

Song amplitude and body size in birds

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Abstract Bird song is a sexually selected multidimensional signal. A fundamental question regarding the evolution of sexually selected signals is what information they convey and how their honesty is maintained. Song amplitude is a performance-related signal trait that varies considerably between individuals, but this signal dimension has been neglected in past studies. I found that median song amplitude in male nightingales (*Luscinia megarhynchos*) and zebra finches (*Taeniopygia guttata*) did not vary significantly with body size or residual body mass. In contrast, I found a significant negative correlation between body size (and also residual mass) and the maximum song amplitude during interactive singing in nightingales. However, the function of these more subtle differences in song amplitude remains to be investigated. By and large, the results of this study suggest that mean song amplitude is unlikely to indicate a bird's body size or current condition (measured as residual mass).

Keywords Animal communication · Bird song · Honest signalling · Performance-related trait · Signal evolution · Song amplitude

Introduction

Inter-individual variation in sexual traits is common in most organisms; thus, it is important to understand how signal variation relates to sexual selection. Bird song is one of the most widely used models in the study of sexual selection, and many studies have shown how individual variation in song characteristics affects reproductive success through mate choice and male–male competition (Catchpole and Slater 2008). However, it is often overlooked that bird song is a multifaceted behaviour that is comprised of a whole set of characters rather than a single trait, and each of these different components can be limited by specific constraints (Gil and Gahr 2002). While many studies have concentrated on song characteristics such as repertoire size, song timing and countersinging patterns, one of the most important parameters for signal transmission, song amplitude, has been neglected, although it may play an important role in encoding information relevant to sexual selection (Gil and Gahr 2002). The potential of song amplitude as an indicator of the singer's quality or condition becomes evident when we consider the great inter-individual variation in this signal trait, which has been shown in several bird species under controlled conditions in sound isolation chambers: Brumm and Todt (2002) found that song amplitude varied by more than 10 dB between six male nightingales (*Luscinia megarhynchos*), in the same number of Bengalese finches (*Lonchura striata*) Kobayashi and Okanoya (2003) measured an average of at least 6-dB difference between individuals, and finally a 14-dB

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difference was found in eleven zebra finches, *Taeniopygia guttata* (Brumm and Slater 2006).

It is well known that frequencies of bird vocalisations can indicate body size. In a comparative study, Ryan and Brenowitz (1985) showed that bigger species tend to produce lower pitched songs. Moreover, the same negative correlation between body size and vocal pitch has also been found within species (e.g. Tubaro and Mahler 1998; Laiolo et al. 2004; Koetz et al. 2007; Geberzahn et al. unpublished data). In addition to frequency parameters, call amplitude is thought to be an honest indicator of body size in insects and, thus, to play a crucial part in sexual selection in this taxon (Simmons 1988; Gray 1997). A similar relationship between vocal intensity and body size could also have evolved in bird song. The vocal amplitude of a particular song element is determined by the air pressure in a bird's air sacs, which is built up by the abdominal expiratory muscles (Plummer and Goller 2008). As the size of these muscles is limited by the size of the bird's body, it follows that vocal amplitude could be an honest signal of body size. Despite the importance of the connexion between body size and song amplitude in birds, there is, as far as I know, only one published study on the topic. Brackenbury (1979) compared vocal sound pressure levels of several bird species and found that the bigger species did indeed tend to produce vocalisations of higher amplitude. However, trends within species have not been shown yet, although these would be much more relevant to communication and sexual selection.

When searching relationships between song amplitude and body size, it is prudent to consider that song amplitude is a flexible trait, which is individually adjusted according to the background noise (reviewed in Brumm and Slabbekoorn (2005)) and the social context (Brumm and Todt 2004; Cynx and Gell 2004; Brumm and Slater 2006; Anderson et al. 2008). Moreover, a recent experiment on courtship song in zebra finches demonstrated that birds can also regulate the amplitude of their songs depending on the distance of the targeted receiver (Brumm and Slater 2006). These causes of song amplitude variation in birds were unknown when Brackenbury (1979) published his comparative study 30 years ago. But in light of the evidence available to us today, clearly, these factors must be taken into account in all studies aiming to glean meaningful measurements of vocal power.

In the current study, I investigated the relationship between song amplitude and body size in two songbird species, the nightingale and the zebra finch, while controlling for social and environmental factors. Nightingales are territorial birds and male advertisement songs are employed in long-range communication (Naguib et al. 2008). In contrast, zebra finches are non-territorial colony breeders, and I investigated their courtship song which is used over

very short distances (Zann 1996; Brumm and Slater 2006). These differences in communication distance might be important because vocal signalling of body size is of particular importance in cases in which receivers cannot assess the size of a singing male by eye. In zebra finches, females can see the courting males; but in nightingales, targeted receivers usually cannot see a singing male and, thus, are not able to visually assess its body size. Thus, a possible correlation between song amplitude and body size might be more pronounced in nightingales than in zebra finches.

Materials and methods

General

The songs of male nightingales and zebra finches were recorded on digital media (DAT or flash card) and, subsequently, morphological measurements of each male were taken. The morphologic data comprised the wing length, length of the third primary feather and the tarsus length as well as the body mass. The nightingales were studied in the wild and in a bioacoustic laboratory, whereas the zebra finches were investigated in the lab only.

To yield reliable measurements of vocal amplitude, it is crucial to consider confounding variables such as the level of masking background noise or the context of singing (solo or interactive singing, distance of targeted receiver, etc.). In the laboratory, background noise could be held constant by using acoustically shielded recording rooms, and the social context could be manipulated by the experimenter. In the field, these variables had to be controlled by careful selection of the test sites and additional measurements of ambient noise characteristics.

Wild nightingales

I used recordings from a previous study of wild nightingales and analysed post hoc the relationship between vocal amplitude and body size. The original study had been undertaken to investigate the Lombard effect in free-ranging nightingales (Brumm 2004). Sound level measurements of ten solo singing males were made in the field with a CEL 314 precision (class 1) sound level metre, and subsequently, the birds were captured to measure their body size and mass. Only those birds, whose territories were not within hearing range of other nightingale territories, were used in this study. This was done to exclude the possible confounding effect of vocal interactions with neighbouring males that might have preceded the measurements. Additionally, I controlled for the Lombard effect, by including the background noise in the birds' territories in the analysis.

On average, I analysed 29 songs per bird (range 13–57 songs). For details of the measuring protocol, see Brumm (2004). Briefly, I measured the peak sound pressure level of each song and the distance of the singing bird from the measuring microphone while controlling for the birds' orientation. This procedure allowed calculating a standardised song level that could then be compared between individuals.

Captive nightingales

I analysed the song performances of ten hand-reared nightingales, which were recorded individually in acoustic chambers in the laboratory. I recorded the spontaneous solo singing of each bird and songs sung in response to a playback simulating a rival male. Calibrated recordings were made on digital tape and the sound level of each song element was measured using Avisoft SASLab Pro (version 3.8; R. Specht, Berlin, Germany). On average, I analysed 16 solo songs (range 15–20 songs) and 13 interactive songs (range 10–20) per bird. The distance and orientation of the subject to the recording device was controlled by placing an omnidirectional microphone in the middle and above the two only perches of the test cage. Immediately after the song recordings, each male was measured and weighed. For details of the recording protocol and the data analysis see Brumm and Todt (2004) and Brumm (2006). Details of the housing are given in Brumm and Hultsch (2001).

Captive zebra finches

I analysed the courtship songs of 41 male zebra finches which were recorded individually in acoustic chambers in the laboratory. Each male was presented with a female 20 cm away to induce courtship. As part of their courtship display, males produce so-called directed song which is targeted at the courted female (Sossinka and Böhner 1980). Calibrated recordings of the directed songs were made with a solid state recorder and the sound level of each song element (syllable) was measured using Avisoft SASLab Pro (version 4.36). On average, I analysed 16 song motifs per bird (range 8–27 motifs). Immediately after the song recordings each male was measured and weighed. For details of the recording protocol and the data analysis, see Brumm and Slater (2006). Briefly, I used a similar array as in the experiments with captive nightingales to control the distance and orientation of the subject to the recording microphone.

Statistical analyses

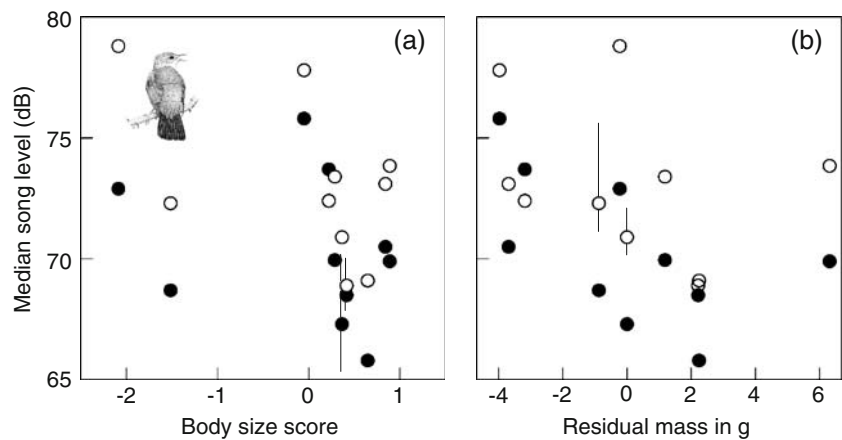
To obtain one measure for body size, principal components analyses with the four initial measures (wing length, length

of the third primary feather, tarsus length and mass) were conducted. For all three datasets, the Kaiser–Meyer–Olkin measure of sampling adequacy was above 0.5, indicating that the correlation of variables was sufficient for the data reduction. For further analysis, I used the first principal component that explained the majority of the variance in the data (74% in the wild nightingales, 76% in the captive nightingales and 51% in the zebra finches). All first components had eigenvalues higher than 1 (2.2 in the wild nightingales, 2.3 in the captive nightingales and 1.5 in the zebra finches), and all four morphological variables loaded positively on PC1. The score on the first principal component was then used as a composite measure of body size (hereafter 'body size score'). In addition to the body size score, I also considered the residual body mass (regressed on the factor scores of a principal component including the three initial body size measures but not the absolute mass). Using the residual mass, I aimed at testing whether vocal amplitude may function as an indicator of the current condition of singing males. Each dataset was evaluated with a general linear model with the song level as a dependent variable. For the lab studies, the body size score and the residual mass were included as covariates in the model. To test the wild nightingale data, I also included the level of environmental background noise as a third covariate to control for the Lombard effect. In the wild nightingales, only the maximum level of each song was recorded, but for the other datasets, I measured the sound level of each song element and calculated the median song level for each song (or song motif in the case of the zebra finches) in addition to the maximum levels. Thus, the average and the maximum vocal intensity were considered in the analysis. Non-significant covariates were removed from the models, and test statistics and *P* values of final models are indicated in the text. In cases where models with two covariates showed a non-significant result, either of the two non-significant covariates was removed from the model and none of the resulting final models indicated a significant relationship between song amplitude on the one side and body size score and residual mass on the other.

Results

Individual differences in median vocal amplitude between males were marked in all data sets, ranging from 10 dB in the captive nightingales to 15 dB in the zebra finches (Figs. 1, 2). Similar differences between individuals were found in the peak performance, i.e. the average maximum song level (Figs. 3, 4, 5): 8–12 dB in the captive nightingales and 15 dB in the wild nightingales and zebra finches. In the following, statistical correlates of this inter-individual variation in song intensity will be investigated.

Fig. 1 Median song levels of captive nightingales ($N=10$ males) and **a** body size and **b** residual body mass (dB re. $20\mu\text{Pa}$). Filled circles spontaneous solo songs; open circles interactive songs in response to con-specific playback. For clarity, interquartiles are given only for the male with the most and the male with the least variation of vocal sound pressure levels



Median song amplitude

In the captive nightingales, the song amplitude variation in the solo songs could not be explained by the general linear model ($F_{2,7}=1.61$, $P=0.266$), i.e. there was no significant relationship between median song intensity and body size or residual body mass. Also in the interactive songs produced in response to con-specific playback, no significant relationship between the birds' median song levels and body size or residual mass could be detected ($F_{2,7}=1.81$, $P=0.232$). In addition to the absolute sound pressure levels I also investigated the relative increase in vocal peak amplitude between solo and interactive songs, i.e. the interactive capacity of the males. But again, this increase in median vocal sound pressure was not related to body size or residual mass ($F_{2,7}=1.83$, $P=0.229$). The same lack of an effect was found in the non-territorial species, the zebra finch, in which the median amplitude of the males' courtship songs also did not reflect the birds' size or residual body mass ($F_{2,38}=0.23$, $P=0.794$).

Maximum song amplitude

In the wild solo singing nightingales, the majority of the inter-individual variation in song amplitude could be

explained by the general linear model ($F_{3,6}=7.51$, $P=0.019$). However, the only significant correlate of individual song amplitude was the level of environmental noise in the birds' territories ($F_{1,8}=17.61$, $P=0.003$; after removal of all non-significant covariates). No significant relationship could be found between song amplitude and body size ($F_{1,6}=0.68$, $P=0.442$) or residual mass ($F_{1,6}=1.06$, $P=0.343$). Like in the wild birds, the maximum solo song amplitudes of the captive nightingales did not vary significantly with their body size or residual mass ($F_{2,7}=2.08$, $P=0.196$). During interactive singing, however, when the males sang with increased vocal sound pressure levels, the variation in peak performance between males could be explained by the general linear model ($F_{2,7}=10.98$, $P=0.007$). The peak sound pressure levels of interactive songs reflected both the body size ($F_{1,7}=10.71$, $P=0.014$) and the residual mass of the singer ($F_{1,7}=6.38$, $P=0.040$). Surprisingly, the relationship between body size and maximum song level was negative, i.e. bigger birds produced lower peak levels (Table 1). A similar negative correlation was found between residual body mass and maximum song level: lighter nightingales sang with higher maximum sound levels. In the zebra finches, the analysis of the males' peak performances yielded comparable results to the

Fig. 2 Median song levels of captive zebra finches ($N=41$ males) and **a** body size and **b** residual body mass (dB re. $20\mu\text{Pa}$). For clarity, interquartiles are given only for the male with the most and the male with the least variation of vocal sound pressure levels

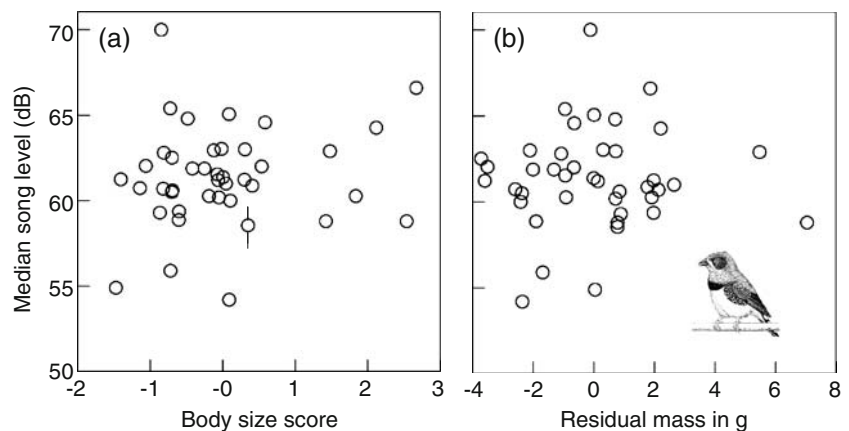
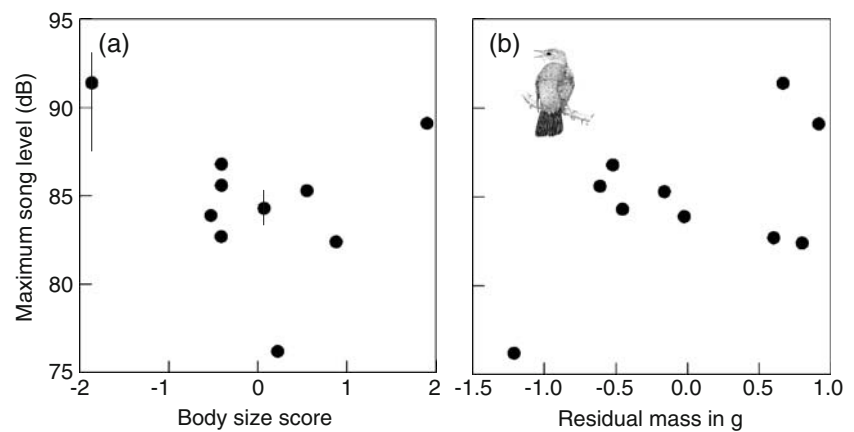


Fig. 3 Maximum song levels of wild nightingales ($N=10$ males) and **a** body size and **b** residual body mass (dB re. $20\mu\text{Pa}$). For clarity, interquartiles are given only for the male with the most and the male with the least variation of vocal sound pressure levels



nightingales' solo songs, i.e. the variation in maximum song amplitude between males was not significantly related to the birds' body size or residual mass ($F_{2,38}=0.395$, $P=0.676$).

Discussion

In this study, I analysed a performance-related signal trait, song amplitude, in nightingales and zebra finches with the aim of finding out whether song amplitude could function as an indicator of body size. The calibrated song recordings revealed striking differences in vocal amplitude between individuals of each species. Differences in median vocal sound pressure levels between males ranged from 10 dB in captive nightingales to 15 dB in wild nightingales and zebra finches. This means, given the logarithmic nature of the decibel scale, that the sound pressure of the loudest males' songs was on the average three to more than five times higher than those of the softly singing birds. A similar magnitude of song level differences between males has also been reported in previous studies on songbirds (Brumm and Todt 2002; Kobayashi and Okanoya 2003; Brumm and Slater 2006). However, the striking individual variation in mean vocal amplitude found in this study was not related to

the differences in body size. At the moment, it is not possible to tell whether there was generally no size effect or whether a small size effect was masked by other factors. In either case, the findings suggest that song amplitude is unlikely to function as an honest signal for body size, as it would not be very informative, if it is easily masked by other, to date unknown, factors. I also found no evidence for a significant relationship between the birds' vocal amplitude and their body mass when controlled for body size. This could be interpreted as an indication that average song amplitude does not signal a male's current condition. However, here, the current condition was assessed indirectly by measuring the males' residual mass. In future studies, a more direct approach including experimental manipulation will be helpful to further clarify the relationship between song amplitude and physical condition.

Studies in anurans and birds have shown that in some cases, vocal signals only encode reliable information about the signaller's body size when the calling animal is challenged by a rival. American toads (*Bufo americanus*), for instance, lower the dominant frequency of their calls when they interact vocally with a rival male, and the lowered call frequencies correlate much more strongly with the toads' body size than their higher pitched non-

Fig. 4 Maximum song levels of captive nightingales ($N=10$ males) and **a** body size and **b** residual body mass (dB re. $20\mu\text{Pa}$). Filled circles spontaneous solo songs; open circles interactive songs in response to con-specific playback. For clarity, interquartiles are given only for the male with the most and the male with the least variation of vocal sound pressure levels

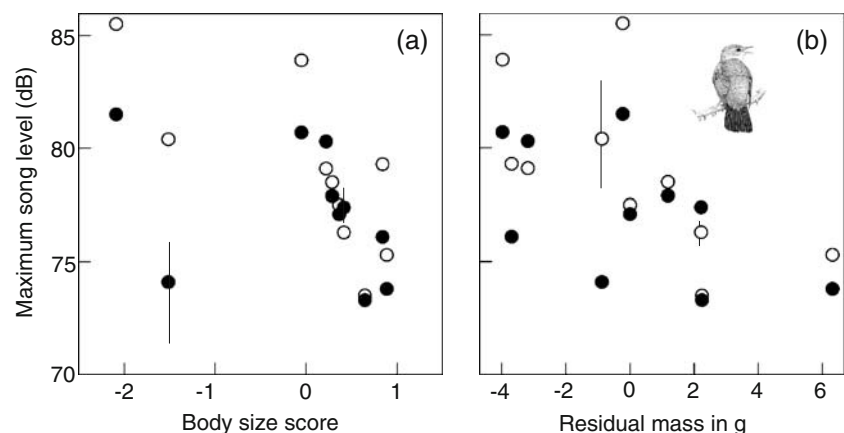
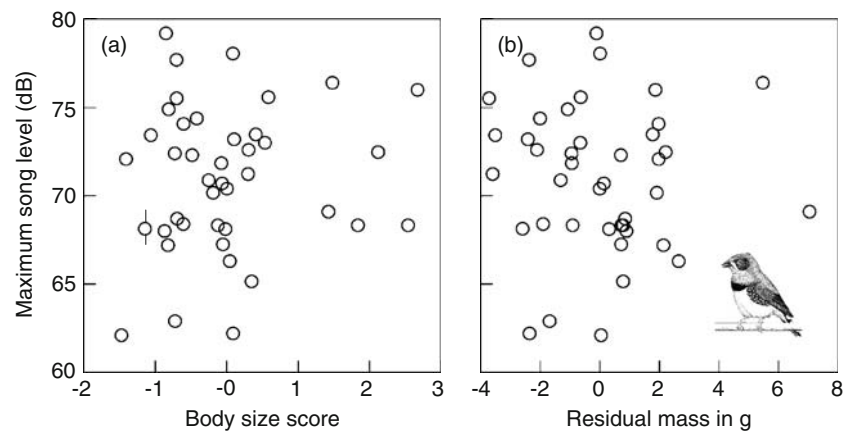


Fig. 5 Maximum song levels of captive zebra finches ($N=41$ males) and **a** body size and **b** residual body mass (dB re. $20\mu\text{Pa}$). For clarity, interquartiles are given only for the male with the most and the male with the least variation of vocal sound pressure levels



interactive calls (Howard and Young 1998). Most recently, Geberzahn et al. (unpublished data) discovered a similar phenomenon in a territorial non-passerine bird, the black coucal (*Centropus grillii*). This species is sex-role reversed, i.e. females defend breeding territories and advertise territory ownership by song, whereas the smaller males rarely vocalise and provide all of the parental care (Goymann et al. 2004). In their analysis of the female singing behaviour, Geberzahn et al. found no correlation between the acoustic characteristics of the female solo songs and the birds' body size. During vocal interactions, however, when the coucals were challenged by the playback of a rival female, the birds lowered the frequencies of their songs which then revealed their body size. A similar phenomenon was found in this study for the maximum amplitudes of nightingale song. Nightingales do not lower their pitch but rather increase the amplitude of their songs during challenged singing (Brumm and Todt 2004), and the results of this study show that body size and residual mass was not reflected in the sound level of solo songs but in the peak levels of interactive songs in response to con-specific playback. However, in contrast to the studies on anurans and coucals, the picture in nightingales is less clear, for a significant relationship between song amplitude and body size and mass was only found in the maximum levels but not in the median song levels. The significance of these more subtle peak differences for

communication and sexual selection is unclear. If strong selection would maintain song amplitude as an indicator of body size, then one would expect overall differences in vocal sound pressure levels to vary with size or condition, which was not the case in the birds studied here. At the moment, it is not possible to tell whether the differences in peak amplitude are used to convey information. Future playback studies will help to elucidate this issue.

Interestingly enough, the correlation between maximum song amplitudes on the one side and body size and current condition on the other was negative, i.e. smaller and lighter males produced higher maximum song levels. This finding suggests that high peak levels in interactive nightingale song do not signal individual quality but rather male singing effort. The smaller males perhaps produced higher peak levels to compensate their low quality, and bigger males, on the other hand, could afford to sing with lower peak levels because they are more likely to win physical combats than small males; thus, they have less need to keep rivals at bay. This notion is in line with other recent findings on individual differences in vocal interactions in nightingales (Schmidt et al 2006, 2008). It is reasonable to assume that bigger and heavier birds are of higher quality because such individuals were found to arrive earlier in their breeding ground after migration, and they also had bigger song repertoires (Kipper et al. 2006). Moreover, male nightingales that arrive earlier on their breeding

Table 1 Correlation coefficients of song amplitude and body size, and song amplitude and residual body mass in songbirds

Species	Recording environment	Social context	Median song amplitude		Maximum song amplitude	
			$r_{\text{body size}}$	r_{mass}	$r_{\text{body size}}$	r_{mass}
Nightingale	Field	Solo singing			-0.487	0.586
	Laboratory	Solo singing	-0.276	-0.566	-0.376	-0.554
	Laboratory	Interactive singing	-0.512	-0.391	-0.734	-0.623
Zebra finch	Laboratory	Courtship song	0.144	0.045	0.108	-0.044

Statistically significant relations detected by GLM procedures are indicated in bold

grounds are more successful in attracting a mate than males returning later from their winter quarters (Amrhein et al. 2007). Schmidt et al. (2008) looked at the spatial behaviour, and the singing activity of nightingales in response to con-specific playback and found that low-quality males (i.e. males that did not succeed in attracting a mate) reacted more strongly to playbacks of simulated weak threat than did high-quality males. Possibly, the playback used in this study, simulating a rival more than 25 m away, was also perceived by the birds as a comparably weak threat. Thus, my finding that small males reacted more strongly (i.e. produced higher song maximum amplitudes) in response to the con-specific playback corroborates the results of Schmidt et al. (2008) on spatial behaviour and singing activity in wild nightingales.

Most interestingly, a similar negative relationship between vocal amplitude and male quality has been found in American bison, *Bison bison* (Wyman et al. 2008). Wyman and her co-workers found no significant relation between a bull's weight and the amplitude of his rutting calls used in male–male competition. However, low quality males that sired only few offspring produced louder calls than high quality males that had more offspring. Thus, it appears that there might be a common principle of signalling intensity and male quality in birds and mammals. However, to my knowledge, the enquiry of Wyman et al. (2008) on bison and this study on song birds are the first to investigate the relationship between vocal amplitude and the size or quality of sexually displaying male mammals or birds, and considering the obvious paucity of comparative data, any conclusions about the generality of the findings are rather premature.

By and large, the findings of this study suggest that song amplitude is unlikely to function as an indicator of body size. However, the question of the significance of higher peak amplitudes of challenged singing in smaller males remains an open one. The rather surprising finding of this negative correlation opens a new avenue for future experimental investigations that eventually may help to find common principles of male–male vocal competition in birds and mammals and also to elucidate a possible common function in terms of sexual selection.

It is important to bear in mind, however, that the immense variation in mean vocal amplitude between individual birds in this study was not the result of differences in body size. So, how can these striking variations in song amplitude then be explained? It is known that song learning and song performance can be affected by the past condition of birds, e.g. by developmental stress (Catchpole and Slater 2008; Holveck et al. 2008). However, a recent study on early nutritional stress in zebra finches showed that the song amplitude of adult birds is not affected by their condition during the nestling and fledgling period (Brumm et al. 2009). Possibly, the individual

differences in song amplitude found in this study reflect differences in motivation. Correlating the hormone levels of birds with their vocal amplitude may help to shed light on this issue. It has been shown in many species that singing activity is closely related to androgen levels (reviewed in Ball (1999)). Moreover, Cynx et al. (2005) demonstrated that high testosterone levels lower the fundamental frequency of zebra finch songs. Perhaps also the loudness of songs is affected by androgens. In this case, vocal amplitude could be an indicator of the singer's endocrine status.

It is conceivable that song amplitude might signal a handicap such that the signal is indicative of quality because signallers of inferior quality cannot afford to bear the costs of signal production (Zahavi 1975, 1977). However, the actual costs of singing loudly still remain to be uncovered (Gil and Gahr 2002). The current picture suggests that energy expenditure plays only a very minor role (Oberweger and Goller 2001; Franz and Goller 2003; Ward et al. 2003, 2004). Most likely, the production of loud songs is primarily constrained by predation and/or social aggression. It has been shown that bird calls can attract predators (Mougeot and Bretagnolle 2000; Krams 2001; Krama and Krams 2005), although none of these studies addressed bird songs. If the songs of birds are used as a cue by predators to find their avian prey, then singing loudly may increase the predation risk since predators are more likely to detect the singing bird. Likewise, louder songs possibly increase the risk of being attacked by con-specific rivals; thus, social aggression may also constrain high song amplitudes. Dabelsteen (1981) and Todt (1981) observed that blackbirds (*Turdus merula*) react more aggressively to playbacks with high volume. However, Anderson et al. (2007) found that male song sparrows (*Melospiza melodia*) responded equally aggressively to two song variants that differed by 21 dB. We clearly lack more quantitative data on the issue and it would be very interesting to systematically investigate social aggression as a limiting cost on the production of loud songs.

In conclusion, the individual differences in mean vocal sound pressure levels in two songbird species were not related to the size or the residual body mass of the birds. This evidence for the lack of a size effect on mean song amplitude suggests that signal intensity is very unlikely to be an indicator of body size and possibly also not of current physical condition. However, further investigations are needed to help us understand the negative correlation between peak amplitudes of interactive nightingale songs and the size and condition of the singer.

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