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Responses to playback of whistle songs and normal songs in male nightingales: effects of song category, whistle pitch, and distance

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Abstract In most species of song birds, males develop song repertoires of several different songs. Among this variety, different songs may be used differently in communication and, thus, may have different functions. Here we studied vocal responses to playback of structurally different songs in male territorial nightingales (*Luscinia megarhynchos*). Nightingales have enormous vocal repertoires of about 200 song types. Among these songs, one category, whistle songs, sticks out syntactically and acoustically. Here we tested whether or not male nightingales match whistle songs with whistle songs and, if so, whether they also match the pitch of the broadcast whistles. Furthermore, we also tested if nightingales treat whistle songs as a separate category of songs. We conducted interactive playback experiments on nocturnal song in which each male received three playback treatments that differed in the number of whistle songs broadcast. Males responded differently during playbacks by singing significantly more whistle songs when the playback tapes contained many whistle songs than when they contained no whistle songs. Males also frequently matched the pitch of the broadcast whistle songs. In contrast to responses during playback, after the playback terminated males sang more whistle songs when no whistle songs were broadcast than when many whistle songs were broadcast. These findings suggest that whistle songs have a specific signal value and that nightingales treat them as a special song category. Electronic supplementary material to this paper can be ob-

tained by using the Springer Link server located at <http://dx.doi.org/10.1007/s00265-002-0511-1>.

Keywords Bird song · Long range communication · *Luscinia megarhynchos* · Song matching · Vocal interactions

Introduction

Male song birds typically use their song to defend a territory and to attract mates. Despite these common functions of bird song, males of different species differ strikingly in the size of their vocal repertoire, their singing style and in the way they use their songs during vocal interactions (Todt and Naguib 2000). Such diversity raises questions as to whether different song patterns have different signal values, a potentially important component in the evolution of signal repertoires. In some species, mostly in those with small song repertoires, males in fact appear to use different songs in different contexts (review in Spector 1992) and different song patterns may elicit different responses by males and females (Vallet and Kreutzer 1995; Ratcliffe and Otter 1996; Vallet et al. 1998). This suggests that in such species different categories of song patterns exist, carrying different kinds of information. However, in species with large vocal repertoires contextual variation in use of songs is less clear (Catchpole and Slater 1995). In addition to correlations between context and the use of different song categories, signal functions of song categories can also be reflected in the way in which the categories are used during vocal interactions. The most commonly studied component in male vocal interactions is song matching, a behavior in which a singer replies with the same song type as sung by its rival. However, males may also reply differently to different song categories, indicating first that they distinguish between the song categories and second that the categories may have different functions in communication. Differential replies to rival songs can thus provide insights into the signal value of the received song and in-

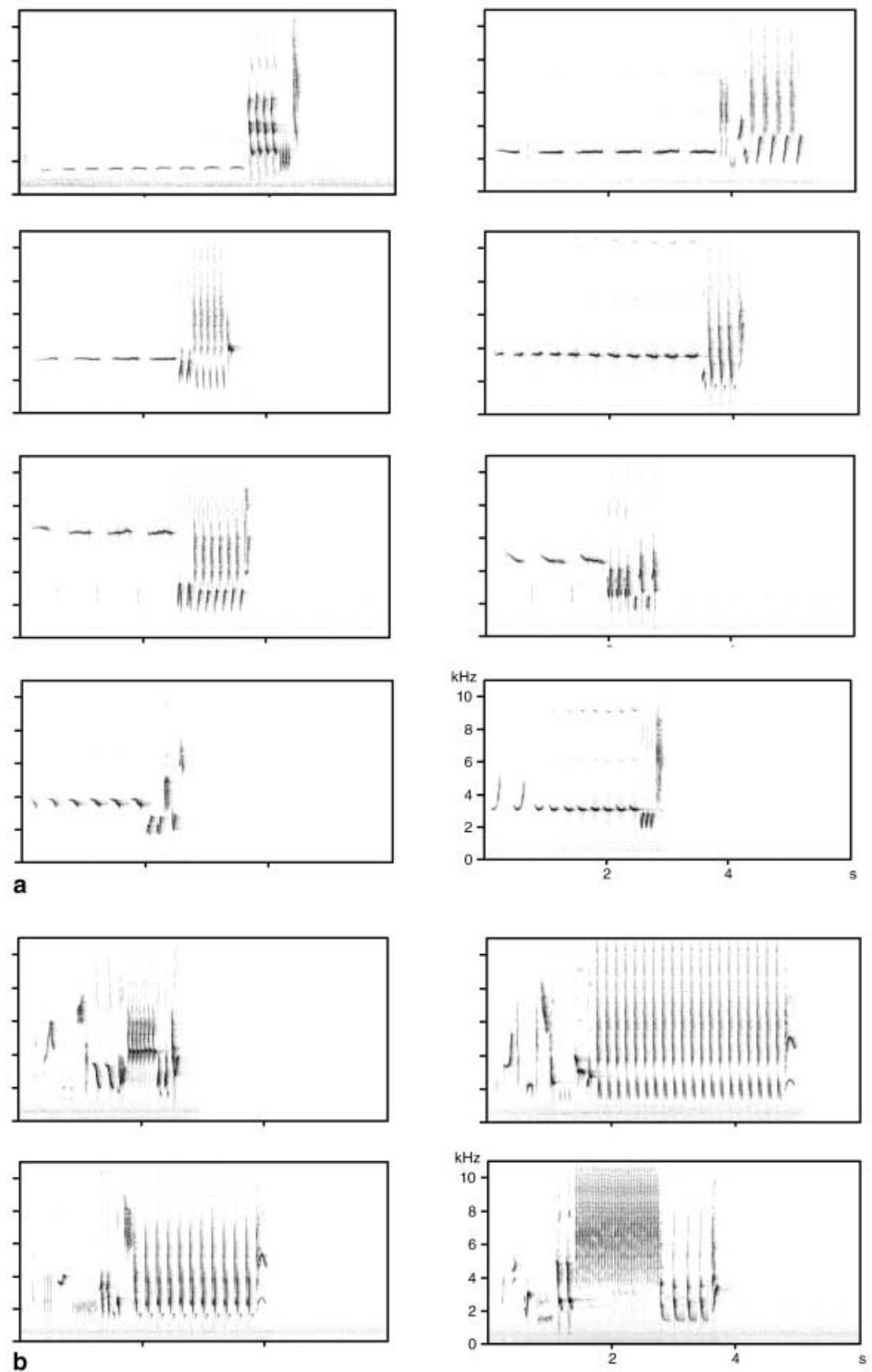
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Fig. 1 Sound spectrogram of (a) eight whistle songs and (b) four 'normal' songs, all recorded from the same male. Electronic supplementary material contains examples for whistle songs (53, 54) and for 'normal' songs (51, 52)



to the way a bird categorizes it (Todt 1971; Simpson 1985; Falls et al. 1988; McGregor et al. 1992; Beecher et al. 1994; Horn and Falls 1996; Stoddard 1996; Todt and Naguib 2000).

The song of male nightingales (*Luscinia megarhynchos*) raises questions about different categories of songs and their use during vocal interactions in an interesting way. Males have much larger vocal repertoires than in

most other species (approximately 200 song types per male; Hultsch and Todt 1981) and within this enormous vocal repertoire, one category of songs, the so-called whistle songs, sticks out syntactically and, at least to the human ear, acoustically (Hultsch 1980; Hultsch and Todt 1996a). While 'normal' songs begin with a series of structurally different elements, whistle songs begin with a regular series of modulated or unmodulated repeated whistles. Each

male has a repertoire of whistle songs with whistles at different frequencies (pitch range of 1.5–8 kHz, Fig. 1) (Hultsch 1980), whereas each whistle song usually contains only similar whistles. Whistle songs are interspersed at varying intervals throughout nocturnal singing bouts without apparent clustering.

In order to test whether whistle songs elicit specific responses during vocal interactions and to test whether they are treated as a specific song category, we carried out interactive playback experiments simulating territorial rivals that differed in the number of whistle songs they produced. Playbacks were conducted at night, when subjects counter-sing with playback without visually searching for a rival so that vocal responses can be studied in isolation from other behaviors. Nocturnal song is produced by unmated males but mated males also resume nocturnal song for a few nights during egg laying by their female (Amrhein et al. 2002). We recorded vocal responses during playback to analyze the specificity of matching responses. In addition, we analyzed responses after playback terminated in order to assess if the different playback treatments affect whistle song rate even without immediate stimulation that permits song matching. Variation in whistle song rate depending on the previous playback treatment would then indicate that whistle songs are treated as a separate category of songs.

Methods

General

We conducted the experiments on 17 territorial nocturnally singing male nightingales between 2300 hours and 0430 hours from 25 to 30 April 1998, in Berlin, Germany. This time period was within the first 10 days after arrival of the first male in the study area. Males singing at night during this early period after arrival have been shown to be unmated (Amrhein et al. 2002).

Playback tapes

We constructed playback tapes from clear recordings of songs made in previous years in areas out of earshot from locations at which we conducted playbacks. All songs were digitized at a sampling rate of 44,100 Hz. We selected 100 songs (50 different normal songs and 50 different whistle songs; examples: see Electronic Supplementary Material 51, 52, 53, 54) from each of four different subjects so that we were able to test statistically for potential effects of males whose songs were used on subjects' responses. From each male we constructed five different playback tapes for each treatment. In order to avoid systematic effects of a particular sequential arrangement of song types or specific whistle songs, different whistle songs were chosen for each tape and no tape contained the same set of normal songs so that each subject received a unique playback tape as a stimulus (Kroodsma 1989; McGregor 2000; Kroodsma et al. 2001). From each male from which we constructed playback tapes we randomly divided the 50 normal songs into blocks of 10 songs and also divided the 50 whistle songs into blocks of 10 songs. We then assigned different sets of these sets of 10 songs to the different tapes. We constructed 20 different playback tapes for each treatment and the tapes for the three different playback treatments differed in the number of whistle songs. Tapes for treatment W0 contained no whistle song and 20 normal songs. Two sets of 10 normal songs were used for a tape and no tape contained the same two sets of songs. However,

each set of 10 normal songs was used in two different tapes. Tapes for treatment W1 contained one randomly selected whistle song and 19 normal songs. Each tape contained a different whistle song that was randomly chosen out of the pool of songs not used on other tapes used for the W1 treatment. The whistle songs replaced a randomly chosen normal song. Each set of 10 normal songs was used in two tapes but no tape contained the same two sets of normal songs. Tapes for treatment W10 contained 10 whistle songs and 10 normal songs. Each tape contained a different set of 10 whistle songs and a different set of 10 normal songs. The tapes for the three treatments that were used for a given subject as playback stimuli were all recorded from the same male, as each playback series consisting of the three treatments was designed to simulate one singing rival. No song (and no song type) occurred twice in the full playback sequence of 60 songs. Within the two treatments containing whistle songs (W1 and W10), half of the tapes started with a whistle song (W1i, W10i) and the other half started with a normal song (W1r, W10r). This allowed us to test if whistle songs have any triggering effects that specifically elicit whistle songs when a stranger starts singing with a whistle song. The order of the remaining whistle songs was then randomized in the sequence. The different percentages of whistle songs sung in such short bouts reflected the extremes in whistle song rates in nocturnal song (unpublished data). We recorded songs on the tapes with only brief silent intervals between songs, so as to be able to play each song interactively, using the pause function to initiate and stop playback of each song separately.

Playback procedure

Each of 17 unmated territorial males received all three playback treatments during the same night, with the order of treatments balanced among subjects. Treatments were separated by 10 min in which no songs were broadcast. We chose subjects opportunistically with the constraint that they were not involved in close range interactions with nearby territorial neighbors. In order to reduce potential effects of the ongoing breeding season we worked in two teams simultaneously at different sites so as to increase the number of subjects per night. We standardized the playback procedure in a joint pilot period and then both teams followed the same procedure using one of two sets of the same equipment. Prior to playback we recorded subjects' song for at least 30 min in order to calculate the base frequency of whistle songs in each subject ($18 \pm 1.7\%$ whistle songs, mean \pm SE; $n=17$). Subjects had repertoires of whistle songs containing whistles ranging from 1,350 to 8,300 Hz (also see Fig. 1). We used interactive playback in order to simulate as naturally as possible a newly appearing rival. We played songs with a SONY WMD 6M tape recorder and used the pause button to broadcast the playback on a song by song basis such that the broadcast songs alternated with the songs sung by the subject (Naguib 1999). The tape recorder was connected to a Visonik A300 Amplifier and to a Canton Plus X passive loudspeaker. The loudspeaker was set up at a height of 1.5–2 m and at a distance between 40 and 100 m from the subject depending on the habitat. At these distances, during the night, nightingales vocally interact with playback and usually do not approach. Broadcast volume was adjusted prior to playback to 88 dB at 1 m distance (CEL 314 precision impulse sound pressure level meter, C-weighting fast response). We recorded subjects' singing responses with a Sennheiser ME66 directional microphone on one channel of a SONY TCD 5M stereo tape recorder. On the other channel we recorded songs broadcast from the loudspeaker using either a Sennheiser ME 66 or a SONY ECM-959 DT microphone. Due to the nature of interactive playback, trials varied in duration but there was no difference in the duration of trials among treatments (W0, 3 min; W1 and W10, 3:10 min; $P=0.20$, $F_{2,16}=1.681$, repeated measures ANOVA). Also subjects' song rate did not differ among playback treatments ($P=0.797$, $F_{2,16}=0.091$, repeated measures ANOVA).

Data analysis

In order to analyze subjects' vocal responses to playback we first digitized the playback songs and the subjects' vocal responses with a sampling rate of 22,050 Hz and 16 bit accuracy using Saslab Pro 3.75 (R. Specht, Berlin). We then determined all whistle songs sung by the subjects and determined their position within the singing sequence. In order to test if the whistle pitch of the broadcast songs influenced the whistle pitch of the subjects' replies, we calculated the average dominant pitch of all whistles within each whistle song using an FFT with 1,024 points, which resulted in a frequency resolution of 27 Hz.

We analyzed the relative number of whistle songs sung by each subject during and after playback using repeated measures ANOVAs (SPSS 10.0.5). For the pairwise comparisons among the playback treatments we used the LSD post hoc tests provided by SPSS in the repeated measures procedure (Snedecor and Cochran 1989). We used exact non-parametric tests when small samples required their use (Siegel and Castellan 1988; Bortz et al. 1990; Mundry and Fischer 1998). All indicated *P* values are two tailed.

Results

Vocal responses during playback

General

The playback treatment significantly influenced the number of whistle songs sung by the subjects ($F_{2, 16}=6.90$, $P=0.003$, repeated measures ANOVA). Subjects sang more whistle songs the more whistle songs were broadcast (Fig. 2a). In pairwise comparisons, this increase in whistle song rate was significant between the treatments W0 (no broadcast whistle song) and W10 (10 out of 20 broadcast songs were whistle songs) ($P=0.001$, $n=17$). The pairwise comparisons of the number of whistle songs between the W1 and W10 treatment and the W0 and the W1 treatment, respectively, were not significant (W1 vs W10, $P=0.076$, $n=17$; W0 vs W1, $P=0.165$, $n=17$). In the W1 treatment, there was no triggering effect in the sense that subjects that received the W1i treatment (which began with the whistle song) sang more whistle songs than did those that received the W1r treatment (where the whistle song was not the first song) (W1i $18\pm3\%$ whistle songs, W1r, $20\pm2\%$ whistle songs, mean \pm SE). Nor did the sequential position of the whistle songs in the W1r treatment affect the number of whistle songs sung during the playback ($r^2=0.066$, $F_{1, 16}=1.054$, $P=0.32$). Furthermore, there was no significant effect of the order of playback treatments on the number of whistle songs ($F_{2, 16}=0.806$, $P=0.46$, repeated measures ANOVA). There also was no influence of the males from which the songs used for playback were recorded on the mean number of whistle songs sung by the subjects during playback ($F_{3, 13}=2.179$, $P=0.14$, one-way ANOVA) or after playback ($F_{3, 13}=0.549$, $P=0.66$, one-way ANOVA). However, subjects differed significantly in the mean number of whistle songs sung during playback ($F_{2, 16}=4.77$, $P<0.001$, two way ANOVA). Whistle song rate also differed among subjects before the onset of playback ($P<0.001$, $df=16$, $\chi^2=41.95$) but there was no correlation between the number of whistle songs sung before and during playback ($r=0.054$, $P=0.84$).

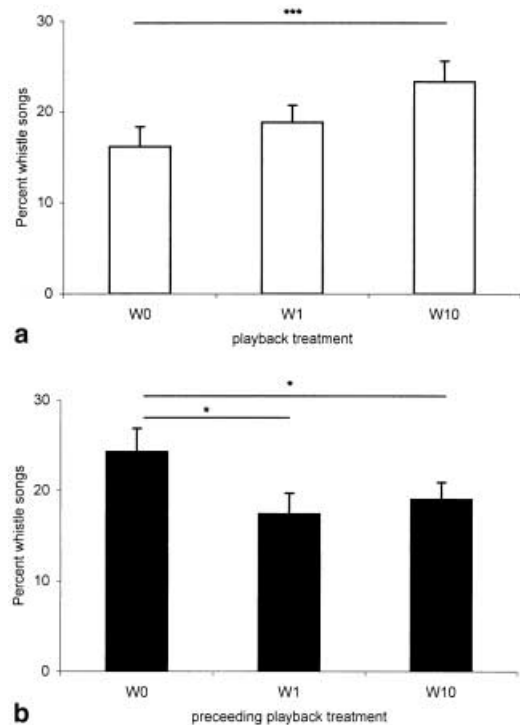


Fig. 2 Mean whistle song rate (a) during the different playback treatments, and (b) after the different playback treatments; each playback consisted of 20 songs that comprised no whistle songs (W0), one whistle song (W1), or ten whistle songs (W10). * $P\leq 0.05$, *** $P\leq 0.001$ in pairwise comparisons

Matching of whistle pitch

In response to the broadcast whistle songs, subjects often directly replied with a whistle song.

W1 treatment. In the W1 treatment, 10 out of the 17 subjects directly replied to the broadcast whistle song with a whistle song. The pitch of the whistles in the broadcast whistle song had a significant influence on the pitch of the whistles in the subjects' replies ($r^2=0.58$, $F_{1, 9}=11.14$, $P=0.01$, linear regression, Fig. 3) with most whistle song replies having whistles of the same or a higher pitch than the pitch of whistles in the broadcast songs. Subjects that received the whistle song as the first song were not more likely to directly reply with a whistle song than were those subjects that received the whistle song at a subsequent position in the playback sequence ($P=0.637$, $n=17$, Fisher Exact test). In all except two cases in which subjects directly replied to the broadcast whistle song with a whistle song, they also overlapped the whistles in the broadcast song with the whistles of their own song ($P=0.11$, $n=10$, binomial test).

W10 treatment. Each subject matched a broadcast whistle song with a whistle song at least once. Subjects on average replied to every second broadcast whistle song ($50\pm6\%$, mean \pm SE) with a whistle song and $80\pm4\%$ (mean \pm SE) of whistle songs sung were direct replies to broadcast whistle songs. Thus, whistle songs sung by

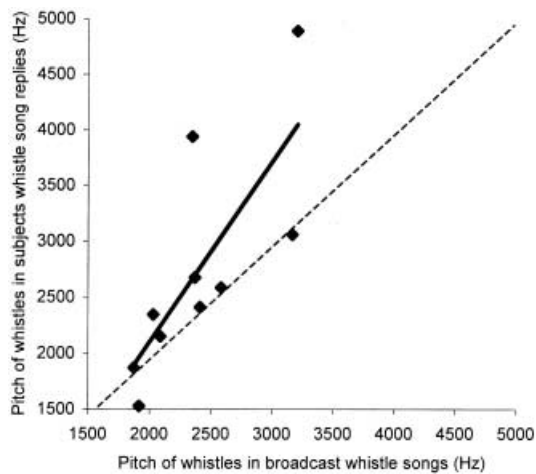


Fig. 3 Regression of the pitch of whistles in subjects whistle song replies on the pitch of the whistles in the broadcast whistle songs in the W1 treatment. The *hatched line* indicates the line of exact pitch matches

subjects were direct replies to the broadcast whistle songs significantly more frequently than replies to normal songs ($P=0.02$, $n=17$, sign test). Occasionally, subjects not only replied to a whistle song with a whistle song but matched the complete broadcast song in the sense that the non-whistle part was also the same as that of the broadcast song. In order to separate such effects of typical song type matching from matching the ‘category’ whistle songs, we removed these song type matches from the data set and repeated the initial repeated measures ANOVA on the influence of playback treatment on whistle song rate. The effect of playback treatment remained when the song type matches were removed ($F_{2, 16}=3.65$, $P=0.037$, repeated measures ANOVA). Thus, the finding that subjects used more whistle songs during playbacks comprising whistle songs was not due to full song type matching.

In all individuals there were positive correlations between whistle pitch in broadcast songs and subjects’ replies ($P<0.001$, $n=12$, sign test; Table 1; five subjects directly replied with a whistle song to a broadcast whistle song two or fewer times so that we could not calculate a regression in these cases). In four subjects there was a significant correlation calculated over all whistle song matches between the pitch of whistles in broadcast whistle songs and the pitch of whistles in subjects’ whistle song replies. In seven subjects there was no such significant correlation, indicating that they did not consistently match the pitch of broadcast whistles when replying with whistle songs to broadcast whistle songs (Table 1). However, all except four subjects matched the pitch of whistles in broadcast whistle song with a pitch difference of less than 500 Hz at least once ($P=0.05$, $n=17$, binomial test).

Effects of playback distance on use of whistle songs

Playback distance had no significant effect on the number of whistle songs sung in any of the three playback treat-

Table 1 Regressions of the mean pitch of whistles in subjects’ direct whistle song replies on the mean pitch of the whistles in the broadcast whistle songs in the W10 treatment. Five subjects directly replied at most two times with a whistle song to a broadcast whistle song so that for these subjects no regression was calculated (see text for details). n =number of whistle song replies to broadcast whistle songs

Individual	r^2	F	P	n	Sign of slope
1	0.134	0.465	0.544	5	+
2	0.023	0.094	0.774	7	+
3	0.538	5.816	0.061†	7	+
4	0.899	44.725	0.001***	7	+
5	0.987	153.419	0.006**	4	+
6	0.031	0.129	0.737	6	+
7	0.097	0.214	0.689	4	+
8	0.018	0.036	0.867	4	+
9	0.925	49.680	0.002**	6	+
10	1.0	2,646.769	0.012*	3	+
11	0.219	0.280	0.690	3	+
12	0.099	0.331	0.605	5	+

† $P<0.1$, * $P<0.05$, ** $P<0.01$, *** $P<0.001$

ments (all $r^2<0.03$, all $P>0.51$; all $n=17$, linear regressions). Also the distance between playback and subject did not affect the probability of a direct whistle song reply in the W1 treatment ($r^2=0.023$, $F_{1, 16}=0.35$, $P=0.56$, linear regression). However, in the W10 treatment playback distance had a significant positive effect on the probability that subjects matched the pitch of the whistle in the broadcast whistle song within a range of 1,000 Hz ($r^2=0.24$, $F_{1, 16}=4.71$, $P=0.047$, linear regression). A regression of the mean differences of whistle pitch in the broadcast songs and the whistles in the whistle song replies on playback distance showed the same positive relation ($r^2=0.17$, $F_{1, 16}=3.09$, $P=0.099$, linear regression).

Vocal responses after playback

When the playback had terminated we continued to record the subjects’ song and then analyzed the percentage of whistle songs over the same number of songs that a subject had sung during playback. In this post-playback period there was again a significant effect of the preceding playback treatment on the number of whistle songs ($F_{2, 16}=5.825$, $P=0.007$, repeated measures ANOVA). Interestingly, this effect was in the opposite direction than that during the playback period itself (Fig. 2b). Subjects sang significantly more whistle songs after the W0 treatment than after the W1 and the W10 treatments (W0 versus W1 treatment, $P=0.012$, $n=17$; W0 versus W10 treatment, $P=0.046$, $n=17$). The number of whistle songs did not differ between the post-playback periods of the W1 and W10 treatments (W1 versus W10 treatment, $P=0.156$, $n=17$).

Discussion

The results show that subjects responded differently to playbacks with different proportions of whistle songs.

During playback, subjects sang significantly more whistle songs when the playback contained many whistle songs than when it contained no whistle song. This effect in part resulted from subjects frequently matching the broadcast whistle songs with whistle songs, but it was not due to full song type matching. Interestingly, after the playback terminated, subjects varied their whistle song rate in the opposite direction than they did during playback. After playback they sang significantly more whistle songs following termination of the W0 treatment than they did following the W10 treatment. Taken together, the different responses during and after playback suggest that whistle songs have a specific signal value, with matching responses during playback reflecting different aspects of whistle songs' use than do responses after playback. Responses during playback show matching of a specific signal parameter, either whistle notes in general or, more specifically, also their pitch, whereas the variation in whistle song rate after playback shows variation in whistle song rate independently of direct responses and provides strong evidence that male nightingales treat whistle songs as a specific category of songs.

In general, matching of whistle songs suggests that whistle songs can be used to address a rival as is the general view for full song type matching (Krebs et al. 1981; Todt 1981; Falls et al. 1982; McGregor et al. 1992; Shackleton and Ratcliffe 1994; Nielsen and Vehrencamp 1995; Beecher et al. 2000; Vehrencamp 2001; reviewed in Todt and Naguib 2000). However, also matching the whistle pitch and the frequent replies with whistle songs that did not match the pitch of the broadcast whistle song indicates that whistle songs can be used at different levels of specificity. The precise matching of the whistle pitch during the W1 treatment in some subjects and the correlation among whistle pitch of the broadcast song and the replies in the W10 treatment are interesting as this pattern of matching differs from typical song type matching. The different levels of specificity with which males can reply to whistle songs in addition to full song type matching of normal and whistle songs allow male nightingales considerable flexibility in matching responses. As each male has a repertoire of several whistle songs covering the whole range of frequencies from about 1 to 8 kHz (unpublished data, Fig. 1), they have the possibility to match a whistle song with almost graded levels of specificity. Whistle song replies thus differ from matching full songs, which is a more discrete 'yes-or-no' response with fewer possible intermediate responses. In addition, full song matches require sharing of song types, whereas whistle song replies do not. Whistle songs thus allow matching at some level of specificity regardless of song type sharing as all males produce whistle songs and also share songs with whistles of similar pitch. In contrast, male nightingales have been shown to share 12–35% of their songs with a neighboring male (Hultsch and Todt 1981). Thus, regardless of song type sharing, whistle songs allow matching and permit complex interactions with different kinds of matching responses even in a species with such a large repertoire.

The result that subjects matched the pitch of broadcast whistles more precisely the more distant the loudspeaker was placed, indicates, in contrast to many other studies, that matching here did not increase with a hypothesized level of threat (Krebs et al. 1981; Vehrencamp 2001). These findings are in line with personal observations that nightingales match whistle songs produced by distant males. Thus, matching may serve different functions depending on the kind of patterns matched, the context and the distance between the singers (Todt and Naguib 2000). Matching whistle songs over long distances, in fact, may function as an attractant rather than being a specific agonistic response strategy. Those individuals that frequently match whistle songs may attract the attention of those singers they are interacting with, in addition to also attracting other listening males or distant females (Naguib and Todt 1997; Naguib et al. 1999; Otter et al. 1999; Peake et al. 2001). The simple acoustic structure of whistles suffers less from degradation during long-range transmission than do more complex song features so that they may be a more effective signal (Wiley and Richards 1982; Naguib and Wiley 2001). Our finding that the probability of matching whistle songs increased with playback distance is consistent with this idea as conspecifics nearby may pay more attention to more complex song components that cannot be recognized so well after long-distance transmission (e.g. Dabelsteen and Pedersen 1993).

That singing behavior after playbacks had terminated further suggests that whistle songs are treated as a specific song category. Birds, after termination of playback, varied their whistle song in the opposite direction than they did during playback. This complements previous findings that showed that whistle songs elicit faster vocal responses in males that do not sing at the onset of playback than do 'normal' songs (Todt and Naguib 2000, p 271). Possibly the nightingale's singing program (Hultsch and Todt 1989, 1996b; Todt and Hultsch 1998) proximately constrains males from deviating for a given time period from their regular whistle song rate. Thus, after a short-term increase or decrease in whistle song rate when responding to rivals, males may 'have to' compensate by then singing songs from this category less or more frequently. Such proximate constraints may also explain why no subject increased its whistle song rate to the level of the broadcast whistle song rate.

Use of different categories of song has so far been described for several species with comparatively small vocal repertoires. Commonly, males sing songs during a given bout of either one or the other category (Lein 1978; Schroeder and Wiley 1983a, b; Lampe and Espmark 1987; Spector 1992; Weary et al. 1994; Wiley et al. 1994). Thus, in these cases a particular singing mode is more clearly associated with a particular context. In nightingales, however, whistle songs are a typical part of male nightingales' vocal repertoire and are used at varying intervals in any singing bout and are usually not clustered in the sense that several whistle songs are sung in immediate succession. Whether or not whistle songs

have similar specific functions in female choice as do some song components in other species (Searcy and Yasukawa 1996), for instance canaries (*Serinus canaria*) (Vallet and Kreutzer 1995; Vallet et al. 1998), remains to be determined.

Taken together, whistle songs appear to have a specific signal value. It remains to be seen whether or not individual differences in responding to whistle songs reflect intrinsic individual variables such as the flexibility of repertoire use which may reflect aspects of male quality. Another interesting question is whether or not differences between males, such as in spatial behavior and dominance (Stamps 1994; Naguib et al. 2001) or other aspects of male quality, are reflected in asymmetries in use of whistle songs between two interacting singers either in terms of matching, overlapping or the specific structure of whistle songs and the frequency with which they are sung.

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