

## Song sharing in the pied bush chat (*Saxicola caprata*)

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**ABSTRACT.** In most oscine passerine bird species, male song is composed of different song types of which some are shared with other males. Our aim for this study was to investigate whether song sharing occurs in the pied bush chat (a tropical species with multiple song types), and if so, whether neighbouring males share significantly more song types than non-neighbouring males and whether song sharing declines with increasing distance between males. A standard song sharing index was used to compare all song types of each male with all song types of all other males. Males had a mean repertoire of  $22.8 \pm 4.4$  song types ranging from 17 to 30 song types. Results revealed that neighbouring males shared significantly more song types than did non-neighbouring males. Nevertheless, no two males shared all song types in their repertoires. Furthermore, we observed a significant decline in the proportion of song repertoire shared with increasing distance between males. Results confirm the presence of song sharing in the pied bush chat, which may help neighbouring males to mediate social relationships.

**KEY WORDS:** pied bush chat, *Saxicola caprata*, song repertoires, song sharing.

### INTRODUCTION

Bird song, among the most acoustically complex of all non-human vocal communication signals (EDA-FUJIWARA et al., 2006), has been attracting the attention of naturalists, zoologists and ornithologists for a long time (DARWIN, 1871; BAKER, 2001; MARLER, 2004). In general, bird song is believed to function as a dual purpose signal aimed to attract mates and/or to repel territorial rivals (CATCHPOLE & SLATER, 2008).

The number of different song types a bird sings is referred to as song repertoire size and may range from 1 to more than 2000 song types in different bird species (CATCHPOLE & SLATER, 2008). The most widely proposed explanation for the evolution of song repertoires is that they have evolved largely because of sexual selection, with females preferring males that sing many song types (SEARCY & ANDERSSON, 1986; ANDERSSON, 1994). The underlying idea is that the development of large repertoires is costly and

only high quality males can afford it (KIEFER et al., 2006).

An alternative hypothesis is that repertoires have evolved to facilitate communication among territorial neighbouring males (BEECHER et al., 1994, 2000; HUGHES et al. 1998; PRICE & YUAN, 2011). Song contests between neighbours may include either 'song type matching' in which one male replies to another with the same song type (KREBS et al., 1981) or 'repertoire matching' in which one male replies to another with a different but shared song type (BEECHER et al., 1996). Studies suggest that territorial neighbouring males use song sharing as an important strategy to address a particular rival and to signal more specific information such as arousal or readiness to escalate a contest. Therefore, by song sharing (song-type matching) a bird may reduce the need for physical battles, thus minimizing the cost and risk of such escalations (KREBS et al., 1981; TODT & NAGUIB, 2000). If song sharing is important in territorial contests between neighbouring males, then it could enhance male

fitness by prolonging territory tenure (HUGHES et al., 2007). Furthermore, a correlation between song sharing and reproductive success has also been established for indigo bunting (*Passerina cyanea*) where males that share their single song type with a neighbour tend to be more successful in mating and in fledging young than those who do not share song (PAYNE et al., 1988). Nevertheless, to understand the adaptive significance of song sharing in any bird species, one has to first ascertain whether song sharing exists in a territorial song-bird species or not.

Song sharing varies considerably between species (RASMUSSEN & DABELSTEEN, 2002). For example, males of several bird species share song types with their neighbours (MCGREGOR, 1980; MCGREGOR & KREBS, 1989; BEECHER et al., 2000; GRIESSMANN & NAGUIB, 2002; ROGERS, 2004; KOETZ et al., 2007) while others do not (SLATER & INCE, 1982; Horn & Falls, 1988) or even share more with non-neighbours than with neighbours (GRANT & GRANT 1979; BRADLEY 1981; BORROR, 1987). Furthermore, in some species, neighbours share more than one might expect (DUFTY, 1985; MORTON, 1987) while in others, sharing falls off rapidly with distance (WILSON et al., 2000; RIVERA-GUTIERREZ et al., 2010). Intraspecific differences in song sharing have also been reported, where sedentary populations of some bird species exhibit higher song sharing while migratory populations exhibit less song sharing (KROODSMA & VERNER, 1978; EWERT & KROODSMA, 1994; NIELSEN & VEHRENCAMP, 1995; NELSON et al., 1996; HUGHES et al., 1998).

*Saxicola* (Family Muscicapidae) is a genus of 15 species of small passerine birds commonly known as stonechats or bushchats. There exists very little information on the singing behaviour of most species in this genus. Species studied for their basic song structure in this genus include the whinchat (*Saxicola rubetra*), stonechat (*S. torquata*) and pied bush chat (*S. caprata*) (GUETTINGER, 1984; SETHI et al., 2012a). Researchers have studied seasonal patterns of song production in the stonechat (GREIG-SMITH,

1982a), correlations between song rates and parental care in the stonechat (GREIG-SMITH, 1982b) and song repertoire sizes of the pied bush chat (SETHI et al., 2011a). Other than this, a survey of the literature reveals that we largely lack fundamental information on the singing behaviour of most species of this genus.

The pied bush chat is a tropical, sedentary and territorial songbird. It is found in open habitats including scrub, grassland and cultivated areas. It is distributed discontinuously from Transcaucasia and the Indian subcontinent to south-east Asia, the Philippines, Indonesia, New Guinea and New Britain (BELL & SWAINSON, 1985; ALI & RIPLEY, 1998). In addition to using a variety of calls (SETHI et al., 2012b), males of this species intensively sing on a daily basis at dawn during the breeding season (late February to July in the study area) (ALI & RIPLEY, 1998; SETHI et al., 2012a). Males have mean ( $\pm$ SD) song repertoires of  $22.2 \pm 6.6$  song types (range = 13–29;  $N = 9$  males) (SETHI et al., 2011a). Males remain on their respective territories throughout the year. Nevertheless, territorial encounters between males are only observed frequently during the breeding season (pers. obs.). Female pied bush chats have also been reported to sing (SETHI et al., 2012c). A female removal experiment in this species suggested that the presence or absence of a mate does not influence male dawn singing behaviour and males seem to direct their songs to neighbouring males (SETHI et al., 2011b). The existence of large song repertoires along with the territorial habit of two or more males that sing in a close-range vocal interaction network make the pied bush chat an excellent model to study song sharing behaviour (SETHI et al., 2011a). Nevertheless, no studies to date have examined song sharing of this species. Therefore, our aim for this study was to investigate whether song sharing occurs in this species, and if so, whether neighbouring males share significantly more song types than do non-neighbouring males and whether song sharing declines with increasing distance between males.

## MATERIAL AND METHODS

This study was carried out in agricultural fields and open grounds at Haridwar (29°55'N, 78°08'E), Uttarakhand State, India during the breeding season, February to July 2013, of the pied bush chat. Songs were recorded of eight males from a color-banded population. We concentrated our study mainly on dawn singing to take advantage of the tendency of males to sing at the highest rate at this time of day (SETHI et al., 2011b). We visited each territory before dawn and recorded the focal male for the entire duration of his dawn singing bout. We always reached the study area before the male started singing and remained there until the completion of the dawn singing. Males start to sing  $51.7 \pm 7.3$  min before sunrise (pers. obs.) and mostly become quiet around sunrise. Thus, 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. Song repertoire size was

defined as the number of different song types used by a male.

On most occasions, two males were recorded each morning by two observers separately using 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).

The eight focal males could be divided into three groups. In the first group, males 1, 2 and 3 were a neighbouring group with male 2 settling between male 1 and male 3. In the second group, males 4 and 5 were immediate neighbours. Males 6, 7 and 8 made the third neighbouring group with male 7 settling between male 6 and male 8. These three groups were at least 2 km. apart and therefore, we believe that they were out of audible range from each other. For the estimation of song repertoires of any male, we visually studied the spectrograms of its entire

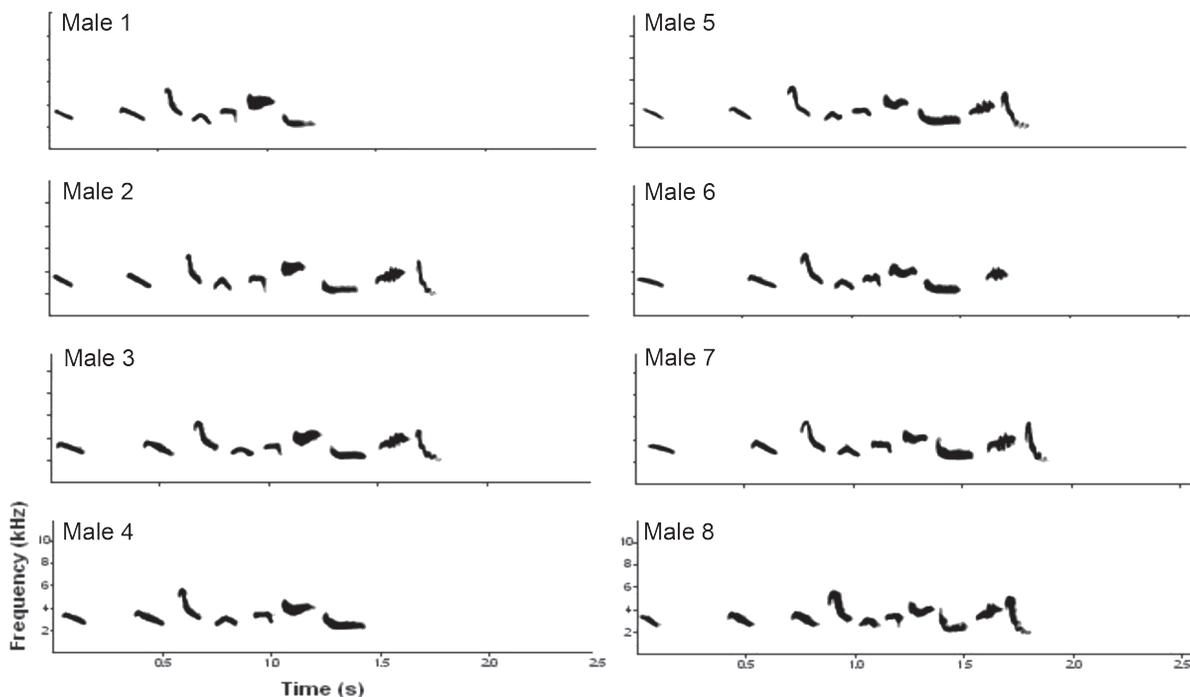


Fig. 1. – Spectrograms of a song type shared by all individuals of the pied bush chat (N=8).

song bout. For each male, a printed library of all used song types was constructed. Each song type was classified either as a new song type or as an already existing one. Each new song type was assigned a unique number. On inter- and intra-individual levels, males rarely used variants of song types, i.e. added or deleted one or two notes at the end of a song type (Figure 1). However, the variation within song types was much less than between song types, and thus, we were able to identify all song types unambiguously. Our previous observations suggested that an inspection of 320 consecutive song types of an individual male pied bush chat can generate its complete song repertoire (SETHI et al., 2011a). Therefore, we inspected around 400 song types for each male. Completeness of repertoires was verified by plotting the cumulative number of new song types against the total number of songs in the subject's repertoire. We were able to estimate the full song repertoires as the cumulative graph reached an asymptote for all males.

To assess the song sharing between males, we compared all song types of each male with all

song types of the other males. In all, 28 pair-wise repertoire comparisons were made, of which 7 and 21 were made among neighbouring and non-neighbouring males respectively. Following MCGREGOR & KREBS (1982) and CATCHPOLE & ROWELL (1993), repertoire sharing was calculated for every pair of males in the population using the standard song sharing index  $S = 2N_s / (R_1 + R_2)$ , where  $N_s$  = the number of shared song types, and  $R_1$  and  $R_2$  are the repertoire sizes of the two males. This gives a song sharing index that expresses the proportion of song types shared between any two males on a scale from 0 (no song types shared) to 1 (all song types shared). A Mann-Whitney U test was used to compare the song sharing index between neighbouring and non-neighbouring males (ZAR, 1999). To determine whether song sharing varies as a function of distance between two males, a Mantel test (MANTEL, 1967) was used through comparing a matrix of sharing indices with a matrix of geographic distance between the males. The distance between two males was measured using a location map and calculated as the shortest land distance between their active nests.

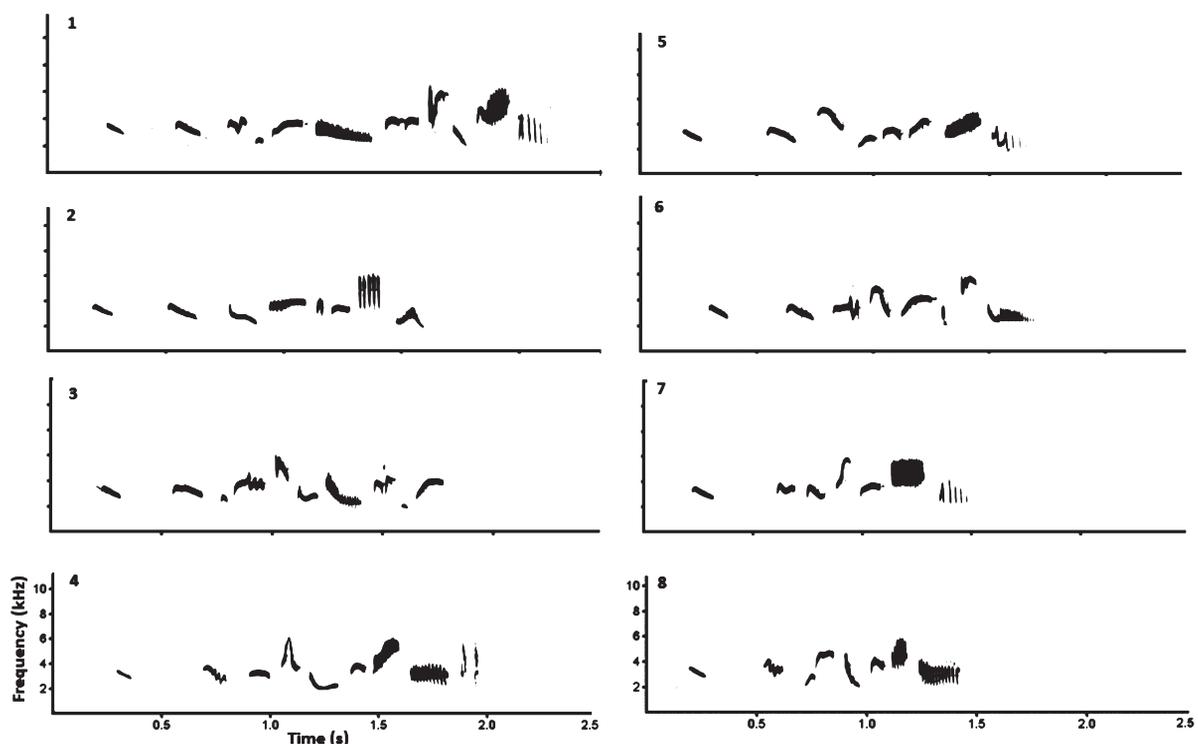


Fig. 2. – Spectrograms of eight song types (out of 20) used by male no. 1.

## RESULTS

Pied Bush Chat males had a mean ( $\pm$ SD) repertoire of  $22.8 \pm 4.4$  song types ( $N = 8$  males). The song repertoire size of these males ranged from 17 to 30 song types. The spectrograms of eight song types (out of 20) delivered by male 1 are shown in Figure 2.

In this study, neighbouring males shared significantly more song types ( $S = 0.52 \pm 0.03$ ; mean  $\pm$ SE) than did non-neighbouring males ( $S = 0.35 \pm 0.02$ ) ( $Z = 3.18$ ,  $P = 0.001$ ). The highest and the lowest similarities of song repertoires were observed in neighbouring ( $S = 0.62$ ) and non-neighbouring pairs ( $S = 0.22$ ) respectively. Nevertheless, no two males shared all song types in their repertoires and all males shared some song types. We found a significant negative correlation between the level of song types shared between two males and their proximity (Mantel  $r = -0.49$ ,  $P > 0.05$ ).

In all, we identified a total of 78 song types in the song repertoires of eight males. Out of 78,

four song types (5%) were common and were delivered by all the males, while 33 (42%) song types were each delivered by one male only (Figure 3). The patterns of song type sharing between male pied bush chats are summarized in Table 1.

## DISCUSSION

Our results indicate that territorial neighbouring male pied bush chats shared songs and that neighbours shared significantly more song types than did non-neighbours. Most studies have suggested a relationship between sedentary behaviour and higher levels of song sharing between territorial neighbours (MCGREGOR & KREBS, 1989; BEECHER et al., 1994; ROGERS, 2004) and our study also supports this correlation. In this study, males did not migrate and were always found in their respective territories throughout the year. Such sedentary habits might allow birds to breed in the same area where they were born and learned their songs (BEECHER et al., 1994). Alternatively, males could exhibit song

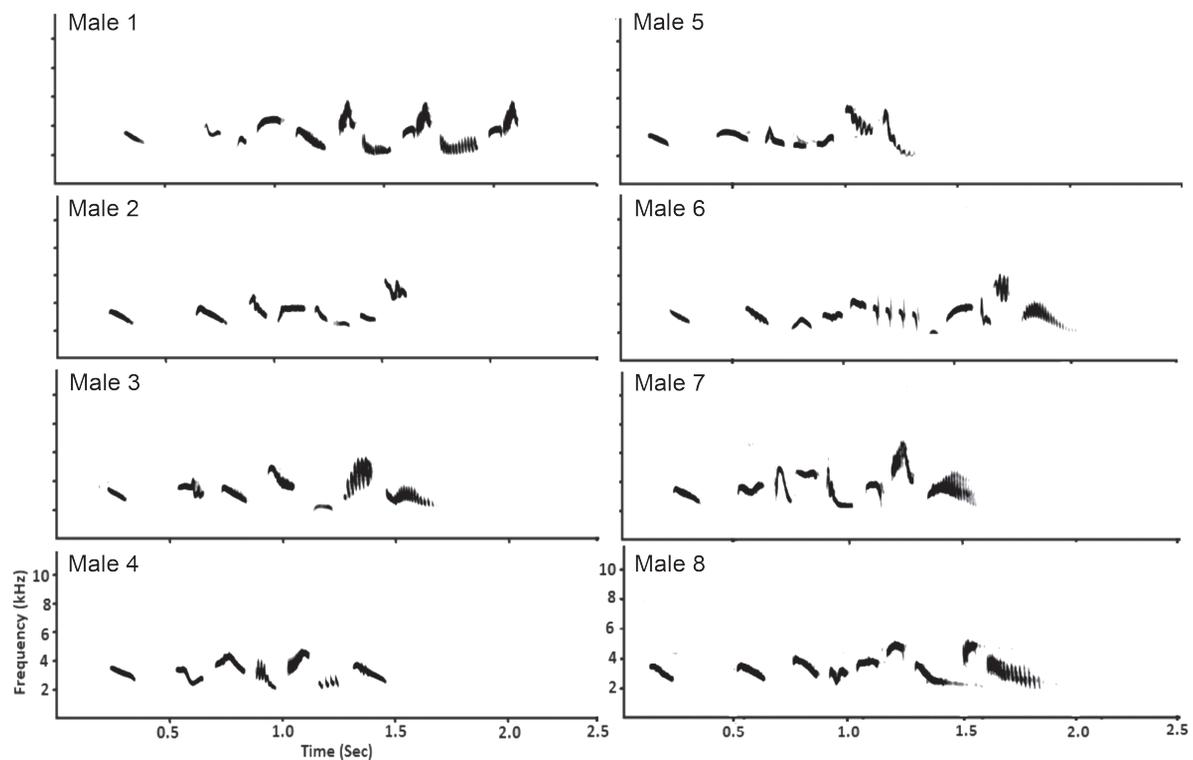


Fig. 3. – Spectrograms of unshared song types from the song repertoires of eight males.

TABLE 1

Patterns of song type sharing in male pied bush chats (N= 8).

| No. of song types (n= 78) | No. of males that shared particular song type | Percentage |
|---------------------------|---|------------|
| 33                        | Unshared (i.e. sung by 1 male only)           | 42.3       |
| 20                        | 2   | 25.6       |
| 10                        | 3   | 12.8       |
| 8                         | 4   | 10.3       |
| 1                         | 5   | 1.3        |
| 1                         | 6   | 1.3        |
| 1                         | 7   | 1.3        |
| 4                         | 8   | 5.1        |
|                           | Total   | 100        |

sharing either by adjusting their song repertoires to the neighbouring males or by settling next to males with similar song repertoires (DEWOLFE et al., 1989; PAYNE & PAYNE, 1993).

Song sharing among neighbouring male songbirds seems to result from at least three non-mutually exclusive processes based on the time of song memorization and song production (NELSON, 1992). The first model suggests that young birds learn their song repertoires from their neighbours or father before dispersal and then settle close to them (MARLER & TAMURA, 1962; CUNNINGHAM & BAKER, 1983; GRANT & GRANT, 1996). The second model suggests that song acquisition occurs after natal dispersal when males establish a territory for the first time (KROODSMA, 1974; PAYNE & PAYNE, 1993). A third model, termed action-based learning (MARLER, 1990), suggests that males produce a variety of songs in their plastic song stage and then select a subset of song(s) for retention in their repertoires based on social interactions with their neighbours (DEWOLFE et al., 1989). However, we do not have any data on song learning by young pied bush chat. Therefore, based on the present study, it is difficult to comment on the evolution of song sharing in the pied bush chat.

The decline of song sharing with distance in the pied bush chat seems to be consistent with the song learning model of BEECHER et al., (1994, 1996) developed for the western

population of the song sparrow. According to this model, young song sparrows memorize songs about two to three months following nutritional independence. During this time, they visit the territories of several adult males to establish their own territory and learn songs from these adult males. The young birds either succeed in occupying a territory near their tutors and exhibit a high level of song sharing with them or they establish their territories farther away from their tutors and exhibit less or no song sharing with them. However, the song learning behaviour in the pied bush chat has not been studied so far and therefore further studies seem necessary to understand the effect of song learning on the song sharing behaviour of this species.

The present study indicates that song sharing is higher between close neighbours than between distant birds. Similarly, a study of syllable sharing in the house finch (*Carpodacus mexicanus*) has revealed a negative correlation between the extent of syllable sharing and distance (BITTERBAUM & BAPTISTA, 1979). Similar relationships have been suggested for Bewick's wren (*Thryomanes bewickii*, KROODSMA, 1974), American redstart (*Setophaga ruticilla*, LEMON et al., 1994), song sparrow (WILSON et al., 2000), and chowchilla (*Orthonyx spaldingii*, KOETZ et al., 2007). In sedentary species, especially those occupying permanent territories such as the pied bush chat, a distance of about 2 km between neighbouring groups might create acoustic isolation, with

males possibly out of earshot from each other. Therefore, in this study, distant males could probably not hear each other and did not show higher levels of song sharing. A similar effect of isolation by distance has been suggested for the great tit (*Parus major*) in which males in closer forest fragments share more song types and the highest levels of sharing are observed among males breeding in the same forest fragment (RIVERA-GUTIERREZ et al., 2010).

Evidence from a variety of species suggests that song sharing, in the form of song-type matching or repertoire-matching, allows males to interact vocally in ways that are impossible without sharing (HUGHES et al., 2007; BEECHER et al., 2000; SEARCY & BEECHER, 2009). Song-type matching may result in escalated aggressive contexts or may be followed by close aggressive approach (NIELSEN & VEHRENCAMP, 1995) while repertoire-matching may direct mild threats to a specific neighbour without escalating the encounter (BEECHER et al., 1996). However, it has been suggested that song matching does not necessarily always evolve through aggressive encounters. It may also help females to compare males and other males to assess the two singers (LOGUE & FORSTMEIER, 2008). Overall, song sharing has the potential to indicate the level of aggression, motivation, experience, abilities, or intent of the territorial singers (SEARCY & BEECHER, 2009; NAGUIB & MENNILL, 2010; PRICE & YUAN, 2011). Although in this study, we did not investigate the type of song sharing (song-type match vs. repertoire match), yet we frequently observed neighbouring males coming to the boundary of their territories, facing each other and performing counter-singing. Such counter-singing between neighbouring males remained common throughout the breeding season suggesting an important role in territorial interactions between neighbouring males. It seems that song sharing in the pied bush chat might help males to mediate social relationship among them to proclaim an established territory. Our previous observations have also suggested that male pied bush chats sing primarily for close-range communication among neighbouring

males to defend their territory (SETHI et al., 2011b).

In conclusion, this study reports the existence of song sharing in the Pied Bush Chat, where neighbouring males share significantly more song types than do non-neighbouring males. We report a decline in the proportion of song repertoires shared with increasing distance between males. Observations also indicate that song sharing in the pied bush chat possibly helps males mediating social relationships via improved acquisition and maintenance of territories. Further experimental studies would be necessary to ascertain the type of song sharing (repertoire or song-type matching) that occurs between neighbouring males along with understanding the song learning behaviour and adaptive significance of song sharing in the pied bush chat.

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## REFERENCES

- ALI S & RIPLEY SD (1998). Handbook of the birds of India and Pakistan (Volume 9: robins to wagtails). Oxford University Press, New Delhi, India.
- ANDERSSON M (1994). Sexual selection. Princeton University Press, Princeton.
- BAKER MC (2001). Bird song research: the past 100 years. *Bird Behavior*, 14:3-50.
- BEECHER MD, CAMPBELL SE & STODDARD PK (1994). Correlation of song learning and territory establishment strategies in the song sparrow.

- Proceedings of the National Academy of Science USA, 91:1450-1454.
- BEECHER MD, STODDARD PK, CAMPBELL, SE & HORNING CL (1996). Repertoire matching between neighboring song sparrows. *Animal Behavior*, 51:917-923.
- BEECHER MD, CAMPBELL, SE & NORDBY JC (2000). Territory tenure in song sparrows is related to song sharing with neighbours, but not to repertoire size. *Animal Behavior*, 59:29-37.
- 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.
- BITTERBAUM E & BAPTISTA LF (1979). Geographical variation in songs of California House finches (*Carpodacus mexicanus*). *Auk*, 96: 462-474.
- BORROR DJ (1987). Song in the white-eyed vireo. *Wilson Bulletin*, 99:377-397.
- BRADLEY RA (1981). Song variation within a population of white-eyed vireos *Vireo griseus*. *Auk*, 98:80-87.
- CATCHPOLE CK & ROWELL A (1993). Song sharing and local dialects in a local population of the European wren *Troglodytes troglodytes*. *Behaviour*, 125:67-78.
- CATCHPOLE CK & SLATER PJB (2008). *Bird Song: Biological Themes and Variations*. Cambridge University Press, Cambridge.
- CUNNINGHAM MA & BAKER MC (1983). Vocal learning in white-crowned sparrows: Sensitive phase and song dialects. *Behavioral Ecology and Sociobiology*, 13:259-269.
- DARWIN C (1871). *The descent of man, and selection in relation to sex*. John Murray, London, U.K.
- DEWOLFE BB, BAPTISTA LF & PETRINOVICH L (1989). Song development and territory establishment in nuttall's white-crowned sparrows. *Condor*, 91:397-407.
- DUFTY AM (1985). Song sharing in the brown-headed cowbird (*Molothrus ater*). *Zeitschrift für Tierpsychologie*, 69:177-190.
- EDA-FUJIWARA H, SATOH R & MIYAMOTO T (2006). Song preferences by females: male song complexity and gene expression in the female brain. *Ornithological Science*, 5:23-29.
- EWERT DN & KROODSMA DE (1994). Song sharing and repertoires among migratory and resident rufous-sided towhees. *Condor*, 96:190-196.
- GRANT BR & GRANT PR (1996). Cultural inheritance of song and its role in the evolution of Darwin's Finches. *Evolution*, 50:2471-2487.
- GRANT PR & GRANT BR (1979). Darwin's finches: population variation and sympatric speciation. *Proceedings of the National Academy Sciences (USA)*, 76:2359-2363.
- GREIG-SMITH PW (1982a). Seasonal patterns of song production by male stonechats *Saxicola torquata*. *Ornis Scandinavica*, 13:225-231.
- GREIG-SMITH PW (1982b). Song-rates and parental care by individual male Stonechats (*Saxicola torquata*). *Animal Behaviour*, 30:245-252.
- GRIESSMANN B & NAGUIB M (2002). Song sharing in neighboring and non neighboring thrush nightingales (*Luscinia luscinia*) and its implications for communication. *Ethology*, 108: 377-387.
- GUETTINGER HR (1984). Comparison of whinchats *Saxicola rubetra* and stonechats *Saxicola torquata* songs. *Journal für Ornithologie*, 261-278.
- HORN AG & FALLS JB (1988). Repertoires and countersinging in western meadowlarks. *Ethology*, 77:337-343.
- HUGHES M, NOWICKI S, SEARCY WA & PETERS S (1998). Song-type sharing in song sparrows: implications for repertoire function and song learning. *Behavioral Ecology and Sociobiology*, 42:437- 446.
- HUGHES M, ANDERSON RC, SEARCY WA, BOTTENSEK LM & NOWICKI S (2007). Song type sharing and territory tenure in eastern song sparrows: Implications for the evolution of song repertoires. *Animal Behaviour*, 73:701-710.
- KIEFER S, SPIESS A, KIPPER S, MUNDRY R, SOMMER C, HULTSCH H & TODT D (2006). First-year common nightingales (*Luscinia megarhynchos*) have smaller song-type repertoire sizes than older males. *Ethology*, 112:1217-1224.
- KOETZ AH, WESTCOTT DA & CONGDON BC (2007). Spatial pattern of song element sharing and its implications for song learning in the chowchilla, *Orthonyx spaldingii*. *Animal Behaviour*, 74:1019-1028.
- KREBS JR, ASHCROFT R & VAN ORSDOL K (1981). Song matching in the great tit *Parus major* L. *Animal Behaviour*, 29:918-923.

- KROODSMA DE & VERNER J (1978). Complex singing behaviors among *Cistothorus* wrens. *Auk*, 95:703-716.
- KROODSMA DE (1974). Song learning, dialects, and dispersal in the Bewick's wren. *Zeitschrift für Tierpsychologie*, 35:352-380.
- LEMON RE, PERREAULT S & WEARY DM (1994). Dual strategies of song development in American Redstarts, *Setophaga ruticilla*. *Animal Behaviour*, 47:317-329.
- LOGUE DM & FORSTMEIER W (2008). Constrained performance in a communication network: implications for the function of song-type matching and for the evolution of multiple ornaments. *The American Naturalist*, 172:34-41.
- MANTEL N (1967). The detection of disease clustering and a generalized regression approach. *Cancer Research*, 27:209-220.
- MARLER P (1990). Song learning: The interface between behaviour and neuroethology. *Philosophical Transactions of the Royal Society of London, Series B*, 329:109-114.
- MARLER P (2004). Bird calls: A cornucopia for communication. In: MARLER P & SLABBEKORN H (eds), *Nature's Music: The Science of Birdsong*, Elsevier, California:132-176.
- MARLER P & TAMURA M (1962). Song dialects in three populations of white-crowned sparrow. *Condor*, 64:368-377.
- MCGREGOR PK & KREBS JR (1982). Mating and song types in the great tit. *Nature*, 297:60-61.
- MCGREGOR PK & KREBS JR (1989). Song learning in adult great tits (*Parus major*): effects of neighbours. *Behaviour*, 108:139-159.
- MCGREGOR PK (1980). Song dialects in the corn bunting. *Zeitschrift für Tierpsychologie*, 54:285-297.
- MORTON ES (1987). The effects of distance and isolation on song-type sharing in the Carolina Wren. *Wilson Bulletin*, 99:601-610.
- NAGUIB M & MENNILL DJ (2010). The signal value of bird song: empirical evidence suggests song overlapping is a signal. *Animal Behaviour*, 80:E11-E15.
- NELSON DA (1992). Song overproduction and selective attrition lead to song sharing in the field sparrow (*Spizella pusilla*). *Behavioral Ecology and Sociobiology*, 30:415-424.
- NELSON DA, MARLER P & MORTON ML (1996). The capacity for song memorization varies in populations of the same species. *Animal Behaviour*, 52:379-387.
- NIELSEN BMB & VEHRENCAMP SL (1995). Responses of songs sparrows to song-type matching via interactive playback. *Behavioral Ecology and Sociobiology*, 37:109-117.
- PAYNE RB & PAYNE LL (1993). Song copying and cultural transmission in indigo buntings. *Animal Behaviour*, 46:1045-1065.
- PAYNE RB, PAYNE LL & DOEHLERT SM (1988). Biological and cultural success of song memes in indigo buntings. *Ecology*, 69:104-117.
- PRICE JJ & YUAN DH (2011). Song-type sharing and matching in a bird with very large song repertoires, the tropical mockingbird. *Behaviour*, 148:673-689.
- RASMUSSEN R & DABELSTEEN T (2002). Song repertoires and repertoire sharing in a local group of blackbirds. *Bioacoustics*, 13:63-76.
- RIVERA-GUTIERREZ HF, MATTHYSEN E, ADRIAENSEN F & SLABBEKOORN H (2010). Repertoire sharing and song similarity between great tit males decline with distance between forest fragments. *Ethology*, 116:951-960.
- ROGERS D (2004). Repertoire size, song sharing and type matching in the Rufous Bristlebird (*Dasyornis broadbenti*). *Emu*, 104:7-13.
- SEARCY WA & ANDERSSON M (1986). Sexual selection and the evolution of song. *Annual Review of Ecology and Systematics*, 17:507-533.
- SEARCY WA & BEECHER MD (2009). Song as an aggressive signal in songbirds. *Animal Behaviour*, 78:1281-1292.
- SETHI VK, BHATT D & KUMAR A (2011a). Song repertoire size of the Pied Bush Chat *Saxicola caprata*. *Current Science*, 100:302-304.
- SETHI VK, BHATT D & KUMAR A (2011b). The effect of mate removal on dawn singing behaviour in male pied bush chats. *Current Zoology*, 57:72-76.
- SETHI VK, BHATT D & KUMAR A (2012a). Dawn singing behavior of a tropical bird species, the Pied Bush Chat *Saxicola caprata*. *Journal of Applied and Natural Science*, 4:241-246.
- SETHI VK, BHATT D & KUMAR A (2012b). Characteristics and behavioral correlates of call types in a tropical bird, the Pied Bush Chat *Saxicola caprata*. *Pakistan Journal of Zoology*, 44:1231-1238.

- SETHI VK, BHATT D & KUMAR A (2012c). Structure and context of female song in a tropical bird, the Pied Bush Chat. *Current Science*, 103:827-832.
- SLATER PJB & INCE SA (1982). Song development in chaffinches: what is learnt and when? *Ibis*, 124:21-26.
- SPECHT R (2002). Avisoft-SAS Lab Pro Sound Analysis and Synthesis Laboratory - a PC-software. Avisoft Bioacoustics, Berlin (<http://www.avisoft.com>).
- TODT D & NAGUIB M (2000). Vocal interactions in birds: the use of song as a model in communication. *Advances in the Study of Behaviour*, 29:247-296.
- WILSON PL, TOWNER MC & VEHRENCAMP SL (2000). Survival and song-type sharing in a sedentary subspecies of the song sparrow. *Condor*, 102:355-363.
- ZAR JH (1999). *Biostatistical Analysis*. Printice Hall, New Jersey.

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