present but unreported; recent work has suggested that female song in oscines is widespread and ancestral (Odom et al. 2014, Webb et al. 2016). Here, we document 2 individual female Costa's Hummingbirds (*Calypte costae*) singing in an undirected fashion from territories held prior to the breeding season.

Costa's Hummingbirds are year-round residents on the University of California, Riverside (UCR) campus. In late fall, females hold feeding territories near blooming flowers in areas where they later nest (nesting begins in approximately Jan). After breeding ends in approximately June, the birds then hold feeding territories centered on flowers. Adults molt from approximately June to October (Baltosser and Scott 1996) while hatch-year (HY) birds may molt later than adults (Pyle et al. 1997), sometimes as late as January (CJC, DR, pers. obs). While adult males are easily identified by their plumage, HY birds resemble adult females. Thus, young pre-molt males can be confused with adult females.

Adult males sing year-round (Baltosser and Scott 1996, Williams and Houtman 2008). HY males begin to sing soon after fledging, and while their initial subsongs are variable and distinctive from adult male song, over the next few months this subsong coalesces into adult song as they go through the stages of song learning (KJ and CJC unpubl.). Thus, when in November we detected a female-plumaged bird singing a male-like song, the most prosaic possibility was that the singer was actually male, for instance a young male that was late to molt but had already developed adult song, or an adult male that for some reason had molted into female plumage. After we determined this bird was actually female, we then sought out additional females to determine whether this was a single aberrant individual or if female song may be a previously overlooked phenomenon present in Costa's Hummingbird.

## Methods

DTR discovered a singing female-plumaged Costa's Hummingbird (hereafter: female #1) holding a feeding territory in the UCR botanical gardens on 4 November 2016. Several other Costa's Hummingbirds held territories in the immediate vicinity, including at least 2 adult males that also sang. Recordings of song were made with a Telinga Pro parabola with a Sennheiser MKH 20 and a Sound Devices 702 24-bit recorder from distances as close as 2 m. Songs were cross-correlated with typical male songs in the software Raven 1.5 ([www.birds.cornell.edu/raven](http://www.birds.cornell.edu/raven)). Videos were recorded with Canon VIXIA HF R500 Digital Camcorder.

We recorded a single 1-hour time budget in the morning to document the presence of singing and other behaviors relevant to ascertaining whether this was a typical bird, such as whether it performed or received courtship displays. To examine whether other female Costa's Hummingbirds sang, we located and recorded comparable single time budgets between 0900 and 1030 h (PST) for 9 additional female Costa's Hummingbirds holding prebreeding territories between 15 November and 21 December 2016. We also made more extensive casual (untimed) observations of some of these females. In all cases, our formal time budget was representative of these further informal observations: birds that never sang during formal observations also never sang during informal observations.

To test the hypothesis that female #1 was male, on 29 November 2016 we collected and prepared her as a study skin (collector number CJC #412, specimen currently housed at UCR) and examined her gonads. A second singing female (female #2) was caught, color marked, banded (band number: K53146), and released.

## Results

### The singing birds were female

Female #1's phenotype was that of a typical female (Supplemental Video 1; <https://youtu.be/k8nXVPNC1UD>). She never engaged in courtship displays (as HY males sometimes do), and she occasionally was the recipient of displays from visiting males. During our observations in November, she did not engage in nest-building or other overt breeding behaviors. Her plumage was fresh, and she appeared to have just finished molting. Her

**Table 1.** Measurements of singing female Costa's Hummingbird and ranges for males and females.

	Female #1	Female #2	Adult males ( $n = 31$ )	Females ( $n = 37$ )	HY males ( $n = 22$ )
Wing chord (mm)	45.7	44.9	42.1–45.9	42.6–47.2	40.9–45.8
Tail length (mm)	23.8	25.5	21.1–26.6	20.7–25.6	20.9–26.5
Exposed culmen (mm)	17.5	17.2	15.2–17.9	15.7–19.6	15.6–18.3
Keel length (mm)	16.3		16.2–18.3	14.9–17.2	16.3–18.1
Weight (g)	3.1	3.5	2.7–3.5	2.6–3.7	2.9–3.7

bill was minimally corrugated, indicating she was adult (Pyle 1997), and her measurements were typical for a female Costa's Hummingbird (Table 1). Upon dissection, her gonad was a granular ovary ~2.5 mm in length (Fig. 1), a size that suggests she was preparing to breed (Williamson 1956). In our formal time budget, this female spent 2% of her hour singing. During informal observations she sometimes sang more frequently, giving the qualitative impression that frequency of song was variable. We digitally recorded 81 songs from 19 song bouts. Adult males holding feeding territories nearby (within 10 m) sang more frequently than this female and sang throughout the day, whereas female #1 sang primarily in the morning.

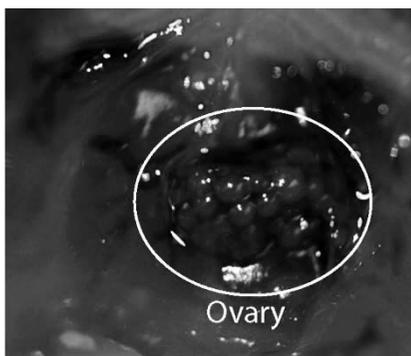
Eight of 9 other observed females never sang, but a ninth one did (hereafter, female #2). In our formal 1-hour time budget, female #2 sang 6 s total (0.17%). However, in an untimed session lasting roughly 40 min in which we recorded 11 song bouts (65 songs total), she sang as often as every 4 min while engaged in building a nest in the middle of campus (GPS: 33.974649, -117.328534). After she laid 2 eggs, she disappeared, meaning we were unable to follow her song ontogeny with the onset of nesting. Weeks later

she was resighted on a nest (and not singing) about 1 km away and ultimately fledged 2 young.

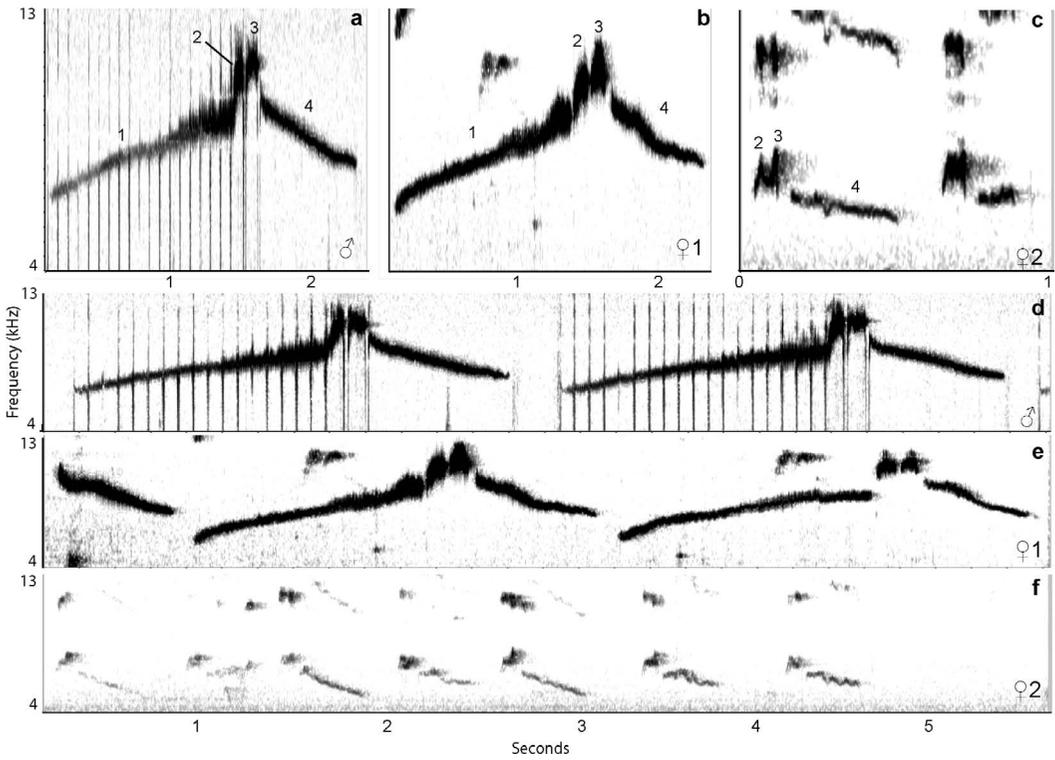
The songs of both females were recognizable as the same type of song that male Costa's Hummingbirds sing, but they nevertheless deviated from a normal male song (Fig. 2). Typical male song consists of an upsweep followed by a downsweep (Fig. 2a), and song bouts comprise several apparently identical songs sung in succession (Fig. 2d). Female #1's song was distinct in 3 ways: (1) it was fainter than male song; (2) element 1 of the song lacked the atonal clicking sound males make (Fig. 2b); and (3) her song always began with an initial downsweep followed by typical song (Fig. 2e). The song of female #2 less closely resembled male song; it did not have this initial upsweep (element 1 was missing entirely), and elements 2, 3, and 4 were lower pitched than in males. Because element 1 was missing from her song, this female's song bouts had a higher song repetition rate than a typical male song bout (Fig. 2f).

We compared the female songs to 7 typical songs of a male Costa's Hummingbird recorded at the Deep Canyon Desert Research Center (GPS: 33.649, -116.376). The cross-correlation between female #1 and these typical songs was (mean [SD]) 0.73 (0.055),  $n = 35$  comparisons to male songs. For comparison, songs from 3 additional male Costa's Hummingbirds had a correlation score of 0.73 (0.062),  $n = 126$  comparisons, with these "typical" songs. Female #2 songs had an average correlation score of 0.33 (0.031),  $n = 28$  comparisons to male songs. We attribute the lower correlation of songs of female #2 to male Costa's song to the missing upsweep and lower frequency.

These 2 females delivered song from territorial perches in an undirected fashion, just as male Costa's Hummingbird do. Other Costa's were usually within earshot of female #1, including multiple males holding feeding territories, which



**Figure 1.** Gonad of singing Costa's Hummingbird #1 (CJC #412). Collected 29 November 2016.



**Figure 2.** Female and male song in Costa's Hummingbird. Individual songs of (a) typical male, (b) female #1, and (c) female #2. Male song contains 4 elements (1–4). Female #1's song contained all 4 elements; female #2's song lacked element 1 entirely, and her elements 2–4 were lower pitched than a typical male song. (d–f) Example song bouts containing multiple songs. (d) Beginning of a typical male song bout (bouts are highly variable in length with subsequent songs identical to initial songs). (e) Female #1 began her bouts atypically, with an isolated element 4, followed by typical songs. Males, by contrast, begin with a normal song (i.e., beginning with element 1). (f) Female #2 partial song bout.

also sang more frequently than female #1. These other birds made it difficult to rule out the hypothesis that her vocalizations were directed at a distant bird, but none of these other individuals was clearly the recipient of her vocalization. Female #2's territory was in an area with few other hummingbirds routinely present, such that most of the time her song had no clear recipient in the vicinity. Both females also produced all of the typical calls of Costa's Hummingbird, such as chip calls and scolding (agonistic) calls that all members of this species produce, meaning that the songs were not simply a malformed version of one of these other vocalizations.

### Discussion

We showed that a small fraction of female Costa's Hummingbirds sing prior to (female #1) or

at the onset of (female #2) nesting. This behavior seems rare; only 1 of 9 randomly selected female Costa's Hummingbird sang (the first singing female was not located randomly). For comparison, most if not all males sing at least a couple of bouts per hour this time of year (Williams and Houtman 2008). Because these songs were produced in an undirected fashion from a territory and were clearly recognizable as the species-specific songs of male Costa's Hummingbird, we are confident we correctly identified these sounds as song, and that this song is homologous to the same vocalization produced by males.

### Does female song have function in Costa's Hummingbird?

Our data provide no clear answer to this question. If female song had a function, why was it apparently expressed by only a small fraction of

**Table 2.** Hummingbird species with reports of female song.

Species	Reference
Costa's Hummingbird ( <i>Calypte costae</i> )	This study
Blue-throated Hummingbird ( <i>Lampornis clemenciae</i> )	Ficken et al. 2000
Blue-fronted Lancebill ( <i>Doryfera johannae</i> )	Mobbs 1982
Long-tailed Hermit ( <i>Phaethornis superciliosus</i> )	Mobbs 1982
Reddish Hermit ( <i>Phaethornis ruber</i> )	Mobbs 1982

females? One possibility is that female song has no function and is expressed simply because it is genetically correlated with male song in Costa's Hummingbird (Lande 1980). In passerines, however, female song often does have function and is associated, for instance, with year-round territoriality and duetting with a mate (Benedict 2008, Odom et al. 2014). Costa's Hummingbirds do not hold shared territories between the sexes and do not hold the same territory year-round. Instead, they shift the location of their nonbreeding territories in response to temporal changes in food availability. Female #1 sang from her territory for nearly a month before we collected her, diminishing the possibility that female song in Costa's only occurs during a short window of a few days, as happens in some passerines (Byers and King 2000). The frequency of female song seemed reduced compared to males at the same time of year, but female #2's singing rate varied substantially.

The function of male song in hummingbirds is little studied. One apparent function is in courtship (Stiles 1982, Clark and Feo 2010), a function that female song clearly does not have. Male Costa's Hummingbirds also sing through the nonbreeding season, implying that song is multifunctional. Perhaps it serves to declare ownership or defense of feeding territories, functions that song could serve for females as well (Krieg and Getty 2016).

### How does female song develop?

Presumably female song is socially learned, as it is in male Costa's Hummingbirds (KJ and CJC, unpubl.). Our future work will document that males raised in isolation chambers absent sufficient tutoring have malformed songs somewhat similar to female

#2's song (KJ and CJC, unpubl.). Our observation of female song suggests that the proximate mechanisms (e.g., brain regions, hormones) responsible for song learning and production are present in some form in female Costa's Hummingbirds. Gahr (2000) reports that 5 female Anna's Hummingbird (*C. anna*) brains lacked song-related areas present in males. Our result suggests Gahr's result is not entirely general. Given that female song may be rare and only expressed by a few individuals, and/or only at the onset of the breeding season, there could be seasonal or individual variation in neural anatomy within females.

### Do other hummingbirds have female song?

Female song is reported in Blue-throated Hummingbird (*Lampornis clemenciae*) as a vocalization produced exclusively by females in the context of male–female interactions (Ficken et al. 2000). Their song is not produced in an undirected fashion or by males, meaning it is not clear whether these vocalizations are homologous to male song or songs of other species. The other reports of female song are from Mobbs (1982). Of dozens of species Mobbs held in captivity, he reported female song in 3 additional species (Table 2), 2 of which are hermits (*Phaethornis* spp.). This finding is somewhat surprising because several species of hermits have been extensively studied in the wild (Stiles and Wolf 1979, Araya-Salas et al. 2017). Males sing on their lek, whereas females do not hold lek territories. Hermits are monochromatic, however, meaning that observation of a singing animal may have caused previous observers to assume it was male, as has also happened in study of song in passerine birds (Odom and Benedict 2018).

### Acknowledgments

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## Nesting association of swifts (Apodidae) and wasps in Brazil

Renata Neves Biancalana<sup>1</sup>

**ABSTRACT**—Associations between social insects, such as wasps and bees, and birds are a common strategy related to nest protection. Several examples exist in the literature of bird–wasp interactions, many in the Neotropics, but some bird families, including swifts (Apodidae), lack information regarding this kind of association. This work reports 2 cases of Neotropical swift species nesting adjacent to wasp nests in southeastern Brazil: the Sooty Swift (*Cypseloides*

*fumigatus*) and Lesser Swallow-tailed Swift (*Panyptila cayennensis*). These are the first records of this kind of association in Brazil. *Received 12 July 2017. Accepted 27 July 2018.*

**Key words:** Brazil, *Cypseloides*, Neotropics, nests, *Panyptila*, swifts, wasps.

### Asociación en la anidación de vencejos (Apodidae) y avisvas en Brasil

**RESUMEN** (Spanish)—la asociación entre insectos sociales, como avisvas y abejas, y las aves es una estrategia común

<sup>1</sup> Programa de Pós-graduação em Zoologia, Universidade Federal do Pará & Museu Paraense Emílio Goeldi, Terra Firme, Belém, PA, Brazil; [renata.biancalana@gmail.com](mailto:renata.biancalana@gmail.com)