

The impact of environmental noise on song amplitude in a territorial bird

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Summary

1. The impact of environmental background noise on the performance of territorial songs was examined in free-ranging nightingales (*Luscinia megarhynchos* Brehm). An analysis of sound pressure levels revealed that males at noisier locations sang with higher sound levels than birds in territories less affected by background sounds.
2. This is the first evidence of a noise-dependent vocal amplitude regulation in the natural environment of an animal.
3. The results yielded demonstrate that the birds tried to mitigate the impairments on their communication caused by masking noise. This behaviour may help to maintain a given transmission distance of songs, which are used in territory defence and mate attraction. At the same time, birds forced to sing with higher amplitudes have to bear the increased costs of singing.
4. This suggests that in songbirds the level of environmental noise in a territory will contribute to its quality and thus considerably affect the behavioural ecology of singing males.

Key-words: acoustical masking, birdsong, Lombard effect, *Luscinia megarhynchos*, vocal amplitude.

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Introduction

Acoustic communication is constrained considerably by environmental factors, such as habitat-dependent sound transmission properties related to microclimate and vegetation structure (Wiley & Richards 1982). Additionally, the level of masking background noise also plays an important role, because detection and recognition of signals depends substantially on the signal-to-noise ratio (Klump 1996). Hence, the transmission distance of a signal is affected crucially by the properties of background noise. In the natural environment vocalizing animals have to face a multitude of noise sources which may be abiotic (caused by wind-induced vegetation movement, rain, flowing water, surf, etc.) or biotic (i.e. interfering sounds produced by other animals). Given a match between noise and signal frequencies, the resulting masking effect by the noise can drive evolutionary changes in the signal structure of vocalizations used for long-range communication. As a result the spectral energy distributions of vocalizations can be shaped to frequency bands that are less or not affected by noise. A particularly severe environmental interference

is the noise produced by torrents and waterfalls. An evolutionary response of frogs and birds living in such habitats is to evade masking by producing high-pitched vocalizations in narrow frequency bands (Dubois & Martens 1984). However, also for less noisy habitats it has been suggested that background sounds can affect the evolution of frequency traits of animal vocalizations (Wiley & Richards 1982; Ryan & Brenowitz 1985; Waser & Brown 1986). Such evolutionary shaping of signal phonetics has been reported recently by Slabbekoorn & Smith (2002) for the songs of little greenbulbs (*Andropadus virens*). In this species, males living in rain forests sing low-frequency notes that are not used by birds in ecotone forests. This song divergence could not be explained by different sound transmission properties between habitats, but by differences in background noise characteristics. In ecotone forests the frequency band of the low-pitched notes is masked by high levels of environmental noise, whereas these frequencies are affected only by low-amplitude noise in rain forest habitats.

In addition to evolutionary changes in signal traits, the intensity of masking background noise can also affect the properties of acoustic signals in the short term. One such short-term adaptation is the Lombard effect, in which a signaller increases the amplitude of its vocalizations in response to an increase of the background noise amplitude (Lombard 1911). However, it

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has been assumed for a long time that birds do not regulate their vocal amplitude, but always vocalize with maximized sound level (Brackenbury 1979; Lengagne *et al.* 1999), thereby overlooking the fact that a variety of birds adjust the intensity of their calls and songs depending on the background noise level (Potash 1972; Cynx *et al.* 1998; Manabe, Sadr & Dooling. 1998). Finally, it emerged that the Lombard effect can even be exhibited in territorial songbirds (Brumm & Todt 2002), demonstrating that male nightingales (*Luscinia megarhynchos* Brehm) do not maximize the amplitude of their advertising full songs, but regulate vocal intensity dependent on the level of masking noise, suggesting that they keep intensity reserves to mitigate masking effects of the acoustic background. In turn, these findings show that songbirds do not necessarily maximize the size of their territories. This conclusion is supported by the study of Lemon *et al.* (1981) on frequency distribution of songs and singing heights in several warbler species.

So far, however, the Lombard effect in birds has been investigated with psychoacoustic experiments in soundproof laboratory settings, but it remains to be examined whether birds also use their potential skills in amplitude regulation in the natural environment where a continuous background sound is present. If songbirds would do so, then one should expect males at more noisy locations to sing with a higher vocal amplitude than birds in less noisy environments. Addressing this issue may help to extend our understanding of how environmental selection pressures can affect acoustic signals and also may contribute to conservation by revealing possible impacts of environmental noise on wildlife.

I studied these topics in common nightingales, a territorial songbird of the south-western Palaearctic. Nightingales show a discontinuous singing style; territorial songs have, on average, a duration of about 3 s and are separated by silent pauses of similar length (Hultsch & Todt 1982).

Methods

GENERAL

I surveyed male territorial nightingales in Berlin, Germany between 05.00 and 10.00 h. Eight birds were studied between 28 April and 1 May 2001 and seven males between 1 May and 12 May 2002. All measurements were taken on working days. In addition the song levels of three birds and the background noise levels in their territories were also assessed on weekend days (when there was less traffic in the morning hours and environmental noise levels were lower) following or preceding the actual survey.

Assessing the sound level of animal vocalizations in the field is a challenging task, because many variables can contribute to differences in measured vocal sound pressure levels. In addition to possible effects of environmental noise, social influences can also play a crucial role in this context. As shown recently for nightingales,

songbirds can increase their vocal amplitude when interacting with rival males (Brumm & Todt 2004). Therefore, only birds holding territories that were not bordered directly by another nightingale's territory (or be within earshot from territorial males farther away) were examined in this study. The territories studied comprised a variety of locations ranging from territories near roads to more remote areas.

All sound level measurements were taken with a CEL 314 precision sound level meter (measuring frequency range 16–20 000 Hz) mounted on a tripod 1.5 m above the ground. A time constant of 125 ms and an 'A' frequency weighting was used. The frequency response curve of the A-filter is approximately flat from 1 kHz to 8 (which is about the frequency range of nightingale songs), but higher and lower frequencies are suppressed. This frequency weighting was chosen because it is noise in the frequency range of their own songs that is crucial for the regulation of vocal amplitude in nightingales (Brumm & Todt 2002). Measurements and recordings were made only when there was no wind (as measured with a Huger WSC 100 H anemometer). The temperature ranged between 8.7 °C and 16.2 °C and relative air humidity was between 60% and 89% (measured with a GFTH 95 Hygro-/Thermometer). All dB values given in this study refer to 20 µPa, except for the power spectra presented in Fig. 1 which were normalized to 0 dB.

SONG LEVEL MEASUREMENTS

Song levels were only measured provided there were no obstacles (leaves, branches, bushes, etc.) between the singing bird and the sound level meter. Because nightingale songs, like most vertebrate vocalizations, show a directional sound radiation pattern (Brumm 2002), it is important to control the angle of incidence between the bird's body and the microphone of the sound level meter when taking measures. The sound pressure level of songs was assessed from below the singing bird (average vertical distance 4.0 m; range 1.6 m–8.1 m) with an angle of incidence of about 90° in relation to the animal's longitudinal axis, and the microphone of the sound level meter pointing directly at the singing bird. For each song the maximum value read from the sound level meter was recorded. Only songs uttered while the bird was facing in the frontal direction with no lateral head movements (Brumm & Todt 2003) were subjected to sound level measurement.

All songs analysed were part of one continuous song bout sung from one perch and were measured from the same position. Therefore, the number of songs measured per bird was limited by the circumstance that the nightingales sooner or later changed their position or stopped singing. The average number of measured songs was 28 (range 12–58 songs).

The sound level meter measured not only the sound level of the nightingale songs but the level of all sounds coming from the direction in which the microphone was facing. Therefore one has to subtract the level of

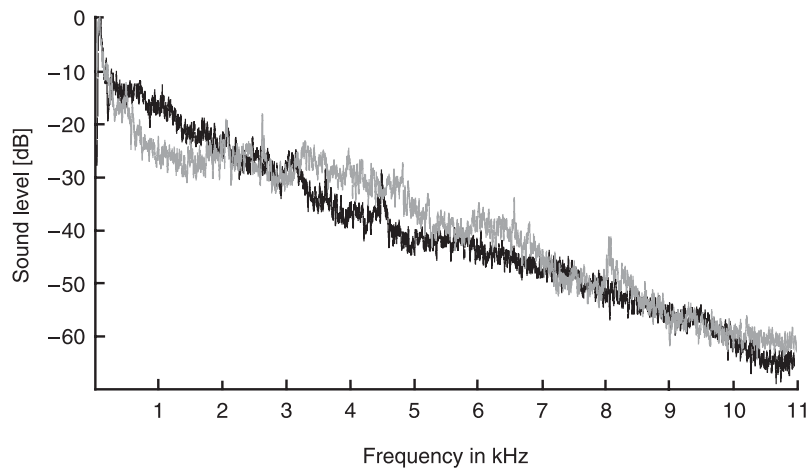


Fig. 1. Environmental noise spectra of two exemplary nightingale territories. Black curve: a territory with high background noise levels (median value 57 dB(A)). At this location the main noise source was traffic sounds from nearby cars, trucks and trains and the songs from great tits (*Parus major* L.). Grey curve: a territory with low background noise levels (median value 45 dB(A)). Here the main noise source was the songs and calls of a multitude of distant birds: blackbird (*Turdus merula* L.), blue tit (*Parus caeruleus* L.), Eurasian cuckoo (*Cuculus canorus* L.), great tit (*Parus major*), greenfinch (*Carduelis chloris* L.) and wood pigeon (*Columba palumbus* L.).

background noise from the value read from the sound level meter to obtain the sound pressure level of a given song. To achieve this, the maximum value of background noise was measured during the silent pause between two successive songs and subtracted from the value measured for the preceding song. This calculation was performed according to the logarithmic computation procedures given in Bradbury & Vehrencamp (1998). [To assess the validity of this method I measured the sound level of sine tones (frequency range: 1–8 kHz, duration: 3 s, separated by pauses of 3 s) played back in nightingale habitats. The difference between these sound level measurements from the field and measurements taken in a sound-shielded room were smaller than 2 dB.]

Finally, following the recording, the horizontal and vertical distance from the position of the bird and the microphone of the sound level meter was assessed with a tape measure.

ENVIRONMENTAL NOISE MEASUREMENT

Immediately following the song level measurements, 2 min of environmental noise was recorded on digital tape with a Sony TCD-D3 DAT recorder from approximately 4 m distance to the bird's songpost. For this purpose I used an omnidirectional microphone (Sennheiser Me 62) mounted facing straight upwards on a tripod 1.5 m above the ground. At the same time, the environmental noise level was measured at the nearest possible position to the bird's songpost, applying the following technique. The sound level meter was aligned horizontal to the ground with one of the four points of the compass (determined by coin toss). Then the environmental sound level (with the settings described above) was measured for 10 s and the maximum value was recorded. After that, the sound level meter was rotated clock-

wise by 90° and the sound level was measured for 10 s, and so on, until eight measurements were taken from each direction.

MEASUREMENTS OF MORPHOLOGICAL TRAITS

A possible noise-dependent difference in vocal amplitude could be due to the regulation of song intensity by the nightingales or the circumstance that birds in louder territories might be able to sing more loudly *per se* because of morphological differences as a confounding variable.

A positive correlation between body size and maximum vocal amplitude seems plausible, because the sound intensity of bird vocalizations could be limited by the size of the respiratory muscles and, connected to this, by the size of the respective bird (Brackenbury 1979). Moreover, such a relationship between body size and vocal amplitude has been found in anurans and insects (review in Gerhardt & Huber 2002).

To examine whether birds in noisier territories were bigger or heavier, I captured the studied males within 6 days after the sound level measurements with mist nets and assessed their wing-length, length of the third primary feather, tarsus length and body mass. These measurements were taken according to the techniques recommended by Svenson (1992). For legal reasons it was not possible to capture all examined birds; therefore, analysis of morphological data is based on 10 males only.

DATA ANALYSES

All sound level values of environmental noise from all directions in a territory were pooled and are given as median values.

The song level measurements from different birds were taken from varying distances. For this reason, it was

necessary to normalize the values to a standard distance in order to compare them between males. First, the direct distance (d) between bird and sound level meter was computed from the horizontal and vertical distances according to Pythagoras's theorem. The average direct distance was 11.1 m (range 8.7–14.1 m). In a second step, the median song level in 1-m distance was calculated for every male according to the following formula based on the spherical spreading loss of sound:

$$L_{1m} = 20 \log d + L_d$$

with L_{1m} being the song level in 1 m distance, d equalling the direct distance between bird and the microphone of the sound level meter and L_d equalling the median song level measured in distance d .

The recording distance did not vary systematically with the median sound pressure level of either the background noise ($r_s = 0.138$, $n = 15$, $P = 0.652$) or the birds' songs ($r_s = 0.163$, $n = 15$, $P = 0.562$).

The 2-min recordings of environmental noise were processed and analysed using Avisoft-SASLab Pro software (version 3.8; R. Specht, Berlin). First, I digitized the recordings with 16-bit resolution and a sampling rate of 22.05 kHz. Then the recordings were divided into sections with a duration of 2 s. Twenty of these sections were chosen randomly and mixed digitally into one section with a duration of 2 s. Finally, a power spectrum was calculated from the mixed section. Each spectrum was smoothed by averaging over 10 Hz and then normalized to 0 dB.

In order to obtain one measure for body size, a principle component analysis with the three initial measures (wing-length, length of the third primary feather, tarsus length) was conducted. The data set was suited for such a data reduction (Kaiser–Meyer–Olkin measure of sampling adequacy: 0.71; Bartlett's test of sphericity: $\chi^2 = 7.85$; d.f. = 3; $P < 0.05$). The principle component analysis yielded one component with an eigenvalue higher than 1 (2.21), which explained 74% of the total variance in the data. The loadings of the three initial measures on this first principle component ranged from 0.827 to 0.864. The score on the first principle component was then used as a composite measure of body size (hereafter 'body size score') for further analyses.

Environmental noise levels may vary in the course of the day, e.g. due to the influence of wind, the high singing activity of birds at dawn (e.g. Dabelsteen & Mathevon 2002) or diurnal variation in man-made noises. Therefore, the time of day was considered in the analysis, to control for a confounding effect.

In order to examine which features of the environment and the bird determine the sound level of songs, I conducted a multiple linear regression with air temperature, humidity, time of day, environmental noise level, body size score and body mass as predictor variables and song level as dependent variable. Because air temperature, humidity and time of day correlated significantly with each other (Spearman's rank correlation: $r_s >$

0.655, $n = 15$, $P < 0.05$), these variables were not used separately in the regression model. Instead a principle component analysis was conducted. The data set was suited for such a data reduction (Kaiser–Meyer–Olkin measure of sampling adequacy: 0.72; Bartlett's test of sphericity: $\chi^2 = 25.94$; d.f. = 3; $P < 0.001$). The principle component analysis yielded one component with an eigenvalue higher than 1 (2.531), which explained 84% of the total variance in the data. The loadings of the three initial measures on this first principle component were 0.947 (temperature), -0.884 (humidity) and 0.923 (time of day). The score on the first principle component was used as a composite measure of weather and time in the multiple regression analysis.

Results

The territories examined differed markedly in the sound level of environmental noise. Mean values of background levels between territories ranged between 40 and 64 dB(A). In the five loudest territories the main noise source was traffic noise from roads, whereas in the remaining territories, traffic sounds played a minor role. At the five locations with the lowest environmental sound level the songs of other bird species were the main source of background noise. However, in all territories high-amplitude regions in the environmental noise spectra coincided with the frequency band of nightingale songs from 1 to 8 kHz (Fig. 1).

The majority of the total variance in song level could be explained by the regression model ($r^2 = 0.819$, $F_{4,5,9} = 5.642$, $P < 0.05$). Air temperature, humidity and time of day had no significant influence on the measured song level of birds (standardized coefficient $\beta = 0.021$, $t = 0.083$, $P = 0.937$). In contrast, a significant relationship between the environmental background noise level in a territory and the sound pressure level of the territory owner's songs was found: nightingales at noisier locations sang with higher song levels ($\beta = 0.794$, $t = 3.151$, $P < 0.05$; Fig. 2). The male holding the territory that was least affected by environmental noise sang with a median sound level of 77 dB(A) (in 1-m distance).

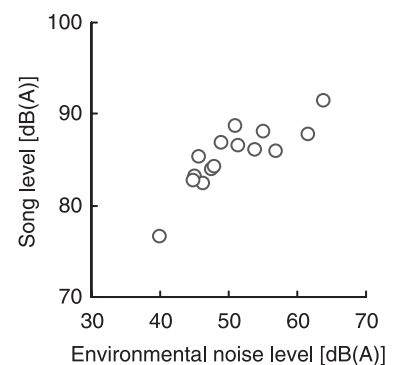


Fig. 2. Relationship between environmental background noise level in a territory and the sound pressure level of the territory owner's songs. Each datapoint represents the median value of one male nightingale (dB re. 20 μ Pa).

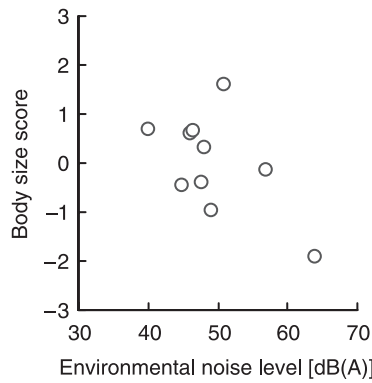


Fig. 3. Body size of male nightingales (principal component on wing-length, length of the third primary feather and tarsus length) and the median environmental background noise level in their territories (dB re. 20 μ Pa).

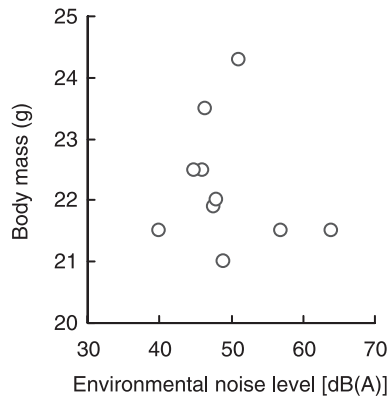


Fig. 4. Body mass of male nightingales and the median environmental background noise level in their territories (dB re. 20 μ Pa).

In contrast, the bird singing in the noisiest territory produced its songs on the average with more than 91 dB(A). Given the logarithmic scaling of level measurements, the detected range of 14 dB in the full song levels of free-ranging nightingales corresponds to a more than fivefold difference in vocal sound pressure.

The revealed correlation between song level and background noise does not necessarily imply causation. However, birds recorded in noisier territories were neither bigger ($\beta = -0.232$, $t = -0.563$, $P = 0.597$; Fig. 3) nor heavier ($\beta = 0.329$, $t = 0.859$, $P = 0.430$; Fig. 4). Furthermore, the additional measurements of song levels on weekend days (when there was less traffic in the morning hours and environmental noise levels were lower) yielded intra-individual changes in vocal intensities dependent on natural variation of noise levels, indicating that the birds indeed adjusted the sound pressure levels of their songs depending on the background noise (Fig. 5).

Discussion

The impact of environmental background noise on the song amplitude of territorial nightingales was studied

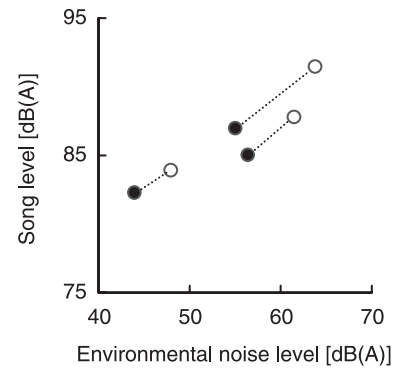


Fig. 5. Individual adjustment of song level in three male nightingales exposed to traffic noise. Data points represent the median sound pressure level of their songs in relation to the median environmental background noise level on weekends (filled circles) and working days (open circles), dB re. 20 μ Pa.

in the birds' natural habitats. The results demonstrate that males in noisier territories sang with higher sound pressure levels than birds at less noisy locations. However, neither bigger nor heavier males were found in louder territories, showing that the observed differences in song amplitude could not be accounted for by morphological differences of the birds. Instead, the revealed song level differences had to be based on a noise-dependent regulation of vocal amplitude. These findings are the first evidence for such a vocal regulation mechanism (also known as the Lombard effect) in the natural environment of an animal.

There are grounds for the assumption that birds in noisier territories produced louder songs to mitigate impairments on the exchange of information between individuals, for this behaviour will help to maintain the distance in which another conspecific can perceive their songs. Thus songsters in noisier territories had to sing with higher vocal amplitude to gain a hearing, e.g. before the background of songs produced by other species or abiotic noise, such as traffic noise from roads.

It is known that disturbance by anthropogenic noise can influence populations of breeding birds. Many studies show evidence for a decline in both number of species and number of individuals due to increased environmental noise levels caused by road traffic (e.g. Reijnen, Foppen & Veenbaas 1997; Weiserbs & Jacob 2001; Forman, Reineking & Hersperger 2002). However, not all species are affected to the same degree, and some species even appear not to be vulnerable to disturbance from traffic noise (Fernández-Juricic 2001; Rheindt 2003). Furthermore, some birds may habituate quickly to environmental noise exposure (Harms, Fleming & Stoskopf 1997), but also less sensitive species that populate noisy habitats can be affected by background sounds, as the findings of this study suggest. Even when there are no obvious influences, environmental noise can have an impact on birds, for species that do not show an effect on density can still be affected by acoustical masking of songs. The masking

of signals can impair acoustic communication severely, thereby leading to difficulties in mate attraction and territory defence.

As the results of this study showed, songbirds counteract these difficulties by increasing vocal amplitude, but as birds are forced to sing louder at noisy locations, they have to face the possible costs related to increased vocal intensities. *Inter alia*, these costs may be a question of energy expenditure, because the production of sounds with a higher sound level requires more energy. In their comparative study on the metabolic costs of singing in passerines, Oberweger & Goller (2001) showed that a 16-dB increase in the song level of starlings (*Sturnus vulgaris*) led to a 16% increase in the rate of oxygen consumption. However, the overall metabolic costs of singing do not seem to be high and other factors such as detection by unwanted receivers (e.g. predators) might also contribute to the costs of increased vocal amplitude. The significance of the costs of singing loudly is emphasized by the fact that territorial birds do not maximize their vocal amplitude *per se* (Brumm & Todt 2002). Therefore, males holding territories exposed to higher environmental noise levels are at a disadvantage because they have to bear the increased costs of singing loudly. Of course, this applies not only to anthropogenic noise, but for all sounds that match the song frequencies of a given bird species. In this context, the sounds emitted by other animals in an ecological community can be of considerable impact, e.g. the intense background sounds produced by chorusing anurans or insects, or the dawn chorus of songbirds.

A special case of an environment with high levels of biotic noise are the breeding grounds of colonial animals. Studies in king penguins (*Aptenodytes patagonicus*) showed how the birds' call recognition system has adapted to the omnipresent acoustic masking of calls by conspecifics in the colony (Aubin & Jouventin 1998). Moreover, king penguins (Lengagne *et al.* 1999) as well as Japanese quail, *Coturnix coturnix japonica* (Potash 1972) are able to increase signal transmission by adjusting the serial redundancy dependent on the environmental noise level or wind condition, i.e. as the noise level increases the birds also increase the number of syllables per call series. In contrast to these findings in birds, it has been shown that common marmosets (*Callithrix jacchus*) do not use such an increased redundancy to cope with interference from background noise; instead, these New World monkeys regulate the duration of call syllables as the noise level varies (Brumm *et al.* 2004). However, in all animals tested so far, these additional forms of noise-dependent vocal plasticity are always exhibited in connection with the Lombard effect, emphasizing the crucial role of amplitude regulation for communication in noise.

Finally, it should not be forgotten that the amplitude of songs plays an important role in the discussion of the sexual selection of signal traits and, connected to this, on the constraints of singing (Gil & Gahr 2002). Due to the difficulties of measuring sound levels in the field,

however, there has been a paucity of studies addressing the intensity of animal vocalizations. To fill this gap, the method for song level measurements in the field presented in this study may be useful.

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