Response of male Bluethroats *Luscinia svecica* to song playback: evidence of territorial function of song and song flights

Jorma Sorjonen & Juha Merilä

Sorjonen, J., Department of Biology, University of Joensuu, P.O. Box 111, FIN-80101, Joensuu, Finland. E-mail Jorma.Sorjonen@Joensuu.Fi
Merilä, J., Section of Population Biology, Department of Zoology, Villavägen 9, S-752 36 Uppsala, Sweden

Male bluethroats (*Luscinia svecica*) have a complex song which is often delivered in the form of song flights. Earlier studies, based upon timing of display, indicate that the chief function of the bluethroat's song was for mate attraction/retention, but the possible territorial function of the song has not been rigorously tested. In song playback experiments performed in the territories of 26 males, a significant increase in song and song flight activity relative to pre-playback levels was observed among males who were not seen to have females in their territories. However, mated males who were seen to be guarding females did not respond to song playbacks, but remained silent, closely guarding their mates. Hence, despite the earlier evidence showing that the bluethroat's song is used to attract a mate, these results suggest that it functions in male–male competition during the pre-mating period and may, in this way, improve a male's mating success.

1. Introduction

The primary functions of bird song are believed to be in mate attraction and territorial defence (Searcy & Andersson 1986). Several studies have demonstrated that large song repertoires and high song rates are associated with enhanced mating success (e.g. Catchpole 1987, Searcy & Andersson 1986). Likewise, large song repertoires (e.g. Krebs 1977a, 1977b, Krebs *et al.* 1978, Yasukawa *et al.* 1980, Krebs *et al.* 1981, Yasukawa 1981, Simpson 1985), high song versatility (Falls & d'Agincourt 1982, d'Agincourt & Falls 1983, Lambrechts & Dhondt 1988) and high singing activity (Lambrechts & Dhondt 1990) are known to be advanta-geous in territorial contests among males in some species. Hence, song in a particular species may have several non-mutually exclusive functions, which may be difficult to assess from purely observational data.

Male bluethroats (*Luscinia svecica*) have a complex song, and they often perform conspicuous song flights of moderate to short duration (e.g. Sorjonen 1986, Cramp 1989, Naguib & Kolb 1992, Merilä & Sorjonen 1994). We (Merilä & Sorjonen 1994) have suggested that the function of the bluethroat's song is primarily to attract a mate, but that song flights may be used both to attract females and to keep intruders away from the males' territory during the pair-formation pe-

riod (Merilä & Sorjonen 1994). This inference was based on the observations that (1) males ceased to sing and make song flights soon after aquiring a mate, (2) no singing was heard or song flights undertaken after the egg-laying period, and (3) the time for mate acquisition was shorter for males making more active song flights. These observations, together with similar results from another study of the same species (Krokene *et al.* 1996), make a strong case that mate attraction is the main function of the bluethroat's song. However, although the previous results are suggestive of this, they do not rule out the possibility that the bluethroat's song and song flights could also be used in territorial defence. Here we will present results of a playback experiment which was designed to answer the question of whether the bluethroat's song, and song flights, may also play a role in territorial defence during acute intrusions of conspecific males.

2. Methods

The bluethroat is a small, insectivorous migratory passerine which arrives at its northern European breeding grounds in late May to early June. According to Järvinen (1994), egg laying commences at Kilpisjärvi between 1 June and 10 July. It is a socially monogamous passerine, although polygamy (Cramp 1989) and extra-pair young can be fairly common (Krokene *et al.* 1996). The nest is located inside of the male's territory; the usual territory size at Kilpisjärvi is 1–1.5 hectares (Järvinen & Pietiäinen 1983). However, great overlap occurs between pairs in foraging territories during the nestling period (Peiponen 1956).

Experiments were carried out between 8 and 10 June 1993, in a subalpine mountain birch forest east of lake Kilpisjärvi (69°50´N, 20°50´E) in Finnish Lapland. Spring was late and cold that year. The mean temperature at Kilpisjärvi in May 1993 was 0.3°C and in June 1993 5.4°C when the average long-term (1961–1990) temperature in May is 1.5°C and 7.5°C in June (Finnish Meteorological Institute 1993). The number of songs and song flights was counted for ten minutes in 26 male bluethroat territories, after which 12 different songs of one strange male of the same population were played back at a standard sound pressure level (about 80 dB) to each male for about three minutes. Although the 12 different playback songs (song length $\bar{x} = 13.7$ s, SD = 9.1, N = 12 and number of syllable types/song $\bar{x} = 15.5$, SD = 5.8, N = 12) belonged to one male, there was great variation in song length (5.8 s to 35.4 s) and song versatility (8 to 24 different syllable types/song) and they represent rather well the mean song of the Kilpisjärvi bluethroat population (song length $\bar{x} = 12.4$ s, SD = 8.3, N = 20 and number of syllables/song $\bar{x} = 13.8$, SD = 11.8, N = 20). Neither song length (Z = – 0.117, P = 0.907) nor song versatility (Z = – 1.54, P = 0.124) differed significantly from the mean songs of the 20 other males (Mann-Whitney U test). Immediately after the playback, after the focal male bluethroat was observed to move towards the loudspeaker, the number of the songs and song flights was re-counted for ten minutes. To enhance the stimulus presented to males, a stuffed male bluethroat was placed about one metre above the ground near the loudspeaker during and after the song playbacks. The countings and playbacks were carried out mostly between 06:00–11:00 (+ 3 h GMT) at a distance of 10 to 15 m from singing males at the territory centre. The males were classified as advertising and guarding individuals. The male was considered to be a guarding male if he was associated with a female in his territory, and an advertising male if no female was observed on his territory during the playbacks and the song recordings.

We used a Sony DAT Walkman TCD-D3 with Sennheiser MKH 60 P microphone when recording 12 different songs of one male in the Kilpisjärvi population. Recording took place on 7 June arround 08:00, at a distance of 10 m. In the playback experiment we used the same Sony DAT recorder with Philips active speaker model SBC BA 130.

Because of the non-normal distribution of the dependent variables, non-parametric tests with two-tailed probability values were used throughout. Unless otherwise stated, all Z-values refer to test-values of Wilcoxon matched-pairs tests.

3. Results

Six of the 26 male bluethroats had a female in their territories. The mean song rate of these males

before ($\bar{x} = 2.2$ songs/10 min, SD = 1.7) and after ($\bar{x} = 2.7$ songs/10 min, SD = 6.5) playback did not differ from each other (Z = -0.7, P = 0.5; Fig. 1a). Only one of these males responded to song playback by increasing song rate and flying towards the loudspeaker and the stuffed male bluethroat. However, the song rate of this male was much lower (10 songs/10 min) than the mean song rate of the advertising males after the playbacks. Song playback did not stimulate the five other guarding males to sing or make song flights, nor did they attack the loudspeaker or the stuffed bluethroat. Instead, these males remained silent, guarding their females by following them closely.

All advertising males responded to song playback by approaching the loudspeaker and the stuffed male bluethroat. Males increased their song rate significantly after they heard the conspecific songs played in their territory — the mean song rate before playback was 8.5 songs/10 min (SD = 9.1, N = 20) and after playback 33.5 (SD = 10.2, N = 20; Z = -3.9, P = 0.001; Fig. 1a). The advertising males also performed song flights significantly more often than before song playback — the mean number of song flights before playback was 0.4 flights/10 min (SD = 0.8, N = 20) as compared to 2.4 flights/10 min after the playback (SD = 0.6, N = 20, Z = -3.0, P = 0.003) (Fig. 1b). Finally, if we calculate the difference in the pre- and post-playback song and song flight rates for individual males, it is clear that the change both in song (Z = -3.5, P = 0.0004; Mann-Whitney) and song flight (Z = -2.5, P = 0.012; Mann-Whitney) rates were greater for advertising males than for guarding males (see also Fig. 1a and 1b).

4. Discussion

The results of this study clearly demonstrate that advertising bluethroat males respond to territorial intrusions of foreign males, as mimicked by a stuffed male and song playback, by increasing their song and song flight rates considerably. Hence, song and song flights in bluethroats would seem likely to play a role in territorial defence before pair formation has occurred. The results indicate that before pair formation male–male competition for best territories was taking place, as well as for a mate. However, those males which
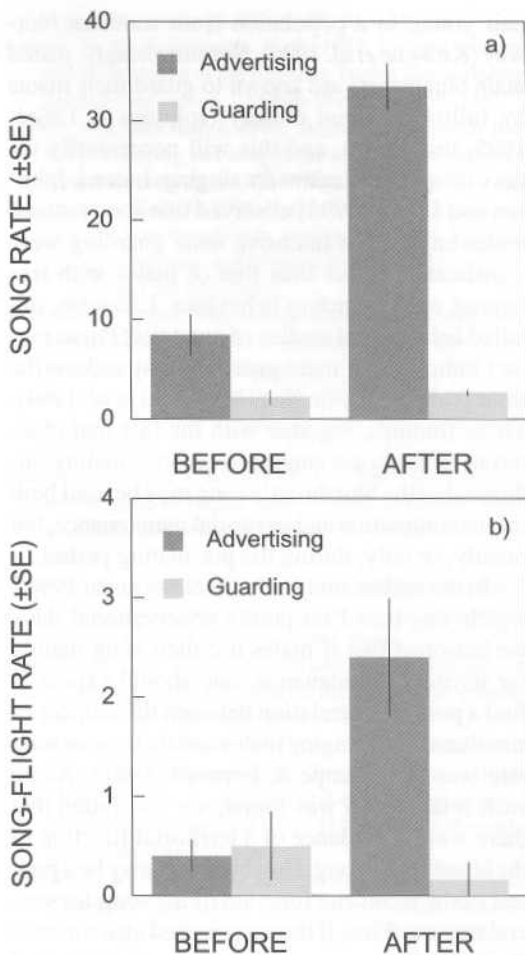

Fig. 1. Mean (±SE) song (a) and song-flight (b) activity of advertising vs. guarding male bluethroats before and after the song playback experiments.

had already acquired a mate did not respond to song playbacks, indicating that they are either unwilling or unable to defend their territories after mating has occurred. As to the former possibility, during the nestling period territorial overlap between different pairs frequently occured during foraging flights, (Peiponen 1956), indicating that a male bluethroat may attach little value to the territory after he has mated. However, it is also clear that males may be constrained from singing during their mates' fertile period when trying to ensure their paternity with close mate guarding. Indeed, the rates of extra-pair paternity are high in this species: 20% of the young were of extra-pair origin, and 35% of broods contained extra-

pair young in a population from southern Norway (Krokene *et al.* 1996). Not surprisingly, mated male bluethroats are known to guard their mates by following them closely (Johnsen & Lifjelt 1995, this study), and this will neccessarily reduce their opportunities for singing. Indeed, Johnsen and Lifjelt (1995) observed that song rates of males engaged in intensive mate guarding were significantly lower than that of males with less intense mate guarding behaviour. Likewise, detailed behavioural studies of great tits (*Parus major*) indicate that mate guarding may reduce the time available for singing (Slagsvold *et al.* 1994). These findings, together with the fact that bluethroat males cease singing soon after mating, indicate that the bluethroat's song may be used both for mate attraction and territorial maintenance, but mainly, or only, during the pre-mating period.

In our earlier study (Merilä & Sorjonen 1994), which was based on purely observational data, we reasoned that if males use their song mainly for territory maintenance, one should expect to find a positive correlation between the number of simultaneously singing males and their mean song rate (see also Lampe & Espmark 1987). As no such relationship was found, we concluded that there was no evidence of a territorial function of the bluethroat's song. However, this may be a poor test of the territorial function of the song for several reasons. First, if the song is used also for mate attraction, the correlation between mean song rate and number of simultaneously singing males in a given day is also highly dependent on mating status of different males. Second, if the territorial context of the song is expressed only, or mainly, during the times when there is a risk of acute intrusions of other males, then the absence of correlation between song rate and the number of simultaneously singing males could result because the singing rate may be high even in a small group if the males are singing near each other, or low in a large group if the males are not in earshot of each other. Finally, it is well known that territorial neighbours may recognise each other from song (Falls 1992, Stoddard 1996); hence, the naturally occurring song rates among close neighbours may be lower than those broadcasted in the presence of a previously unknown individual. Therefore, the more direct approach used in this study

avoids these caveats, and clearly uncovers the territorial function of song.

Selostus: **Sinirintakoiraiden reakointi playback-kokeeseen: todistus laulun toimimisesta reviirin puolustuksessa**

Sinirinta koiraiden laulu on vaihtelevan monipuolinen ja se esitetään näkyvältä paikalta ja usein ilmasta ns. laululentona. Koiraan laulun on todettu houkuttelevan naaraita, mutta laulun mahdollista merkitystä reviirin puolustmisessa ei ole aiemmin perusteellisimmin tutkittu. Tässä työssä tutkittiin Kilpisjärvellä 26:n sinirintakoiraan reaktioita niile nauhalta soitetuun vieraan sinirintakoiraan lauluun. Koiraat, joiden reviireillä ei havaittu naaraita lisäsivät laulu- ja laululentoaktiivisuuttaan huomattavasti kuultuaan vierasta laulua nauhalta kun taas koiraat, jotka tavattiin reviiriltään naaraan seurassa eivät lisänneet laulu- tai laululentoaktiivisuuttaan vaan vartioivat naarasta seuraamalle sitä kaikkialle muutaman metrin etäisyydellä. Ennen koiraiden pariutumista näyttäisi laululla olevan merkitystä koiraiden välisissä yhteydenotoissa ja parantavan siten koiraan mahdollisuutta houkutella naaras reviirilleen.

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