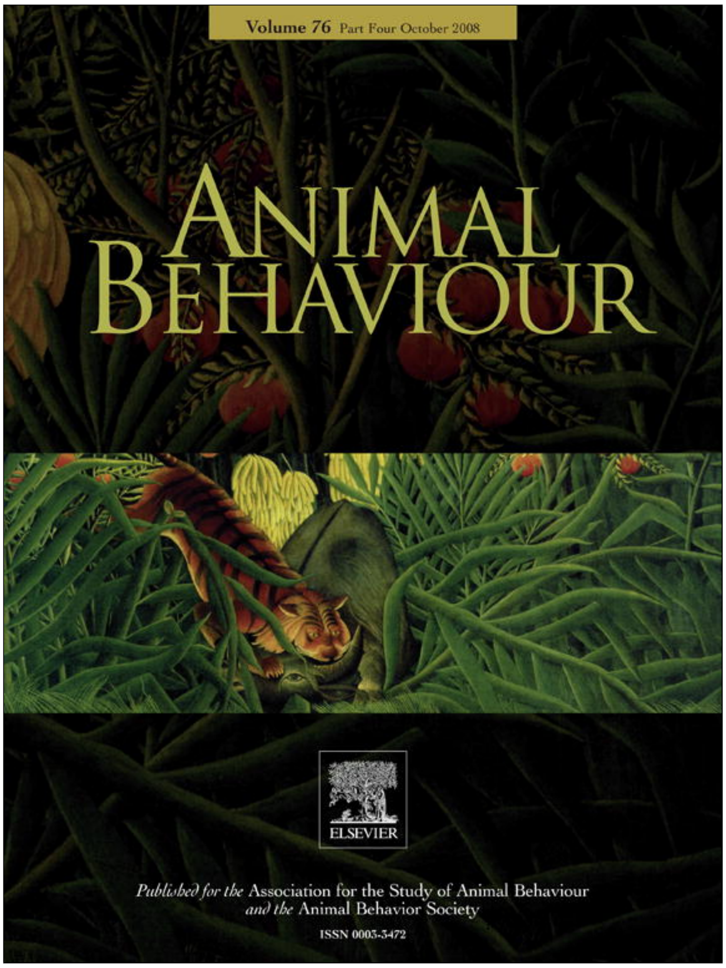
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Acoustic directionality of red-winged blackbird (*Agelaius phoeniceus*) song relates to amplitude and singing behaviours

GAIL L. PATRICELLI*, MARC S. DANTZKER† & JACK W. BRADBURY‡
*Section of Evolution and Ecology, University of California, Davis
†Bioacoustics Research Program, Cornell Laboratory of Ornithology
‡Macaulay Library, Cornell Laboratory of Ornithology

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Sound waves typically radiate from a vocalizing animal with unequal amplitude in different directions; this may profoundly affect communication, favouring adaptations that use or compensate for this directionality. Previous studies suggest that variation in directionality among vocalization types is related to function, with vocalizations such as alerts being relatively omnidirectional, thus maximizing the number of surrounding receivers, and vocalizations such as courtship calls being relatively directional, thus reducing eavesdropping by beaming sounds at the targeted receiver. Here we examine variation within a vocalization type, bird songs, to test hypotheses about how variation in song directionality relates to singing behaviour and the social context of singing. We measured the directionality and amplitude of red-winged blackbird songs in the field using calibrated microphones encircling the bird. We found variation in directionality among song types, possibly allowing males to select songs from their repertoires with directionality to suit the social context. We found support for the hypothesis that the amplitude and directionality of songs are related, with more-directional songs delivered at higher amplitudes. In addition, we found support for the hypothesis that directionality is negatively related to the degree of male rotation on the perch between vocalizations, suggesting that males may combine omnidirectional songs and rotation to broadcast their songs, and may face the receiver and produce directional songs during direct interactions. We also observed variation in directionality among note types within songs. These results suggest that directionality plays an important role in shaping song structure and singing behaviour in red-winged blackbirds.

Keywords: active space; *Agelaius phoeniceus*; amplitude; bird song; communication; directionality; red-winged blackbird

Sound waves radiate in all directions from a vocalizing animal; when sounds are not equally loud in every direction, the vocalization is considered to be directional. Directional radiation of signals can occur in all modalities: acoustic, visual, chemical, vibrational and electrical (e.g. Bradbury & Vehrencamp 1998; McNett et al. 2006; Peters & Evans 2007). For example, the radiance received by a female assessing a structural colour patch on a male will vary depending on the orientation of the male relative to the sun and to the female (e.g. Endler 1992; Sweeney et al. 2003; Fleishman et al. 2006). Directionality in radiating signals is likely to have important implications in animal communication and thus the signal-production structures and behaviours that affect directionality may be subject to selection, similar to other features of signals that can affect the efficacy of transmission, such as frequency and temporal patterning in acoustic signals (Marler 1955; Morton 1975; Richards & Wiley 1980; Nowicki 1987; Podos 1997, 2001).

Correspondence: G. L. Patricelli, Section of Evolution and Ecology, 2320 Storer Hall, One Shields Avenue, University of California, Davis, CA 95616, U.S.A. (email: gpatricelli@ucdavis.edu). M. S. Dantzker and J. W. Bradbury are at the Cornell Laboratory of Ornithology, 159 Sapsucker Woods Road, Ithaca, NY 14850, U.S.A.

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There are a number of means by which directionality may affect the quality of the signal received, as well as the number and identity of receivers for a signal. Because higher frequency sounds are more directional than lower frequency sounds, receivers may assess the spectral properties of a vocalization to determine whether the sender is facing the receiver (Witkin 1977; Hunter et al. 1986; Larsen & Dabelsteen 1990; Dantzker et al. 1999; Miller 2002; Lammers & Au 2003). Because the sender's orientation relative to the receiver will affect the amplitude received, directionality will affect the receiver's ability to assess information about the sender conveyed by amplitude, such as size (Morton 1982; Arak 1983). Directionality may also affect the shape and size of the 'active space' of the vocalization, the area in which the signal can be detected, because active space is determined in part by the amplitude of the sound waves relative to background noise (Brenowitz 1982a). Furthermore, directionality will affect the number and identity of receivers for a signal. More-omnidirectional vocalizations will maximize the number of surrounding receivers that detect the vocalization, whereas more-directional vocalizations will allow animals to beam the sound to a target receiver and decrease eavesdropping (Witkin 1977; Larsen & Dabelsteen 1990; Dantzker et al. 1999; Brumm & Todt 2003; Dabelsteen 2005). Thus, omnidirectional vocalizations may also be beneficial when the receiver's location is unknown, whereas directional location may be used when receiver location is known. These effects of directionality on acoustic communication may select for adaptations that allow animals to either compensate for directionality or make use of directionality when communicating.

In most birds, models of sound production predict that radiation patterns will be bilaterally symmetrical, with their maximum radiation point in front of the beak (Hunter et al. 1986; Fletcher & Tarnopolsky 1999). These models predict that the shape and directionality of the radiated sound field will mainly be determined by the acoustic frequency, the position of the head and body, the size and morphology of the beak and the amount of beak movement during vocalization (Hunter et al. 1986; Larsen & Dabelsteen 1990; Fletcher & Tarnopolsky 1999; Nelson et al. 2005). Therefore variation in frequency and posture among call types may affect directionality, as will variation in morphology among species. Previous measurements of directionality in vertebrates range from highly directional signals in echolocating bats and cetaceans and in displaying greater sage grouse (approximately 20−30 dB difference in amplitude between the loudest and the quietest angle measured; Hartley & Suthers 1987; Dantzker et al. 1999; Madsen 2005) to moderately directional signals in songbirds and dogs (approximately 3−10 dB difference; Witkin 1977; Hunter et al. 1986; Larsen & Dabelsteen 1990; Brumm 2002; Frommolt & Gebler 2004; Nelson et al. 2005; Patricelli et al. 2007) to nearly omnidirectional signals in anurans (Gerhardt 1975). Measures of acoustic signals in insects similarly range from omnidirectional to highly directional (e.g. Forrest 1991; Michelsen & Elsner 1999; Michelsen & Fonseca 2000; Jerome et al. 2005).

An additional mechanism by which animals may alter the directionality of their vocalizations is by turning on their perch when they vocalize. Brumm & Todt (2003) found that male nightingales, *Luscinia megarhynchos*; have a moderately directional song and that they rotate on their perch when there is no known receiver, possibly to radiate their song omnidirectionally, and they face their rival when location is known, possibly to beam their sounds towards their rival. These rotation behaviours probably also facilitate visual surveying and visual signalling. Similar behaviours have been described in male northern mockingbirds, *Mimus polyglottos* (Breitwisch & Whitesides 1987). Therefore males may have behavioural strategies to complement the directionality of their vocalizations, and directionality may play an important role in shaping male singing behaviours.

Previous studies have found evidence that the directionality of different classes of vocalizations may be adapted to the function of that vocalization in communication (Larsen & Dabelsteen 1990; Patricelli et al. 2007). For example, Patricelli et al. (2007) found that red-winged blackbird calls used to communicate with multiple receivers (alarm 'cheers' and 'checks' used as conspecific alert and contact calls; Beletsky et al. 1986; Burton & Yasukawa 2001) are more directional than sexually selected vocalizations (precopulatory calls and 'oak-a-lee' songs, Peek 1972; Searcy & Brenowitz 1988; Searcy 1989). Directionality may vary not only among classes of vocalizations, but also within classes. Therefore birds may use song or call variants with appropriate directionality in different situations. Birds with song repertoires may use this tactic. Many species use songs both for advertisements (long-distance attraction of females and defining territory boundaries) and for direct interactions (courtship of females or confrontations with neighbouring conspecifics) (Catchpole & Slater 1995). If songs within a repertoire vary in directionality, males may use song variants or song types that match the social context. Consistent with this possibility, Patricelli et al. (2007) found that red-winged blackbird songs have moderate directionality relative to the birds' other vocalizations, but have the highest standard deviation in directionality among vocalization types. Birds may also alter their rotation behaviours and/or singing amplitudes to complement or counteract the directionality of the song type they are singing and thereby influence how far and to whom the signal is radiated. These possibilities have not yet been explored in any species.

We measured the directionality of oak-a-lee songs used by territorial male red-winged blackbirds. Red-winged blackbirds are polygynous, with harems of up to 15 females nesting on their territories (mean harem size ranges from 1.6 to 6.2 among populations; Searcy & Yasukawa 1995). The oak-a-lee song of the red-winged blackbird is used during direct interactions with rival males and is important in maintaining territory boundaries (Peek 1972); songs are also important in acquiring mates (Peek 1972) and elicit copulation-solicitation behaviours in females (Searcy & Brenowitz 1988). Males have repertoires of five to seven songs (Smith & Reid 1979), and during the breeding season, male song is often accompanied by the song-spread visual display (Peek 1972). Red-winged blackbirds are ideal for the study of directionality in the field because their marsh-grass habitat is open, with few features that reflect sound; they readily vocalize from man-made perches in their territories and their use of songs in different social contexts is well studied (Searcy & Yasukawa 1995).

In this study, we tested hypotheses about how directionality within and among song types relates to male singing behaviours and the social context in which songs are used. First, we tested the hypothesis that there are significant differences in directionality among song types, which would facilitate selective use of songs within the repertoire to match the social context. Second, we tested the hypothesis that there is a relationship between directionality and the amplitude at which songs are produced. A positive relationship between amplitude and directionality would be expected if males sing at higher amplitudes during direct interactions, as has been found in nightingales (Brumm & Todt 2004; see also Dabelsteen 1981). A negative relationship would be expected if males sing at lower amplitudes during direct interactions, for example, the use of soft song during courtship in many species (e.g. Dabelsteen et al. 1998). Third, we tested the hypothesis that directionality varies with the song-spread visual display that accompanies songs. Because red-winged blackbirds give higher-intensity visual displays during direct interactions with males and females (Peek 1972), we predicted a positive relationship between directionality and the intensity of the visual display. Fourth, we tested the hypothesis that there is a relationship between the directionality of songs and rotation behaviour while singing. A negative relationship between rotation and directionality would be expected if males beam their songs during direct interactions by facing the receiver and using directional songs and combine less-directional songs and rotation to broadcast their songs widely (no rotation would be required if song were truly omnidirectional, e.g. Forrest 1991; but this is not the case with red-winged blackbirds and other passerines measured thus far; Hunter et al. 1986; Larsen & Dabelsteen 1990; Brumm 2002; Nelson et al. 2005; Patricelli et al. 2007). Fifth, we tested the hypothesis that directionality varies among notes within each song, which may allow males to direct the same songs at different receivers.

METHODS

Field Site

The field site was located at the Cornell Experimental Ponds Facility approximately 10 km north of Ithaca, New York, U.S.A. (42.50°N, 76.46°W). This site consisted of man-made ponds and marshes, interspersed with grassland habitat. We made directionality measurements on six male red-winged blackbirds in their territories during the breeding season, between 28 April and 10 June, 2003. Throughout this time, we measured temperature, wind speed, humidity and atmospheric pressure at 5-min intervals using a Davis Vantage Pro weather station. The weather station was placed at a central location on the field site, within 0.5 km of the recording perches. We estimated weather conditions at the time of each vocalization (to within 1 s) by linear interpolation in MATLAB (1998; Mathworks, Inc., Natick, Massachusetts, U.S.A.); we used these data to estimate the speed of sound for acoustic localization (see below).

The Recording Perch

The acoustic directionality recording rig consisted of a perch encircled by a steel ring, around which eight calibrated microphones and three video cameras were arrayed (see Patricelli et al. 2007). To ensure that vocalizations were recorded in the far field (Bradbury & Vehrencamp 1998), microphones were placed at least 0.9 m from the singing bird (at least ~3 wavelengths). Recordings were made over grass, not marsh groundcover. The top of the perch was 2.31 m from the ground, and the tops of the microphone capsules were 2.3 m from the ground; the exact height of each microphone from the ground varied within ~0.25 m among recording sites depending upon whether the perch was placed on a slope (see Patricelli et al. 2007 for detailed measurements of perch geometry). Because our microphones were >2 m from the ground and approximately 1 m from the vocalizing bird, we assumed that environmental transmission effects between the microphone and the bird were negligible and equal along all paths. Any differential effects on these amplitude measures from ground reflections (which should be small at this angle, ~27°, and with a dense cover of grass on the ground) should not bias the results of this study.

Metal fence posts were placed in the territories of male red-winged blackbirds throughout the field site. We monitored perches for the identities of the singing males (all but two males were banded from a previous study; the two unbanded males simultaneously held territories on opposite sides of the field site and therefore cannot have been the same individual). We replaced the favoured fence-post perch in each male's territory with the recording perch in the afternoon or evening and recorded birds on the subsequent days between dawn (ca. 0545 hours) and late morning (ca. 1000 hours).

Video Recording and Analysis

We used video to measure the orientation of the bird relative to the microphones during each vocalization. We recorded the video with three black-and-white, closed-circuit security cameras placed around the ring of the recording perch (see Patricelli et al. 2007 for details about the recording equipment); Fig. 5 shows one of the three camera views for each song. Video data were digitized for frame-by-frame analysis in Macintosh iMovie. To determine bird orientation for each vocalization, we compared the multiplexed video image of the vocalizing bird to video images of a model bird rotated in 15° increments. We scored the orientation of the bird's head and body separately relative to 0 and used the head orientation for analyses. If the orientation of the bird's head differed from that of its body by ≥30° or if the body or head position changed during the vocalization, we did not include that vocalization in the analysis. We measured 'rotation' for each vocalization from videos as the absolute value of the difference in head orientation between the current and the previous vocalization (observed min = 0°, observed max = 180°); we $\log_{10}$ transformed the rotation to achieve normality for statistical tests.

Intensity of the Visual Display

We scored the intensity of the song-spread displays from videos as falling into four categories defined by Peek (1972): (1) incipient displays, in which the red of the epaulets is slightly exposed, but the wings are folded and the tail is only partially spread; (2) low-intensity displays, in which the epaulets are exposed, wings are slightly out from the body and tail is lowered and fanned; (3) medium-intensity displays, in which epaulets are exposed and raised, wings are well extended from the body in a flat plane and the tail is lowered and fanned; and (4) high-intensity displays, in which the epaulets are exposed and raised, wings are fully extended from the body and lowered downward and the tail is extremely fanned and nearly touches the wing tips (Fig. 5 shows a high-intensity display). All videos were scored by G.L.P., who was blind to the amplitude and directionality of the displays.

Audio Recording and Measurement of Amplitude

We recorded audio with a Mark of the Unicorn (MOTU) Audio 896, which digitized and recorded audio directly to hard disk on a PowerMac G3 laptop. We used MOTU Digital Performer (version 6) for audio acquisition and audio–video synchronization. We used Sennheiser K6 microphones with ME62 omnidirectional capsules and MZW64 wind screens. We recorded digital audio at 44.1 kHz with 16 bits per sample. To allow calibration for variation in microphone, cable and preamp sensitivity among channels (see below), we recorded a 114-dB test tone from a Larson and Davis CAL250 precision calibrator; to allow calibration for variation in gain settings each day we recorded a tone from a Shure in-line tone generator (AT15TG).

Wave files were visualized as spectrograms in Raven (Cornell Laboratory of Ornithology, 2002); we excluded vocalizations from the analysis if visual inspection of the spectrogram revealed overlapping vocalizations or excessive background noise. For each song, we chose seven notes for measurement of amplitude, directivity index (DI) and peak frequency (see below); notes were chosen consistently within each song type and silent gaps between notes were not included in analyses. For measures of the DI, amplitude and peak frequency of the entire song (e.g. Figs 2–5), we used the mean measure among notes weighted by the duration of the note. For analyses of note types within songs (e.g. Figs 1 and 6), we divided notes into four categories that were comparable by ear across song types (see Fig. 1 for examples from three song types): introductory notes (the first one to three notes), 'oak' notes (the next two to four notes), 'a' notes (one or two notes preceding the trill) and 'lee' notes (concluding trills, one note). For each note category, we used mean measures of included notes weighted by note duration (the weighted mean was calculated as the sum of the products of duration and the focal variable for each note, divided by the sum of durations).

For each vocalization at each microphone, we calculated the sound pressure level in decibels (dB SPL re 20 μPa) at 1 m from the sound source using a MATLAB routine. This routine first measured the path length between the sound source and each microphone using acoustic localization (Spiesberger & Fristrup 1990) and normalized these measures to 1 m using the assumption of spherical spreading (path lengths varied slightly, ca. ±0.1 m, because of the geometry of the recording perch and the position of the bird while singing). Second, we measured amplitude from sound files in the frequency domain (FFT size 512, overlap 0.7, Hann window) and corrected these measures for variation in recording gain and system sensitivity using calibration tones (see above). Patricelli et al. (2007) provide details on calibration and the measurement of amplitude. For analyses including amplitude, we used the maximum amplitude measure among the eight microphones for each vocalization, typically in front of the bird.

Songs were categorized into song types by visual inspection of spectrograms. We found 14 song types present in our 166 recorded songs from our six study males. Five of these songs were shared by more than one male (see Table 1). We recorded an average of 3.16 ± 0.75 songs (ranging from 1 to 6 songs) from the study males; the repertoire size of males in another population of red-winged blackbirds in New York was 5–7 songs (Smith & Reid 1979).

Directivity Measurements and Polar Plots

We quantified the patterns of acoustic radiation for each vocalization using both the DI and the difference in dB SPL between the quietest and the loudest of the eight measures of amplitude for the focal vocalization (Diff; Dantzker et al. 1999). The directivity index compares the intensity of the maximum lobe of a two-dimensional beam pattern with the intensity of a uniform source radiating the same total power output (Dantzker et al. 1999). For comparison, an omnidirectional vocalization would have a DI of 0, red-winged blackbird vocalizations ranged from a mean DI of 2.72 (Diff = 7.16 dB) for the 'check' alert call to 3.98 (Diff = 9.59 dB) for the 't'chit' call (Patricelli et al. 2007), and the highly directional 'whistle' note of the sage grouse strut display has an average DI of 4.4 (Diff = 14 dB) and a maximum DI of 6.7 (Diff = 22.9 dB; Dantzker et al. 1999). For the average DI of a song or note type, we used a mean of the DI values for each of the notes, weighted by the duration of the note (see above).

We visualized radiation patterns using polar plots of amplitude at each microphone for the region of interest within the song. All polar plots were in decibels, with the loudest value normalized to 0 dB (outermost circle on the plot) and an origin at −12 dB. To create average radiation plots for each note type (presented in Fig. 1), we used linear interpolation to estimate the amplitude at 24 locations around the bird for each vocalization (there were 24 possible microphone locations among vocalizations, because we scored the direction that the bird was facing to within

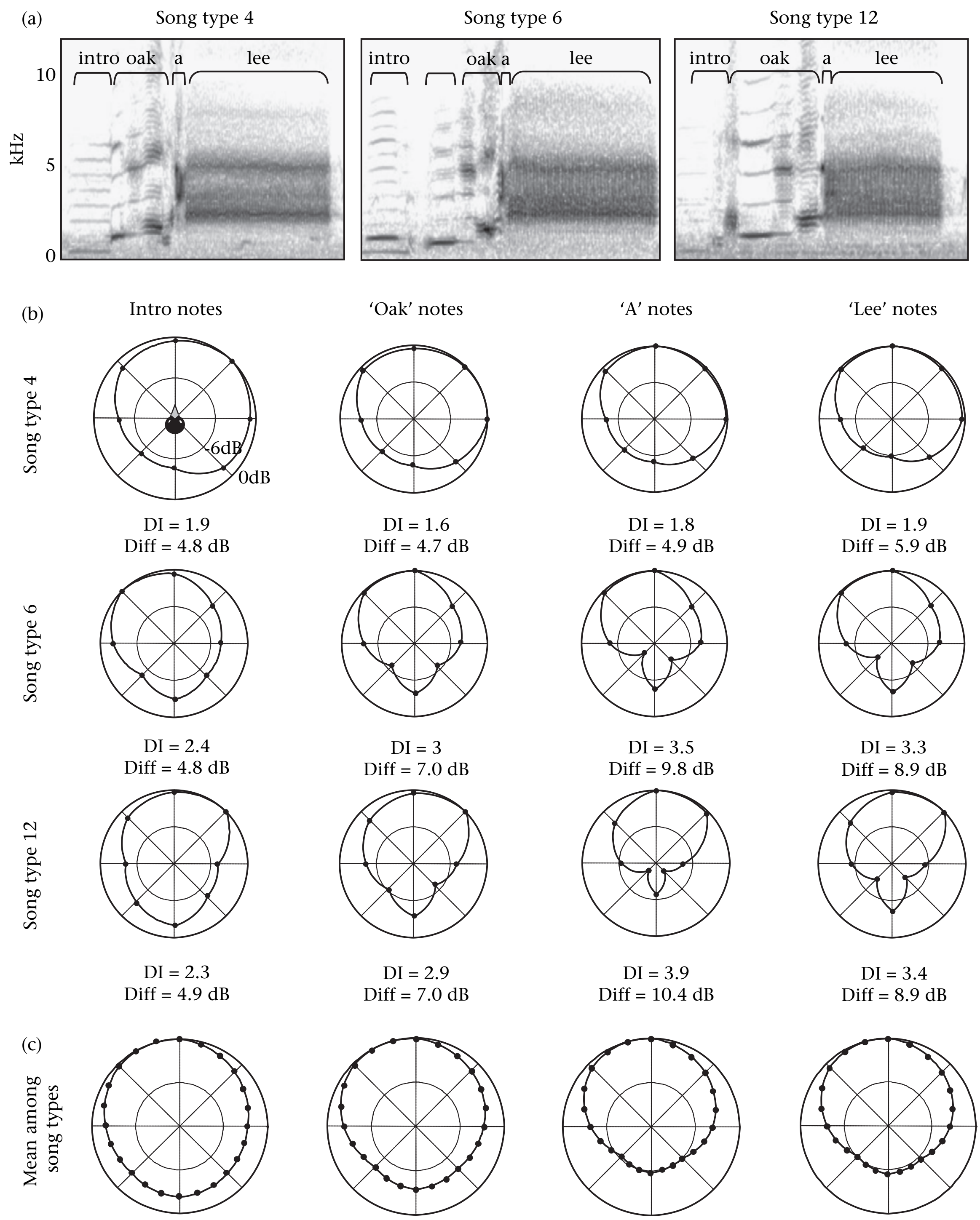

Figure 1. Acoustic radiation plots of red-winged blackbird vocalizations. (a) Spectrograms showing examples of three songs from three song types; examples were chosen to illustrate songs with relatively low (song type 4), moderate (song type 6) and high directionality (song type 12). The assignment of notes within each category is shown on the spectrogram. (b) Polar plots of acoustic radiation for the three songs shown in (a) (in rows); separate plots are shown for each note type (in columns). Points on each plot represent the amplitude as measured at each of the eight microphones, connected by linear interpolation. All polar plots are in decibels, with the loudest value normalized to 0 dB (outermost circle on the plot) and an origin at −12 dB. All plots are oriented so that the bird's head is facing upward. The directivity index (DI) and min—max difference (Diff) are given under the vocalization. (c) Average radiation plots for each note type, pooled among all males, songs and song types (see Methods for details).

Table 1. Descriptive statistics for each song type, pooled among males

		Directionality	Min–max difference (dB SPL)	Max amplitude* (dB SPL)	Peak frequency (kHz)
Song type 1, *N*=29, 1 male	Mean	3.27	7.02	83.12	3.08
	SD	0.51	0.82	0.73	0.09
	Min	2.07	5.17	81.29	2.87
	Max	4.19	8.41	84.00	3.21
Song type 2, *N*=22, 1 male	Mean	3.09	6.92	84.79	3.22
	SD	0.42	0.84	0.58	0.14
	Min	2.29	4.96	83.59	2.99
	Max	3.75	8.24	85.80	3.53
Song type 3, *N*=19, 2 males	Mean	2.74	6.61	83.25	3.14
	SD	0.64	0.73	1.40	0.38
	Min	1.89	5.24	81.36	2.72
	Max	4.18	7.88	86.03	3.64
Song type 4, *N*=7, 1 male	Mean	2.39	6.06	81.79	2.91
	SD	0.40	0.45	0.53	0.025
	Min	1.81	5.28	80.99	2.89
	Max	2.85	6.58	82.58	2.95
Song type 5, *N*=8, 1 male	Mean	2.79	7.13	84.23	2.90
	SD	0.60	0.87	0.86	0.04
	Min	1.67	5.46	82.64	2.83
	Max	3.40	8.10	85.39	2.95
Song type 6, *N*=7, 1 male	Mean	2.90	6.85	81.59	2.67
	SD	0.67	1.43	1.14	0.06
	Min	1.94	4.74	79.77	2.60
	Max	3.64	8.11	82.69	2.77
Song type 7, *N*=9, 2 males	Mean	2.80	6.60	82.51	2.55
	SD	0.71	1.05	1.45	0.08
	Min	1.62	4.59	79.81	2.41
	Max	3.67	7.78	83.96	2.65
Song type 8, *N*=5, 1 male	Mean	3.36	7.17	83.62	2.48
	SD	0.11	0.37	0.31	0.03
	Min	3.26	6.89	83.13	2.45
	Max	3.54	7.73	83.92	2.52
Song type 9, *N*=11, 2 males	Mean	2.58	6.64	82.55	2.79
	SD	0.50	0.93	0.72	0.16
	Min	1.81	4.26	81.31	2.60
	Max	3.34	7.62	83.52	3.10
Song type 10, *N*=11, 2 males	Mean	3.30	7.19	82.59	2.54
	SD	0.80	1.24	1.04	0.17
	Min	1.50	4.88	80.40	2.40
	Max	3.98	8.38	83.53	2.94
Song type 11, *N*=31, 2 males	Mean	3.23	7.75	83.08	3.18
	SD	0.77	1.39	1.20	0.15
	Min	1.97	5.48	80.68	2.83
	Max	4.44	9.93	85.35	3.37
Song type 12, *N*=5, 1 male	Mean	3.36	7.92	84.86	2.90
	SD	0.97	1.06	1.15	0.14
	Min	1.89	6.13	83.11	2.75
	Max	4.26	8.89	85.94	3.12
Song type 13, *N*=1	Value	2.18	4.92	84.98	3.06
Song type 14, *N*=1	Value	3.82	7.72	81.79	2.46
Mean of song means, *N*=14	Mean	2.99	6.89	83.20	2.85
	SD	0.44	0.76	1.16	0.27
	Min	2.18	4.92	81.59	2.48
	Max	3.82	7.92	84.98	3.22

The arithmetic mean, standard deviation (SD) and minimum and maximum values for four different measurements made on each of the 14 song types are shown. The number of songs used in these analyses (*N*) is given under each song title, as well as the number of males whose repertoires included that song type. All vocalizations are pooled among males; these statistics thus describe the sample of vocalizations and are not estimates of population values among males.

*Max amplitude is the highest amplitude measure among the eight microphones for each vocalization (typically in front of the bird); see Methods for descriptions of other measures.

15°; each set of amplitude measures was shifted so that the bird was facing the top of the plot). The 24 points on the plot each represent the mean of amplitude measures for that location pooled among males and among song types.

Peak Frequency Measurements

To measure the peak frequency (the frequency at which the highest amplitude occurs) of each note on which directionality was calculated, we found the frequency bin with the highest amplitude in each window of the spectrogram (window size 512), then we took the average of those frequency values among windows. Thus our measure of 'peak frequency' represents the average peak frequency through the duration of the note (the same region from which the directionality is calculated), not the frequency of the single highest-energy window within the note, because the latter measure would be highly sensitive to FFT window size and short-term fluctuations in amplitude. For the average peak frequency of a song or note type, we used a mean of the peak frequency measures for each of the notes, weighted by the duration of the note (see above).

Statistical Analyses

All statistical analyses were conducted using SAS 8.01. We used a Kruskal–Wallis nonparametric ANOVA to compare directionality among song types, because the extreme homoscedasticity of DI values among the 14 song types precluded the use of parametric statistics. We used a mixed-model ANOVA to compare directivity among display-intensity levels and note types using PROC MIXED. Male identity was considered a random block effect because we measured multiple types of vocalizations on each male; the interaction between male and call type was also modelled as a random effect. The dependent variable was DI in all ANOVA models. We used the variance components (VC) covariance structure to model the covariance of the repeated measures (the multiple recording of each call type for each male); we tested eight models, and the VC model showed the best fit using the Akaike and Schwartz' Bayesian information criteria (Littell et al. 1996). To examine relationships between variables, we use least-squares regression and Pearson correlations. All statistical tests were two-tailed.

RESULTS

First, we tested the hypothesis that song types differ in directionality. Supporting this hypothesis, we found a highly significant difference in directionality among song types in a nonparametric ANOVA (Kruskal–Wallis test, $\chi^2_{13} = 35.2$, $P < 0.001$; Table 1). Figure 1 shows polar plots of examples from three song types.

Second, we tested the hypothesis that there is a relationship between directionality and the amplitude at which songs are delivered. We did not find a significant relationship between DI and amplitude (using the maximum amplitude measure among the eight microphones for each vocalization, typically in front of the bird) among song types, using the mean DI and amplitude values among males for each song type (regression: $R^2 < 0.001$, $F_{1,13} < 0.001$, $P > 0.9$). However, supporting this hypothesis, all six males had positive slopes of DI on amplitude, and the average slope was significantly different from 0 (*t* test: $t_5 = 4.8$, $P = 0.005$; Fig. 2). There was no relationship between the peak frequency and the amplitude of songs within each male; the average slope among males did not differ significantly from 0 (*t* test: $t_5 = 0.06$, $P > 0.9$).

Third, we tested the hypothesis that directionality varies with the song-spread visual display that accompanies songs. Our results did not support this hypothesis; we found no significant relationship between directionality and the intensity of the visual display in a mixed-model, repeated measures ANOVA (Fig. 3a). We also examined whether other behavioural variables change with song-spread intensity. We found no significant differences in amplitude among intensity levels (Fig. 3b). We found a nonsignificant tendency for rotation behaviour to differ among intensity levels (Fig. 3c), with males tending to rotate more while producing higher-intensity displays.

Fourth, we tested the hypothesis that there is a relationship between the degree to which a male rotates on his perch and the directionality of songs produced. Supporting this prediction, we found a highly significant negative relationship between directionality and rotation (the amount that the male rotates, in degrees, between the previous and the current vocalization) using the average value among males for each song type (Pearson correlation: $R = -0.78$, $N = 14$, $P < 0.002$; Fig. 4). In addition, we examined whether DI and rotation were related within individual males; five of the six males had the predicted negative slopes of DI on rotation, though the average slope did not differ significantly from 0 in a *t* test (*t* test: $t_5 = 2.15$, $P = 0.08$). Figure 5 shows male rotation behaviour in subsequent songs during the dawn chorus. Male rotation between songs ranged from 0 to 180°.

Fifth, in addition to examining variation in directionality among songs, we tested the hypothesis that different notes of the oak-a-lee song differ in directionality, such that songs may function in multiple contexts simultaneously. Supporting this hypothesis, we found that DI is highly significantly different among note types in a mixed-model, repeated measures ANOVA (ANOVA: $F_{3,15} = 64.88$, $P < 0.0001$; Fig. 6, Table 2). Figure 1 shows polar plots of each note for three song types.

DISCUSSION

We found strong support for the hypothesis that there is variation in directionality among song types. The differences in amplitude between the quietest and the loudest amplitude measures of each song rendition (Diff) ranged from 4.98 to 9.93 dB, with an average of 6.98 dB among songs (see Table 1). With spherical spreading alone, this average difference in source amplitude would translate to more than a halving of the distance at which the song could be detected by a receiver, and more than a doubling in received amplitude at a given distance. However, spherical

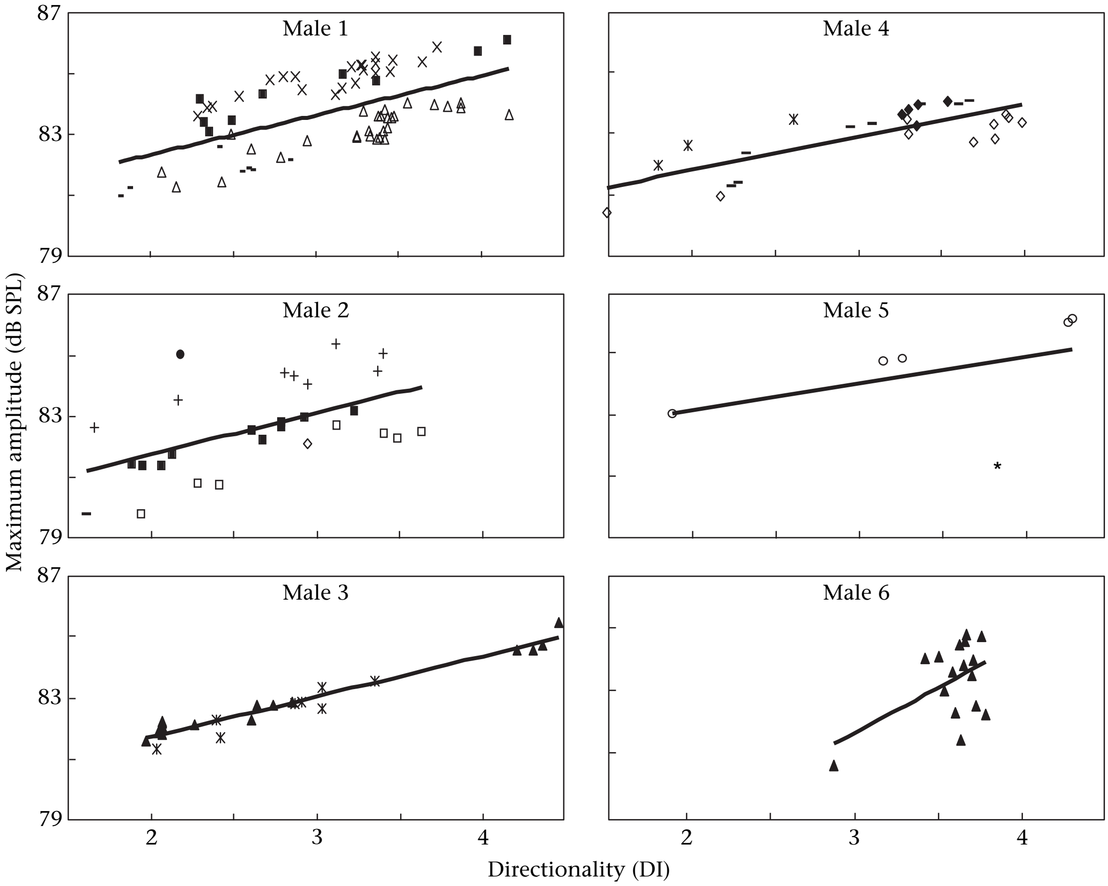

Figure 2. The relationship between maximum amplitude and directionality for each male. Each song type is shown with a different symbol; the best-fit line and slope for each male is calculated using all song types. There is a strong and strikingly linear relationship between DI and amplitude for all but one male (male 6), especially comparing songs of the same type. The average slope of directionality on amplitude among males is significantly different from 0 ($t_5 = 4.8$, $P = 0.005$), supporting the prediction that there is a positive relationship between directionality and amplitude among songs of individual males.

spreading alone will overestimate the importance of source directionality, because excess attenuation (EA) increases with distance (i.e. the loudest amplitude measure will be more strongly affected by EA than the quietest because it propagates farther, which shrinks the propagation difference between them). Because EA depends on frequency, habitat, weather and singing location (Embleton 1996) and because directionality is also determined in part by frequency (Hunter et al. 1986; Fletcher & Tarnopolsky 1999), the amplitude of a particular song at a given distance from the sender will reflect a complex interaction between source directionality, EA and frequency. Brenowitz (1982a) found that EA of red-winged blackbird songs was trivial within 30 m of the signaller (also measured at a study site in Ithaca, New York); therefore EA will primarily reduce the impact of directionality on received amplitude during long-distance communication.

The observed variation in directionality among song types may be unrelated to functional context in which the song is used, or males may selectively use songs from their repertoires in different contexts, choosing more-directional song types in direct interactions and more-omnidirectional song types in broad advertisements. We do not have information about the context in which songs in this study were used, so we cannot directly examine whether males select song types in this way. Smith & Reid (1979) report anecdotal evidence that male red-winged blackbirds do not favour particular song types during particular social contexts, and males tend to cycle through their repertoires, which suggests that males are unlikely to match their song type to the social context (Yasukawa 1981; Searcy & Yasukawa 1990); however, the possibility of contextual song type use has not been eliminated. Selective use of song types is not the only means by which males may match directionality to social context; males could also adjust directionality for a particular song rendition, for example, by adjusting the fundamental frequency or harmonic weighting of the song or their body posture and beak opening while singing (Hunter et al. 1986; Larsen & Dabelsteen 1990).

We found support for the hypothesis that the amplitude and directionality of songs are related; there was a highly significant positive relationship between directionality and maximum amplitude within individual males (Fig. 2). However, we found no relationship between the mean directionality and the mean amplitude among song types when using an average for each song type. This suggests that amplitude and directionality strongly covary among each male's song types and among each male's renditions

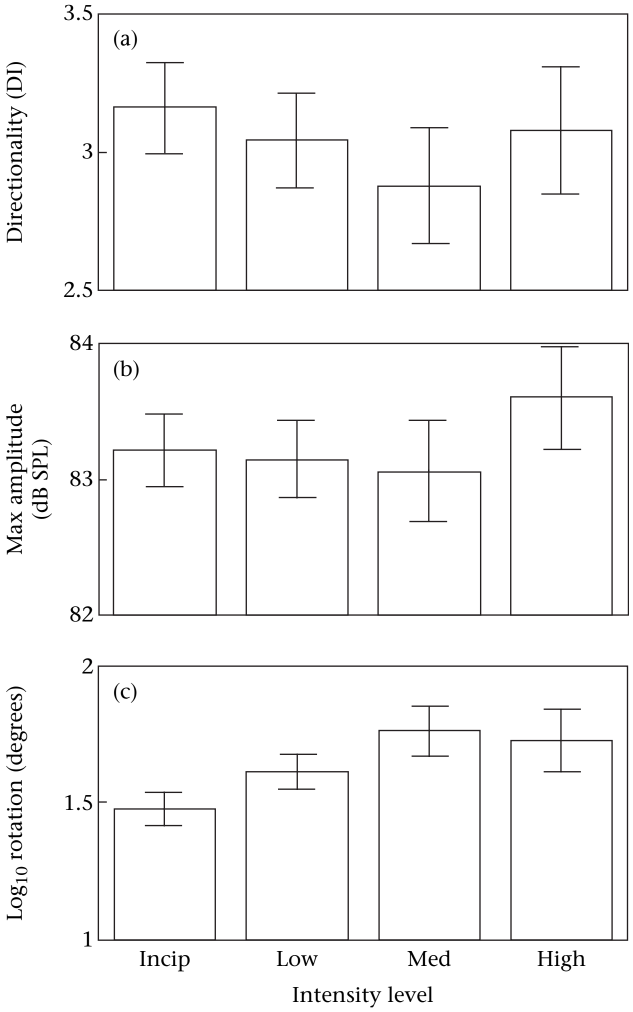

Figure 3. Comparison among display-intensity levels. The least-squares mean directivity index of each display-intensity level (incipient, low intensity, medium intensity and high intensity; Peek 1972), with standard error bars, is shown. We found no significant differences among display-intensity levels in (a) directionality (ANOVA: $F_{3,11} = 0.7$, $P = 0.57$), (b) amplitude (ANOVA: $F_{3,11} = 0.67$, $P = 0.59$) or (c) rotation behaviour while singing (ANOVA: $F_{3,10} = 2.89$, $P = 0.09$).

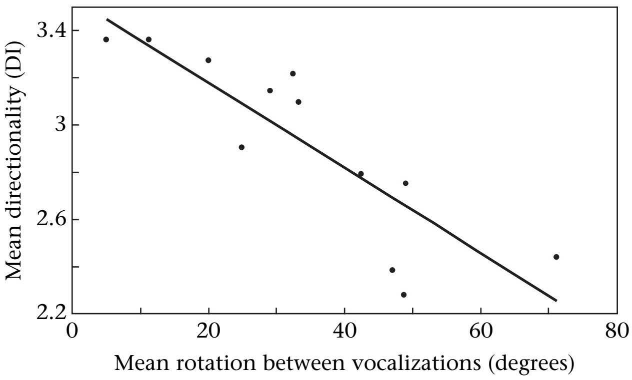

Figure 4. Directionality and rotation behaviours. We found a highly significant negative relationship between directionality and rotation using the average rotation and DI values among males for each song type (Pearson correlation: $R = -0.78$, $N = 14$, $P < 0.002$). By using relatively omnidirectional songs while rotating on the perch, males should increase the number of neighbouring conspecifics who detect the song.

of the same song type, but that there are differences among males in the directionality and/or amplitude at which they deliver particular song types. Brumm & Todt (2004) found that male nightingales sing at higher amplitudes in direct interactions with rivals than during undirected songs (see also Dabelsteen 1981). If red-winged-blackbirds do the same, then the results presented here suggest that males beam their sounds at rivals during direct interactions by using more-directional songs. Covarying directionality and amplitude may also benefit males in intersexual interactions; Searcy (1996) found that females showed an increase in solicitation behaviour in response to high-amplitude songs, so males may benefit from singing at higher amplitude during courtship.

An alternative explanation for the relationship between amplitude and directionality is that these two song features are linked due to the mechanism of sound production. One possibility for linkage is that directional songs have higher maximum amplitude because the sound energy is directed forward, rather than radiated omnidirectionally. This is unlikely, because models of sound production predict that directional patterns emerge primarily through interference effects cancelling sound energy and by the sound shadow caused by the head (Hunter et al. 1986; Fletcher & Tarnopolsky 1999). However, a physiological link remains possible. For example, fundamental frequency and amplitude may both vary with subsyringeal air-sac pressure and beak opening (Goller et al. 2004; Nelson et al. 2005; e.g. Westneat et al. 1993). Because higher frequencies are more directional, the relationships observed here between directionality and amplitude may be a consequence of change in frequency and/or beak opening and not evidence of selection acting on directionality. Arguing against this explanation, we did not find any relationship between the amplitude and the peak frequency of songs. Furthermore, directionality and amplitude do not covary among call types in this species; Patricelli et al. (2007) found that 'cheer' alarm calls have the highest amplitude and relatively low directionality, and 't'chit' calls have the highest directionality and the lowest amplitude. This suggests that directionality and amplitude can be modulated independently among call types. However, the relationships between DI and amplitude are strikingly linear and strikingly similar for all but one male in this study (Fig. 2), suggesting that a physiological linkage between amplitude and directionality may occur in song production, even if the pattern does not hold when comparing different types of vocalizations. Studies of sound production physiology that measure air-sac pressure, fundamental frequency, directionality and amplitude are needed to address this possibility.

We found support for the hypothesis that there is a relationship between the amount of rotation among songs and the directionality of songs. We found a highly significant negative relationship between average rotation and average directionality among song types. We also found a nonsignificant tendency for individual males to have negative slopes between rotation and directionality. These

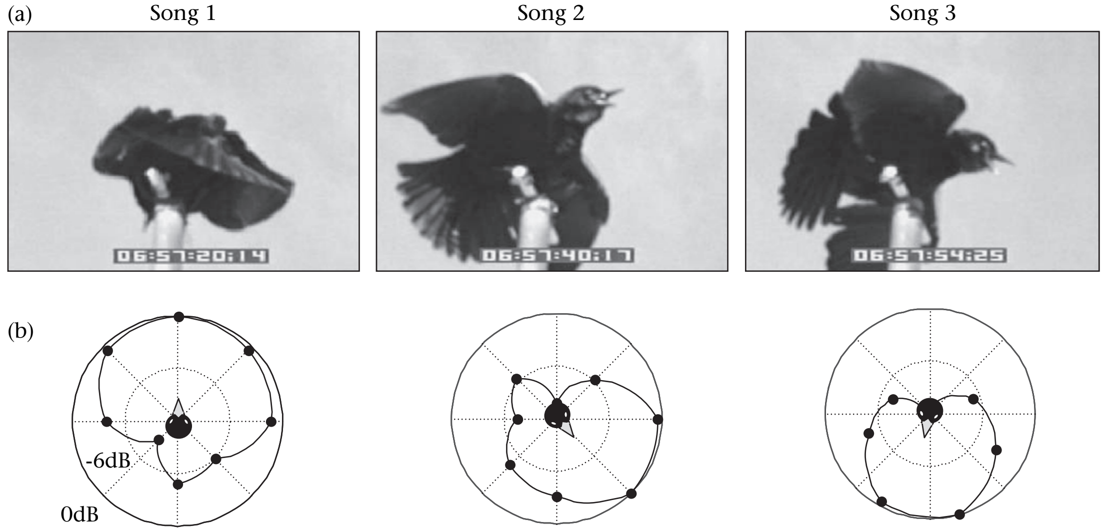

Figure 5. Three songs during the dawn chorus. (a) Video stills showing male position on the recording perch while singing three songs in sequence during the dawn chorus. (b) Resulting radiation plots. Plots shift in orientation with male rotation; the icon in the centre indicates which direction the bird is facing. These plots show that by rotating while singing, males can broadcast their songs more widely.

results suggest that males combine less-directional songs and increased rotation behaviours, which will broadcast songs more widely, and combine directional songs and less rotation, which will beam their signals in a narrower pattern. Further research is needed to determine whether males use these narrower beams in direct interactions and wider beams in broad advertisements. Male nightingales and northern mockingbirds rotate less during direct interactions, orienting toward their intended target (Breitwisch & Whitesides 1987; Brumm & Todt 2003); we do not yet know whether the degree of rotation and directionality of vocalizations covary within or among males in these species or any others. In contrast, Forrest (1991) found that cricket species with directional radiation of calls rotated while vocalizing, whereas crickets with omnidirectional radiation of calls did not rotate, opposite to the relationship between directionality and rotation reported here. This difference in behaviour between crickets and birds is probably because, first, rotation behaviour was observed in the crickets during advertisement calling only, in which maximization of radiation should be favoured; this yields the opposite prediction of a comparison of advertisement and direct interaction, as discussed here. Second, the calls of the omnidirectional crickets in the Forrest (1991) study have virtually omnidirectional radiation in the vertical

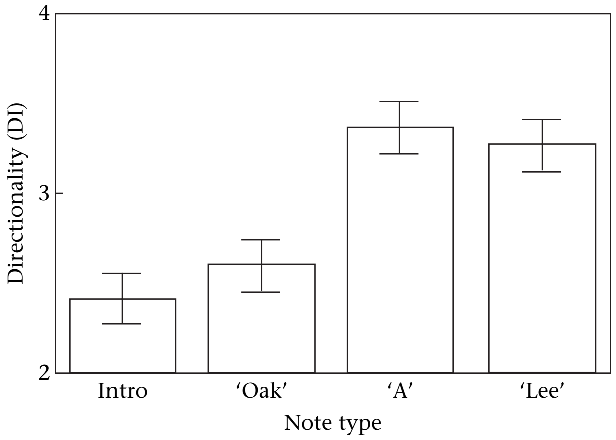

Figure 6. Comparison of directionality among note types. The least-squares mean DI of each note type, with standard error bars, is shown. DI is highly significantly different among note types in a mixed-model, repeated measures ANOVA ($F_{3,15} = 64.88$, $P < 0.0001$).

Table 2. Descriptive statistics for each note type, pooled among songs and among males

		Directivity index	Max–min difference (dB SPL)	Max amplitude* (dB SPL)	Peak frequency (kHz)
Introductory notes	Mean	2.33	4.58	68.15	1.04
	SD	0.63	0.94	4.27	0.31
	Min	0.99	2.36	59.01	0.22
	Max	4.07	7.13	76.04	2.73
'Oak' notes	Mean	2.53	5.60	79.03	2.32
	SD	0.60	1.04	4.38	0.43
	Min	1.00	2.63	68.98	1.30
	Max	3.99	8.00	85.49	3.07
'A' notes	Mean	3.28	7.90	87.04	3.55
	SD	0.70	1.50	4.06	0.48
	Min	1.58	3.87	75.72	1.89
	Max	5.39	12.41	95.03	4.66
'Lee' notes	Mean	3.19	7.48	84.26	3.15
	SD	0.71	1.19	1.52	0.29
	Min	1.46	4.53	80.81	2.72
	Max	4.64	10.54	87.51	4.13

The arithmetic mean, standard deviation (SD) and minimum and maximum values for four different measurements made on each of the four note types are shown. All vocalizations were pooled among males; these statistics thus describe the sample of vocalizations and are not estimates of population values among males; see Fig. 6 for population estimates of directionality.

*Max amplitude is the highest amplitude measure among the eight microphones for each vocalization (typically in front of the bird); see Methods for descriptions of other measures.

plane and thus rotation would not improve broadcast, whereas even the least-directional songs of red-winged blackbirds differ significantly from omnidirectional radiation (e.g. Fig. 1 and Table 1); therefore male red-winged blackbirds must adjust their posture to achieve omnidirectional rotation. These differences between crickets and birds highlight how sound production mechanisms, directionality, and the functional context of signals may interact to shape signalling behaviours.

An alternative explanation for the observed relationship between rotation behaviour and directionality is that rotation behaviour is influenced by the visual, rather than the acoustic, component of signalling. When receiver location is unknown, males benefit both by singing less-directional songs and by rotating to monitor their surroundings visually. By doing so, males may increase their ability to detect the positions of rival males and potential mates. In contrast, males in direct interactions may benefit from using more-directional songs and facing the receiver. By doing so, males may better observe receiver response and increase perception by the receiver of the visual signal (the song-spread display) that often accompanies song (Breitwisch & Whitesides 1987; Brumm & Todt 2003). Both the visual and the acoustic demands of singing may combine to cause the relationship between rotation and directionality observed in red-winged blackbirds; therefore, male red-winged blackbirds must adjust their posture to achieve omnidirectional rotation (Fig. 5).

Peek (1972) found that males performed moderate- and high-intensity displays far more frequently in the presence of male or female conspecifics than in their absence; we tested the hypothesis that males would use more-directional vocalizations while producing higher-intensity song-spread displays. We did not find support for this hypothesis; there was no relationship between intensity and directionality. We also found no evidence of variation in amplitude among intensity levels, as would be expected if higher-amplitude calls are used in direct interactions (Dabelsteen 1981; Brumm & Todt 2004). We found a nonsignificant tendency for rotation behaviour to differ among intensity levels, but if anything the results show a tendency to rotate less at incipient/low-intensity levels, whereas we would predict less rotation during direct interactions (i.e. higher intensity) if males face the target male or female (Breitwisch & Whitesides 1987; Brumm & Todt 2003). The apparent lack of relationship between intensity, amplitude and rotation behaviour suggests that these behaviours are not all associated with direct interactions in red-winged blackbirds. Experimental introductions of model males and females are needed to determine which of these behaviours are consistently associated with direct interactions (discussed further below). It is also interesting to note that even though male singing posture is extremely different among intensity levels (Peek 1972), there is no consistent difference in the directionality of the songs produced. That suggests that body posture (i.e. body angle, wing and tail position) is not a major determinant of directionality in this species. Other aspects of body position that may affect directionality, such as degree of beak opening (Hunter et al. 1986; Larsen & Dabelsteen 1990; Nelson et al. 2005), could not be measured using the data available from this study.

In addition to examining variation among song types and renditions, we tested the hypothesis that different notes of the oak-a-lee song differ in directionality. Supporting this hypothesis, we found highly significant differences in directionality among note types. This variation in directionality may be an epiphenomenon of selection for variation in frequency among notes; regardless of whether the variation in directionality was selected directly, it may have functional consequences in communication. Miller (2002) reported mixed directionality among different harmonic components of killer whale calls, which provides information about whether the signaller is moving towards or away from the receiver and may thus facilitate coordinated movements (see also Lammers & Au 2003). Coordination of movements is a less likely explanation for mixed directionality among notes in red-winged blackbird songs, because there is no evidence that songs are used to coordinate flight or flocking behaviours (Searcy & Yasukawa 1995). However, mixed directionality may allow receivers to estimate the orientation of the signaller and thus determine whether they are the intended receiver of the song (Witkin 1977; Hunter et al. 1986; Larsen & Dabelsteen 1990). Eurasian blackbirds, *Turdus merula*, have a full song that combines a loud, long-ranging component that is predicted to be relatively omnidirectional, followed by quieter, short-ranged twitter with moderate directionality (Dabelsteen & Pedersen 1988; Larsen & Dabelsteen 1990). Larsen & Dabelsteen (1990) proposed that the ratio of the high- to low-frequency components of these song components may allow receivers to assess sender orientation. Playback studies of songs differing in power spectra are needed to test this hypothesis directly.

A non-mutually exclusive alternative explanation is that the notes may have different intended receivers and thus may function in different social contexts (Dabelsteen & Pedersen 1988). Indeed, previous studies of red-winged blackbirds have found that males and females respond differently to the notes of the oak-a-lee song. Trills ('lee' notes) are used in long-distance communication of species identity and are necessary and sufficient to elicit an aggressive response from conspecific males; males do not respond more strongly to a full song than to trills only (Brenowitz 1982b). Full songs, however, are significantly more potent in eliciting solicitation behaviour from oestradiol-treated females than trills alone (Searcy & Brenowitz 1988). Thus females attend to all notes and males attend primarily to trills. We found that the introductory notes and 'oak' notes have the lowest directionality. These notes are also given at lower amplitude and are within a frequency range masked by low-frequency background noise at this location (2.5–4 kHz; Brenowitz 1982b); therefore these notes would be ineffective for long-range communication. These less-directional notes are likely to be detected by males with adjacent territories and multiple females in a male's harem. The 'a' notes have the highest directionality and are also the loudest; trills also have relatively high directionality and amplitude. These notes are both within the frequency range that propagates well (Brenowitz 1982b) and would thus be effective for long-distance communication. Notes used in both short-range and long-range communication, however, could be used in interactions with either a single or multiple receivers and may be directed towards males or females; it is thus difficult to make predictions about how different notes should be structured in this species. Experimental presentations of model males and females, as discussed below, would help us to understand how these notes are used in different social contexts and whether mixed directionality allows a single song to fulfil multiple social functions.

Because we did not have information about the social context of the songs in this study, we could not directly test the hypothesis that more-directional songs are used in direct interactions and more-omnidirectional songs are used in advertisements. This hypothesis could be tested directly though experimental presentations of an intruding male and a visiting female to each male's territory and measurement of directionality of the elicited songs (as well as song amplitude and male rotation behaviour). In spring 2004, we attempted such an experiment using taxidermic mounts of male and female red-winged blackbirds. Experimental presentations of model males failed, however, because target males inconveniently attacked the models without first stopping to vocalize on the recording perch. When we experimentally presented females, the males flew to the ground near the female and called, and again, we were unable to record calls from the perch. Male and female presentation experiments would probably be more successful with a less arousing stimulus and/or a larger microphone array that encircles the experimental stimulus and provides multiple perches for the focal male; in this case, excess attenuation would need to be measured along the paths between the bird and each microphone to reconstruct source directionality (Dantzker et al. 1999). Although further experimental and/or observational studies are needed to test directly the hypothesis that directionality is adjusted to match the social context of songs, the results presented here highlight the potential importance of directionality in acoustic communication and other signalling modalities in influencing both the structure of animal signals and their signalling behaviours.

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