Female song in the Cyprus Wheatear *Oenanthe cypriaca*

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Abstract
Female song is widespread across bird species yet rarely reported. Here, we report the first observations and description of female song in the Cyprus Wheatear *Oenanthe cypriaca* and compare it to male song during the breeding season. Twenty-five percent of colour-ringed females were observed singing at least once, predominantly in April, compared to 71% of males that continued singing through the breeding period. We suggest that female song may have multiple functions in this species, but it may be especially important in territorial defence and mate acquisition.

Keywords Female bird song · Female songbirds · Passerine · Muscicapidae

Zusammenfassung
Weibchengesang beim Zypernsteinschmätzer *Oenanthe cypriaca*
Weibchengesang kommt bei vielen Vogelarten vor, es wird aber nur selten darüber berichtet. Hier präsentieren wir erste Beobachtungen und Beschreibungen des Weibchengesangs beim Zypernsteinschmätzer *Oenanthe cypriaca* und vergleichen diesen mit dem Gesang der Männchen während der Brutzeit. Im Vergleich zu 71% der Männchen, die über die Brutzeit hinweg sangen, wurden 25% der farbberingten Weibchen zumindest einmal beim Singen beobachtet, vorwiegend im April. Wir nehmen an, dass der Weibchengesang bei dieser Art vielfältige Funktionen erfüllt, vermutlich aber besonders wichtig für Revierverteidigung und Partnerfindung ist.

Introduction
Bird song was long assumed to be a primarily male trait, but recent work has shown female song to be widespread across bird species and ancestral (Odom et al. 2014; Riebel et al. 2019). Female song is rarely reported (Odom and Benedict 2018), particularly in less intensively studied taxa (Garamszegi et al. 2007), and singing females can be confused for males in sexually monomorphic species so that singing females are often overlooked (Langmore 1998; Kirschel et al. 2009a). Female song is suggested to have multiple functions including territorial defence, mate defence, mate attraction, coordination of breeding activities, and in intrasexual communication (e.g. duetting) (Langmore 1998).

Avian researchers have been called to address the lack of documented female song to facilitate understanding of its prevalence, function, and evolution (Odom and Benedict 2018). Here, we report the first observations of female song in the Cyprus Wheatear *Oenanthe cypriaca*, describe its song structure, compare its occurrence in relation to male song, and investigate some of the circumstances that may be associated with it.

Methods

Study species

Cyprus Wheatears are obligate migrants that breed in Cyprus and migrate to eastern sub-Saharan Africa for the non-breeding season (Xenophontos et al. 2017). Male song occurs during the breeding season when they are regularly observed singing from high perches and treetops (Collar...
and Christie 2019). Male song occurs in a frequency range between 4 and 7 kHz, and three song types were previously identified based on song structure (Sluys and van den Berg 1982). Male song has been described as a ‘monotonous, noisy, harsh buzzing or sawing’ (Flint 1995) and ‘a series of phrases consisting of rapid buzzes’ (Collar and Christie 2019), whilst to our knowledge, there are no reports or descriptions of female song in this species.

Both male and female Cyprus Wheatears have similar black and white plumage during spring and summer but can be distinguished in the field (see Christensen 1974; Flint 1995). The black mantle and wings on males are glossy and intense, whilst the same areas on females range from dull black to dark brown. Males tend to have a pure white forehead, crown and nape, whilst these areas in females vary from greyish to a dirty white.

Field site and data collection

Data were collected daily during the breeding season between 1 April and 31 July in 2019 and 2020 within the National Forest Park of Troodos, Cyprus (34°56′N, 32°51′E), where a colour-ringed population of Cyprus Wheatears has been actively monitored since 2009 (n=1043 colour-ringed individuals) (Xenophontos and Cresswell 2016). Each bird had a unique combination of four colour rings, that includes a metal ring provided by BirdLife Cyprus, and was aged and sexed when captured using plumage characteristics. Colour-ringed birds were monitored throughout the breeding season and so their behaviour also confirms their sex: only females build nests and incubate eggs. Plumage differences between the sexes are also very distinct when both the male and female of a pair are observed together.

Data were collected opportunistically during weekly visits to each breeding territory (n=86 territories in 2019 and n=73 in 2020) between 05:30 and 19:30. For each observation (n=1743 total observations of n=207 total individuals; April: n=605 observations and n=167 individuals; May: n=596 and 128, June: n=412 and 115, July: n=130 and 64, respectively), we recorded the bird’s ID, location, date, time and whether they were singing or not. We classed an observation as singing when we could visually observe the bird singing. We did not include observations when individuals were not detected, and we did not record the duration of individual observations. We recorded if birds older than two years occupied their territory from the previous year and if their partner returned or not. Where possible we recorded additional contextual information including when female–female conflict occurred, if birds were solo singing, or if a female was observed singing whilst a male (partner or otherwise) was present within the same territory. Ages are given as exact number of calendar years when birds were either ringed as juveniles or first-year birds, otherwise the age is suffixed with a plus to indicate their minimum possible age.

Song recording

We recorded female (n=2 individuals; n=7 recordings) and male (n=4 individuals; n=11 recordings) Cyprus Wheatear song during the 2020 field season using a Marantz PMD661 recorder (16-bit, 48 kHz sampling rate) and Sennheiser MKH8020 microphone housed in a Telinga parabolic reflector. We defined a note as a continuous sound without a gap, and we defined distinct series of notes as song bouts. Recordings were analysed in Raven Pro version 1.5 (Center for Conservation Bioacoustics 2014), where we visually inspected spectrograms to identify song bouts and to classify song types. We classified song types based on their note structure and then categorised each song bout by its song type. We analysed only those song bouts that did not overlap spectrally with calls and songs of other birds (conspecific or heterospecific), leaving n=33 female and n=45 male song bouts for analysis. From each song bout, we determined the peak frequency from the power spectrum of a song selection box drawn around the entire song on the spectrogram (Fast Fourier transform [FFT] size=512) using Raven Pro’s default settings, song rate, and duration. We calculated song rate as the number of notes in the song bout minus one, divided by the time from the beginning of the first note to the beginning of the last note (Kirschel et al. 2009b). The final note was excluded because song rates based on the full song bout omit the ‘gap’ after the last note, biasing the rate upward in songs with fewer notes. We noted evidence of faint harmonics in some recordings, but these were not consistently recorded and of low amplitude, so we focused our analysis on the fundamental frequency signal. Recordings are available at https://doi.org/10.7479/8vys-c734.

Statistical analysis

We compared the proportion of singing females with males for each month of the study. We used a logistic generalized linear mixed model (GLMM) with birdID and year as random intercepts, and included fixed effects of sex, month and age and interactions between sex and month, and sex and age in the model. We categorised age as a two-level factor with birds classed as either first-year or older than first-year. We used a logistic GLMM (i.e. binomial family) because the response variable was coded as zero or one depending on whether the observation included singing. Significance of model terms was tested using the Wald chi-squared statistic.

We tested for differences between the sexes in song parameters using a linear mixed model (LMM) with sex as a fixed effect and birdID as a random effect. We
log-transformed the response variable duration to ensure normally distributed residuals. We only used observations of song type 1 to test for differences between the sexes because this was the most common song type and was performed by both sexes. We used the Bonferroni p value adjustment for multiple comparisons because we tested for sex differences in song three ways: peak frequency, song rate and song duration. The analyses were carried out in R version 4.0.3 (R Core Team 2020) using the lme4 package (Bates et al. 2014). Results are reported as mean ± 1 standard error unless otherwise stated.

Results

We observed 21 of 84 (25%) individual colour-ringed female Cyprus Wheatears singing at least once, and 87 of 123 (71%) males. There were 28 separate occurrences of singing from 589 observations (4.8%) of colour-ringed females, and 401 of 1154 (34.7%) observations of males. The proportion of birds singing differed significantly between months (main effect of month, Wald test: $X^2 = 25.4$, $df = 3$, $p < 0.001$) and between sex and month (interaction between sex and month, Wald test: $X^2 = 10.9$, $df = 3$, $p = 0.012$) (Fig. 1). The proportion of birds singing was not significantly different between age groups (main effect of age, Wald test: $X^2 = 0.57$, $df = 1$, $p = 0.45$) nor between sex and age groups (interaction between sex and age, Wald test: $X^2 = 0.2$, $df = 1$, $p = 0.65$). Most observations of female song occurred in April, whilst observations of males singing peaked in April and continued through May and June, although the proportion of singing males decreased each month (Fig. 1).

Singing occurred for females returning to a previously held territory and regardless of whether their partner returned. Singing also occurred when moving to a new territory (Table SI) and in one of these cases a female sang from treetops in two territories before moving out of the field site, indicating potential prospecting behaviour. Two observations of females singing occurred alongside female-female conflict (2/28 = 7%) that involved ‘wing flicking’ and chasing. Two observations occurred with a single male present (2/28 = 7%). Two observations of female singing occurred when two males were present (2/28 = 7%) (Table SI); one female was a first-year and the other a returning adult where the two males present were not the partner from the previous year even though he returned. Three observations of female singing appeared to occur directly in response to the approach of an observer (3/28 = 10%).

We identified five song types in Cyprus Wheatear, two of which occurred in both males and females (type 1 and type 2 song, see Fig. 2 and Table SII). Type 1 song consisted of a broadband, high entropy buzzy sound, which varied in structure both within and among individuals but along an apparent continuum (Fig. 2a–e). It corresponded with song type c described by Sluys and van den Berg (1982). Type 2 comprised one or two tonal frequency overslurs (Fig. 2f–g), and was somewhat similar to Sluys and van den Berg (1982) song type b. Whilst the male and female song sounded similar, we found that peak frequency in type 1 song was significantly higher in female song than in males ($494 ± 121$ Hz, $t = 4.10$, $df = 4.5$, $p = 0.04$), but there was no significant difference in song rate (difference: $−1.59 ± 1.72$ notes s$^{−1}$, male: $4.90 ± 0.93$ notes s$^{−1}$, female: $3.31 ± 1.45$ notes s$^{−1}$, $t = −0.93$, $df = 4.5$, $p = 0.31$) or duration (difference: $0.71 ± 0.89$ log s, male: $3.9 ± 1.6$ s, female: $1.9 ± 1.2$ s, $t = −1.0$, $df = 4.8$, $p = 0.99$) (Fig. 3a–c). Across all song types, the maximum duration for female song bouts was 5.2 s, whilst song bout duration was greater than this in 11/45 (24%) of male song bouts, with a maximum song bout duration in males of 36.5 s (Table SII). Peak frequency ranged between approximately 4.8–6.2 kHz in males, and 4.1–6.8 kHz in females (Table SII). We also observed male and female Cyprus Wheatear singing simultaneously (see Fig. S1).

Discussion

Observations of female song were relatively uncommon in comparison to males but occurred in a variety of contexts suggesting that female song in Cyprus Wheatear might have multiple functions. Female song predominantly occurred during April, suggesting that females might compete for territories or partners on arrival from migration, and may also announce their fertility to males (Langmore 1998). Two
observations of female–female aggression coincident with singing suggest that at least one function of female song in this species is for territorial defence and this has been observed in a few other species (e.g. Reichard et al. 2018; Kirschel et al. 2020), and two further observations of female song occurred when two males were present suggesting that it may be involved in signalling fertility, mate choice (Langmore 1998), or pair bonding (Sethi and Bhatt 2012).

Female singing presumably occurred predominantly in April because singing later whilst incubating could increase chances of predation (Kleindorfer et al. 2016), and although survival during the breeding period is high in Cyprus Wheatears, the female mortality that does occur is associated with predation whilst on the nest (Xenophontos and Cresswell 2016). Furthermore, the functions of song in attracting a mate and intrasexual competition must be greatest on arrival.

Fig. 2 Spectrograms showing song types for female (left column) and male (right) Cyprus Wheatears. Type 1 (a–e); type 2 (f–g); type 3 (h); type 4 (i); and type 5 (j). Spectrograms were produced in Raven Pro 1.5 with an FFT size = 512 samples.
Female song has been reported in other European passerines, including in the *Oenanthe* genus, but over half of the species were data deficient (see Garamszegi et al. 2007 for review), highlighting the need for female song to be documented. The fact that female song has not previously been reported in Cyprus wheatear is perhaps not surprising since males and females appear similar, and singing females may have been incorrectly assumed to be male. For example, previous work has used the presence of singing as a feature to identify males in this species (Christensen 1974). Future research in this species should use playback experiments to determine the functions of both female and male song.

**Supplementary Information** The online version contains supplementary material available at https://doi.org/10.1007/s10336-021-01902-z.

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from spring migration. Males, however, continue singing through the breeding season and this may be directed toward other males to aid in maintaining their territories (Kroodsma and Byers 1991) and may also aid in re-mating after nest predation or after female desertion (Rodrigues 1996). It could also be directed toward females to indicate that the male is present and no predators are nearby (Johnson and Kermott 1991), or it may act as a mate guarding function (Moller 1991; Seddon and Tobias 2006), or to advertise for extra-pair copulations (Foote and Barber 2009).

Singing females were rarely heard after April except five times when females had hatched or fledged chicks. Female song in these cases may have been directed toward their partner to alert them of predation risk to the offspring (Halkin 1997), which in this case may have been the presence of the observer, but we note that there were many occasions where observers approached females with hatched or fledged chicks that did not give rise to song. It is unlikely that female song during the breeding season was produced to alert chicks to that did not give rise to song. It is unlikely that female song in these cases may have been directed toward their partner to indicate that the male is present and no predators are nearby (Johnson and Kermott 1991), or it may act as a mate guarding function (Moller 1991; Seddon and Tobias 2006), or to advertise for extra-pair copulations (Foote and Barber 2009).

We have tentative evidence that female song might be higher pitched than in males, and it is likely that only males perform longer duration song bouts. We also noted the occurrence of both a male and female singing concurrently (Fig. S1), and whilst it appears that the male modulated pitch when the female sings, it is likely coincidental rather than for signal jamming (e.g., Tobias and Seddon 2009). Based on our observations of just a few individuals, we also consider it likely that there is high inter- and intra-individual variability in song structure and song type. We note caution with these interpretations though because our sample size of recorded individuals was small.
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