Current Biology

Bird song plasticity and multimodal shift along noisy rivers

--Manuscript Draft--

Manuscript Number:	CURRENT-BIOLOGY-D-25-01205R1
Full Title:	Bird song plasticity and multimodal shift along noisy rivers
Article Type:	Report
Corresponding Author:	Henrik Brumm Max Planck Institute for Biological Intelligence Seewiesen, GERMANY
First Author:	Léna de Framond
Order of Authors:	Léna de Framond
	Stuart P. Sharp
	Kevin Duclos
	Thejasvi Beleyur
	Henrik Brumm
Abstract:	Environmental noise can severely impair acoustic communication thereby affecting key behaviors, such as predator avoidance1,2, territory defense3,4, and reproduction5-7. Persistent noise in some habitats is thought to have favored the emergence of multimodal communication systems 8-10. Multimodal signals, which integrate information across several sensory channels, can enhance signal detection, and improve message clarity in challenging environments11. The capacity to flexibly adjust signaling strategies in response to noise is considered critical to the resilience and evolutionary success of communication systems12,13. However, direct evidence for noise-induced shifts between sensory modalities—termed multimodal shift—remains scarce11. Although river noise has been linked to the evolution of multimodal displays14,15 and shifts16 in torrent frogs, examples from other taxa are lacking. Here, we investigate how the white-throated dipper (Cinclus cinclus), a riverine songbird, modulates both acoustic and visual signaling along noisy rivers. We find that the dippers adjust their songs to the ambient noise level. In addition, they use, conspicuous blinking with white-feathered eyelids to compensate for acoustic masking in high-noise environments. Blinking rate was linked to local river noise, aggressive behaviour, and conspecific presence. Calibrated field measurements revealed a negative correlation between song amplitude and blinking rate, consistent with a noise-driven multimodal shift. This indicates that song plasticity operates in tandem with visual signaling, showing that animals can dynamically reallocate investment across modalities in response to fluctuating environmental pressures. The fine-tuning of both signal performance and modality underscores the critical role of noise interference and signal flexibility in the evolution of complex communication systems.
Additional Information:	
Question	**Response**
Standardized datasets A list of datatypes considered standardized under Cell Press policy is available here. Does this manuscript report new standardized datasets?	No
Original code Does this manuscript report original computer code, algorithms, or computational models?	No

Bird song plasticity and multimodal shift along noisy rivers

Léna de Framond (1), Stuart P. Sharp (2), Kevin Duclos (1), Thejasvi Beleyur (1, 3, 4), Henrik Brumm (1) *

(1) Animal Communication & Urban Ecology Group, Max Planck Institute for Biological Intelligence, 82319 Seewiesen, Germany

(2) Lancaster Environment Centre, Lancaster University, Lancaster, LA1 4YQ, UK

(3) Active Sensing Collectives Group, Centre for the Advanced Study of Collective Behaviour, University of Konstanz, 78464 Konstanz, Germany

(4) Max Planck Institute of Animal Behavior, 78315 Radolfzell, Germany

* Correspondence: henrik.brumm@bi.mpg.de

Lead contact: Henrik Brumm (henrik.brumm@bi.mpg.de)

Keywords

Ambient noise, animal communication, blinking, *Cinclus*, Lombard effect, songbird, song amplitude

Summary

Environmental noise can severely impair acoustic communication thereby affecting key behaviors, such as predator avoidance[1,2], territory defense[3,4], and reproduction[5-7]. Persistent noise in some habitats is thought to have favored the emergence of multimodal communication systems[8-10]. Multimodal signals, which integrate information across several sensory channels, can enhance signal detection, and improve message clarity in challenging environments[11]. The capacity to flexibly adjust signaling strategies in response to noise is considered critical to the resilience and evolutionary success of communication systems[12,13]. However, direct evidence for noise-induced shifts between sensory modalities—termed *multimodal shift*—remains scarce[11]. Although river noise has been linked to the evolution of multimodal displays[14,15] and shifts[16] in torrent frogs, examples from other taxa are lacking. Here, we investigate how the white-throated dipper (*Cinclus cinclus*), a riverine songbird, modulates both acoustic and visual signaling along noisy rivers. We find that the dippers adjust their songs to the ambient noise level. In addition, they use, conspicuous blinking with white-feathered eyelids to compensate for acoustic masking in high-noise environments. Blinking rate was linked to local river noise, aggressive behaviour, and conspecific presence. Calibrated field measurements revealed a negative correlation between song amplitude and blinking rate, consistent with a noise-driven multimodal shift. This indicates that song plasticity operates in tandem with visual signaling, showing that animals can dynamically reallocate investment across modalities in response to fluctuating environmental pressures. The fine-tuning of both signal performance and modality underscores the critical role of noise interference and signal flexibility in the evolution of complex communication systems.

Results and discussion

We studied white-throated dippers (*Cinclus cinclus*) because they are fast-flowing river specialists[17] living in naturally noisy environments. Their song is surprisingly low in amplitude compared to other birds and relative to their noisy habitat[18,19]. Like other dipper species[20], white-throated dippers have distinctive snow-white eyelids that contrast sharply with their brown plumage when they blink, making this behaviour an ideal candidate for a visual component in a multimodal signal. In a color-banded population of dippers[21], systematic observation and acoustic measurements allowed us to relate their blinking rate to the river noise level and the presence of conspecifics. Using calibrated microphones, we measured the birds' song source amplitudes to carefully investigate noise-induced song plasticity in naturally noisy conditions, and to determine the presence and context of multimodal shifts.

Dipper blinks as a signal

On average, dippers blinked 54.9 ± 9.7 times per minute (mean ± SD, N = 403 observations of 22 birds), which is similar to the blinking rate reported for American dippers (*Cinclus mexicanus*)[20] and more than three times higher than that of the similar-sized European blackbird (Figure S1). Dippers' snow-white feathered eyelids, which contrast sharply with the dark-brown plumage on their heads (Figure 1A), make their blinks highly conspicuous, even to the naked eye of human observers[22]. Dippers are territorial birds; when presented with simulated intruders in a playback experiment, the birds that defended their territory most aggressively (approaching the loudspeaker faster and closer, flying more, singing more during playback, and resuming singing after playback) also had a higher blinking rate (Figure 1B, Table S1). Overall, blink rate varied by about 30% between the least and most aggressive birds. Taken together, these findings suggest that dippers may use each other's blinking to determine the aggressiveness of an opponent during territorial disputes. Since bird song serves as an aggressive signal in territorial defense, there is at least partial redundancy in the information provided by blink rate and song, which is a prerequisite for a signal to be used as part of a multimodal system[11]. Although birds' eyes and eyelids have a small surface area, some species use blinks and eyelid color for communication, e.g., to establish hierarchies[23] or to indicate attentional state[24]. Similarly, iris displays are used during sexual displays in bowerbirds[25]. Exposing contrasting plumage colors is also common in avian sexual displays[26-28], along with various strategies to increase the contrast between the signal color and the background[26,29].

Blink rate as a function of river noise and social context

We analyzed whether dippers use their blinking to increase communication efficiency in noisy environments; hence, we tested statistically if the birds increased blink rate when the river was louder, and in the presence of conspecifics. We found a strong interaction between river noise and the presence of a conspecific, such that birds increased their blink rate by an average of 2.3 blinks per minute when the river noise increased by 6 dB(A) in the presence of a conspecific within 25 m (Figure 1C, Table S2). In other words, the predicted change in blink rate across the entire range of river noise levels (50-85 dB(A)) is 16 blinks per minute, approximately 30% of the average rate. However, solitary birds did not adjust their blink rate to the river noise (Figure 1C, Table S2). One important requirement for the dipper blinks to be used as a signal to rescue acoustic communication is that its salience over the background noise is sufficient. Torrents not only produce acoustic noise, but also visual noise (e.g., splashes, foam, moving water) in which a visual signal could be masked. Supporting the role of blinking in multimodal communication, we observed that the birds only adjusted their blink rate to river noise when the targeted receiver was in close proximity (Figure 1C). Songbirds can perceive polarized light[30], and reflections from water surfaces are polarized[31], which may increase the saliency of the white feathers against the polarized river. In addition, the temporal regularity of blinks contrasts with the random nature of water movements, which could further increase signal salience. Adaptations to visual noise that increase signal detectability have been demonstrated in lizards, which use abrupt movements to contrast with slow, wind-induced vegetation movements, and they increase their movements as visual noise increases[32].

Blink rate and song amplitude integration into a multimodal signal

In multimodal signals, the same information can be encoded in different communication channels. Redundant information in one channel can enhance the perception of the information in the other channel (multimodal enhancement)[11]. In this case, we expect the signal intensity in both channels to increase in parallel. In a multimodal shift, however, we expect the signal intensity in one channel to be inversely proportional to that in the other channel[11]. To investigate the presence of multimodal enhancement or multimodal shifts in dippers, we recorded the birds' song with a calibrated microphone while measuring blink rate and ambient noise.

The dippers increased song amplitude at noisier song posts (Figure 2B, Table S3). This noise-dependent regulation of vocal amplitude is known as the *Lombard effect*[33], seen widely across birds and mammals[34]. In the dippers, the Lombard effect was independent of the presence of conspecifics (GLMM, effect of doubling river noise acoustic energy (6 dB(A)) on song amplitude [95% credible interval] = 1.2 [0.6, 1.7] dB, Table S3, Figure 2B). The strength of the response was in the range of the observed magnitude of the Lombard effect in other bird species[19]. In line with the multimodal-shift hypothesis, the birds traded-off blinking for song amplitude. When a conspecific was present, dippers switched from loud songs with low blink rate to fainter songs with high blink rate (Figure 1C, d, Table 1), suggesting that the proportion of visual and acoustic signaling is plastically adjusted to the external conditions. To our knowledge, there is only one other documented instance of a noise-induced multimodal shift in birds: white crowned sparrows (*Zonotrichia leucophrys*) may increase the frequency of wing fluttering during agonistic interactions in urban, but not rural areas[35] Our findings provide one of the clearest demonstrations to date of context-dependent reallocation between sensory channels in a wild vertebrate. This behavioral flexibility highlights how animals can fine-tune multimodal signals in real time to overcome environmental constraints, expanding our understanding of communication plasticity in natural systems.

Song plasticity in noise and its role in multimodal signaling

Our calibrated field recordings also revealed how dippers adjust the spectral and temporal structure of their songs in response to fluctuating natural noise levels. Such plasticity is common in birds exposed to anthropogenic noise[36], but our study shows that even species adapted to chronically noisy environments—such as fast-flowing rivers—modulate their acoustic signals to mitigate increased masking. Dippers are likely open-ended learners and have a complex song with a repertoire of several hundred syllables[37] (Figure 2A). We classified syllables according to four complexity criteria (Figure 2C): syllables with rapid frequency modulations, with trills (i.e. more than three rapid frequency modulations in opposite directions), with several temporally separated elements separated by short pauses, and with several temporally overlapping elements indicating simultaneous use of both sides of the syrinx (two-voiced syllables). Each syllable was visually scored according to these criteria and assigned to one or more categories. At noisier locations, dippers increased the proportion of syllables with rapid frequency modulations and trills (that typically have a narrow frequency range of 0.9 ± 0.3

kHz) while decreasing the proportion of long, temporally complex syllables (Figure 2D, Table 2). These variations in song syllable use along a noise gradient were mostly due to behavioral plasticity, as opposed to individual differences, that is, individual birds chose different syllables in noise (Table 2, Table S4).

In terms of signal perception, long, constant-frequency sounds are easier to perceive in noise because of the temporal summation of signal energy in the vertebrate inner ear[38]. Our results show that the dippers adjusted their songs by (1) decreasing the bandwidth and (2) decreasing the use of complex elements and short syllables in noisy conditions, which in turn may have increased perception in noise. Increased signal duration, and in some cases also increased frequencies, are a common phenomenon observed in parallel with the Lombard effect[34]. In addition, syllable selection for increased signal perception in noise has been suggested in blackbirds and is thought to be adaptive in noise-polluted urban areas[39]. Yet, even with such plasticity, acoustic communication remains constrained in high-noise conditions[1,40]. Crucially, we observed that—in the presence of conspecifics—dippers did not rely solely on vocal compensation. Instead, they simultaneously reduced song amplitude and increased blink rate, consistent with a noise-driven multimodal shift. This finding complements the observed Lombard effect by indicating that in social contexts, dippers may trade off acoustic intensity for enhanced visual signaling. Rather than simply amplifying or modifying song structure, the birds flexibly shifted investment across sensory channels. This dual flexibility—in both acoustic characteristics and channel prioritization—supports the view that multimodal communication systems may evolve not just through redundancy, but through dynamic reallocation in response to environmental constraints. Together, these findings offer a comprehensive picture of how song plasticity functions not in isolation, but as part of a broader multimodal communication strategy shaped by real-time ecological pressures. A test of the dippers' response to the blinks would be necessary to establish that they are indeed being used as signals. Our playback experiment tested blink rate in the context of territorial defense, which is only one of the various functions of bird song. However, our findings and the presence of contrasting feathered eyelids in all five dipper species suggest an important evolutionary function of the contrasting white flash of dipper blinks, especially as fully-feathered eyelids are rare in songbirds[20].

Another conspicuous visual behavior of dippers is their frequent curtsy movements, or dipping.[17] However, in a pilot study using an unmarked population in Germany, we found that dippers did not dip while singing. Instead, they markedly increased dipping before flying off or diving. Thus, we speculate that this behavior is not a visual signal but is rather related to the birds' three-dimensional visual perception. Therefore, we decided not to record dipping in this study.

Our study provides compelling evidence that white-throated dippers adjust their communication strategies in response to ambient river noise by reallocating investment between acoustic and visual signals. The observed trade-off between song amplitude and blink rate represents a rare example of a noise-induced multimodal shift in a wild animal. This flexible integration of signals across modalities demonstrates how animals can dynamically optimize information transfer in challenging environments. Beyond documenting an underappreciated signaling behavior — the conspicuous blinking of feathered eyelids — our findings underscore the role of behavioral plasticity in maintaining communication efficacy under environmental constraints. Given the prevalence of anthropogenic and natural noise in animal habitats, such plastic multimodal strategies may be more widespread than currently recognized, offering important insights into the adaptive evolution of complex signaling systems.

Resource availability

Lead contact

Requests for further information and resources should be directed to, and will be fulfilled by, the lead contact, Henrik Brumm (henrik.brumm@bi.mpg.de).

Materials availability

This study did not generate new unique reagents.

Data and code availability

- All data connected to this paper are available with the following doi: 10.5281/zenodo.15395603
- All code connected to this paper are available with the following doi: 10.5281/zenodo.15395603
- Any additional information required to reanalyze the data reported in this paper is available from the lead contact upon request.

Acknowledgments

We are grateful to the local land owners and the Yorkshire Dales National Park for granting us access to the riverbanks. We would also like to thank A. Rogers and P. Mawby for their help and support in the field, E. de Framond for his assistance with the pilot experiments, and S. A. Zollinger for providing equipment. Also, we acknowledge the contributions of W. M. X. Zimmer and K. Beedholm, who helped with the microphone calibration and acoustic analyses, J. de Framond, who revised the Python codes, and E. Udino, who provided assistance with the statistical analyses. Thanks also go to W. Goymann, A. Kirschel, and the anonymous reviewers for their comments on the manuscript and to M. Baldwin for her generous support. This study was funded by the Max Planck Society.

Author contributions

Conceptualization: LdF, HB; Methodology: LdF, HB, SPS, TB; Investigation: KD, LdF, SPS; Data curation: LdF, KD; Formal analysis: LdF; Software: LdF; Supervision: HB, SPS, TB; Validation: LdF, TB; Visualization: LdF; Funding acquisition: HB; Writing – original draft: LdF, HB; Writing – review & editing: all authors

Declaration of Interest

The authors declare no competing intersts.

Figure legends

Figure 1. White-throated dippers shift from loud songs to increased blinking frequency when river noise increases and conspecifics are present.

(A) A white-throated dipper with its eyes open (top) and closed, exposing the white eyelid (bottom). Photographs by K. Duclos. (B) Number of blinks in relation to the aggression score before (green) and after (blue) simulated territorial intrusion and in relation to (C) river noise, both with and without a conspecific within 25 m. (D) Blink rate as a function of maximum song amplitude, with and without a conspecific within 25 m. River noise is colour-coded. (B–D) Raw data are shown together with the model posterior mean (line) and 95% credible interval (ribbon). See also Figure S1 and Tables S1 and S2.

Figure 2. Dippers adjust song amplitude and syllable type in response to river noise.

(A) An example of a five-second spectrogram of dipper song (Hanning window, 512 samples, overlap 99%, dB range: -50 to -25 dB). (B) Dipper song source level in relation to river noise (model estimate and 95% credible interval in purple, raw data points in black). (C) Spectrograms of exemplary syllables illustrating the complexity criteria (each spectrogram is 250 ms long). (D) Proportion of syllables in each complexity category as a function of river noise amplitude. Model posterior mean and 95% credible intervals are shown in purple, individual slopes as short grey lines in the background, and raw data as black dots. See also Tables S3 and S4.

Tables

Table 1. In the presence of conspecifics, dippers trade-off song amplitude against blink rate. Estimate (posterior mean) and 95% credible interval of the Gaussian GLMM examining the effects of river noise, song amplitude, and the presence of a conspecific on dipper blinking rate on the subset of data for which we recorded both blink rate and song simultaneously (N=113, 11 dippers)

Predictor	**Estimate [95% credible interval]**
(intercept)	**56.63 [49.55, 63.27]**
River noise level (per 6 dB (A))	1.21 [-0.55, 2.94]
Conspecific present	-1.05 [-5.48, 3.45]
Song source level (per 6 dB)	0.31 [-1.73, 2.42]
Song source level:conspecific present	**-6.45 [-11.65, -1.14]**
Variance of random effect (bird ID)	*58.7*
Variance of residuals	*57.3*

Table 2. Dippers use different syllable types depending on the background noise level. Estimate (posterior mean) and 95% credible interval of the logistic GLMM examining the effects of river noise, blink rate, and the presence of a conspecific on the proportion of each syllable type (based on N=5409 syllables from 13 dippers for whicheboth song amplitude and blink rate were available). Estimates are on the logit scale.

Proportion of syllables with…	**… two voices**	**… trills**	**… fast frequency modulations**	**… several elements**
Predictor	Estimate [95% cri]	Estimate [95% cri]	Estimate [95% cri]	Estimate [95% cri]
(intercept)	**-1.88 [-2.41, - 1.49]**	**-0.57 [-0.82, - 0.27]**	**-0.91 [-1.45, - 0.42]**	**-0.84 [-1.12, - 0.55]**

River noise level (per 6 db(a))	-0.05 [-0.13, 0.03]	**0.12 [0.06, 0.19]**	**-0.10 [-0.17, -0.03]**	**-0.23 [-0.30, -0.16]**
Individual mean (quantifying inter-individual differences)	*0.06 [-0.25, 0.41]*	***0.21 [0.01, 0.39]***	*0.05 [-0.33, 0.42]*	*-0.15 [-0.37, 0.05]*
Deviation from individual mean (quantifying behavioural plasticity)	*-0.06 [-0.15, 0.03]*	***0.11 [0.05, 0.18]***	***-0.11 [-0.18, -0.03]***	***-0.24 [-0.31, -0.17]***
Conspecific present	-0.04 [-0.16, 0.26]	-0.09 [-0.25, 0.06]	0.12 [-0.05, 0.28]	-0.02 [-0.18, 0.15]
Sex (male)	0.19 [-0.29, 0.82]	-0.10 [-0.44, 0.21]	0.25 [-0.35, 0.93]	0.13 [-0.19, 0.46]
Peak frequency	**-0.13 [-0.20, -0.05]**	**0.12 [0.06, 0.19]**	0.02 [-0.04, 0.08]	0.02 [-0.04, 0.07]
Signal to noise ratio (6 dB)	-	-	-0.01 [-0.02, 0]	-
Variance of random effect (bird ID)	*0.04*	*0.02*	*0.11*	*0.02*
Variance of residuals	*0.13*	*0.22*	*0.21*	*0.21*

STAR methods

EXPERIMENTAL MODEL AND STUDY PARTICIPANT DETAILS

We studied a free-ranging color-banded population of white-throated dippers[21] in Yorkshire Dales National Park, Cumbria, northwest England (54.32°N, -2.53°E) in February and March 2024. The birds were ringed under a British Trust for Ornithology license held by SPS.

METHOD DETAILS

Observations took place from sunrise onwards. When a bird was singing, one observer (LdF) counted through a telescope or binoculars the number of blinks for 30 seconds. We noted the actual duration of the sampling period (in case the bird flew away before 30 seconds) to calculate minute-wise blinking rate. We waited at least thirty seconds between counts to minimize the risk of temporal autocorrelation. Simultaneously, a second observer (KD) recorded the birds' song with a directional microphone (Sennheiser MKH 416 with windshield Nanoshield, Rycote, UK, hand-held recorder Portacapture X6, Tascam) for at most 1 minute at a time. We noted the position of the bird, whether another dipper was within 25m of the focal bird (estimation of distance), and the focal bird's ring colors. We also noted the gain setting of the recorder and measured the distance between the bird and the microphone with a laser-range finder (6x24 Range finder and speedmeter, Bresser, UK), the ambient temperature and relative humidity (portable weather station Kestrel 4000 Pocket weather Tracker, Kestrel Instruments, USA), and we matched recordings to blink counts.

We observed birds for a maximum of four hours at a time, at the end of which we measured the river noise level at each song post (or the closest accessible point) using an SPL meter (peak LAF, fast mode, Casella Cel 240, TSI Incorporated, Minessota, USA) oriented horizontally towards the river over 15 seconds. To ensure that the measures from a distance to a song post were still representative of the true river amplitude at the song post, we measured the river noise amplitude from three different points in an easily accessible song post. River noise level varied by less than 3 dB at these three locations, which is negligible compared to the range the river noise level covered overall (30 dB; the loudest point had more than 30 times more sound energy than the faintest point).

Playback experiment

We downloaded five dipper song recordings from the Xeno-Canto Database, band-pass filtered them (2-10 kHz), and extracted 30 seconds of good-quality audio. The source recordings were made at locations outside of Britain. We calibrated the playbacks to play the playbacks at a peak amplitude of 85 dB(A) RMS SPL at 1m. We placed a remote-controlled loudspeaker (Turtlebox Gen 1.5) on the riverbank less than 100m from a dipper nest. When a bird came close to the speaker (i.e. at the nest or within 50 m) and sang, we counted the number of blinks for one minute, then triggered the playback. We noted the number of flights, whether the bird sang during the playback presentation, then counted the number of blinks again for one minute as soon as the bird settled. We also measured the distance between the bird and the speaker a the start of the playback and the minimum distance during the playback presentation.

QUANTIFICATION AND STATISTICAL ANALYSIS

Aggression score

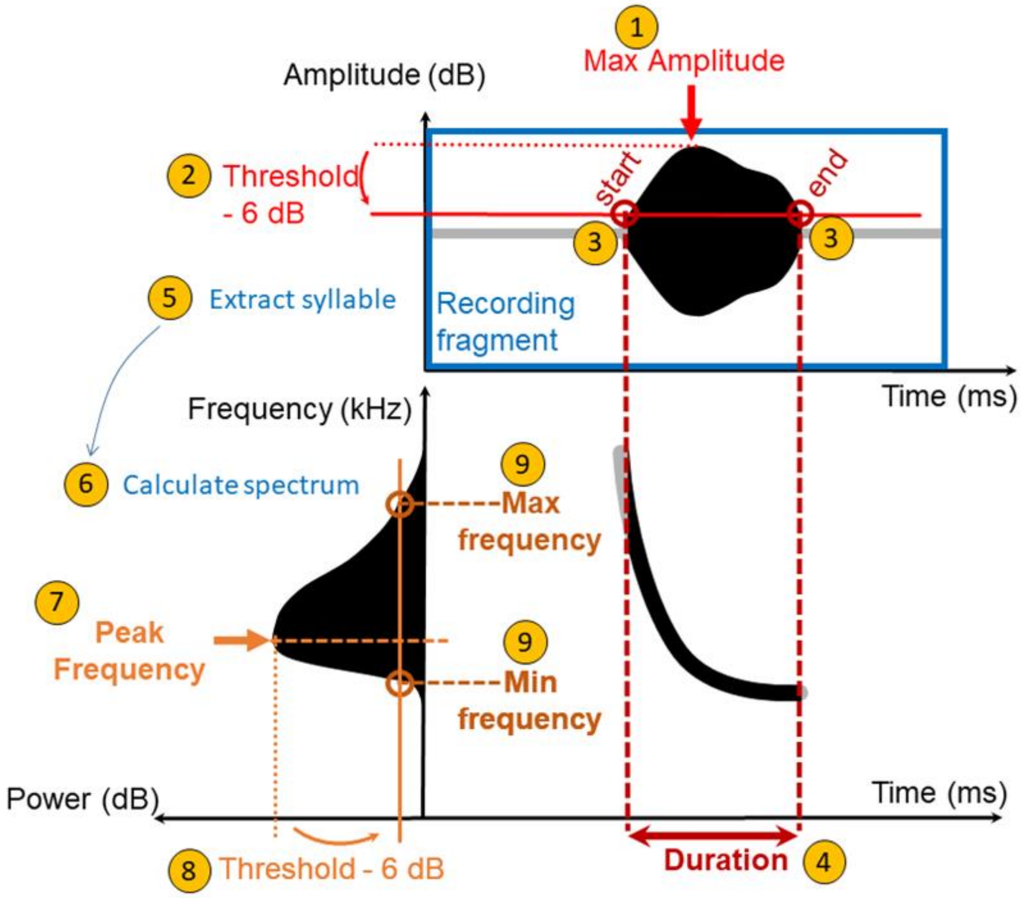
We built a composite measure of the aggressive response of the birds to conspecific songs by employing a PCA on five single behavioral aggression measures (song during and after broadcast, number of flights during broadcast, number of flights after broadcast, and minimum distance to the speaker; Figure S2). We used the first component (59% of variance explained) as a measure for the bird’s aggression (negative values indicate more aggressive birds).

Acoustic analyses

All acoustic analyses were performed in Python v. 11.3. The recording chain was calibrated in the lab to obtain the frequency response and sensitivity (see supplements for the details). Before analysis, we corrected all recordings for the frequency response of the microphone. We detected bird song syllables in the four-time down-sampled recordings using cross-correlation with a 10-ms downwards sweep (7-3 kHz). We extracted a segment of the original recording when the smoothed cross-correlation envelope (10-ms running average) surpassed its own mean + SD, with a 30-ms buffer before and after. On a spectrogram (512 window size, overlap 90%, Hanning window). We detected the highest frequency peak per window. Since river noise is typically of lower frequency than bird song, this procedure resulted in a bimodal distribution. We performed a kernel clustering analysis (2 clusters, one “noise”, lower frequencies, and one “bird”, the highest frequencies) and used the 10th percentile – 1 kHz and 90th percentiles + 2 kHz to build a band-pass filter (5th-order Butterworth second-order section filter[49]). We then calculated the smoothed Hilbert envelope (10 ms running average) and defined the start and end of the syllable when the envelope crossed the 6-dB threshold below the maximum amplitude. Because the 6-dB threshold was often buried in the noise, we needed an alternative way of determining the call start and end. A call with a duration longer than 90% of the call window was likely badly defined. Because we already assigned each spectrogram window's highest peak to a "bird" or a "river" cluster, we used the first and last peak assigned to the "bird" category as the start and end of the syllable. If this method still gave too long call durations, we used the results of the cross-correlation threshold crossing directly. We additionally extracted an audio segment of the same duration immediately before the call segment as a reference for the noise level.

We measured the peak, highest, and lowest frequency (6 dB below peak[52]) on the average spectrum. We used the highest and lowest frequencies to calculate the call's bandwidth. If the peak frequency was lower than the filter frequency, we reduced the cut-off frequency of the high-pass filter by 500 Hz. We computed the signal energy of both the bird and the noise segment, then calculated the difference between the bird and the noise energy, which we divided by the duration of the segment and square-rooted the resulting value to obtain the RMS full-scale received level. This result was then converted into received sound pressure levels using the microphone's sensitivity and recording gain, and the bird's source level was reconstructed by correcting for distance-dependent spherical spreading using the inverse square law.

We measured the signal-to-noise ratio as the difference between the noise (filtered with the same high-pass filter) and the call's RMS amplitude. We discarded syllables of SNR < 1 dB as an accurate estimation of the source level would not be possible[49], too short (below 5 ms), and too long (above 1 second) syllables. We detected over 19000 syllables, which we manually checked in a custom-written user interface. We corrected occurrences where the algorithm had detected only one unit of a several-unit syllable or the 6-dB threshold did not accurately represent the whole syllable (more than half of the duration missing). We excluded syllables detected but not clearly visible on the spectrogram, as the species could not be determined with certainty. We checked that the start and end of each syllable matched with the spectrogram and corrected occurrences where the algorithm had detected only one unit of a several-unit syllable or the 6-dB threshold did not accurately capture the entire syllable (more than half of the duration missing). Finally, the frequency and amplitude parameters were recalculated for each call.



Workflow of the automatic acoustic measurements on the recordings. We determined the maximum amplitude in the waveform (1) and used a threshold 6 dB below the peak (2) to determine the start and end (3) of each syllable. Start and end where then used to measure the syllable duration (4) and extract the syllable (5) from the recordingfile. In a next step, we computed an average (Welsh) power spectrum for the syllable (6, left panel) to determine the peak frequency as the frequency of maximum power (7). Finaly, we used a threshold 6 dB below the maximum power (8) to determine the maximum and minimum frequency of the syllable (9) and calculate bandwidth.

Microphone calibration procedure

Microphones were calibrated using the free-field substitution method[53]. In the substitution method the same sound is recorded using two microphones, one with a known frequency-response and a target microphone whose frequency-response needs to be measured. A calibration-grade condenser microphone (46 BF (1/4”), G.R.A.S. Sound & Vibration, Holte, Denmark) with a flat frequency response (0.1-10 kHz <0.5 dB variation) was placed at a distance of 5 m from a speaker (VIFA speaker, Avisoft Bioacoustics, Glienicke, Germany) at height 1.4 m playing back a linear sweep (10-1 kHz, 7 ms). Having removed the calibration microphone, the target microphone (Sennheiser MKH 416 with windshield) was then placed at the same distance and height. The same speaker playback was also recorded. Microphone positions were verified to be the same relative to the speaker using cross-hair lasers for alignment and a range-finders (BOSCH GLM 50C, Leinfelden-Echterdingen, Germany) for height from ground and distance to the speaker. The microphone and speaker pair were placed in a line at the centre of the room (3.3 × 8.4 m and 2.9 high) – as far as possible from the walls and other reflective surfaces.

The playback had linear sweeps of three durations (3, 5, 7 ms), and finally only the 7 ms sweep was used as it resulted in the most consistent frequency-responses. Despite optimizing speaker-microphone placement, the sweep recordings had non-negligible reflections due to the duration of the sweeps and shape of the room. The direct path of the sweep was obtained by first deconvolving with the known linear sweep template, removing the reflection peaks, and then convolving the original sweep. The sensitivity of the GRAS 46BF was measured using a calibrator playing a 1 kHz tone at 94 dB SPL (B&K Type 4231, Virum, Denmark). All recordings were made using an handheld recorder (Tascam Portacapture X6) running at 96 kHz sampling rate and the appropriate gain values for each recording were noted to compensate for final sensitivity calculations.

Using the known sensitivity of the GRAS 46BF, the spectral received levels in dB SPL rms were calculated for each frequency band of the linear sweep. For the target microphone, the spectral received levels of the linear sweep in arbitrary units RMS was calculated. The final sensitivity of the target microphone was calculated by dividing the known sound-pressure-level with the received level in arbitrary units.

Song amplitude quality check

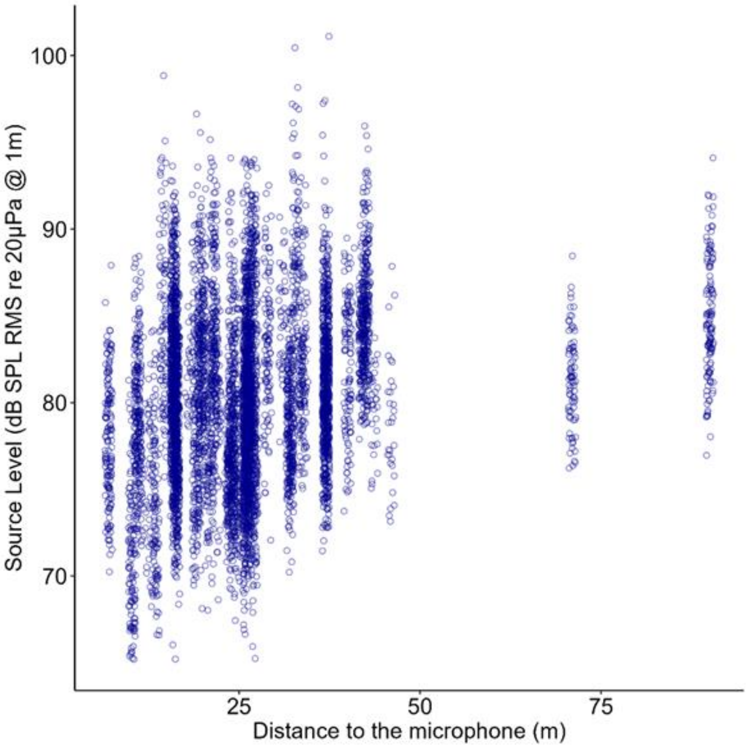
In addition to the spherical spreading of sound, the fading of sounds over distance is also partly due to the absorption of sound energy by the air (atmospheric attenuation), and the attenuation coefficients are frequency- and weather-dependent[50]. Since the microphone was placed on the riverbank, the river noise recorded originated from closer to the microphone than the bird’s song; therefore, correcting for atmospheric attenuation directly in the recordings would result in overcompensating the noise level. To avoid this, we calculated the atmospheric attenuation at the syllable’s peak frequency using ambient temperature and humidity at the time of recording to calculate the atmospheric attenuation bias, that is, by how much we underestimated the source level by not correcting for atmospheric attenuation at the peak frequency[48],

In a quality-check step, we looked at how our measures of song amplitude varied according to the syllable detection method (-6 dB threshold below maximum amplitude on the envelope, frequency peak detection, cross-correlation window, or manual definition), the distance to the microphone, and the atmospheric attenuation bias. We built a Gaussian GLMM (identity link function) with the bird ID and recording number as random effects. The effect size of the atmospheric attenuation bias on the song source level was close to -1 dB, indicating that we slightly underestimated the source level by the amount of atmospheric attenuation we did not correct for. Hence, we corrected the source level by the amount of the atmospheric attenuation bias and used this measure in further analyses.

Quality check of the song source level measures.
Estimate (posterior mean) and 95% credible interval of the Gaussian GLMM examining the effects of measurement methods on the song source level (N=7482, 14 dippers). Results which credible interval does not overlap zero are shown in bold. The reference level is the syllable definition using the -6-dB threshold below peak amplitude with average distance to the microphone and atmospheric attenuation bias.

	Predictor	**Estimate [95% credible interval]**
	(Intercept)	**80.37 [79.10, 81.60]**
Potential bias due to the recording method	Distance to the microphone (10m)	**1.20 [0.73, 1.68]**
Potential bias due to non compensations	Atmospheric attenuation bias (dB)	**-0.92 [-1.09, -0.73]**
Potential bias due to the measurment method	Syllable definition (manual)	**-1.12 [-1.28, -0.96]**
	Syllable definition (frequency tracking)	**-3.87 [-4.24, -3.48]**
	Syllable definition (cross correlation)	**-2.98 [-3.35, -2.58]**
Random effects	*Variance of random effect (recording)*	*9.98*
	Variance of random effect (Bird ID)	*1.65*
	Variance of residuals	*10.39*

The bias due to distance was especially strong here since we used the entire dataset for this analysis. In practice, the signal-to-noise ratio of the recording decreased drastically when a bird was farther away because the received level of the song decreases proportionally to the square of the distance while the ambient noise remains unchanged. However, as shown below, the highest source level did not change with the distance from the microphone. This shows that the bias due to distance was correctly corrected in the acoustic analysis.



Song source level as a function of the distance to the microphone. Note that the average source level increases when the birds are further away, which is due to the filtering of fainter syllables that are drowned out by the noise when the bird is further away from the microphone. However, the maximum source level as a function of the distance remains constant.

Syllable complexity score

We scored the syllable complexity according to four criteria: presence of several, non-temporally overlapping units; trills (at least three reversal frequency modulations not separated by silences); several units overlapping in time suggesting the use of the two sides of the syrinx independently; and ratio between the syllable bandwidth and duration (i.e. index of frequency modulation) lower than 0.25. Each syllable was scored for each of the four categories (trait present/absent).

Blinking rate and song amplitude

Since we recorded only one measure of blink rate per recording, and each recording contained 1-164 song syllables, we selected in each recording the 95th percentile of the RMS syllable amplitude of trilled single-element syllables, which were reliably present in all recordings. The 95th percentile is a reliable estimate of the maximum amplitude[51, 52, 54].

Statistical analysis

All statistical analyses were performed in R v 4.2.2 in a Bayesian framework with the packages *rstanarm* v. 2.32.1 and *bayesplot* v. 1.10.0. Models were run with default, non-informative priors. We ensured the models had mixed correctly by inspecting chain plots, and we checked model fit by performing posterior-predictive checks as advised by Gabry (2022)[55].

Statistical model parameters

Model	Response variable	Fixed effects	Random effects	Sample size	Family	Link function	Number of iterations	Warm-up	Thin rate	Results
Quality check	RMS song level	Call detection method Distance to the bird Atmospheric attenuation bias	Bird ID Recording ID	7520 syllables, 14 birds	Gaussian	identity	5000	1000	10	STAR methods: Quality check of the song source level measures
Song amplitude according to other parameters	RMS song level corrected for atmospheric attenuation	Trill criterion Element criterion Two-voice criterion Fast FM criterion Syllable duration Bandwidth Peak frequency Sex River noise	Bird ID Recording ID	7482 syllables, 14 birds	Gaussian	identity	5000	1000	10	Table S3
Trill composition	Trill criterion	River noise Blink rate Presence of conspecific Sex Peak frequency	Bird ID	7482 syllables, 14 birds	Binomial	logistic	4000	1000	4	Table 2
Composition in syllables with several elements	Element criterion	River noise Blink rate Presence of conspecific Sex Peak frequency	Bird ID	7482 syllables, 14 birds	Binomial	logistic	4000	1000	4	Table 2

Two-voice syllable composition	Two-voice criterion	River noise Blink rate Presence of conspecific Sex Peak Frequency	Bird ID	7482 syllables, 14 birds	Binomial	logistic	4000	1000	4	Table 2
Fast FM syllable composition	Fast FM criterion	River noise Blink rate Presence of conspecific Sex Peak frequency	Bird ID Recording ID	7482 syllables, 14 birds	Binomial	logistic	4000	1000	4	Table 2
Blinking response to playback	Blinking rate	Playback phase Aggressivity score	Bird ID	30 observations, 15 birds	Gaussian	identity	5000	1000	5	Table S1
Blinking rate according to river noise	Blinking rate	River noise Conspecific presence River noise : conspecific presence Sex Observer ID	Bird ID	403 observations, 22 birds	Gaussian	identity	5000	1000	5	Table S2
Blinking rate according to song amplitude	Blinking rate	River noise Song level Conspecific presence Song level : conspecific presence	Bird ID	114 observations, 11 birds	Gaussian	identity	5000	1000	5	Table 1

Plasticity in song complexity

To assess whether birds modified their song structure in response to river noise, we quantified the proportion of syllables that met one or several complexity criteria across noise levels (Table S4). For this, we built one binomial model for each criterion with a score of whether or not a syllable satisfed this criterion as a resonse variable, and river noise, peak frequency, blink rate, bird sex, and the presence of a conspecific as fixed predictors, and bird ID as a random factor.

Noise-related differences in song structure could arise from two sources: (1) behavioural plasticity within individuals, or (2) consistent differences between individiuals. To distinguish between these possibilities, we performed two types of inter-individual comparisons. First, we decomposed the noise predictor into two components: inter-individual variation (i.e., subject-specific mean noise level) and intra-individual variation (i.e., deviations from the subject mean). We then refitted the binomial GLMMs used to examine the proportion of syllables in each criterion substituting raw noise level with the two noise components[56].

A statistically meaningful effect of the subject meanwould suggest that the differences in song structure were primarily due to inter-individual variation, reflecting population-level differences. Conversely, a statistically meaningful effect of the deviation from the subject mean would indicate that the observed changes were driven primarily by within-individual plasticity. When evidence pointed towards plasticity, we conducted a second analysis—a random regression—to test whether individuals differed in how they adjusted their song structures in response to noise.

Because random regressions with binomial response variables can be insensitive, we first validated our approach using a simulated data set with the same structure as the real data and known individual variation in response slopes (randomly sampled between 0 and 3 on the log-odds scale)[57]. We refitted the initial model, which included river noise level, conspecific presence, and focal bird sex as fixed effects, under three scenarios:

1. no random effects
2. Bird ID as a random intercept only (replicating the original model)
3. Bird ID as a random intercept and noise as a random slope

We compared the predictive performance of these models using the Leave-One-Out Cross-Validation (LOO)[58], which yields an estimate of the Expected Log-Predictive Density (ELPD) and its standard deviation (SD). The model with the highest ELPD was considered the best. We deemed differences in model performance statistically meaningful when the ELPD of a lower-ranked model plus twice its SD was still lower than the ELPD of the top model[58]. In the simulated data, the model including random slopes outperformed the other two, confirming that our approach was sufficiently sensitive to detect inter-individual differences in noise-related song adjustment. Results of the simulation are shown below. We applied this full procedure across all four syllable complexity criteria.

Leave-One-Out Comparison on the simulated data, to test if the model would be able to detect differences in behavioural plasticiy based on our dataset using random structures.

The simulated slopes for the 13 birds were 0.13, 0.33, 0.75, 10.3, 1.12, 1.21, 1.74, 1.95, 2.03, 2.06, 2.15, 2.57, and 2.73. The model with random slope has more predictive power than the other two models, indicating that comparing the models with and without random slopes will enable the detection of significant differences in behavioural plasticity in our dataset. ELPD: expected log-predictive density.

Model	**ELPD difference**	**Standard error of ELPD difference**	**Model has worse predictive power**
Random slope and intercept	0	0	(best model)
Random intercept only	-95.357	13.345	Yes
No random effect	-228.092	19.899	Yes

References

1. Templeton, C.N., Zollinger, S.A., and Brumm, H. (2016). Traffic noise drowns out great tit alarm calls. Curr. Biol. 26, R1173–R1174. doi:10.1016/j.cub.2016.09.058.
2. Zhou, Y., Radford, A.N., and Magrath, R.D. (2019). Why does noise reduce response to alarm calls? Experimental assessment of masking, distraction and greater vigilance in wild birds. Funct. Ecol. 33, 1280–1289. doi:10.1111/1365-2435.13333.
3. Kleist, N.J., Guralnick, R.P., Cruz, A., and Francis, C.D. (2016). Anthropogenic noise weakens territorial response to intruder’s songs. Ecosphere 7, e01259. doi:10.1002/ecs2.1259.
4. Sebastianutto, L., Picciulin, M., Costantini, M., and Ferrero, E.A. (2011). How boat noise affects an ecologically crucial behaviour: the case of territoriality in *Gobius cruentatus* (Gobiidae). Environ Biol Fish 92, 207–215. doi:10.1007/s10641-011-9834-y.
5. Senzaki, M., Barber, J.R., Phillips, J.N., Carter, N.H., Cooper, C.B., Ditmer, M.A., Fristrup, K.M., McClure, C.J.W., Mennitt, D.J., Tyrrell, L.P., et al. (2020). Sensory pollutants alter bird phenology and fitness across a continent. Nature 587, 605–609. doi:10.1038/s41586-020-2903-7.
6. de Jong, K., Forland, T.N., Amorim, M.C.P., Rieucau, G., Slabbekoorn, H., and Sivle, L.D. (2020). Predicting the effects of anthropogenic noise on fish reproduction. Rev. Fish. Biol. Fisheries 30, 245–268. doi:10.1007/s11160-020-09598-9.
7. Aulsebrook, L.C., Bertram, M.G., Martin, J.M., Aulsebrook, A.E., Brodin, T., Evans, J.P., Hall, M.D., O’Bryan, M.K., Pask, A.J., Tyler, C.R., et al. (2020). Reproduction in a polluted world: implications for wildlife. Reproduction 160, R13–R23. doi:10.1530/REP-20-0154.
8. Brumm, H., and Slabbekoorn, H. (2005). Acoustic Communication in Noise. Advances in the Study of Behavior 35, 151–209. doi:10.1016/S0065-3454(05)35004-2.
9. Hebets, E.A., and Papaj, D.R. (2005). Complex signal function: developing a framework of testable hypotheses. Behav Ecol Sociobiol 57, 197–214. doi:10.1007/s00265-004-0865-7.
10. Partan, S.R., and Marler, P. (2005). Issues in the classification of multimodal communication signals. Am. Nat. 166, 231–245. doi:10.1086/431246.
11. Partan, S.R. (2017). Multimodal shifts in noise: switching channels to communicate through rapid environmental change. Anim. Behav. 124, 325–337. doi:10.1016/j.anbehav.2016.08.003.
12. Wiley, R.H. (2015). Noise matters. The Evolution of Communication (Harvard University Press).
13. Wong, B.B.M., and Candolin, U. (2025). Behavioural Responses to a Changing World (Oxford University Press).

14. Chen, P., Liu, S., Wu, Y., Liu, G., Jin, Y., and Zhang, F. (2024). Female frogs communicate with males through blinking. Curr. Biol. 34, R191–R192. doi:10.1016/j.cub.2024.01.023.

15. Grafe, T.U., Preininger, D., Sztatecsny, M., Kasah, R., Dehling, J.M., Proksch, S., and Hödl, W. (2012). Multimodal communication in a noisy environment: A case study of the Bornean rock frog *Staurois parvus*. PLOS ONE 7, e37965. doi:10.1371/journal.pone.0037965.

16. Grafe, T.U., and Tony, J.A. (2017). Temporal variation in acoustic and visual signalling as a function of stream background noise in the Bornean foot-flagging frog, *Staurois parvus*. Journal of Ecoacoustics, 1:#X74QE0. doi:10.22261/JEA.X74QE0.

17. Tyler, S., and Ormerod, S. (1994). The Dippers (T & AD Poyser Ltd).

18. Villain, A. (2016). Acoustic communication in female songbirds : functions, flexibility and plasticity in calls. https://theses.hal.science/tel-02017944.

19. Brumm, H., de Framond, E., Kikodze, E., and de Framond, L. (in press). A comparative analysis of song amplitude across and within bird species. Proc. R. Soc. B

20. Goodge, W.R. (1960) Adaptations for amphibious vision in the dipper (*Cinclus mexicanus*). J. Morphol. 107:79-91. doi:10.1002/jmor.1051070106.

21. Crowther, W., Magoolagan, L., Mawby, P.J., Whitehead, F.A., Wright, P.M., and Sharp, S.P. (2018). Winter territoriality and its implications for the breeding ecology of White-throated Dippers *Cinclus cinclus*. Bird Study 65, 471–477. doi:10.1080/00063657.2018.1541963.

22. Townsend, C.W. (1925). The winking of the water Ouzel. The Condor 27, 143–144. doi:10.2307/1362991.

23. Verbeek, N.A.M. (1972). Comparison of displays of the Yellow-billed Magpie (Pica nuttalli) and other corvids. J Ornithol 113, 297–314. doi:10.1007/BF01647510.

24. Guillemain, M., Fouque, C., and Figuerola, J. (2012). Consistent contrast between eyelid and iris brightness supports a role for vigilance signalling in ducks. Ibis 154, 461–467. doi:10.1111/j.1474-919X.2012.01240.x.

25. Corbett, E.C., Brumfield, R.T., and Faircloth, B.C. (2024). The mechanistic, genetic and evolutionary causes of bird eye colour variation. Ibis 166, 560–589. doi:10.1111/ibi.13276.

26. Martin, R.P., Carr, E.M., and Sparks, J.S. (2025). Does biofluorescence enhance visual signals in birds-of-paradise? R. Soc. Open Sci. 12, 241905. doi:10.1098/rsos.241905.

27. Hogan, B.G., and Stoddard, M.C. (2018). Synchronization of speed, sound and iridescent color in a hummingbird aerial courtship dive. Nat Commun 9, 5260. doi:10.1038/s41467-018-07562-7.

28. Fialko, K., and Price, T.D. (2025). Use of visual display in dark, cluttered environments. Ornithology, ukaf004. doi:10.1093/ornithology/ukaf004.

29. McCoy, D.E., Feo, T., Harvey, T.A., and Prum, R.O. (2018). Structural absorption by barbule microstructures of super black bird of paradise feathers. Nat Commun 9, 1. doi:10.1038/s41467-017-02088-w.

30. Åkesson, S. (2024). Polarization Vision in Birds. In Polarization Vision and Environmental Polarized Light, G. Horváth, ed. (Springer Nature Switzerland), pp. 299–306. doi:10.1007/978-3-031-62863-4_18.

31. Horváth, G. (2014). Polarization patterns of freshwater bodies with biological implications. In Polarized light and polarization vision in animal sciences, G. Horváth, ed. (Springer), pp. 333–344. doi:10.1007/978-3-642-54718-8_16.

32. Peters, R.A. (2013). Noise in Visual Communication: Motion from Wind-Blown Plants. In Animal Communication and Noise, H. Brumm, ed. (Springer). pp. 311-3307. Doi:10.1007/978-3-642-41494-7_11

33. Zollinger, S.A., and Brumm, H. (2011). The Lombard effect. Curr. Biol. 21, R614–R615. doi:10.1016/j.cub.2011.06.003.

34. Brumm, H., and Zollinger, S.A. (2011). The evolution of the Lombard effect: 100 years of psychoacoustic research. Behaviour 148, 1173–1198. doi:10.1163/000579511X605759.

35. Akçay, Ç., Beck, M. L., & Sewall, K. B. (2020). Are signals of aggressive intent less honest in urban habitats?. Behavioral Ecology, 31(1), 213-221. doi:10.1093/beheco/arz179 .

36. Brumm , H., and Zollinger, S. A. (2013) Avian vocal production in noise. In Animal Communication and Noise. H. Brumm, ed. (Springer). pp. 187-227. doi:10.1007/978-3-642-41494-7_7

37. Magoolagan, L., Mawby, P.J., Whitehead, F.A., and Sharp, S.P. (2019). The structure and context of male and female song in White-throated Dippers. J Ornithol 160, 195–205. doi:10.1007/s10336-018-1599-z.

38. Heil, P., and Neubauer, H. (2003). A unifying basis of auditory thresholds based on temporal summation. PNAS 100, 6151–6156. doi:10.1073/pnas.1030017100.

39. Nemeth, E., Pieretti, N., Zollinger, S.A., Geberzahn, N., Partecke, J., Miranda, A.C., and Brumm, H. (2013). Bird song and anthropogenic noise: vocal constraints may explain why birds sing higher-frequency songs in cities. Proc. R. Soc., B 280, 20122798. doi:10.1098/rspb.2012.2798.

40. Nemeth, E. and Brumm, H. (2010). Birds and anthropogenic noise: are urban songs adaptive? Am Nat 176: 465-475. DOI: 10.1086/656275

41. Virtanen, P., Gommers, R., Oliphant, T.E., Haberland, M., Reddy, T., Cournapeau, D., Burovski, E., Peterson, P., Weckesser, W., Bright, J., et al. (2020). SciPy 1.0: fundamental algorithms for scientific computing in Python. Nat Methods 17, 261–272. doi:10.1038/s41592-019-0686-2.

42. Ulloa, J.S., Haupert, S., Latorre, J.F., Aubin, T., and Sueur, J. (2021). scikit-maad: An open-source and modular toolbox for quantitative soundscape analysis in Python. Methods Ecol. Evol. 12, 2334–2340. doi:10.1111/2041-210X.13711.

43. Harris, C.R., Millman, K.J., van der Walt, S.J., Gommers, R., Virtanen, P., Cournapeau, D., Wieser, E., Taylor, J., Berg, S., Smith, N.J., et al. (2020). Array programming with NumPy. Nature 585, 357–362. doi:10.1038/s41586-020-2649-2.

44. Hunter, J.D. (2007). Matplotlib: A 2D graphics environment. Comput. Sci. Eng. 9, 90–95. doi:10.1109/MCSE.2007.55.

45. Pedregosa, F., Varoquaux, G., Gramfort, A., Michel, V., Thirion, B., Grisel, O., Blondel, M., Prettenhofer, P., Weiss, R., Dubourg, V., et al. (2011). Scikit-learn: Machine learning in Python. J. Mach. Learn. Res. 12, 2825–2830.

46. Goodrich, B., Gabry, J., Ali, I., and Brilleman, S. (2020). rstanarm: Bayesian applied regression modeling via Stan. Version 2.21.1.

47. Gabry, J., and Mahr, T. (2019). Plotting for Bayesian Models. Version 1.10.0.

48. The SciPy community (2025). Signal processing in SciPy - Filter design. https://docs.scipy.org/doc/scipy/tutorial/signal.html#filter-transformations.

49. Araya-Salas, M., Smith-Vidaurre, G., and Webster, M. (2019). Assessing the effect of sound file compression and background noise on measures of acoustic signal structure. Bioacoustics 28, 57–73. doi:10.1080/09524622.2017.1396498.

50. Goerlitz, H.R. (2018). Weather conditions determine attenuation and speed of sound: Environmental limitations for monitoring and analyzing bat echolocation. Ecol. Evol. 8, 5090–5100. doi:10.1002/ece3.4088.

51. Surlykke, A., and Kalko, E.K. (2008). Echolocating bats cry out loud to detect their prey. PLoS one 3, e2036.

52. de Framond, L., Beleyur, T., Lewanzik, D., and Goerlitz, H.R. (2023). Calibrated microphone array recordings reveal that a gleaning bat emits low-intensity echolocation calls even in open-space habitat. Journal of Experimental Biology 226, jeb245801. doi:10.1242/jeb.245801.

53. Zuckerwar, A.J., Herring, G.C., and Elbing, B.R. (2006). Calibration of the pressure sensitivity of microphones by a free-field method at frequencies up to 80kHz. J. Acoust. Soc. Am. 119, 320–329. doi:10.1121/1.2141360.

54. Holderied, M.W., and von Helversen, O. (2003). Echolocation range and wingbeat period match in aerial-hawking bats. Proc.Roy. Soc. B 270, 2293–2299. doi:10.1098/rspb.2003.2487.

55. Gabry, J. (2022). Graphical posterior predictive checks using the bayesplot package. https://mc-stan.org/bayesplot/articles/graphical-ppcs.html.

56. Van De Pol, M., and Wright, J. (2009). A simple method for distinguishing within- versus between-subject effects using mixed models. Anim. Behav. 77, 753–758. doi:10.1016/j.anbehav.2008.11.006.

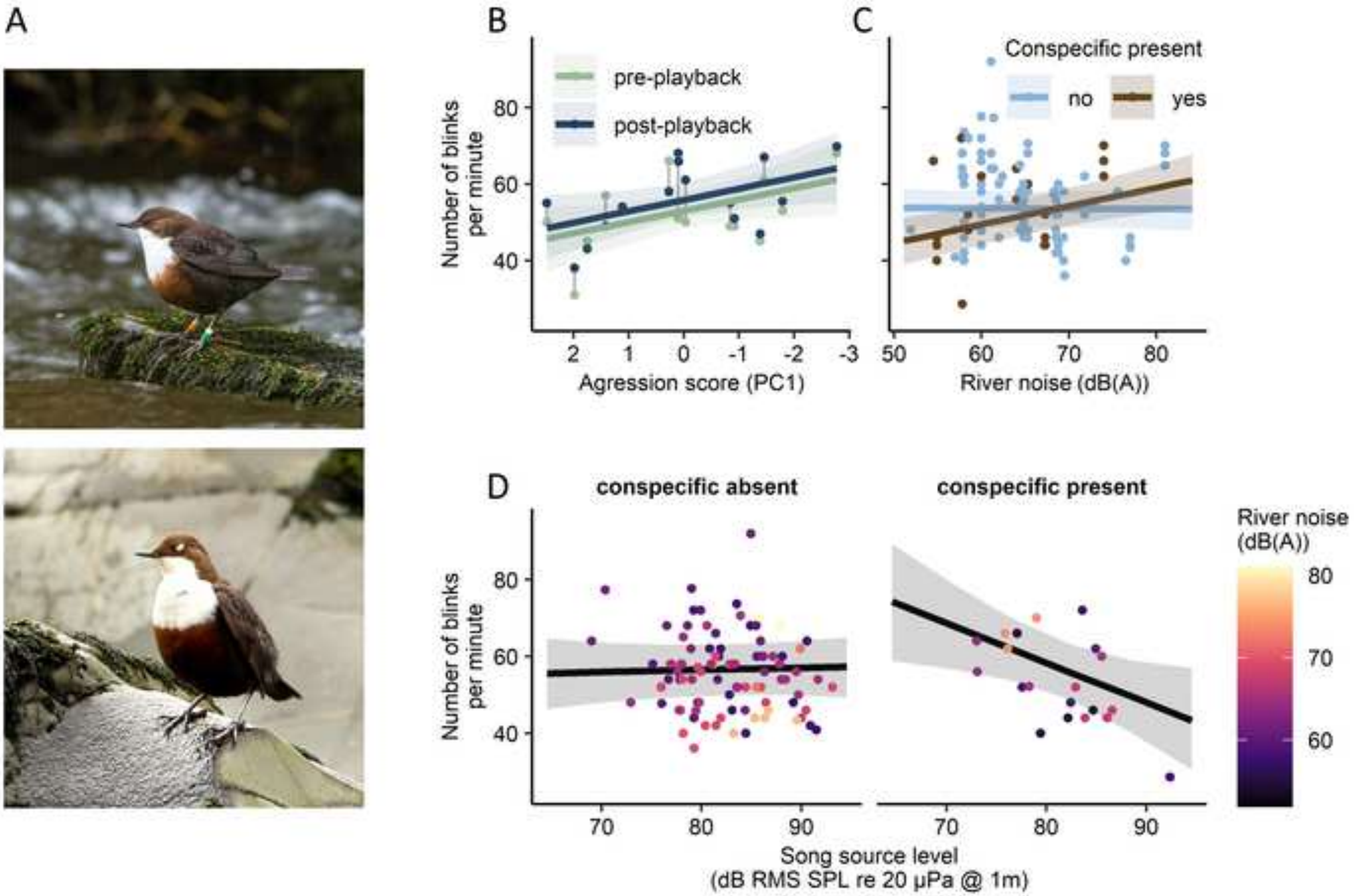
57. Udino, E., and Mariette, M.M. (2022). How to Stay Cool: Early Acoustic and Thermal Experience Alters Individual Behavioural Thermoregulation in the Heat. Front. Ecol. Evol. 10. doi:10.3389/fevo.2022.818278.

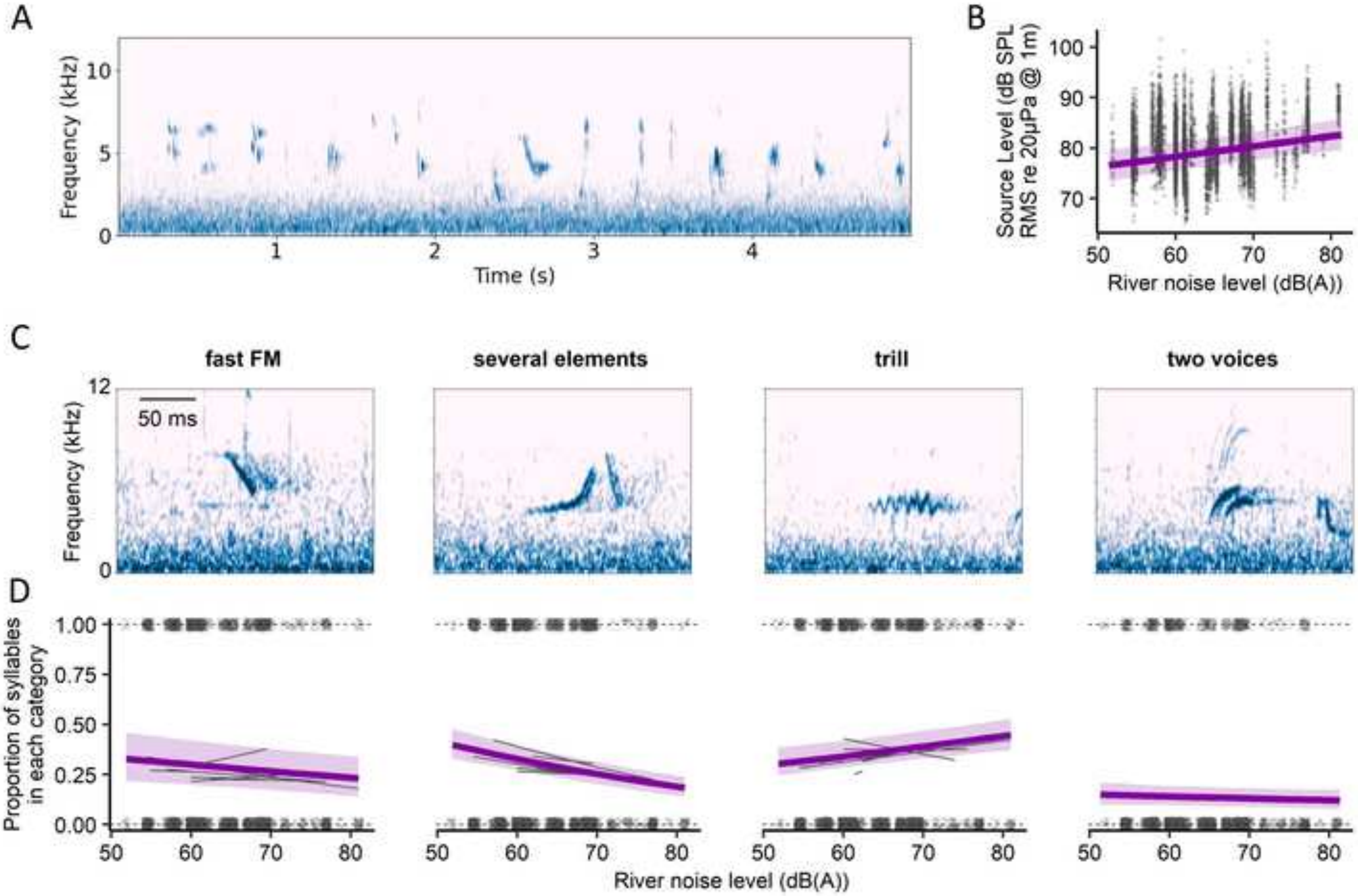
58. Vehtari, A., Gelman, A., and Gabry, J. (2017). Practical Bayesian model evaluation using leave-one-out cross-validation and WAIC. Stat Comput 27, 1413–1432. doi:10.1007/s11222-016-9696-4.

KEY RESOURCES TABLE

RESOURCE	SOURCE	IDENTIFIER
Software and Algorithms		
Python version 3.11	Python Software Foundation	http://www.python.org
Package *scipy* version 1.13.0	Virtanen et al.[41]	https://scipy.org/
Package *Scikit-maad* version 1.4.2	Ulloa et al.[42]	https://scikit-maad.github.io/
Package *Numpy* version 1.26.4	Harris et al.[43]	https://numpy.org/
Package *Matplotlib* version 3.8.4	Hunter[44]	https://matplotlib.org/
Package *Soundfile* version 0.12.1	B. Bechtold	https://python-soundfile.readthedocs.io/
Package *Scikit-learn* version 1.5.0	Pedregosa et al.[45]	https://scikit-learn.org/
R version 4.2.2	The R Foundation for Statistical Computing	R: The R Project for Statistical Computing, https://www.r-project.org
Package *rstanarm* version 2.32.1	Goodrich et al.[46]	https://mc-stan.org/rstanarm
Package *bayesplot* version 1.10.0	Gabry & Mahr[47]	https://mc-stan.org/bayesplot/

Figure 1


A
B
C
D
pre-playback
post-playback
Number of blinks per minute
80
60
40
2
1
0
-1
-2
-3
Agression score (PC1)
Conspecific present
no
yes
50
60
70
80
River noise (dB(A))
conspecific absent
conspecific present
River noise (dB(A))
80
70
60
Number of blinks per minute
80
60
40
70
80
90
70
80
90
Song source level
(dB RMS SPL re 20 μPa @ 1m)


A
Frequency (kHz)
10
5
0
1
2
3
4
Time (s)
B
Source Level (dB SPL RMS re 20µPa @ 1m)
100
90
80
70
50
60
70
80
River noise level (dB(A))
C
fast FM
several elements
trill
two voices
12
50 ms
Frequency (kHz)
0
D
Proportion of syllables in each category
1.00
0.75
0.50
0.25
0.00
50
60
70
80
River noise level (dB(A))

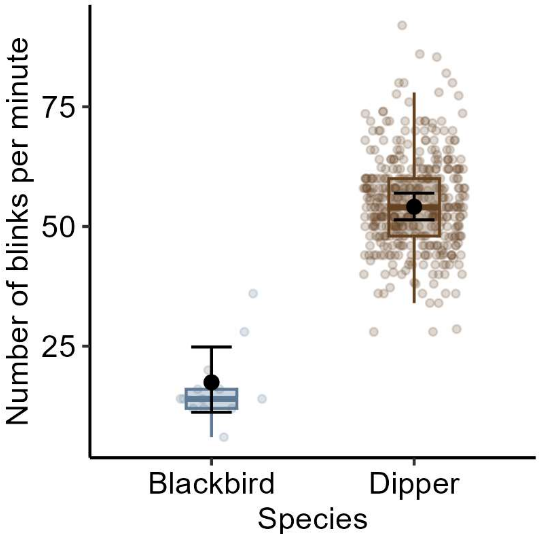


Figure S1. Blink frequency differences between blackbirds and dippers.
The blackbird data are based on 13 observations of six birds. On average, the blackbirds blinked 16.4 ± 7.8 times per minute. Dippers blinked markedly more frequently, with 36.6 [29.1, 43.5] more blinks per minute than the blackbirds (Gaussian GLMM with bird ID as a random effect and species as a fixed effect). Related to Figure 1.

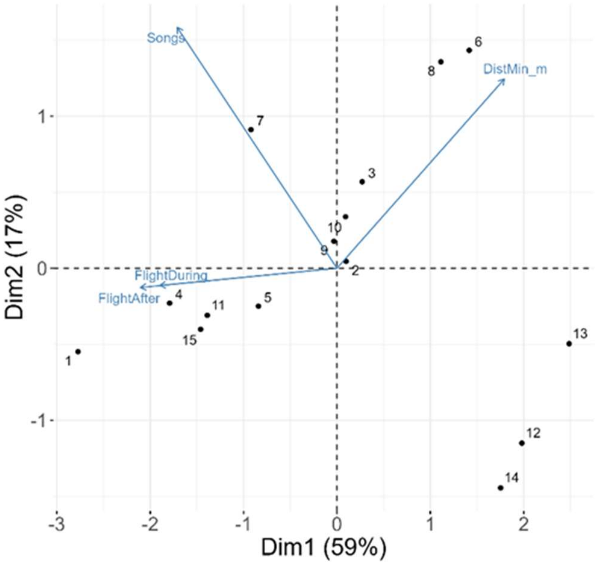


Figure S2. Principal Component Analysis (PCA) biplot of the aggression score of dippers in response to playback presentation.
The plot shows the relationships between 15 observations and 5 behavioral variables. Obser-vations are represented as points (labeled 1–15), while variables are shown as blue arrows indicat-ing their contribution and direction in the reduced two-dimensional PCA space (Dim1 and Dim2). The length and orientation of the arrows represent the strength and direction of each variable’s influence. Related to STAR Methods.

Predictor	**Estimate [95% credible interval]**
(Intercept)	**52.99 [48.33, 57.61]**
Playback phase (after)	2.85 [-0.95, 6.70]
Aggression score (PC1, negative => more aggressive)	**-2.98 [-5.82, -0.13]**
Variance of random effect (Bird ID)	*34.3*
Variance of residuals	*13.5*

Table S1. Dippers blink more when they respond more aggressively.
Estimate (posterior mean) and 95% credible interval of the Gaussian GLMM examining the effects of playbacks on dipper blink rate (N=15 dippers). Results which credible interval does not overlap zero are shown in bold. Reference level is r the blinking rate before the playback started in birds with an average aggression score. Related to Figure 1.

Predictor	**Estimate [95% credible interval]**
(Intercept)	**53.55 [48.72, 58.19]**
River noise level (per 6 dB(A))	-0.06 [-0.96, 0.80]
Conspecific present	-1.22 [-3.40, 0.98]
River noise level:conspecific present	**2.95 [1.17, 4.84]**
Sex (Male)	1.40 [-4.71, 7.71]
Observer 2	-3.29 [-7.63, 0.60]
Observer 3	2.07 [-6.05, 11.26]
Variance of random effect (Bird ID)	*26.5*
Variance of residuals	*57.3*

Table S2. Dippers blink more when a conspecific is within 25m.
Estimate (posterior mean) and 95% credible interval of the Gaussian GLMM examining the effects of river noise and the presence of a conspecific on the dipper blink rate on the full dataset (N=403, 22 dippers). Results which credible interval does not overlap zero are shown in bold. The reference level is female birds with no conspecific within 25 m and at average river noise level. Related to Figure 1.

Predictor		**Estimate [95% credible interval]**
	(Intercept)*	**78.45 [75.63, 81.40]**
Environmental parameters	**River noise level (doubling energy, +6 dB(A))**	**1.14 [0.59, 1.66]**
	Conspecific present	0.36 [-1.04, 1.72]
	Sex (male)	0.62 [-2.99, 3.98]
Acoustic syllable parameters	**Duration (10 ms)**	**-0.04 [-0.07, -0.01]**
	Peak frequency (1 kHz)	**-0.13 [-0.22, -0.04]**
	Bandwidth (1 kHz)	**-1.21 [-1.36, -1.06]**
Syllables category	**2 voices**	**0.39 [0.17, 0.60]**
	Trill	**0.76 [0.59, 0.92]**
	Several elements	0.15 [-0.02, 0.35]
	Fast FM	**0.73 [0.51, 0.93]**
Measurement method	**Syllable definition (manual)**	**-0.81 [-0.99, -0.64]**
	Syllable definition (frequency tracking)	**-3.62 [--3.98, -3.27]**
	Syllable definition (cross correlation)	**-2.72 [-3.11, -2.33]**
	Variance of random effect (recording)	*9.93*
	Variance of random effect (Bird ID)	*3.85*
	Variance of residuals	*9.94*

Table S3. Dipper song syllable source level according to the context, acoustic parameters and measurement parameters.

Estimate (posterior mean) and 95% credible interval of the Gaussian GLMM examining the effects of context and syllable characteristics on the syllable source level (N=7482, 14 dippers). Results for which the credible interval does not overlap zero are shown in bold. Related to Figure 2.

* The reference level is female birds with no conspecific within 25m, with average river noise level and syllable parameters, and a syllable belonging to none of the complexity categories. The reference syllable definition is the -6dB threshold below peak amplitude.

Proportion of syllables with	**Model**	**ELPD difference**	**Standard error of ELPD difference**	**Model has worse predictive power**
several elements	Random slope and intercept	0	0	(best model)
	Random intercept only	-0.914	1.711	No
	No random effect	-11.796	5.156	Yes
trills	Random slope and intercept	0	0	(best model)
	Random intercept only	-4.755	2.731	No
	No random effect	-15.378	5.621	Yes
fast FM	Random slope and intercept	0	0	(best model)
	Random intercept only	-0.979	2.302	No
	No random effect	-18.161	6.272	Yes

Table S4. Leave-One-Out Comparison of the models with different random structures to test for individual differences in noise-induced adjustments of song composition. Results for which the credible interval does not overlap zero are shown in bold. ELPD: expected log-predictive density. Related to Figure 2.