

JOURNAL OF AVIAN BIOLOGY

Short communication

Comparisons of acoustic structures between sexes in a duetting, montane bird

Huan Liu^{1,2,3}, Fanghong Yang⁴, Qi Zhang⁴, Pengfei Liu✉⁴ and Yuehua Sun✉¹

¹Key Laboratory of Animal Ecology and Conservation Biology, Institute of Zoology, Chinese Academy of Sciences, Beijing, China

²University of Chinese Academy of Sciences, Beijing, China

³Wildlife Conservation Monitoring Centre, National Forestry and Grassland Administration, Beijing, China

⁴School of Life Sciences and Technology, Longdong University, Qingyang, China

Correspondence: Pengfei Liu (pfliu0120@126.com), Yuehua Sun (sunyh@ioz.ac.cn)

Journal of Avian Biology

2024: e03249

doi: [10.1111/jav.03249](https://doi.org/10.1111/jav.03249)

Subject Editor: Martin Paeckert

Editor-in-Chief: Jan-Åke Nilsson

Accepted 15 July 2024



Female song in birds is more widespread than previously thought, and studies across different species are critical for better understanding the entire evolutionary process of bird song. In this study, we recorded the songs of males and females in a duetting, montane bird species, the Elliot's laughingthrush *Trochalopteron elliotii*, across consecutive breeding seasons. We specifically focused on identifying the number and structure of different song types by males and females, and compared these acoustic structures between the sexes. Our findings revealed that both males and females sang sex-specific solos. More specifically, females sang a single type of solo that varied significantly in the number of notes, whereas males produced three different solos composed of 2, 3, or 4 notes, respectively. Female solos exhibited significantly more notes and longer song duration compared to males. Male solos typically had a significantly higher maximum frequency for the entire song. No significant differences were observed in the duration of the first note, song rate, and other frequency characteristics between male and female solos. Furthermore, paired males and females coordinated their sex-specific solos to form duets when challenged by conspecific territory intruders, both within and outside the breeding season. Sex-specific solos suggested that male and female songs play different roles and may be subject to different selective pressures. Further research is necessary for elucidating the functions of male song, female song, and duets in this montane bird species.

Keywords: duetting, female song, pair bond, social selection

Introduction

Mate attraction and territory defence are widely considered to be the two primary functions of male song in songbirds (Catchpole and Slater 2008). Song complexity or repertoire size often represents an honest signal of male quality (Searcy and Andersson 1986, Gil and Gahr 2002), a trait which is subject to both intra- and inter-sexual selection



www.avianbiology.org

© 2024 The Author(s). Journal of Avian Biology published by John Wiley & Sons Ltd on behalf of Nordic Society Oikos

This is an open access article under the terms of the Creative Commons Attribution License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.

(Westcott 1992, Nolan and Hill 2004). In contrast to male song, information on the temporal structure and functions of female song is limited (Langmore 1998, Riebel et al. 2005). However, recent researches have revealed that female song in oscine passerines is widespread and ancestral, occurring in approximately 60–70% of passerine species (Garamszegi et al. 2007a, Odom et al. 2014, Webb et al. 2016), but which, across several avian families (Icteridae, Muscicapidae, and Fringillidae) has been repeatedly lost (Garamszegi et al. 2007b, Price 2009, Price et al. 2009, Odom et al. 2015). These findings challenge the traditional view that female song is rare, and in fact suggest a more complex and diverse pattern of vocal communication, in which female bird song may have a similar biological significance to male song and play an important role in survival and breeding (Langmore 1998, Hall and Langmore 2017). Despite these recent advances, there remains a lack of research comparing song structure and song behaviour between the sexes.

In some tropical bird species, females sing solos of similar complexity to males (Brunton and Li 2006, Price et al. 2008), which suggests that females may use song to compete for resources, strengthen pair bonds, and allow mate guarding (Tobias and Seddon 2009, Hall et al. 2015, Reichard et al. 2018). Females and males can also form duets by coordinating their vocalizations temporally (Benedict 2008), and these duets also play a role in territory defence, mate-guarding, and reproductive synchronization (Hall 2004, Dahlin and Benedict 2014). Despite accumulating evidence indicating that female song serves numerous functions (Cain et al. 2015, Kirschel et al. 2020), there have been few investigations of female song (Odom and Benedict 2018), particularly for temperate species (Malacarne et al. 1991, Benedict 2008).

Elliot's laughingthrush *Trochalopteron elliotii* is a sexually monomorphic and socially monogamous montane songbird endemic to China (Liu and Sun 2016). During the breeding season, the species inhabits alpine habitats with open woodlands, shrubs, and cultivated lands, but migrates to lower altitudes for the non-breeding winter season. During winter individuals form flocks, while mated males and females maintain their pair bonds and, in some instances, occupy and defend separate territories (Lei and Lu 2006). In the pre-breeding season, females typically sing, especially when they are unpaired or in flocks. Paired males are known to sing solos, duets, or choruses with other males throughout the year. While the vocal behaviour of Elliot's laughingthrush has been described previously, to our knowledge at least, the structure of female song has yet to be analysed due to its scarcity (Opaev et al. 2017). Here, for the first time, we present a comparative analysis of song structure between the sexes in this montane passerine species during consecutive breeding seasons.

Material and methods

Study site and species

The fieldwork was conducted in the Lianhuashan Nature Reserve (34°58'16"N, 103°45'30"E; 2040 m a.s.l.), located

on the eastern edge of the Qinghai-Tibet Plateau in central China. The study area is mainly composed of cultivated farmlands, open woodlands, and orchards, as well as abandoned fields dominated by scrub vegetation. Since 2013, we have been studying the ecology of the resident Elliot's laughingthrush population at this site and, each year, catch and colour-band males and females with a unique combination of colour rings for sex and individual identification. The sex of all marked individuals was determined by the swelling of the male gonads and differences in morphological size (Liu and Sun 2016).

Field observation and vocalization recording

From 5 March to 20 May 2021, and 5 April to 13 June 2022, we observed male and female singing behaviour every three days during suitable weather conditions. All observations were conducted between 08:00 and 11:00. Within each territory, we conducted one-hour long observations, during which we recorded the date, sex of the singer, time, singing contexts (agonistic interactions, spontaneous singing, chorus singing), presence of intruders, and whether the focal pair divorced. For each singing individual, we collected solos and duets using a TASCAMHD-P2 sound recorder (44.1 kHz, 16 bits) and a Sennheiser MKH416 P48 shotgun microphone at a distance of 5–10 m from the singing birds. We also recorded solos from unpaired males, which were determined through direct observations of male–female interactions, and from observations made at nests being attended by these same males.

Acoustic structure

Avisoft-SASLab Pro was used to analyse the song structure of all recordings. The sampling rate was 22.05 kHz, with a sample size of 16 bits, the FFT length was 512 points, the frequency resolution was 43 Hz, the temporal resolution was 2.9 ms, and the window used was FlatTop, with an 87.5% overlap. The simplest elements of the song on the sonogram are referred to as 'notes'. We defined a discrete song as being made up of two or more consecutive notes, typically separated by a brief pause (Brenowitz et al. 1997). Solo songs refer to the distinctive individual songs produced by a single bird (either male or female). All definitions of songs and notes are illustrated in Fig. 1A.

For each individual, the following song characteristics were recorded: the total number of notes within a song, duration of song, first note duration of a song, the speed of a song (the number of notes within a song per second), maximum frequency, minimum frequency, and frequency range of the song, the first and last note. To determine these parameters, we analysed two solos from each female and male. In order to include a diverse range of variation in vocal characteristics within individuals, we only selected recordings that were both high-quality and representative of the individual's vocal repertoire.

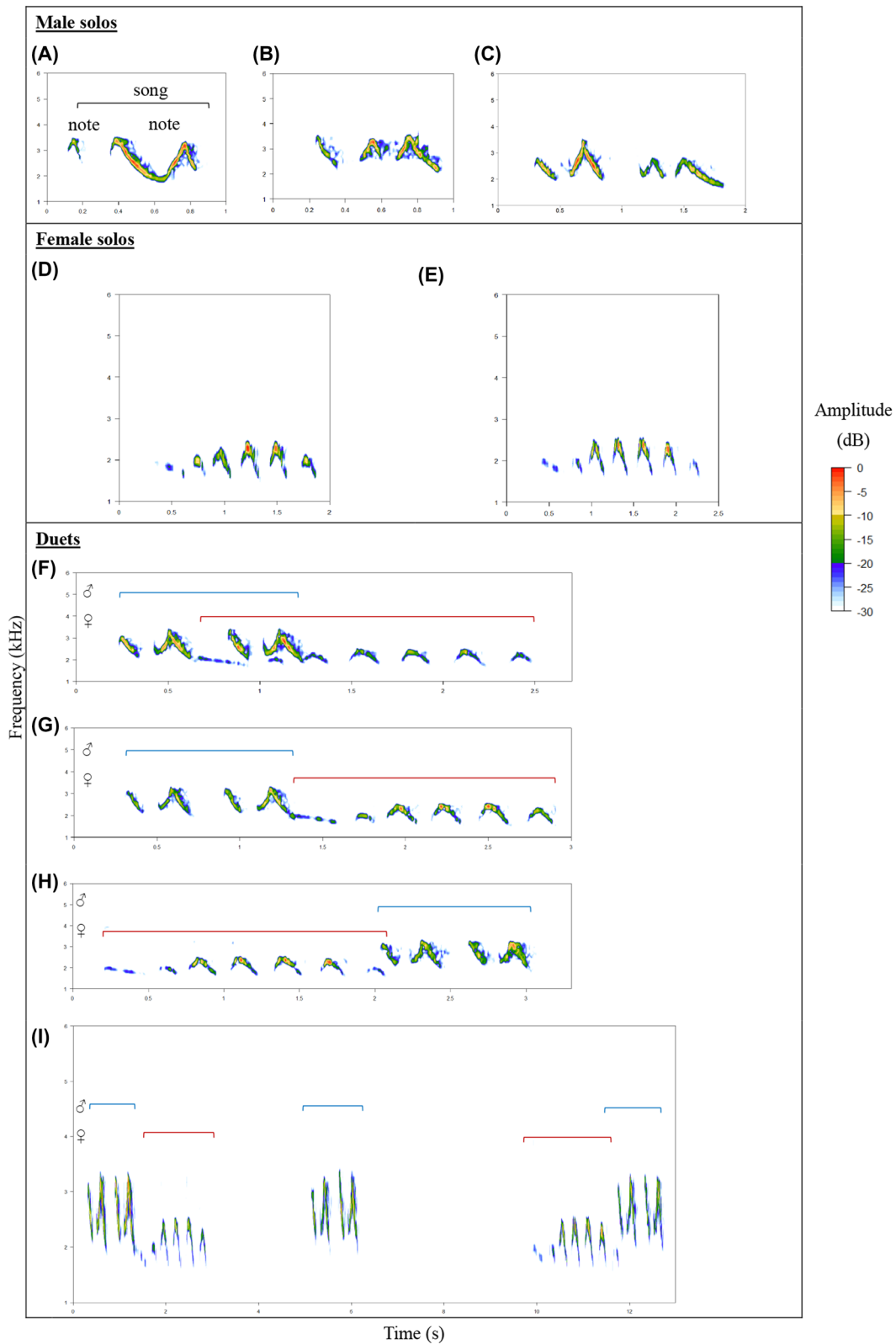


Figure 1. Spectrograms and song parameters of male solos, female solos, and duets in Elliot's laughingthrush *Trochalopteron elliotii*. (A–C): spectrograms depicting representative male Elliot's laughingthrush solos with 2, 3, 4 notes, respectively. (D), (E): spectrograms depicting representative female Elliot's laughingthrush solos with 6 or 7 notes. (F): male-initiated overlapping type duet. (G): male-initiated alternating duet. (H): female-initiated alternating duet. (I): coordinated alternating type duet.

Spectrograms creation

Spectrograms were extracted using R package 'Seewave' with an FFT-window length of 512 and an overlap of 87.5% (Sueur et al. 2008). The 'tuneR' package was used to load sound files in WAV format as an object (Ligges et al. 2013). In a spectrogram, time is displayed on the x-axis, frequency on the y-axis, and amplitude is represented by colour intensity.

Statistical analysis

Wilcoxon rank sum tests were used to determine if each of the vocal characteristics (the number of notes, speed, duration, first note duration) and frequency of the song differed between males and females. Bonferroni correction was used to adjust the p-values in the analysis. All statistical analyses were conducted using R ver. 4.1.3 (www.r-project.org). Values are given as mean $\pm$ SE, with Bonferroni corrected p value < 0.004 .

Results

During the breeding seasons of 2021 and 2022, observations were conducted on 27 pairs, none of which were observed repeatedly in both years. In total, we recorded 64 solos from 23 different paired males, 15 solos from 9 unpaired males, and 27 solos from 19 different paired females. Additionally, we documented 31 duets from 17 different mated pairs. In each pair, at least one individual was marked, ensuring the determination of the singer's sex.

Elliot's laughingthrush produced sex-specific solos. Male repertoires include three song types, which consist of 2, 3, and 4 notes, respectively (Fig. 1A–C). In male solos all three song types were used in different contexts: two-note types were used exclusively during daytime choruses, whereas three- and four-note types were used exclusively in agonistic

behaviours among males. Duetting males displayed only song types including three or four notes.

Female repertoires included a single song type, with the number of notes varying from 2 to 7 (Table 1, Fig. 1D–E). Both sexes were capable of coordinating their song to form duets. In 90.3% of duets (28 out of 31), males initiated the duetting, and females overlapped (Fig. 1F) or alternated with their partners' songs (Fig. 1G, I). Duets were also initiated by females, with males alternating their songs (Fig. 1H–I).

Significant differences were observed in solos between the sexes: females had significantly more notes ($p < 0.001$) and longer song duration ($p < 0.001$) compared to males (Table 1, Fig. 2). Males exhibited a significantly higher maximum frequency of the entire song ($p < 0.001$; Table 1, Fig. 2). No significant differences were observed in the duration of the first note, song rate, and other frequency characteristics between male and female solos ($p > 0.004$; Table 1, Fig. 2).

Discussion

Our results showed that female Elliot's laughingthrush sang, and that both sexes exhibited sex-specific songs. Males were observed to produce three distinct song types, whereas females sang a single song type that varied in the number of notes within songs of each singing bout. Females produced a significantly higher number of notes and longer songs compared to males, while the frequency of female songs was significantly lower than that of males. The differences in song structures between sexes may suggest that the male and female songs are subject to different selective pressures (Odom et al. 2015). For example, the low-frequency songs produced by females may serve as a signal of body size to males, indicating a better capacity to defend a territory (Ryan and Brenowitz 1985, Gil and Gahr 2002). Sex-specific song has also been reported in other laughingthrush species (Vencl and Soucek 1976, Lei and Lu 2006, Weng et al. 2012, Liu et al. 2022), and in

Table 1. Comparisons of temporal characteristics and frequency of song in male and female Elliot's laughingthrush *Trochalopteron elliotii*.

Parameters	Males (n = 113)	Females (n = 35)	Test statistic (W)	p value
Number of notes within a song	2.85 $\pm$ 0.08 (2–4)	4.09 $\pm$ 0.24 (2–7)	2976	< 0.001
Duration of the whole song (s)	0.82 $\pm$ 0.03 (0.33–1.65)	1.27 $\pm$ 0.08 (0.48–2.08)	3107	< 0.001
First note duration of a song (s)	0.19 $\pm$ 0.01 (0.05–0.83)	0.23 $\pm$ 0.02 (0.04–0.43)	2407	0.053
The speed of the whole song ^a	3.65 $\pm$ 0.08 (1.73–6.10)	3.28 $\pm$ 0.08 (2.59–4.32)	1419	0.012
Maximum frequency (kHz)	3.55 $\pm$ 0.03 (2.49–4.30)	3.41 $\pm$ 0.10 (2.67–5.51)	1206	< 0.001
Minimum frequency (kHz)	1.60 $\pm$ 0.03 (1.10–3.70)	1.61 $\pm$ 0.05 (1.20–2.49)	1908	0.752
Frequency range ^b (kHz)	1.96 $\pm$ 0.04 (0–2.80)	1.80 $\pm$ 0.09 (1.20–3.02)	1390	0.008
Maximum frequency of the first note (kHz)	3.21 $\pm$ 0.04 (2.40–4.04)	3.09 $\pm$ 0.08 (2.06–4.30)	1589	0.079
Minimum frequency of the first note (kHz)	1.78 $\pm$ 0.03 (1.10–2.41)	1.83 $\pm$ 0.07 (1.10–3.35)	1973	0.986
Frequency range of the first note ^c (kHz)	1.43 $\pm$ 0.03 (0.60–2.40)	1.26 $\pm$ 0.06 (0.52–2.15)	1447	0.017
Maximum frequency of the last note (kHz)	3.35 $\pm$ 0.03 (2.20–4.10)	3.29 $\pm$ 0.11 (2.40–5.51)	1461	0.019
Minimum frequency of the last note (kHz)	1.68 $\pm$ 0.02 (1.11–2.50)	1.77 $\pm$ 0.05 (1.29–2.49)	2341	0.098
Frequency range of the last note ^d (kHz)	1.67 $\pm$ 0.03 (0.80–2.60)	1.52 $\pm$ 0.09 (0.77–3.02)	1352	0.005

^aSpeed of the whole song calculated by dividing the number of notes in one song by the duration of the song.

^bFrequency range of the whole song calculated as maximum frequency minus minimum frequency of the song.

^cFrequency range of the first note calculated as maximum frequency minus minimum frequency of the first note in the song.

^dFrequency range of the last note calculated as maximum frequency minus minimum frequency of the last note in the song. Bonferroni corrected p value = 0.004. Significant differences between males and females are highlighted in bold.

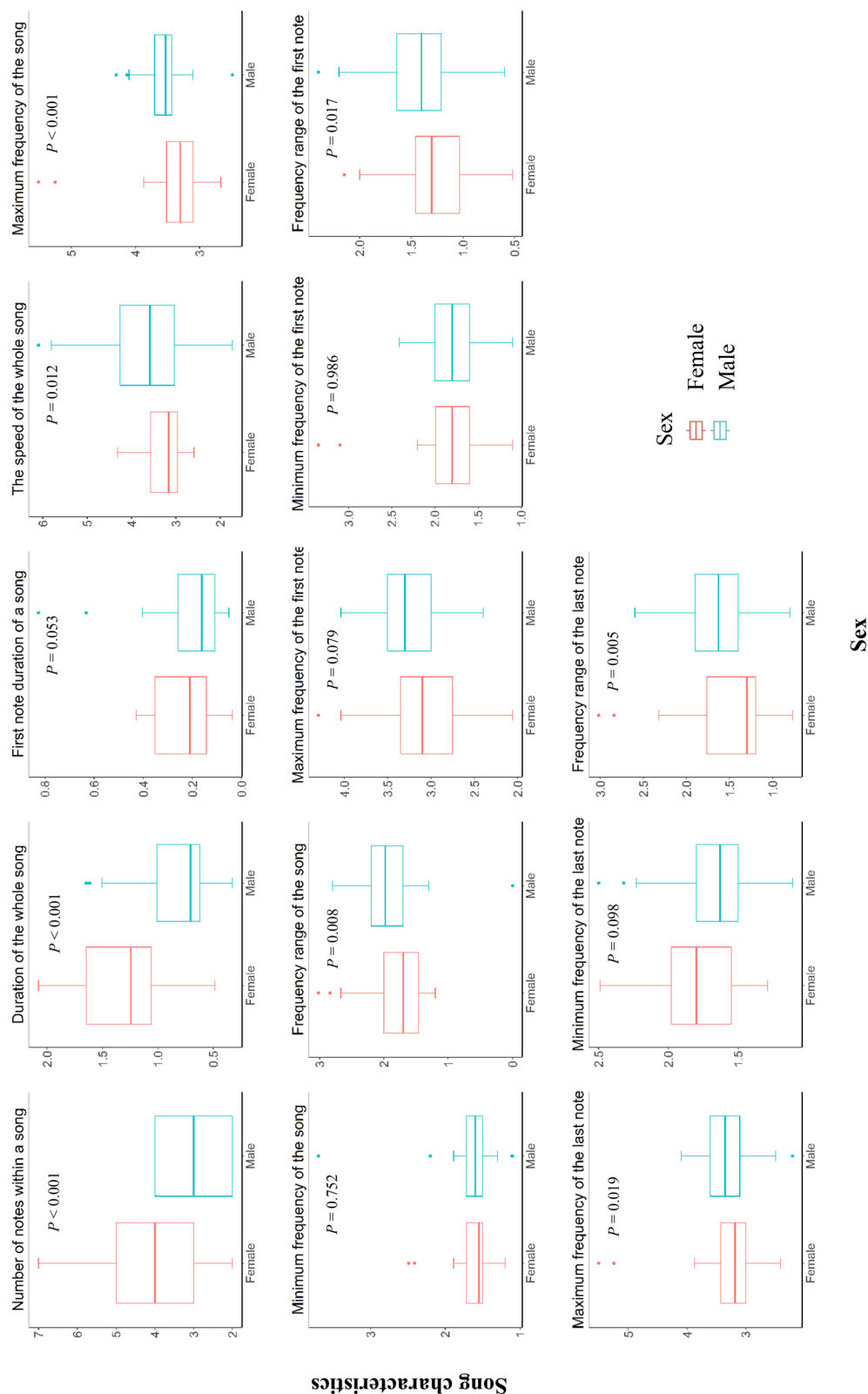


Figure 2. The boxplots display the comparison of song characteristics between males and females. Each boxplot represents the median (line inside the box), lower quartile (bottom of the box), upper quartile (top of the box), and the range of the data (whiskers). Outliers are displayed as points.

other babblers including red-billed leiothrix *Leiothrix lutea*, hwamei *Garrulax canorus*, brown-cheeked laughingthrush *Trochalopteron henrici*, and snowy-cheeked laughingthrush *Lanthocincla sukatschewi* (P. Liu unpubl.).

During the two consecutive breeding seasons, both males and females sang solos or duets within their territories during the day, and paired females sang in response to their male partners. Paired males used 2-note solos to interact with neighbouring males. Unpaired males exhibited wide-ranging movements while singing solos consisted of 3- or 4-notes. A study in a population of this babbler found that Elliot's laughingthrush sing three solo types: two types consist of three notes and are more often used in interactions with neighbouring males; the third type consists of two notes and appears to be used in male–female duetting (Opaev et al. 2017). In our study population, it may be the case that unpaired males use 3- or 4-note solos to attract mates, while paired males use 2-note solos to advertise ownership of their territories. Outside the breeding season, males may also form duets with females or engage in chorusing with other males when gathering in flocks, even when defending separate territories, whereas females sing to form duets with their mates when occupying winter territories. Further work is needed to determine the context in which the same song types are used during the non-breeding season; e.g. whether they function for mate attraction, intersexual competition, or territory defence (Langmore et al. 1996, Gil and Gahr 2002, Krieg and Getty 2016).

In our study population of Elliot's laughingthrush, males and females coordinated their songs into duets, a behaviour which has also been observed in another population of this species (Opaev et al. 2017). We found that male and female Elliot's laughingthrush sang both coordinated alternating and overlapping duets. A potential benefit of alternate duets may be that they extend the duration of the vocal display, potentially increasing the signal of joint resource defence or pair-bonding (Hall 2004), while the overlapping duets may represent conflict between the pairs, including mate-guarding, paternity guarding and extra-pair mating (Hall 2004, Dahlin and Benedict 2014). Females of some passerine species may prevent potential extra-pair copulation by forming duets with jamming notes, thus serving as a deterrent (Tobias and Seddon 2009). Furthermore, in the Elliot's laughingthrush, both male and female initiated duets. For many species, duets are initiated by members of both sexes (Dahlin and Benedict 2014, Dingle and Slabbekoorn 2018), thus duets are the products of both male and female behaviour. In our population, the majority of duets were initiated by males, indicating that females rarely leave their mates to sing alone, which suggests that there may be a higher cost to females in allowing the male to sing on his own, as it might attract rival females. In grey-breasted wood-wrens *Henicorhina leucophrys*, male and female initiation rates in duets indicate potential functions in joint territory defence and defending mates (Dingle and Slabbekoorn 2018). Studies on the plain laughingthrush *Pterorhinus davidi* found that duetting is primarily used for cooperative territorial defence and shared resource defence

(Liu et al. 2023). Additionally, the most frequent context of duetting by Elliot's laughingthrush is aggressive interactions with other pairs or individuals, suggesting a possible role in advertising pair bonds (e.g. white-throated dipper *Cinclus cinclus*: Magoolagan et al. 2019).

From our quantitative assessment of male and female songs and identification of sex-specific songs, Elliot's laughingthrush can be added to the growing list of bird species in which female song plays a significant functional role in within-pair communication (Cooper et al. 2023), mate guarding (Rogers et al. 2007), or nest defence (Dalziel and Welbergen 2016). Furthermore, the frequent singing of unpaired females suggests that female song may also function in mate attraction (Morton et al. 2000). To further enhance our understanding of bird song evolution and animal communication in general, more experimental research is required to document and quantify female songs of this and other species, especially in the montane areas and northern temperate zones where research on female song is severely lacking.

Acknowledgements – We would like to express our gratitude to Gesang Wangjie, Jingyi Yang, and Meixiu Chen for their invaluable assistance during the field work. We also thank Huw Lloyd for revising and polishing the manuscript.

Funding – The research was supported by the National Natural Science Foundation of China (project 32370526, 32070452).

Permits – The experiments were conducted under the approval of the Animal Care and Ethics Committee and carried out in accordance with the guidelines for the use of Animals in Research issued by the Institute of Zoology, Chinese Academy of Sciences (permission no. 2013/108).

Author contributions

Huan Liu: Conceptualization (equal); Formal analysis (equal); Investigation (equal); Methodology (equal); Visualization (equal); Writing – original draft (lead); Writing – review and editing (equal). **Fanghong Yang:** Data curation (equal); Investigation (equal); Software (equal). **Qi Zhang:** Data curation (equal); Investigation (equal); Software (equal). **Pengfei Liu:** Conceptualization (equal); Formal analysis (equal); Investigation (equal); Methodology (equal); Writing – original draft (equal); Writing – review and editing (equal). **Yuehua Sun:** Conceptualization (equal); Funding acquisition (equal); Project administration (equal); Supervision (equal); Writing – review and editing (equal).

Transparent peer review

The peer review history for this article is available at <https://www.webofscience.com/api/gateway/wos/peer-review/jav.03249>.

Data availability statement

Data are available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.bnzs7h4kc> (Liu et al. 2024).

References

- Benedict, L. 2008. Occurrence and life history correlates of vocal duetting in North American passerines. – *J. Avian Biol.* 39: 57–65.
- Brenowitz, E. A., Margoliash, D. and Nordeen, K. W. 1997. An introduction to birdsong and the avian song system. – *J. Neurobiol.* 33: 495–500.
- Brunton, D. H. and Li, X. 2006. The song structure and seasonal patterns of vocal behavior of male and female bellbirds (*Anthornis melanura*). – *J. Ethol.* 24: 17–25.
- Cain, K. E., Cockburn, A. and Langmore, N. E. 2015. Female song rates in response to simulated intruder are positively related to reproductive success. – *Front. Ecol. Evol.* 3: 119.
- Catchpole, C. K. and Slater, P. J. 2008. Bird song: biological themes and variations. – Cambridge Univ. Press.
- Cooper, J. E. J., Garcia-del-Rey, E. and Lachlan, R. F. 2023. Evolution of female song and duetting in the chaffinch (*Fringilla*) species complex. – *J. Avian Biol.* 2023: e03069.
- Dahlin, C. R. and Benedict, L. 2014. Angry birds need not apply: a perspective on the flexible form and multifunctionality of avian vocal duets. – *Ethology* 120: 1–10.
- Dalziel, A. and Welbergen, J. 2016. Elaborate mimetic vocal displays by female superb lyrebirds. – *Front. Ecol. Evol.* 4: 34–46.
- Dingle, C. and Slabbekoorn, H. 2018. Multiple functions for pair duets in a Neotropical wren *Henicorhina leucophrys*. – *Anim. Behav.* 145: 67–76.
- Garamszegi, L., Eens, M., Pavlova, D., Avilés, J. and Møller, A. P. 2007a. A comparative study of the function of heterospecific vocal mimicry in European passerines. – *Behav. Ecol.* 18: 1001–1009.
- Garamszegi, L. Z., Pavlova, D. Z., Eens, M. and Møller, A. P. 2007b. The evolution of song in female birds in Europe. – *Behav. Ecol.* 18: 86–96.
- Gil, D. and Gahr, M. 2002. The honesty of bird song: multiple constraints for multiple traits. – *Trends Ecol. Evol.* 17: 133–141.
- Hall, M. 2004. A review of hypotheses for the functions of avian duetting. – *Behav. Ecol. Sociobiol.* 55: 415–430.
- Hall, M. L. and Langmore, N. E. 2017. Fitness costs and benefits of female song. – *Front. Ecol. Evol.* 5: 48–49.
- Hall, M. L., Rittenbach, M. R. and Vehrencamp, S. L. 2015. Female song and vocal interactions with males in a Neotropical wren. – *Front. Ecol. Evol.* 3: 12.
- Kirschel, A. N., Zanti, Z., Harlow, Z. T., Vallejo, E. E., Cody, M. L. and Taylor, C. E. 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.
- Krieg, C. A. and Getty, T. 2016. Not just for males: females use song against male and female rivals in a temperate zone songbird. – *Anim. Behav.* 113: 39–47.
- Langmore, N. E. 1998. Functions of duet and solo songs of female birds. – *Trends Ecol. Evol.* 13: 136–140.
- Langmore, N. E., Davies, N., Hatchwell, B. and Hartley, I. R. 1996. Female song attracts males in the Alpine accentor *Prunella collaris*. – *Proc. R. Soc. B* 263: 141–146.
- Lei, F. M. and Lu, T. C. 2006. China endemic birds. – Science Press.
- Ligges, U., Krey, S., Mersmann, O. and Schnackenberg, S. 2013. tuneR: analysis of music. – <http://r-forge.r-project.org/projects/tuner>.
- Liu, H., Yang, F., Zhang, Q., Liu, P. and Sun, Y. 2024. Data from: Comparisons of acoustic structures between sexes in a duetting, montane bird. – Dryad Digital Repository, <https://doi.org/10.5061/dryad.bnzs7h4kc>.
- Liu, P., Lou, Y., Lloyd, H. and Sun, Y. 2023. Multiple field study approaches reveal the functions of female song and duets in a temperate songbird. – *Anim. Behav.* 206: 1–11.
- Liu, P. F. and Sun, Y. H. 2016. Sexual size dimorphism and assortative mating in Elliot's laughingthrush *Trochalopteron elliotii*. – *Ardea* 104: 177–181.
- Liu, P. F., Lai, M., Wang, M. J. and Sun, Y. H. 2022. Females and males sing distinctly different songs in a temperate zone songbird. – *Ardea* 110: 99–105.
- Magoollagan, L., Mawby, P. J., Whitehead, F. A. and Sharp, S. P. 2019. The structure and context of male and female song in white-throated dippers. – *J. Ornithol.* 160: 195–205.
- Malacarne, G., Cucco, M. and Camanni, S. 1991. Coordinated visual displays and vocal duetting in different ecological situations among western Palearctic non-passerine birds. – *Ethol. Ecol. Evol.* 3: 207–219.
- Morton, E. S., Derrickson, K. C. and Stutchbury, B. J. M. 2000. Territory switching behavior in a sedentary tropical passerine, the dusky antbird (*Cercomacra tyrannina*). – *Behav. Ecol.* 11: 648–653.
- Nolan, P. M. and Hill, G. E. 2004. Female choice for song characteristics in the house finch. – *Anim. Behav.* 67: 403–410.
- Odom, K. J. and Benedict, L. 2018. A call to document female bird songs: applications for diverse fields. – *Auk Ornithol. Adv.* 135: 314–325.
- Odom, K. J., Hall, M. L., Riebel, K., Omland, K. E. and Langmore, N. E. 2014. Female song is widespread and ancestral in songbirds. – *Nat. Commun.* 5: 3379.
- Odom, K. J., Omland, K. E. and Price, J. J. 2015. Differentiating the evolution of female song and male–female duets in the New World blackbirds: can tropical natural history traits explain duet evolution? – *Evolution* 69: 839–847.
- Opae, A. S., Liu, M. and Kang, Z. 2017. Behavioral ecology of Elliot's laughingthrush (*Trochalopteron (Garrulax) elliotii*, Timaliidae, Aves): 2. Vocal repertoire. – *Biol. Bull.* 44: 1100–1110.
- Price, J. J. 2009. Evolution and life-history correlates of female song in the New World blackbirds. – *Behav. Ecol.* 20: 967–977.
- Price, J. J., Yunes-Jiménez, L., Osorio-Beristain, M., Omland, K. E. and Murphy, T. G. 2008. Sex-role reversal in song? Females sing more frequently than males in the streak-backed oriole. – *Condor* 110: 387–392.
- Price, J. J., Lanyon, S. M. and Omland, K. E. 2009. Losses of female song with changes from tropical to temperate breeding in the New World blackbirds. – *Proc. R. Soc. B* 276: 1971–1980.
- Reichard, D. G., Brothers, D. E., George, S. E., Atwell, J. W. and Ketterson, E. D. 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., Hall, M. L. and Langmore, N. E. 2005. Female songbirds still struggling to be heard. – *Trends Ecol. Evol.* 20: 419–420.
- Rogers, A. C., Langmore, N. E. and Mulder, R. A. 2007. Function of pair duets in the eastern whipbird: cooperative defense or sexual conflict? – *Behav. Ecol.* 18: 182–188.
- Ryan, M. J. and Brenowitz, E. A. 1985. The role of body size, phylogeny, and ambient noise in the evolution of bird song. – *Am. Nat.* 126: 87–100.
- Searcy, W. A. and Andersson, M. 1986. Sexual selection and the evolution of song. – *Annu. Rev. Ecol. Syst.* 17: 507–533.
- Sueur, J., Aubin, T. and Simonis, C. 2008. Seewave, a free modular tool for sound analysis and synthesis. – *Bioacoustics* 18: 213–226.

- Tobias, J. A. and Seddon, N. 2009. Signal jamming mediates sexual conflict in a duetting bird. – *Curr. Biol.* 19: 577–582.
- Vencl, F. and Soucek, B. 1976. Structure and control of duet singing in the white-crested laughing thrush (*Garrulax leucolophus*). – *Behaviour* 57: 206–225.
- Webb, W. H., Brunton, D. H., David, A. J., Thomas, D. B., Mihai, V. and James, D. 2016. Female song occurs in songbirds with more elaborate female coloration and reduced sexual dichromatism. – *Front. Ecol. Evol.* 4: 22–29.
- Weng, Y. S., Yuan, H. W., Yao, C. T. and Hsieh, C. F. 2012. Male and female Steere's liocichlas respond differently to solo and stereo duet playback. – *Anim. Behav.* 83: 487–493.
- Westcott, D. 1992. Inter-and intra-sexual selection: the role of song in a lek mating system. – *Anim. Behav.* 44: 695–703.