

Differences in acoustic directionality among vocalizations of the male red-winged blackbird (*Agelaius phoeniceus*) are related to function in communication

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Abstract Studies of animal acoustic communication have found that the frequency and temporal structure of acoustic signals can be shaped by selection for efficient communication. The directionality of acoustic radiation may also be adapted for communication, but we know relatively little about how directionality varies with signal function, sender morphology, and the environment in which the sound is transmitted. We tested the hypothesis that the directionality of a vocalization is adapted to its function in communication. This hypothesis predicts that vocalizations that are directed to multiple conspecifics (e.g., advertisements and alarms) will be relatively omnidirectional because this will maximize the number of neighbors and mates that receive the signal, and that vocalizations directed to particular individuals will be relatively directional because this will maximize detection of the signal by the targeted receiver and minimize eavesdropping. To test these predictions, we measured the directionality and amplitude of red-winged blackbird (*Agelaius phoeniceus*) vocalizations in the field by recording vocalizations simultaneously on eight calibrated microphones encircling the bird. We found significant variation in directionality among vocalizations. Supporting our predictions, we found that the most omnidirectional vocalizations were those used to alert conspecifics to danger, and the most directional vocal-

izations are those used during courtship and solicitation of copulation, when the costs of eavesdropping are likely to be high. These results suggest that the directionality of red-winged blackbird vocalizations is shaped by selection for effective communication. This study is the first to provide statistical support for the hypothesis that directionality is related to the function of a signal in communication.

Keywords Bird song · Directionality · Communication · Red-winged blackbird

Introduction

Studies of animal communication have contributed to our understanding of natural selection by examining the degree to which animal signals are shaped by their social function, the physiology of the sender and receiver, and the environment in which signals are transmitted. Many of these studies have focused on acoustic signals, and in particular, on the spectral and temporal properties of acoustic signals (e.g., amplitude and frequency modulation, frequency spectrum, and bandwidth) because they are relatively easy to quantify (Morton 1975; Richards and Wiley 1980; Wiley and Richards 1982; Nowicki 1987; Westneat et al. 1993; Podos 1997; Hoese et al. 2000; Podos 2001). An important component of acoustic communication has been largely left out of these studies—the directionality of acoustic radiation—because it is difficult to measure. In this study, we describe a method for measuring acoustic radiation in the field and compare the directionality of different red-winged blackbird vocalizations, discussing the implications of this directionality for communication.

Sound waves radiate in all directions from a vocalizing animal, but the sound may not be equally loud in each

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direction. When this is so, the vocalization is considered to be directional. Models of single source internal sound production—like that found in most birds, anurans, bats, and humans—suggest that radiation patterns will be bilaterally symmetrical with their maximum radiation point in front of the vocal emission structure (Hunter et al. 1986; Larsen and Dabelsteen 1990). Despite the relative simplicity of this model, the degree of directionality is likely to be highly variable between species and between vocalization types, and may be partially controlled by the calling animal (Dantzker et al. 1999). In birds, the shape and directionality of the radiated sound field will likely be a factor of frequency, beak morphology, and vocalization posture (e.g., head and beak position, Hunter et al. 1986; Larsen and Dabelsteen 1990). Thus, variation in frequency and posture among call types may affect directionality, as will variation in morphology among species. Indeed, the handful of directionality measurements available indicate that vertebrate vocalizations range from highly directional (up to a 30 dB difference in amplitude around the animal) to omnidirectional across species and vocalization types (Flanagan 1972; Gerhardt 1975; Hunter et al. 1986; Larsen and Dabelsteen 1990; Dantzker et al. 1999; Brumm 2002; Miller 2002; Frommolt and Gebler 2004; Nelson et al. 2005).

Spatial variability in the amplitude of radiating sound is likely to have important implications in animal communication. Directionality will affect the receiver's ability to assess the sender if amplitude conveys information about the sender's location, size, or vigor (Morton 1982; Arak 1983) because the sender's orientation relative to the receiver will affect the amplitude detected. This issue has also complicated attempts to test hypotheses about the role of amplitude in communication because the orientation of the sender relative to a researcher's microphone will affect receive levels (Gerhardt 1998). Directionality will also affect signal transmission. A change in amplitude as small as 3 dB can translate to a 40% change in propagation distance, and thus directionality will affect the active space of the call, the area over which the vocalization can be detected (e.g., Brenowitz 1982). Directionality may also affect the number and identity of receivers. Omnidirectional vocalizations may maximize the number of neighbors that detect the vocalization, whereas more directional vocalizations may allow birds to beam the sound to a single receiver and decrease the possibility of eavesdropping (Witkin 1977; Larsen and Dabelsteen 1990; Dantzker et al. 1999; Brumm and Todt 2003; Dabelsteen 2005). Because higher frequencies are more directional than lower frequencies, 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 and Dabelsteen 1990; Dantzker et al. 1999). These potentially important effects of directionality on acoustic communica-

tion may select for adaptations that allow animals to either compensate for directionality or make use of directionality when communicating. Relatively, little is known about how directionality varies with signal function, sender morphology and behavior, and the environment in which the sound is transmitted. This is an important gap in our current understanding of acoustic communication, and one that is relevant to the broader issue of how traits, such as communication signals, are shaped by functional necessity and mechanistic constraint.

Acoustic directionality has been measured using both laboratory and field methods. In lab studies, live animals are coaxed to vocalize in anechoic chambers or sounds are broadcast through the carcasses of dead animals (Larsen and Dabelsteen 1990; Gerhardt 1998; Brumm 2002; Frommolt and Gebler 2004; Nelson et al. 2005). This method controls for environmental effects and allows detailed measurement of directionality in three dimensions, but removes animals from the context in which the vocalization is used and is logistically infeasible with many species. Field studies have been conducted by repositioning two microphones around the animal during subsequent vocalizations to reconstruct a sound field for each call type (e.g., Gerhardt 1975; Hartley and Suthers 1987; Larsen and Dabelsteen 1990; Au et al. 1995). This method can be used only in the small number of species that will vocalize repeatedly without changing orientation as the researcher moves microphones around them, and assumes that there is little intraindividual variation in directionality. So, while these methods have provided very important information about directionality, they have limited our ability to test hypotheses about directionality and amplitude in animal communication. Dantzker et al. (1999) improved upon these methods by simultaneously measuring amplitude at eight locations around vocalizing greater sage grouse (*Centrocercus urophasianus*) in the field using an array of microphones. In this study, we update these methods with digital audio recording technology and adapt the system for use on passerines by situating the eight-microphone array around a calling perch. This system measures directionality in the horizontal plane and thus is limited to studies of animals that communicate primarily in this plane.

We measured the directionality of different vocalizations used by territorial male red-winged blackbirds to test the hypothesis that the directionality of a vocalization reflects its function in communication. 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 and Yasukawa 1995). Redwings 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 territory, and because their vocal repertoire is well-

studied (Searcy and Yasukawa 1995). We measured the directionality of five types of vocalizations made by male red-winged blackbirds: the “oak-a-lee” song, the precopulatory call, “check” calls, “cheer” calls, and “t’chit” calls. We predicted that vocalizations that are directed to multiple conspecifics would be relatively omnidirectional because this will maximize the number of neighbors and mates that receive the signal, and that vocalizations directed to particular individuals would be relatively directional because this will maximize detection of the signal by the targeted receiver and minimize eavesdropping (Witkin 1977; Larsen and Dabelsteen 1990; Dantzker et al. 1999; Brumm and Todt 2003; Dabelsteen 2005). Specific predictions for each type of vocalization are detailed below.

The “oak-a-lee” song functions in territorial defense (Peek 1972) and elicits courtship and copulation in females (Searcy and Brenowitz 1988). During the breeding season, male song is often accompanied by the song-spread visual display (Yasukawa and Searcy 1995). Males use these songs both in direct interactions with males and females, and as advertisements to attract mates or define their territory. These two contexts predict different degrees of directionality: in a direct interaction with a neighboring male or a female, we predict that males will use highly directional vocalizations to beam the sound at the targeted receiver; whereas, in broad advertisement, we predict lower directionality because this will maximize the number of receivers for the song (Larsen and Dabelsteen 1990). These are conflicting predictions, so we may thus expect songs to be a compromise between these extremes, or that males shift their directionality in different contexts.

The precopulatory call (also known as the “ti-ti-ti” call), is used in the context of courtship and is often accompanied by a crouching display by males (Yasukawa and Searcy 1995). Playback of precopulatory calls to receptive females elicits copulation–solicitation postures (Searcy 1989). We predict that precopulatory calls will be highly directional to avoid eavesdropping by neighboring males because neighbors will interrupt copulation (Larsen and Dabelsteen 1990; Searcy and Yasukawa 1995).

Territorial males give the various “check” vocalizations almost continuously throughout the breeding season (Beletsky et al. 1986). Checks are thought to function as contact calls (Yasukawa and Searcy 1995), and alert calls (Beletsky et al. 1986; Burton and Yasukawa 2001). Males match the calls of their neighbors and indicate alarm by switching call types (Beletsky et al. 1986). Similar to check calls, the “cheer” is similarly used to indicate general alarm (Beletsky et al. 1986), but may also signify particular predators, such as hawks (Yasukawa and Searcy 1995). Because the receivers of check and cheer calls are conspecifics, we predict that these calls will be relatively omnidirectional in radiation, to maximize the number of

receiving neighbors and mates (Larsen and Dabelsteen 1990). Note that if these calls were used to signal to predators that they had been detected, we would instead predict these calls to be directional and “aimed” at the predator.

The “t’chit” call has not been previously described. The call is structurally similar to the “check” calls, and may similarly function as an alert call, predicting relatively omnidirectional radiation. However, we only observed males in our study population giving the t’chit call before and after courtship chases with females (G. Patricelli, personal observation). If t’chit calls function in courtship, we would predict that it to have similar directionality to the precopulatory notes. However, because the role of this call has not been tested, we cannot make a priori prediction for this call.

We compare the directionality of each type of vocalization, and we compare the directionality of two classes of vocalizations for which the function is known, the alert calls (checks and cheers) and sexually selected vocalizations (precopulatory calls and male song).

Materials and methods

Field site

The field site was located at the Cornell Experimental Ponds Facility approximately 10 km north of Ithaca, NY, USA (42.50° N, 76.46° W). Directionality measurements were made on six male red-winged blackbirds in their territories during the breeding season, between April 28 and June 10, 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. Weather conditions at the time of each vocalization (to within 1 s) were estimated by linear interpolation in MATLAB (Mathworks 1998).

The recording perch

The acoustic directionality recording rig consists of a perch encircled by a steel ring, around which eight calibrated microphones and three video cameras are arrayed (Fig. 1). To assure that vocalizations were recorded in the far field (Bradbury and Vehrencamp 1998), microphones were placed at least 0.9 m from the singing bird (at least ~3 wavelengths). The geometry of the array was measured with a Sokkia DOI343 theodolite surveying system; detailed measures are presented on Fig. 1. The top of the perch was 2.31 m from the ground, the top of the microphone capsules were 2.3 m from the ground; the exact height of each microphone from the ground varied within

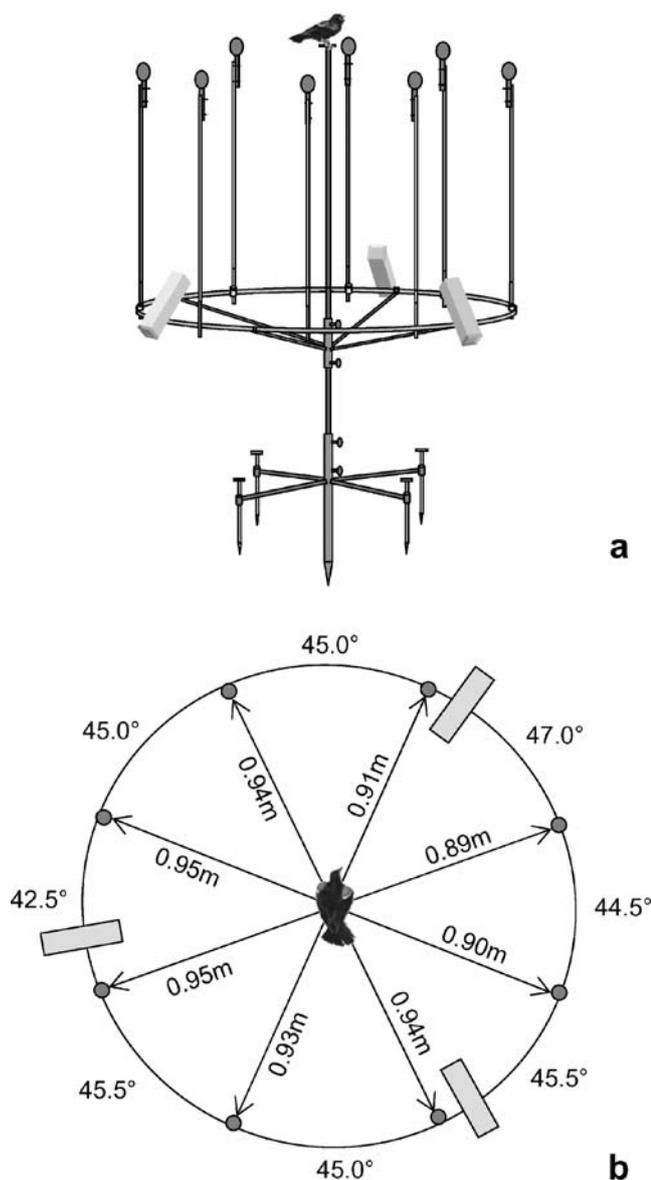


Fig. 1 The recording perch. **a** A diagram of the perch used to record red-winged blackbird vocalizations, showing the central perch, surrounded by a 2-m diameter steel ring around which eight calibrated microphones and three video cameras are arrayed. This perch was placed in a male redwing blackbird's territory; digital audio was recorded to hard disk in a nearby blind. **b** The geometry of the recording perch. The diagram shows the bird on the central perch and the path lengths from the perch to each of the eight microphones, with the angles between each microphone. For analyses, the actual path length from the sound source (i.e., the bird's beak) to the microphone was measured for each vocalization using acoustic localization (see "Materials and methods" section), and normalized to 1 m

~0.25 m among recording sites depending upon whether the perch was placed on a slope.

Metal fence posts were placed in the territories of male red-winged blackbirds throughout the field site. Perches were monitored for the identity 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 thus cannot have been the same individual). The favored fence-post perch in each male's territory was replaced by the recording perch in the afternoon or evening and birds were recorded in subsequent days between dawn (ca. 0545 hours) and late morning (ca. 1000 hours). Recordings were made only at times with no precipitation and wind <12 km/h (wind speed and other weather measures were not significant as covariates in the ANOVA, see below).

Video recording and analysis

We used video to confirm species identity and measure the orientation of the bird relative to the microphones during each vocalization. Video was recorded with three black and white closed circuit security cameras (Sony SSC-M183 cameras with Tamron 13VG550-SQ 5–50 mm lenses) in weatherproof housing (Ultrak UL-HEM12). Video from all three cameras was multiplexed (EverPlex 8BQ multiplexer) and recorded on a single Hi-8 video deck (Sony GV-A500). To allow frame-accurate synchronization of audio and video data, longitudinal time code (LTC) was generated by a Mark of the Unicorn (MOTU) Midi Timepiece AV, and imprinted on the video image with a Horita window dub inserter (TRG-50PC). LTC was also recorded on the audio channel of the videotape. Video data was 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, and used the head orientation for analyses; vocalizations where the orientation of the bird's head differed from the orientation of the bird's body by $\geq 30^\circ$ were not included in the analysis.

Audio recording and analysis

We recorded audio with a MOTU Audio 896, which digitized and recorded audio directly to hard disk on a PowerMac G3 laptop. We used MOTU Digital Performer (v.6) for audio acquisition and audio-video synchronization using LTC (see above). We used Sennheiser K6 microphones with ME62 omnidirectional capsules and MZW64 windscreens; the MOTU 896 provided phantom power to the microphones. Digital audio was recorded at 44.1 kHz with 16 bits per sample.

Our recording system involved two potential sources of variation in amplitude among channels: recording gain and microphone sensitivity. We controlled for this variation by recording test tones that were used for calibration during the measurement of amplitude. To calibrate for any variation in recording gain among days and/or among channels, we recorded a test tone from a microphone input

tone generator (Shure A15TG) on each channel each day. To calibrate for variation in microphone sensitivity, we recorded a 114 dB SPL test tone (10.02 Pascals (Pa)) from a microphone calibrator (Larson Davis CAL250 Precision Calibrator) on each channel; this measurement was made once at the end of the field season. We used the same configuration of microphones and cables on each recording day, so this test tone allowed us to control for variation in cable and audio recorder sensitivity as well as microphone sensitivity. In addition to controlling for variability among recording channels, these test tones allowed us to convert our measures to dB SPL (see details below).

Audio files were exported from Digital Performer as single-track wave files; these files were merged into an eight-track wave file for each recording session using MATLAB (Mathworks 1998). Eight-track wave files were then visualized as spectrograms in Raven (Cornell Laboratory of Ornithology 2002); all recorded vocalization were included in the analysis unless visual inspection of the spectrogram revealed overlapping vocalizations or excessive background noise. For each vocalization, we chose the regions to include for analysis from a spectrogram in MATLAB; for checks and cheers, we included the entire vocalization, for t-chits and precopulatory notes, we measured each note in a call separately and used an average for analysis (excluding the pauses between notes). For oak-a-lee songs, we included four notes from each song (two introductory “oak” notes, the “a” note, and the concluding trill). Because these notes vary in duration (on average, the trill is more than three times longer than the other three notes combined), we used a mean directionality weighted by the duration of the note.

Amplitude measurements

For each vocalization at each microphone, we calculated the sound pressure level in decibels (dB SPL) at 1 m from the sound source using a MATLAB routine. This measurement involved three steps, which will be described in detail in the following paragraphs: first, we corrected the wave file for variation in the path length between the sound source and each microphone, second, we measured mean energy (ME) from a spectrogram of the vocalization, and third, we converted ME to dB SPL and controlled for variation in recording gain and system sensitivity.

First, to correct for variation in the path length between the sound source and each microphone (Rho), we multiplied every value in the wave file by Rho; this normalized the wave files to Rho = 1 m using the assumption of spherical spreading. The measured value of Rho for each vocalization depended on the location of the microphone on the steel ring (which is constant and approximately 1 m, see Fig. 1) and the location of the sound source, which may

change slightly if the bird is not centered on the perch (e.g., if the bird tilts forward while vocalizing). Thus, we estimated the location of the sound source relative to the microphones using acoustic localization (Spiesberger and Fristrup 1990). Our localization routine uses delays in the time at which the sound reached each of the eight microphones to estimate the location of the sound source (see Dantzker et al. 1999 for detailed methods); the speed of sound was estimated using measurements of temperature at the time of the vocalization.

Second, to measure mean energy from a spectrogram of the vocalization (fft size=128, overlap=0.7, Hann window), we took the square root of the power spectral density (calculated using Welch’s method). In addition to measuring ME on vocalizations, we measured ME on both gain and sensitivity test tones (see above) for calibration.

Third, to convert ME to dB SPL and to correct for variation in recording gain and system sensitivity, we calibrated each vocalization to standardized test tones (see above). We used the following equation to calibrate each channel for each vocalization:

$$\text{Vocalization in Pa} = \text{vocalization in ME} * \left(\frac{GT_1}{GT_2} \right) \left(\frac{10.02 \text{ Pa}}{ST} \right)$$

where GT_1 is the gain test tone for the day on which the vocalization was recorded, measured in ME; GT_2 is the gain test tone on the day that system sensitivity was measured, in ME; 10.02 Pa is the factory-measured pressure of the sensitivity test tone, and ST is our measurement of this sensitivity test tone in ME. The vocalization in Pascals is then converted to dB SPL and reported as dB SPL re 20 μ Pa at 1 m from the source. Because our microphones were placed 2.3 m from the ground and approximately 1 m from the vocalizing bird, we assume that environmental transmission effects between the microphone and bird are negligible and equal along all paths. Any differential effects on these amplitude measures from ground reflections (which should be small at this angle, $\sim 27^\circ$, and with a dense cover of grass on the ground) and should not bias the results of this study.

Directivity measurements

We quantified the patterns of acoustic radiation for each vocalization using both the Directivity Index (DI, see Appendix 3 of ref. Dantzker et al. 1999), and the difference in dB SPL between the quietest and loudest of the eight measures of amplitude for the focal vocalization (“Diff”, see Dantzker et al. 1999). The DI quantifies how much the observed two-dimensional radiation pattern differs from spherical spreading; for comparison, an omnidirectional vocalization would have a DI of zero and the highly

directional “whistle” note of the sage-grouse strut display was observed to have an average DI of 4.4 (Diff=14 dB) and a maximum DI of 6.7 (22.9 dB) (Dantzker et al. 1999). In addition, we estimate the mean amplitude in front of the bird (“mean amplitude in front”) as the average amplitude in dB PL of interpolated points anterior to the sound source. To do so, we used linear interpolation in MATLAB to produce 120 estimates of amplitude equally spaced in a circle around the sound source, and calculated the average of all points between 271 and 89° (with 0° defined as directly anterior to the bird’s beak). By using a mean of interpolated measures, we minimized artifacts caused by differences in the location of the microphones relative to the bird’s head among recordings. “Mean amplitude behind” was similarly calculated as the mean of all interpolated measures between 269 and 91°.

Peak frequency measurements

To measure the peak frequency of each note on which directionality was calculated, we found the frequency with the highest amplitude in each window of the spectrogram (window size = 128 samples), 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 vocalization (across which the directionality of the note is calculated), not the frequency of the single highest energy window within the vocalization (the latter measure would be highly sensitive to fft window size and short-term fluctuations in amplitude). For t-chits and precopulatory notes, we measured “peak frequency” on each note in the call separately and we present an average on Table 1 (excluding the pauses between notes). For the “oak-a-lee” song, we used a mean of the “peak frequency” values for each of the four notes, weighted by the duration of the note (similar to our calculation of directionality).

Statistical analyses

We used a mixed model ANOVA to compare directivity among vocalization types using PROC MIXED in SAS© 8.01. 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 directivity index in all ANOVA models. We included the following variables as covariates in all models: wind speed, temperature, humidity, and barometric pressure. In all tests, we sequentially dropped the most nonsignificant covariates (all $P > 0.5$) until only significant covariates remained in the final model; all weather variables were dropped as nonsignificant in all 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). Where appropriate, we included a priori orthogonal contrasts between means in the ANOVA model. Statistical tests are two-tailed; P -values are not corrected for multiple comparisons (Moran 2003; Nakagawa 2004). All means are presented \pm SE, unless otherwise noted.

Results

We measured directionality for five types of red-winged blackbird vocalization. We found that all five vocalizations had a directionality index significantly greater than zero in our samples (a DI of zero would be an omnidirectional sound)(t tests with all vocalizations pooled among males: oak-a-lee $t=58.6$, precop call $t=76.9$, check $t=50.5$, cheer $t=26.6$, t’chit $t=122.7$; all with $P < 0.00001$). Descriptive statistics for directionality and amplitude for each call type are presented in Table 1; the acoustic radiation pattern for each type of vocalization is presented as a polar plot showing amplitude at each of the eight microphones around the vocalizing bird (Fig. 2).

While all five types of vocalizations were significantly directional, we found variation in the degree of directionality among vocalization types. Analysis of variance revealed a significant difference among vocalization types in directivity index (Table 2). To explore these differences, we included two a priori contrasts into our ANOVA model to compare the two functional classes of vocalizations: the alert calls (checks and cheers) and sexually selected vocalizations (precopulatory calls and male song). We found that sexually selected vocalizations are significantly more directional than the alert calls (F test: $F_{1,8}=10.55$, $P=0.012$). The difference in directionality between these functional classes is greater if we include t’chit calls in the sexually selected category (F test: $F_{1,8}=17.07$, $P=0.003$).

In addition, we used pair-wise comparisons among call types to test predictions about the directionality of each vocalization. We predicted that precopulatory calls would be highly directional relative to the alert calls (checks and cheers); we find that the precopulatory calls are significantly more directional than both types of alert calls (Table 2). We predicted that alert calls would have low directionality, and supporting this prediction we see that the two alert calls have approximately equal directionality and are the least directional of measured calls. We predicted that the oak-a-lee song would be directional in interactions and less directional in advertisements, or that the song would be moderately directional as a compromise. Our results suggest that male song is moderately directional, falling

Table 1 Descriptive statistics for each type of vocalization

Measurement	Oak-a-lee	Precop	T'chit	Check	Cheer	All calls ^a
Number of calls (<i>n</i>)	167	36	90	90	16	5
Directivity index						
Mean	3.06	3.96	3.98	2.72	2.74	3.31
SD	0.65	0.19	0.49	0.51	0.41	0.63
Min	1.62	3.42	2.54	1.61	1.90	2.72
Max	4.55	4.31	4.69	3.86	3.57	3.98
Max–min difference (dB SPL)						
Mean	7.17	8.96	9.59	7.16	6.88	8.00
SD	1.14	0.52	1.07	1.31	1.33	1.20
Min	3.97	7.83	7.18	4.01	4.39	6.88
Max	10.06	10.12	12.62	11.46	9.73	9.59
Max amplitude ^b (dB SPL)						
Mean	84.0	84.1	79.4	82.2	94.1	84.8
SD	1.5	1.4	1.7	2.2	1.9	5.5
Min	79.8	79.7	75.4	78.1	90.1	79.4
Max	86.8	87.1	85.4	88.5	95.9	94.1
Mean amplitude in front (dB SPL)						
Mean	82.1	81.4	76.7	80.5	92.4	82.7
SD	1.3	1.5	1.7	2.0	1.8	5.8
Min	78.5	76.8	73.2	77.0	88.9	76.7
Max	84.7	84.4	82.8	86.4	94.3	92.4
Mean amplitude behind (dB SPL)						
Mean	78.4	77.0	71.6	77.2	89.0	78.7
SD	1.3	1.4	1.9	1.9	2.2	6.4
Min	75.8	72.4	68.9	73.6	84.4	71.6
Max	82.0	79.6	77.6	82.2	91.3	89.0
Peak frequency (kHz)						
Mean	3.25	3.65	3.87	3.57	3.51	3.59
SD	0.22	0.17	0.63	0.54	0.28	0.19
Min	2.70	3.22	2.48	1.78	3.27	3.34
Max	3.66	3.99	5.40	4.61	3.95	3.87

Table shows the arithmetic mean, standard deviation (SD), minimum and maximum values for six different measurements made on each of the five types of vocalization. See “Materials and methods” section for descriptions of other measures. All vocalizations are pooled among males; thus, these statistics describe the sample of vocalizations and are not estimates of population values; see Fig. 3 for population estimates of directionality.

^a The “all calls” column is the mean, SD, min, and max among the five types of vocalizations.

^b “Max amplitude” is the highest amplitude measure among the eight microphones for each vocalization (typically in front of the bird)

between the alert calls and the other sexually selected vocalizations. Male song is significantly less directional than the t'chit, but not significantly less than the precopulatory note; song is more directional than the check and the cheer, but not significantly so. The t'chit call had the highest mean directivity index; and the t'chit was significantly more directional than the check, cheer and display vocalizations, though not the precopulatory note Fig. 3.

Discussion

Directionality

We measured directionality for the five types of red-winged blackbird vocalization: checks, cheers, displays, precopula-

tory notes, and t'chits. We found that all five vocalizations were directional: on average among vocalization types, there was an 8.0 dB difference between the loudest and quietest measure of amplitude, with a maximum of 9.59 dB and a minimum of 6.88 dB. Thus, even the least directional red-winged blackbird vocalization would be more than twice as loud to a receiver at the loudest location (typically anterior to the bird's beak) than to a receiver in the quietest location (typically behind the bird). These measurements are slightly more directional than other measures in passerines. Larsen and Dabelsteen (1990) found a difference of 4 dB between the loudest and quietest measures of the 2.5 kHz “chook” call of the blackbird (*Turdus merula*), with increasing directivity in higher frequency vocalizations. Nelson (2000) found a 2–3 dB front–back difference in SPL in the 2–4.5 kHz call of eastern towhees (*Pipilo*

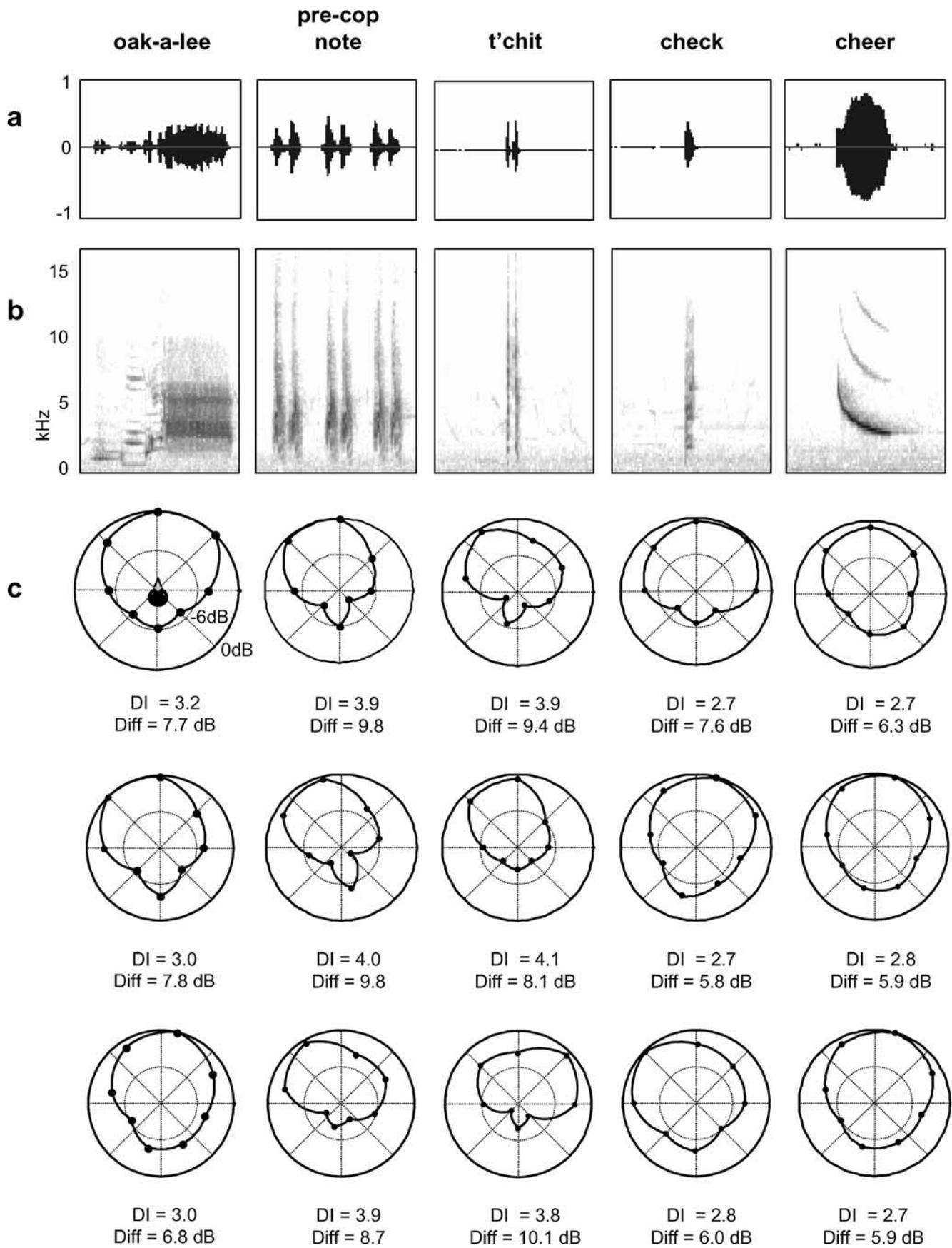


Table 2 Results from analysis of variance and pair-wise comparisons of directivity index (DI)

Effect	S.E.D.	<i>df</i>	<i>F</i>	<i>P</i>
Call type		4,8	6.60	0.0120
Call types				
T'chit vs check	0.2023	8	4.43	0.0022
T'chit vs cheer	0.2570	8	3.41	0.0092
T'chit vs display	0.1870	8	3.17	0.0131
T'chit vs precop	0.2581	8	0.06	0.9503
Check vs cheer	0.2239	8	-0.08	0.9349
Check vs display	0.1409	8	-2.15	0.0640
check vs Precop	0.2714	8	-3.24	0.0119
Cheer vs display	0.2194	8	-1.29	0.2318
Cheer vs precop	0.3192	8	-2.70	0.0272
Display vs precop	0.2551	8	-2.26	0.0535

Table shows the degrees of freedom (*df*), *F* statistic, and two-tailed probability (*P*) for each factor in the final ANOVA model. The dependent variable is directivity index. This analysis included all frequencies in the sound files (0–22 kHz).

erythrophthalmus), and Brumm (2002) found a 4.6 dB front–back difference in the 1–8 kHz song of nightingales (*Luscinia megarhynchos*). Variation among studies in measurements of directionality is likely due in part to differences in the vocalizations, body size, and morphology of the focal bird species (Hunter et al. 1986; Larsen and Dabelsteen 1990), and in part to differences in methodologies (i.e., whether the researchers report front–back differences or maximum–minimum differences). Indeed the difference between our measures of mean amplitude in front of the bird and behind the bird (similar to the methods used in other studies) produces a result more similar to results from other species: a mean of 4 dB among vocalizations. In nonpasserine vertebrates, directionality measurements range from highly directional, with up to a 22-dB difference in amplitude in the strut display of greater sage grouse to nearly omnidirectional in anuran calls (e.g., Flanagan 1972; Gerhardt 1975; Dantzker et al. 1999; Brumm 2002; Frommolt and Gebler 2004).

In addition, we compared directionality among vocalization types to test specific predictions about the role of

Fig. 2 Acoustic radiation plots of red-winged blackbird vocalizations. **a** Oscillograms of each vocalization; y-axis units are proportional to pressure. **b** Spectrograms of each vocalization. **c** Polar plots of acoustic radiation for three example vocalizations that have directionality index (DI) values near the mean for that type of vocalization. Points on each plot represent the amplitude as measured at each of the eight microphones, connected by linear interpolation. All polar plots are in decibel, 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 DI and min–max difference (“Diff”) is given under the vocalization

directionality in communication. We found support for the prediction that precopulatory calls would be relatively directional and that alert calls (checks and cheers) would be relatively omnidirectional. We did not have clear prediction for the oak-a-lee song—we predicted that the song would be directional in interactions and less directional in advertisements, or would be moderately directional as a compromise. The observed mean directionality of male song is indeed moderate relative to other vocalizations, but the standard deviation of song is higher than that of other vocalizations (see Table 1). Thus, it is not clear whether males have a moderate directional song or whether they shift directionality among contexts. Future work will be needed to address these two alternatives. We also did not have clear predictions for the t'chit call because the function of this call is not yet established. We found that the t'chit call had the highest mean directivity index; and the t'chit was significantly more directional than all vocalizations except the precopulatory note. This is consistent with observations from the field that the t'chit is used before and after courtship chases with females (Patricelli, personal observation), but further observation of how birds use the t'chit call is needed to verify the function of this vocalization. In addition to comparisons among call types, we compared the two functional classes of vocalizations: the alert calls (checks and cheers) and sexually selected vocalizations (precopulatory calls and male song). We found that sexually selected vocalizations are significantly more directional than the alert calls. Taken together, these results suggest that the directionality of a vocalization is shaped by its function in communication.

The alarm calls of many vertebrate species have a high frequency relative to other call types, predicting a directional pattern of radiation (Marler 2004). The high frequency of many alarm calls (as well as the gradual

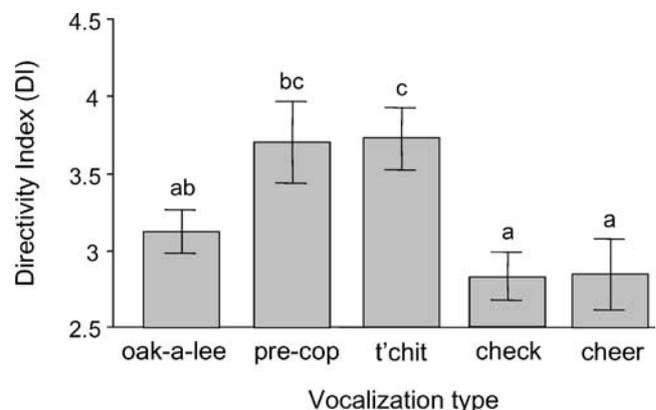


Fig. 3 Comparison of different red-winged blackbird vocalizations. The least squares mean directivity index of each call type, with standard error bars. Those means that share the same letter are not significantly different. See Table 2 for results from an ANOVA comparing these means

onset) is thought to reduce the ability of predators to locate the signaler (very high and low frequencies are more difficult to localize using binaural cues; Marler 1955; Bradbury and Vehrencamp 1998), and to reduce the active space of the vocalization (higher frequencies attenuate more quickly; Morton 1975). In contrast, we found that alert and alarm calls of red-winged blackbirds have the least directional radiation patterns of measured vocalizations and an average peak frequency similar to other vocalizations. Previous studies have demonstrated that red-winged blackbird alarm calls are used to communicate with surrounding conspecifics and mates (Beletsky et al. 1986; Searcy and Yasukawa 1995; Burton and Yasukawa 2001), which would favor the lower directionality observed in this system. The high amplitude of the “cheer” call (94.1 dB SPL) further suggests that this alarm call is structured to increase, rather than decrease active space. Calls may also provide cues to sender orientation relative to the receiver if the calls have broad bandwidth (i.e., mixed directionality; Witkin 1977; Hunter et al. 1986; Larsen and Dabelsteen 1990; Miller 2002). Higher frequency components will be more directional than lower frequency components of the call and, thus, the received power spectrum will differ depending on the sender’s orientation. This may provide information to predators about whether they are being watched, and information to conspecifics about the location of the predator (i.e., if the caller is facing the predator). The low directionality and narrow bandwidth of the cheer would reduce information about orientation. While there is some evidence that spectral cues may be used to localize sounds (Gold and Knudsen 1999, 2000; Gill et al. 2000; Arthur 2004), we do not yet know if red-winged blackbirds or their predators attend to spectral cues from directional vocalizations to determine orientation. Further research is needed to assess how different call features combine to determine the effectiveness of alarm and alert calls (e.g., Nelson and Suthers 2004; Nelson et al. 2005). These results highlight the importance of considering directionality and amplitude when discussing how selection shapes alarm call structure (Witkin 1977; Hunter et al. 1986; Larsen and Dabelsteen 1990).

Previous studies of directionality in birds have been limited to small sample sizes due to logistic difficulty and/or the need to sacrifice target animals (Hunter et al. 1986; Larsen and Dabelsteen 1990; Dantzker et al. 1999; Brumm 2002; Nelson et al. 2005). This limited sample size precluded the use of population statistics in the data analysis and, thus, allowed only speculation about variation among vocalizations in directionality. The advances in digital recording technology utilized in this study have made the measurement of directionality increasingly feasible. However, measurement remains difficult to complete during the breeding season of the target species. Thus,

while our sample size of six individuals is larger than many previous studies of directionality, it remains a small sample size for statistical analysis. The SAS mixed model procedure increased the power of our test by allowing us to make use of the many measurements of each vocalization type for each male (this program models the covariance among repeated measurements and thus avoids problem of pseudoreplication). Nonetheless, we cannot rule out the possibility that sampling error influenced our estimates of population parameters.

Mechanisms of variation in directionality

Frequency is known to affect the directionality of radiating sounds, with lower frequency sounds having less directional patterns of radiation than higher frequency sounds (Bradbury and Vehrencamp 1998). The frequency content of a vocalization is affected by beak and body morphology (Nowicki 1987; Westneat et al. 1993; Podos 1997, 2001; Hoese et al. 2000) and may be shaped by selection for efficient propagation in the habitat in which it is used, or to increase or decrease the ability of the receiver to locate the sender (Marler 1955; Morton 1975; Richards and Wiley 1980; Wiley and Richards 1982). Because shifts in the frequency of a vocalization cause changes in acoustic directionality (Hunter et al. 1986; Larsen and Dabelsteen 1990; Nelson et al. 2005), there may be evolutionary tradeoffs between optimizing calls for directivity vs optimizing calls for propagation or localizability when the optimal frequencies for these selective factors are different. The consequences of these potential tradeoffs are an exciting area for future research.

Little is known about what, besides frequency, causes within-individual variation in directionality. The model of passerine vocalization developed by Hunter et al. (1986) includes as parameters the acoustical impedance of the air, the frequency of the vocalization, and the radius of the acoustical baffle. In Hunter et al.’s model, the acoustical baffle was estimated as the size of bird’s head; however, the bird’s body may also contribute to the baffle, and thus variation in male body posture (e.g., the song-spread display, Peek 1972) may influence directionality. In addition, beak opening has been shown to affect directionality (Larsen and Dabelsteen 1990; Nelson et al. 2005; but see Hunter et al. 1986). So, while frequency is the major determinant of directionality, other factors may also contribute to variation in directionality among call types.

There is an additional mechanism by which birds may alter the directionality of their vocalizations: by turning on their perch when they sing. Brumm and Todt (2003) found that male nightingales have a moderately directional song and that they rotate on their perch when there is no known receiver, presumably to radiate their song omnidirection-

ally, and they face their rival when location is known, presumably to beam their sounds toward them. Similar behaviors have been described in male northern mockingbirds and crickets (Breitwisch and Whitesides 1987; Forrest 1991). Animals producing less directional vocalizations would be expected to rotate less while vocalizing. Thus, males may have behavioral strategies to counteract or capitalize on the directionality of their vocalizations, and directionality may play an important role in shaping male singing behaviors.

Conclusions

We found that the vocalizations of male red-winged blackbirds have a directional pattern of acoustic radiation and that this directionality varies among types of vocalizations. In addition, we found that this variation is related to the function of the vocalization in communication—sexually selected vocalizations that are used in interactions with females are more directional than alert calls used to warn conspecifics of danger. This result suggests that directionality is adapted to minimize eavesdropping by unwanted receivers in the former context and maximize the number of receivers in the latter context. Acoustic radiation patterns are as fundamental to our knowledge of acoustic communication, as they are still unknown. Advances in audio recording technology and analysis should allow a new phase of research that integrates issues of directionality and amplitude into studies of acoustic communication.

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