

DIRECTIONALITY OF THE DRUMMING DISPLAY OF THE RUFFED GROUSE

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Abstract. Directionality is a key feature of vocalizations in birds and can provide insight into vocalizations' function and propagation. Despite recent interest in birds' production of nonvocal acoustic signals, little is known about the directionality of these sounds. Here, we examine the directionality of the drumming display of male Ruffed Grouse (*Bonasa umbellus*), a nonvocal acoustic signal used in mate attraction and territorial defense. We recorded drumming males with a low-frequency microphone and measured sound-pressure levels with a sound-level meter from three orientations: front (0°), behind (180°), and side (90°). The sound-pressure level was significantly higher in front of and behind a drumming male than on the sides, indicating that the drumming sound radiates primarily along the displaying bird's longitudinal axis. Spectral analyses of the recordings did not, however, yield consistent differences in frequency among the three orientations. The acoustic radiation pattern of the drumming display differs from that of vocalizations in that the sound-pressure levels are just as high behind the bird as they are in front of it. This directionality likely affects estimation of distance by predators and intended receivers as well as potentially limiting the number of receivers able to perceive the signal.

Key words: acoustic directionality, grouse, communication, courtship.

Direccionalidad del Despliegue de Tamborileo de *Bonasa umbellus*

Resumen. La direccionalidad es una característica clave de las vocalizaciones en las aves y puede ayudar a entender la función y propagación de las vocalizaciones. A pesar del interés reciente en la producción de señales acústicas no vocales en las aves, poco se sabe sobre la direccionalidad de estos sonidos. Aquí examinamos la direccionalidad del despliegue de tamborileo del macho de *Bonasa umbellus*, una señal acústica no vocal usada para la atracción de la pareja y la defensa del territorio. Registramos machos realizando el tamborileo con un micrófono de baja frecuencia y medimos los niveles de presión del sonido con un contador del nivel del sonido desde tres orientaciones: frente (0°), detrás (180°) y costado (90°). El nivel de presión del sonido fue significativamente más alto en frente de y detrás de un macho tamborileando que en los costados, indicando que el sonido de tamborileo se irradia principalmente a lo largo del eje longitudinal de despliegue del ave. Los análisis espectrales de las grabaciones, sin embargo, no arrojaron diferencias consistentes en la frecuencia entre las tres orientaciones. El patrón de irradiación acústica del despliegue de tamborileo se diferencia del de las vocalizaciones en que los niveles de presión del sonido son tan altos detrás del ave como lo son en frente de ella. Esta direccionalidad probablemente afecta las estimaciones de distancia de los depredadores y de los receptores deseados y también limita potencialmente el número de receptores capaces de percibir la señal.

INTRODUCTION

Most studies of avian vocal communication have focused on spectral and temporal features of vocalizations. Sound waves radiate out from vocalizing individuals, but, depending on the posture of the individual and the type of vocalization, the sound may not be equally loud in all directions (Dantzker et al. 1999, Patricelli et al. 2007, Yorzinski and Patricelli 2010). Determining the directionality, that is, the extent to which the sound radiates more in one direction than another, of an acoustic signal is therefore critical for a number of reasons. First, the extent to which a signal is directional can affect the receiver's ability to assess the sender because the

amplitude of the signal might convey information about the sender's size, condition, and/or location (Brumm and Naguib 2009). Second, variations in amplitude can significantly affect how far a sound propagates (Brenowitz 1982, Brumm and Naguib 2009). Third, a highly directional signal allows a bird to beam a signal to an individual receiver, whereas an omnidirectional signal maximizes the number of receivers (Bradbury and Vehrencamp 1998, Dantzker et al. 1999). Thus, determining the directionality of a signal has significant implications for understanding how far it propagates (Bradbury and Vehrencamp 1998, Brumm and Naguib 2009) and how the signal is being used (Patricelli et al. 2007, Brumm et al. 2011, Yorzinski and Patricelli 2010).

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Several studies of the directionality of avian vocalizations have demonstrated that some vocalizations are more directional than others. For example, alarm calls of the Red-winged Blackbird (*Agelaius phoeniceus*) are less directional than vocalizations used in courtship or copulation solicitation, presumably to reduce the costs of eavesdropping by unintended receivers (Patricelli et al. 2007). The calls the Greater Sage-Grouse (*Centrocercus urophasianus*) uses in its courtship display are all directional, but the primary direction varies with the call type. For example, “coos” beam primarily from in front of the bird, whereas “whistles” beam laterally and “pops” beam out in front but are highly variable in their radiation pattern (Dantzker et al. 1999). These and other studies of directionality (Hunter et al. 1986, Larsen and Dabelsteen 1990, Brumm and Naguib 2002, Yorzinski and Patricelli 2010) suggest that measuring the directionality of vocalizations could provide insight into understanding how the vocalizations are used.

Vocalizations are not, however, the only sounds birds produce for acoustic communication. Birds produce a diverse range of snaps, whistles, and other sounds by mechanical means (Bostwick 2006, Hingee and Magrath 2009). Despite detailed studies of the physics and underlying morphology of the production of nonvocal sound (Bostwick and Prum 2003, 2005, Bostwick 2006, Clark 2008, Clark and Feo 2008, Hingee and Magrath 2009, van Casteren et al. 2010), little to no information is available on the directionality of these signals. Because these nonvocal sounds are generally produced as part of a courtship display, directionality should play a critical role in the function and propagation of these sounds, just as it does for vocalizations.

One species of particular interest with respect to the directionality of a nonvocal acoustic signal is the Ruffed Grouse (*Bonasa umbellus*). Male Ruffed Grouse produce a low-frequency sound (Fig. 1) known as “drumming” by beating their

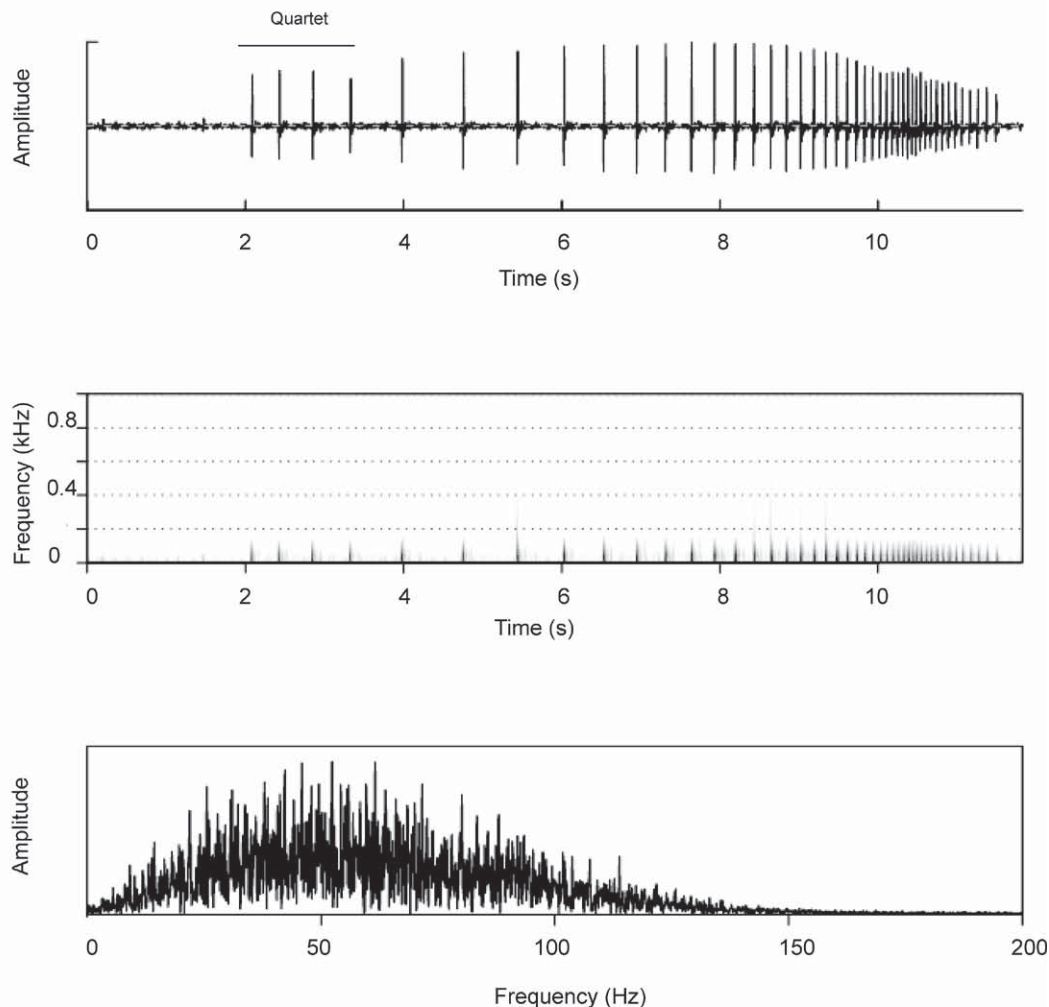


FIGURE 1. A waveform (top), spectrogram (middle), and a frequency-response graph (bottom) of a representative bout of drumming recorded from a male Ruffed Grouse. For both the waveform and spectrogram, time is along the x axis in seconds. Frequency is shown in kilohertz (kHz), and the normalized amplitude is shown in volts. The “quartet” shown in the waveform marks the beginning of a drumming bout.

wings 40–50 times in rapid succession over 8–11 sec (Hjorth 1970, Aubin 1972). Early descriptions of the drumming suggested that the sound was produced by the wings beating against the log on which the bird was standing, the flanks, or each other, but analyses of air movement and films of drumming males by Hjorth (1970) indicate that this is not the case. Like song or other courtship displays, the drumming serves to defend a territory and attract females (Allen 1934, Bump et al. 1947, Brander 1967, Hjorth 1970, Atwater and Schnell 1989). Unlike most birds that produce nonvocal acoustic signals (Bostwick and Prum 2003, 2005, Bostwick 2006, Clark 2008, Clark and Feo 2008, Hingee and Magrath 2009, van Casteren et al. 2010), male Ruffed Grouse do not fly or alter their posture while producing the sound, which allows for recordings and detailed measurements of sound-pressure level (SPL) to be taken around a displaying individual.

Archibald (1974) obtained an estimate of the directionality of Ruffed Grouse drumming, but it was based on playing back drumming sounds captured on videotape that were amplified and then measured only the loudest wingbeat with a sound-level meter. Here, we measure SPLs with a sound-level meter at three different orientations around displaying Ruffed Grouse as well as analyze spectrograms of recordings taken at the same three orientations to better characterize the directionality of the drumming.

MATERIALS AND METHODS

STUDY SITE

We studied male Ruffed Grouse on public lands near Buck Lake (52.97° N, 114.77° W) in western Alberta, Canada. This area is covered with mixed boreal forest consisting of stands of poplar (*Populus tremuloides* and *P. balsamifera*) and White Spruce (*Picea glauca*) interspersed with small muskeg patches dominated by Black Spruce (*Picea mariana*). The understory is dominated by rose (*Rosa acicularis*), Saskatoon (*Amelanchier alnifolia*), snowberry (*Symphoricarpos albus*), dogwood (*Cornus stolonifera*), raspberry (*Rubus idaeus*), shrubby willows (*Salix bebbiana*), and assorted grasses and forbs. The shrubs and poplars are leafless until mid-late May, toward the end of the drumming season. We located drumming males during the spring (1 April–9 May) of 2011 by walking along transect lines along or within this poplar/spruce forest from 04:00 to 12:00. Once we heard a drumming male, we localized the log on which it was standing and marked its coordinates with a hand-held GPS unit (± 3 –5 m).

MEASUREMENTS OF SOUND-PRESSURE LEVEL

We measured SPL with a sound-level meter (Extech Instruments, model 407732, ± 1.5 dB, range 35–130 dB) that was calibrated before each measurement with a sound-level calibrator (Extech Instruments, model 407722, 94 dB and 114 dB, ± 0.5 dB). We measured distances to the drumming logs with a laser range-finder (Bushnell Scout 1000ARC, ± 1 m). For every male, we attempted to record 10 SPL measurements from each of three orientations: front (0°), behind (180°), and side (90°). In some cases, this was not possible because of differences in the distance

at which the grouse flushed and the structure of the habitat surrounding different logs. For example, at some logs we could not obtain measurements from one of the directions because there were too many fallen trees blocking the approach. There was no difference in the average distance at which we took measurements among the three orientations around all 13 males ($F = 3.13$, $df = 2, 23$, $p = 0.06$), but there was a tendency for measurements taken from the side of the bird to be taken at a shorter distance (15.8 ± 6.5 m, mean \pm sd) than from the other two orientations (front = 24.3 ± 7.2 m; behind = 25.5 ± 8.9 m).

All of the readings were taken from a distance of 7–40 m (mean = 23 ± 7 m). We calculated the SPL at the source (i.e., distance of 1 m) as $SPL_{\text{source}} = SPL_{\text{measured}} + 20 \times \log_{10}(\text{distance})$. Although this provides an estimate at 1 m rather than an actual reading, there was little to no vegetation between the sound-level meter and the drumming bird, the SPL readings were above ambient noise, and, given the sounds' low frequencies (Fig. 1), it is unlikely that attenuation would deviate significantly from that predicted from spherical spreading alone (Wiley and Richards 1982, Bradbury and Vehrencamp 1998). To alleviate the potential for our measurements to be affected by ground effects (Wiley and Richards 1982, Bradbury and Vehrencamp 1998), we kept the height of the sound meter relatively constant (60 ± 10 cm) at approximately the same height from the ground as the bird's chest.

To analyze differences among the three orientations, we compared the means of all birds by one-way analyses of variance (ANOVAs) and tested for differences among the males for which we had SPLs for all three orientations, using male, orientation, and their interaction as terms in a factorial ANOVA. When we detected significant effects, we used post-hoc Tukey–Kramer HSD tests, as implemented in JMP version 9 (SAS Institute), to compare all means.

RECORDINGS AND SPECTRAL ANALYSES

We recorded drumming males with a G.R.A.S. 46AE microphone (frequency response = 5 Hz to 10 kHz ± 1 dB) and a Marantz PMD 661 digital recorder (sampling frequency = 44.1 Hz) at a distance of 7–40 m, as measured with the laser rangefinder. To obtain a good signal-to-noise ratio we made all recordings in areas with a vegetation density as low as possible. Although we attempted to record from all three orientations whenever possible, as stated above, habitat structure and individual differences in flight distance prevented us from obtaining all three from all of the males.

For all analyses we used Avisoft SASLab-Pro (version 5.1; Specht 2004). Because before drumming Ruffed Grouse often make several “silent” wingbeats (Hjorth 1970, Aubin 1972, Samuel et al. 1974), which were barely detectable or absent in the bulk of our recordings, we considered a bout of drumming to begin at the onset of the first quartet of steady wingbeats (Fig. 1) that is found in all recordings. Note that Aubin (1972) and Samuel et al. (1974) used the same criterion to define the beginning of a drumming bout. Using the

quartet as a starting point, we then analyzed spectrograms of the recordings. From the energy spectrum averaged over each drumming bout (Fig. 1), we calculated the 25%, 50%, and 75% quartiles (Q25, Q50, and Q75, all in Hz). The quartiles characterize the distribution of energy across the frequency spectrum and divide it into four equal parts. For example, the Q25 is the frequency below which 25% of the total energy of the drumming in a bout occurs. In addition to the quartiles, we measured the peak frequency (Hz), which was the frequency with the highest amplitude within each drumming bout. We calculated the mean Q25, Q50, Q75, and peak frequency for each orientation for each male and compared them with an ANOVA. For those individual males for which we could obtain recordings from all three orientations, we also ran a factorial ANOVA of all recordings for Q25, Q50, Q75, and peak frequency with male, orientation, and the interaction effect as terms. Again, we used post-hoc Tukey–Kramer HSD tests to compare all means if the ANOVAs revealed significant effects.

RESULTS

MEASUREMENTS OF SOUND-PRESSURE LEVEL

We recorded a total of 191 SPL measurements from 13 males (average 15 per male). The average number of SPL measurements recorded for each male was as follows: front = 8, (range 4–15); behind = 7, (range 4–10); side = 5 (range 3–9). In many cases, we could not detect SPLs above ambient noise when measuring from the sides of displaying birds. Of the 13 males, we obtained measurements for all three orientations from five, of two orientations from three males, and one of orientation from the remaining five.

Overall, the average SPL from the front of a drumming bird was 66.2 ± 1.7 dB (mean \pm SD, $n = 9$ males; Fig. 2a). This was slightly larger than the average from behind (65.2 ± 1.8 dB, $n = 11$ males), and both were much larger than that measured from the side (58.9 ± 1.5 dB, $n = 6$ males). We were unable to record SPLs from both right and left sides of individual birds, but when we compared SPLs from the left ($n = 3$) and the right ($n = 3$) of these six males, we found no significant difference ($t = -0.74$, $df = 4$, $p = 0.52$). An ANOVA across the averages of the males yielded a significant difference among the orientations ($F = 30.63$, $df = 2, 20$, $p < 0.01$). The post-hoc analyses revealed that the SPLs from the side were significantly lower than those from the front or behind but revealed no significant difference between front and behind.

An ANOVA restricted to the five males for which we had measurements from all three orientations also yielded significant differences ($F = 53.34$, $df = 14, 85$, $p < 0.01$). There was not only a significant difference in orientation ($F = 276.34$, $df = 2, 85$, $p < 0.01$), but also among males ($F = 7.41$, $df = 4, 85$, $p < 0.01$) and in the interaction effect between male and orientation ($F = 12.59$, $df = 8, 85$, $p < 0.01$). Post-hoc tests revealed that some males were louder than others at specific orientations, but the largest effect was the difference in SPL among the three orientations. SPLs from the front (least-squares mean

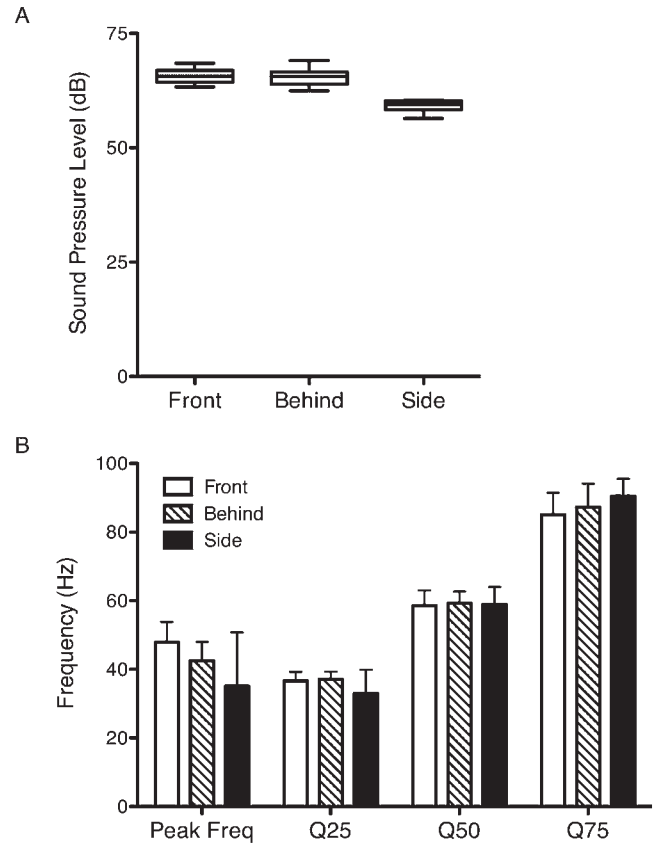


FIGURE 2. (A) Boxplots (minimum–maximum) of mean sound-pressure level (SPL) measured in decibels (dB) of bouts of drumming of 13 male Ruffed Grouse at three different orientations: front, behind, and side. (B) The average frequency (Hz \pm standard deviation) measured for peak frequency and the 25th, 50th and 75th quartiles from spectrograms of bouts of drumming recorded from 11 male Ruffed Grouse at three different orientations: front, behind and side.

= 66.17 dB) were significantly larger than from behind (least-squares mean = 64.96 dB), and both were significantly larger than from the side (least-squares mean = 59.21 dB). Thus the drumming is primarily directed toward the front of a displaying bird with significantly less energy emanating from the other two directions.

SPECTRAL ANALYSES

We analyzed 165 drumming bouts recorded from 11 males (8–22 per male). ANOVAs across the averages of the males for the Q25 ($F = 2.33$, $df = 2, 23$, $p = 0.12$), Q50 ($F = 0.07$, $df = 2, 23$, $p = 0.94$), and Q75 ($F = 1.09$, $df = 2, 23$, $p = 0.35$) frequencies, did not yield any significant differences among the three orientations (Fig. 2b). We did detect a significant difference in peak frequency ($F = 7.59$, $df = 2, 23$, $p < 0.01$), and post-hoc tests indicated that this was due to peak frequencies recorded from the side (28.2 ± 18.8 Hz) significantly lower than those taken from the front of (47.9 ± 6.0 Hz) or behind (42.6 ± 5.5 Hz) a drumming bird (Fig. 3).

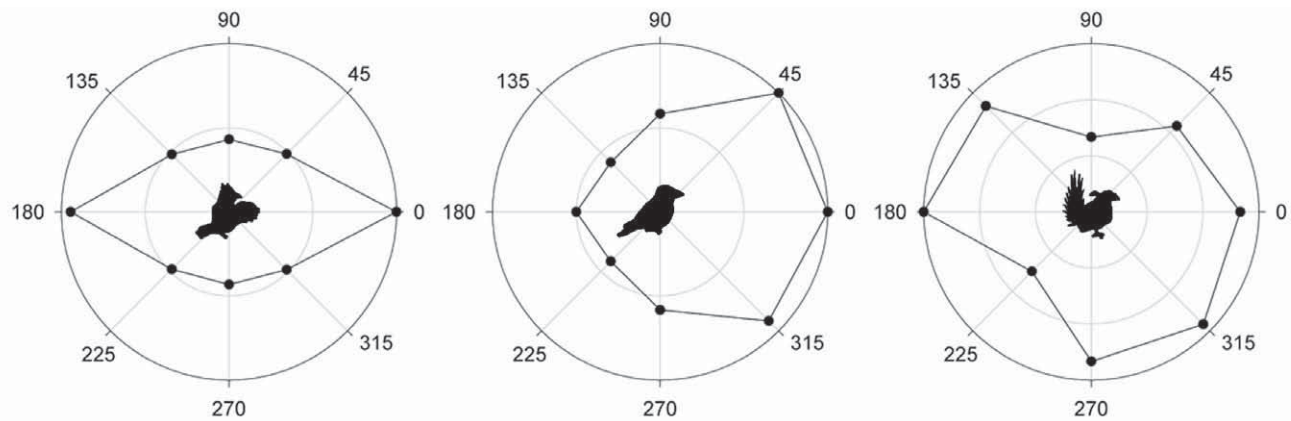


FIGURE 3. Polar plots depicting the pattern of acoustic radiation of (from left to right) Ruffed Grouse drumming, the Red-winged Blackbird's "oak-a-lee" call (Patricelli et al. 2007), and the Greater Sage-Grouse's "coo 1" (Dantzker et al. 1999). The direction in the polar plots (in degrees) for all three species rostral is at 0°, caudal at 180°, and lateral at 90° and 270°. The radial divisions are in intervals of 6 dB, just as in Patricelli et al. (2007) and Dantzker et al. (1999). Points shown for the Ruffed Grouse at 45°, 135°, 225°, and 315° are based on interpolation and recordings from two males (numbers 147 and 135) at 45° and 225°.

We were able to obtain recordings with good signal-to-noise ratios for all three orientations from only three males (Table 1). Factorial ANOVAs of all recordings of these three males, which included male, orientation, and their interaction as effects, were significant for Q25 ($F = 44.99$, $df = 8, 42$, $p < 0.01$), Q50 ($F = 26.75$, $df = 8, 42$, $p < 0.01$), Q75 ($F = 12.98$, $df = 8, 42$, $p < 0.01$) and peak frequency ($F = 3.34$, $df = 8, 42$, $p < 0.01$). In the ANOVAs of both the Q25 and peak frequency, male, orientation, and the interaction effects were all significant (all $p < 0.01$). For the Q50, male, and the interaction effect were significant ($p < 0.01$), but orientation was not ($p = 0.19$), and for the Q75, male and orientation were significant ($p < 0.01$), but the interaction effect was not ($p = 0.15$). Post-hoc tests indicated that the majority of these effects were due to frequencies recorded from the side (Table 1) being lower than those recorded from the front and behind.

DISCUSSION

Overall, our results clearly indicate that the Ruffed Grouse drumming is directional and beams primarily from the front of a male, with a significant decrease of -7.3 dB (on average) from the sides (Fig. 3). We did detect some differences among the three orientations in the spectral analyses, but they were inconsistent.

The acoustic radiation pattern of Ruffed Grouse drumming differs from that of vocalizations in two respects. First, the SPLs were much lower than those for birdsong or other courtship vocalizations normalized to a distance of 1 m. Songbirds generally sing at a peak SPL of 80–94 dB (Brenowitz 1982, Larsen and Dabelsteen 1990, Patricelli et al. 2007), and Butler et al. (2010) reported a similar intensity for booming Lesser Prairie-Chickens (*Tympanuchus pallidicinctus*), whereas the drumming of Ruffed Grouse is much quieter (64–70 dB). Second, the shape of the acoustic radiation pattern of the drumming is markedly different from that of vocalizations (Fig. 3). Most avian vocalizations share a similar directionality; the song or call is loudest directly in front of and quietest directly behind the bird (Hunter et al. 1986, Larsen and Dabelsteen 1990, Dantzker et al. 1999, Brumm and Naguib 2002, Patricelli et al. 2007, Yorzinski and Patricelli 2010). In contrast to this typical pattern of vocalizations, drumming radiates almost equally in front of and behind a displaying bird; radiation occurring perpendicular to this axis is significantly less (Fig. 3). This pattern approximates that of an acoustic dipole in which sound radiates equally in two directions along an axis, but perpendicular to this axis, little to no sound radiates (Bradbury and Vehrencamp, 1998, Blackstock 2000). Drumming is produced by rapid wing movements along the bird's longitudinal axis in the same fashion as the back-and-forth vibration of an idealized

TABLE 1. Means of peak frequency (Hz) and 25th, 50th, and 75th percentile frequencies (Q25, Q50, and Q75) measured from three male Ruffed Grouse from which we recorded drumming from three orientations: front, behind, and side.

Male	n	Peak			Q25			Q50			Q75		
		Front	Behind	Side	Front	Behind	Side	Front	Behind	Side	Front	Behind	Side
130	12	44.74	44.41	7.57	33.33	31.69	23.38	53.22	49.13	52.23	77.27	71.41	85.29
144	17	47.62	42.94	51.11	37.76	36.53	39.61	58.38	59.70	63.03	86.25	85.89	90.61
145	22	51.72	45.97	34.48	39.47	38.50	32.99	59.87	59.53	57.71	84.13	86.48	88.67

dipole, so the acoustic radiation pattern of the drumming is therefore unsurprising. Considering a drumming bird as a dipole also provides an explanation for the amplitude of drumming being lower than that of vocalizations. At low frequencies (i.e., long wavelengths), the amplitude that a dipole can produce is much lower than that a monopole can produce (Blackstock 2000). A Ruffed Grouse produces wavelengths (25–90 Hz, Garcia et al. 2012) that are much longer (3.8–13.6 m) than its body size, resulting in amplitudes much lower than vocalizations of other species (Bradbury and Vehrencamp 1998).

A dipole's acoustic radiation pattern of a low-frequency sound also has implications for localizing a displaying male. For example, the amplitude that a receiver detects will provide a poor estimator of distance unless both the source amplitude and the orientation of the displaying male are known a priori. In fact, a displaying male generates the same SPL directly in front of it at 256 m as it does at 128 m to its sides. Observers' inability to judge distance to a drumming male effectively is mentioned repeatedly in the literature, drumming birds thought distant being only a few meters away (Bump et al. 1947, Gullion 1984), and we experienced this regularly in the field when trying to locate drumming grouse. Distance estimation is not, however, the only problem facing intended receivers (males or females). Low frequencies attenuate less and travel farther through complex environments, but they are difficult to localize (Bradbury and Vehrencamp 1998). The very low frequencies produced by drumming (Fig. 1, Garcia et al. 2012) therefore pose a significant problem for conspecifics because lower frequencies are inherently difficult to localize, especially for bird with an inter-aural distance much smaller than the wavelengths it is attempting to localize (Klump 2000). Thus, both location of and distance to a drumming bird are difficult for receivers to estimate. How females find drumming males is unknown, but could involve anatomical specializations in the auditory system to enhance perception of low frequencies.

The fact that the males cannot alter their position while displaying also has implications for how the drumming sound radiates. Unlike vocalizing species, which can readily alter position while displaying (Dantzker et al. 1999, Patricelli et al. 2007, Yorzinski and Patricelli 2010, Brumm et al. 2011), drumming males must be oriented perpendicular to the longitudinal axis of their drumming log. Although this could constrain a male to broadcasting in only two directions, many males use more than one log within the breeding season and swap logs within a day. At least six of our males used more than one log over the course of our study, and two of them used three or more logs within one morning. The alternative logs were not perfectly parallel to the original log, so the use of multiple logs could provide a means of broadcasting in several directions. Thus changing the drumming log through the day or season would overcome the constraint of a fixed posture while drumming and provide a means of beaming this

directional signal to a larger area, thereby enhancing the probability of being heard by potential mates or competing males. Whether males change drumming logs more frequently in response to hearing another male drumming or an approaching female is not known, but the answer could provide some insight into the potential importance of maintaining more than one drumming log.

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