

# The ecology of vocal signaling: male spacing and communication distance of different song traits in nightingales

Marc Naguib,<sup>a,b</sup> Rouven Schmidt,<sup>b,c</sup> Philipp Sprau,<sup>a,b</sup> Tobias Roth,<sup>d,e</sup> Cornelia Flörcke,<sup>b</sup> and Valentin Amrhein<sup>d,e</sup>

<sup>a</sup>Netherlands Institute of Ecology (Nioo-KNAW), Department of Population Biology, Heteren, The Netherlands, <sup>b</sup>Faculty of Biology, Animal Behaviour, University Bielefeld, Bielefeld, Germany, <sup>c</sup>Max Planck Institute for Ornithology, Seewiesen, Germany, <sup>d</sup>Research Station Petite Camargue Alsacienne, Saint-Louis, France, and <sup>e</sup>Evolutionary Biology, Zoological Institute, University of Basel, Basel, Switzerland

The ecology of a species and its communication system require mutual adaptations. Specifically, information transfer between individuals needs to be adapted to the social and ecological requirements and constraints. As a consequence, constraints on signal transmission are likely to play a role in the evolution of spatiotemporal behavior and settlement and vice versa. In long-distance signaling, such as in bird song, adaptations can be reflected in specific signal structures that transmit to a socially relevant distance without degradation masking the coded information. Here, we studied sound transmission properties of 2 different song components in male nightingale (*Luscinia megarhynchos*) territorial song, i.e., transmission of whistle songs and songs with rapid broadband trills. We also determined spacing of nocturnal song posts using a global positioning system. The results revealed highly significant differences in transmission of the 2 functionally different song traits, with information in whistles traveling well beyond the typical spacing between neighboring individuals. Information coded in trills bandwidth did not even travel the average distance toward the nearest neighbor, showing that information coded in trill bandwidth is not available for receivers at typical spacing distances. The results emphasize that for a better understanding of evolutionary processes in communication, ecological components such as spatial distance as well as signal structure and signal degradation have to be taken into account. *Key words:* bird song, environmental acoustics, GPS, sound transmission, territorial settlement. [*Behav Ecol* 19:1034–1040 (2008)]

## INTRODUCTION

Signals and their information content play a central role in individual decision-making processes. The ecology of a species and its social system thereby require specific adaptations in communication so that the information that is signaled can be received and processed by intended receivers. The structure of the habitat and the spacing of individuals, for instance, have strong implications on the evolution of a signaling system (Endler 1993). Likewise, the distance up to which socially relevant signals can propagate may constrain the spacing patterns of territorial individuals so that constraints on signal transmission may have affected the evolution of spatial behavior and strategies that regulate spacing. Understanding the evolution of spatial settlement patterns and long-distance communication thus requires mutual consideration. Signals degrade and attenuate during transmission from the source to a receiver so that the structure and the information content of a signal at its source differ from its structure and information content at the position at which a receiver makes a decision (Wiley and Richards 1978, 1982; Dabelsteen et al. 1993; Mathevon et al. 1996; Endler and Basolo 1998; Naguib and Wiley 2001; Mathevon et al. 2008). Thus, in natural situations, it is not always evident which information is available for an individual when responding to a signal as individual spacing

and environmental constraints will limit an individual's ability to extract all information coded by a signaler in a signal. Yet, analyses of signals or experiments testing the responses to signals commonly use settings in which a full, clear and undegraded signal is the unit of investigation. In order to understand the role of information coded in a signal in decision-making processes, however, it also needs to be determined which information is actually transmitted.

Among the diversity of signals used by animals, alarm calls (Krams et al. 2007) and sexually selected advertisement signals (Searcy and Nowicki 2005) have provided particularly deep insights into information content of signals and their processing by receivers. Advertisement signals usually are long ranging and provide information on the signalers' motivation and quality. In complex signals, such as birdsong, such information may be coded in specific acoustic traits that do not necessarily transmit the same distance as other traits of the signal.

Among the diversity of songbirds, the nightingale (*Luscinia megarhynchos*) is a particularly interesting species to assess differences in function and transmission distance of specific song traits. Males have large song repertoires (Kipper et al. 2006), and some structurally different songs can be assigned to different functional categories, for example, whistle songs (Naguib et al. 2002) and songs with rapid broadband trills (Kunc et al. 2006; Schmidt et al. 2008). Whistle songs are characterized by being initiated with a series of whistles with minor frequency modulation (Hultsch and Todt 1996). These songs attract attention specifically in long-distance communication and are hypothesized to play an important role in female attraction during nocturnal song (Naguib et al. 2002; Kunc et al. 2005). Such whistles in general have been argued to act as

Address correspondence to M. Naguib. E-mail: m.naguib@nioo.knaw.nl.

Received 12 March 2008; revised 25 April 2008; accepted 7 May 2008.

alerting components (Richards 1981) and by accumulating reverberation within their narrow frequency band to use the otherwise detrimental effects of reverberation in a beneficial way (Slabbekoom et al. 2002). Songs with rapid broadband trills, in contrast, are used specifically in short-range aggressive interactions between males (Kunc et al. 2006; Schmidt et al. 2006, 2008) and elicit stronger territorial responses than do songs without such trills (Schmidt et al. 2008). Trills reverberate rapidly in dense vegetation and therefore are not well suited for long-range communication (Naguib 2003). Moreover, as a broadband signal, trills will be increasingly affected by irregular amplitude fluctuations and frequency-dependent attenuation with increasing propagation distance (Marten and Marler 1977; Piercy et al. 1977; Richards and Wiley 1980). Despite these gross differences in structure of song components and the associated predictions regarding propagation distance, there still is little information available on the actual differences in transmission distance relative to the spacing of communicating individuals.

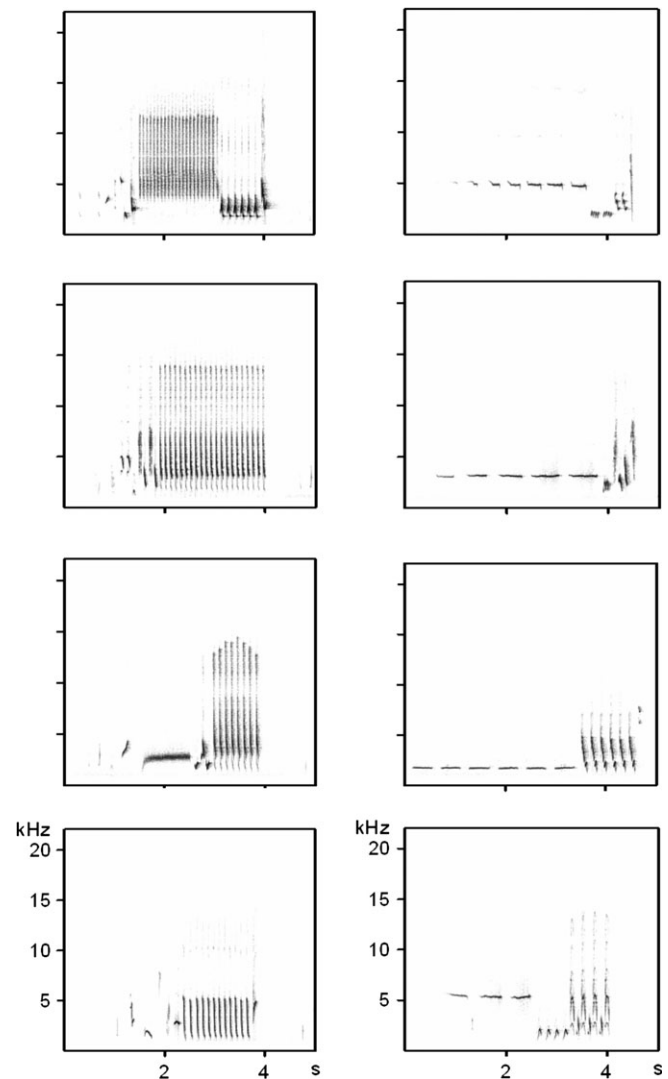
Here, we report a sound transmission experiment using 2 functionally relevant song components in nightingale song. We broadcast songs containing rapid broadband trills and whistle songs over different distances across different transects within nightingales' typical habitat. Furthermore, we determined nocturnal song post distances using a global positioning system (GPS) in order to quantify typical spacing of nocturnally singing nightingales. Combining these methods allowed determining the structure of specific song traits at different transmission distances and comparing the results with actual spacing patterns of naturally communicating individuals.

## METHODS

We conducted the sound transmission experiments between 00:00 and 03:00 h CEST on 29 April and 2 May 2007 at the Petite Camargue Alsacienne in France, 10 km north of Basel, Switzerland. The habitat here is highly fragmented and nightingales settle along hedgerows and canals as well as in groups of bushes. Vocal long-distance communication thus takes place across open areas such as water or fields with low ground vegetation, along hedgerows or heterogeneous mosaic of bushes. Therefore, song degradation mainly results from frequency-dependent attenuation and irregular amplitude fluctuations rather than from reverberation (Richards and Wiley 1980).

### Determination of song post distances

We used a GPS to determine distances among nocturnal song posts of 139 nightingales in the larger vicinity of the area (about 18 km<sup>2</sup> in and near the Petite Camargue Alsacienne) during nocturnal rounds made every night from 10 April until 20 May. These song posts give a good indication of typical spacing of individuals and reflect communication distance between males at night, which is the time of particularly high song output in unmated males (Amrhein et al. 2002; Amrhein et al. 2004a, 2004b). Mated females usually are within the territory of their mates at night, as evidenced by radio-tracking data (Amrhein V, Kunc HP, Naguib M, unpublished data), so that these distances also are a good approximation for listening distance by mates and average distance between males being on their territory (Naguib et al. 2001). While using a fixed route during the rounds at night to cover the whole study area, song posts were approached with caution, and GPS readings could usually be taken within 5 m of the song posts without disturbing the singing bird. Based on all GPS data, the metric distances between all possible pairs of individuals were determined. We used these data to determine the distance to the nearest neighbor on the day of settlement and at the end



**Figure 1**  
Songs with rapid broadband trills (left panel) and whistle songs (right panel) as used in the sound transmission experiment.

of the season. We further calculated the number of neighbors within radii of 32, 64, and 128 m (distances used in the sound transmission experiments) and also within larger radii of 200 and 400 m.

### Selection of songs

As broadcast stimuli, we used 11 whistle songs and 11 songs containing rapid broadband trills (Figure 1). Songs were recorded from males in the study population in previous years. Recordings were made on nocturnal song within 10 m of the song post using a Sennheiser ME66/K6 microphone (Sennheiser electronic cooperation, Wedemark, Germany) and Sony TCD5M tape recorders (Sony Ltd, Tokyo, Japan). Songs were digitized on a PC with a sample rate of 44 100 Hz using Cool Edit 2000 (Syntrillium Software Cooperation, Phoenix, AZ.). Each song was taken from a different male, and songs were selected on the basis to cover the within-song category variation. Whistle songs used covered the natural range (Naguib et al. 2002) and had whistles with peak frequencies of  $3198 \pm 1600$  Hz (mean  $\pm$  standard deviation; range 1330–6240 Hz). Broadcast rapid broadband trills had  $16 \pm 5$  repeated elements (range 8–23 elements), an element

repetition rate of  $11.1 \pm 2.5$  elements/s (range 8.5–16.5 elements/s) and a bandwidth at  $-10$  dB from the peak frequency of  $4334 \pm 1699$  Hz (range 2930–7918 Hz; FFT length, 1024 point; frequency resolution, 43 Hz). Songs were compiled into 1 file with 11 whistle songs followed by 11 songs with rapid broadband trills. The set of songs was then repeated 2 times so that the broadcast file contained 3 replicates for each song. Each song was normalized separately in peak amplitude using Adobe Audition 1.0 (Adobe Systems Incorporated).

### Sound transmission experiments

All songs were broadcast as wave files from a Trekstore i.Beat drive 2.0 digital player connected to a Blaupunkt MPA 2 amplifier and a Canton S loudspeaker. The loudspeaker was connected to a telescopic pole and positioned at 2 m height, which is a common perch height in singing nightingales. Sounds were broadcast with 93.3 dB as measured at 1 m using a Voltcraft 322 sound pressure level (SPL) meter (C settings, fast response) on a 5-s 1-kHz sine tone of equal peak amplitude as the songs of the broadcast sound file. Songs were rerecorded successively at 32, 64, 128, and 256 m using a Sennheiser ME 64/K6 microphone connected to a digital Marantz PMD 660 solid-state digital recorder. At 16 m, we measured the sound pressure level (SPL) of the 1 kHz sine tone and recorded it on the Marantz recorder using the identical recording settings as used for the larger distances. We used 16 m as reference point at half the distance to our first recording distance (rather than 32 m, our first full recording distance) to obtain a better signal/noise ratio for the reference tone when determining SPL with the omni directional SPL meter. The SPL of this tone was then used to calibrate the software for sound analysis (see below). The microphone was connected to a telescopic pole and was, as was the loudspeaker, positioned at 2 m height to simulate the situation at which birds on their song posts perceive rivals' song. In order to control for effects of the sound equipment on spectral song characteristics, we broadcast the complete file in a soundproof chamber at the University of Bielefeld and rerecorded the sounds using the same equipment as used in the field. Here, sounds were broadcast with 92.7 dB at 1 m. The control measures at 1 m distance were then taken

from these rerecorded sounds rather than from the original sounds in the wave file used for playback.

Songs were broadcast and rerecorded along 4 transects, 3 of which were along hedgerows and 1 across an open field with soft soil and no ground vegetation. The loudspeaker on the pole always was positioned in a bush, i.e., at typical singing position of a nightingale and directed toward the microphone. The microphone was also positioned in a bush along the hedgerow, except at the open field where the pole was positioned on the field, i.e., with no vegetation nearby.

### Analysis of sounds

All sounds were analyzed on a PC using Saslab Pro (Version 4.39; Raimund Specht, Berlin, Germany). We first used the rerecorded sine tone at 16 m to calibrate Saslab. All SPL measures taken from the larger recording distances were then calculated with reference to that tone. In order to quantify spectral changes with transmission distance, we calculated sound spectrograms (FFT length, 1024 point, frequency resolution, 43 Hz) from which we calculated power spectra. From the power spectra, we took the following measures: 1) bandwidth at  $-10$  dB below the peak, 2) highest frequency at  $-10$  dB below the peak, 3) peak frequency (=frequency at peak amplitude), and 4) amplitude at peak frequency. We used  $-10$  dB as threshold frequency to be able to take the same measure of bandwidth at all propagation distances. Due to the low signal to noise ratio at 256 m, we were not able to extract these parameters from most songs so that we excluded this distance from the analysis.

For analysis, we used for each of the sound parameters general linear models (GLMs) for repeated measures with distance as the repeated factor (4 levels: 1, 32, 64, and 128 m) and song category (whistle or trill) and transect (4 levels) as fixed factors. Differences between the 4 transects were not significant in the initial model for most parameters except for amplitude at peak frequency (Table 1) so that transect was excluded as factor from the respective final models. Some songs, mainly trills, had degraded below background noise at 128 m so that the final sample size for trills is lower than for whistles; overall trill sample size was  $N = 35$  ( $N = 34$  for bandwidth), and overall whistle sample size was  $N = 44$  ( $N = 43$  for bandwidth).

**Table 1**  
Results of the final GLM using distance as repeated factor and transect and song category as independent factors

Variable	Bandwidth		Maximum frequency		Peak frequency		Amplitude at peak frequency	
	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>
Distance	49.44 <sup>a</sup>	<0.000001	51.33 <sup>b</sup>	<0.000001	9.06 <sup>c</sup>	0.001	3896.20 <sup>d</sup>	<0.000001
Song category	206.05 <sup>c</sup>	<0.000001	26.40 <sup>f</sup>	<0.000001	0.51 <sup>g</sup>	0.48	4.17 <sup>h</sup>	0.45
Transect		ns		ns		ns	1.81 <sup>i</sup>	0.15
Distance x song category	50.99 <sup>a</sup>	<0.000001	52.25 <sup>b</sup>	<0.000001	8.04 <sup>c</sup>	0.002	16.96 <sup>d</sup>	<0.000001
Distance x transect		ns		ns		ns	3.94 <sup>d</sup>	0.001

Entries with 'ns' indicate that the factor was not significant in the initial model and thus removed for the final model.

<sup>a</sup>  $F_{3,92.1}$ .

<sup>b</sup>  $F_{3,94.6}$ .

<sup>c</sup>  $F_{3,112.1}$ .

<sup>d</sup>  $F_{3,141.6}$ .

<sup>e</sup>  $F_{1,75}$ .

<sup>f</sup>  $F_{1,76}$ .

<sup>g</sup>  $F_{1,77}$ .

<sup>h</sup>  $F_{1,71}$ .

<sup>i</sup>  $F_{3,71}$ .

We used Huynh-Feldt corrections, as criteria for sphericity were not met. Residuals for most models were not normally distributed even after transformation. However, because we obtained similar results with separate Friedman analyses of variance, we here report the results from the GLMs, which additionally allowed studying the interactions. Statistical analysis was conducted with SPSS 14.0.

## RESULTS

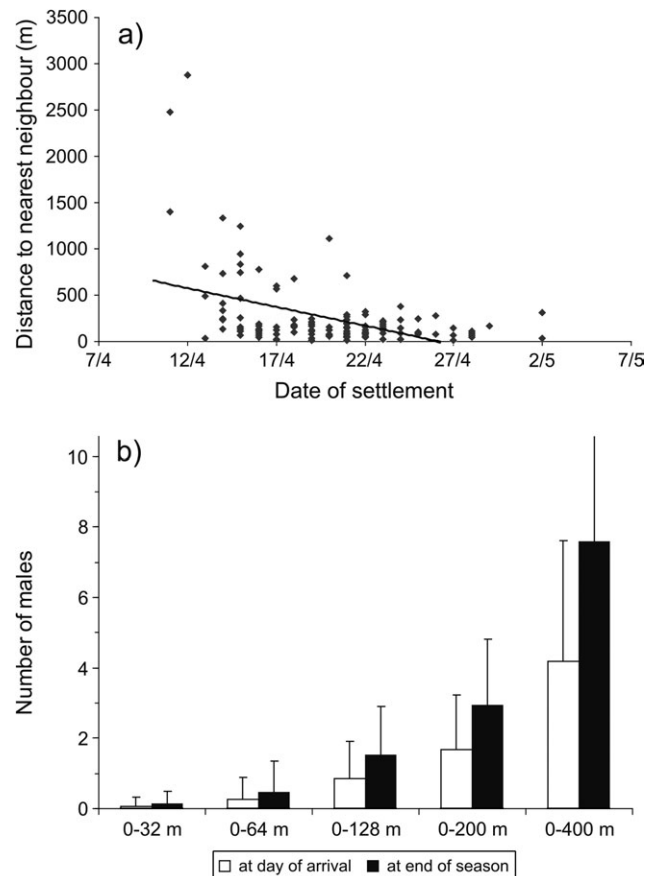
On the day of settlement, the median distance between a male's nocturnal song post and that of the nearest neighbor of 139 sampled males was 129 m (Figure 2a). This distance to the nearest neighbor on the day of settlement decreased significantly over the season even though some early arriving males already settled close to each other (regression,  $r^2 = 0.193$ ,  $P < 0.0001$ , Figure 2a). The number of neighbors increased from the day of settlement toward the end of the season and with increasing radii. However, for the shorter radii over which song can be heard well, i.e., below 32 and 64 m, as shown below, the average number of males toward the end of the season was still well below one neighbor (Figure 2b).

The sound transmission experiments revealed highly significant structural changes with increasing distance specifically for trills and highly significant differences in transmission of trills and whistles (Table 1, Figures 3 and 4). The differences among the song types were most pronounced in the 2 bandwidth measures, frequency bandwidth, and highest frequency at  $-10$  dB from the peak. Whistles did not change much with increasing propagation distances, whereas trill bandwidth decreased highly significantly with distance. This decrease in bandwidth in trills was statistically significant in all distance comparisons (all  $P < 0.001$ , least-significant difference post hoc tests) but in absolute values most pronounced within the first 32 m (Figure 3). Trills thus degraded in bandwidth below the distance to the nearest neighbors, whereas whistle songs maintained their spectral characteristics even well beyond the distance to the nearest neighbor. Transect had no significant effect on any of the measured parameters except for a significant interaction between transect and distance and between transect and song category for amplitude at peak frequency. This effect mainly resulted from sounds being louder at long distances in transect 4 (the open field) compared with the other transects (hedgerows).

## DISCUSSION

The experiments revealed significant differences in the communication distance of whistles and rapid broadband trills. Whistles did not degrade in spectral structure with increasing propagation distance, whereas rapid broadband trills did so substantially. Thus, the experiments show that information coded in the 2 different song components has different communication distances. Most interestingly, the sound transmission experiments in combination with GPS measurements of nearest neighbor distances revealed that information coded in the bandwidth of broadband trills was lost even below the typical spacing of neighboring nightingales. Information coded in the whistles' spectral domain, in contrast, transmitted well across the regular communication distance of neighboring and even more distant individuals.

Such differences in transmission distance in different signal components have fundamental implications for our understanding of communication systems and understanding communication in the light of the ecology of a species. Studies on communication distance of signals usually focus on the complete signal as a unit. Use of low-amplitude song (soft song) in songbirds, for instance, has been shown to be a signal

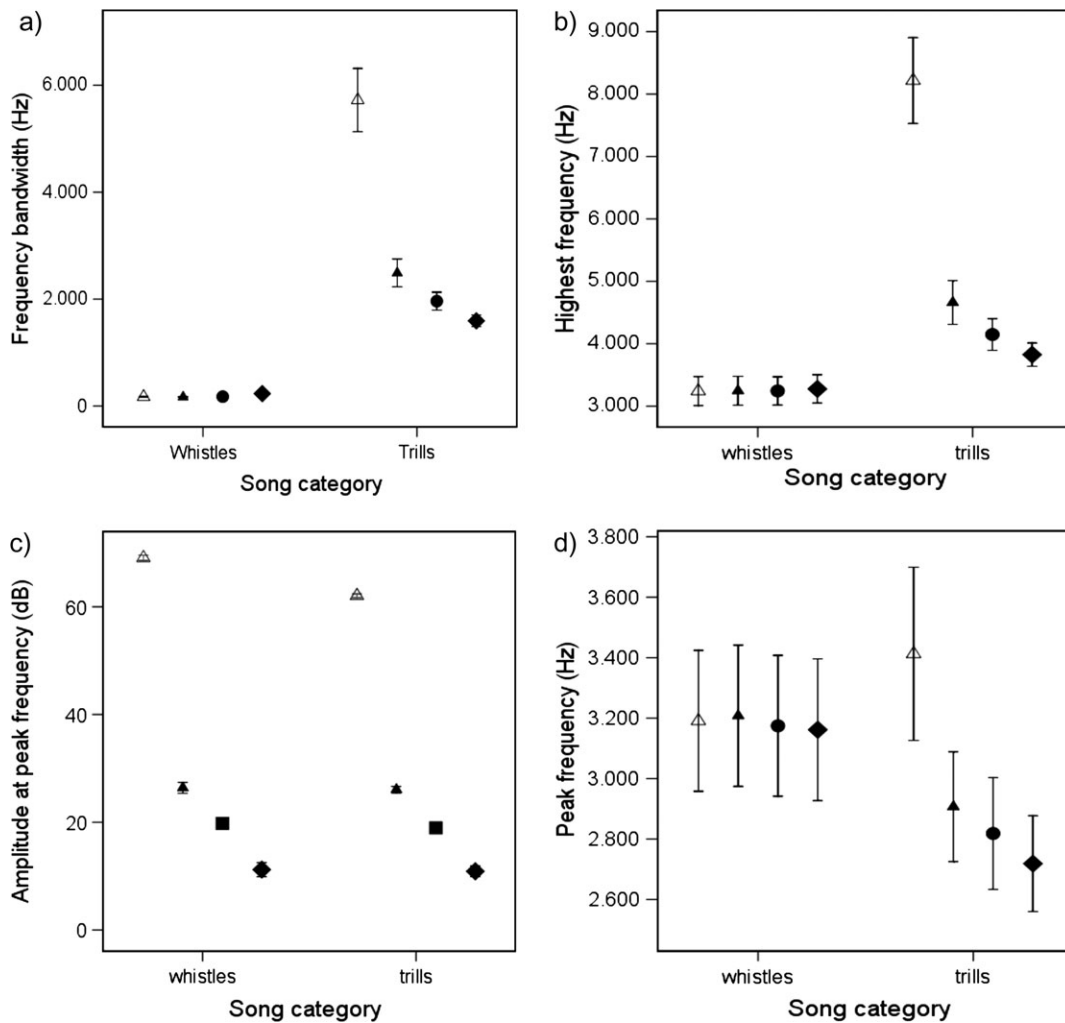


**Figure 2**

Settlement patterns of male nightingales. (a) Distance to the nearest neighbor plotted against the date of settlement. Distances were measured based on GPS coordinates taken at nocturnal song posts (b) Mean ( $\pm$  standard error) number of neighbors within the radii used for sound transmission playback (32, 64, and 128 m) and in larger radii (200 and 400 m).

specifically used in short-range communication (Dabelsteen et al. 1998; Anderson et al. 2007). These signals as a whole are designed for short-range communication and minimize the possibility for distant individuals to eavesdrop on the interaction (Naguib et al. 2004). In other words, if the intended receiver is close by, and if information may not be in the sender's interest to reach other individuals, there are mechanisms to accomplish this interest. Likewise, in long-distance communication, birds have been shown to increase the amplitude of their song under noisy conditions, presumably to maintain communication distance under unfavorable acoustic conditions (Brumm and Todt 2002; Brumm 2004). The differential transmission of different song components, as quantified in our experiment, is functionally different from an overall change in amplitude as males could vary transmission distance of specific information by selecting specific songs without affecting the more general signal value in territory advertisement.

The strong spectral degradation of the trills in combination with our data of spacing of song posts indicates that information coded in trill bandwidth is not available for vocal communication between neighbors at their typical communication distance. This applies not only to the early arriving males as shown by the settlement data but also to males that settle subsequently at a closer distance which on average is still beyond the propagation distance of the trill bandwidth. These



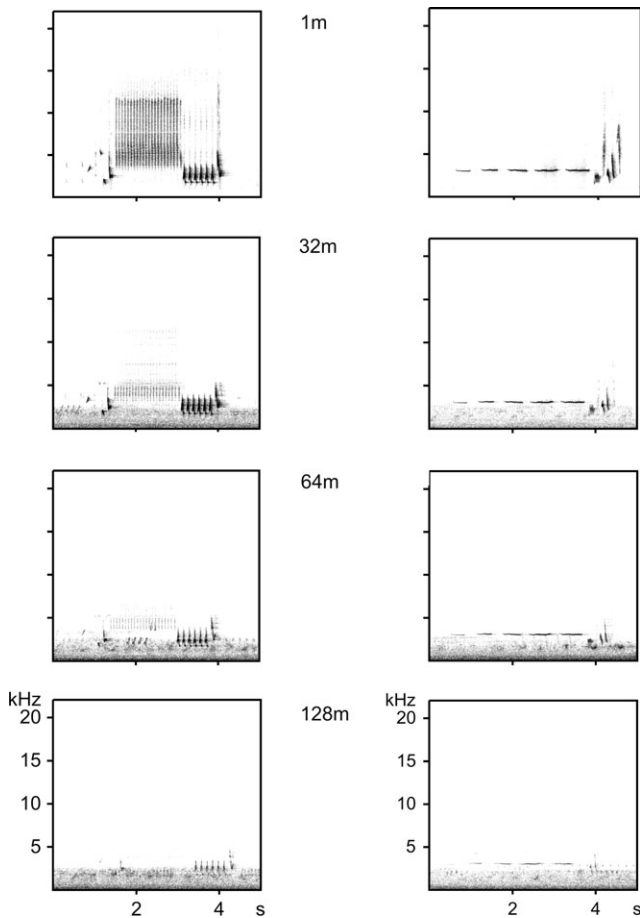
**Figure 3**

Degradation of whistles and trills across distance. Different symbols indicate the different distances from left to right, 1 m (open triangles), 32 m (filled triangles), 64 m (filled squares), 128 m (filled diamonds). Shown are means  $\pm$  standard error: (a) frequency bandwidth, (b) highest frequency, (c) amplitude at peak frequency, and (d) peak frequency (frequency at amplitude peak).

findings are particularly interesting as trills have been shown to be of specific signal value for males and females (Ballentine et al. 2004; Illes et al. 2006; Schmidt et al. 2008). Production constraints on rapid trills with broad bandwidth have been taken to suggest that these signals reflect aspects of male quality (Podos 1996, 1997). Males have to open and close their beaks widely and rapidly and to coordinate these beak movements on a fine scale with breathing patterns and syringeal activity, resulting in a trade-off between bandwidth and trill element repetition rate (Hoese et al. 2000). Whereas in some species rapid trills have been shown to correlate with female choice (Vallet and Kreuzer 1995; Ballentine et al. 2004), songs with rapid broadband trills in nightingales rather function as agonistic signal in male-male interactions (Kunc et al. 2006; Schmidt et al. 2006, 2008). In vocal interactions among nightingales and other songbirds with similar song traits and spacing patterns, however, the information coded in trill bandwidth is apparently not available at typical communication distances. In other words, a male needs to approach closely and below the typical distance between nocturnal song posts in order to decide how broadband the trills really are. Likewise, also females would not be able to assess neighboring males based on these song traits unless approaching. A possi-

ble function of trill bandwidth as aggressive signal thus will not be available unless at very close range, which may at least partly explain why males intrude into neighbors' territories when these are challenged by a unfamiliar rival (Naguib et al. 2004). These considerations suggest that in male-male interactions, trills seem to function as close-range signal of motivation rather than as a general long-range signal of quality as the latter information should be coded in traits traveling at least to the next potential receiver. Whether or not the trill bandwidth functions as a short-range signal to reassure the own quality to the mate is a possibility that remains to be tested. The rapid loss of bandwidth in trills over 32 m also makes these signals a good candidate to assess distance (Naguib 1995). Distance becomes particularly important at close range as the probability of a physical encounter increases with decreasing distance, so that the ability of accurate distance assessment at short range may have played a role in the evolution of these signal components (Naguib and Wiley 2001).

Whistles transmit over a given distance with little spectral degradation and transmit beyond the typical spacing of the closest territorial neighbors as revealed by our analyses. Indeed, male nightingales tend to become more responsive to whistle songs the further away the rival is. Playback



**Figure 4**  
Spectrograms of a song with rapid broadband trills (left panel) and of a whistle song (right panel) as recorded at different transmission distances.

experiments showed that males increase the accuracy of matching the whistle pitch with larger distances (Naguib et al. 2002). In the absence of strong reverberation (Slabbekoorn et al. 2002), whistles also provide very little specific distance information, except that their overall attenuation along with the full song provides distance cues (Naguib 1997). Even though there is still little evidence on the function and consequences in use of such long-distance signals, they may be important in maintaining a status within the wider neighborhood. Extraterritorial forays by males of varied song bird species indicate that social and spatial relations exist even beyond the specific relation between nearest neighbors (Hanski 1992; Chandler et al. 1997; Pitcher and Stutchbury 2000; Naguib et al. 2001), and such relations may be important for territorial and non-territorial eavesdropping conspecifics (Naguib et al. 2004; Amrhein et al. 2004a). It also has been hypothesized that whistle songs have a specific function in nocturnal song to attract attention by females (Naguib et al. 2002; Kunc et al. 2005). Whistle songs thus may either have a specific function to maintain social relations on a distant level or act as alerting component to draw attention to attend to the singer and facilitate perception of other song components (Richards 1981).

Taken together, the experiments show that long-distance communication cannot be understood fully without taking into account differential transmission of different signal components relative to the spacing of individuals. Communication and ecological spacing patterns thus are intrinsically linked

to each other, and combining the 2 reveals important insights in processes of communication and spatial ecology.

## FUNDING

Swiss Association Pro Petite Camargue Alsacienne, by a grant from the Treubel Fonds to V.A.; German Science Foundation (Na 335/8) to M.N.

We thank Alexandra Wolf and Sébastien Goumon for assistance in the field and Indrikis Krams and an anonymous reviewer for comments on the manuscript.

## REFERENCES

- Amrhein V, Korner P, Naguib M. 2002. Nocturnal and diurnal singing activity in the nightingale: correlations with mating status and breeding cycle. *Anim Behav*. 64:939–944.
- Amrhein V, Kunc HP, Naguib M. 2004a. Non-territorial nightingales prospect territories during the dawn chorus. *Proc R Soc Lond B* 271 (Suppl):S167–S169.
- Amrhein V, Kunc HP, Naguib M. 2004b. Seasonal patterns of singing activity vary with time of day in the nightingale. *Auk*. 121:110–117.
- Anderson CA, Nowicki S, Searcy WA. 2007. Soft song in song sparrows: response of males and females to an enigmatic signal. *Behav Ecol Sociobiol*. 61:1267–1274.
- Ballentine B, Hyman J, Nowicki S. 2004. Vocal performance influences female response to male bird song: an experimental test. *Behav Ecol*. 15:163–168.
- Brumm H. 2004. The impact of environmental noise on song amplitude in a territorial bird. *J Anim Ecol*. 73:434–440.
- Brumm H, Todt D. 2002. Noise-dependent song amplitude regulation in a territorial songbird. *Anim Behav*. 63:891–897.
- Chandler CR, Ketterson ED, Nolan V. 1997. Effects of testosterone on use of space by male dark-eyed juncos when their mates are fertile. *Anim Behav*. 54:543–549.
- Dabelsteen T, Larsen ON, Pedersen SB. 1993. Habitat-induced degradation of sound signals—quantifying the effects of communication sounds and bird location on blur ratio, excess attenuation, and signal-to-noise ratio in blackbird song. *J Acoust Soc Am*. 93:2206–2220.
- Dabelsteen T, McGregor P, Lampe HM, Langmore N, Holland J. 1998. Quiet song in song birds: an overlooked phenomenon. *Bioacoustics*. 9:89–105.
- Endler JA. 1993. Some general comments on the evolution and design of animal communication systems. *Philos Trans R Soc Lond B*. 340:215–225.
- Endler JA, Basolo AL. 1998. Sensory ecology, receiver biases and sexual selection. *Trends Ecol Evol*. 13:415–420.
- Hanski IK. 1992. Territorial behaviour and mixed reproductive strategy in the chaffinch. *Ornis Scand*. 23:475–482.
- Hoese WJ, Podos J, Boetticher NC, Nowicki S. 2000. Vocal tract function in birdsong production: experimental manipulation of beak movements. *J Exp Biol*. 203:1845–1855.
- Hultsch H, Todt D. 1996. Rules of parameter variation in homotype series of birdsong can indicate ‘sollwert’ significance. *Behav Proc*. 38:175–182.
- Illes AE, Hall ML, Vehrencamp SL. 2006. Vocal performance influences male receiver response in the banded wren. *Proc R Soc Lond B*. 273:1907–1912.
- Kipper S, Mundry R, Sommer C, Hultsch H, Todt D. 2006. Song repertoire size is correlated with body measures and arrival date in common nightingales, *Luscinia megarhynchos*. *Anim Behav*. 71:211–217.
- Krams I, Krama T, Igaune K, Mand R. 2007. Long-lasting mobbing of the pied flycatcher increases the risk of nest predation. *Behav Ecol*. 18:1082–1084.
- Kunc HP, Amrhein V, Naguib M. 2005. Acoustic features of song categories of the nightingale (*Luscinia megarhynchos*) and its implications for communication. *Behaviour*. 142:1083–1097.
- 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.

- Marten K, Marler P. 1977. Sound transmission and its significance for animal vocalizations. I. Temperate habitats. *Behav Ecol Sociobiol.* 2:271–290.
- Mathevon N, Aubin T, Dabelsteen T. 1996. Song degradation during propagation: importance of song post for the wren *Troglodytes troglodytes*. *Ethology.* 102:397–412.
- Mathevon N, Aubin T, Vielliard J, da Silva M-L, Sebe F, Boscolo D. 2008. Singing in the rain forest: how a tropical bird song transfers information. *PLoS ONE.* 3(2):e1580.
- Naguib M. 1995. Auditory distance assessment of singing conspecifics in Carolina wrens: the role of reverberation and frequency-dependent attenuation. *Anim Behav.* 50:1297–1307.
- Naguib M. 1997. Use of song amplitude for ranging in Carolina wrens, *Thryothorus ludovicianus*. *Ethology.* 103:723–731.
- Naguib M. 2003. Reverberation of rapid and slow trills: implications for signal adaptations to long range communication. *J Acoust Soc Am.* 133:1749–1756.
- Naguib M, Altenkamp R, Griebmann B. 2001. Nightingales in space: song and extra-territorial forays of radio tagged song birds. *J Ornithol.* 142:306–312.
- Naguib M, Amrhein V, Kunc HP. 2004. Effects of territorial intrusions on eavesdropping neighbors: communication networks in nightingales. *Behav Ecol.* 6:1011–1015.
- Naguib M, Mundry R, Hultsch H, Todt D. 2002. Responses to playback of whistle songs and normal songs in male nightingales: effects of song category, whistle pitch, and distance. *Behav Ecol Sociobiol.* 52:216–223.
- Naguib M, Wiley RH. 2001. Estimating the distance to a source of sound: mechanisms and adaptations for long-range communication. *Anim Behav.* 62:825–837.
- Piercy JE, Embelton TFW, Sutherland LC. 1977. Review of noise propagation in the atmosphere. *J Acoust Soc Am.* 61:1403–1418.
- Pitcher TE, Stutchbury BJM. 2000. Extraterritorial forays and male parental care in hooded warblers. *Anim Behav.* 59:1261–1269.
- Podos J. 1996. Motor constraints on vocal development in a songbird. *Anim Behav.* 51:1061–1070.
- Podos J. 1997. A performance constraint on the evolution of trilled vocalizations in a songbird family (Passeriformes: Emberizidae). *Evolution.* 51:537–551.
- Richards DG. 1981. Alerting and message components in songs of rufous-sided towhees. *Behaviour.* 76:223–249.
- Richards DG, Wiley RH. 1980. Reverberations and amplitude fluctuations in the propagation of sound in a forest: implications for animal communications. *Am Nat.* 115:381–399.
- Schmidt R, Kunc HP, Amrhein V, Naguib M. 2006. Responses to interactive playback predict future mating status in nightingales. *Anim Behav.* 72:1355–1362.
- Schmidt R, Kunc HP, Amrhein V, Naguib M. 2008. Aggressive responses to broadband trills are related to subsequent pairing success in nightingales. *Behav Ecol.* 19:635–641.
- Searcy WA, Nowicki S. 2005. The evolution of animal communication. Reliability and deception in signaling systems. Princeton, NJ: Princeton University Press.
- Slabbekoorn H, Ellers J, Smith TB. 2002. Birdsong and sound transmission: the benefits of reverberations. *Condor.* 104:564–573.
- Vallet E, Kreutzer M. 1995. Female canaries are sexually responsive to special song phrases. *Anim Behav.* 49:1603–1610.
- Wiley RH, Richards DG. 1978. Physical constraints on acoustic communication in the atmosphere: implications for the evolution of animal vocalizations. *Behav Ecol Sociobiol.* 3:69–94.
- Wiley RH, Richards DG. 1982. Adaptations for acoustic communication in birds: sound transmission and signal detection. In: *Acoustic communication in birds*, Vol. 2 (Kroodsma DE, Miller EH, eds). New York: Academic Press; 131–181.