

The signal function of overlapping singing in male robins

TORBEN DABELSTEEN*, PETER K. MCGREGOR*†, JO HOLLAND*,
JOE A. TOBIAS‡ & SIMON BOEL PEDERSEN*

*Department of Population Biology and Centre for Sound Communication, Zoological Institute,
University of Copenhagen

†Behaviour & Ecology Research Group, Department of Life Science, University of Nottingham

‡Department of Zoology, University of Cambridge

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Abstract. Songbirds can vary the timing of song production with respect to other singing individuals on a song-by-song timescale, for example birds may overlap songs or alternate singing and thereby avoid overlap. Playback was used to study the information contained in such timing of song exchanges in territorial male robins, *Erithacus rubecula*. The results are consistent with the idea that interacting with a singer either by overlapping or alternating is a way of indicating the intended receiver whereas non-interactive (loop) playback does not give this information. Furthermore, an overlapping pattern of singing generally elicited responses characteristic of highly aroused males. In robins this is shown by a rapid approach and change to an almost continuous, low amplitude pattern of singing referred to as twittering. Thus overlapping could be taken as indicating a high degree of arousal or a willingness to escalate. The response changed during the experimental period, with twittering responses becoming more common regardless of playback treatment. This result is consistent with experimental males having gathered information from interactions between playback and their neighbours in previous trials, that is, they collected information by eavesdropping.

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Songbirds are usually within hearing range of several other conspecifics in the local population and can therefore be considered as members of a communication network in which the individuals have a number of options for gaining information. They can listen to the widely broadcast full songs of other individuals, either by concentrating on specific individuals or by focusing their attention on their interactions (eavesdropping), or they can gain information in a more direct way through active participation in vocal interactions with each other (Dabelsteen & Pedersen 1991; Dabelsteen 1992; McGregor 1993; Dabelsteen & McGregor 1996; McGregor & Dabelsteen 1996). Concentrat-

ing on a single individual implies that the receiving bird extracts information from structural sound parameters such as frequency level, singing rate and sound type. Eavesdropping and active interaction with other individuals allow the added possibility of extracting information from interaction phenomena such as interactive selection of the song types from the repertoire available and timing of the singing interactions. The information carrying capacity of structural parameters has been documented in several studies, for example, discrimination between species, populations and individuals (e.g. Dabelsteen & Pedersen 1985, 1992, 1993; Nelson 1988; Weisman & Ratcliffe 1989; Weisman et al. 1990; see also Becker 1982 for a review). However, the signal value of the majority of interaction phenomena is more or less unknown because equipment for interactive playback experiments has only recently been developed and applied (e.g. Dabelsteen & Pedersen 1990, 1991; McGregor et al. 1992; Bradbury & Vehrencamp 1994; Otter et al. 1994; Dabelsteen et al. 1996).

Correspondence: T. Dabelsteen, Department of Population Biology and Centre for Sound Communication, Zoological Institute, Tagensvej 16, DK-2200 Copenhagen N, Denmark (email: tdabelstee@zi.ku.dk). P. K. McGregor is at the Department of Life Science, University of Nottingham, University Park, Nottingham NG7 2RD, U.K. J. A. Tobias is at the Department of Zoology, University of Cambridge, Downing Street, Cambridge CB2 3EJ, U.K.

One of the most intriguing aspects of male songbirds' vocal interactions is the timing of singing. Males can simply attempt to avoid simultaneous singing (e.g. Ficken et al. 1974; Wasserman 1977). They may also coordinate singing in an alternating pattern, sometimes with the result that the interacting individuals appear to adopt leader and follower roles. The latter phenomenon has been described in the marsh wren, *Cistothorus palustris* (Kroodsma 1979). Finally, the males may overlap each other's songs as has been reported from interactions in the great tit, *Parus major* (e.g. McGregor et al. 1992; J. P. Tavares, personal communication). In extreme instances each song of the opponent can be overlapped. Robins, *Erithacus rubecula*, both overlap and alternate songs during singing interactions with rivals, for example neighbours and unknown trespassers. Whereas overlapping typically occurs when an opponent is close to the singer, alternating can be performed at any distance (e.g. Brindley 1991).

The contexts in which overlapping and alternating occur in robins are quite similar to those of other species in which these phenomena have been described, for example great tits also overlap at close range during escalated song duels and show associated aggressive postures (e.g. P. K. McGregor & T. Dabelsteen, personal observation; J. P. Tavares, personal communication; also Hinde 1952 for a description of skirmishes and singing during lulls in skirmishing). The contexts of overlapping and alternating together and the associated aggressive behaviour of the birds using these two singing patterns have generated three different hypotheses about the signal function of alternating and overlapping. The first states that neither alternating nor overlapping has signal value: both of the two singing patterns are more or less random phenomena. The second states that the two patterns have the same signal value and function to indicate an intended receiver. The third hypothesis also states that the two patterns constitute ways of indicating an intended receiver, but that the signal value of the two patterns are different because overlapping represents a higher arousal of the singer than alternating.

We have tested the three hypotheses in interactive playback experiments with territory-holding male robins. We simulated an intruder that started to sing the full song and then, after the territory owner had started to countersing

with the full song, the intruder either continued with non-interactive singing (loop playback) or changed to an overlapping or alternating singing pattern. If hypothesis 1 is correct we should predict similar responses to the three treatments. If hypothesis 2 is correct we should predict similar responses to overlapping and alternating but a weaker response to non-interactive loop playback because being targeted as the receiver must, all other things being equal, be taken as a greater threat than not being targeted. If hypothesis 3 is correct we should again predict the weakest response to loop playback and a stronger response to alternating, but the strongest response would be elicited by overlapping because a highly aroused male must constitute a greater threat than a less aroused male.

METHODS

Playback Equipment and Test Songs

For the playback experiments we used the second version of a digital sound emitter system (DSE-2) consisting of a notebook PC and a small external D/A unit which was connected to the parallel port of the PC. The D/A unit contained a digital-to-analogue converter and a signal micro-processor that controlled the converter and enabled the songs stored in the PC to be played back through the converter immediately a key of the PC keyboard was activated. For details of the DSE system and how playback songs were loaded, see Dabelsteen & Pedersen (1991).

In this experiment the PC was loaded with 10 different songs from the same individual. The songs are typical of the full song of the robin (Fig. 1). They were recorded from a male in the study area in 1991 and therefore it is highly unlikely that this individual was also present in 1995. The programming of the PC allowed the songs to be played back in an interactive way or as a tape loop. In the loop mode the songs were played back with their natural inter-song pauses inserted. Songs and inter-song pauses had durations of respectively 2.59 ± 0.58 s and 4.15 ± 1.03 s ($\bar{X} \pm \text{SE}$), values that correspond to a relatively highly aroused singing robin (e.g. Brémond 1968). In the interactive playback mode the songs were played in the same order as in the loop, but the inter-song pauses were determined by the experimenter because the next song was

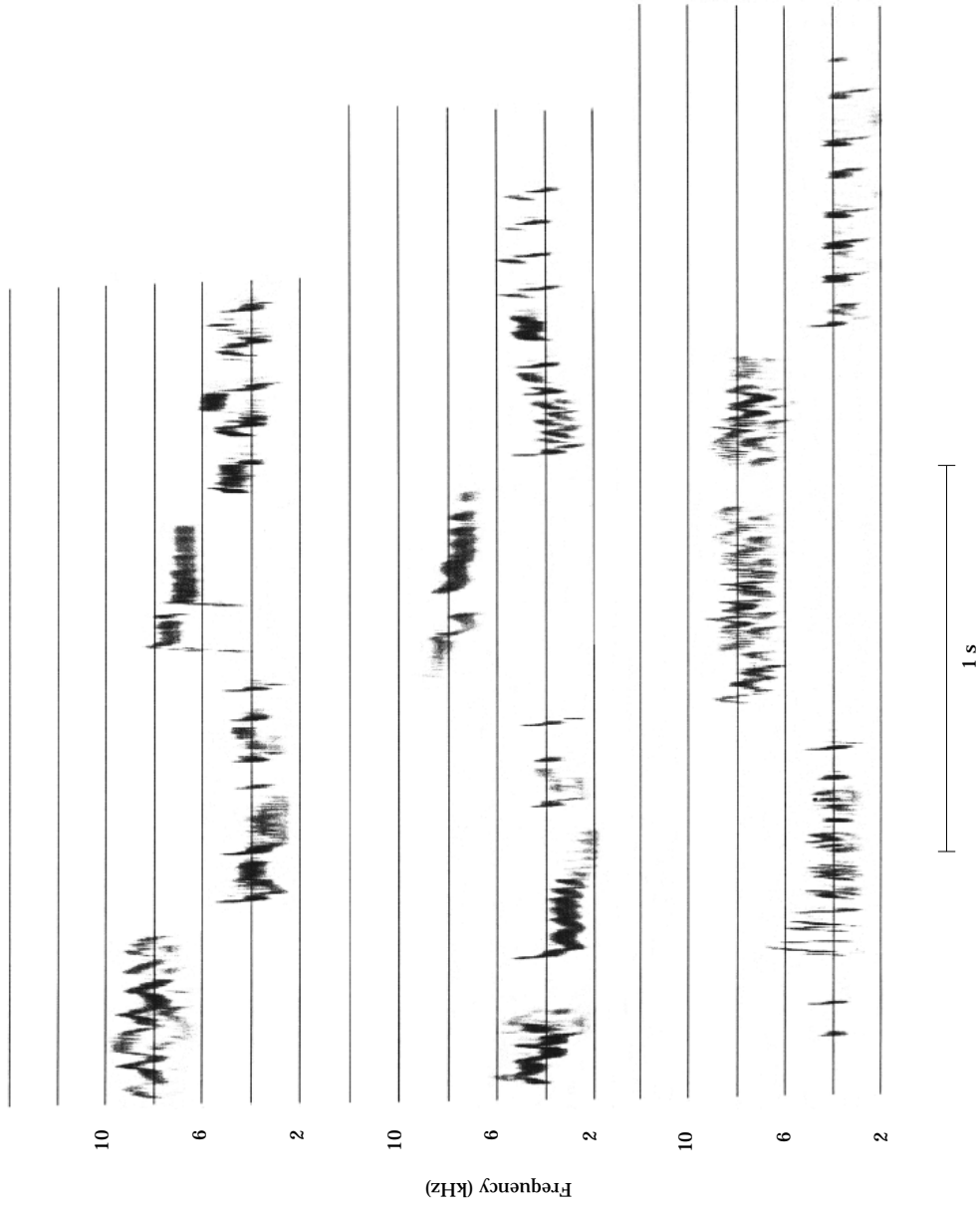


Figure 1. Three of the robin test songs showing the species-characteristic alternation between high and low frequency phrases of full songs.

played immediately the proper key was pressed. An experienced controller of the DSE was able to press the key less than 1 s after a test bird's song started or stopped (Dabelsteen et al. 1996).

The songs were amplified by means of a Denon DCA-400 power amplifier and connected through a 20 m cable to a small (diameter 4.5 cm, weight 120 g) loudspeaker (Vifa D26NC-05-06 Neodymium Tweeter) from which they were broadcast with a natural sound pressure level (i.e. about 65 dB(A) measured at a distance of 10 m from the front of the speaker).

Experimental Design

We carried out the experiments in mixed deciduous forest at Strødam Biological Field Station between 0800 and 1300 hours local time, from 30 April to 5 May 1995 with 54 territory-holding males. Some of the males were colour ringed, but most were identified by their territories which had been mapped a few days prior to, or during, the experimental period. The mapping was done according to the standard recommendations of the mapping method (e.g. Enemar 1959; Svensson 1970) and was therefore based primarily on locations of simultaneously singing males and males engaged in border disputes, but also on the locations of silent and vocalizing males to some extent. To reduce the risk of neighbours responding to an experiment, we always placed the speaker in the middle of the test bird's territory, typically some 3–4 m above ground level, fixed to a thin branch or twig and broadcast away from the observers. Observers and speaker were in place 5 min before the start of playback, and we ensured that the test male was present, silent and not engaged in courting or fighting behaviour.

We stimulated the males to sing full song by means of loop pre-playback. If the subjects did not sing within 2 min, we waited about 1 min and then played the loop again. If the subject did not sing after a further 2 min, the subject was abandoned. When the pre-playback loop had elicited singing we continued with the test playback which lasted for 3 min. There were three different treatments: (1) non-interactive loop playback; (2) alternating interactive playback: each song of the test male was immediately followed by a playback song, that is, we activated the keyboard immediately after the song of the test male stopped; and (3) overlapping interactive playback: each song of

the test male was overlapped by a playback song, that is, we activated the keyboard immediately the song of the test bird started.

Each of the 54 test males was tested only once, that is, each male was played one of the treatments only, and each treatment was given to the same number of males ($N=18$). The order in which the three treatments were played varied between the 6 experimental days, but each type of treatment was played approximately the same number of times per day.

Measuring Responses

One observer monitored the songs of the test bird and controlled the output of the DSE-2. A second observer recorded the entire test using a Sony TCD-D10 PRO DAT recorder and a Sennheiser MKH 816T directional microphone. A third observer watched the test male and noted its singing response and its approach response including any change in location and visual behaviour. We recorded visual and acoustic behaviour for the 3 min of test playback and for 3 min after playback had stopped. The DSE-2 output was stored automatically in the DSE-2 during each test and thus served as an extra check of the experiments. The sound recordings were analysed on a Kay Elemetrics Corp. DSP 5500 sonagraph (bandwidth 300 Hz, frequency range 0–8000 Hz).

Response Measures

Pilot experiments on colour-ringed robins in the Cambridge University Botanical Garden, U.K. and at Strødam Biological Field Station showed that test males responded to playback in one of two ways: they either approached a little and continued with full singing, or they came very close to the speaker and produced quiet twitter song (high-pitched squealing, Lack 1969). During natural aggressive interactions an intruder is quickly approached and twittering is performed only when in close proximity (less than 3 m, approximately). This twitter song close to an opponent is usually accompanied by posturing in which the twittering male stretches to present its red breast feathers to the opponent and/or sways from side to side. The robin's threat display is described in full by Lack (1969). Any robin revealing itself to a territorial male in this state of high

arousal, as indicated by twittering and posturing, will be physically attacked. Because the two types of singing behaviour are so very different we cannot use the same response measures for twittering and non-twittering males.

Twittering is very difficult to overlap or to alternate with using full songs because it is more or less continuous. Pilot experiments show that overlapping almost inevitably leads to many more songs being played back than does alternating because one automatically attempts to overlap all of the twittering but cannot identify the pauses during which the alternating songs should be played. Such a large difference in number of songs played would, of course, make it impossible to interpret any difference in treatment effect because this could have been caused either by the difference in amount of song played back or by the timing of playback, that is whether we alternated, overlapped or used loop playback. For twittering males we therefore measured only the latency to twittering expressed in seconds to start of twittering and the number of playback songs played before the start of twittering.

For non-twittering males we quantified the singing response and the approach response, both during and after playback. We measured singing by counting the number of songs sung, the approach responses by measuring closest approach to the speaker and time spent within 10 m of the speaker. In the approach response we also included a measure of agitation, number of flights over 0.1 m.

RESULTS

Number of Twittering and Non-twittering Males

There was a non-significant tendency for more males to twitter in response to overlapping playback (13/18 twittered to overlapping, 8/18 to alternating and 9/18 to loop playback; $G_2=3.26$, $P>0.05$). Considerably more males twittered in the second half of the experiment (Table I). In the first half there was a non-significant tendency for males to twitter more to overlapping song (6/9 males twittered to overlapping, 2/9 to alternating and 2/10 to loop playback; $G_2=5.48$, $P>0.05$; note that $G_{crit\ 5\%}=5.99$). In the second half all three treatments elicited twittering from most test males (7/9 males twittered to overlapping, 6/9 to alternating and 7/8 to loop playback; $G_2=1.06$, $P>0.05$).

Table I. Number of males twittering and non-twittering in the two halves of the experiment

| | Twittering | Non-twittering |
|----------|------------|----------------|
| 1st half | 10 | 18 |
| 2nd half | 20 | 6 |

G (with Williams' correction applied)=9.28, $df=1$, $P<0.01$.

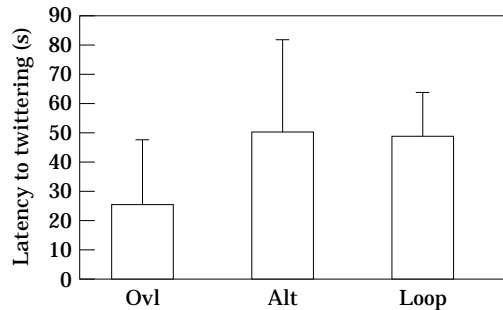


Figure 2. Mean (+SE) latency to start of twittering in response to overlapping (Ovl, $N=13$), alternating (Alt, $N=8$) and loop (Loop, $N=9$) playback.

Table II. Number of males twittering after one or two playback songs and after more than two songs

| | Overlapping | Alternating | Loop |
|-----------|-------------|-------------|------|
| 1–2 songs | 9 | 3 | 0 |
| >2 songs | 4 | 5 | 9 |

Playback was either overlapping, alternating or loop. $G_2=13.78$, $P<0.01$.

Response of Twittering Males

Males started to twitter sooner to overlapping playback; the latency to twittering was twice as long to alternating and loop playback (Kruskal–Wallis test: $H_2=10.17$, $P<0.01$; Fig. 2). The majority of the males also started to twitter to overlapping playback almost immediately (after only one or two test playback songs), and some of the males started to twitter almost immediately to alternating playback, but no males did so to loop playback (Table II).

Response of Non-twittering Males

The number of songs played back to males that did not twitter varied significantly between the

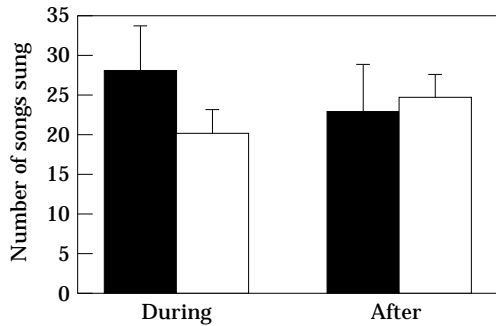


Figure 3. Mean (\pm SE) number of songs sung by non-twittering males during and after playback. ■: Overlapping playback ($N=5$); □: loop playback ($N=9$). Mann–Whitney U -test, two-tailed: during: $U=7$, $N_1=5$; $N_2=9$, $P<0.05$; after: $U=21.5$, $N_1=5$, $N_2=9$, ns.

three treatments ($\bar{X} \pm$ SE; overlapping, 29.4 ± 4.6 , $N=5$; alternating, 23.6 ± 2.5 , $N=10$; loop, 27.1 ± 0.4 , $N=9$; Kruskal–Wallis test: $H_2=10.38$, $P<0.01$). Subsequent pair-wise comparisons showed significant differences between alternating and overlapping (Mann–Whitney U -test, two-tailed: $U=7.5$, $N_1=5$, $N_2=10$, $P<0.05$) and alternating and loop playback ($U=10$, $N_1=9$, $N_2=10$, $P<0.02$). There was no significant difference between overlapping and loop playback ($U=9$, $N_1=5$, $N_2=10$, $P<0.10$). We therefore compared the response to overlapping and loop playback. The non-twittering males sang significantly more during overlapping playback than during loop playback (Fig. 3), whereas none of the approach measures varied significantly between the two treatments (Table III). There were no significant differences between the two treatments after playback ceased (Fig. 3, Table III).

DISCUSSION

The quiet twitter song accompanied by posturing is performed only in close proximity to an opponent and is indicative of a highly aroused male (Lack 1969). Therefore, it is clear from our results that overlapping playback aroused the test birds more than either of the other two treatments; overlapping elicited twittering in more test birds, at least in the first half of the experimental period, overlapping elicited twittering sooner, and it also elicited more singing from males that did not twitter. That overlapping and loop playback

Table III. Non-twittering males' approach response ($\bar{X} \pm$ SE) during and after overlapping and loop playback, see text

| Response measure | Overlapping ($N=5$) | Loop ($N=9$) |
|---------------------------------------|-----------------------|-----------------|
| No. of flights >0.1 m | | |
| During | 3.4 ± 1.6 | 6.2 ± 3.4 |
| After | 1.0 ± 0.9 | 1.7 ± 1.0 |
| Closest approach to speaker (m) | | |
| During | 10.8 ± 6.1 | 10.6 ± 7.1 |
| After | 14.6 ± 3.9 | 12.9 ± 5.9 |
| Time (s) spent within 10 m of speaker | | |
| During | 11.0 ± 14.5 | 68.7 ± 53.8 |
| After | 32.0 ± 64.9 | 58.6 ± 53.0 |

elicited the same approach response from non-twittering males is perhaps not really surprising because a characteristic of male robins singing full song is that they stay at some distance from each other. The equal approach responses elicited by these two treatments therefore does not change our conclusion that overlapping elicits the strongest response. The fact that alternating sometimes elicited immediate twittering whereas loop playback never did suggests that alternating may be a stronger stimulus than loop playback. This is also supported by the number of songs played to the non-twittering males during alternating playback. Since the alternating treatment is driven by the bird, the number of songs played during this treatment is indicative of the number of songs sung by the test male, and more songs were played during alternating than were sung by the test male during loop playback, cf. Fig. 3. Therefore, our result most closely fits the predictions of hypothesis 3 which states that overlapping and alternating constitute alternative ways of indicating an intended receiver, but that overlapping expresses a higher degree of arousal of the singer than alternating. The escalation sequence from alternating to overlapping, then an approach, close range twittering and posturing, then an attack can be observed in natural interactions. Similar experiments with great tits have led to the same conclusion (Dabelsteen et al. 1996).

The finding that all three treatments elicited twittering in the majority of the test males in the second half of the experimental period, but not in the first, suggests that the test males' response threshold had somehow been lowered between the

Table IV. Total number of neighbours and number of previously stimulated neighbours during the two halves of the test period ($\bar{X} \pm SE$)

| Neighbours | 1st half | 2nd half | Mann-Whitney U-test, two-tailed |
|---------------------------|-----------------|-----------------|------------------------------------|
| Total no. | 2.96 \pm 0.59 | 2.88 \pm 0.45 | Z=0.116, P<0.84 |
| No. previously stimulated | 0.46 \pm 0.33 | 1.08 \pm 0.37 | Z=2.44, P<0.014 |

two periods. Such a general change in responsiveness could have been caused by several factors related to habitat, climatic or social conditions. In this study habitat-related factors can have had only a minor influence since the test males in the two periods occupied the same habitat. The weather was similar over the whole period except that the average overnight temperatures increased from about 3.4°C to 9.1°C. We cannot exclude the possibility that this overnight temperature difference contributed to the effect we observed, but this influence would have been slight because singing activity, which indicates responsiveness to intruders, was high throughout the period. An important social factor could have been the number of neighbours surrounding a test male because this may be positively related to the amount of social stimulation experienced. The number of neighbours did not differ significantly between the first and second halves of the experimental period; however, there was a significant difference in the number of neighbours stimulated in previous experiments (Table IV). In the second half of the period twice as many neighbours had been experimental subjects as in the first half. This, of course, is not conclusive evidence of a causal relationship, but it could suggest that the test males in the second half of the experimental period had been influenced by the previous experiments with their neighbours. It seems possible that the test males had been eavesdropping on the interactions between their neighbours and the unknown rival with a repertoire of 10 songs (i.e. playback). This interpretation would agree with the idea that local populations of birds constitute communication networks in which individuals extract information by interacting with each other and from eavesdropping on interactions between others. It should be emphasized that there is no significant difference between the three treatments in the number of previously stimulated neighbours for either twittering males (Kruskal-Wallis test:

$H_2=0.05$, $P<0.98$) or for non-twittering males ($H_2=0.19$, $P<0.95$). Our main conclusion about the different signal function of overlapping and alternating therefore stands firm.

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