Articles

The predictive value of trill performance in a large repertoire songbird, the nightingale *Luscinia megarhynchos*

Philipp Sprau, Tobias Roth, Valentin Amrhein and Marc Naguib

P. Sprau (psprau@orn.mpg.de) and M. Naguib, Netherlands Inst. of Ecology (NIOO-KNAW), Dept of Animal Ecology, PO Box 50, NL-6700 AB Wageningen, the Netherlands. Present address for PS: Max Planck Inst. for Ornithology (MPIO), Eberhard-Gwinner-Strasse, DE-82319 Seewiesen, Germany. MN also at: Behavioural Ecology Group, Dept of Animal Sciences, Wageningen Univ., De Elst 1, NL-6708 WD Wageningen, the Netherlands. – T. Roth and V. Amrhein, Research Station Petite Camargue Alsacienne, Rue de la Pisciculture, FR-68300 Saint-Louis, France. TR and VA also at: Zoological Inst., Univ. of Basel, Vesalgasse 1, CH-4051 Basel, Switzerland.

In animal communication, elaborate signals have been shown to be under sexual selection and often to reliably indicate a signaler's quality, condition, or motivation. For instance, the performance of physically challenging signals such as trills – i.e. rapidly repeated elements of broad frequency bandwidth – is considered to reflect signaler quality. Nightingales *Luscinia megarhynchos* are renowned for their outstanding song repertoire sizes, and most songs include a variety of complex trills. In the present study, we examined whether performance of trills can reliably reflect male quality. We show that vocal performance of trills predicts the age of a male. Older males sang trills that were closer to the performance limit than did younger males. Moreover, males with narrower beaks sang more consistent trills than did males with wider beaks. Vocal performance of trills, however, did not significantly predict other measures of biometric quality such as body size or body condition of the males. The findings suggest that receivers could benefit from the predictive value of physically demanding song traits in assessing age as an important quality component of potential mates or rivals. Particularly in species with high singing versatility, signaler assessment based on readily assessable structures may be adaptive, as this will allow receivers to quickly gather relevant information about the singer without attending to the full song repertoire.

In competition over mates and resources, animals often use sexually selected signals (Andersson 1994, Andersson and Simmons 2006). Bird-song is one of the key models for research in the principles of sexual selection (Searcy and Nowicki 2005) as it expresses motivational, conditional and qualitative state of males affecting female choice and male resource defence (Gil and Gahr 2002, Catchpole and Slater 2008).

Song repertoire size, for instance, can provide valuable information on the signalers' reproductive success (Catchpole 1980, McGregor and Krebs 1982, Lambrechts and Dhondt 1986, Hasselquist et al. 1996), age (Forstmeier et al. 2006, Kiefer et al. 2006), or body condition (Reid et al. 2005, Kipper et al. 2006). However, assessing individuals based on the number of different songs may be difficult in species with large repertoires, as it takes long periods of time to cycle through the repertoire (Hartshorne 1973), and singers may not even use their full song repertoire ('silent song types', Geberzahn et al. 2002). Thus, in species with large repertoires, receivers could potentially avoid costs of prolonged listening by attending to traits other than song repertoire that are more readily available (Botero et al. 2009).

For quick assessment of signalers, structural song traits such as trills, i.e. rapidly repeated elements that have a wide

frequency bandwidth, may be particularly relevant. Signalers are usually limited in the performance of rapid broadband trills, as they face a tradeoff between repeating trilled elements at a high rate, while at the same time singing trill elements of high frequency bandwidth (Podos 1997). In swamp sparrows *Melospiza georgiana*, this tradeoff has been shown to be strongly affected by beak movements, with wide beak gapes resulting in high frequency bandwidths, and fast opening and closing leading to the high repetition rates of the trills (Westneat et al. 1993). Because individuals are limited in the performance of trills, singing close to the performance limit, i.e. singing trills with a high repetition rate and a high frequency bandwidth, is considered a trait that honestly reflects the quality of a signaler. Indeed, trill performance has been shown to encode information such as age (Ballentine 2009, de Kort et al. 2009), body condition (Weiss et al. 2012), or morphological characteristics (including bill morhology; Ballentine 2006, 2009, Derryberry 2009, Sockman 2009). Such information may be used by conspecifics to assess signallers. For instance, females have been shown to prefer males that are singing higher performance trills (Draganoiu et al. 2002, Ballentine et al. 2004). So far, however, studies testing the predictive value of trill performance mainly considered species with small

song repertoires such as canaries *Serinus canaria* or swamp sparrows with a single or a few types of trills.

In contrast, nightingales *Luscinia megarhynchos*, have large song repertoires of about 180 different song types per male (for a recent review on nightingale singing versatility, Naguib et al. 2011), and most of the songs contain trills. Such trills can be highly versatile in terms of element repetition rate, frequency bandwidth, number of repeated elements and position within a song. Among the large variety of trills, 'rapid broadband trills' are particularly conspicuous (Fig. 1d–e): about 20% of nightingale songs (Sprau et al. 2010b) contain rapid broadband trills that are characterized by particularly large frequency bandwidths (≥ 6000 Hz), high element repetition rates (≥ 8.5 elements s^{-1}), at least five repeated elements, and they typically occur in the terminal section of the song (Naguib et al. 2008, 2011).

Rapid broadband trills quickly degrade with distance (Naguib et al. 2008) and are predominantly used as an aggressive signal in close-range interactions (Kunc et al. 2006, Schmidt et al. 2006, Sprau et al. 2010a). Thus, trills are not only conspicuous with regard to their spectral characteristics but also with regard to their function. Yet, to date it is unknown whether rapid broadband trills encode information about signaller age and/or morphological characteristics in large repertoirc songbirds. In this study, we investigated 1) the predictive value of trill performance in a songbird species with a large song repertoire, and 2) more specifically whether the distinct functional category of rapid broadband trills could not only provide information on aggression, but could predict quality of signallers as reflected in traits such as age, body condition, or beak morphology.

Methods

Study site and subjects

Data were collected from 19 male nightingales recorded in our long-term study population located in the Petite
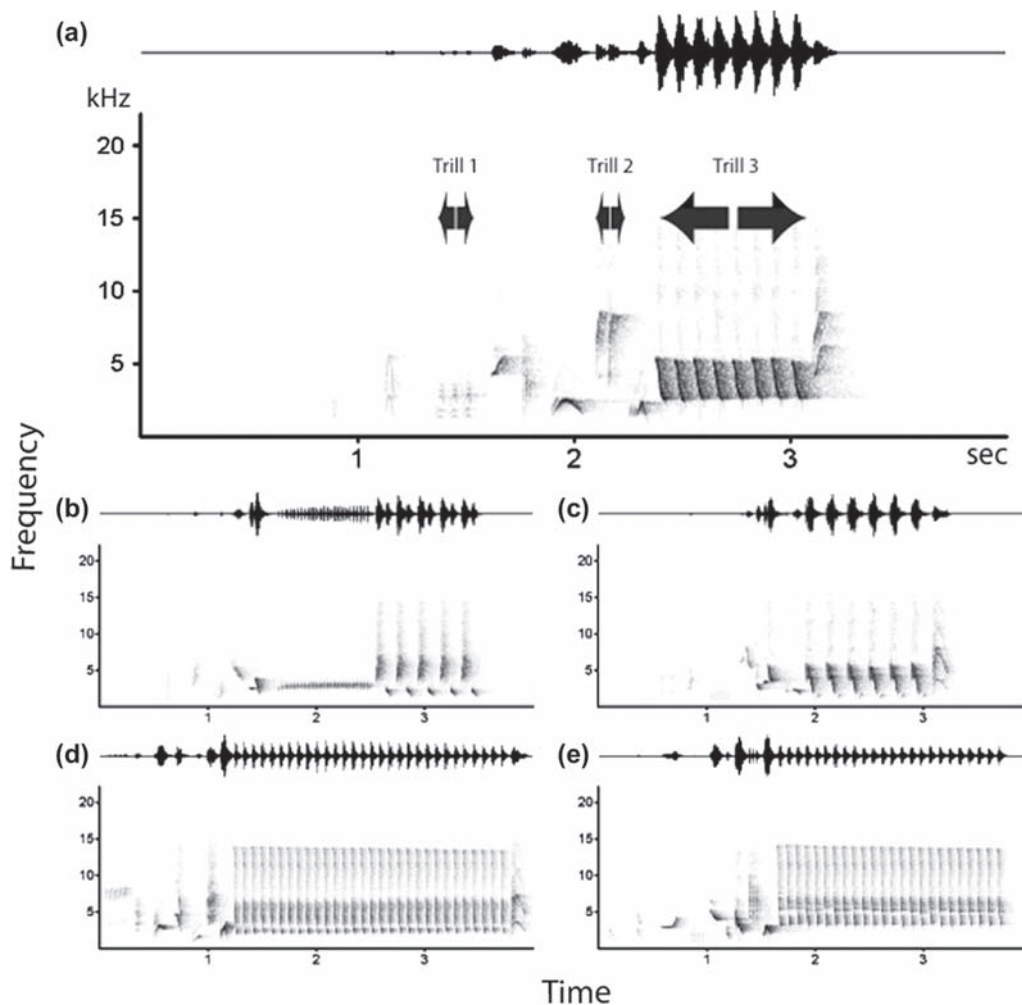

Figure 1. Examples of spectrograms and oscillograms of nightingale songs. Trills were defined as an at least twofold repetition of the same element. In (a), three trills within one song are shown; (b) shows an example of a buzz, i.e. a very rapid narrowband trill-like structure, (c) an example of a slow trill, and (d) and (e) show two rapid broadband trills, i.e. songs with trills with a frequency bandwidth of > 6 kHz, a repetition rate of > 8.5 elements s^{-1}, and $\geq$ five repeated elements in the terminal part of a song (for details see text).

Camargue Alsacienne (47°37′20N, 7°32′13E; France). In this nature reserve, about 200–240 male nightingales settle each year in an area of 18 km² (Amrhein et al. 2007). The 19 males were captured between 14 April and 25 May 2008. From the 19 males, two remained unpaired throughout the season whereas the remaining 17 males successfully attracted a female. We placed mist nets in the territories of males that had been singing for at least three consecutive nights. Mist nets were opened at twilight for a maximum of three hours. From the captured males, we measured 1) bill length (mm; accuracy 0.1 mm), 2) bill depth (mm; accuracy 0.1 mm), 3) wing length (mm; accuracy 0.1 mm), 4) body condition, and 5) age (second calendar year and older). Bill length was measured from the tip of the bill to the base of the skull, and measurements for bill width were taken at the base of the bill. To assess wing size, we measured the length of the third primary from the left wing. Body condition was measured as the body mass corrected for body size (weight (g)/tarsus length (mm; accuracy 0.1 mm)), which indicates the energetic state of an animal (Schulte-Hostedde et al. 2005). As nightingales differ in song between age classes (Kiefer et al. 2006, 2009), we also determined whether males were 'second calendar year' (SCY) or fully mature males (i.e. 'after second calendar year' (ASCY)). Age was determined based on plumage characteristics (Svensson 1992, Mundry and Sommer 2007). Accordingly, six males were determined as second calendar year and 13 males as after second calendar year individuals. In order to avoid observer effects, the same person measured all individuals. Two birds were not weighed, so we did not have measurements on condition of these birds. After measurement, males were ringed in their territory and released within 15 min of capture. None of the males deserted its territory after capture.

Recordings and analysis of songs

We recorded nocturnal song of the same males that were measured, using microphones connected to a digital solid state recorder. To minimize spectral degradation, all males were recorded from a distance of max. 6 m from their nocturnal song perches. Audio recordings were made from nocturnal song between 23:45 and 01:45 h from 14 April to 2 May 2008. All 19 males were unpaired at the time of recording.

For the analysis of trill performance, we randomly chose 30 songs from the first 300 recorded songs of each of the 19 different males. Each of these 570 songs was then high-pass filtered at 500 Hz to remove low frequency noise, and their amplitude was normalized to 80% using Adobe Audition 1.0. For all song measurements we used the sound analysis software Avisoft SASlab Pro 4.4 (R. Specht, Berlin, Germany). In a first step, we measured trill rate (number of elements/s) from oscillograms and frequency bandwidth (Hz) from sound spectrograms (FFT length: 1024, frequency resolution 43 Hz) for all trills ('overall trills'), which were defined as repeating one element or syllable at least once (Fig. 1). Following Podos (1997), frequency bandwidth was measured at −24 dB relative to the peak amplitude frequency in the song using power spectra. In total, we measured 1715 trills from 568 songs of the 19 individuals

(two songs did not include trills). In order to determine whether only the frequency of occurrence (Kunc et al. 2006, Schmidt et al. 2006, Sprau et al. 2010b), or also the performance of rapid broadband trills encodes information that may be used to assess singers, we first selected all trills and then in a second step selected the subset of rapid broadband trills for specific analysis. Rapid broadband trills were defined as trills containing ≥5 repeated elements with a frequency bandwidth of ≥6000 Hz (measured at −24 dB) and an element repetition rate of ≥8.5 elements s⁻¹ and making up the terminal section of the song (Naguib et al. 2008). Thus, short rapid broadband trills that often consist of about two notes in the initial part of the song were not included in this category (Fig. 1). For three of the 19 males we did not find rapid broadband trills in any of the 30 analyzed songs. We did not include pairing status in the analysis given the unequal distribution of paired (n = 17) and unpaired males (n = 2).

In a second analysis we assessed the consistency of a trill, i.e. the spectral similarity between consecutive trill notes within a song, to see whether trill consistency predicts quality and biometric traits of signallers (de Kort et al. 2009). We randomly selected three rapid broadband trills and three non-rapid broadband trills from each of the 30 songs of the 19 males used for the analysis of trill performance. From these selected trills, we extracted clips of individual trill notes. The clips for the trill notes in a given song were then subjected to spectral cross-correlation using the 'Classify .wav or .son files' function in Avisoft SASlab Pro 4.4. Spectral cross-correlations provide a measure of similarity between notes by comparing the spectral information in a spectrogram display. A coefficient of 0
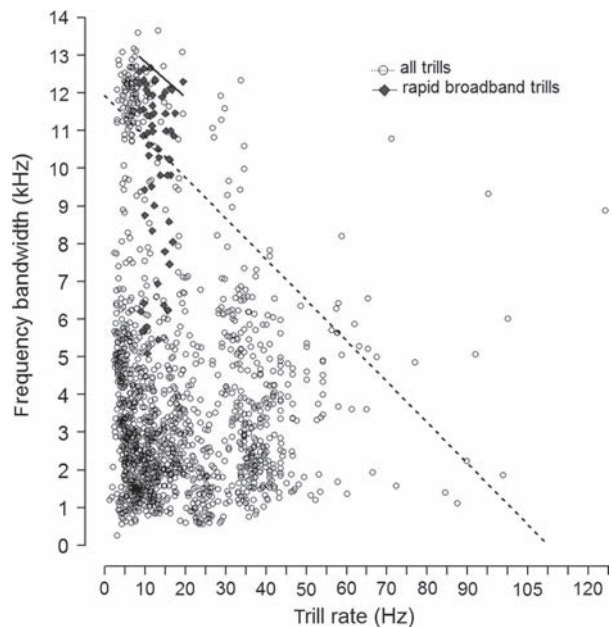

Figure 2. Trill performance limit for 1715 trills from 568 songs of 19 male nightingales, as measured using a quantile regression from frequency bandwidth (kHz) on trill rate (no. s⁻¹). Rapid broadband trills were defined as having trill rates ≥8.5 Hz (elements s⁻¹), frequency bandwidths ≥6 kHz (measured at −24dB), and having five repeated elements in the terminal part of a song.

indicates no similarity, while a coefficient of 1 implies that two notes are identical. Each trill note was compared with all other trill notes of the same trill. The values of all comparisons were averaged, resulting in a consistency value for each song.

Statistical analysis

Data were analyzed using R 2.15.1. We estimated how trill rate and frequency bandwidth was related to trill duration using the lme function in R (package 'nlme', ver. 3.1–97),
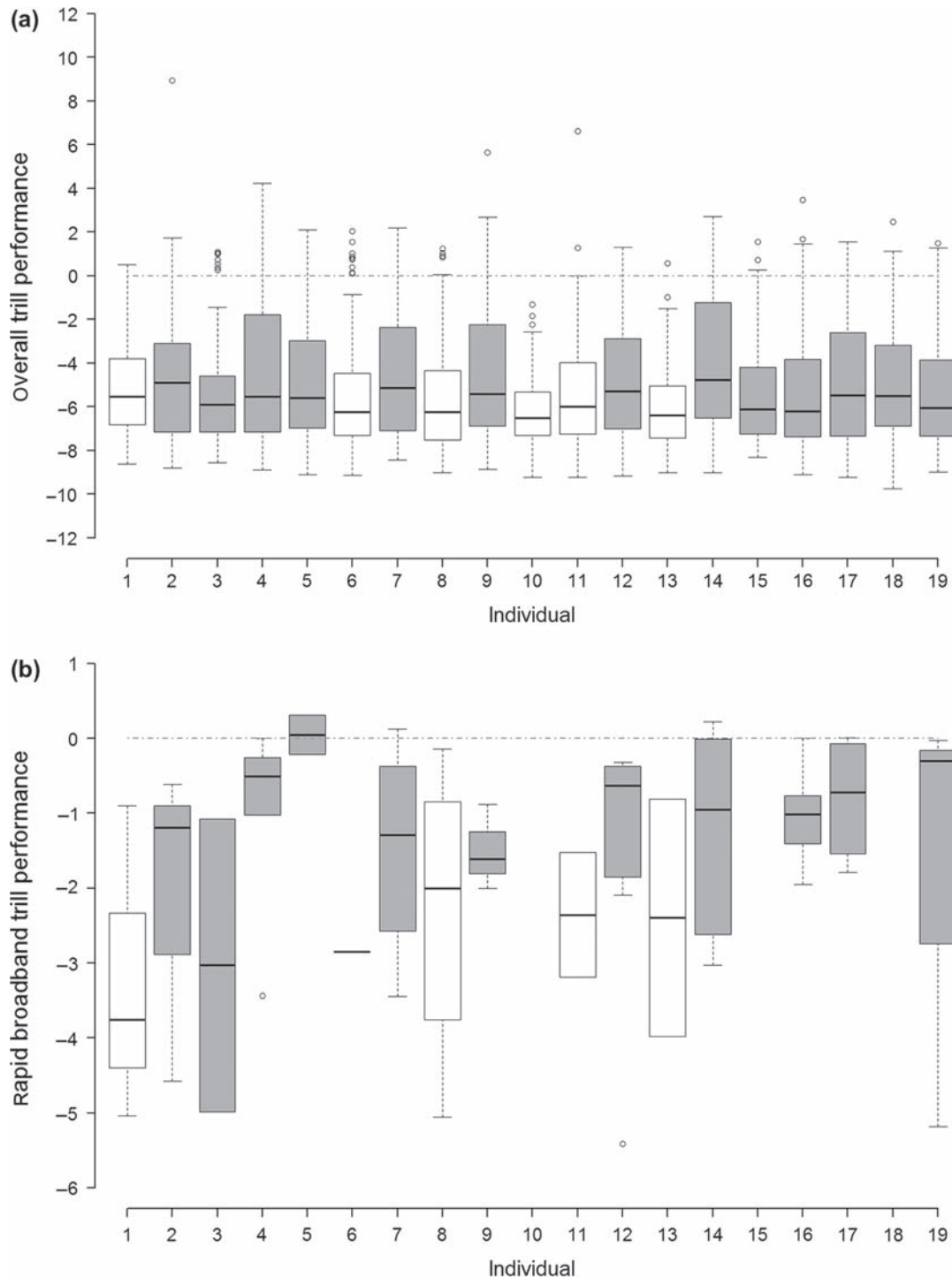

Figure 3. Individual variation of trill performance indices measured as orthogonal distance from the quantile regression line to each trill for (a) all trills and for (b) rapid broadband trills sung by n = 19 nightingales. Trills with index values close to the regression line (i.e. ∘ in the figure) considered to reflect high performance, whereas trills with strongly negative values are considered to reflect low performance. White bars represent individuals in their second calendar year, grey bars represent individuals after their second calendar year. Note that individuals 10 and 15 did not sing any rapid broadband trill in any of the 30 analyzed songs. Shown are medians and quartiles, open points are outliers.

using linear mixed-effect models (LMM) with trill duration as response variable and trill rate and frequency bandwidth as fixed effects. Because several trills were measured from the same subjects, we included individual male as a random factor. The significance of the fixed factors was assessed using likelihood ratio (LR) tests using the maximum likelihood method (Zuur 2009). For the analysis of the performance limit of trills, we used regression quantiles (RQ; Koenker and Bassett 1978, Koenker 2005), using the function 'rq' of the R package 'quantreg' (ver. 4.44, Koenker 2009), with tau (i.e. the quantile) set to 0.9. In contrast to the often used upper bound regression (Blackburn et al. 1992), quantile regression analysis reliably estimates upper bounds of density distributions (Cade et al. 1999, Cade and Noon 2003). We used quantile regressions separately for all analyzed trills ('overall trills') and for rapid broadband trills only (Fig. 2). We then measured orthogonal distance from the regression line to each trill to obtain an index for vocal performance of the trill. Trills that were close to or above the 90%-quantile regression line (i.e. trills that had small negative or positive index values) were considered to reflect high trill performance. Indices were calculated separately for the datasets including all trills and including rapid broadband trills only. From these indices we then calculated the maximum and the average of overall and of rapid broadband trill performance for each individual (Cardoso et al. 2009). Maximum and average indices were used as response variables in linear models (LM) using the R-function 'lm'. As fixed factors we used bill length, bill depth, wing size and condition (continuous variables), and male age (factor with two levels). We were particularly interested in bill length and bill depth because the performance of both overall trills and rapid broadband trills is partly limited by rapid vocal tract movements (such as opening and closing of the beak; Westneat et al. 1993). We also tested whether trill consistency depended on morphological characteristics and age by using the spectral cross-correlation coefficients as response variable. For all models, we removed non-significant terms from the maximal model starting with the least significant term (Crawley 2007). We visually checked homogeneity of variance and normality of error in the final models using plots of standardized residuals against quantiles from a normal distribution.

Results

Because we would expect most trills to be produced below the performance maxima and because the analyses for maximum and average trill performances led to largely the same results (i.e. the same significant effects), we here focus on the results for the average performances of all trills and specifically for rapid broadband trills. Trill duration was significantly related to trill rate and to frequency bandwidth. Trills with higher rate and smaller frequency bandwidth were significantly shorter than slower trills with high bandwidth (LMM: trill rate LR = 361.78, DF = 1, p < 0.001; frequency bandwidth LR = 219.94, DF = 1, p < 0.001). In contrast, when considering only rapid broadband trills, trill duration was not significantly related to trill rate or frequency

Table 1. Results from backward selection of linear models predicting vocal performance of all trills and of only rapid broadband trills of n = 19 male nightingales. Sample sizes vary because in the random samples of songs of some of the males, no rapid broadband trills were detected, or the body weight was not taken. See text for further details.

Response variable	Estimate	SE	DF	t	p
Overall trills					
intercept	−5.57	0.18	17	−31.41	< 0.001
bill length	0.06	0.09	13	0.69	0.50
bill width	0.11	0.28	12	0.38	0.71
wing size	−0.01	0.05	11	−0.26	0.80
body condition	1.86	1.89	14	0.98	0.34
age	0.81	0.21	17	3.76	0.002
Rapid broadband trills					
intercept	−2.63	0.31	14	−8.44	< 0.001
bill length	−0.09	0.21	11	−0.4	0.70
bill width	−0.57	0.4	12	−1.43	0.18
wing size	−0.12	0.07	13	−1.75	0.10
body condition	1.11	3.76	8	0.3	0.78
age	1.21	0.38	14	3.22	0.006

bandwidth (LMM: trill rate LR = 2.85, DF = 1, p = 0.10; frequency bandwidth LR = 0.32, DF = 1, p = 0.57).

Vocal performance for all trills significantly varied with frequency bandwidth and trill rate; i.e. the higher the element repetition rate, the narrower the frequency bandwidth (y = 11.93–0.11x, p < 0.001; Fig. 2). However, we found no significant correlation between frequency bandwidth and element repetition rate when considering only rapid broadband trills (y = 13.07–0.06x, p = 0.66; Fig. 2). Between-individual variation in trill performance, measured as standard deviation from the performance indices, was significantly higher in the indices of rapid broadband trills than in that of all trills (variance test: F = 3.17, DF = 18, p = 0.023; Fig. 3).

Male vocal performance of all trills was not significantly predicted by morphological characteristics (LM: all t < 0.98, all p > 0.34; Table 1, Fig. 4). However, older males sang trills that were closer to the upper bound than did males that were in their second calendar year (LM: age, estimate ± SE = 0.81 (± 0.21), DF = 17, p = 0.002; Table 1, Fig. 4a). Likewise, age (LM: age, estimate ± SE = 1.21 (± 0.38), DF = 14, p = 0.006, but not morphological characteristics (LM: all t < 0.3, all p > 0.10; Table 1), predicted vocal performance of rapid broadband trills, with older males performing rapid broadband trills that were closer to the performance limit (Fig. 4b).

Overall trill consistency, measured as the spectral cross-correlation between individual trill notes, was significantly related to bill width; males with broader bills sang less consistently (LM: bill width, estimate ± SE = −0.03 (± 0.02), DF = 17, p = 0.033; Table 2). Trill consistency for rapid broadband trills only, however, was not significantly related to any of the predictors (LM: all t < 1.48, all p > 0.15; Table 2).

Discussion

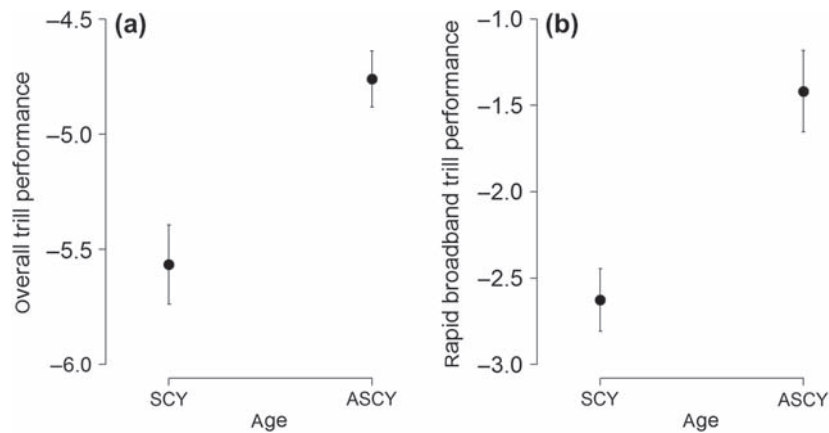Male age predicted vocal performance of trills, with older nightingales performing trills that were closer to the

Figure 4. Average (± SE) trill performance indices of male nightingales measured as orthogonal distance from the quantile regression line to each trill for (a) all trills and for (b) rapid broadband trills in their second calendar year (SCY, n = 6) and after their second calendar year (ASCY, n = 13).

performance limit than did younger males. Similar observations were recently made in swamp sparrows that also show an increase in trill performance with age (Ballentine 2009). Our findings suggest that vocal performance of trills can reliably encode information on age of the signaler also in songbird species with a large song repertoire, and thus may function as an indicator of male quality. By mating with older males, females may gain fitness benefits, as older males often have higher reproductive success (Nol and Smith 1987, Forslund and Pärt 1995). Moreover, in territorial species, older males are often more successful in defending their territories (Hyman et al. 2004), so that rivals may assess the competitive ability of a territory owner before challenging it. An alternative explanation for our findings may be that trill performance does not increase with age but that males with better trill performance have higher survival and thus tend to be older. Yet, regardless of the causes of the age-differences in trill performance, from a receiver perspective, trill performance is likely to be a useful indicator of age, allowing for relatively fast assessment of signaler quality.

So far, a relation of male quality traits and vocal performance of trills was described for species with small repertoires and with little variation in trill structure (Dreiss et al. 2008, Ballentine 2009, de Kort et al. 2009, Derryberry 2009, Sockman 2009). Our study suggest that encoding individual information in trill performance is not restricted to species that have only few trills in their repertoires or where the entire song repertoire consists of a single trill; also a species such as the nightingale with large song repertoire and many different trill types can apparently encode valuable information in the performance of trill structures. Particularly for such species with large song repertoires, information encoded in traits other than repertoire size may be beneficial in situations where it is important to readily assess signalers without the need to listen to the songs of conspecifics for long periods of time. Recently, so called buzzes, i.e. rapid narrowband trill-like structures of low frequency (Fig. 1b), have been found to be another structural trait in the large repertoire of nightingales that reliably encodes quality-indicating traits of signalers (in this case, body weight) and that evokes

strong reactions in females (Weiss et al. 2012). Those findings highlight the importance of physically challenging song traits such as trills or buzzes for fast assessment of a signaler. Together with the study on buzzes (Weiss et al. 2012), our study shows that high versatility in complex song structures can allow fine-tuned encoding of information that likely enables quick and reliable assessment of signaler quality for potential rivals and mates.

Vocal performance of trills, i.e. singing close to the performance limit, did not significantly predict other measures of biometric quality of the males such as beak morphology, condition and wing size. However, males with narrower bills sang more consistent trills, suggesting that consistency in trill note production may be limited by beak morphology. Correlations between other song traits such as repertoire size and vocal performance of buzzes and male body measures have previously been found in nightingales (Kipper et al. 2006, Weiss et al. 2012). Also in other species, body measures have been found to correlate with song characteristics such as trill performance (Palacios and Tubaro 2000, Christensen et al. 2006, Derryberry 2009). Indeed, nightingales may use the full spectrum of their song versatility to encode different information on

Table 2. Results from backward selection of linear models predicting trill consistency of all trills and of only rapid broadband trills of n = 19 male nightingales.

Response variable	Estimate	SE	DF	t	p
Overall trills					
intercept	0.99	0.07	17	13.42	<0.001
bill length	<0.001	0.01	15	0.08	0.94
bill width	−0.03	0.02	17	−2.31	0.033
wing size	<0.001	<0.001	14	−0.11	0.91
body condition	0.01	0.12	11	0.06	0.95
age	0.01	0.02	16	0.75	0.46
Rapid broadband trills					
intercept	0.77	0.11	15	73.09	<0.001
bill length	−0.01	0.01	12	−0.74	0.47
bill width	−0.04	0.02	14	−1.50	0.15
wing size	<0.001	<0.001	11	−0.48	0.64
body condition	0.10	0.20	8	0.51	0.62
age	0.03	0.02	13	1.48	0.16

Table 3. Overview of vocal performance of trills for different oscine passerines.

Species/family	Common name	Observed max. frequency bandwidth (kHz)	Observed max. trill rate (Hz)	Upper bound regression	Reference
Emberizidae		~8	~48	$y = 7.55 - 0.12^*x$	Podos 1997
Melospiza lincolnii	Lincoln's sparrow	~3	~16	$y = 2.90 - 0.07^*x$	Sockman 2009
Melospiza georgiana	swamp sparrow	~6.5	~14	$y = 6.55 - 0.10^*x$	Ballentine et al. 2004
Zonotrichia leucophrys	white crowned sparrow	~4	~21	$y = 2.32 - 0.02^* x$	Podos 1997, Derryberry 2009
Junco hyemalis	dark-eyed junco	~6	~22	–	Cardoso et al. 2007
Thryothorus pleurostictus	banded wren	~4.2	~20	$y = 4.64 - 0.17^*x$	Illes et al. 2006
Serinus canaria	canary	~7	~30	–	Draganoiu et al. 2002
Ageliaus phoeniceus	red winged blackbird	~7	~22	$y = 7.13 - 0.14^*x$	Cramer and Price 2007
Geospiza spec.	Darwin's finch	~7	~20	–	Podos 2001
Camarhynchus parvulus	Darwin's small tree finch	~6	~12	–	Christensen et al. 2006
Dendroica petechia	yellow warbler	~5.2	~10	$y = 6.06 - 0.23^*x$	Beebee 2004
Luscinia megarhynchos	nightingale	13.66	124.29	$y = 11.93 - 0.11^*x$	This study (Fig. 2)

signaler characteristics such as age, condition, and morphology, by using different song traits. Listeners may assess body condition of a singing nightingale based on its repertoire size (Kipper et al. 2006) or buzz performance (Weiss et al. 2012), they may use trill consistency to assess morphological traits (this study), and they may assess age of a nightingale based on repertoire size (Kiefer et al. 2006) or vocal performance of trills (this study).

Our specific analysis of rapid broadband trills led to similar results as the analysis of all trills combined. Again, older males sang rapid broadband trills that were closer to the performance limit than did younger males. The performance of rapid broadband trills, however, was more strongly affected by frequency bandwidth compared to trill rate as shown by the small negative slope of the regression line. We also found that the performance of rapid broadband trills varied more among singers than did the performance of other trills. Thus, rapid broadband trills apparently do not only signal motivational aspects in close-range interactions (Kunc et al. 2006, Schmidt et al. 2006, Sprau et al. 2010b), but could also be used to discriminate among males of different age classes or to discriminate among singers. In comparison to other investigated species, trill performance of nightingales is much more extreme (Table 3): nightingales use frequency bandwidths and element repetition rates that are more than twice as wide or fast than that measured in other species. In addition to the outstanding variability in using many different song types, nightingales are thus exceptional also in the performance of trills, making nightingales one of the most sophisticated singers in the Western Palearctic.

Our study supports previous findings demonstrating the predictive value of trills in songbirds, and extends on earlier findings by showing that also a songbird species with large song repertoire can encode valuable information such as signaler age in the performance of physically challenging trills. These characteristics make trills a suitable song trait that may enable listeners to readily assess male quality.

References

Amrhein, V., Kunc, H. P., Schmidt, R. and Naguib, M. 2007. Temporal patterns of territory settlement and detectability in mated and unmated nightingales *Luscinia megarhynchos*. – Ibis 149: 237–244.

Andersson, M. 1994. Sexual selection. – Univ. Press Princeton.

Andersson, M. and Simmons, L. W. 2006. Sexual selection and mate choice. – Trends Ecol. Evol. 21: 296–302.

Ballentine, B. 2006. Morphological adaptation influences the evolution of a mating signal. – Evolution 60: 1936–1944.

Ballentine, B. 2009. The ability to perform physically challenging songs predicts age and size in male swamp sparrows, *Melospiza georgiana*. – Anim. Behav. 77: 973–978.

Ballentine, B., Hyman, J. and Nowicki, S. 2004. Vocal performance influences female response to male bird song: an experimental test. – Behav. Ecol. 15: 163–168.

Beebee, M. D. 2004. The functions of multiple singing modes: experimental tests in yellow warblers, *Dendroica petechial*. – Anim. Behav. 67: 1089–1097.

Blackburn, T. M., Lawton, J. H. and Perry, J. N. 1992. A method of estimating the slope of upper-bounds of plots of body size and abundance in natural animal assemblages. – Oikos 65: 107–112.

Botero, C. A., Rossman, R. J., Caro, L. M., Stenzler, L. M., Lovette, I. J., De Kort, S. R. and Vehrencamp, S. L. 2009. Syllable type consistency is related to age, social status and reproductive success in the tropical mockingbird. – Anim. Behav. 77: 701–706.

Cade, B. S. and Noon, B. R. 2003. A gentle introduction to quantile regression for ecologists. – Front. Ecol. Environ. 1: 412–420.

Cade, B. S., Terrell, J. W. and Schroeder, R. L. 1999. Estimating effects of limiting factors with regression quantiles. – Ecology 80: 311–323.

Cardoso, G. C., Atwell, J. W., Ketterson, E. D. and Price, T. D. 2007. Inferring performance in the songs of dark-eyed juncos (*Junco hyemalis*). – Behav. Ecol. 18: 1051–1057.

Cardoso, G. C., Atwell, J. W., Ketterson, E. D. and Price, T. D. 2009. Song types, song performance, and the use of repertoires in dark-eyed juncos (*Junco hyemalis*). – Behav. Ecol. 20: 901–907.

Catchpole, C. K. 1980. Sexual selection and the evolution of complex songs among European warblers of the genus *Acrocephalus*. – Behaviour 74: 149–166.

Catchpole, C. K. and Slater, P. J. B. 2008. Bird song: biological themes and variation. – Cambridge Univ. Press.

Christensen, R., Kleindorfer, S. and Robertson, J. 2006. Song is a reliable signal of bill morphology in Darwin's small tree finch *Camarhynchus parvulus*, and vocal performance predicts male pairing success. – J. Avian Biol. 37: 617–624.

Cramer, E. R. A. and Price, J. J. 2007. Red-winged blackbirds *Agelaius phoeniceus* respons differently to song types with different performance levels. – J. Avian Biol. 38: 112–127.

Crawley, M. J. 2007. The R book. – Wiley.

de Kort, S. R., Eldermire, E. R. B., Valderrama, S., Botero, C. A. and Vehrencamp, S. L. 2009. Trill consistency is an age-related assessment signal in banded wrens. – Proc. R. Soc. B 276: 2315–2321.

Derryberry, E. P. 2009. Ecology shapes birdsong evolution: variation in morphology and habitat explains variation in white-crowned sparrow song. – Am. Nat. 174: 24–33.

Draganoiu, T. I., Nagle, L. and Kreutzer, M. 2002. Directional female preference for an exaggerated male trait in canary (*Serinus canaria*) song. – Proc. R. Soc. B 269: 2525–2531.

Dreiss, A. N., Navarro, C., De Lope, F. and Møller, A. P. 2008. Effects of an immune challenge on multiple components of song display in barn swallows *Hirundo rustica*: implications for sexual selection. – Ethology 114: 955–964.

Forslund, P. and Pärt, T. 1995. Age and reproduction in birds – hypotheses and tests. – Trends Ecol. Evol. 10: 374–378.

Forstmeier, W., Hasselquist, D., Bensch, S. and Leisler, B. 2006. Does song reflect age and viability? A comparison between two populations of the great reed warbler, *Acrocephalus arundinaceus*. – Behav. Ecol. Sociobiol. 59: 634–643.

Geberzahn, N., Hultsch, H. and Todt, D. 2002. Latent song type memories are accessible through auditory stimulation in a hand-reared songbird. – Anim. Behav. 64: 783–790.

Gil, D. and Gahr, M. 2002. The honesty of bird song: multiple constraints for multiple traits. – Trends Ecol. Evol. 17: 133–141.

Hartshorne, C. 1973. Born to sing. – Indiana Univ. Press.

Hasselquist, D., Bensch, S. and von Schantz, T. 1996. Correlation between male song repertoire, extra-pair paternity and offspring survival in the great reed warbler. – Nature 381: 229–232.

Hyman, J., Hughes, M., Searcy, W. A. and Nowicki, S. 2004. Individual variation in the strength of territory defense in male song sparrows: correlates of age, territory tenure, and neighbor aggressiveness. – Behaviour 141: 15–27.

Illes, A. E., Hall, M. L. and Vehrencamp, S. L. 2006. Vocal performance influences male receiver response in the banded wren. – Proc. R. Soc. B 273: 1907–1912.

Kiefer, S., Spiess, A., Kipper, S., Mundry, R., Sommer, C., Hultsch, H. and Todt, D. 2006. First-year common nightingales (*Luscinia megarhynchos*) have smaller song-type repertoire sizes than older males. – Ethology 112: 1217–1224.

Kiefer, S., Sommer, C., Scharff, C., Kipper, S. and Mundry, R. 2009. Tuning towards tomorrow? Common nightingales *Luscinia megarhynchos* change and increase their song reper-toires from the first to the second breeding season. – J. Avian Biol. 40: 231–236.

Kipper, S., Mundry, R., Sommer, C., Hultsch, H. and Todt, D. 2006. Song repertoire size is correlated with body measures and arrival date in common nightingales, *Luscinia megarhynchos*. – Anim. Behav. 71: 211–217.

Koenker, R. 2005. Quantile regression. – Econometric Soc. Monogr. 38.

Koenker, R. 2009. Quantreg: quantile regression. – R package ver. 4.44, <http://CRAN.R-project.org/package=Quantreg>.

Koenker, R. and Bassett, G. 1978. Regression quantiles. – Econometrica 46: 33–50.

Kunc, H. P., Amrhein, V. and Naguib, M. 2006. Vocal interactions in nightingales, *Luscinia megarhynchos*: more aggressive males have higher pairing success. – Anim. Behav. 72: 25–30.

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

McGregor, P. K. and Krebs, J. R. 1982. Mating and song types in the great tit. – Nature 297: 60–61.

Mundry, R. and Sommer, C. 2007. A new character in the pattern of feather colouration for age determination in common nightingales. – Limicola 21: 131–139.

Naguib, M., Schmidt, R., Sprau, P., Roth, T., Flörcke, C. and Amrhein, V. 2008. The ecology of vocal signaling: male spacing and communication distance of different song traits in nightingales. – Behav. Ecol. 19: 1034–1040.

Naguib, M., Kunc, H. P., Sprau, P., Roth, T. and Amrhein, V. 2011. Communication networks and spatial ecology in nightingales. – Adv. Study Behav. 43: 239–271.

Nol, E. and Smith, J. N. M. 1987. Effects of age and breeding experience on seasonal reproductive success in the song sparrow. – J. Anim. Ecol. 56: 301–313.

Palacios, M. G. and Tubaro, P. L. 2000. Does beak size affect acoustic frequencies in woodcreepers? – Condor 102: 553–560.

Podos, J. 1997. A performance constraint on the evolution of trilled vocalizations in a songbird family (Passeriformes: Emberizidae). – Evolution 51: 537–551.

Podos, J. 2001. Correlated evolution of morphology and vocal signal structure in Darwin's finches. – Nature 409: 185–188.

Reid, J. M., Arcese, P., Cassidy, A., Marr, A. B., Smith, J. N. M. and Keller, L. F. 2005. Hamilton and Zuk meet heterozygosity? Song repertoire size indicates inbreeding and immunity in song sparrows (*Melospiza melodia*). – Proc. R. Soc. B 272: 481–487.

Schmidt, R., Kunc, H. P., Amrhein, V. and Naguib, M. 2006. Responses to interactive playback predict future pairing success in nightingales. – Anim. Behav. 72: 1355–1362.

Schulte-Hostedde, A. I., Zinner, B., Millar, J. S. and Hickling, G. J. 2005. Restitution of mass-size residuals: validating body condition indices. – Ecology 86: 155–163.

Searcy, W. A. and Nowicki, S. 2005. The evolution of animal communication: reliability and deception in signaling systems. – Princeton Univ. Press.

Sockman, K. W. 2009. Annual variation in vocal performance and its relationship with bill morphology in Lincoln's sparrows, *Melospiza lincolnii*. – Anim. Behav. 77: 663–671.

Sprau, P., Roth, T., Schmidt, R., Amrhein, V. and Naguib, M. 2010a. Communication across territory boundaries: distance-dependent responses in nightingales. – Behav. Ecol. 21: 1011–1017.

Sprau, P., Schmidt, R., Roth, T., Amrhein, V. and Naguib, M. 2010b. Effects of rapid broadband trills on responses to song overlapping in nightingales. – Ethology 116: 300–308.

Svensson, L. 1992. Identification guide to European passerines. – Br. Trust Ornithol., Thetford.

Weiss, M., Kiefer, S. and Kipper, S. 2012. Buzzwords in females' ears? The use of buzz songs in the communication of nightingales (*Luscinia megarhynchos*). – PLoS One 7: e45057.

Westneat, M. W., Long, J. H., Hoese, W. and Nowicki, S. 1993. Kinematics of birdsong – functional correlation of cranial movements and acoustic features in sparrows. – J. Exp. Biol. 182: 147–171.

Zuur, A. F. 2009. Mixed effects models and extensions in ecology with R. – Springer.