

# The effect of mate removal on dawn singing behaviour in male pied bush chats

Vinaya Kumar SETHI\*, Dinesh BHATT, Amit KUMAR

Avian Diversity and Bioacoustics Lab, Department of Zoology and Environmental Science, Gurukul Kangri University, Haridwar 249 404, Uttarakhand, India

**Abstract** To determine the influence of pairing status on dawn singing behaviour in pied bush chats *Saxicola caprata*, we conducted mate removal experiments across eight territories. The experiment was divided into three stages: pre-removal (pairs were present on their respective territories), removal (females were experimentally removed), and returned (females were released into the focal pairs' territories). Dawn bout length, song rate, song complexity, percentage performance time, song perch height, and distance of singing location to territory boundary were measured for each male during each experimental stage. We did not find an effect of mate removal on any dawn song characteristics of male pied bush chats suggesting that the presence or absence of a mate does not influence male dawn singing behaviour. Our findings further suggest that males use dawn chorus to mediate social relationships with neighbouring males to proclaim an established territory [*Current Zoology* 57 (1): 72–76, 2011].

**Key words** Dawn chorus, Mate removal, Pied Bush Chat, *Saxicola caprata*

The breeding season of many avian species is characterized by particularly high singing activity at dawn, referred to as the dawn chorus (Catchpole and Slater, 1995). The functions of this dawn chorus have been speculated on extensively and hypotheses such as environmental pressures, hormone-related cycles and social functions (Staicer et al., 1996) have been proposed. Social functions can be split into two groups following the generally accepted dual function of song, territorial defense and mate attraction (McGregor, 1991). For example, dawn singing may have a strong intrasexual component and be addressed mainly to males as territory defense (Slagsvold et al., 1994; Kunc et al., 2005), or to maintain and adjust the social relationship among neighbours (social dynamic hypothesis, Staicer et al., 1996). However, in some species, dawn singing has been demonstrated to have a strong intersexual component and functions to attract and stimulate the social female to copulate (Mace, 1986), attract extra-pair females (Kempnaers et al., 1997), or as a form of mate guarding (Welling et al., 1995).

Further evidence that males sing to attract females comes from female-removal experiments. In several species of song bird levels of male song output are directly related to the presence of the mate within the territory, and if the mate is experimentally removed males

change singing behavior dramatically. Males increase song output by increasing the amount of time spent singing (Krebs et al., 1981; Cuthill and Hindmarsh, 1985; Mace, 1986; Otter and Ratcliffe, 1993), by increasing the length of song (Cuthill and Hindmarsh, 1985), or by changing the composition of the repertoire of songs to types associated with pair formation (Kroodsma et al., 1989). The increase in song output may aid in re-establishing contact with the mate or attracting a replacement (Otter and Ratcliffe, 1993).

The pied bush chat *Saxicola caprata* (Order Passeriformes, Family Muscicapidae) is a tropical songbird found in open habitats including scrub, grassland and cultivated areas. Males are highly territorial and deliver a dawn chorus from their respective territories during the breeding season (Ali and Ripley, 1998). We have observed up to 29 different song types produced by males. A spectrogram of a male's song type is shown in Fig. 1. Territory size of pied bush chat ranges from 2327.7 m<sup>2</sup> to 5229.3 m<sup>2</sup> with an average of 3941.5 ± 951.1 m<sup>2</sup> ( $n = 8$ ) (pers. obs.). This species appears to be socially monogamous, and each pair produces two to three broods during each breeding season (Bell and Swainson, 1985).

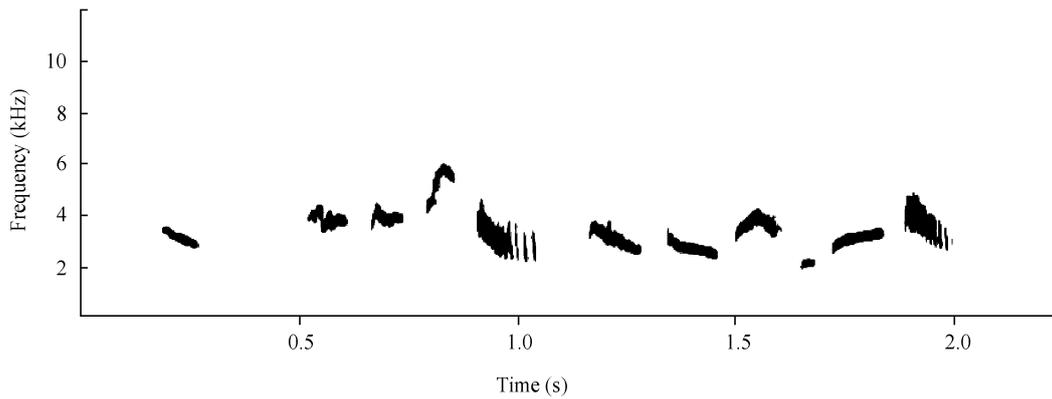
To investigate the function and social influence of dawn singing behaviour in pied bush chats we conducted

---

Received June 13; 2010; accepted Sept. 10, 2010

\* Corresponding author. E-mail: vinaya ksethi@yahoo.co.in

© 2011 *Current Zoology*



**Fig. 1** Spectrogram of a song type of the male pied bush chat *Saxicola caprata*

mate removal experiments. We removed a focal male's mate from different territories to determine how a focal male might change his dawn singing behaviour. We predicted a significant increase in the dawn chorus of male pied bush chats following mate removal. We concentrated our study on singing behaviour during the dawn period to take advantage of the tendency of males to sing maximally at this time of day.

## 1 Materials and Methods

This study was carried out from March to June 2009 in agricultural fields and open grounds with scattered bushes at Haridwar (29°55'N, 78°08'E), Uttarakhand State, India. We recorded the dawn singing behaviour of eight territorial male pied bush chats from a color-banded population during nest-building and incubation periods. Male territories were mapped by noting locations of singing and boundary encounters. We visited each territory before dawn and recorded the entire chorus. Males start to sing  $51.7 \pm 7.3$  min before sunrise (pers. obs.). Most males become quiet around sunrise and sunrise was used as the cutoff point defining the end of dawn singing. However, sometimes males stopped singing approximately 20 min before sunrise and engaged in an alternate activity such as foraging. In these cases we considered the dawn chorus as finished when the male did not sing for a minimum of 5 min. Observations were made during daytime also between 15:00–18:30 h.

Songs were recorded from 4 to 6 m without influencing the singing behaviour of 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 24000 Hz and sample format of 16 bit.

Spectrograms were prepared with Avisoft SASLab Pro 4.1 software (Specht, 2002).

To determine the influence of pairing status on dawn singing behaviour we conducted eight female removal experiments across eight pairs and territories. Removals took place on 27 March, 6, 16, 21 and 22 April, 16 and 18 May, and 17 June. The experimental set up was divided into three stages. In the first stage, termed 'pre-removal', the dawn songs of males were recorded when their mates were present on their respective territories. In the second stage, termed 'removal', females were captured using mist nets at around 14:00 h and on the following day males were recorded during the dawn. We released females within the focal pairs' territories within two to four hours after recording dawn singing during the 'removal' stage. All females returned to their territories and joined their mates within hours on the day they were released. The next morning we recorded each male a third time ('returned stage').

The following dawn song characteristics and measurements were measured for each male during each stage: (i) dawn bout length (min), (ii) song rate (estimated as number of song types delivered by each male during 10 min continuous song section), (iii) song complexity (estimated as number of different song types delivered by each male during a 10 min continuous song section), (iv) percentage performance time (computed as song length divided by the sum of song length and pause length multiplied by 100, Lambrechts and Dhondt, 1988), (v) song perch height (m), (vi) distance from singing location to territory boundary (m). We used Wilcoxon matched-pairs signed rank tests to compare male singing behaviour between the pre-removal and removal and the pre-removal and returned stages (Zar, 1999). Results are reported as means  $\pm$  SD unless otherwise noted.

## 2 Results

After removal of their mates, male pied bush chats did not alter their dawn singing patterns or associated behaviour. Males neither increased nor shortened the length of their dawn song bouts when their mates were removed or returned. Likewise, there was no significant difference in song rate, song complexity, percentage performance time, song perch height or distance of singing location to territory boundary among experimental stages (Table 1).

Males frequently tried to establish contact with their lost mate within hours of removal. For example, within two hours of the mate removal experiment all males entered their respective nest cavity at least four times and increased their movements within the territory. Further, one male entered the nest cavity five times and another male 11 times before going to roost on the day their mates were removed. In contrast, during pre-removal and returned stages, males merely perched nearby the nest cavity (where females were nest building or incubating) probably to guard the female and rarely or only occasionally entered the nest cavity during day time.

At dawn, neighbouring males frequently came to the boundary of their territories, faced each other and performed counter-singing. Males used low perches for dawn chorus (range: ground level to 2 m during pre-removal and returned stages, and ground level to 1.5 m during removed stage), which did not vary significantly among experimental stages (Table 1). The use of low perches during dawn chorus was in marked contrast to the perches males used during daytime singing. During the day males usually sang near the top of the canopy, on the edge of a building or on an electricity

pole with a mean height of  $5.8 \pm 1.6$  m (range: 2 to 8 m,  $n = 9$ ).

The mean distance between neighbouring dawn singing males was relatively low ( $12.1 \pm 5.4$  meter), when compared to the mean distance between singing males and their roosting mates' ( $29.8 \pm 10.1$  meter), suggesting that during dawn males were in the close range of vocal interaction with neighbouring males as compared to their mate. Additionally, female pied bush chats approached their respective males within 20 min ( $16.95 \pm 3.54$  min,  $n = 19$ ) of the commencement of the dawn chorus, whereas males continued to sing for more than 30 min during dawn.

## 3 Discussion

We did not detect any significant difference in the dawn song of male pied bush chats following the removal of their mates. This suggests that the presence or absence of a mate does not strongly influence male dawn singing behaviour. In contrast the dawn chorus of male pied bush chats appears to function primarily for close-range communication among neighbouring males. For example, irrespective of the presence or absence of their mate, neighboring male pied bush chats frequently selected dawn singing locations close to, and on opposite sides of, their shared territorial boundary. Neighbouring males used these perches consistently to interact vocally often performing counter-singing at high rates for extended periods throughout the breeding season. Males occasionally sang during the day, however, such close-range counter-singing was common only at dawn but not during the day. Overall, these observations are consistent with the social dynamics hypothesis for the functional significance of dawn singing, which suggests that this behaviour functions in the maintenance and

**Table 1** Dawn singing behaviour of male pied bush chats (N = 8) in relation to presence or absence of their mate

Dawn song characteristics	Status of female			Wilcoxon Signed Ranks Test	
	Pre-removal	Removed	Returned	Pre-removal versus removed	Pre-removal versus returned
Bout length (min)	42.3±2.7	46.7±2.9	43.3±2.0	$t = 6, P = 0.090$	$t = 15.5, P = 0.725$
Song perch height (m)	0.8±0.2	0.8±0.1	1.0±0.2	$t = 6, P = 0.655$	$t = 5, P = 0.480$
Distance of singing location to territory boundary (m)	9.6±1.4	8.7±1.4	10.3±1.8	$t = 6, P = 0.343$	$t = 7.5, P = 0.527$
Song rate (no. of songs/10 min)	154.3±9.8	158.5±6.0	149.5±4.9	$t = 14, P = 0.575$	$t = 14, P = 0.575$
Song complexity (no. of song types/10 min)	18.6±2.0	19.3±1.9	18.8±1.7	$t = 5, P = 0.119$	$t = 7, P = 0.892$
Percentage performance time	36.2±1.9	37.1±1.9	35.3±1.9	$t = 11.5, P = 0.362$	$t = 16, P = 0.779$

Values are means  $\pm$  SE.

adjustments of social relationships among neighbouring males (Staicer et al., 1996; Liu and Kroodsma, 2007). We cannot rule out that dawn singing by male pied bush chats does function to attract females for extrapair copulations, as has reported for other species (Welling et al., 1995; Kempenaers et al., 1997).

Male pied bush chats used low perches for dawn chorus which did not vary significantly among experimental stages. Additionally, the mean distance between neighbouring dawn singing males was relatively low, when compared to the mean distance between singing males and their roosting mate. Singing from the ground or low perches is more suitable for short-range communication than for long-range communication (Wiley and Richards, 1982), and studies indicate that males may sing from low perches to communicate in a close-range vocal interaction network, often with neighbouring males (Lein, 2007; Liu and Kroodsma, 2007). Our results also indicate that male pied bush chats were probably directing their dawn chorus towards their close-range neighbouring males and not to their mate roosting farther from the dawn chorus perches.

Male birds generally sing from the central area of their territory or near to the nest during dawn in order to direct their songs at their mate. If females are experimentally removed males try to establish contact with their mates either by entering the nest cavity or by increasing movement around the territory (Otter and Ratcliffe, 1993). Here, male pied bush chats always used locations close to their shared boundary and did not sing near their nest cavity or female roosting sites during dawn. Of further interest is our observation that during the removal stage, males did not try to search for their lost mates and continued to sing their dawn chorus from almost the same perches that were used during the pre-removed and returned stages. This suggests that it is less likely that the dawn chorus is in fact directed at their mate.

Male pied bush chats sang inconsistently and for short periods during the early breeding season when males were establishing territories. The dawn chorus reached its peak only after most neighbouring males had settled on their territories (pers. obs.). The dawn chorus of male pied bush chats appears to play a role in social relationship among males. Similar observations have been reported for mate removal experiments carried out on six pairs in chipping sparrows *Spizella passerina* (Liu, 2004). However, other studies suggest that males direct their dawn chorus towards their mates. For example, Mace (1986) found that time spent singing at dawn

in male great tits *Parus major* was directly proportional to the time after dawn that the female emerges from the nest cavity. Similarly, Part (1991) and Otter and Ratcliffe (1993) found that male collared Flycatchers *Ficedula albicollis* and black-capped chickadees *Parus atricapillus* end the dawn song with the arrival of their mate. In contrast, female emergence did not appear to have any affect on dawn singing behaviour in pied bush chat as males continued to sing even after female arrival.

In conclusion, dawn song characteristics and singing behavior in male pied bush chats appears to be unaffected by the removal of their female mate. Thus, our findings suggest that male pied bush chats may not direct their dawn chorus primarily to their mate. In contrast, for several reasons, male pied bush chats seemed to direct their dawn chorus towards their neighboring males, supporting the hypothesis that resident males may sing at dawn to defend their territory and to mediate social relationships with neighbouring males to proclaim an established territory (Staicer et al., 1996; Kunc et al., 2005; Amrhein and Erne, 2006).

**Acknowledgements** We thank the Head, Department of Zoology and Environmental Science, Gurukul Kangri University Haridwar, India for providing infrastructure. Many thanks to Shivchand Arora for assistance recording songs in the field. We are grateful to Valentin Amrhein, University of Basel, Switzerland and two anonymous referees for feedback on an earlier version of this paper. Funding and permission was obtained from the Department of Science and Technology (sanction no. SR/SO/AS/73/2006).

## References

- Ali S, Ripley SD, 1998. Handbook of the Birds of India and Pakistan (Robins to Wagtails). New Delhi: Oxford University Press.
- Amrhein V, Erne N, 2006. Dawn singing reflects past territorial challenges in the winter wren. *Anim. Behav.* 71: 1075–1080.
- Bell HL, Swainson GW, 1985. The colonization, ecology and breeding of the pied stonechat *Saxicola caprata* at Port Moresby, Papua New Guinea. *Ibis* 127: 74–83.
- Catchpole CK, Slater PJB, 1995. Bird Song: Biological Themes and Variations. Cambridge: Cambridge University Press.
- Cuthill I, Hindmarsh A, 1985. Increase in starling song activity with removal of mate. *Anim. Behav.* 33: 326–335.
- Kempenaers B, Verheyen GR, Dhondt AA, 1997. Extrapair paternity in the blue tit *Parus caeruleus*: Female choice, male characteristics, and offspring quality. *Behav. Ecol.* 8: 481–492.
- Krebs JR, Avery M, Cowie RJ, 1981. Effect of removal of mate on the singing behavior of great tits. *Anim. Behav.* 29: 635–637.
- Kroodsma DE, Bereson RC, Minear E, 1989. Use of song types

- by the chestnut-sided warbler: Evidence for both intra- and inter-sexual functions. *Can. J. Zool.* 67: 447–456.
- Kunc HP, Amrhein V, Naguib M, 2005. Seasonal variation in dawn song characteristics in the common nightingale. *Anim. Behav.* 70: 1265–1271.
- Lambrechts M, Dhondt AA, 1988. The anti-exhaustion hypothesis: a new hypothesis to explain song performance and song switching in the great tit. *Anim. Behav.* 36: 327–334.
- Lein MR, 2007. Patterns of dawn singing by buff-breasted flycatchers. *J. Field Ornithol.* 78: 343–351.
- Liu WC, 2004. The effect of neighbors and females on dawn and daytime singing behaviors by male chipping sparrows. *Anim. Behav.* 68: 39–44.
- Liu WC, Kroodsma DE, 2007. Dawn and daytime singing behavior of chipping sparrows *Spizella passerina*. *Auk* 124: 44–52.
- Mace R, 1986. Importance of female behavior in the dawn chorus. *Anim. Behav.* 34: 621–622.
- McGregor PK, 1991. The singer and the song: On the receiving end of bird song. *Biol. Rev.* 66: 57–81.
- Otter K, Ratcliffe L, 1993. Changes in singing behavior of male black-capped chickadees *Parus atricapillus* following mate removal. *Behav. Ecol. Sociobiol.* 33: 409–414.
- Part T, 1991. Is dawn singing related to paternity insurance? The case of the collared flycatcher. *Anim. Behav.* 41: 451–456.
- Slagsvold T, Dale S, Saetre GP, 1994. Dawn singing in the great tit *Parus major*: Mate attraction, mate guarding, or territorial defense? *Behaviour* 131: 115–138.
- Specht R, 2002. Avisoft-SASLab Pro Sound Analysis and Synthesis Laboratory. Berlin: Avisoft Bioacoustics (<http://www.avisoft.com>).
- Staicer CA, Spector DA, Horn AG, 1996. The dawn chorus and other diel patterns in acoustic signaling. In: Kroodsma DE, Miller EH ed. *Ecology and Evolution of Acoustic Communication in Birds*. Ithaca: Cornell University Press, 426–453.
- Welling P, Koivula K, Lathi K, 1995. The dawn chorus is linked with female fertility in the willow tit *Parus montanus*. *J. Avian Biol.* 26: 241–246.
- Wiley RH, Richards DG, 1982. Adaptations for acoustic communication in birds: Sound transmission and signal detection. In: Kroodsma DE, Miller EH, Ouellet H ed. *Acoustic Communication in Birds*. New York: Academic Press, 131–181.
- Zar JH, 1999. *Biostatistical Analysis*. New Jersey: Prentice-Hall.