

was 10 mm day<sup>-1</sup> compared to the expected values of 11.5 mm day<sup>-1</sup>. While in July the mean observed interception was 22 mm day<sup>-1</sup> compared with the expected values of 27.0 mm day<sup>-1</sup>.

It was found that in all the lower rainfall months there was a marked increase in interception with increase in crown area. Examinations of interception in periods of several consecutive rainy days have confirmed that interception is greatly reduced by the rainfall remaining from previous day's rain. This could be due to reduced evaporation or due to minimum absorption by the foliage.

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## Structure and context of female song in a tropical bird, the Pied Bush Chat

Vinaya Kumar Sethi, Dinesh Bhatt\* and Amit Kumar

Avian Diversity and Bioacoustics Laboratory,  
Department of Zoology and Environmental Science,  
Gurukula Kangri University, Haridwar 249 404, India

**Songbirds have been regarded as an important model system in the field of animal communication focusing mainly on songs by male birds. However, the occurrence, structure and sociobiological significance of song in female birds have been a long-neglected field. We describe here the structure and context of female song in a tropical avian species, the Pied Bush Chat (*Saxicola caprata*). All the females sang occasionally prior to nest-building through egg-laying and rarely during incubation. We did not find significant difference in any of the song type characteristics of the female song when compared with male. However, mean song repertoire size for females was significantly smaller than males. Females sang during aggressive interactions with floater or neighbouring females. Females also sang during intersexual vocal communi-**

\*For correspondence. (e-mail: dineshharidwar@gmail.com)

**cation through song-answering. Observations suggest that females use song for mate defence and probably to convey some pair bond information to the mate. This study provides evidence for the occurrence of female song in the Pied Bush Chat which has otherwise been widely overlooked so far.**

**Keywords:** Female song, Pied Bush Chat, song answering, song repertoire, tropical songbird.

BIRD song is generally considered to be the preserve of male songbirds and functions primarily in territory defence and mate attraction<sup>1</sup>. In those species where females do sing, they often sing less frequently and with less complexity than males<sup>2-5</sup>. However, there is growing evidence that female song is not so uncommon as previously thought, but instead may be an adaptive plastic trait in females<sup>6-8</sup>.

The role of female song has been a matter of much speculation. Initially, female song was considered as a functionless by-product of temporarily high levels of androgen<sup>9</sup>. However, later studies have emphasized the biological relevance of female song<sup>6</sup>. For example, in some species female song may serve the same function as in males<sup>1,4</sup> especially to deter intrasexual competitors for mates or resources<sup>10-17</sup>. Female song may also play role in mate attraction<sup>18-20</sup> and maintaining intra-pair contact to coordinate breeding activities<sup>17,21-25</sup>.

In the Indian subcontinent situated in the tropical monsoon belt, systematic studies on bird song behaviour have been recently started<sup>26,27</sup>. Consequently, we largely lack fundamental data on song characteristics and singing behaviour of most of the songbirds of the Indian subcontinent. There are some studies on Indian bird models dealing with the structure and possible function of song in male<sup>26,28-30</sup>. However, female song seems a widely neglected area of research in the Indian subcontinent and appears to be described for only one song bird species so far<sup>31</sup>.

The objective of this study was to provide a description of the structure and context of female song in a tropical song bird, the Pied Bush Chat and to study the intersexual differences in song structure.

The Pied Bush Chat is found in open habitats, including scrub, grassland, cultivated areas and partially developed human settlements. However, it mostly prefers open grounds with small patches of bushy vegetation. Field work was undertaken from February to July 2010 in open/scrub lands within a 10 km radius at Haridwar (29°55'N, 78°08'E), Uttarakhand, India.

The Pied Bush Chat is a tropical sedentary species. The male is mostly black with a white rump, wing patch and lower belly, whereas the female is largely drab brown. Males are territorial and deliver short-whistled songs during breeding season that extends from late February to July in the study area<sup>32,33</sup>. The structure and song repertoire size of male Pied Bush Chat has been studied<sup>29</sup>.

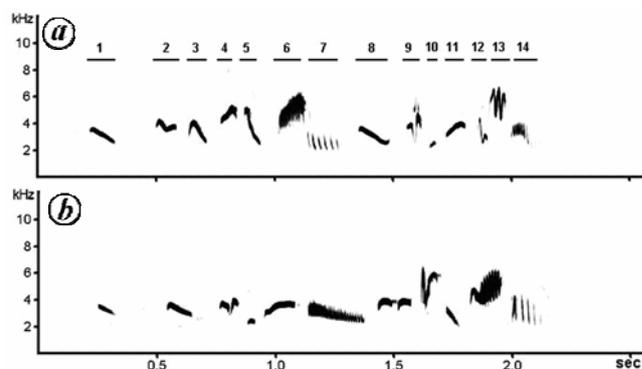
Moreover, mate removal experiment has suggested that males use dawn chorus to mediate social relationships with neighbouring males to proclaim an established territory<sup>30</sup>. However, the female song behaviour of this species has been widely overlooked and there appears no information on the structure, context of singing and even the prevalence of female song for the Pied Bush Chat.

We monitored 12 pairs of the Pied Bush Chat, where all the individuals were ringed with a unique combination of coloured plastic rings. Given that the Pied Bush Chat is a dawn singer, most observations began about an hour before sunrise and continued intermittently during daytime also. Female Pied Bush Chat sings spontaneously (pers. obs.) and thus, we made no systematic efforts to record female songs; rather recordings were obtained coincidentally while recording males.

We used a Sennheiser ME 67 directional microphone attached to a Marantz PMD 670 portable solid state sound recorder (D&M Holdings Inc, Kanagawa, Japan). Songs were saved to a computer as Wav files with input sampling frequency of 24,000 Hz and sample format of 16 bit. Spectrograms were prepared with Avisoft SASLab Pro software<sup>34</sup>. We compared different song-type parameters between females and males such as minimum frequency, maximum frequency, duration, number of notes in the song type and type of note in the song type. To test whether these characteristics and song repertoire size differ between sexes, Mann-Whitney *U*-test was applied<sup>35</sup>. Results are reported as mean  $\pm$  SE.

The females of all 12 pairs sang during this study. Like males, songs of females were found varied and complex with each song type consisting of a series of notes (Figure 1). We did not find significant difference in any of the song type characteristics of the female song when compared with the male (Table 1).

Mean song repertoire size for males and females was observed to be  $22.6 \pm 1.56$  and  $2.0 \pm 0.30$  song types respectively, and the difference was found highly significant



**Figure 1.** Spectrogram of song types used by female (a; out of four song types; delivered during aggression to floater female) and male (b; out of 28 song types; delivered during dawn chorus) individuals of the Pied Bush Chat (bird no. Med 10). Numeric digits (1–14) indicate different note-types used in the song type.

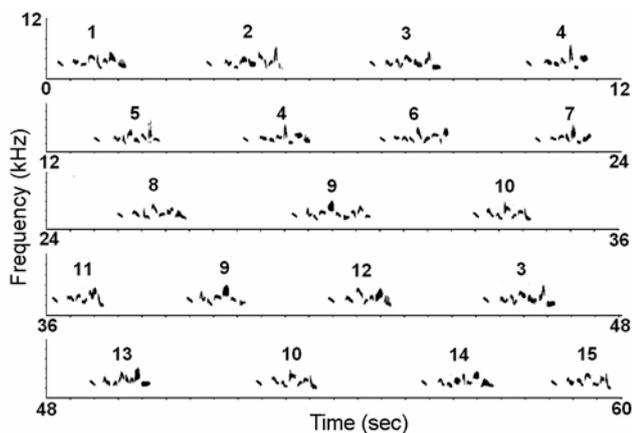
**Table 1.** Sex differences in the song type characteristics of the Pied Bush Chat

Song type characteristics	Male (94 song types)			Female (24 song types)			Mann–Whitney <i>U</i> -test	
	Minimum	Maximum	Mean $\pm$ SE	Minimum	Maximum	Mean $\pm$ SE	<i>Z</i>	<i>P</i> -Value
Minimum frequency (kHz)	1.5	2.39	1.92 $\pm$ 0.01	1.64	2.2	1.92 $\pm$ 0.03	0.118	0.906
Maximum frequency (kHz)	4.26	7.68	5.93 $\pm$ 0.05	4.26	7.03	6.05 $\pm$ 0.13	1.385	0.166
Duration (sec)	0.73	2.22	1.43 $\pm$ 0.02	0.92	2.22	1.50 $\pm$ 0.05	1.030	0.303
No. of notes in a song type	5	14	8.15 $\pm$ 0.16	5	13	8.45 $\pm$ 0.39	0.857	0.391
Type of note in a song type	4	14	8.01 $\pm$ 0.16	5	13	8.25 $\pm$ 0.40	0.694	0.488

**Table 2.** Song repertoire size and song sharing observed in the Pied Bush Chat

Bird no.	Song repertoire size (no. of different song types observed)		No. of song types a female shared with its mate
	Male	Female	
Med10	28	4	4
Cn10	19	1	1
Frnk10	29	2	2
Pnd10	19	2	1
Dvn10	26	4	3
Rd10	13	2	1
Tw10	29	1	0
Dav10	27	2	2
Cnf10	15	1	1
Hry10	24	1	1
Bp10	22	2	1
Tmb10	21	2	0
Mean $\pm$ SE	22.6 $\pm$ 1.56	2.0 $\pm$ 0.30	

Difference in song repertoire size between sexes:  $Z = 4.172$ ,  $P = 0.00003$ .



**Figure 2.** Spectrogram of a 60 sec segment of song of male Pied Bush Chat. Each one continues from the panel immediately above and song types are identified by the number in each panel.

( $Z = 4.172$ ,  $P = 0.00003$ ; Table 2). We observed song-type sharing between individuals of a mated pair. Most females ( $N = 10$ ) shared all, most or at least one song type with their mates. However, two females (Tw10 and Tmb10) did not share song types with their mate (Table 2). In fact, females exhibit large variations in sharing

song types with their mates or neighbouring males (manuscript under preparation).

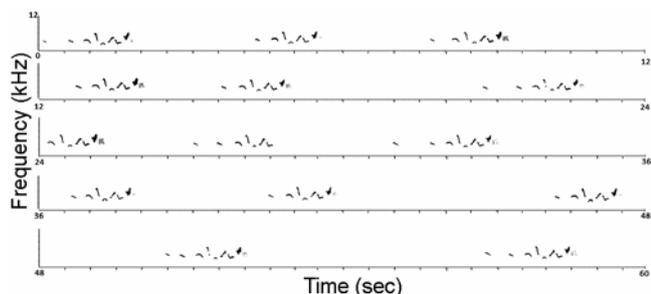
We observed intersexual differences in other aspects of song behaviour also. The most striking feature that differed between sexes was the song delivery pattern. Male Pied Bush Chat sings with immediate variety where successive song types are different from one another<sup>29</sup> (Figure 2). However, in this study females always sang with eventual variety where a single song type is repeated several times (Figure 3). Moreover, males sang on a daily basis primarily during dawn at a stretch for about 30 min (median = 30.5 min; range = 15–46 min), whereas singing females were observed only occasionally and mostly for 6–10 sec with 70 sec being the maximum singing duration. In addition, males started singing during February, i.e. about one month earlier than females and sang throughout the breeding season, whereas females sang almost exclusively during the period just prior to nest building through incubation (Table 3).

We observed singing females under two circumstances. First, females sang during aggressive interactions with floater or neighbouring females ( $n = 37$  for 11 females). As soon as the resident female observed any other female inside or nearby the territorial boundary, she sang and chased it for a long distance in circles both in the air and

**Table 3.** The contexts of female song in the Pied Bush Chat

Female	Singing contexts	
	Aggression to floater/ neighbouring female	Song-answering to mate
F-Med10	Observed <sup>A(2)</sup>	Observed <sup>B(2)</sup>
F-Cn10	Observed <sup>A(2),B(4)</sup>	Not observed
F-Frnk10	Observed <sup>B(5)</sup>	Observed <sup>A(1)</sup>
F-Pnd10	Observed <sup>D(2)</sup>	Not observed
F-Dvn10	Observed <sup>B(3),C(1)</sup>	Observed <sup>B(3)</sup>
F-Rd10	Observed <sup>C(1)</sup>	Observed <sup>B(1)</sup>
F-Tw10	Observed <sup>A(4)</sup>	Observed <sup>C(1)</sup>
F-Dav10	Observed <sup>D(2)</sup>	Not observed
F-Cnf10	Not observed	Observed <sup>B(2)</sup>
F-Hry10	Observed <sup>C(2)</sup>	Observed <sup>A(1),B(3)</sup>
F-Bp10	Observed <sup>A(4),C(2)</sup>	Not observed
F-Tmb10	Observed <sup>A(3)</sup>	Not observed

Alphabets in superscript indicate the breeding stages: A, nest-site selection; B, nest-building; C, egg-laying; D, incubation and numbers in the superscript (in parenthesis) indicate the total sightings females sang during these breeding stages.



**Figure 3.** Spectrogram of a 60 sec segment of song of a female Pied Bush Chat. Each panel continues from the one immediately above.

on the ground. We also observed a fight between females ( $n = 7$  for three females) that included bodily contact and pecking. During such agonistic interactions, the resident male was perched and visible but he did not participate in the fight. It was also interesting to note that resident females responded only to intruding females and were neutral towards intruding males. However, resident male quickly chased off any intruder male observed in the vicinity of his territory.

Second, the female used songs while answering her mate. On several occasions during daytime, both male and female were silent for several minutes and when the male sang, the female immediately answered him. In this study, seven out of 12 females performed such ‘song-answering’ to their mates. During song-answering, the female either initiated her song within approximately 1 sec of the male song, or midway through the song of the male (Figure 4). The female answered the song of her mate most often before nest completion and song-answering was rare thereafter (Table 3). We did not observe females choosing any specific song type for delivery under these two contexts. In other words, the song types used by the female during one context (aggression

to floater/neighbouring females) were used in another context (song answering to mate) also. For example, females F-Tw10 and F-Hry10 had only one song type each in their song repertoires and these females sang their single song type during both contexts.

On one occasion, a male was observed escorting his mate to a crevice in a ground-pit. When the female was inspecting the crevice, the male flew over the pit and produced a song which was immediately answered by his mate. Eventually, this site was selected for nesting and the pair successfully raised four young ones. On another occasion, we observed a female flying over her mate and apparently pecking his head with her beak. The female repeated this action three times and thereafter the male flew towards an almost completely built nest on the ground in a bush. The male entered the bush and stayed there for about a minute. As soon as the male came out, he sang a song type which was answered instantly by his mate. After a minute or so the male again sang, which was again answered by his mate through overlapping his last song and then they both performed ‘song-answering’ for about 40 sec. Thereafter, the male chased the female around the territory and eventually copulation occurred.

In the literature we do not find any information on the prevalence and context of female song in the Pied Bush Chat. Here we describe the female song in this species and provide evidence that the female song in the Pied Bush Chat is not rare and females do sing essentially during certain breeding stages.

There exists considerable variation in intersexual song structure across bird species. For example, in some species, females sing songs similar to males<sup>7,21,36-39</sup>. In others, however, females sing less developed or often immature songs than the males<sup>9,37,40-42</sup>. In this study, song repertoire size differed significantly between sexes; however, we did not detect any significant difference in basic song-

type characteristics between males and females (Table 1). Similarity in the basic structure of song types between sexes may indicate an equal capacity for female song learning in the Pied Bush Chat. However, it would be further interesting to look into the song learning in female Pied Bush Chat.

We witnessed several vocal and behavioural responses of the resident female in which she exhibited agonistic response towards the intruder female. In addition, females responded their mates through song answering also. Agonistic response of resident female to the intruder suggests that the female song may deter rivals from territories, resources or mate (see introduction). Rather, resource defence by female has been suggested as a common feature in birds where females may sing throughout the year or seasonally<sup>4</sup>. In addition, overlapping songs by members of a mated pair (song-answering) may also play a role in joint territorial defence<sup>36,43</sup>.

For several reasons, however, female song in the Pied Bush Chat does not appear to play a role in territorial defence. For example, we typically found male Pied Bush Chat beginning to sing and defend territories in early February, whereas females sang during mid or late March when territories had already been established. Given that the Pied Bush Chat is multi-brooded and vigilance of territory boundaries seems to be maintained regularly, males may use song on a daily basis for long duration to defend their territory and to mediate social relationships with neighbouring males<sup>30</sup>. However, females sang almost exclusively during the early breeding stages and not in a predictable manner as their mates. Moreover, if song plays a role in territorial defence, the male and female should approach intruders of either sex together<sup>37,44,45</sup>. However, the female Pied Bush Chat responded (vocally and physically) to only intruder females and never to the intruder males, even though instances of the intrusion by males inside the territory of the resident male were common during breeding season.

There is a suggestion that in some species, the female has to defend the territory because of the involvement of the male in other activities besides territorial establishment<sup>4</sup>. For example, Superb fairy-wren *Malurus cyaneus* males often remain absent from the territory for obtaining

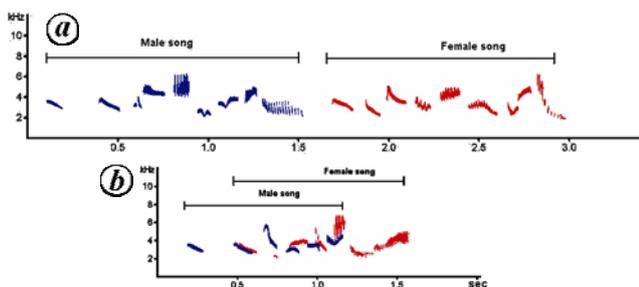
extra-pair matings leaving the territory undefended for a long time. Therefore, females have to sing to defend the territory<sup>13</sup>. However, in the Pied Bush Chat, males are highly territorial and deliver dawn chorus from the boundary of their territories facing each other<sup>30</sup> and do not leave the territory undefended. Under such a situation, it seems less likely that females may need to sing for the purpose of territorial defence.

There is a possibility that female song in Pied Bush Chat could play a role in mate defence. During this study, we observed paired males trying to attract a second female either by escorting her to inspect an unoccupied cavity in their territory ( $n = 7$ ) or by spreading their tails (a common feature during mate attraction) before the intruder female ( $n = 5$ ). Such observations indicate that Pied Bush Chat males seek opportunities to engage in extra-pair copulations and thus, females show agonistic response coupled with song to deter the same sex rival in for mate defence.

We also observed song answering in the Pied Bush Chat, where females responded immediately to the song of their mates with their own songs. Song answering by female to her mate song is a common feature for many bird species and has been suggested as the strategy adopted by the female for mate defence in duetters<sup>4</sup>. However, it does not explain why the female Pied Bush Chat sings only for certain phases of the breeding and not for the entire breeding season.

There are suggestions that female song may be important to coordinate breeding activities for a mated pair. Thorpe<sup>46</sup> pointed out that precisely timed mutual singing between mates of songbirds may maintain or strengthen the pair-bond relationship. In other species also, females use song to coordinate nest relief, to locate fledglings, to encourage male parental care, to maintain group cohesion, and for provisioning to young ones<sup>6</sup>. In this study, vocal response of the majority of females to songs by males was restricted to the early breeding phase(s), suggesting that song-answering may convey information in the synchronization of breeding activities such as female's readiness to breed or some other pair-bond information. However, observations for such interpretation seem suggestive and need further studies.

To sum up, there was no significant difference between song-type characteristics of males and females. However, males had large song repertoire size. Females used songs in inter- and intrasexual communication. Observations also indicated that female song in the Pied Bush Chat is not rare or an anomaly, but may be an adaptive trait that needs to be studied further.



**Figure 4.** Spectrogram showing song-answering in the Pied Bush Chat. Female song type either followed (a) or overlapped (b) the male song type.

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