

Long-term effects of early parasite exposure on song duration and singing strategy in great tits

Linda L. Bischoff,^a Barbara Tschirren,^b and Heinz Richner^a

^aEvolutionary Ecology Laboratory, Institute of Ecology and Evolution, University of Bern, Baltzerstrasse 6, 3012 Bern, Switzerland and ^bDepartment of Animal Ecology, Lund University, Sölvegatan 37, 22362 Lund, Sweden

Song is a sexually selected trait in many bird species and has been suggested to function as a signal of a male's health and parasite resistance. Here we present an experimental field study on the long-term effects of parasite exposure early in life on adult bird song. We exposed nestling great tits (*Parus major*) to ectoparasitic hen fleas (*Ceratophyllus gallinae*) and on their recruitment into the local breeding population assessed the response to a playback of a challenging male in their breeding territory. We show, to our knowledge for the first time in a wild bird population, that parasite exposure early in life affects bird song: song duration of males that were exposed to parasites early in life was reduced by 32% compared with males that grew up in a flea-free environment. Early parasite exposure also significantly reduced the degree of song overlap with the playback, which has been shown to correlate with social status. There was no effect of early parasite exposure on the number of different song types sung or on the latency until the males started the vocal response to the playback. These results suggest that mates or rivals can use song duration and song overlap as proxies for an individual's exposure to parasites early in life. It thereby highlights both the importance of parasites in maintaining honesty of sexually selected traits and the costs of parasitism in terms of reduced attractiveness and competitiveness. *Key words:* bird song, developmental stress hypothesis, ectoparasites, honest signaling, *Parus major*, sexual selection. [*Behav Ecol* 20:265–270 (2009)]

The song of male birds often has a dual signaling function in both female attraction and repulsion of competing males (Darwin 1871; Catchpole 1982; Searcy and Andersson 1986; Catchpole and Slater 1995). Singing is energetically costly for males (Brackenbury 1979; Lambrechts and Dhondt 1988; Vehrencamp et al. 1989; Grafen 1990; Eberhardt 1994), implying that higher quality males can afford to display more costly song types, song structures, or song rates. Numerous studies have shown that a male's present condition influences song rate and song repertoire (e.g., Buchanan et al. 1999; Berg et al. 2005). More recently, it has been suggested that a male's song might also be affected by environmental conditions experienced early in life. Indeed, several studies (Nowicki et al. 2002; Buchanan et al. 2003) have shown that nutritional stress during early development can affect song development (i.e., the nutritional stress hypothesis, Nowicki et al. 1998). This hypothesis has been expanded to other stress factors, for example, early parasite exposure, that might have long-lasting effects on song characteristics in adulthood (i.e., the developmental stress hypothesis, Spencer et al. 2003; Buchanan et al. 2004; Nowicki and Searcy 2004; but see Gil et al. 2006).

Song has thereby the potential to function as a multiple signal of both a male's past growth and development (Buchanan et al. 2003; Spencer et al. 2003; Spencer, Buchanan, et al. 2005) and/or of his current condition (Buchanan et al. 1999). By assessing song rates and song structures during mate choice, females might thus gain honest information not only about a male's current status but potentially also on past environmental conditions experienced by the male early in life (Catchpole 1996; Buchanan 2000; Buchanan and Catchpole 2000; Doutrelant et al. 2000).

Honest information about male quality is relevant not only for female mate choice but also for male–male competition. Males often eavesdrop on the neighbor's song to get honest information on the motivation, condition, or health status of potential contrahents (Peake et al. 2005). Two important aspects of intrasexual vocal signaling are song matching, where an individual repeats the song pattern of the competitor (Krebs et al. 1981; McGregor et al. 1992; Nielsen and Vehrencamp 1995; Beecher et al. 2000; Vehrencamp 2001), and song overlapping, where an individual, depending on its relative dominance status, times its song relative to the opponent's song with various degrees of overlap (Dabelsteen et al. 1997).

To date, studies testing the effects of early environmental conditions on song development have been performed mainly under laboratory or aviary conditions (Buchanan et al. 2003; Spencer et al. 2004), whereas in the wild, evidence for effects of stress experienced early in life on song development remains scarce. In particular, the effect of parasitism experienced early in life on the development of song and adult singing performance has, to our knowledge, not been tested in wild-living birds so far. Here we investigated if early developmental stress, resulting from exposure to a common ectoparasite during the nestling period, can affect song traits and song overlap of males under natural conditions. We experimentally infested nestling great tits (*Parus major*) after hatching with hen fleas (*Ceratophyllus gallinae*) and recorded their song after recruitment into the local breeding population the following years. Hen fleas are common ectoparasites of great tits. They live in the nest material of their hosts and suck blood from the nestlings (Tripet and Richner 1997). If early developmental conditions have long-term consequences for adult song, we predict a shorter duration of singing and/or a smaller number of different song types sung within the recording period in males that were exposed to hen fleas early in life. Furthermore, we predict that males raised in a parasite-free nest are more competitive and thus show a higher degree of song overlap with a competing male.

Address correspondence to L.L. Bischoff. E-mail: linda.bischoff@esh.unibe.ch.

Received 5 September 2008; revised 23 December 2008; accepted 6 January 2009.

MATERIALS AND METHODS

Manipulation of early parasite exposure

The study was performed in a population of great tits breeding in nest-boxes in a forest close to Bern, Switzerland ("Forst," 46°54'N, 7°17'E/46°57'N, 7°21'E). During the breeding seasons of 1998–2004, we manipulated the load of hen fleas in the nests. First, we microwaved the nesting material of all nests 2 days after hatching of the nestlings. This procedure kills all nest-based ectoparasites naturally present in the nests (Richner et al. 1993). Thereafter, half of the nests were experimentally infested with 40 female and 20 male fleas originating from old nests collected within the same forest before the breeding season, whereas the other nests remained flea free. Nests were randomly assigned to 1 of the 2 treatment groups. All nestlings were ringed with individually numbered aluminum rings when 9 days old. Fifteen days after hatching, toward the end of the nestling stage, the nestlings' body mass and metatarsus length were measured. These manipulations were part of a longer term study on host adaptations to ectoparasitism.

Twenty-two males (13 from experimentally infested nests and 9 from flea-free nests) were recaptured as breeders in 2005 in the local population. All recruits originated from different broods (i.e., they were not siblings). One of these males was born and manipulated in 1998 (no fleas), 3 males were born and manipulated in 2002 (2 with fleas and 1 without fleas), and the rest of the males were born and manipulated in 2004 (11 with fleas and 7 without fleas).

Recording and analysis of song

To create the song stimuli, we recorded the songs of 5 great tit males in another population ("Birchiwald," Bremgarten b. Bern, 46°58'N, 7°25'E, Switzerland, distance to study area ~10 km) during 45 min each. The songs were recorded from a distance of approximately 10–15 m with a condenser shotgun microphone (Georg Neumann, Berlin, Germany, KMR 82 i) via a preamplifier (SHURE, Niles, IL, FP23) to the program Sound Studio 2.1 (Kwok 2003) on a laptop. We used these digitized songs to create 5 different song stimuli of 20 min duration each in the programs Sound Studio 2.1 (Kwok 2003) and Raven 1.2.1 (Charif et al. 2004) (see details below).

The song of great tits has a typical structure (Figure 1): a combination of 1–5 notes (Krebs 1976; McGregor and Krebs 1982b) is called a phrase (about 0.2–0.5 s; Figure 1). Phrases are usually repeated and form a strophe (McGregor and Krebs 1982b; Lambrechts and Dhondt 1986). Strophes are typically separated by an interstrophe pause before they are repeated again. Repeated strophes based on the same kind of phrase are called a song type (sometimes also called song unit, Lambrechts and Dhondt 1988). A male great tit has a song repertoire of 1–9 distinct song types (McGregor et al. 1981; McGregor and Krebs 1982a; Otter et al. 1999). Females are attracted to males with larger song repertoires (Baker et al. 1986). Generally, great tits sing strophes of the same song type for several minutes before switching to another song type (Krebs 1976).

Some song types are more common than others (Bischoff LL, personal observations). We used the most common song type (used by 57% of males in the population) (Figure 1) to create the different song stimuli. Single phrases of this song type were extracted and multiplied 6 times using Sound Studio 2.1 (Kwok 2003) to create a stimulus strophe of 4 s followed by 3 s of silence (i.e., the interstrophe pause, Figure 1). The duration of strophe and pause was based on a preliminary study and represents an average song unit in the study population (Bischoff LL, unpublished data). The song unit (i.e., the strophe and pause) was then repeated to create 1-min stimulus sequences. Each stimulus contained the song of 1 male only. This approach allowed us to standardize the stimulus structure while still covering a range of natural variation in song between different males.

We recorded the males' response to a playback during the breeding season 2005. We recorded the songs of all males with an aluminum ring but analyzed only recordings of recruits from manipulated broods for this study. All recordings were performed between 6 AM and 1 PM on the day the clutch contained the fourth egg. We played a noninteracting 20-min song stimulus in the male's breeding territory using an iPod mini with the full uncompressed WAVE/AIFF format setting and a loudspeaker (Yamaha, Rellingen, Germany, AA5), which was placed 1 m away from the nest-box on the ground. The amplitude of the song stimulus was standardized to 83 ± 2 dB measured 1 m in front of the loudspeaker using a sound pressure level meter (Voltcraft Plus, SL-300).

For the song recordings of the target males, we first played a 5-min song stimulus sequence (as described above) in each male's territory, followed by 30 s of silence. Then, we played 6 times a 2-min song stimulus followed by a 30 s of silence to make up for a total of 20 min of playback in each male's territory. Thus, each target male was exposed to 1 song stimulus selected at random from the 5 available stimuli (systematic randomization to assure that all stimuli were used equally often). All stimuli were played to males originating from both parasite-infested and parasite-free nests, respectively (stimulus 1: without fleas $n = 3$, with fleas $n = 2$; stimulus 2: without fleas $n = 1$, with fleas $n = 3$; stimulus 3: without fleas $n = 2$, with fleas $n = 2$; stimulus 4: without fleas $n = 1$, with fleas $n = 3$; and stimulus 5: without fleas $n = 2$, with fleas $n = 3$), and stimulus number (1–5) was included as a random effect in the statistical analyses to control for variation in the males' response due to variation among stimuli.

The song of the focus males was recorded during the entire 20-min trial period using a condenser shotgun microphone (Georg Neumann, KMR 82 i) via a preamplifier (SHURE, FP23) to the program Sound Studio 2.1 (Kwok 2003) on a laptop. The spectrograms were analyzed blindly with respect to the parasite treatment of the males using the program Raven 1.2.1 (Charif et al. 2004). We measured the summed duration of all song units (i.e., the combined duration of strophe plus interstrophe pause, see Figure 1 and definition above) during the 20-min recording (thereafter called song duration), the number of different song types sung within these 20 min, the summed duration of all strophe lengths during the 20 min

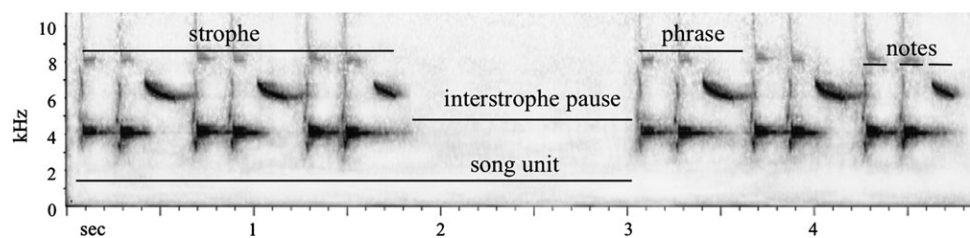


Figure 1
Spectrogram of a typical great tit song.

(thereafter called strophe length), the summed duration of all interstrophe pauses during the 20 min (thereafter called interstrophe pause length), and the time until the focus male responded to the playback (thereafter called latency). Latency is likely influenced by the location or distance of the male from the nest-box at the start of the playback (e.g., males that are closer to the nest-box respond more quickly). We also counted the number of times a target male overlapped his song with the stimulus (song overlap). Only cases where the target bird responded after the stimulus strophe (for definition of song strophe, see Figure 1) had started were counted as song overlap, whereas all cases where the target male had started before the stimulus strophe were ignored. Percentage of song overlap was then calculated as the number of overlapping strophes/number of total strophes \times 100.

Clutch size and breeder morphology

Clutch size was recorded at the start of incubation, and brood size was recorded 15 days after hatching. All breeding parents were captured 12 days after hatching of their brood using a door trap inside the nest-box, and their metatarsus length and body mass were measured. Their body condition was calculated as the residuals of a regression of body mass on tarsus length.

Statistical analyses

We used general linear mixed models to analyze the effect of early flea exposure on the song duration, the number of different song types sung, the latency until the males started their vocal response to the playback, and the percentage of song overlap. Song stimulus (1–5) was included as a random factor in all statistical analyses to control for differences in a male's vocal response due to variation among playback stimuli. Residuals of the models were tested for normality using Shapiro–Wilk tests and homoscedasticity using Bartlett tests to ensure that the assumptions for parametric testing were fulfilled. All tests were 2-tailed with a significance level of 0.05. Means \pm 1 standard error are presented in the results and the figures. Statistical analyses were performed in the program JMP IN 5.1 (Sall and Lehmann 1996).

RESULTS

Effects of experimental flea exposure on song

Males raised in a parasite-infested nest responded vocally for a significantly shorter period (364 ± 55 s) during the playback

trials than males brought up in a parasite-free nest (536 ± 39 s; $F_{1,16} = 5.396$, $P = 0.034$). This longer song duration of birds raised in a parasite-free nest was due to a tendency for longer strophe lengths ($F_{1,16} = 4.179$, $P = 0.057$) as well as longer interstrophe pauses ($F_{1,16} = 8.595$, $P = 0.009$). Males raised in a parasite-free nest also overlapped their song significantly more with the playback ($62.9 \pm 10.3\%$) than males from an infested nest ($48.3 \pm 10.7\%$; $F_{1,16} = 10.209$, $P = 0.006$). This effect became even more significant ($F_{1,15} = 21.972$, $P < 0.001$) when including song duration ($F_{1,15} = 8.634$, $P = 0.010$) as a covariate into the analysis of song overlap, showing that early flea exposure influenced song overlap and song duration independently (Figure 2).

Early flea exposure did not significantly influence the number of different song types sung during the playback trials (with fleas: 3.3 ± 0.6 , without fleas: 3.0 ± 0.4 ; $F_{1,16} = 0.171$, $P = 0.684$) or the latency until the males started their vocal response to the playback (with fleas: 170.1 ± 63.9 s, without fleas: 148.2 ± 98.3 s; $F_{1,16} = 0.038$, $P = 0.847$).

Correlates of song

Song duration during the playback trials was not significantly influenced by a male's body condition as an adult ($F_{1,16} = 0.137$, $P = 0.716$) or as a nestling ($F_{1,16} = 0.004$, $P = 0.948$), and it was independent of male age ($F_{1,16} = 0.003$, $P = 0.954$) or the date ($F_{1,16} = 0.408$, $P = 0.532$) or time of day of song recording ($F_{1,16} = 0.475$, $P = 0.501$).

Similarly, song overlap was not significantly influenced by a male's nestling body condition ($F_{1,16} = 0.094$, $P = 0.763$), male age ($F_{1,16} = 0.848$, $P = 0.371$), or the time of day of song recording ($F_{1,16} = 0.147$, $P = 0.706$). We found a tendency for males in better adult body condition to overlap their song more with the playback ($F_{1,16} = 3.846$, $P = 0.068$) and also a decrease of song overlap with the ongoing breeding season ($F_{1,16} = 4.275$, $P = 0.055$). However, the effect of flea treatment on song overlap remained significant ($F_{1,14} = 8.274$, $P = 0.012$) when including adult condition and date of song recording as covariates into the statistical model.

Females laid larger clutches when mated to a male, which sang for a longer period in response to the playback ($F_{1,16} = 5.138$, $P = 0.038$; Figure 3). This was due to a positive correlation between both clutch size and strophe length ($F_{1,16} = 6.22$, $P = 0.022$) as well as clutch size and interstrophe pause length ($F_{1,16} = 7.23$, $P = 0.014$). No other aspect of song was significantly correlated with clutch size (all $P > 0.160$) or male adult condition ($P = 0.343$). No significant

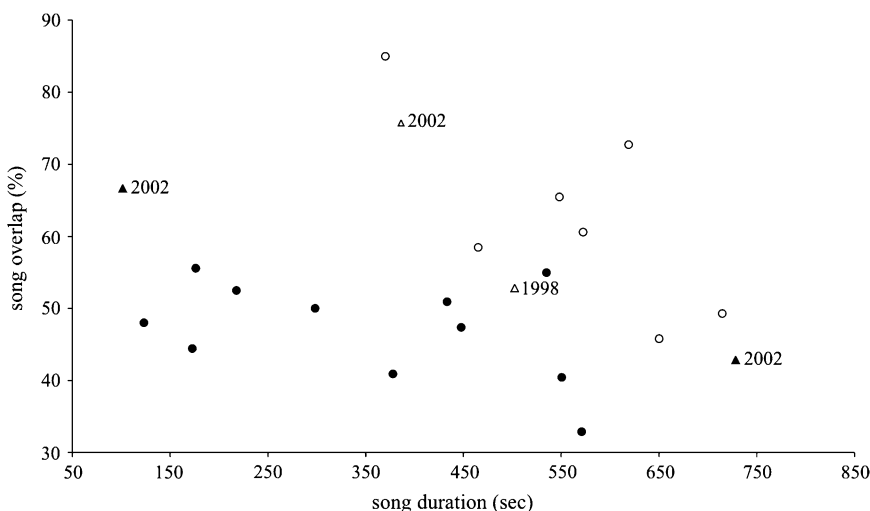


Figure 2

Relationship between song duration and song overlap of adult males raised in a flea-infested ($n = 13$; black) or a parasite-free nest ($n = 9$; white). The triangles indicate old males (year of birth shown) and the points indicate 1-year-old males (born in 2004). Song overlap (percentage of number of strophes overlapping with playback) and song duration were recorded during a 20-min period in response to a playback.

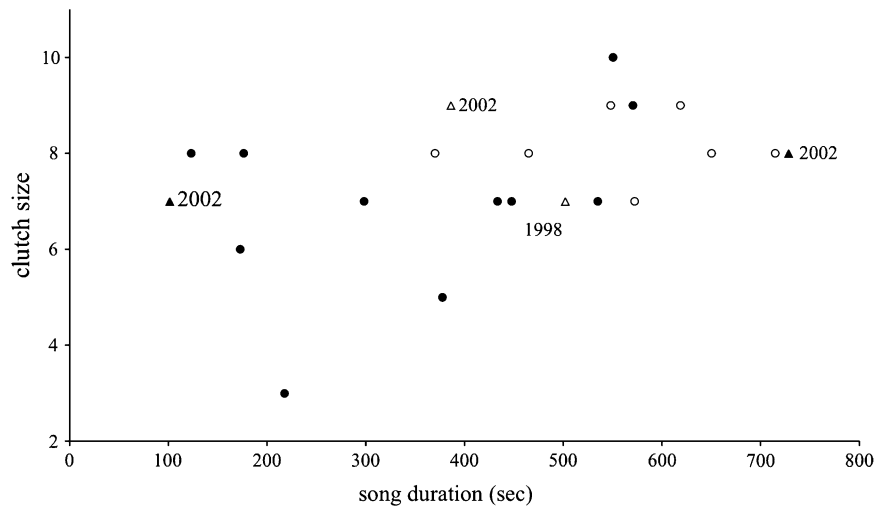


Figure 3

Relationship between song duration and clutch size. Black signs indicate males infested with fleas early in life ($n = 13$) and white signs represent uninfested males ($n = 9$). The triangles indicate old males (year of birth shown) and the points indicate 1-year-old males (born in 2004). Song duration was recorded during a 20-min period in response to a playback.

relationship between song duration and brood size 15 days after hatching was observed ($F_{1,16} = 0.60$, $P = 0.450$). There was no significant correlation between female and male condition ($F_{1,19} = 0.387$, $P = 0.541$), indicating that there was no assortative mating for body condition.

DISCUSSION

Several studies have shown that the brain structures associated with song learning are costly to produce and thus vulnerable to stress (e.g., Catchpole 1996; Nowicki et al. 1998; but see Gil et al. 2006). In swamp sparrows (*Melospiza georgina*), for example, nutritional limitation during growth had a negative effect on the development of the song nuclei in the brain (Nowicki et al. 2002). Similarly, nestling development was a predictor of adult song repertoire size in great reed warblers (Nowicki et al. 2000). Furthermore, male European starlings (*Sturnus vulgaris*) that experienced an unpredictable food supply early in life produced a smaller repertoire of song phrases than males with a constant food supply (Spencer et al. 2004).

Beside these well-documented effects of nutritional stress on song development, a recent study by Spencer, Buchanan, et al. (2005) demonstrated that an infection with blood parasites early in life can similarly affect song development. Captive male canaries (*Serinus canaria*) that were infected with malaria parasites (*Plasmodium relictum*) during development produced simpler songs (number of different syllables) as adults and had a significantly smaller volume of the nucleus hyperstriatalis ventrale pars caudale (i.e., the “high vocal center” in the brain) compared with uninfected males. Our study demonstrates that similar effects of early parasite exposure on song development occur in the wild as well: male great tits that had been exposed to ectoparasitic hen fleas early in life sang for a shorter period in response to a playback than unexposed males. This is in agreement with the hypothesis that song development is costly (Eberhardt 1994; Gaunt et al. 1996), and it indicates that parasites might mediate the trade-off between investing limited resources in the development of song-related brain structures and parasite defense, respectively. It thereby highlights the importance of parasites in ensuring honesty of sexually selected traits (Hamilton and Zuk 1982).

Interestingly, the effects of early parasite exposure on song duration were independent of adult or nestling condition. Furthermore, the number of different song types sung within the recording period and the latency until the male started their vocal response to the playback were not affected by the infes-

tation experiment. This is surprising because Spencer et al. (2004) and Spencer, Buchanan, et al. (2005) have found that nutritional stress affects song repertoire size in passerines. It suggests that food restriction and parasite exposure affect song development in different ways, and it shows that song does contain not only multiple information about a male's condition over different timescales (see also Scheuber et al. 2003a, 2003b) but also information about the specific type of stressor a male was exposed to early in life.

We found a positive correlation between a male's song duration and his partner's clutch size, which might indicate that song duration is a sexually selected trait in our study population (see also Houtman 1992; Collins et al. 1994; Gil and Gahr 2002; Garamszegi and Møller 2004; Spencer, Wimpenny, et al. 2005). This effect is unlikely due to assortative mating because male and female conditions were not significantly correlated. However, it might reflect an increased female investment in the current brood when mated to an attractive partner (i.e., the differential allocation hypothesis; Burley 1988; Sheldon 2000; Gil et al. 2004). It thus demonstrates the benefits of a high song output for a male's fitness and reveals the cost of parasitism for males in terms of reduced attractiveness.

Beside the effects of early ectoparasite exposure on the duration of singing, which might be especially important in intersexual selection (see above), we also found that parasite-exposed males overlapped the song of a challenger (i.e., the playback) less than unexposed males. Several studies have demonstrated that song overlapping is important in male-male competition as a signal of aggressiveness (Todt 1981; Brindley 1991; McGregor et al. 1992; Dabelsteen et al. 1996, 1997; Naguib et al. 1999; Langemann et al. 2000; Mennill and Ratcliffe 2004b) and dominance (Hyman et al. 2004; Mennill and Ratcliffe 2004a, 2004b). Males that overlap their opponent's song in male-male competition may therefore be more likely to find a mating partner or to gain access to higher quality territories and might thereby achieve a higher reproductive success. In support of this hypothesis, Kunc et al. (2006) found that the subsequent pairing success of male nightingales (*Luscinia megarhynchos*) was related to the frequency of song overlap in male-male interactions during the time of mate attraction. Also, in a dual-speaker choice experiment, female little blue penguins (*Eudyptula minor*) preferred the song of males with a higher degree of song overlap (Miyazaki and Waas 2002). Furthermore, in an experiment with alternating and overlapping playback, corn bunting males (*Miliaria calandra*) approached the loudspeaker more

quickly and spent more time close to the loudspeaker when the playback was alternated rather than when it was overlapping with their own song (Osiejuk et al. 2007), indicating that competitors are less likely to challenge overlapping singers (Todt and Naguib 2000; Osiejuk et al. 2004). Together, these studies suggest that parasite exposure early in life does affect not only a male's attractiveness but also his territory defense behavior and competitiveness in intrasexual encounters by altering its singing strategy.

To summarize, we experimentally show, to our knowledge for the first time in a wild bird population, that parasite exposure early in life affects song duration in response to a playback and the timing of singing of adult great tits. It demonstrates that song development is costly and highlights both the importance of parasites in maintaining honesty of sexually selected traits and the costs of parasitism in terms of reduced attractiveness and competitiveness.

FUNDING

Swiss National Science Foundation (3100A0-102017 to H.R., fellowship number PA00A3-121466 to B.T.); Canton of Bern to L.L.B.

We thank Martin C. Fischer for the assistance with the song analysis and for comments during preparation of the manuscript, Verena Saladin for field assistance and comments on the manuscript, and Katharina Gallizzi for comments on statistical questions. The experiments were conducted under a license of the Ethical Committee of the Office of Agriculture and Nature of the Canton Bern, Switzerland.

REFERENCES

- Baker MC, Bjerke TK, Lampe H, Espmark Y. 1986. Sexual-responses of female great tits to variation in size of males' song repertoires. *Am Nat.* 128:491–498.
- Beecher MD, Campbell SE, Burt JM, Hill CE, Nordby JC. 2000. Song-type matching between neighbouring song sparrows. *Anim Behav.* 59:21–27.
- Berg ML, Beintema NH, Welbergen JA, Komdeur J. 2005. Singing as a handicap: the effects of food availability and weather on song output in the Australian reed warbler *Acrocephalus australis*. *J Avian Biol.* 36:102–109.
- Brackenbury JH. 1979. Power capabilities of the avian sound-producing system. *J Exp Biol.* 78:163–166.
- Brindley EL. 1991. Response of European robins to playback of song—neighbour recognition and overlapping. *Anim Behav.* 41:503–512.
- Buchanan KL. 2000. Stress and the evolution of condition-dependent signals. *Trends Ecol Evol.* 15:156–160.
- Buchanan KL, Catchpole CK. 2000. Song as an indicator of male parental effort in the sedge warbler. *Proc R Soc Lond B Biol Sci.* 267:321–326.
- Buchanan KL, Catchpole CK, Lewis JW, Lodge A. 1999. Song as an indicator of parasitism in the sedge warbler. *Anim Behav.* 57:307–314.
- Buchanan KL, Leitner S, Spencer KA, Goldsmith AR, Catchpole CK. 2004. Developmental stress selectively affects the song control nucleus HVC in the zebra finch. *Proc R Soc Lond B Biol Sci.* 271:2381–2386.
- Buchanan KL, Spencer KA, Goldsmith AR, Catchpole CK. 2003. Song as an honest signal of past developmental stress in the European starling (*Sturnus vulgaris*). *Proc R Soc Lond B Biol Sci.* 270:1149–1156.
- Burley N. 1988. The differential-allocation hypothesis: an experimental test. *Am Nat.* 132:611–628.
- Catchpole CK. 1982. The evolution of bird sounds in relation to mating and spacing behaviour. In: Kroodsma DE, Miller EH, editors. *Acoustic communication in birds*. New York: Academic Press. p. 297–319.
- Catchpole CK. 1996. Song and female choice: good genes and big brains? *Trends Ecol Evol.* 11:358–360.
- Catchpole CK, Slater PJB. 1995. *Bird song*. Biological themes and variations. Cambridge (UK): Cambridge University Press.
- Charif RA, Clark CW, Fistrup KM. 2004. Raven 1.2, Cornell Laboratory of Ornithology, Ithaca, NY.
- Collins SA, Hubbard C, Houtman AM. 1994. Female mate choice in the zebra finch—the effect of male beak color and male song. *Behav Ecol Sociobiol.* 35:21–25.
- Dabelsteen T, McGregor PK, Holland J, Tobias JA, Pedersen SB. 1997. The signal function of overlapping singing in male robins. *Anim Behav.* 53:249–256.
- Dabelsteen T, McGregor PK, Shepherd M, Whittaker X, Pedersen SB. 1996. Is the signal value of overlapping different from that of alternating during matched singing in great tits? *J Avian Biol.* 27:189–194.
- Darwin C. 1871. *The descent of man and selection in relation to sex*. London: Murray.
- Doutrelant C, Blondel J, Perret P, Lambrechts MM. 2000. Relationship between song repertoire size and male quality in blue tits. *J Avian Biol.* 31:360–366.
- Eberhardt LS. 1994. Oxygen-consumption during singing by male carolina wrens (*Thryothorus ludovicianus*). *Auk.* 111:124–130.
- Garamszegi LZ, Møller AP. 2004. Extrapair paternity and the evolution of bird song. *Behav Ecol.* 15:508–519.
- Gaunt AS, Bucher TL, Gaunt SLL, Baptista LF. 1996. Is singing costly? *Auk.* 113:718–721.
- Gil D, Gahr M. 2002. The honesty of bird song: multiple constraints for multiple traits. *Trends Ecol Evol.* 17:133–141.
- Gil D, Leboucher G, Lacroix A, Cue R, Kreutzer M. 2004. Female canaries produce eggs with greater amounts of testosterone when exposed to preferred male song. *Horm Behav.* 45:64–70.
- Gil D, Naguib M, Riebel K, Rutstein A, Gahr M. 2006. Early condition, song learning, and the volume of song brain nuclei in the zebra finch (*Taeniopygia guttata*). *J Neurobiol.* 66:1602–1612.
- Grafen A. 1990. Biological signals as handicaps. *J Theor Biol.* 144:517–546.
- Hamilton WD, Zuk M. 1982. Heritable true fitness and bright birds—a role for parasites. *Science.* 218:384–387.
- Houtman AM. 1992. Female zebra finches choose extra-pair copulations with genetically attractive males. *Proc R Soc Lond B Biol Sci.* 249:3–6.
- Hyman J, Hughes M, Searcy WA, Nowicki S. 2004. Individual variation in the strength of territory defense in male song sparrows: correlates of age, territory tenure, and neighbor aggressiveness. *Behaviour.* 141:15–27.
- Krebs JR. 1976. Habituation and song repertoires in great tit. *Behav Ecol Sociobiol.* 1:215–227.
- Krebs JR, Ashcroft R, Vanorsdol K. 1981. Song matching in the great tit *Parus major* L.. *Anim Behav.* 29:918–923.
- Kunc HP, Amrhein V, Naguib M. 2006. Vocal interactions in nightingales, *Luscinia megarhynchos*: more aggressive males have higher pairing success. *Anim Behav.* 72:25–30.
- Kwok L. 2003. Sound Studio 2.1. Felt Tip Inc., Brooklyn, NY.
- Lambrechts M, Dhondt AA. 1986. Male quality, reproduction, and survival in the great tit (*Parus major*). *Behav Ecol Sociobiol.* 19:57–63.
- Lambrechts M, Dhondt AA. 1988. The anti-exhaustion hypothesis—a new hypothesis to explain song performance and song switching in the great tit. *Anim Behav.* 36:327–334.
- Langemann U, Tavares JP, Peake TM, McGregor PK. 2000. Response of great tits to escalating patterns of playback. *Behaviour.* 137:451–471.
- McGregor PK, Dabelsteen T, Shepherd M, Pedersen SB. 1992. The signal value of matched singing in great tits—evidence from interactive playback experiments. *Anim Behav.* 43:987–998.
- McGregor PK, Krebs JR. 1982a. Mating and song types in the great tit. *Nature.* 297:60–61.
- McGregor PK, Krebs JR. 1982b. Song types in a population of great tits (*Parus major*)—their distribution, abundance and acquisition by individuals. *Behaviour.* 79:126–152.
- McGregor PK, Krebs JR, Perrins CM. 1981. Song repertoires and lifetime reproductive success in the great tit (*Parus major*). *Am Nat.* 118:149–159.
- Mennill DJ, Ratcliffe LM. 2004a. Do male black-capped chickadees eavesdrop on song contests? A multi-speaker playback experiment. *Behaviour.* 141:125–139.

- Mennill DJ, Ratcliffe LM. 2004b. Overlapping and matching in the song contests of black-capped chickadees. *Anim Behav.* 67:441–450.
- Miyazaki M, Waas JR. 2002. 'Last word' effects of male advertising calls on female preference in little blue penguins. *Behaviour.* 139:1413–1423.
- Naguib M, Fichtel C, Todt D. 1999. Nightingales respond more strongly to vocal leaders of simulated dyadic interactions. *Proc R Soc Lond B Biol Sci.* 266:537–542.
- Nielsen BMB, Vehrencamp SL. 1995. Responses of song sparrows to song-type matching via interactive playback. *Behav Ecol Sociobiol.* 37:109–117.
- Nowicki S, Hasselquist D, Bensch S, Peters S. 2000. Nestling growth and song repertoire sire in great reed warblers: evidence for song learning as an indicator mechanism in mate choice. *Proc R Soc Lond B Biol Sci.* 267:2419–2424.
- Nowicki S, Peters S, Podos J. 1998. Song learning, early nutrition and sexual selection in songbirds. *Am Zool.* 38:179–190.
- Nowicki S, Searcy WA. 2004. Song function and the evolution of female preferences—why birds sing, why brains matter. *Ann NY Acad Sci.* 1016:704–723.
- Nowicki S, Searcy WA, Peters S. 2002. Brain development, song learning and mate choice in birds: a review and experimental test of the "nutritional stress hypothesis". *J Comp Physiol A.* 188:1003–1014.
- Osiejuk TS, Ratynska K, Cygan JP. 2004. Signal value of alternating and overlapping singing in the yellowhammer *Emberiza citrinella*. *J Ethol.* 22:55–61.
- Osiejuk TS, Ratynska K, Cygan JP. 2007. Corn bunting (*Miliaria calandria*) males respond differently to alternating and overlapping playback of song. *J Ethol.* 25:159–168.
- Otter K, McGregor PK, Terry AMR, Burford FRL, Peake TM, Dabelsteen T. 1999. Do female great tits (*Parus major*) assess males by eavesdropping? A field study using interactive song playback. *Proc R Soc Lond B Biol Sci.* 266:1305–1309.
- Peake TM, Matessi G, McGregor PK, Dabelsteen T. 2005. Song type matching, song type switching and eavesdropping in male great tits. *Anim Behav.* 69:1063–1068.
- Richner H, Oppliger A, Christe P. 1993. Effect of an ectoparasite on reproduction in great tits. *J Anim Ecol.* 62:703–710.
- Sall J, Lehmann A. 1996. JMP start statistics. New York: Duxbury Press.
- Scheuber H, Jacot A, Brinkhof MWG. 2003a. Condition dependence of a multicomponent sexual signal in the field cricket *Gryllus campestris*. *Anim Behav.* 65:721–727.
- Scheuber H, Jacot A, Brinkhof MWG. 2003b. The effect of past condition on a multicomponent sexual signal. *Proc R Soc Lond B Biol Sci.* 270:1779–1784.
- Searcy WA, Andersson M. 1986. Sexual selection and the evolution of song. *Annu Rev Ecol Syst.* 17:507–533.
- Sheldon BC. 2000. Differential allocation: test, mechanisms and implications. *Trends Ecol Evol.* 15:397–402.
- Spencer KA, Buchanan KL, Goldsmith AR, Catchpole CK. 2003. Song as an honest signal of developmental stress in the zebra finch (*Taeniopygia guttata*). *Horm Behav.* 44:132–139.
- Spencer KA, Buchanan KL, Goldsmith AR, Catchpole CK. 2004. Developmental stress, social rank and song complexity in the European starling (*Sturnus vulgaris*). *Proc R Soc Lond B Biol Sci.* 271: S121–S123.
- Spencer KA, Buchanan KL, Leitner S, Goldsmith AR, Catchpole CK. 2005. Parasites affect song complexity and neural development in a songbird. *Proc R Soc Lond B Biol Sci.* 272:2037–2043.
- Spencer KA, Wimpenny JH, Buchanan KL, Lovell PG, Goldsmith AR, Catchpole CK. 2005. Developmental stress affects the attractiveness of male song and female choice in the zebra finch (*Taeniopygia guttata*). *Behav Ecol Sociobiol.* 58:423–428.
- Todt D. 1981. On functions of vocal matching—effect of counter-replies on song post choice and singing. *Z Tierpsychol.* 57:73–93.
- Todt D, Naguib M. 2000. Vocal interactions in birds: the use of song as a model in communication. *Adv Study Behav.* 29:247–296.
- Tripet F, Richner H. 1997. The coevolutionary potential of a 'generalist' parasite, the hen flea *Ceratophyllus gallinae*. *Parasitology.* 115: 419–427.
- Vehrencamp SL. 2001. Is song-type matching a conventional signal of aggressive intentions? *Proc R Soc Lond B Biol Sci.* 268: 1637–1642.
- Vehrencamp SL, Bradbury JW, Gibson RM. 1989. The energetic cost of display in male sage grouse. *Anim Behav.* 38:885–896.