



Female song in the Cyprus Wheatear *Oenanthe cypriaca*

Robert Patchett¹ · Alexander N. G. Kirschel² · Joanna Robins King¹ · Patrick Styles¹ · Will Cresswell¹

Received: 25 February 2021 / Revised: 6 May 2021 / Accepted: 14 May 2021
© The Author(s) 2021

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 through 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

Communicated by T. S. Osiejuk.

✉ Robert Patchett
robertpatchett@gmail.com

¹ Centre for Biological Diversity, University of St Andrews, Fife, St Andrews KY16 9TH, UK

² Department of Biological Sciences, University of Cyprus, PO Box 20537, 1678 Nicosia, Cyprus

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′11″ N, 32°51′48″ 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 \pm 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).

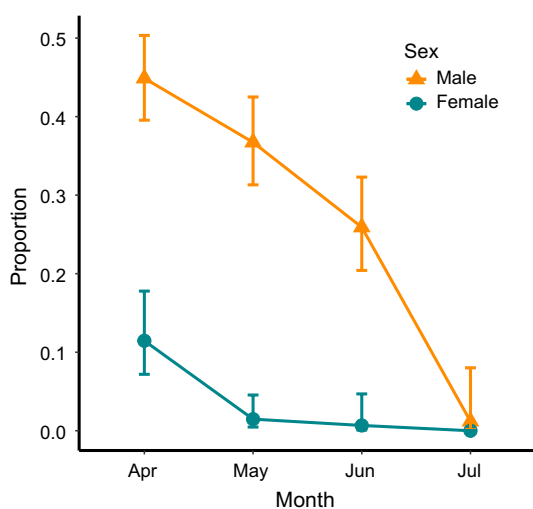


Fig. 1 Proportion of female and male Cyprus Wheatear observations where singing occurred estimated from a GLMM. Error bars show 95% confidence intervals. No females were observed singing in July

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} , $t = -0.93$, $df = 4.9$, $p = 0.93$) 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

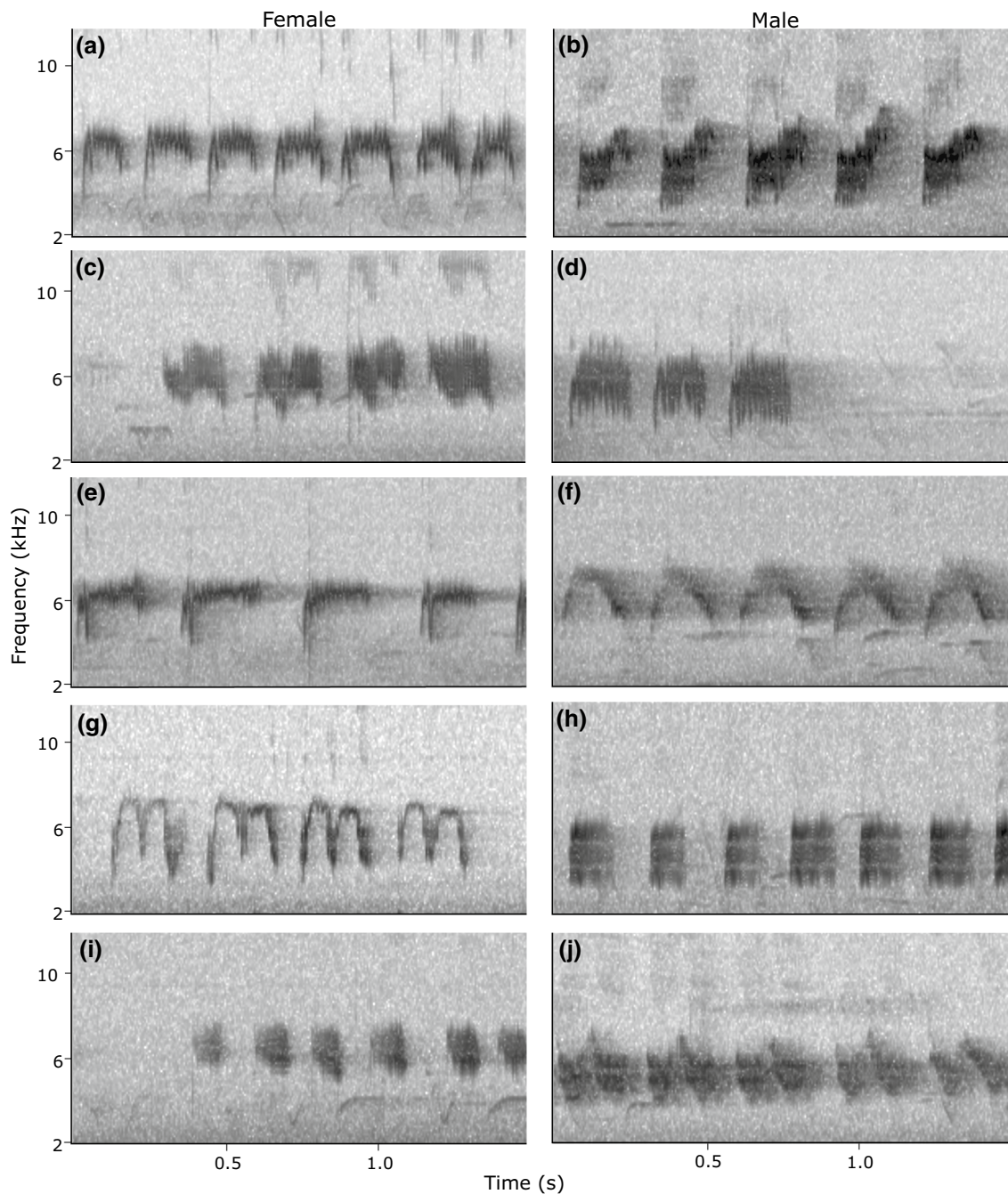


Fig. 2 Spectrograms showing song types for female (left column) and male (right) Cyprus Wheatears. Type 1 (a–e); type 2 (f–g); type 3 (h); type 4 (i); and type 5 (j). Spectrograms were produced in Raven Pro 1.5 with an FFT size=512 samples

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 (Xenophonos and Cresswell 2016). Furthermore, the functions of song in attracting a mate and intrasexual competition must be greatest on arrival

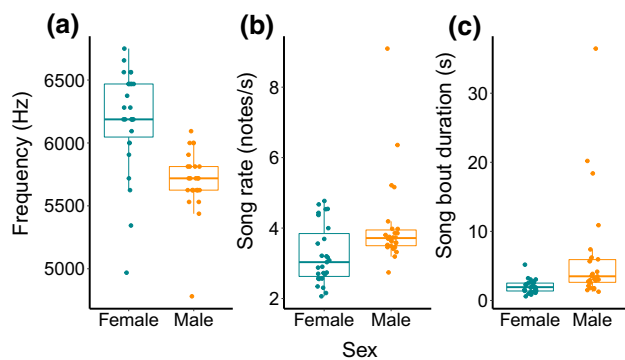


Fig. 3 Comparison of type 1 song between male and female Cyprus Wheatear, comparing **a** peak spectrum frequency, **b** song rate and **c** song bout duration

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 (Møller 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 period was produced to alert chicks to the presence of a predator (i.e. the observer) because Cyprus Wheatear produce specific alarm calls for this purpose (Randler 2013). Female song could also have been used to communicate fertility (Langmore 1998), e.g. for a second brood, but note that one of the cases of female song was from a female who had already hatched a second brood.

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 variabilities in song structure and song type. We note caution with these interpretations though because our sample size of recorded individuals was small.

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>.

Acknowledgements We thank the A.P. Leventis Conservation Foundation for supporting this work, Michaela Moysi for logistical help, Bird-Life Cyprus and the Game and Fauna Service of Cyprus for granting us permission to carry out this research, and five anonymous referees for their comments that substantially improved this paper.

Open Access This article is licensed under a Creative Commons Attribution 4.0 International License, which permits use, sharing, adaptation, distribution and reproduction in any medium or format, as long as you give appropriate credit to the original author(s) and the source, provide a link to the Creative Commons licence, and indicate if changes were made. The images or other third party material in this article are included in the article's Creative Commons licence, unless indicated otherwise in a credit line to the material. If material is not included in the article's Creative Commons licence and your intended use is not permitted by statutory regulation or exceeds the permitted use, you will need to obtain permission directly from the copyright holder. To view a copy of this licence, visit <http://creativecommons.org/licenses/by/4.0/>.

References

- Bates D, Maechler M, Bolker B, Walker S (2014) Fitting linear mixed-effects models using lme4. *J Stat Softw* 67:1–48
- Center for Conservation Bioacoustics (2014) Raven Pro: Interactive Sound Analysis Software
- Christensen S (1974) Notes on the plumage of the female cyprus Pied Wheatear *Oenanthe pleschanka*. *Ornis Scand* 5:47–52
- Collar N, Christie DA (2019) Cyprus Wheatear (*Oenanthe cyprica*). In: del Hoyo J, Elliott A, Sargatal J, Christie DA, de Juana E (eds) Handbook of the birds of the world alive. Lynx Edicions, Barcelona
- Flint P (1995) Separation of cyprus pied wheatear from pied Wheatear. *Br Birds* 88:230–241
- Foote JR, Barber CA (2009) Paired male song sparrows sing more when their mate is incubating. *Wilson J Ornithol* 121:819–822
- Garamszegi LZ, Pavlova DZ, Eens M, Moller AP (2007) The evolution of song in female birds in Europe. *Behav Ecol* 18:86–96
- Halkin SL (1997) Nest-vicinity song exchanges may coordinate biparental care of northern cardinals. *Anim Behav* 54:189–198
- Johnson LS, Kermott L (1991) The functions of song in male house wrens (*Troglodytes aedon*). *Behaviour* 116:190–208

- Kirschel ANG, Earl DA, Yao Y et al (2009a) Using songs to identify individual Mexican antthrush *formicarius moniliger*: comparison of four classification methods. *Bioacoustics* 19:1–20
- Kirschel ANG, Blumstein DT, Smith TB (2009b) Character displacement of song and morphology in African tinkerbirds. *Proc Natl Acad Sci USA* 106:8256–8261
- Kirschel ANG, Zanti Z, Harlow ZT et al (2020) Females don't always sing in response to male song, but when they do, they sing to males with higher-pitched songs. *Anim Behav* 166:129–138
- Kleindorfer S, Evans C, Mahr K (2016) Female in-nest chatter song increases predation. *Biol Lett* 12:20150513
- Kroodsma DE, Byers BE (1991) The function(s) of bird song. *Integr Comp Biol* 31:318–328
- Langmore NE (1998) Functions of duet and solo songs of female birds. *Trends Ecol Evol* 13:136–140
- Møller AP (1991) Why mated songbirds sing so much: mate guarding and male announcement of mate fertility status. *Am Nat* 138:994–1014
- Odom KJ, Benedict L (2018) A call to document female bird songs: applications for diverse fields. *Auk* 135:314–325
- Odom KJ, Hall ML, Riebel K et al (2014) Female song is widespread and ancestral in songbirds. *Nat Commun* 5:3379
- R Core Team (2020) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna
- Randler C (2013) Alarm calls of the Cyprus Wheatear *Oenanthe cyprica*—one for nest defence, one for parent-offspring communication? *Acta Ethol* 16:91–96
- Reichard DG, Brothers DE, George SE et al (2018) Female dark-eyed juncos *Junco hyemalis thurberi* produce male-like song in a territorial context during the early breeding season. *J Avian Biol* 49:e01566
- Riebel K, Odom KJ, Langmore NE et al (2019) New insights from female bird song: towards an integrated approach to studying male and female communication roles. *Biol Lett* 15:20190059
- Rodrigues M (1996) Song activity in the chiffchaff: Territorial defence or mate guarding? *Anim Behav* 51:709–716
- Seddon N, Tobias JA (2006) Duets defend mates in a suboscine passerine, the warbling antbird (*Hypocnemis cantator*). *Behav Ecol* 17:73–83
- Sethi VK, Bhatt D (2012) Structure and context of female song in a tropical bird, the pied bush chat. *Curr Sci* 103:828–832
- Sluys R, van den Berg M (1982) On the specific status of the Cyprus pied wheatear *Oenanthe cyprica*. *Ornis Scand* 13:123–128
- Tobias JA, Seddon N (2009) Signal jamming mediates sexual conflict in a duetting bird. *Curr Biol* 19:577–582
- Xenophontos M, Cresswell W (2016) Survival and dispersal of the Cyprus wheatear *Oenanthe cyprica*, an endemic migrant. *J Ornithol* 157:707–719
- Xenophontos M, Blackburn E, Cresswell W (2017) Cyprus wheatears *Oenanthe cyprica* likely reach sub-Saharan African wintering grounds in a single migratory flight. *J Avian Biol* 48:1–7

Publisher's Note Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.