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Hushed disputes between noisy neighbours: ovenbirds vary song amplitude during conflicts with territorial rivals

Connor S. Acorn [a, *], Jennifer R. Foote [b, 1], Daniel J. Mennill [a]

[a] Department of Integrative Biology, University of Windsor, Windsor, ON, Canada
[b] Department of Biology, Algoma University, Sault Ste Marie, ON, Canada

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Vocal amplitude represents an important source of variation in animal acoustic signals, yet amplitude is not well studied for most species, especially in field settings where amplitude is challenging to quantify. Previous studies have shown that vocal amplitude is a flexible trait that songbirds can control. In this study, we explored variation in the amplitude of the primary songs of male ovenbirds, *Seiurus aurocapilla*, to address the question: do ovenbirds modulate their song amplitude in different social contexts? We present the context-dependent amplitude hypothesis: that animals adjust their vocal amplitude across social contexts to maximize communication with intended receivers while minimizing detection by nonintended receivers. We used a high-precision, field-portable sound level meter to measure the amplitude of 213 songs sung by 30 male ovenbirds on their breeding territories. We categorized the contexts in which these songs were sung as either distant countersinging (i.e. directed back-and-forth interactions with a rival male >20 m away in a separate territory), close countersinging (i.e. directed back-and-forth interactions with a rival male <10 m away) and broadcast singing (i.e. singing without back-and-forth interactions with other males). Our recordings demonstrate that ovenbirds sing high-amplitude songs, with a median average amplitude of 76.0 dB(A) (interquartile range: 73.2–77.9, $N = 213$) across the entire song and a median maximum amplitude of 98.8 dB(A) (interquartile range: 96.0–101.0, $N = 213$). Our field data reveal that ovenbirds exhibit differences in the amplitude of their songs between the close countersinging context and the broadcast singing and distant countersinging contexts. Songs had higher amplitudes during the broadcast singing and distant countersinging contexts and the lowest amplitudes during the close countersinging context. We conclude that ovenbirds change their vocal amplitude between social contexts and that vocal amplitude is important to ovenbird communication.

Animals exchange vital information through acoustic communication, particularly during the breeding season, when vocalizations can function both as courtship displays to attract mates and as territorial displays to defend resources from conspecific rivals (Beecher & Brenowitz, 2005; Catchpole & Slater, 2008; Conti et al., 2015; Gustison & Townsend, 2015). Diverse features of acoustic signals, including frequency, rate and repertoire size, can affect an individual's ability to perform these functions, thus influencing their fitness (Collins, 2004). However, another important dimension of acoustic signals, amplitude, has received considerably less attention, especially in field settings (Brumm, 2009; Zollinger & Brumm, 2015). The amplitude of a sound is often measured in terms of sound pressure level, which is the ratio of the pressure of a sound wave to a reference pressure, which is commonly 20 μPa for sounds travelling through air (Jakobsen et al., 2021). A sound's amplitude determines, in part, how far it will travel through its environment and how loud the sound will be perceived by other animals (Erbe et al., 2022; Jakobsen et al., 2021). Vocal amplitude is an important part of acoustic communication that varies between social contexts (Dunlop, 2016; Gustison & Townsend, 2015; Vargas-Castro et al., 2017). Previous research on songbirds shows that song amplitude is a flexible trait that animals can vary with social context (Brumm & Todt, 2004; Cynx & Gell, 2004; Kobayasi & Okanoya, 2003). Most studies of song amplitude have been conducted in laboratory settings where environmental conditions are more easily controlled (Zollinger & Brumm, 2015). In field

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* Corresponding author.
E-mail address: connoracorn1@gmail.com (C. S. Acorn).
[1] *E-mail address:* jennifer.foote@algomau.ca (J. R. Foote).

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settings, diverse conditions must be accounted for when measuring vocal amplitude, posing challenges for researchers to study amplitude in wild, free-living animals. In recent years, however, innovations in technology and methods have made field studies on vocal amplitude more feasible (e.g. Brumm & Ritschard, 2011; Derryberry et al., 2017; Menezes & Podos, 2025; Patricelli et al., 2007; Podos & Cohn-Haft, 2019).

Countersinging (interactively singing back-and-forth with other individuals) is a common behaviour used by territorial songbirds to defend their territories from conspecific rivals (reviewed in Logue, 2021; Todt & Naguib, 2000). There are several different contexts in which rivals may interact with one another, including countersinging over a long distance from within their own territories or countersinging over shorter distances during territorial intrusions and boundary disputes (Naguib, 2005). Evidence suggests that songbirds increase their song amplitude when countersinging with distant rivals compared to when broadcast singing (i.e. singing that is not directed at specific territorial neighbours; Brumm & Todt, 2004). When distantly countersinging, higher-amplitude songs may most effectively reach the rival bird and facilitate communication (Brumm & Todt, 2004; Logue, 2021). Distant countersinging interactions between neighbours can escalate into close-range countersinging when animals approach each other, sometimes involving one bird entering the territory of its rival (Naguib, 2005; Todt & Naguib, 2000). During close countersinging interactions, the interacting birds often alter aspects of their singing, such as singing rate, song type, song matching and song overlapping (Beecher et al., 2000; Benedict et al., 2012; Sprau et al., 2010; Vehrencamp et al., 2014). If close countersinging interactions continue to escalate, they may reach a stage where low-amplitude soft songs are used as aggressive signals that predict physical attack (Dabelsteen et al., 1998; Searcy & Beecher, 2009). The use of soft songs as signals of aggression has been documented in diverse songbird species (Anderson et al., 2008; Hof & Hazlett, 2010; Moran et al., 2018). Soft songs may reduce eavesdropping from nearby conspecific birds during the most aggressive territorial interactions (Akçay et al., 2015; Dabelsteen et al., 1998; Fitzsimmons et al., 2008; Moran et al., 2018). These lower-amplitude soft songs are sometimes structurally identical to songs used in other contexts or may have their own distinct structure, but they are consistently defined by low amplitude (Searcy & Beecher, 2009).

Ovenbirds, *Seiurus aurocapilla*, are migratory North American wood warblers known for the clamorous songs sung by breeding males (Lein, 1981). Despite their reputation as boisterous singers (Lemon et al., 1981), song amplitude has not been described in ovenbirds or any other wood warbler species. Male ovenbirds sing two main song types: an often-sung primary song used both in mate attraction and territory defence, and an extended flight song that is uttered rarely during nocturnal displays (Spector, 1992). Primary songs (hereafter referred to simply as ‘songs’) consist of a phrase of three to five notes ranging in frequency from 2000 to 10000 Hz, uttered repeatedly with increasing amplitude (Hughes, 2011; Lein, 1981). Songs are typically 2–4 s long and have their greatest concentration of energy at 3000–5000 Hz (Lein, 1981). A recent paper by Menezes and Podos (2025) found that the peak frequency of ovenbird songs decreases and is more variable at higher amplitudes. As in many temperate songbirds, breeding male ovenbirds routinely engage in directed countersinging interactions with neighbouring males during the dawn and morning periods (Popp, 1989; Spector, 1992). Males may distantly counter-sing with one another from within their own territories or counter-sing during close-range confrontations associated with territorial intrusions (Lein, 1981; Popp, 1989). When countersinging during close confrontations, male ovenbirds have been observed singing songs that are noticeably lower in amplitude than their normal songs, although the precise amplitude of these songs has not been quantified (Lein, 1981). This behaviour may be akin to the low-amplitude soft songs used as aggressive signals in other songbird species (Anderson et al., 2008; Hof & Hazlett, 2010; Moran et al., 2018).

Animals, including songbirds, may vary their vocal amplitude in different social contexts, modulating their amplitude with the distance of their target audience. We call this the context-dependent amplitude hypothesis, whereby animals adjust their vocal amplitude across social contexts to maximize communication with intended receivers while minimizing detection by non-intended receivers. In the present study, our objective was to explore this hypothesis through field-based amplitude recordings of male ovenbirds engaged in different singing behaviours. Our first goal was to describe ovenbird song amplitude, and our second goal was to test predictions of the context-dependent amplitude hypothesis. Given that males of other songbird species increase song amplitude when countersinging with distant conspecific males (e.g. common nightingales, *Luscinia megarhynchos*, sing higher-amplitude songs when playback simulates a male >25 m away; Brumm & Todt, 2004), we predicted that male ovenbirds would sing higher-amplitude songs when engaged in interactive countersinging with distant rivals compared to when they were broadcasting song outside of a countersinging context (Fig. 1). In a distant countersinging context, higher-amplitude songs would benefit males' ability to be heard by conspecifics at greater distances. Higher-amplitude songs could be less beneficial when broadcast singing since males may not know how far away their audience is, or whether one is even present. We also predicted that male ovenbirds would sing lower-amplitude songs when engaged in close-range territorial confrontations with conspecific males. This prediction is based on previous findings showing that other songbirds produce lower-amplitude songs during escalated territorial interactions (Fig. 1; Anderson et al., 2008; Hof & Hazlett, 2010; Moran et al., 2018). We were motivated by a desire to apply a quantitative approach to studying vocal amplitude through field studies of one of North America's noisiest singing wood warblers.

METHODS

General Field Methods

We studied ovenbirds inhabiting the Coldwater Creek Trail section of the Hiawatha Highlands Conservation Area in Sault Ste Marie, Ontario, Canada (46°34′08″N, 84°17′44″W). We recorded male ovenbird songs during the breeding season from May to June 2023. This population of ovenbirds has been the focus of ongoing study since 2013 (Ehnes & Foote, 2015; Foote et al., 2017, 2018). Birds in this population are not banded but we differentiate between birds based on their individually distinctive songs and their territorial positions within the forest, a strategy that has proven effective through numerous previous field studies (Ehnes & Foote, 2015; Foote et al., 2017, 2018; Jagielski & Foote, 2023). We assessed the territory boundaries of male ovenbirds by tracking their movements with a hand-held global positioning system (GPSMAP 64sx; Garmin, Olathe, KS, U.S.A.), allowing us to record the areas occupied by each individual and map their territories. Using their known territories and individually distinctive song structures (Jagielski & Foote, 2023; Lein, 1981), we could readily differentiate between individuals.

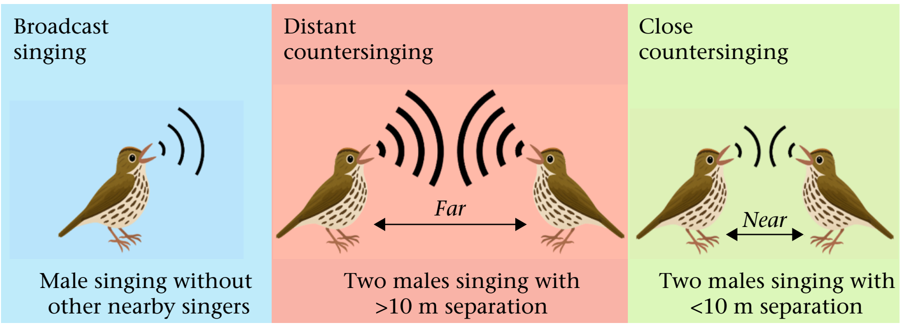

Figure 1. Visual representation of our predictions of the context-dependent amplitude hypothesis that animals adjust their vocal amplitude across social contexts to maximize communication with intended receivers while minimizing detection by nonintended receivers. We predicted that ovenbird song amplitude would be the greatest during distant countersinging interactions between males, lowest during the close countersinging interactions between males and intermediate during nondyadic broadcast singing, based on findings in the literature that have quantified song amplitude in other birds.

Sound Level Measurements

We measured the amplitude of ovenbird songs using a Larson Davis 831C SoundAdvisor sound level meter equipped with a free-field omnidirectional condenser microphone and preamplifier (Larson Davis, Depew, NY, U.S.A.). This high-precision sound level meter has been used in previous field-based studies to accurately quantify the amplitude of birdsong for wild, free-living songbirds (Menezes & Podos, 2025; Podos & Cohn-Haft, 2019). At the beginning of each field day, we calibrated the sound level meter with a Larson Davis CAL200 acoustic calibrator. We recalibrated the device approximately once every hour. We configured the sound level meter to measure two amplitude parameters of each recorded ovenbird song, Leq and Lpeak, both in A-weighted amplitude, over time windows of 20 ms, as in Podos and Cohn-Haft (2019). Leq measures the average amplitude of a sound throughout its specified duration, while Lpeak measures the maximum amplitude reached at any point in the duration of a sound (Jakobsen et al., 2021). Amplitude was measured using an A-weighting at a reference pressure value of 20 μPa, consistent with many previous studies on avian vocal amplitude, facilitating direct comparisons with other birds (Menezes & Podos, 2025; Opaev & Shishkina, 2020; Podos & Cohn-Haft, 2019). In addition to the measurements of sound amplitude, the sound level meter simultaneously recorded audio files of the measured sounds (48 kHz sampling frequency; 16-bit accuracy; WAV format), which allowed us to visualize sound spectrograms of the field recordings.

We began measuring song amplitude during the early morning at approximately 0700 hours and continued until midday when ovenbird singing activity decreased. All recorded songs were uttered spontaneously without the use of playback or other lures to elicit singing. For each song bout measured with the sound level meter, we recorded the context in which the focal male was singing. We categorized song bouts into the following three social contexts. (1) We classified male singing behaviour as ‘distant countersinging’ if the subject male was engaged in a back-and-forth singing pattern with a neighbouring male (at least 50% of songs in the singing bout were sung within a few seconds of a neighbouring male's song) in an adjacent territory, with at least 20 m distance of separation between the males. (2) We classified male singing behaviour as ‘close countersinging’ if the subject male was engaged in a back-and-forth singing pattern with another male, with less than 10 m distance of separation between the males and often including chases. We did not observe countersinging interactions at distances of 10–20 m. (3) We classified male singing behaviour as ‘broadcast singing’ if the subject male was singing without any noticeable back-and-forth interactions with other males (the male sang without vocal responses from any immediate neighbours).

We measured the linear distance between the sound level meter and the ovenbird using a laser rangefinder (TecTecTec VPRO500; TecTecTec, Houston, TX, U.S.A.). The median distance between the sound level meter and singing ovenbird during amplitude measurements was 11 m (range 5–22 m). We observed singing males using binoculars (10 × 50 magnification) and estimated their head orientation relative to the sound level meter in intervals of 15° between a range of 0° (i.e. a male was facing directly towards the sound level meter) and 180° (i.e. a male was facing directly away from the sound level meter; as in Podos & Cohn-Haft, 2019). Measurements of the distance between the sound level meter and the singing bird, as well as measurements of the bird's head orientation, were made by the individual operating the sound level meter but were occasionally taken by multiple observers. We made all song amplitude measurements with clear paths between the sound level meter and the singing bird, with no vegetation blocking our line of sight. Linear distance and head orientation were measured for each individual song, and any songs in which distance or head orientation changed during the song were not included.

Acoustic Analyses

We examined audio recordings in the sound analysis program Raven Pro (Cornell Lab of Ornithology, Ithaca, NY, U.S.A.) to locate songs measured by the sound level meter with minimal background noise. We then used the program G4 (Larson Davis) to calculate amplitude measurements for these songs. To account for background noise potentially affecting amplitude measurements, we applied an equation that corrects measurements of signal amplitude for the effects of background noise:

$$\left(L_{\text{signal}} = 10\log_{10}\left(10^{\left(\frac{L_{\text{signal+noise}}}{10}\right)} - 10^{\left(\frac{L_{\text{noise}}}{10}\right)}\right)\right) \tag{1}$$

L_{signal} is the amplitude of the signal, L_{noise} is the amplitude of background noise present in the recording, and $L_{\text{signal+noise}}$ is the measurement (Brumm et al., 2009; Hardman et al., 2017). For each song, we selected a 1 s segment of background noise from directly before or after the song. We calculated the mean LAeq during each 1 s segment to use in the noise correcting equation. The amplitude of a signal dissipates as it spreads out from its source at a rate of 6 dB for each doubling of distance in a process known as spherical spreading (Wahlberg & Larsen, 2017). To account for this, we standardized the measurements of song amplitude by applying an equation that approximates the amplitude of the song 1 m away from the source:

$$L_{1\mathrm{m}} = 6\,\log_2(\mathrm{d}) + L_d \qquad (2)$$

$L_{1\mathrm{m}}$ is the amplitude of the song at 1 m away from the source, d is the distance between the singing bird and the measuring device and L_d is the amplitude measured at that distance (Brumm & Ritschard, 2011; Brumm & Zollinger, 2011). The noise-correcting equation and distance-correcting equation were applied to each of the amplitude measurements made every 20 ms during songs.

We compared the amplitude of ovenbird songs across the three social contexts with three measurements (Fig. 2): (1) the average song amplitude across the entire song calculated as the average LAeq value across all notes; (2) the average amplitude of the final three song phrases, calculated as the average LAeq value of the final three phrases in the song (the portion of the ovenbird song that routinely has the highest signal-to-noise ratio due to increasing amplitude throughout the song; Lein, 1981); and (3) the maximum song amplitude, calculated as the highest LApeak value reached at any point in the song.

We limited our data to a maximum of five songs per individual in a single context. In instances where we recorded more than five songs per individual in a single context, we randomly selected five songs for inclusion in our analyses. We measured the amplitude of 213 songs from 30 individual male ovenbirds, using an average of 7.1 songs per individual (range 2–15 songs) and an average of 3.9 songs per individual per context (range 1–5 songs). There were six individual males for whom we measured songs in all three contexts and another 14 for whom we measured songs in two of the three contexts. We measured songs from 18 individuals during the broadcast singing context, from 26 individuals during the distant countersinging context and from 11 individuals during the close countersinging context.

Statistical Analyses

We conducted our statistical analyses in R (version 4.4.2; R Core Team, 2024). We calculated the median values for average song amplitude, average amplitude of the final three song phrases and maximum song amplitude for each song ($N = 213$) in our data set. We used generalized linear mixed models with the function ‘glmmTMB’ from the R package glmmTMB (Brooks et al., 2017), using a Gaussian distribution family, with social context and head orientation as fixed effects and ordinal day and individual as random effects. Ordinal day and individual identity were included as random effects to account for potential differences in amplitude on different days and between individuals. Separate models were made for average song amplitude, average amplitude of the final three song phrases and maximum song amplitude, with each as the response variable. We used generalized linear mixed models due to their ability to account for both fixed and random effects, as well as their robustness to nonnormal data (Schielzeth et al., 2020). We used the function ‘testDispersion’ from the R package DHARMa (Hartig, 2024) to test model assumptions and ensure adequate model fit. We used post hoc pairwise Tukey's honestly significant difference tests with the function ‘emmeans’ in the R package emmeans (Lenth et al., 2025) for each of the three song amplitude variables to determine how the three contexts differed from each other. Tukey's tests allowed us to make multiple pairwise comparisons between groups in our data set (Aghilone & Cavacece, 2015). We also used Kendall's rank correlations with the function ‘cor.test’ in R to study the relationship between song length and each of the three song amplitude variables.

Instead of communicating findings as either significant ($P < 0.05$) or not significant ($P > 0.05$), we describe findings following the ‘language of evidence’ approach suggested by Muff et al. (2022), where we consider $P > 0.10$ to be no evidence, $0.05 < P < 0.10$ as weak evidence, $0.01 < P < 0.05$ as moderate evidence, $0.001 < P < 0.01$ as strong evidence and $P < 0.001$ as very strong evidence. We present the interquartile range for each of our reported measurements.

Ethical Note

Our field methods were approved and permitted by the Animal Care Committee of the University of Windsor (Animal Use Protocol Permit: 20-09). We used only noninvasive methods that did not involve handling or physically interacting with any birds. Observations and manual measurements of ovenbird songs were made at an adequate distance to reduce disturbance of the birds’ natural behaviour.

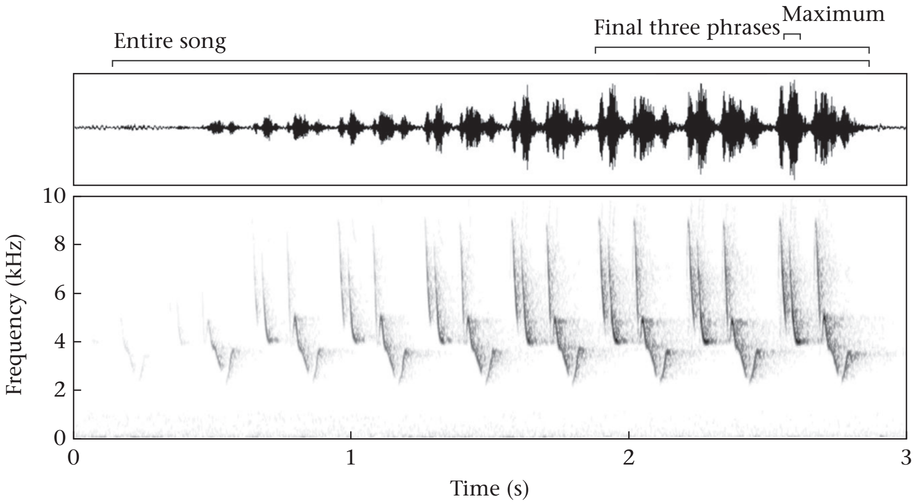

Figure 2. An ovenbird song shown in the format of a waveform (top) and spectrogram (bottom), highlighting the portions of the song that we measured with field-based recordings using a calibrated sound level meter.

RESULTS

Amplitude of Ovenbird Songs

We found substantial variation in the amplitude of male ovenbird songs across 213 songs (Fig. 3). The median average amplitude across the entire song was 76.0 dB(A) (interquartile range: 73.2–77.9, $N = 213$) sound pressure level re. 20 μPa at 1 m distance; the median average amplitude across the final three song phrases was 82.2 dB(A) (79.7–84.4, $N = 213$); and the average maximum song amplitude was 98.8 dB(A) (96.0–101.0, $N = 213$). Songs included 5–16 phrases repeated in succession, with a median of 9 (8–10) phrases per song. Song phrases comprised three to six unique notes, spanning a frequency range of 2000–10000 Hz (Fig. 2). The length of songs varied from 1.44 s to 4.14 s, with a median length of 2.6 s (interquartile range: 2.44–3.02 s, $N = 213$).

The well-known song of ovenbirds features a gradual crescendo from lower-amplitude phrases at the start of the song to the higher-amplitude phrases towards the end of the song. We found that the moment of maximum amplitude occurred most often during the penultimate phrase (33.3% of songs), followed by the antepenultimate (31.0%), final (26.8%), fourth-last (8%) and fifth-last (0.9%) phrases ($N = 213$).

Song length varied with song amplitude. We found moderate evidence of a weak negative association between song length and average amplitude across the entire song, where longer songs

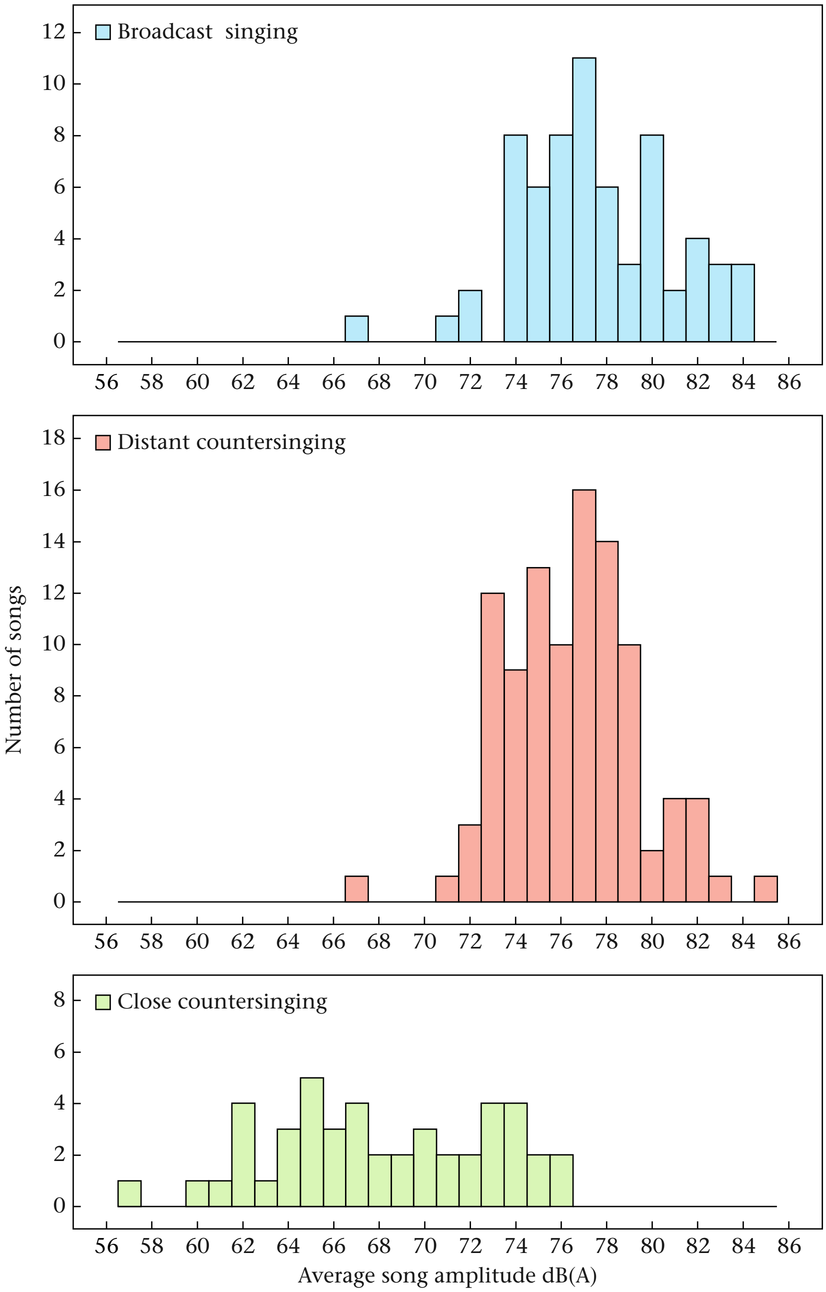

Figure 3. Histograms showing the distributions of average song amplitude during the broadcast singing (66 songs from 18 males), distant countersinging (101 songs from 26 males) and close countersinging (46 songs from 11 males) contexts.

tended to have lower amplitudes (Kendall's rank correlation: $z = -2.04$, $P = 0.04$, $\tau = -0.10$). We found no evidence of an association between song length and average amplitude across the final three song phrases ($z = 1.39$, $P = 0.16$, $\tau = 0.06$). We found strong evidence that maximum song amplitude had a weak positive correlation with song length, where longer songs had higher amplitudes ($z = 2.74$, $P = 0.006$, $\tau = 0.13$).

Song Amplitude Variation Across Contexts

Ovenbirds changed their song amplitude in different contexts, and this pattern was present whether we focused our analysis on the average measured amplitude of the entire song, the final three song phrases or the maximum amplitude of the song. We found very strong evidence that average amplitude across the entire song varied between social contexts (Table 1): the median value of average song amplitude was 77.2 dB(A) (75.3–80.2, $N = 66$) during broadcast singing, 76.6 dB(A) (74.5–78.0, $N = 101$) during distant countersinging and 67.8 dB(A) (65.1–72.6, $N = 46$) during close countersinging. We found very strong evidence that average song amplitude varied between close countersinging and both broadcast singing and distant countersinging. We found no evidence of a difference in average song amplitude between the broadcast singing and distant countersinging contexts (Table 2, Fig. 4a).

As with the average amplitude across the entire song, average amplitude across the final three song phrases varied between social contexts (Table 1). The median average amplitude across the final three song phrases was 83.5 dB(A) (81.6–85.6, $N = 66$) during broadcast singing, 82.8 dB(A) (81.3–84.7, $N = 101$) during distant countersinging and 73.6 dB(A) (69.8–79.3, $N = 46$) during close countersinging. This reveals very strong evidence of a difference in amplitude between close countersinging and both distant countersinging and broadcast singing, but no evidence of a difference between broadcast singing and distant countersinging (Table 2, Fig. 4b).

Table 1

Generalized linear mixed models output showing the influence of the fixed effects, social context (broadcast singing, distant countersinging, close countersinging) and head orientation on the three measurements of song amplitude and the influence of the random effects, ordinal day and individual on the models

	Estimate	SE	z	Pr(>|z|)
Average song amplitude				
Fixed effects				
Intercept	77.00	0.78	99.16	<0.0001
Close countersinging	-6.82	0.78	-8.69	<0.0001
Distant countersinging	-1.05	0.55	-1.92	0.06
Head orientation	-0.01	0.01	-1.64	0.10
Random effects	**Variance**	**SD**		
Ordinal day	3.95	1.99		
Individual	4.69	2.16		
Final three phrases average amplitude				
Fixed effects				
Intercept	82.49	0.79	104.33	<0.0001
Close countersinging	-6.66	0.84	-7.92	<0.0001
Distant countersinging	0.17	0.46	0.36	0.72
Head orientation	0.01	0.01	0.39	0.70
Random effects	**Variance**	**SD**		
Ordinal day	6.77	2.60		
Individual	3.68	1.92		
Maximum song amplitude				
Fixed effects				
Intercept	99.29	0.89	111.01	<0.0001
Close countersinging	-5.75	0.72	-7.96	<0.0001
Distant countersinging	-0.04	0.46	-0.08	0.94
Head orientation	-0.01	0.01	-1.24	0.21
Random effects	**Variance**	**SD**		
Ordinal day	9.48	3.08		
Individual	5.52	2.35		

Table 2

Estimates of the relationship between the three variables of song amplitude and context (broadcast singing, distant countersinging, close countersinging) using post hoc Tukey's tests of honestly significant differences for the results of the generalized linear mixed models shown in Table 1

Contexts	Estimate	SE	*df*	*t* ratio	*P*
Average song amplitude					
Broadcast vs close	6.82	0.78	204	8.69	<0.0001
Broadcast vs distant	1.05	0.55	204	1.92	0.14
Close vs distant	-5.77	0.70	204	-8.19	<0.0001
Final three phrases average amplitude					
Broadcast vs close	6.66	0.84	204	7.92	<0.0001
Broadcast vs distant	-0.17	0.46	204	-0.36	0.93
Close vs distant	-6.83	0.81	204	-8.47	<0.0001
Maximum song amplitude					
Broadcast vs close	5.75	0.72	204	7.96	<0.0001
Broadcast vs distant	0.04	0.46	204	0.08	0.99
Close vs distant	-5.71	0.72	204	-7.91	<0.0001

As with whole songs and the final three phrases, we also found very strong evidence that maximum song amplitude varied between social contexts (Table 1). The median value of maximum song amplitude was 100.3 dB(A) (97.8–101.8, $N = 66$) during broadcast singing, 99.3 dB(A) (97.7–101.5, $N = 101$) during distant countersinging and 90.9 dB(A) (86.8–96.0, $N = 46$) during close countersinging. There was very strong evidence that maximum amplitude varied between close countersinging and both broadcast singing and distant countersinging. However, there was no evidence of a difference in maximum amplitude during broadcast singing and distant countersinging (Table 2, Fig. 4c).

Head Orientation

We found no evidence of a relationship between the amplitude of ovenbird songs and the singer's head orientation relative to the sound level meter for any of the three amplitude variables (Table 1). Our field observations revealed that ovenbirds tilt their head back and orient their beak skyward when singing.

DISCUSSION

Through field-based studies of vocal amplitude, measured with portable sound level meters, we found substantial variation in ovenbird song amplitude and strong evidence that amplitude varies with behavioural context. Our results matched our prediction that territorial male ovenbirds would sing lower-amplitude songs during close countersinging. For each of our three amplitude variables, we found strong evidence that amplitude varied between the close countersinging context (lower-amplitude songs) compared to the broadcast singing and distant countersinging contexts (higher-amplitude songs). The average and maximum amplitudes of songs performed during the close countersinging context were approximately 10 dB(A) lower than songs performed during the other two contexts. This reduction in amplitude during the close countersinging contexts shows that male ovenbirds change their song amplitude when interacting with other males during certain social contexts. Our results did not match our other prediction that song amplitude would be highest during the distant countersinging context; we found no evidence of a difference between broadcast singing and distant countersinging for average song amplitude, average amplitude of the final three phrases or maximum amplitude. Overall, our results offer support for the context-dependent amplitude hypothesis,

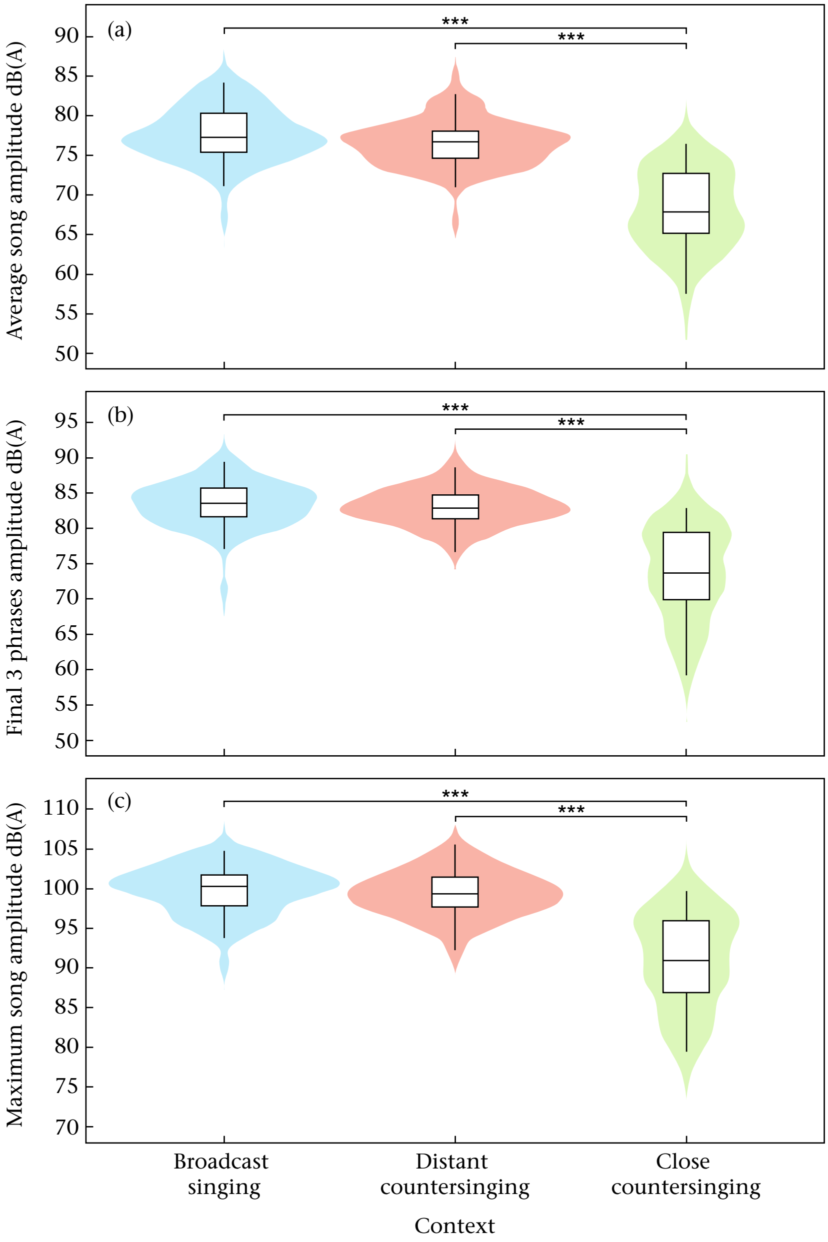

Figure 4. (a) Average amplitude of 213 ovenbird songs recorded in three different contexts: broadcast singing (66 songs), distant countersinging (101 songs) and close countersinging (46 songs). Data are shown as box plots (thick line show medians; boxes show 25th to 75th percentile, whiskers show 10th to 90th percentile) as well as violin plots. (b) Average amplitude of the final three phrases of ovenbird songs recorded in three different contexts: broadcast singing, distant countersinging and close countersinging. (c) Maximum amplitude of ovenbird songs recorded in three different contexts: broadcast singing, distant countersinging and close countersinging.

revealing that ovenbirds vary their vocal amplitude in different social contexts.

The similarity in amplitude during the broadcast singing and distant countersinging contexts suggests that male ovenbirds sing at a higher amplitude when not engaged in an escalated close countersinging conflict, regardless of whether they are interacting with neighbouring males or singing independently of an interaction. A previous experiment conducted on captive male common nightingales found that males increased their song amplitude when exposed to playback of male conspecific songs compared to singing independent of playback (Brumm & Todt; 2004). The difference in our field findings and the findings of this previous laboratory experiment may be due to differences between species or may be due to the presence of eavesdropping females in a field setting. Female songbirds have been shown to prefer males that sing higher-amplitude songs (Ritschard et al., 2010; Searcy, 1996), and females have been shown to eavesdrop on singing interactions between males to assess the interacting males (Mennill et al., 2002; Otter et al., 1999). For the purpose of attracting females, it may be beneficial for male ovenbirds to sing at their highest amplitudes during both the broadcast singing and distant countersinging contexts. Singing at higher amplitudes may also be beneficial in discouraging territorial intrusions from eavesdropping male neighbours during the broadcast singing and distant countersinging contexts, extending the range over which songs can be heard (Fitzsimmons et al., 2008). Higher-amplitude songs would be audible to neighbouring males and females over longer distances due to the spherical spreading of sound (Brumm &

Slabbekoorn, 2005). A recent study by Menezes and Podos (2025) on the relationship between vocal frequency and amplitude in various songbird species found that the peak frequency of ovenbird songs decreased slightly as amplitude increased. This decrease in peak frequency at higher amplitudes may also extend the range of ovenbird songs, as environmental factors that degrade sounds tend to have a stronger effect at higher frequencies (Embleton, 1996).

The amplitude of songs in the close countersinging context was, on average, 10 dB(A) lower than that of songs in the broadcast singing and distant countersinging contexts. Recognizing that the decibel scale is logarithmic, this means that songs in the close countersinging context were half the amplitude of the other contexts. The close countersinging context featured a mix of songs similar in amplitude to the other two contexts, as well as many lower-amplitude songs (Fig. 3). Rather than having two distinct modes of ‘loud song’ and ‘quiet song’, our data suggest that male ovenbirds sing across a continuous range of amplitudes and tend to use lower amplitudes during close countersinging interactions. The lower-amplitude songs may have been used as signals of aggression during particularly hostile moments, similar to low-amplitude songs in other songbird species (Akçay et al., 2015; Anderson et al., 2008; Moran et al., 2018). Songbirds may use lower-amplitude songs to signal aggression as a strategy for reducing eavesdropping by distant individuals while their countersinging rival is still close enough to hear (Dabelsteen et al., 1998; Fitzsimmons et al., 2008). Reducing eavesdropping could be beneficial for a songbird engaged in a close-range countersinging interaction if it allows them to avoid advertising that they are engaged in escalated territorial disputes (Dabelsteen et al., 1998).

We found no evidence that ovenbird song amplitude was related to head orientation relative to the sound level meter. The direction a male was facing when he sang did not affect our song amplitude measurement. In contrast to our findings in ovenbirds, previous research has demonstrated that song amplitude varies directionally in other bird species (Brumm, 2002; Patricelli et al., 2007). The singing posture of ovenbirds may help to explain this difference. When male ovenbirds sing, they tilt their head back so that their beak is pointed upward, a phenomenon known from previous studies (Hann, 1937) and substantiated from our own observations during this investigation. This upwards-oriented singing posture may result in songs radiating omnidirectionally from a singing male ovenbird, and this could account for the lack of acoustic directionality we observed in our amplitude measurements. Future investigations using multiple microphones (as in Patricelli et al., 2007) could help to confirm whether the radiation pattern of ovenbird song is truly omnidirectional.

Overall, male ovenbirds sang high-amplitude songs with a median average amplitude of 76.0 dB(A) across the entire song, a median average amplitude of 82.2 dB(A) during the final three phrases of the song and a median maximum amplitude of 98.8 dB(A). This large difference between the average amplitude of the entire song and the maximum amplitude arises due to the amplitude ‘crescendo’ that defines ovenbird song, where males begin singing at lower amplitudes before increasing throughout the song to reach an amplitude peak near the song's end (Lein, 1981). This explains why the amplitude of the final three song phrases is greater than the amplitude measured across the entire song. The final three phrases in an ovenbird song are the highest-amplitude phrases and contain the moment of maximum amplitude, with the moment of maximum amplitude typically happening during the penultimate phrase. We found strong evidence of a weak positive association between maximum song amplitude and song length, but no evidence of an association between song length and average amplitude of the final three phrases, and moderate evidence of a weak negative association between song length and average amplitude of the entire song. This suggests that longer songs build to a slightly greater peak, but include more of the lower-amplitude phrases at the beginning of the song, making the average amplitude slightly lower throughout.

Our results suggest that male ovenbirds sing at high amplitudes, reaching maximum levels (median of 98.8 dB(A)) that exceed those recorded for several other temperate-breeding songbird species, including great tits, *Parus major* (86.8 dB; Blumenrath & Dabelsteen, 2004), dusky warblers, *Phylloscopus fuscatus* (83.3 dB(A); Opaev & Shishkina, 2020), Radde's warblers, *Phylloscopus schwarzi* (73 dB(A); Opaev & Shishkina, 2020), song sparrows, *Melospiza melodia* (85 dB; Anderson et al., 2008), and common nightingales (91 dB(A); Brumm, 2004). The highest-amplitude birdsongs recorded to date are the songs of screaming pihas, *Lipaugus vociferans*, and white bellbirds, *Procnias albus*, two tropical species where singers are capable of reaching maximum amplitudes in excess of 115 dB(A) and 125 dB(A), respectively (Podos & Cohn-Haft, 2019), far surpassing our measurements of temperate ovenbirds. There is little data on the song amplitude of many songbird species, including the closest relatives to ovenbirds, other species in the Parulidae family. This gap in the existing literature restricts our ability to compare the song amplitude of ovenbirds with the 114 other Parulidae wood warblers (Lovette et al., 2010), and further investigations will be needed to determine whether high-amplitude songs are sung throughout the family or are unique to ovenbirds. Plasticity in vocal amplitude is not limited to songbirds and is also present in many mammals (Dunlop, 2016; Gustison & Townsend, 2015; Vargas-Castro et al., 2017) and reptiles (Brumm & Zollinger, 2017; Wang et al., 2007). However, there is significant room for new research on the vocal amplitude and context-dependent variation in all animals that vary the amplitude of their vocalizations. With novel tools, including sensitive field-portable sound level meters, future research should focus on quantifying the amplitude of the vocalizations of animals across different social contexts.

Our study provides the first description of the amplitude of ovenbird songs and is one of the few studies to show evidence of songbirds changing song amplitude across social contexts. Our results provide support for the context-dependent amplitude hypothesis and the established idea that vocal amplitude is a flexible trait in songbirds. Future studies could build on our findings by measuring the song amplitude of other songbird species in diverse singing contexts. Such studies would allow for a better understanding of how song amplitude varies between species and potentially illuminate any amplitude-related idiosyncrasies that may exist in the singing behaviour of individual species compared to the few species that have already been studied. Another worthwhile future direction of research would be to study whether ovenbird song amplitude varies between intersexual and intrasexual contexts, as the scope of this study did not include any direct interactions between male and female ovenbirds.

Author Contributions

Connor S. Acorn: Writing – original draft, Visualization, Methodology, Investigation, Formal analysis, Conceptualization. **Jennifer R. Foote:** Writing – review & editing, Validation, Supervision, Resources, Project administration, Methodology, Investigation, Funding acquisition, Conceptualization. **Daniel J. Mennill:** Writing – review & editing, Visualization, Validation, Supervision, Resources, Project administration, Methodology, Funding acquisition, Conceptualization.

Data Availability

Research data and R scripts are available as Supplementary Material.

Declaration of Interest

The authors have no conflicts of interest to declare.

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Supplementary Material

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