Acoustic features of song categories and their possible implications for communication in the common nightingale (*Luscinia megarhynchos*)

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Summary

In many passerine species, males sing more than one distinct song type. Commonly, songs are assigned to different song types or song categories based on phonological and syntactical dissimilarities. However, temporal aspects, such as song length and song rate, also need to be considered to understand the possible functions of different songs. Common nightingales (*Luscinia megarhynchos*) have large vocal repertoires of different song types but their songs additionally can be grouped into two distinct categories (particular groups of song types): whistle songs and nonwhistle songs. Whistle songs are hypothesised to be important to attract migrating females. We studied temporal properties of whistle songs and nonwhistle songs and examined the relationship between those song parameters and song output parameters, such as song rate and song length. To investigate how song parameters vary among males, we calculated the coefficients of variation for different song traits. We found that the variation in the proportion of whistle songs was significantly higher among males than variation in other song parameters. Furthermore, the proportion of whistle songs was negatively correlated with other song output patterns. These findings suggest that the production of whistle songs might be constrained and/or that whistle songs and their succeeding pauses may act as a functional unit in communication.

Keywords: *Luscinia megarhynchos*, repertoire, sexual selection, song category, whistle song.

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Introduction

Many passerine species sing more than one distinct song type (Kroodsma, 1982; Horn & Falls, 1996). Different song types can vary in their structural complexity and in their temporal structure such as song length. Similar song types can then be grouped into different song categories (e.g., song types a1, a2, a3 can be grouped into song category A). Evidence for functional divergence among songs includes their differential use during mate attraction and territory defence. For example, in some species long songs are directed towards females, whereas short songs are directed towards males (e.g., willow warbler, *Phylloscopus trochilus*, Järvi et al., 1980; great reed warbler, *Acrocephalus arundinaceus*, Catchpole, 1983; redwing, *Turdus iliacus*, Lampe & Espmark, 1987). Furthermore, playback experiments in several species have shown that males respond differently to different song categories or song types (Ficken & Ficken, 1970; Järvi et al., 1980; Schroeder & Wiley, 1983; Simpson, 1985; Catchpole et al., 1986; Nelson & Croner, 1991; Searcy & Nowicki, 2000; Naguib et al., 2002).

Commonly, songs are assigned to different song categories based on structural dissimilarities, such as the presence or absence of specific song components, or on the syntactical organization (reviewed in Becker, 1982; Spector, 1992; Lambrechts, 1996; Kroodsma, 2004). However, songs that are assigned to different song categories based on specific structural components often differ also in several other song parameters (Becker, 1982), which may be equally important as the trait used for classifying songs into different song types or song categories. Some of these song parameters (e.g., song length) have been shown to be sexually selected (e.g., Catchpole & Slater, 1995; Garamszegi & Møller, 2004).

Nightingales have large vocal repertoires (up to 260 different song types; Hultsch & Todt, 1981; Kipper et al., 2004) and their songs can be grouped into two distinct song categories: whistle songs and nonwhistle songs (Figure 1; Hultsch & Todt, 1996; Naguib et al., 2002; Kunc et al., in press a). The first part of a whistle song consists of a series of pure-tone elements with little or no frequency modulation (Hultsch & Todt, 1996). Each male has a repertoire of whistle songs with whistles at different frequencies (pitch range of about 1.5-8 kHz; Hultsch, 1980; Naguib et al., 2002). Nonwhistle songs begin with structurally different elements, and the structural variability among songs within this song category is high (Figure 1; Todt, 1970, 1971).

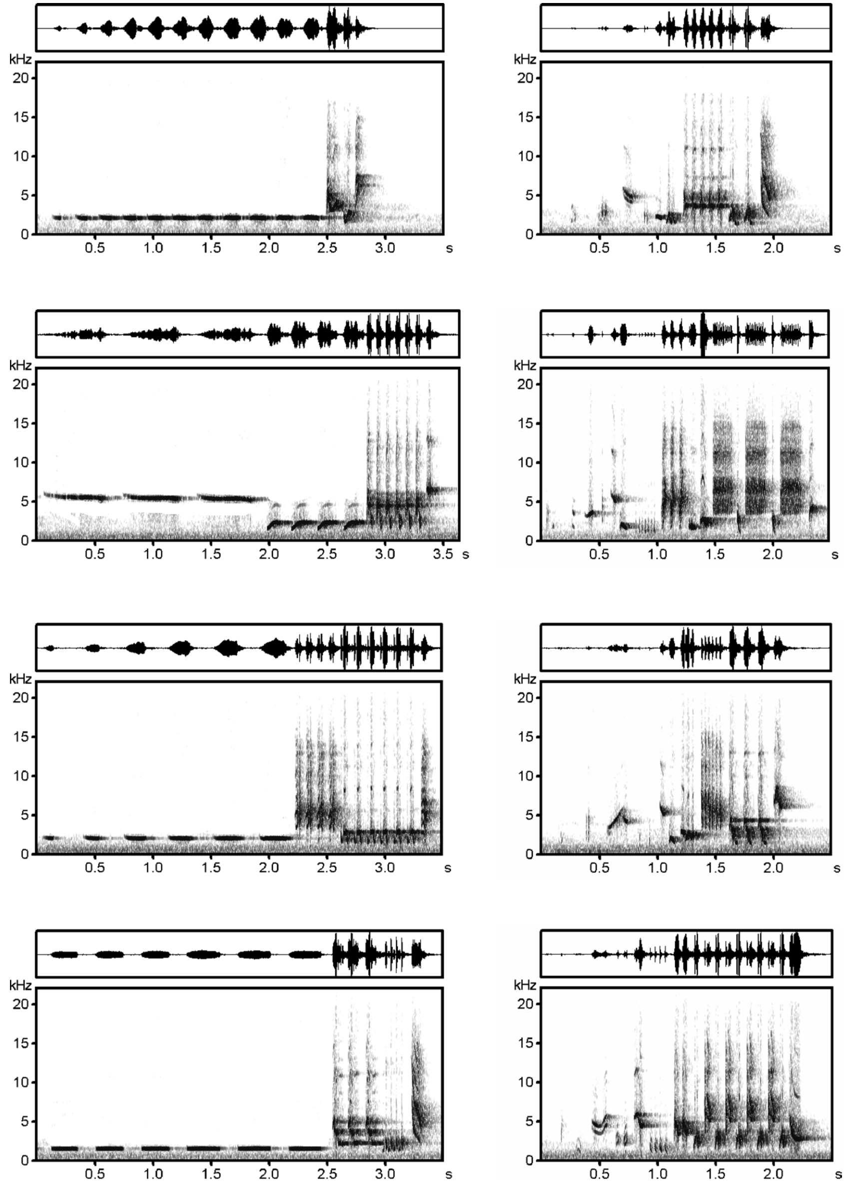

Figure 1. Oscillograms (above) and spectrograms (below) of songs of the two different categories. Left side: whistle songs, and right side: nonwhistle songs of male nightingales. Songs are sung with immediate variety.

The function of whistle songs is unclear but it is hypothesised that whistle songs might be important to attract females (Hultsch, 1980; Glutz von Blotzheim, 1988). As structurally simple whistles suffer less from spectral degradation than more complex song features do (Wiley & Richards, 1982; Slabbekoorn et al., 2002), whistle songs may be a particularly effective signal over longer distances to attract females migrating at night. Previous studies on nightingales have shown that playback of whistle songs and nonwhistle songs elicit different responses among males (Naguib et al., 2002; Kunc et al., in press b), indicating that male nightingales discriminate between songs of these two structurally different categories.

Here, we analyzed temporal properties of whistle songs and nonwhistle songs and the relationships between song categories and temporal song parameters in order to determine whether or not whistle songs differ from nonwhistle songs also in other than the phonological traits that are used to categorize them. Furthermore, we investigated how structural and temporal song parameters vary among males by calculating the coefficients of variation (CV) for different song traits, to obtain a better understanding how sexual selection may act on these traits.

Methods

Study site, study species, and general procedures

The study was carried out in April 2001 and 2002 at the Petite Camargue Alsacienne in France (Amrhein et al., 2002, 2004). We observed the first males singing after their arrival from migration on 3 April in 2001 and on 12 April in 2002. All males were unpaired when their songs were recorded.

Recording methods, sonographic analysis, and song classification

Nocturnal song recordings were made between 00:00 and 03:30 CEST, using a Sennheiser ME66/K6 directional microphone and either a Sony TC-D5M or a Sony WM-D6C tape recorder. We digitized recordings on a PC using Cool Edit 2000 (Syntrillium Cooperation, USA, sample frequency: 44.1 kHz, resolution: 16 bit). We analysed song characteristics with the software package Avisoft SASLab Pro 3.5 (R. Specht, Berlin; time resolution: 5.8 ms, FFT: 256). We randomly chose and analysed 10 minutes of nocturnal song of 34 different males. Whistle songs can clearly be identified on the basis of their syntactical and phonological structure (see Figure 1; Hultsch & Todt, 1996; Naguib et al., 2002). In the spectrographic analysis, we distinguished visually between the two song categories: whistle songs and nonwhistle songs.

We measured the following song parameters: (a) overall song rate (number of songs per minute), and (b) the percentage of whistle songs sung. For each song category we measured separately: (c) song length (length of a song in seconds), and (d) pause length (the interval between the end of one song and the beginning of the next song in seconds).

Analysis of song variability and statistical analysis

To compare variation of different song traits with different means we used the coefficient of variation (CV). The CV was calculated by dividing the standard deviation by the mean of the sample multiplied with 100 (Sokal & Rohlf, 1995). To test for differences between the CVs of song parameters we used the test statistic C (Dawkins & Dawkins, 1973). To test if pause length depended on the preceding song category or on song length, we used a single univariate general linear model, because it has the advantage that the effect of the covariate (song length) on the dependent variable (pause length) is removed from the unexplained variability by regression analysis. The final model tests the difference between factor level means, adjusted for the effect of the covariate (Quinn & Keough, 2002). To test how song output parameters (song length, pause length, and song rate) influenced each other, we used a multivariate general linear model, because these song output parameters were correlated with each other. Furthermore, to test for the effect of whistle songs on the song output parameters, the proportion of whistle songs was included as a covariate. All statistical tests were performed with SPSS 11.0. Results are given as mean ± SD and all reported tests are two-tailed.

Results

Variability of song characteristics among males

The coefficient of variation showed the highest variation in the percentage of whistle songs compared to the other song traits among males (Table 1). The

Table 1. Variability of song characteristics among males ($N = 34$).

Song parameter	Mean	SD	Range	CV (%)
Percentage of whistle songs	20.40	6.46	26.80	31.67
Song rate	8.98	1.47	5.76	16.37
Whistle song length	3.51	0.54	2.63	15.38
Nonwhistle song length	2.53	0.27	1.28	10.67
Song length	2.72	0.27	1.29	9.93

variability in song rate and whistle song length was approximately half of the variation of the percentage of whistle songs. Song length and nonwhistle song length had the lowest coefficient of variation of the measured song parameters. The coefficient of variation of the proportion of whistle songs was significantly higher than the second ranked coefficient of song rate ($C = 6.4$, $p < 0.05$).

Differences between whistle songs and nonwhistle songs

Whistle songs and nonwhistle songs differed significantly in all measured song parameters (Table 2). Nonwhistle songs occurred more often than whistle songs. Whistle songs were longer than nonwhistle songs, and pauses following whistle songs were longer than pauses following nonwhistle songs. The longer pauses following whistle songs could be explained in two ways: First, longer songs generally demand longer subsequent pauses, or second, specifically the whistle songs have longer subsequent pauses independent of their length. To test if pause length depended on the length of the preceding song or on the preceding song category, we ran a general linear model, which revealed that pause length depended on the preceding song category ($F_{1,65} = 4.88$, $p = 0.031$) but not on the length of the preceding song ($F_{1,65} = 1.16$, $p = 0.29$).

Relationship among song parameters

To asses how the percentage of whistle songs depended on other song parameters, we analysed how the percentage of whistle songs sung interacted with overall song length, overall pause length and song rate by using a multivariate general linear model. Males singing a higher percentage of whistle songs made longer pauses ($F_{1,32} = 11.83$, $p = 0.002$; Figure 2), and sang

Table 2. Differences between two different song categories in the nocturnal song of *Luscinia megarhynchos* (mean ± SD; for all tests: $N = 34$).

Song parameter	Whistle songs	Nonwhistle songs	t	p
Percentage	20.4 ± 6.5	79.6 ± 6.5	26.5	<0.001
Song length	3.5 ± 0.5	2.5 ± 0.3	−11.7	<0.001
Pause length	4.7 ± 1.6	4.0 ± 1.1	4.3	<0.001

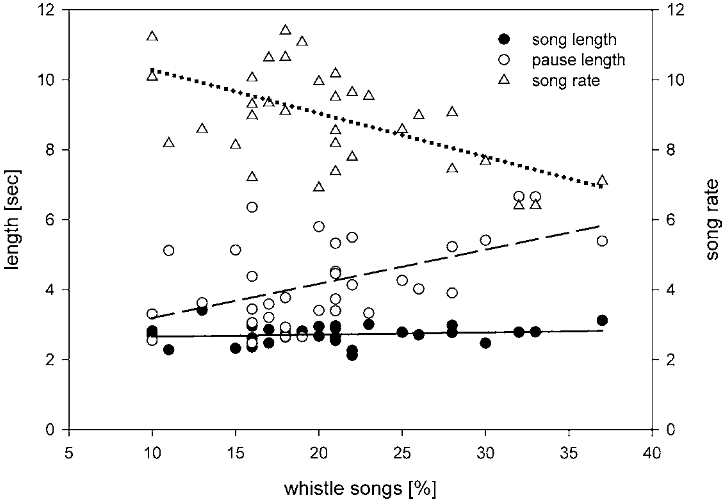

Figure 2. Relationships between the percentage of whistle songs and overall song length (straight line), overall pause length (dashed line) and song rate (dotted line).

with a lower song rate ($F_{1,32} = 12.96$, $p = 0.001$), but did not change the length of overall songs ($F_{1,32} = 0.73$, $p > 0.4$).

We did not find significant correlations between song rate and any measure of song length (all $r_P < 0.07$, all $p > 0.4$, Figure 3a), i.e., individuals did not significantly vary the length of songs when varying song rate. However, we found a strong negative correlation between song rate and all measures of pause length (all $r_P > -0.89$, all $p < 0.001$, Figure 3b), indicating that a nightingale's song rate depends mainly on the length of the pauses between the songs.

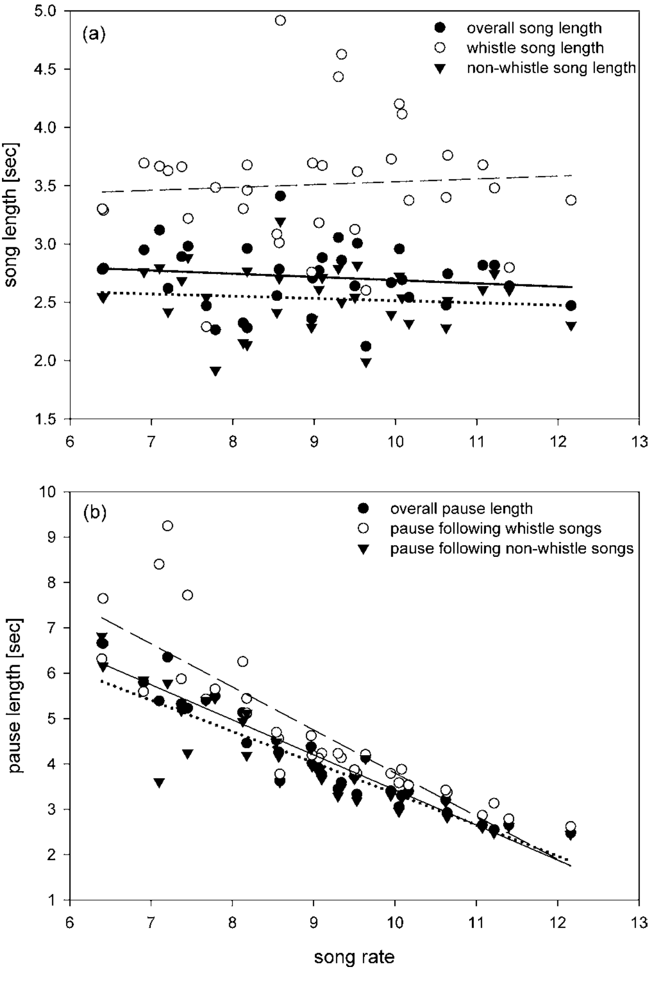

Figure 3. Correlations between (a) song rate and overall song length, whistle song length, and nonwhistle song length and (b) song rate and pause length, pauses following whistle songs and pauses following nonwhistle songs. Lines are for illustration only; straight line: (a) overall song or (b) pause length; dashed line: (a) whistle song length or (b) pauses following whistle songs, dotted line: (a) nonwhistle song length or (b) pauses following nonwhistle songs.

Discussion

Variability of song characteristics

The comparison of the coefficients of variation calculated for five song traits in the nocturnal song of the nightingale revealed that the among-male variability was significantly higher in the percentage of whistle songs than in the second ranked coefficient of variation of song rate. A high inter-individual variability in a trait could reflect that no strong selection acts on that trait as one may well argue that sexual selection should reduce variability rather than enlarge it. In any case, a trait with high inter-individual variability provides the opportunity for receivers to discriminate among males on a finer scale than it would be the case with traits that are less variable. Even though we cannot rule out the former possibility, it seems likely that whistle songs are under sexual selection as they appear to have a specific signal value in mal-male vocal interactions (Naguib et al., 2002) and are linked to male reproductive success (Kunc, 2004). Thus, the high variability may well be used to discriminate among males even though it remains unclear which factors maintain the high variability if directional selection acts on the amount of whistle songs.

In general, in bird species like the nightingale with a highly versatile song repertoire (Todt, 1970), selection may not act strongly on song output parameters such as song rate and song length like in species with smaller and less complex song repertoires (song rate: willow warbler, *Phylloscopus trochilus*, Radesäter et al., 1987; Arvidsson & Neegaard, 1991; pied flycatcher, *Ficedula hypoleuca*, Alatalo et al., 1990; European starling, *Sturnus vulgaris*, Eens et al., 1991; blackcap, *Sylvia atricapilla*, Hoi-Leitner et al., 1995; willow tit, *Parus montanus*, Welling et al., 1997; song length: great reed warbler, *Acrocephalus arundinaceus*, Catchpole, 1983; great tit, *Parus major*, Lambrechts & Dhondt, 1986, 1987; blue tit, *Parus caeruleus*, Kempenaers et al., 1997; white-throated sparrows, *Zonotrichia albicollis*, Wassermann & Cigliano, 1991; hoopoe, *Upupa epops*, Martin-Vivaldi et al., 2002). In species like the nightingale, sexual selection might rather act on structural song traits like whistle songs, which may have a specific signal value, because males respond differently to whistle songs and nonwhistle songs during playback experiments (Naguib et al., 2002; Kunc et al., in press b).

Differences between whistle songs and nonwhistle songs

Whistle songs and nonwhistle songs differed significantly in song length, pause length, and in the percentage of their occurrence. The difference in song length between whistle songs and nonwhistle songs can be explained by the fact that whistle songs contain a long series of mostly unmodulated whistles, whereas nonwhistle songs consist of a series of shorter elements (cf. Todt, 1970). Pauses following whistle songs were significantly longer than pauses following nonwhistle songs. This may arise because after a longer song an individual might need to make a longer pause. Neuromuscular fatigue has been suggested as a factor limiting song length in song birds that sing with eventual variety (Lambrechts & Dhondt, 1988; but see Weary & Lemon, 1988; Gaunt et al., 1996). However, this argument does not apply well to birds like the nightingale that sing with immediate variety. Furthermore, pause length was not influenced by length of the preceding song but by the category of the preceding song. This and the less frequent occurrence of whistle songs compared to nonwhistle songs may be taken to suggest that whistle songs underlie some constraint, but it remains uncertain what kind of constraint this might be. Possibly, one constraint could be that whistle songs are energetically more costly to produce. However, the overall metabolic costs of bird song seem to be low (Oberweger & Goller, 2001; Franz & Goller, 2003; Ward et al., 2003, 2004), so that it seems unlikely that a particular song category is energetically more costly to produce than another one, at least not to an extent of evolutionary significance. Another constraint could be that pure tone signals like whistles are more difficult to generate. Pure tones like unmodulated whistles in nightingales are a common and widespread phenomenon in birds (e.g., in white-crowned sparrows, *Zonotrichia* spp., Lampe & Baker, 1994; European starling, *Sturnus vulgaris*, Eens, 1997). However, the mechanism how unmodulated tones such as whistles are produced is still debated (e.g., Nowicki, 1987; Ballintijn & ten Cate, 1998; Gaunt & Nowicki, 1998; Gardner et al., 2001; Beckers et al., 2003; Podos & Nowicki, 2004). Because nightingales made longer pauses after whistle songs, it could be that the production and control of such pure tone song is more demanding in terms of neuromuscular exhaustion. Alternatively, the longer pauses after whistle songs may not be linked to such possible proximate constraints but function to attract attention (Richards, 1980; Todt & Naguib, 2000). Longer pauses after whistle songs may then emphasize the signal value of whistle songs as the time to process them by receivers before the next song is sung is expanded. Moreover, as whistle songs can elicit very specific matching responses, i.e., replies with whistle songs, males also may expand the silent intervals after whistle songs in order to be able to listen to such possible replies without being overlapped.

Thus, the functional unit in communication may not be just the song but the song with its succeeding pause. Any possible constraints on producing whistle songs, either proximate or ultimate, cannot be detected by a correlative study as the one presented here. We can only speculate about the mechanism responsible for the high inter-male variation in the proportion of whistle songs. If there are no production constraints, then factors such as experience or the conditions during the early period of song learning should be included in further studies.

Relationships between song parameters

To increase song rate, birds can either shorten the length of single songs or reduce pauses between songs. Here we found that song rate correlated negatively with all measures of pause length (overall pause length, pauses following whistle songs, pauses following nonwhistle songs), but song rate did not correlate with song length. The negative correlation between song rate and pause length indicates that nightingales reduce the pauses between songs to increase song rate, which is the most common pattern in song birds (Catchpole & Slater, 1995). The percentage of whistle songs was significantly negatively correlated with song rate and significantly positively correlated with pause length. But the percentage of whistle songs did not correlate with song length. It seems not only that pause length depends on the preceding song category, but also that there is a constraint on singing more whistle songs. This again may suggest that whistle songs underlie either some proximate constraint or that whistles songs and their succeeding pause have a specific signal value, as discussed above.

To summarize, the significantly higher coefficient of variation for the percentage of whistle songs compared to the other song traits may be taken as support for the idea that whistle songs are important in communication as they allow to distinguish among males on a finer scale. The negative correlation between song rate and a complexity parameter, i.e., the percentage of whistle songs, demonstrates that further studies should include analyses of relationships between song output and complexity parameters. Such studies may enable a deeper understanding of the constraints acting on song parameters and should allow identifying those traits that are most likely under sexual selection.

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References

Alatalo, R.V., Glynn, C. & Lundberg, A. (1990). Singing rate and female attraction in the pied flycatcher: an experiment. — Anim. Behav. 39: 601-603.

Amrhein, V., Korner, P. & Naguib, M. (2002). Nocturnal and diurnal singing activity in the nightingale: correlations with mating status and breeding cycle. — Anim. Behav. 64: 939-944.

Amrhein, V., Kunc, H.P. & Naguib, M. (2004). Seasonal patterns of singing activity vary with time of day in the nightingale (*Luscinia megarhynchos*). — Auk 121: 110-117.

Arvidsson, B.L. & Neegaard, R. (1991). Mate choice in the willow warbler – a field experiment. — Behav. Ecol. Sociobiol. 29: 225-229.

Ballintijn, M.R. & ten Cate, C. (1998). Sound production in the collared dove: a test of the 'whistle' hypothesis. — J. Exp. Biol. 201: 1637-1649.

Becker, P.H. (1982). The coding of species-specific characteristics in bird sounds. — In: Acoustic communication in birds (Kroodsma, D.E. & Miller, E.H., eds). Academic Press, New York.

Beckers, G.J.L., Suthers, R.A. & ten Cate, C. (2003). Pure-tone birdsong by resonance filtering of harmonic overtones. — PNAS 100: 7372-7376.

Catchpole, C.K. (1983). Variation in the song of the great reed warbler *Acrocephalus arundinaceus* in relation to mate attraction and territorial defence. — Anim. Behav. 31: 1217-1225.

Catchpole, C.K., Leisler, B. & Dittami, J. (1986). Sexual differences in the responses of captive great reed warbles (*Acrocephalus arundinaceus*) to variation in song structure and repertoire size. — Ethology 73: 69-77.

Catchpole, C.K. & Slater, P.J.B. (1995). Bird song: biological themes and variations. — Press Syndicate University of Cambridge, Cambridge.

Dawkins, R. & Dawkins, M.S. (1973). Decisions and the uncertainty of behaviour. — Behaviour 45: 83-103.

Eens, M. (1997). Understanding the complex song of the European starling: an integrated ethological approach. — Adv. Stud. Behav. 26: 355-434.

Eens, M., Pinxten, R. & Verheyen, R.F. (1991). Male song as a cue for mate choice in the European starling. — Behaviour 116: 210-238.

Ficken, M.S. & Ficken, R.W. (1970). Responses of four warbler species to playback of their two song types. — Auk 87: 296-304.

Franz, M. & Goller, F. (2003). Respiratory patterns and oxygen consumption in singing zebra finches. — J. Exp. Biol. 206: 967-978.

Garamszegi, L.Z. & Møller, A.P. (2004). Extrapair paternity and the evolution of bird song. — Behav. Ecol. 15: 508-519.

Gardner, T., Cecchi, G., Magnasco, M., Laje, R. & Mindlin, G.B. (2001). Simple motor gestures for birdsongs. — Phys. Rev. Letters 8720.

Gaunt, A.S., Bucher, T.L., Gaunt, S.L.L. & Baptista, L.F. (1996). Is singing costly? — Auk 113: 718-721.

Gaunt, A.S. & Nowicki, S. (1998). Sound production in birds: acoustics and physiology revisited. — In: Animal acoustic communication (Hopp, S.L., Owen, M.J. & Evans, C.S., eds). Springer, Berlin-Heidelberg.

Glutz von Blotzheim, U.N. (1988). Handbuch der Vögel Mitteleuropas. Band 11/1. — AULA-Verlag, Wiesbaden.

Hoi-Leitner, M., Nechtelberger, H. & Hoi, H. (1995). Song rate as a signal for nest site quality in blackcaps (*Sylvia atricapilla*). — Behav. Ecol. Sociobiol. 37: 399-405.

Horn, A.G. & Falls, J.B. (1996). Categorization and the design of signals: the case of song repertoires. — In: Ecology and evolution of acoustic communication in birds (Kroodsma, D.E. & Miller, E.H., eds). Cornell University Press, Ithaca, p. 121-134.

Hultsch, H. (1980). Beziehungen zwischen Struktur, zeitlicher Variabilität und sozialem Einsatz des Gesangs der Nachtigall (*Luscinia megarhynchos*). — PhD thesis, Freie Universität Berlin.

Hultsch, H. & Todt, D. (1981). Repertoire sharing and song-post distance in nightingales (*Luscinia megarhynchos*). — Behav. Ecol. Sociobiol. 8: 183-188.

Hultsch, H. & Todt, D. (1996). Rules of parameter variation in homotype series of birdsong can indicate a ‘sollwert’ significance. — Behav. Proc. 38: 175-182.

Järvi, T., Radesäter, T. & Jakobson, S. (1980). The song of the willow warbler *Phylloscopus trochilus* with special reference to singing behaviour in agonistic situations. — Orn. Scan. 11: 236-242.

Kempenaers, B., Verheyen, G.R. & Dhondt, A.A. (1997). Extrapair paternity in the blue tit (*Parus caeruleus*): female choice, male characteristics, and offspring quality. — Behav. Ecol. 8: 481-192.

Kipper, S., Mundry, R., Hultsch, H. & Todt, D. (2004). Long-term persistence of song performance rules in nightingales (*Luscinia megarhynchos*): a longitudinal field study on repertoire size and composition. — Behaviour 141: 371-390.

Kunc, H.P. (2004). Song and sexual selection in the nightingale (*Luscinia megarhynchos*). — PhD thesis, University of Bielefeld.

Kunc, H.P., Amrhein, V. & Naguib, M. (in press a). Seasonal variation of dawn song characteristics in the common nightingale. — Anim. Behav.

Kunc, H.P., Amrhein, V. & Naguib, M. (in press b). Vocal interactions in common nightingales: more aggressive males have higher pairing success. — Anim. Behav.

Kroodsma, D.E. (1982). Song repertoires: problems in their definition and use. — In: Acoustic communication in birds (Kroodsma, D.E. & Miller, E.H., eds). Academic Press, New York, p. 125-146.

Kroodsma, D.E. (2004). The diversity and plasticity of birdsong. — In: Nature’s music (Marler, P. & Slabbekoorn, H., eds). Elsevier Academic Press.

Lambrechts, M.M. (1996). Organization of birdsong and constraints on performance. — In: Ecology and evolution of acoustic communication in birds (Kroodsma, D.E. & Miller, E.H., eds). Cornell University Press, London.

Lambrechts, M.M. & Dhondt, A.A. (1986). Male quality, reproduction, and survival in the great tit (*Parus major*). — Behav. Ecol. Sociobiol. 19: 57-63.

Lambrechts, M.M. & Dhondt, A.A. (1987). Differences in singing performance between male great tits. — Ardea 75: 43-52.

Lambrechts, M.M. & Dhondt, A.A. (1988). The anti-exhaustion hypothesis: a new hypothesis to explain song performance and song switching in the great tit. — Anim. Behav. 36: 327-334.

Lampe, H.M. & Baker, M. (1994). Behavioural response to song playback by male and female white-crowned sparrows of two subspecies. — Bioacoustics 5: 171-185.

Lampe, H.M. & Espmark, Y.O. (1987). Singing activity and song pattern of the redwing *Turdus iliacus* during the breeding season. — Orn. Scan. 18: 179-185.

Martin-Vivaldi, M., Martinez, J.G., Palomino, J.J. & Soler, M. (2002). Extrapair paternity in the hoopoe *Upupa epops*: an exploration of the influence of interactions between breeding pairs, non-pair males and strophe length. — Ibis 144: 236-247.

Naguib, M., Hultsch, H., Mundry, R. & Todt, D. (2002). Responses to playback of whistle songs and normal songs in male nightingales: effects of song category, whistle pitch, and distance. — Behav. Ecol. Sociobiol. 52: 216-223.

Nelson, D.A. & Croner, L.J. (1991). Song categories and their functions in the field sparrow (*Spizella pusilla*). — Auk 108: 42-52.

Nowicki, S. (1987). Vocal tract resonances in oscine bird sound production: evidence from birdsongs in a helium atmosphere. — Nature 325: 53-55.

Oberweger, K. & Goller, F. (2001). The metabolic cost of birdsong production. — J. Exp. Biol. 204: 3379-3388.

Podos, J. & Nowicki, S. (2004). Performance limits on bird song. — In: Nature's music (Marler, P. & Slabbekoorn, H., eds). Elsevier Academic Press.

Quinn, G.P. & Keough, M.J. (2002). Experimental design and data analysis for biologists. — Cambridge University Press, Cambridge.

Radesäter, T., Jakobson, S., Andbjer, N., Bylin, A. & Nyström, K. (1987). Song rate and pair formation in the willow warbler, *Phylloscopus trochilus*. — Anim. Behav. 35: 1645-1651.

Richards, D.R. (1980). Alerting and message components in songs of rufous-sided towhees. — Behaviour 76: 223-249.

Schroeder, D.J. & Wiley, R.H. (1983). Communication with repertoires of song themes in tufted titmice. — Anim. Behav. 31: 1128-1138.

Searcy, W.A. & Nowicki, S. (2000). Male-male competition and female choice in the evolution of vocal signaling. — In: Animals signals: Signal design in animal communication (Espmark, Y., Amundsen, T. & Rosenqvist, G., eds). Tapir Academic Press, Trondheim.

Simpson, B. (1985). Effects of location in territory and distance from neighbours on the use of song repertoires by Carolina wrens. — Anim. Behav. 33: 793-804.

Slabbekoorn, H., Ellers, J. & Smith, T.B. (2002). Birdsong and sound transmission: The benefits of reverberations. — Condor 104: 564-573.

Sokal, R.R. & Rohlf, F.J. (1995). Biometry. The principles and practice of statistics in biological research. — Freemann, New York.

Spector, D.A. (1992). Wood-warbler song systems a review of Paruline singing behaviors. — In: Current ornithology (Power, D.M., ed.). Plenum Press, New York, p. 199-238.

Todt, D. (1970). Zur Ordnung im Gesang der Nachtigall (*Luscinia megarhynchos* L.). — Verh. Deutsch. Zool. Ges. 64: 249-252.

Todt, D. (1971). Äquivalente und konvalente gesangliche Reaktionen einer extrem regelmäßig singenden Nachtigall (*Luscinia megarhynchos*). — Z. vergl. Physiol. 71: 262-285.

Todt, D. & Naguib, M. (2000). Vocal interactions in birds: the use of song as a model in communication. — Adv. Stud. Behav. 29: 247-296.

Ward, S., Lampe, H.M. & Slater, P.J.B. (2004). Singing is not energetically demanding for pied flycatchers, *Ficedula hypoleuca*. — Behav. Ecol. 15: 477-484.

Ward, S., Speakman, J.R. & Slater, P.J.B. (2003). The energy cost of song in the canary, *Serinus canaria*. — Anim. Behav. 66: 893-902.

Wassermann, F.E. & Cigliano, J.A. (1991). Song output and stimulation of the female in white-throated sparrows. — Behav. Ecol. Sociobiol. 29: 55-59.

Weary, D.M. & Lemon, R.E. (1988). Evidence against the continuity-versatility relationship in bird song. — Anim. Behav. 36: 1379-1383.

Welling, P.P., Rytkönen, S.O., Koivula, K.T. & Orell, M.I. (1997). Song rate correlates with paternal care and survival in willow tits: advertisement of male quality? — Behaviour 134: 891-904.

Wiley, R.H. & Richards, D.G. (1982). Adaptations for acoustic communication in birds: sound transmission and signal detection. — In: Acoustic communication in birds (Kroodsma, D.E. & Miller, E.H., eds). Academic Press, New York, p. 131-181.