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What is the whistle all about? A study on whistle songs, related male characteristics, and female song preferences in common nightingales

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Abstract In many passerine species certain song structures have evolved to convey information to conspecific males or females. For example, in the common nightingale *Luscinia megarhynchos*, the 'whistle part' is a striking acoustic feature of some song types. Whistle songs have been suspected to be particularly well suited to attract females and/or to be important during female choice, but this has never been tested directly. In this study, we used a two-pronged approach for addressing the function of whistle songs in intersexual communication. First, we analysed relationships between whistle song features and male characteristics reflecting overall male quality. We found that the number of whistle songs produced and acoustic consistency of single whistle elements predicted male body measures, i.e., males who sang more whistle songs were heavier and larger, and produced whistle elements with higher consistency. Second, we conducted playback experiments with females either with or without whistle songs. Females responded more strongly to whistle songs by moving and vocalizing more during the whistle playback. We conclude that whistle songs might play an important role in nightingale mating, as they evoke high arousal in females, and different whistle song features may signal different aspects of male quality to females.

Keywords Song category · Song consistency · Male quality · Field data · Female choice · Playback experiment

Zusammenfassung

Der Pfeifgesang der Nachtigall: korrelierte Männchenmerkmale und weibliche Gesangspräferenzen

Bei vielen Singvogelarten haben sich bestimmte Gesänge entwickelt, die an artgleiche Männchen oder Weibchen adressiert werden. So sind beispielsweise die sogenannten Pfeifstrophen ein sehr auffälliges Merkmal im Gesang der Nachtigall *Luscinia megarhynchos.* Obwohl dieser Pfeifgesang bereits seit Längerem im Verdacht steht eine besondere Bedeutung vor allem bei der Werbung der Weibchen zu haben, existierte hierfür bislang kein direkter Nachweis. In der vorliegenden Studie wurde diese für den Verpaarungskontext postulierte Funktion des Pfeifgesanges unter Anwendung zweier verschiedener Ansätze genauer untersucht. Zum einen wurde geprüft, inwieweit sich Beziehungen zwischen spezifischen Aspekten des Pfeifgesanges und anderen Männchenmerkmalen, die im Allgemeinen die Qualität eines Männchens anzeigen, nachweisen lassen. Hier ergaben die Analysen, dass die Häufigkeit der vorgetragenen Pfeifstrophen im nächtlichen Gesang der Nachtigall stark mit bestimmten Körperabmessungen männlicher Tiere korreliert. So sangen schwerere und größere Männchen in der Regel mehr Pfeifstrophen. Ein ähnlicher Zusammenhang ließ sich auch bezüglich einer erhöhten Kopiertreue beim Vortragen der einzelnen aufeinanderfolgenden Pfeifelemente nachweisen. Darüber hinaus wurde die Wirkung des Pfeifgesanges auf weibliche Nachtigallen untersucht. Hierzu wurden den Weibchen verschiedene Männchengesänge vorgespielt, die entweder einen hohen Anteil an Pfeifstrophen aufwiesen,

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oder aber gar keine Pfeifstrophen enthielten. Dabei reagierten die Weibchen eindeutig stärker auf die Gesänge mit hohem Pfeifstrophenanteil. Aufgrund dieser Befunde kommen wir zu der Schlussfolgerung, dass der Pfeifstrophengesang der Nachtigall in der Tat eine wichtige Rolle in Verpaarungskontexten übernimmt, da er zum einen stimulierend auf die Weibchen wirkt und zum anderen als Indikator für diverse Qualitätsaspekte der Männchen fungieren kann.

Introduction

Bird song has traditionally been investigated in the framework of the 'dual function hypothesis', which posits that male song primarily serves the purposes of mate attraction and rival deterrence (Searcy and Andersson 1986; Catchpole and Slater 2008). Therefore, the evolution of song is thought to be strongly driven by factors such as female song preferences and/or the use of song in male–male vocal interactions. A key notion of most theories on song evolution is that song serves as indicator of signaller condition or viability (Nowicki and Searcy 2005). In order to serve as honest signals during communication, the expression and maintenance of these signals must be associated with costs (Zahavi 1975; Grafen 1990). As a consequence, song features should be related to male traits, since only superior males can afford to sing high quality songs (Gil and Gahr 2002). The link between song and male quality is closely enmeshed in the evolution of female song preferences (Searcy and Yasukawa 1996). By choosing their mates on the basis of indicative song features, females may ensure both mating with genetically as well as phenotypically superior males, which finally improves female fitness, and/or the female's own survival and fecundity (Andersson 1994; Møller and Jennions 2001).

In many passerine species, these processes have presumably led to the development of multiple versions of a song (Beecher and Brenowitz 2005), where highly specific song patterns can be assigned to different behavioural contexts such as courtship (e.g., Sossinka and Böhner 1980; Beletsky 1983; Catchpole 1983; Gaddis 1983; Weary et al. 1994; Brunner and Pasinelli 2010; Petruskova et al. 2014). Songs that share the same function often appear to be syntactically and acoustically similar within one species (e.g., Byers 1996; Trillo and Vehrencamp 2005) or even across species (e.g., trill songs: Podos 1997; rattle songs: Galeotti et al. 1997; Illes et al. 2006), and based on these similarities have been described to form song categories (e.g., Nelson and Croner 1991; Whaling et al. 1997; Bolsinger 2000). In species that have evolved large song repertoires, vocal complexity has long been investigated as a likely parameter of female choice (Catchpole 1987; Searcy 1992a). The signal value of repertoires as an indicator for male quality is assumed to be maintained by developmental costs of brain structures underlying song learning during early life (Nowicki et al. 2002). For some species, females have been shown to be attracted to more complex song, whereas other studies have challenged the role of repertoires as an important mating signal (Byers and Kroodsma 2009). Aside from song inventories, recent studies have additionally focused on the fine tuning of song structures, such as trills (syllables with a rapidly repeated series of elements that often cover broad frequency ranges, Wilson et al. 2014), or the ability of males to produce songs with high consistency (Sakata and Vehrencamp 2012). Since the production of these structures seems to be a physically challenging task for males, females might use individual differences in vocal performance to assess male quality (e.g., Ballentine et al. 2004; Byers 2007; Searcy et al. 2010).

The common nightingale *Luscinia megarhynchos* is among the most versatile singers in the temperate zone, with males having very large repertoires (on average 180 different song types per male; Kipper et al. 2004; Kiefer et al. 2006). This huge complexity makes the nightingale a suitable candidate to investigate the possible function of different song types and other, more subtle song features. To date there is only limited knowledge on the usage of song in mating contexts. For example, despite the fact that large repertoires correlate with aspects of male quality (Kipper et al. 2006), it is unclear whether female nightingales indeed prefer large repertoire singers. Considering the numerous different song types, different song categories have been identified in nightingale singing (whistle song: Hultsch 1980; Naguib et al. 2002; trill song: Kunc et al. 2006, 2007; buzz song: Weiss et al. 2012). The only direct evidence that categories are meaningful to females as well was provided for buzz songs (Weiss et al. 2012). Another song category, the whistle song, has long been hypothesized to play a role in mating (Hultsch 1980). This category comprises song types that contain a homotype series of repeated whistle elements with little or no frequency modulation in the first part of the song (Hultsch and Todt 1996b). Whistle series either directly start a song, or they are preceded by one soft element or a short sequence of heterotype elements. Males have repertoires of different whistle song types that differ in whistle frequency, whistle element or series duration, whistle modulation and the following (often trilled) song part (Hultsch 1980; Naguib et al. 2002; Kunc et al. 2005b; see Fig. 1a–c for examples of different whistle song types). Whistle

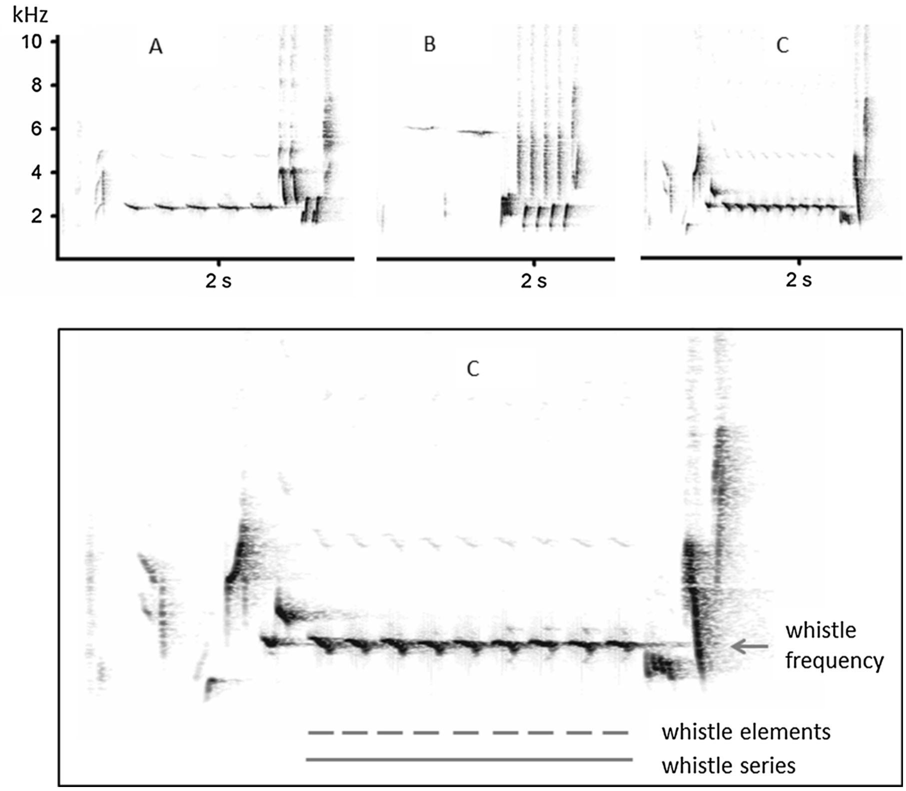

Fig. 1 Examples of different whistle song types frequently sung by males of our study population. Depicted are three types that differ in, e.g., whistle frequency, duration of whistle series and duration of single whistle elements or duration of pauses between whistle elements. Type (C) was analysed with respect to its acoustic fine structure

songs have been shown to matter in male–male interactions (e.g., Naguib et al. 2002). Additionally, several findings point to a function as a mating signal. First, their acoustic structure permits transmission over long distances (Richards 1981; Wiley and Richards 1982; Dabelsteen et al. 1993; Naguib et al. 2008), and whistle songs are therefore expected to serve long-range communication to attract the attention of conspecifics (Naguib and Wiley 2001; Naguib et al. 2002). Second, whistle songs often occur in the nocturnal singing of unpaired males at the beginning of the breeding season (~15–20 % of all songs are whistle songs, Hultsch 1980; Kiefer et al. 2006), whereas their occurrence during dawn singing is lower (only ~2–14 % of all songs; Hultsch 1980; Kunc et al. 2005a). At night, migrating females arrive at the breeding grounds and prospect male territories (Glutz von Blotzheim and Bauer 1989; Roth et al. 2009). The high rate of whistle songs at that time was suspected to serve female attraction. During nocturnal singing, males vary in the proportion of whistle songs (Kunc et al. 2005b; Kiefer et al. 2006); this might constitute a basis for female mate choice. A recent study suggested that males respond to the presence of a female (mimicked by a call playback) by maintaining or increasing whistle song rate (Kipper et al. 2014). Finally, data suggest that whistle songs influence female mating decisions in the field (unpublished data PhD thesis Kunc 2004).

To shed further light on the function of whistle songs in intersexual communication, we followed two approaches. First, we analysed several whistle song features in recordings from free-ranging male nightingales, and related these to male traits that have repeatedly been used as measures of male quality in nightingales and other songbirds (e.g., Kipper et al. 2006; Kipper and Kiefer 2010; Gil and Gahr 2002). Assuming that the production of whistle song imposes some kind of costs to males, we predicted that whistle song features would be related to male traits in order to serve as indices of male quality. Second, to test for the role of whistle songs in mate attraction, we conducted experiments with females, by playing songs either with or without whistle songs. We hypothesized that if whistle songs are important cues for females, females will respond more strongly to whistle songs. Studies investigating female song preferences in other species have used several behavioural responses to evaluate female responses to male song. These responses include behaviours that are clearly associated with sexual contexts, such as copulation solicitation displays (CSD), or more subtle behaviours such as postures, movements, or calls that indicate increased activity and female arousal (Searcy 1992b). To date, only one study reported an experimental test of song preferences in nightingales (Weiss et al. 2012). According to this study, we expected more location changes and certain postures in response to whistle song playbacks. Since a recent study pointed to the potential importance of calling in the species (Kipper et al. 2014), we also expected females to emit more calls when hearing whistle songs.

Methods

Males

Male data were obtained in a long-term field project on nightingale song (e.g., Bartsch et al. 2014; Bartsch et al. 2015), carried out on population of nightingales in the Golmer Luch, Potsdam, Brandenburg (52.4°, 12.97°). Between 2009 and 2012, males settling in this area were monitored regularly throughout the breeding season from mid-April to mid-June. For the study presented here, we used data from 23 resident males who had established territories in at least 1 year (each individual only contributed once).

When male nightingales settle in a territory, they start nocturnal singing (besides diurnal song), which they only cease after pair formation (Grüll 1981; Amrhein et al. 2002). We documented male settling (as determined by at least three consecutive nights of singing from the same song post) and nocturnal singing activity by regular night rounds (at least every second night) between 2330 and 0200 h. Thus, male arrival dates were approximated by their first night of nocturnal song in a territory. To compare arrival dates across years, we determined the median of each year's arrival dates and used this as a reference, with earlier arrival dates being negatively and later dates being positively signed. Subjects were recorded during their first nights of singing when all males were most probably still unpaired (Amrhein et al. 2002). Singing was recorded with a Marantz PMD-660 Compact Digital Recorder connected to a Sennheiser ME66/K6 directional microphone. After having recorded the males, they were captured using Ecotone mist nets (http://www.econtone.pl). During banding, each male was fitted with a unique colour ring combination for identification. We measured wing length (±0.5 mm), length of the eighth primary (counted from the innermost primary towards the tip of the wing, ±0.5 mm), length of the tibiotarsus (±0.1 mm) and weight. Male age was determined (yearling or older) by feather characteristics (Svensson 1992; Mundry and Sommer 2007). Later on in the breeding season, we regularly (rotational every 1–3 days) returned to the territories to confirm male identity and pairing status via visual observations.

Song analysis

All sound analyses were conducted with the software Avisoft SASlab Pro 4.52 (R. Specht, Berlin, Germany). Recordings were down-sampled to 22.05 kHz, high pass filtered (0.8 kHz, Butterworth) and amplitude was normalized to 75 %. For each recording, we analysed several different song parameters. First, we determined the repertoire size of males via visual inspection of 533 consecutive songs (equalling about 1 hour of nocturnal song), which has been shown to result in saturated repertoire curves (for details, see Kipper et al. 2004). We further determined whistle song repertoire size (i.e., the number of different whistle song types within 533 consecutive songs). A whistle song type was operationally defined as each song type starting with or containing a series of at least two (usually more) homotype whistle elements (e.g., Naguib et al. 2002) characterised by low frequency modulation and a low frequency coverage of elements (opposite to trills that cover larger ranges; see Fig. 1 for examples). In addition, we determined whistle song occurrence (i.e., all whistle songs independent of types). Finally, we calculated an overall mean whistle frequency per male by averaging the mean frequency of a whistle series across all whistle song types. A higher value indicates a male singing predominantly whistle songs in higher frequencies, whereas a lower value would indicate a male singing mostly lower frequency whistle songs.

To further inquire into the acoustic fine structure of whistle songs, we chose one whistle song type that occurred in most of our subjects (20 out of 23 males; accordingly, three males did not contribute to this part of the analysis) and was sung at least twice by all males (see Fig. 1c). For this type, we determined the duration of the whole whistle series (s) by measuring the time from the onset of the first whistle element to the offset of the last one, and counted the number of whistle elements. From that, we calculated the whistle rate (number of whistles/second). As song consistency has been shown to encode signaller quality and/or motivation in different species including nightingales (Botero et al. 2009; de Kort et al. 2009; Rivera-Gutierrez et al. 2010; Sprau et al. 2013), we further generated a parameter related to the consistency of whistle elements, including temporal as well as frequency measures. To do so, we determined the duration and the frequency of each single whistle element and averaged values across all whistle elements. We then calculated the coefficient of variation (CV) for both measures, which is defined as the ratio of the standard deviation to the mean, and averaged both CVs. The coefficient of variation has been frequently used to describe song variability within or between individuals (e.g., Kunc 2005b; Byers 2007; Węgrzyn et al. 2010).

The recordings used to produce the spectrograms in Fig. 1 are available from the Animal Sound Archive at the Museum für Naturkunde, Berlin (http://www.animalsoundarchive.org; see Electronic Supplementary Material).

Playbacks with females

To test responses of females to whistle songs, we conducted playback experiments with females raised under controlled conditions in the laboratory as part of a study on male song learning and female preference learning (e.g., Kiefer et al. 2014 for details on the hand-raising procedure and tutoring). Females went through two phases of song tutoring during their first year of life. The first started soon after fledging (June–July 2006), i.e., during the first sensitive phase of male auditory song learning (Hultsch and Kopp 1989). Some of the songs were re-tutored in the following spring, resulting in overall exposures of between 27 and 40 times per song type. Tutoring frequencies within this range are sufficient for learning in male nightingales (Hultsch and Todt 2008). Birds were tutored with whistle and non-whistle songs in proportions reflecting those of natural singing (Kiefer et al. 2006). Some, but not all, song types that were used in the playback experiment (see below) were tutored previously (proportion of playback song types that were tutored: 25 ± 2 % Mean ± SD); the respective proportion did not differ between whistle and non-whistle playbacks (Mann–Whitney U test, $N_1 = N_2 = 7$, $W = 25$, $P = 1$).

For our playback experiment, we tested nine adult females in June 2008. During this time, females were kept separately in cages (50 × 120 × 50 cm) under weekly changing light conditions reflecting the natural conditions during the breeding season (in the week of experiments: lights on 0500–2130 h). Cages were equipped with perches, grit covering the ground, and water and food, which was available ad libitum. As in many other laboratory studies, responsiveness to song (i.e., showing copulation solicitation displays) seemed possible only when treating females with estrogen (Searcy and Marler 1981; Catchpole et al. 1984). Thus, 8–10 days before to the experiments started, females were treated with estrogen to increase their responsiveness to the playback. Five females were implanted subcutaneously (skin covering the breast muscle) with an estradiol pellet. The four remaining females were treated the same, but received only a sham-implant (pellets composed of pure Silastic adhesive without estradiol; for details on estradiol treatment, see Weiss et al. 2012). During playbacks, the data of two females were lost due to technical failure of the recording equipment in the sham-implanted group. The resulting small sample size (only two females in the sham-implanted group) did not allow for testing of the influence of the implantation on female responses. However, looking at the data distribution across response variables did not reveal any systematic difference between the two groups, and thus, data for all females were pooled (resulting in a sample size of seven tested females).

Song stimuli

Playback songs were derived from high quality recordings of nocturnal song of free-ranging males (different from tutor-song males). Recordings were obtained between 2005 and 2008 at several places in Berlin that were different from the female removal site, using the same equipment as for male recordings, or alternatively, in some cases a SONY TCD D-100 DAT recorder. Songs were recorded from 3 to 8 m distance. All songs were digitised at 44 kHz and with 16 bit accuracy, high-pass-filtered at 500 Hz (Hamming window) to remove low-frequency background noise, and separately normalized at 75 % using the sound analysis program Avisoft Saslab Pro Version 5.0.07 (R. Specht, Berlin). To avoid pseudo-replication, each female heard a unique playback that was presented in two qualities (whistle and non-whistle treatment) from seven different males. Each playback consisted of 20 different song types (i.e., each type occurred just once) that were frequently sung by males of a Berlin nightingale population (based on repertoire comparison of 40 birds; Kipper et al., unpublished data). For the whistle playback, we selected 18 different whistle song types from a male's recording and added two non-whistle types. This is at the upper range of whistle song rate in natural singing, as we wanted to make playback effects more detectable. For the non-whistle playback, we selected 20 non-whistle song types from each male's recording. In all playbacks, the 20 song types were shuffled and ~2.5 s of silence was inserted between song types.

Experimental setup and playback design

On the day of the experiment, cages were transferred to a separate room and females were given 30 min for acclimatisation before the playback started. Cages were mounted on a 0.8 m high table in front of a video camera for audio-visual recording of female behaviour. Additionally, a Marantz PMD connected to a Sennheiser ME66/K6 directional microphone was used for audio recordings. Each playback session consisted of a whistle and a non-whistle treatment. Based on preliminary observations and studies of female preferences in other species, we expected large intra-individual and inter-individual variability in response behaviour. Given our rather small sample size, each treatment (consisting of 20 songs) was played twice with a short pause of 30 s to increase response probability. Between treatments there was a longer pause of 10 min. The order of treatments (i.e., which playback started, either whistle or non-whistle) was randomized across females to avoid effects of playback order.

Female responses

No female showed copulation solicitation displays in this or other playback experiments (see Weiss et al. 2012), regardless of whether they were treated with estradiol or not. Thus, we used other behavioural parameters to assess female responses to the different song qualities. To determine general behavioural activity, we counted the number of location changes within the cage (including hops between perches or at the ground and flights) and the number of tail lifts. These parameters have been used as proxy for female song preferences before (Baker 1983; Caro et al. 2010; Weiss et al. 2012). Also, we counted the number of vocalizations emitted by females (e.g., short calls like "huit" and "karr", Glutz von Blotzheim and Bauer 1989; Kipper et al. 2014) during each treatment to further evaluate female song responsiveness. As each treatment was played twice, the values for response measures were summed. To account for slight differences in total playback time between different females, we calculated the rate of each behaviour (behaviour/min). We also measured the latency (in seconds) until the first location change during each treatment. To do so, we averaged the times across the two stimuli presentations. When a female did not move at all during one song presentation, latency was set to the longest stimuli duration (longest playback = 156 s). To account for individual differences in female behaviour, we additionally analysed female behaviour prior to song broadcast by comparing female responses during the 3-min pre-playback phases. For the treatment that was presented second, we used the last 3 min of the 10 min pause between treatments as the pre-playback phase.

Statistics

All data were analysed using R (R Development Core Team, version 3.1.1) and statistical significance was set at $\alpha = 0.05$ (two-sided testing for data on male song; one-sided testing for female data under the hypothesis that whistle songs induce stronger responses). Male data (song parameters and male characteristics) were analysed in several steps. In a first step, we tested if repertoire size, whistle repertoire size, whistle occurrence and mean frequency were correlated to each other to decrease the number of inter-correlated measures using Pearson correlations. We likewise proceeded with song measures related to the acoustic fine structure of one whistle type. For further analyses, these parameters were treated separately (i.e., data across all whistle songs and data on the fine structure of one specific type entered different models). Finally, we investigated whether male characteristics were predicted by different whistle song features by calculating linear models (LM) using the 'lm' function, or generalized linear models (GLM) using the 'glm' function in R. To do so, the respective male trait [male body weight, tarsus and wing length, arrival date, age (as assigned to either age class, yearling or older)] and pairing status (i.e., paired or unpaired) were set as response variables and as fixed factors, we used the whistle song parameters (i.e., either parameters derived from analyses across all whistle songs or parameters concerning one whistle type, see also Table 1). Since whistle repertoire size is highly correlated with overall repertoire size (Kiefer et al. 2006, see also results), we included repertoire size as a covariate in the models. For all models, we always started with the maximum model and removed nonsignificant terms by using the 'step' function (default for direction is backward selection) in R. For the final models, we visually checked if residuals of all models were normally distributed and variances were homogenous (residual plots).

Differences in responses of females to whistle and non-whistle playbacks are shown as side-by-side plots in Figs. 4, 5, 6 and 7. Generally, due to small sample size and marked differences with respect to location and shape of data, the data set should be statistically tested only with caution. We used a paired permutation test as implemented in the R package exactRankTests Version 0.8-27. To get an impression of female baseline behaviour prior to the treatments, we used the same approach by comparing female behaviour during the 3-min pre-playback phases. As only five out of seven females vocalized during the playbacks, only five females entered the statistical analysis for this specific response measure.

Results

Whistle songs as predictors of male quality

We first analysed how repertoire size, whistle repertoire size, whistle occurrence and mean whistle frequency were related to each other. As previously reported by Kiefer et al. (2006), we found that whistle song repertoire size was positively correlated with repertoire size (Pearson correlation, $n = 23$, $r = 0.80$, $p < 0.001$; data not shown). All other parameters (including parameters related to the fine structure of one whistle type) showed no correlation, and thus were also included into further analyses. Most noteworthy here, whistle song occurrence and mean whistle frequency were both independent of whistle repertoire size (Pearson correlation, whistle song occurrence: $n = 23$, $r = 0.08$, $p = 0.71$; mean frequency: $n = 23$, $r = -0.02$, $p = 0.91$; data not shown).

Next, we analysed whether male traits related to quality were predicted by whistle song features. We found that

Table 1 Overview on results of song analysis. Shown are means and standard deviations (SD) for each song parameter

	(Unit)	N	Mean	±SD
Song characteristic				
Repertoire	No. of different song types	23	171	32
Whistle song repertoire	No. of different whistle song types	23	27	5
Whistle song occurrence	No. of whistle songs	23	74	13
Mean whistle frequency	Hz	23	3460	328
Whistle song type characteristic				
Whistle series duration	s	20	2.18	1.11
Whistle rate	Elements/s	20	6.53	0.37
Mean coefficient of variation		20	0.08	0.02

For the fine tuning of whistle song type characteristics, only 20 males entered the analyses, since only these males had this specific song type in their repertoire

Table 2 Results from backward selection of LM or GLM on whistle song characteristics predicting male characteristics (a) $n = 23$ (b) $n = 20$

Response variable	Predictor variables	Estimate	SE	df	t/z	P
(a) $n = 23$						
Body weight	Whistle song occurrence	0.05	0.03	19	1.95	0.07
Tarsus length	Whistle song occurrence	0.03	0.01	19	2.22	0.04*
Wing	Repertoire size	0.10	0.03	19	3.11	0.007**
	Whistle repertoire size	0.51	0.21	19	−2.49	0.02*
	Whistle occurrence	0.12	0.05	19	2.30	0.04*
	Mean whistle frequency	0.00	0.00	19	−2.22	0.04*
Arrival	repertoire size	−0.18	0.07	19	−2.43	0.03*
	Whistle repertoire size	1.06	0.44	19	2.43	0.03*
	Whistle occurrence	−0.17	0.11	19	−1.54	0.14
Age	Repertoire size	0.13	0.05	22	2.42	0.02*
Status	Repertoire size	−0.06	0.02	22	−2.50	0.01*
(b) $n = 20$						
Body weight	Mean coefficient of variation	−61.23	21.75	16	−2.81	0.012*
Tarsus length	Mean coefficient of variation	−37.99	9.78	16	−3.88	0.001**
Wing	Duration whistle series	−0.48	0.43	16	−1.12	0.28
Arrival	Duration whistle series	1.85	1.06	16	1.75	0.10
Age	Whistle rate	1.70	1.42	16	1.20	0.23
Status	Mean coefficient of variation	−31.70	34.38	16	−0.92	0.36

Sample sizes vary due to missing values of the respective measures

males who had larger tarsi, longer wings and weighed more sang more whistle songs (LM: tarsus length, $n = 21$, estimate ± SE = 0.03 ± 0.01, $df = 19$, $p = 0.04$; wing length, $n = 21$, estimate ± SE = 0.12 ± 0.05, $df = 19$, $p = 0.04$; body weight, $n = 21$, estimate ± SE = 0.05 ± 0.03, $df = 19$, $p = 0.07$; Table 2a; Fig. 2). Wing length was additionally predicted by repertoire size (LM, $n = 21$, estimate ± SE = 0.10 ± 0.03, $df = 19$, $p = 0.007$), whistle repertoire size (LM, $n = 21$, estimate ± SE = 0.51 ± 0.21, $df = 19$, $p = 0.02$) and mean whistle frequency (LM, $n = 21$, estimate ± SE = 0.00 ± 0.0, $df = 19$, $p = 0.04$; Table 2a). Furthermore, arrival date was predicted by both repertoire and whistle repertoire size (LM, repertoire size: $n = 21$, estimate ± SE = −0.18 ± 0.07, $df = 19$, $p = 0.03$; whistle repertoire size: $n = 21$, estimate ± SE = 1.06 ± 0.44, $df = 19$, $p = 0.03$; Table 2a). With respect to the fine tuning of whistle song, larger and heavier males had lower mean coefficients of variation, i.e., they sang whistle elements of a certain whistle song type with higher consistency (LM: tarsus length, $n = 18$, estimate ± SE = −37.99 ± 9.78, $df = 16$, $p = 0.0013$; body weight, $n = 18$, estimate ± SE = −61.23 ± 21.75, $df = 16$, $p = 0.012$; Table 2b; Fig. 3). Finally, male age and pairing status were both predicted by repertoire size (GLM: age, $n = 23$, estimate ± SE = 0.13 ± 0.02, $df = 22$, $p = 0.02$; status, $n = 23$, estimate ± SE = −0.06 ± 0.02, $df = 22$, $p = 0.01$; Table 2a).

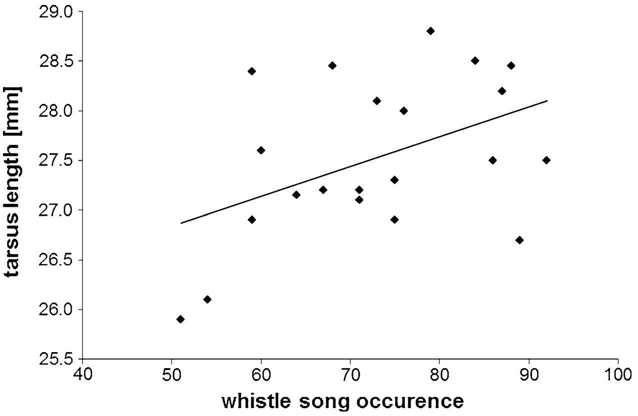

Fig. 2 Relation between tarsus length and whistle song occurrence ($n = 21$)

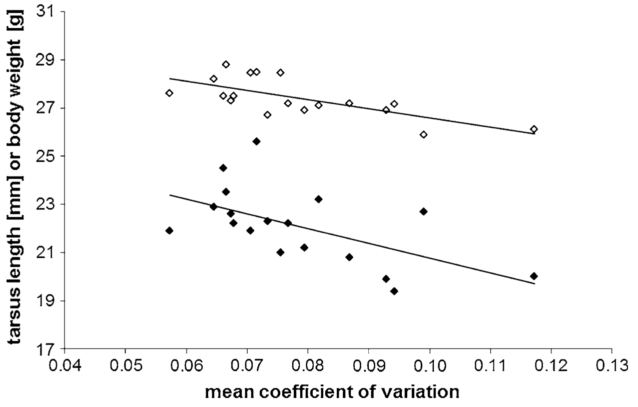

Fig. 3 Relation between male body measures (*open diamonds* body weight, *black diamonds* tarsus length) and mean coefficient of variation (n = 18)

Playback experiments with females

Before the playbacks, females did not differ in their behaviour in any of the response parameters (paired permutation test, all $n = 7$, all $p > 0.1$). During the playbacks, females showed different responses to playbacks containing many whistle songs or no whistle songs: almost all females responded more strongly to the whistle playback with significant differences (paired permutation test, one-sided, all $n = 7$, all $p = 0.047$) in the number of location changes (non-whistle: Mean ± SD = 16 ± 18, whistle: Mean ± SD = 27 ± 14; Fig. 4), number of tail lifts (non-whistle: Mean ± SD = 11 ± 9, whistle: Mean ± SD = 18 ± 11; Fig. 5), and latency to the first location change (non-whistle: Mean ± SD = 65 s ± 62 s, whistle: Mean ± SD = 22 s ± 33 s; Fig. 6). Also, all females vocalized more during the whistle treatment (non-whistle: Mean ± SD = 10 ± 22, whistle: Mean ± SD = 23 ± 28; Fig. 7), although this was not statistically significant (paired permutation test, one-sided, $n = 5$, $p = 0.06$).

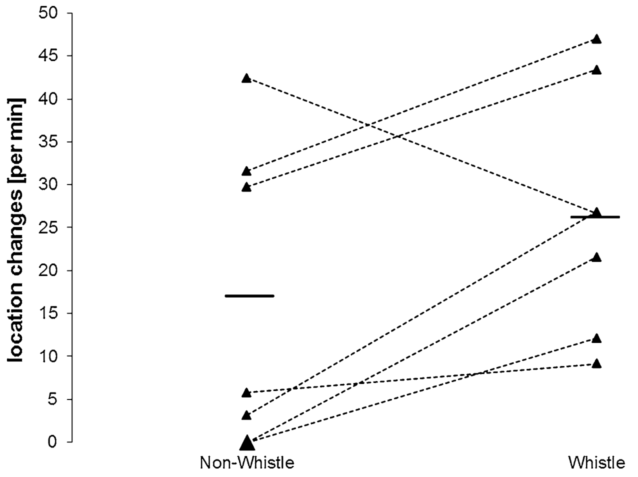

Fig. 4 Number of location changes (per minute) that females performed during playbacks either containing many whistle songs or non-whistle songs only. *Triangles* indicate values for individual birds; *lines* indicate mean values ($n = 7$)

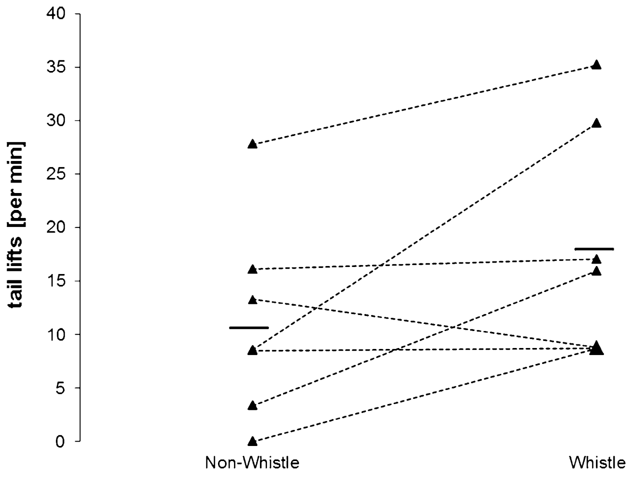

Fig. 5 Number of tail lifts (per minute) that females performed during playbacks either containing many whistle songs or non-whistle songs only. *Triangles* indicate values for individual birds; *lines* indicate mean values ($n = 7$)

Discussion

The results of our study support the idea that whistle songs are important in nightingale mating contexts. First, we found relationships between different whistle song features and male traits reflecting different aspects of quality in free-ranging male nightingales. Most striking is that males of better body condition (indicated by longer tarsi, longer wings and more weight) sang more whistle songs and additionally, whistled with higher consistency. Besides relations of whistle song and male quality, overall song repertoire size was related to male age and pairing status (with older and paired males having larger song type

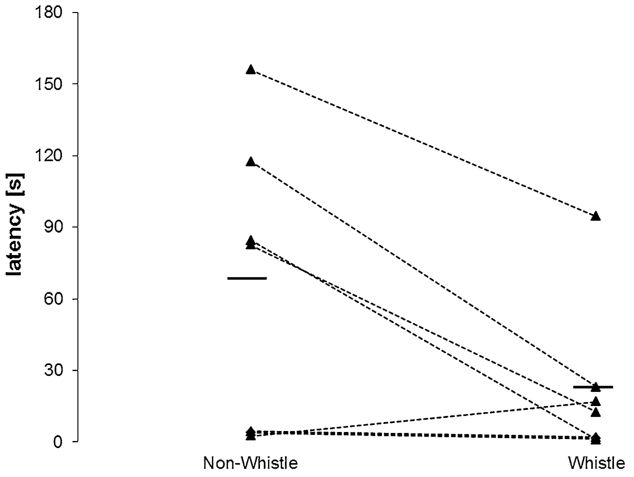

Fig. 6 Latency to first location change (in seconds) of females during playbacks either containing many whistle songs or non-whistle songs only. *Triangles* indicate values for individual birds; *lines* indicate mean values ($n = 7$)

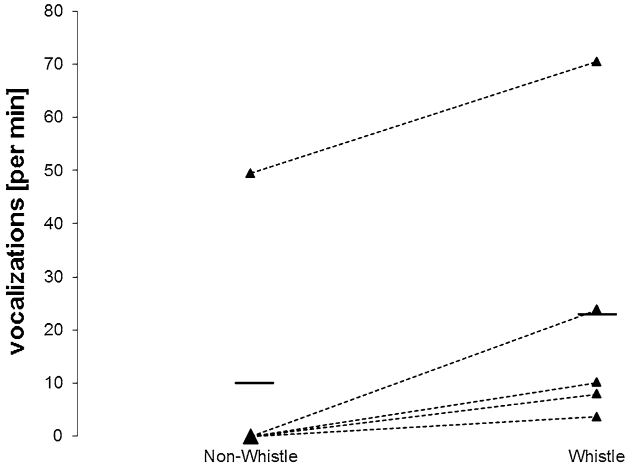

Fig. 7 Female vocalization behaviour during playbacks either containing many whistle songs or non-whistle songs only. *Triangles* indicate values for individual birds; *lines* indicate mean values ($n = 5$)

repertoires), suggesting that multiple song characteristics convey multiple pieces of information in nightingales. Second, female nightingales responded stronger to playbacks containing whistle songs.

The fact that whistle song features predict male quality traits suggests that these features are well suited to serve as indicator signals and therefore might play a role in female mating decisions. Here, whistle song occurrence (including repetitions of any whistle song type) during nocturnal singing seems to be of particular importance. As described earlier (Kunc et al. 2005b; Kiefer et al. 2006), the proportion of whistle songs during nocturnal singing varies remarkably across males, which could provide important cues for females to choose among males. Following hypotheses on the function of whistle songs as long-range communication signals, the production of many whistle songs would enhance the proposed signal value. Besides that, our data show that males vary in their whistle consistency. The ability of males to perform songs with high consistency has been shown to be relevant in female mate choice (Sakata and Vehrencamp 2012). Whistle consistency, for example, is related to harem size in great reed warblers *Acrocephalus arundinaceus* (Węgrzyn et al. 2010). Our results confirm that in species with large song repertoires, the fine tuning of song structures might have been selected to function in communication as well (Drăgănoiu et al. 2002; Botero et al. 2009; Weiss et al. 2012; Geberzahn and Aubin 2014).

Whether the production of whistle songs underlies physical constraints in nightingales (equivalent to models on performance constraints in trill production, e.g., Podos 1997) is not known. To date, the production mechanism of whistle-like sounds in birds is not fully understood. Here, both pure aerodynamic models and vibratory syrinx mechanisms have been proposed (e.g., Gaunt et al. 1982; Ballintijn and ten Cate 1998; Larsen and Goller 1999). The involvement of vibratory syringeal movements during whistle song production might constitute a basis for whistle songs being costly to produce. Especially, the fast production of consistent whistle elements and pauses in between may require a fine coordination of syringeal and respiratory muscles (Sakata and Vehrencamp 2012). For nightingales, Kunc et al. (2005b) showed that whistle songs are followed by longer pauses than non-whistle songs, which might point to some constraint mechanism. Our results support this view. We found that whistle song features are strongly related to male body measures such as tarsus or wing length and body weight. Especially tarsus length as a skeleton measure, and to a lesser extent wing measure, are stable traits that are partly heritable and partly influenced by environmental conditions in early development (Lindström 1999; Metcalfe and Monaghan 2001). These measures have frequently been used to assess body size in birds (Rising and Somers 1989; Gosler et al. 1998), and have been linked to male quality as for example, early nutritional condition (Searcy et al. 2004), increased individual survival (Alatalo et al. 1990b) or a higher dominance status (Garnett 1981). Assuming that larger male nightingales are 'better' males and knowing that whistle song features predict male size, female nightingales might choose males of better condition on the basis of whistle song features.

Our study provides experimental evidence that females react stronger to whistle than to non-whistle songs. Assuming that their increased responses during the whistle treatment reflect increased arousal or even a preference for whistle songs (Searcy 1992b), we conclude that whistle songs serve in mate attraction in nightingales, a notion that had been previously proposed by several authors (e.g., Hultsch 1980; Kunc 2004, 2005a, b; Todt and Hultsch 2006; Naguib et al. 2008). Especially female vocalization behaviour during the playbacks can be seen as a strong indicator of female song preference (Nagle et al. 2002; Dunning et al. 2014; Amy et al. 2015). In nightingales, both sexes possess call repertoires that are used in many different situations during courtship and breeding (Horstkotte 1965; Glutz von Blotzheim 1989). Since only whistle songs elicited the emission of calls in the majority of females (only one female called in the non-whistle treatment), female calls might be seen as some kind of response to whistling males. This is further corroborated by several anecdotal field observations where we observed females emitting calls when they approached a singing male (personal observation). Furthermore, the increased activity of females when hearing whistle songs (more location changes and tail lifts, shorter latency to start moving) might indicate their readiness to move towards the whistle source. So far, we only tested female responses to the mere presence of whistles songs in a playback. Future studies could be designed to test female preferences for more distinct whistle song features, and if females do indeed pay attention to finer structural features of whistle songs (e.g., artificially manipulated element consistency) to assess male quality.

Overall, Hultsch (1980) proposed three main functions of whistle songs: species recognition, long-distance communication among males, and alerting and attraction of females. All three functions might be realized by whistle songs or different aspects of whistling, such as the occurrence of whistle songs, frequencies and fine-tuning (e.g., consistency) of whistle elements. Future studies are needed to disentangle the function of whistle song features and their relevance in different behavioural contexts.

Conclusion

The role of whistle songs in male–male vocal communication has already been addressed in several studies, while our results expand on the knowledge of the function of whistle songs in intersexual communication. By detecting relationships between whistle song and male quality, and by showing that females show stronger responses to whistle songs than to non-whistle songs, results of this study suggest that whistle songs provide cues for females that play an important role during mate choice. We conclude that whistle songs in nightingales are multifunctional and encode multiple messages for different receivers.

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