Vocally-mediated consensus decisions govern mass departures from jackdaw roosts

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eTOC blurb: *Vast groups of roosting birds often suddenly take to the skies together in the early morning. Using field recordings and a large-scale field experiment, Dibnah et al show that jackdaws use vocalisations to coordinate these mass departures. This provides empirical evidence for vocally-mediated consensus decision-making in large animal groups.*

In the early morning, large groups of up to hundreds or even thousands of roosting birds, sometimes comprising the entire roost population, often take off together in sudden mass departures. These departures commonly occur in low light conditions and structurally complex habitats where access to visual cues is likely to be restricted. Roosting birds are often highly vocal, leading us to hypothesise that vocalisations, which can propagate over large distances, could provide a means of enabling individuals to agree on when to depart – that is to establish a consensus[1] – and thus coordinate the timing of mass movements. Investigations of the role of acoustic signals in coordinating collective decisions have been limited to honeybees[2] and relatively small vertebrate groups (<50 individuals)[3-5] and have rarely included experimental validation[2,3]. Here, by combining field recordings with a large-scale experimental manipulation, we show that jackdaws (*Corvus monedula*) use vocalisations to coordinate mass departures from winter roosts. This provides empirical evidence for vocally-mediated consensus decision-making in large vertebrate groups.

Maintaining group cohesion can provide substantial benefits, including reduced predation risk, improved foraging efficiency and greater access to mates and social information[6]. To stay together and maintain these benefits, animals may have to reach consensus about when to move[1,7]. We investigated consensus decision-making in jackdaws, a highly social corvid species that forms winter roosts of up to many thousands of individuals from different age classes and breeding colonies (see Supplemental Methods for further details). Roosting jackdaws (see Figure 1A) tend to vocalise loudly over long periods leading up to mass departures around sunrise. To understand the potential role of vocalisations in coordinating mass departures, we collected acoustic and video data across the winter months from six jackdaw roosts in Cornwall, UK (roost size: 160-1470 individuals), and quantified vocalisation intensity leading up to and immediately prior to departure.

While on some mornings jackdaws departed in a stream of small groups of individuals over a period of up to 22 minutes, on most mornings (21 out of 33 mornings) a majority of roost members, or even the entire roost, departed together (Figure S1A). These mass departures occurred almost instantly (mean time for all birds in the group to take off = 4.32 seconds; range: 1.03-7.81s; Figure S1A), with birds remaining together in cohesive flocks following departure, suggestive of a consensus decision-making process (see Supplemental Methods: "Jackdaw Roosts" and Supplemental Videos).

We found that the timing of departures was linked to calling within the roost. As corvid winter roost departures correlate strongly with the time of sunrise (see Supplemental Methods: "Meteorological variables"), we calculated departure times relative to sunrise. Across mornings, there was substantial variation in the timing of the largest group departure (containing 15-1410 birds leaving together in the same direction), which ranged from 45 minutes before to 15 minutes after sunrise (mean = 21.5 min before sunrise). Roosting jackdaws began calling long before sunrise (mean time from first minute of continuous calling until sunrise: 101 min; range: 65-138 min). To quantify the intensity of calling over time, we calculated power spectral density (PSD), which captures the power (in dB) of each frequency component (Hz) of a signal across time. Thus, a greater intensity of calling reflects more simultaneous callers and/or louder calling. On 73.3% of mornings (out of 30 mornings with available acoustic data), calling intensity showed an overall increase over the hour before the largest group departure (Figures 1B, S1A). Rain and heavy cloud cover delayed departures (Table S1A,C). When accounting for meteorological variables, departures occurred earlier when there was a steeper rise in calling (Figure 1C; Table S1A,C). For every 10% increase in the steepness of the rise in calling intensity, departures occurred 1.32 minutes earlier (up to a maximum increase in calling intensity of 60%). We found qualitatively the same effect if we considered the time of the first (rather than the largest) departure or if we excluded mornings where the largest subgroup departed late in the morning (see Supplemental Results, Section 3(iii)). Given that the amplitude of calls heard will depend on an individual's position in the roost, temporal changes in calling intensity may provide a particularly reliable source of information to heighten and synchronise activity levels and so prime groups for departure (c.f.[4]).

Calling was also linked to the temporal coordination among departing roost members. Specifically, temporal coordination (measured as the proportion of roost members in the largest departing group) was best predicted by the final calling intensity in the minute before departure, with meteorological variables playing no significant role (Table S1B,D; Supplemental Results, Sections 3(ii), 3(iii)). This relationship was non-linear, with a sharp increase in the proportion of roost members leaving together with increasing final calling intensity (Figure 1D). This is reminiscent of theoretical[1] and empirical[3,5,8,9] work on quorum-based group decisions, whereby collective action is triggered when a minimum "quorum threshold" is reached. However, it is also possible that once jackdaws are sufficiently primed by the build-up of calling, reaction to some external stimulus or individual movements are sufficient to trigger the whole group to leave together. The final calling intensity was only weakly correlated with the rate of change in calling intensity (see Supplemental Methods, Section (ii)), suggesting that both factors may provide complementary information that is used in collective decisions of when to leave. Specifically, while a steeper rise in calling intensity increases the likelihood of birds departing earlier, cohesive mass departures are likely triggered if a sufficiently heightened level of calling is reached, providing indication of a consensus.

To test for a causal link between vocalisations and collective departures, we conducted playback experiments within one roost to investigate if we could artificially advance the moment of mass take-off. Specifically, to generate an earlier onset and peak of calling, we broadcast recordings of roosting calls from multiple speakers within the roost. This resulted in the first mass departure (which always contained ≥50% of the roost leaving together) occurring on average 6.57 minutes earlier than during control playbacks of wind noise, which in turn did not differ from natural departure times with no playbacks (Figure 1E; Table S1E). These results indicate that the earlier departures were caused by birds responding to the increase in conspecific calls and not simply to noise more generally, likely linked to the overall calling intensity building up earlier than normal because of the addition of the playback calls (Figure S1B,C). While correlations between acoustic signals and group movements have been reported in a range of species (reviewed in [4]), experimental evidence of acoustically-mediated consensus decisions has been limited to two kin-based societies: meerkats (*Suricata suricatta*)[3] and *Apis* honeybees[2] (whose waggle dances incorporate acoustic signals). Adding to this body of experimental evidence, we show that vocal mechanisms have the power to enable consensus decisions even where groups are large, dispersed and contain unrelated individuals.

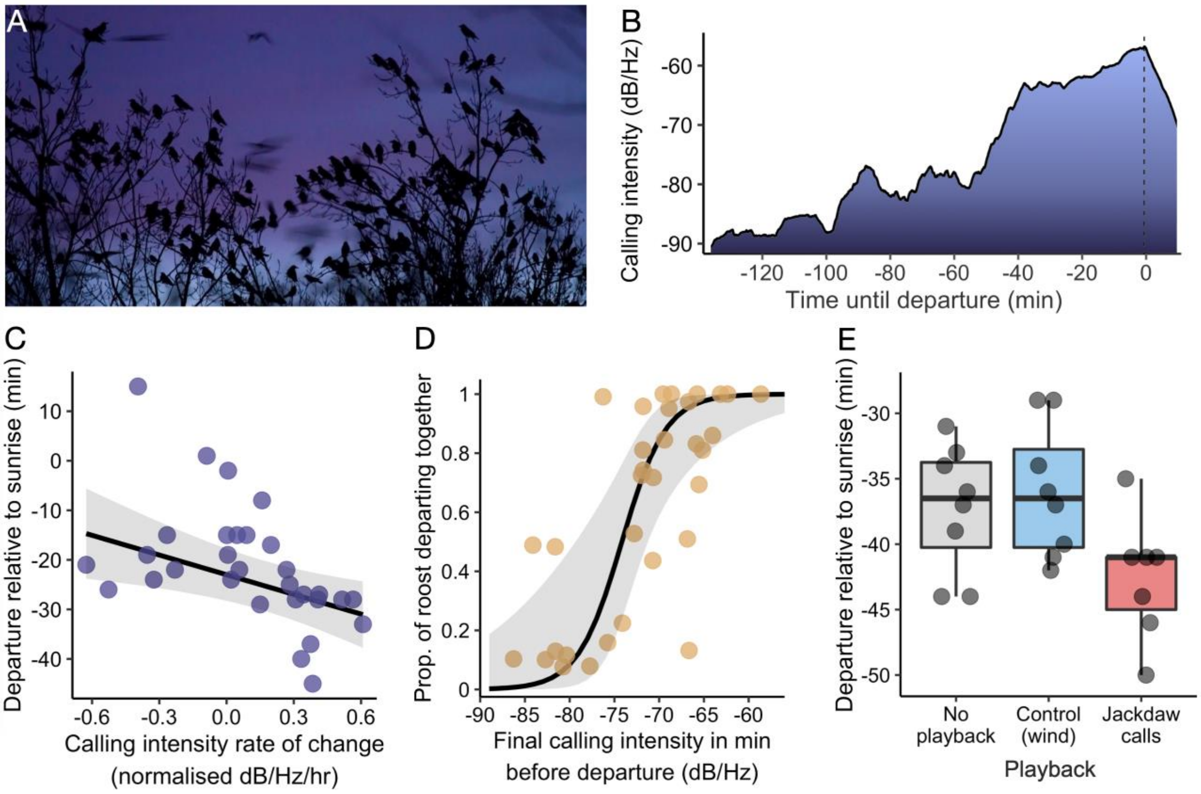

Figure 1. (A) A winter roost moments prior to a mass departure (photo by J.W. Jolles). **(B)** Example of a rise in calling intensity before departure in one of the observed roosts with a mass departure. **(C)** Departures occur earlier when the rate of change in calling intensity is higher (negative departure times indicate minutes before sunrise). **(D)** Non-linear relationship between calling intensity in the final minute before departure and the proportion of roost members departing together, showing a sharp increase when calling intensity is between -80 and -70 dB/Hz. **(E)** Playbacks of jackdaw roost calls trigger earlier mass departures than control playbacks (wind noise) or no playbacks.

Through their calls, jackdaws appear to effectively signal their willingness to leave, providing large groups with a means of achieving consensus to perform cohesive, collective departures from the roost. By establishing consensus to leave the roost early and in large flocks, birds may reduce predation risk, facilitate access to useful foraging information, and lengthen the time available for foraging during the short days and harsh conditions of the winter months[10]. Our observational data indicate that consensus is achieved through the effect of calling build-up (excitation) to the point where mass collective departures can be triggered (activation). Our playback experiments provide strong evidence for a causal link between calling and the timing of mass departures. Together, this work provides important insights into the mechanisms underpinning the mass movements of large animal groups under natural conditions.

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DECLARATION OF INTERESTS

The authors declare no competing interests.

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Supplemental information: *Vocally-mediated consensus decisions govern mass departures from jackdaw roosts*

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(1) SUPPLEMENTAL METHODS

(i) Study system and data collection procedures

Jackdaw roosts

Jackdaws (*Corvus monedula*) are a highly social, colony-breeding corvid species, widely distributed across Eurasia. During the winter months, flocks of jackdaws travel from foraging grounds spread over a wide area and fly in large flocks[S1,2] to congregate in roosts where they spend the night. These roosts can contain hundreds or even thousands of individuals of different age classes, with birds from many different breeding colonies as well as non-breeders[S3-7]. Thus, roost populations contain a wide mixture of both relatives and non-relatives.

In the morning, jackdaws commonly depart suddenly from the roost in large flocks. Departing flocks always remained cohesive, with flock members moving in the same direction, often performing synchronised aerial manoeuvres (see Supplementary Videos A-F). These large flocks then tend to split into smaller flocks that fly together towards foraging sites or breeding colonies[S6-8]. In Supplementary Video A, all birds can be seen leaving the roost within the space of 2.4 seconds, save for two individuals. Notably, the two individuals that remain behind are carrion crows (*Corvus corone*) and not jackdaws, like the rest of the group members. This suggests that group departures are linked to selective responses to conspecific vocalisations and are a distinct phenomenon from simply a sudden mass escape response to the presence of a predator.

Roosting sites

We searched for jackdaw roosts within a 15 km radius of Penryn in Cornwall, UK. We found a total of nine active roosts for the current study, based on (i) consistently containing at least 50 birds over at least three consecutive roosting nights and (ii) jackdaws settling at and departing from roughly the same location each day, which allowed consistent monitoring. Some roosts were located within large stretches of woodland, whereas others were confined to smaller, sometimes irregularly-shaped woodland patches carved out by roads or agricultural fields. Roosts were located at a minimum of 2.78 km from each other, except for two roosts located within the same woodland but 300 m apart and at differing elevations (one in a valley; the other on the slope of a hill). Pilot observations confirmed that these two roosts within the same woodland could be treated as independent as both departure timing and direction of travel differed consistently between them. We carried out observations and audio recordings during the winter period (Nov-Mar) across two subsequent winters (2018-2019 and 2019-2020). During this period, we visited roosts on average four times a week.

Roost observations

Observations of roosts were made by a single observer from 60 min before sunrise until after all roosting birds had departed. To record departures from the roost, observations were made with binoculars and filmed using a Canon EOS 550D camera with a zoom lens (300 mm; aperture ranged from f4.5 to f5.6 at ISO 800 or 1600). To minimize disturbance, observations were made from a standardised position at least 50 m away from each roost with a clear viewpoint of the departures. When ≥10 jackdaws flew away from the roost at the same time (i.e., within a 10-second window) in the same direction and were separated by ≥15 seconds from prior or subsequent departing groups, this was defined as a ‘group departure’. We collected 55 mornings of departure time data in total.

Counting the total number of roost members

To estimate the number of jackdaws in each roost and in each morning departure and thus, the proportion of roost members in the largest departure (referred to as “temporal coordination of departures”), we reviewed video records of birds arriving at the roost in the evening or leaving in the morning frame-by-frame. We counted birds using Adobe Photoshop by covering each bird visible in the frame with a coloured marker of the same size and shape and then tallying the total number of markers. Consecutive 1-second frames were used to track the trajectory of birds in flight and ensure that none were counted twice when new birds became visible. For three out of nine roosts, it was only possible to establish total roost population counts from one morning departure or one afternoon roost arrival due to poor lighting and video quality. In these cases, and where video footage and personal observation could qualitatively verify consistent numbers of birds across multiple mornings at the same roost and departures occurred in the same direction at similar times, the same population counts were shared across multiple days. An independent coder blind to our hypotheses and predictions recounted 16% of video-recorded departures, covering five roosts of varying population sizes (ca. 160-1470 individuals). Inter-rater reliability was high, with an intra-correlation coefficient (ICC) of 0.999 ($p < 0.001$) and a 95% confidence interval of 0.995 and 1.

Meteorological variables

Previous research shows that the timing of corvid roost departures is known to be strongly linked to the time of sunrise[S9,10] and this is borne out in our own data (Pearson's correlation test: $r = 0.96$, lower/upper 95% CI = 0.94/0.98, $t = 25.82$, $p < 0.001$; $n = 55$). We therefore calculated departure time relative to sunrise, with negative values indicating minutes before sunrise. Sunrise times at the nearest village/town to the roost (max. distance: 4.20 km) were obtained from the UK Met Office (www.metoffice.gov.uk). As departures may also be influenced by other meteorological conditions[S9,10], we acquired hourly local cloud coverage, barometric air pressure, humidity, temperature, and wind speed from 'World Weather Online' (www.worldweatheronline.com) and noted whether it rained within 30 minutes of departure.

Acoustic recordings

We were able to collect acoustic data at six roosts out of the nine active roosts identified in the area. Out of these six, we sampled each roost for a minimum of two weeks, except in three roosts, where activity diminished substantially after 5-12 days as birds began to abandon the roost (around February and March as winter was ending) or unexpectedly changed roosting locations mid-way through winter. For mornings where data were available for departure time and temporal coordination, we obtained a total of 30 mornings of acoustic data that covered the hour before departure and 33 mornings of acoustic data for the final minute prior to departure. We programmed SM3 Wildlife Acoustic recorders (Wildlife Acoustics, Inc, Maynard, MA, USA) to record for four hours each morning, starting three hours before sunrise. Mornings when equipment failed, or strong wind/rain masked jackdaw calls, were excluded from analyses. We used six recorders in the winter of 2018/2019 and four recorders in 2019/2020 (due to equipment failures), deploying and retrieving them during the daytime to avoid disturbing roosting birds. Within a given roost, we strapped recorders to trees at a height of 2.5 m, equally-spaced and roughly 40 m apart in square grids. Recorder positions remained fixed at each roost throughout the study once our pilot observations had confirmed the location of the roosting area and that recorders were positioned as centrally around it as possible. Before deployment, we activated the recorders simultaneously and used a loud hand clap to produce a clear acoustic signal that could later be used to synchronise the audio files (.wav) from all the recorders in Audacity (www.audacityteam.org). Here, we also applied 6 dB of noise reduction to reduce the amplitude of continuous background sounds (i.e., low frequency hums or buzzes) picked up by the microphones while leaving jackdaw calls unaffected.

Acoustic analysis

To determine the rate of change in calling intensity over the hour leading up to the largest group departure and the final calling intensity in the minute before departure, we performed spectral analyses in MATLAB[S11]. This involved estimating the power spectral density (PSD) to quantify calling intensity, which captures the power (in dB) of each frequency component (Hz) of a signal across a unit of time (here, per second and an average over the final minute). We restricted PSD estimates to the frequency range of jackdaw calls (480-4000 Hz) by adding low and high pass filters. We also normalised all PSD estimates for each morning (between 0 and 1) to account for differences in recorder sensitivity and position relative to the jackdaws. We then took the mean of each normalised PSD estimate across all recorders to produce a representative measure of calling intensity throughout the central roosting area. To calculate the rate of change in calling intensity, we performed linear regressions on the normalised PSD data per morning, with normalised PSDs being analysed as a function of time (s). This produced regression slope estimates for each morning with units of normalised dB/Hz/s, which were later converted into units of normalised dB/Hz/hr to increase the scale of regression model coefficients that used this variable in our statistical analysis. To estimate the final calling intensity before departure, we calculated a single PSD estimate over the final minute for each morning. As collective departures may also be influenced by background noise, such as strong winds or road traffic noise, we quantified levels of low frequency background sounds (0-400 Hz) outside the range of jackdaw vocalisations. As before, we used PSD estimates to calculate the rate of change and final minute amplitude of low frequency background noise and included them as covariates in our analyses where relevant. Note that the rate of change in calling intensity was calculated over a period of one hour prior to departure because this encompasses the time period over which intensity begins to build: while calling began on average 101 minutes before sunrise, there were mornings where virtually no calling occurred until an hour before departure. To further examine the robustness of our findings, we also tested the effects of changing the time period over which the rate of change and final intensity were calculated, and focused on the effects of calling in relation to the first, rather than the largest group departure. None of these analyses qualitatively changed our conclusions: see section 4(iii) for details.

Finally, it is important to note that jackdaws commonly call when flying off from the roost, but we took great care to ensure this post-departure calling was excluded from our analyses. Immediately after a mass take-off, there were consistently sudden peaks in calling intensity as birds took flight, which were clearly evident in the recordings. The sound of many flapping wings and the sharp drop off in calling that proceeded were also clear indications that the birds had taken off. Using these indications, coupled with personal observations of departures with binoculars and a camera, as well as synchronous video recordings, we were able to accurately pinpoint when mass departures occurred and exclude any calling after departure.

Playback experiments

We used one of the six roosts (near College Reservoir, Penryn) where we collected observational and acoustic data during the first winter of this study for playback experiments during the second winter, using loudspeakers to broadcast audio from within the roost. This roost was selected because it showed consistent activity and collective departures throughout the preceding winter periods. The roost population was estimated as 150-200 individuals over the period of the experiment. 15-minute-long playbacks either broadcasted jackdaw calls or white (wind) noise as a control around 20 minutes before the expected time of departure (based on sunrise time). We also recorded the times of natural, unmanipulated departures to determine whether the noise from control playbacks caused birds to react differently compared to when no playbacks were used. Due to the early natural departure times at this roost and low light levels, it was not possible to use video footage to determine the size of the largest departing group. Throughout the entire experiment, there were 12 mornings in which all roost members left together in a single mass departure (‘whole roost departures’) and 11 mornings in which there were two mass departures, each containing roughly 50% of the roost population. We therefore conducted two separate analyses (each with n = 23 mornings). The ‘first’ departure analysis contained the times of all the ‘whole roost departures’ and the first departures on mornings where there were two departures. The ‘final’ departure time analysis included the times of all ‘whole roost departures’ and all second departure times. The two analyses produced quantitatively similar results (see below).

(a) Construction of playback tracks

To avoid possible confounds of differential responses to known versus unfamiliar calls, playback tracks used only recordings collected at the roost where the experiment was conducted. We selected a single recorder to construct playback tracks from, which was the recorder with the most sensitive microphones and highest quality audio (determined by comparing the highest average amplitude (dB) between each recorder across a sample of five mornings). To create playback tracks, we extracted 15-minute samples from the final 30 minutes before the moment of (first) departure in our recordings. Track length was designed such that it was long enough to allow jackdaws to detect temporal changes in calling intensity. We also constructed 15-minute control playbacks of wind noise (obtained from www.whitenoisemp3s.com). Wind noise, like jackdaw calling in the roost, shows oscillating peaks and troughs of intensity as gusts of wind rise and die down, providing a useful comparison to test whether birds respond specifically to jackdaw calls or simply react to comparable, increased noise levels introduced by the loudspeakers prior to departure. Since we aimed to conduct ten trials per playback treatment, we created ten unique playback tracks for each (ten with jackdaw calls and ten with wind). All playback track audio was faded in and out at the beginning and end to avoid unnatural sudden bursts or cessations of sound, respectively. We also applied a high pass filter at 250 Hz to remove very low frequency continuous background sounds that were outside of the jackdaw calling frequency range (480-4000 Hz) and improve the clarity of broadcasted audio.

Our observational data indicated a sharp increase in the temporal coordination of departures (i.e., the proportion of roost members leaving together) when the calling intensity was between -80 and -70 dB/Hz (see main text, Figure 1D). We calibrated the playback audio to mimic natural calling amplitudes, such that the combined signal of the playback plus natural calls would exceed this level of calling intensity. To achieve this, we repeatedly broadcasted a 30-second sample of calling at increasing volumes from two speakers positioned either side of a single recorder within the roost. Between broadcasts, we left a 30-second gap to allow time to increase the volume setting on the remote control and note down each setting change. The recorder was placed 20 m away from each playback speaker to mirror the approximate distance recorders would be located relative to jackdaws roosting in trees above. The aim of this test was to match the amplitude (in dB) of the live recording of jackdaw calling with the amplitude of the recording of jackdaw calling played from the speaker. The volume setting on the speaker that matched the original recording's amplitude was used for all playback experiments. To determine this, we used Audacity to compare the average root-mean-square (RMS) sound pressure (a measure of average amplitude across a given section of audio). This method was repeated for control (wind noise) playbacks. We performed these tests during the daytime at the roost and prior to any playback experiments.

We programmed the loudspeakers to automatically start broadcasting playbacks 20 minutes before the first jackdaws were predicted to depart (playback start ranged from 49 to 64 minutes before sunrise; note that at this point birds the roosting birds were awake and had already been calling for 40-60 minutes). By using a 15-minute track length, we ensured there would be around a 5-minute buffer between the end of the playback and the predicted first departure to account for error in our departure time prediction (if the playback had no influence on the birds). To ensure playbacks began at precisely the desired time, 15-18 hours of silence were added at the beginning of the track, depending on how many hours prior to the predicted departure time we had arrived at the roost in the afternoon. This allowed us to set the speakers up in the roost in the afternoon before the experimental trial, begin the playback tracks, and leave them overnight to play silence before the treatment audio began automatically at the desired time the following morning. This removed the need to get close to the roosting birds to be within range to trigger the speakers remotely, which could have caused disturbance or even scared birds into a pre-mature take-off. To predict departure times, we used a linear regression model that fitted natural departure times relative to sunrise recorded at the same roost earlier that winter as the response term and forecasted rain and cloud cover conditions as explanatory terms. Prior to each playback trial, forecasted meteorological data could then be entered into the model to estimate when departure was likely to occur.

(b) Playback procedure

We conducted playback experiments from 13 December 2019 to 20 March 2020. To avoid the artificiality of calls coming from a single point location, we broadcasted playbacks simultaneously from four remote-controlled loudspeakers. Before deployment in the roost, we covered four FoxPro Fury 2 loudspeakers with waterproofing material (leaving the speaker cones exposed) and attached them to external battery packs placed in a waterproof box. We strapped the loudspeakers to trees at a height of 2.5 m in a grid 40 m apart to achieve a broad coverage of acoustic stimuli throughout the roost. To avoid disturbance, all recorder and playback equipment was set up and retrieved during the daytime, with batteries recharged overnight. Before strapping speakers to trees, we used a single remote control to trigger the playback track to begin on all loudspeakers simultaneously. This caused speakers to immediately start playing the designated number of hours of silence that preceded the treatment audio, which would then automatically begin 20 minutes prior to the predicted departure of jackdaws from the roost each morning.

Experiments followed a repeated measures design, with the playback treatment type (control or experimental) being selected pseudo-randomly, such that the same treatment was never used on two or more mornings in a row to minimise the risk of habituation. To avoid pseudoreplication, we used different audio for each playback track for each trial, but all speakers within a trial played the same track. To reduce disturbance and the risk of habituation to playbacks, we left at least a one-day gap between trials, as well as between playback trials and mornings when we recorded natural departure times. We aimed to avoid rainy days as previous work in corvids has indicated that they are associated with later roost departures[S9,10]. However, since rain sometimes occurred even on forecasted dry mornings, we had to remove a number of trials. After also removing trials due to technical issues with the loudspeakers failing to broadcast audio, our analyses included 23 trials (eight no treatment, eight control and seven experimental).

Ethics

This research was approved by the University of Exeter Bioscience Ethics committee (reference eCORN000644) and followed the ASAB Guidelines for the Treatment of Animals in Behavioural Research and Teaching[S12].

(ii) Statistical analyses

We carried out all statistical analyses in R 4.0.5[S13] and built mixed-effects models using *lme4*[S14] and *lmerTest*[S15]. Model selection was carried out using an information theoretic (IT) approach and models were ranked by Akaike's information criterion corrected for small sample sizes (lowest to highest AICc)[S16]. In all analyses, we assessed residual plots for violations of model assumptions[S17] and tested for multicollinearity between predictors by assessing the variance inflation factor (VIF). Roost site was fitted as a random effect in all mixed model analyses. To avoid fixed effect bias when estimating variance components, all linear mixed effects models (LMMs) were fitted by maximum likelihood (ML) before model selection. However, we refitted the final, best-fitting model by restricted maximum likelihood (REML) to minimize small sample size bias and prevent inflation of type-I errors[S18]. We then generated regression coefficients of the best-fitting model using *ggeffects*[S19], which were plotted along with the raw data using *ggplot2*[S20]. R^2 estimates were calculated using *performance*[S21]. As any combination of our meteorological and acoustic variables were biologically plausible influences on departures, we used the *dredge* function from the *MuMin* package[S22] to determine which variable combinations best predicted the response term and generate a table of models ranked by AICc. Models with a ΔAICc ≤ 6 made up the 'top set'. We then implemented the 'nesting rule', described by Richards[S23], whereby models in the top set that were more complex versions of nested, better performing models with lower AICc were disregarded. More complex models were only retained if they had a lower AICc than a simpler, nested model.

Influence of calling on departure time

We first conducted preliminary analyses on the full dataset of available departure times to establish the influences of meteorological variables on departure time (n = 55).

These analyses revealed that the most important meteorological predictors of departure time were rain before departure, cloud coverage and barometric air pressure. Here, departure time was delayed when there was rain (mean ± SE = 9.11 ± 2.11, lower/upper 95% confidence interval = 4.98/13.17, $t = 4.32$, $p = <0.001$), greater cloud cover (%) (0.11 ± 0.03, lower/upper CI = 0.05/0.16, $t = 3.71$, $p = <0.001$) and lower barometric air pressure (mPa) (-0.18 ± 0.08, lower/upper CI = -0.33/-0.02, $t = 2.21$, $p = 0.032$). These variables were then carried over as covariates in LMMs that used a restricted dataset ($n = 30$) (for which audio recordings were available) to test whether a steeper rise in calling intensity and greater final calling intensity in the minute prior to departure were associated with earlier departures.

Influence of calling on the temporal coordination of departures

To test whether a greater proportion of the roost population left together (i.e., “temporal coordination”) when there was a steeper rise in the rate of change in calling intensity and a greater final calling intensity, we constructed generalised linear mixed models (GLMMs) with a binomial error structure ($n = 30$). Temporal coordination was fitted as the response variable, with the number of birds in the largest departing group as the numerator and the total number of roosting birds as the denominator. Wind speed and rain were included as covariates to account for their potential influence, e.g., by influencing the propagation of acoustic signals and their effect on group cohesion and social information transfer. Initial analyses showed that the temporal coordination of departures was not influenced by cloud cover (-0.03 ± 0.02, lower/upper CI = -0.09/0.02, $z = -1.17$, $p = 0.242$) and barometric air pressure (0.00 ± 0.05, lower/upper CI = -0.10/Inf, $z = 0.07$, $p = 0.945$), so these variables were not included in models to avoid over-parametrisation.

Playback experiments

To test the effect of playback treatments on departure time, we used multiple linear regression. We modelled the times of the ‘first’ and ‘final’ departure relative to sunrise as response variables in separate models, with playback treatment type as the key explanatory variable, along with cloud coverage and barometric air pressure as covariates. Initial analyses revealed no effects of these meteorological variables, so we constructed simple linear regression models with playback treatment as the only predictor to avoid overparameterising the model. We also used linear regression to test for the effects of different playback treatments on the rise in calling intensity over the hour period before departure, comparing these to natural departures. Finally, a linear regression was used to determine the effects of control and jackdaw calling playbacks on the time difference between the end of the playback audio and the time of the first mass departure.

Additional analyses

(a) Relationship between the rate of change in calling intensity and final intensity

The rate of change in calling intensity and the final calling intensity were only weakly correlated, with the rate of change only predicting 15.7% of the variation in final calling intensity (8.67 ± 3.47, lower/upper CI = 1.88/16.42, t = 2.50, p = 0.019, marginal R^2 = 0.16). When modelled together as predictors of departure time and temporal coordination, they also displayed very weak multicollinearity. This justified our decision to treat them as independent explanatory variables in our analyses.

(b) Additional explanatory variables

Larger or more irregularly-shaped roosting areas could, in principle, hinder the propagation of vocalisations through the roost, making it more difficult for roosting birds to reach a consensus. To address this possibility, we conducted additional analyses using a subset of data (n = 27 mornings) where we were able to establish the total number of roosting birds, the size of the central roosting area (m^2, estimated using Google Maps and field observations) and shape irregularity (quantified using the fractal dimension index for estimating shape complexity[S24]). In LMM analyses with meteorological and acoustic variables we found no evidence that any of these variables influenced departure time or the proportion of roost members departing together. As none of these variables were present in the top set during model selection, they were subsequently removed from all analyses.

(2) SUPPLEMENTAL VIDEOS AND DATA ACCESSIBILITY

Data, R scripts, full model selection tables are available in the figshare repository: https://doi.org/10.6084/m9.figshare.19076825.v2, along with multiple videos illustrating mass departures and cohesive post-departure flocking and social behaviour: https://doi.org/10.6084/m9.figshare.19076858.v1. We have also included an additional figure in the figshare repository, showing spectrograms of a morning when calling increased overall leading up to departure and another of a morning where calling decreased: https://doi.org/10.6084/m9.figshare.19076849.v1.

(3) SUPPLEMENTAL RESULTS

(i) Influence of calling on departure time

Mass departures occurred earlier when the rise in calling intensity was steeper. Rain and greater cloud cover were linked to later departures (Table S1A, C). Accounting for these meteorological conditions, there was strong support for the rate of change in calling intensity as a key predictor of departure times: this variable featured in the two highest-ranked models and had robust effects (Table S1A,C). We found weak support for an additional effect of the final calling intensity. Although this variable featured in the highest-ranked model, the effect was not robust (Table S1C).

(ii) Influence of calling on the temporal coordination of departures

The number of birds leaving simultaneously in the largest departure ranged from 15 to 1410 individuals, with the proportion of the total roost population in the largest departure ranging from 7.68 to 100%. After applying the nesting rule, the best-fitting model contained only the final calling intensity (Table S1B,D). As illustrated in Figure 1D in the main text, there was a sharp, non-linear increase in the temporal coordination of departures as the final calling intensity increased. Although the final calling intensity was the best predictor of temporal coordination, there was some, albeit weaker support for an effect of the rate of change in calling intensity (Table S1B). The second best-fitting model contained only the rate of change in calling intensity, which had a weaker but similar non-linear relationship, with a sharp increase in temporal coordination when the rate of change was positive (7.73 ± 2.83, lower/upper CI = 3.38/15.12, $z = 2.83$, $p = 0.006$).

(iii) Effects of changes in criteria for calling intensity and departure time

To determine whether our results could be influenced by criteria used to calculate acoustic parameters and determine departure times in the observational data, we carried out additional analyses.

The analyses reported in the main text and Table S1 below focus on the impact of the rate of change in calling rate measured over 1 hour prior to the largest group departure, and the final calling intensity in the minute prior to this departure. Calculating the rate of change in calling intensity over a period of 1.5 hours produced qualitatively the same effects on the timing of departures, groups leaving earlier when the rate was higher (-32.25 ± 13.93, lower/upper CI = -58.09/-6.24, t = -2.32, p = 0.035). We also found a similar effect of higher calling intensity linked to a larger proportion of the flock leaving together (greater temporal coordination) if final intensity was calculated over a period of 5 minutes or 30 seconds prior to departure (5 mins: 0.37 ± 0.12, lower/upper CI = 0.17/0.67, z = 3.01, p = 0.003; 30 s: 0.33 ± 0.10, lower/upper CI = 0.16/0.58, z = 3.17, p = 0.002).

Focusing on the largest group departure could conceivably influence our findings if, for instance, many birds had already left alone or in small groups before the largest group left, such that declines in calling intensity are an artefact of declining numbers of birds in the roost. However, Figure S1A shows that this cannot be the case because patterns of increasing or decreasing calling rate are evident long before birds start leaving the roost. To further address this issue, we also examined the effects of changing criteria such that the rate of change in calling intensity in the hour period before departure and final calling intensity in the minute before departure were determined with respect to the first departure instead of the largest. We also conducted separate analyses using partitioned data that excluded mornings where the largest departure was not the first departure.

Our results remained qualitatively the same as our original analyses. We found that, as before, the rate of change in calling intensity was in the best-fitting model predicting departure time, with steeper rises in calling intensity being associated with earlier departures (-14.08 ± 3.80, lower/upper 95% CI = -21.23/-6.90, t = -3.70, p = 0.001). The final calling intensity was also in the best-fitting model predicting the temporal coordination of departures, with greater final intensity predicting greater temporal coordination (0.41 ± 0.14, lower/upper 95% CI = 0.19/0.77, z = 2.92, p = 0.004). Similarly, when excluding mornings where the largest departure was not the first, a greater rate of change in calling intensity predicted earlier departures (10.88 ± 2.44, lower/upper 95% CI = -15.79/-6.39, t = -4.46, p < 0.001) and a greater final calling intensity was associated with greater temporal coordination, albeit this effect was weaker (0.43 ± 0.24, lower/upper 95% CI = 0.10/1.08, z = 1.80, p = 0.072). These results, along with Figure S1A, indicate that patterns of calling were evident long before departure and that birds departing before the largest departure did not strongly influence our acoustic data and overall findings.

(iv) Playback experiments

Combined with naturally occurring jackdaw calls, our playback experiments caused an overall steeper rise in calling intensity over the hour period before departure (see examples in Figure S1B). The rise in calling intensity before the first departure was significantly flatter for trials with no playback treatment (n = 8 mornings; -0.20 ± 0.08, lower/upper CI = -0.37/-0.03, t = -2.41, p = 0.026) compared to playbacks of jackdaw calls (n = 6, where one recording was unusable due to high winds). In contrast, the rise in acoustic intensity did not differ between playbacks of jackdaw calls and control playbacks of wind noise (n = 8, -0.01 ± 0.08, lower/upper CI = -0.18/0.16, t = -0.10, p = 0.925).

Linear regression models showed a clear effect of playback treatment. Experimental playbacks of roost recordings resulted in the first mass departure (i.e., where ≥ 50% of roost members departed simultaneously) occurring 6.57 minutes earlier compared to control playbacks with white noise, which in turn did not differ from mornings with no playbacks (Table S1E). Analyses of the final mass departure (on mornings when the entire roost did not leave in a single mass departure) showed qualitatively the same results (Table S1F). In all but two of the trials where we broadcasted jackdaw calls, the first departure occurred before the end of the playback, whereas departures never occurred before the end of control (wind noise) playbacks. Relative to the end of the playback, departures occurred 8.73 minutes earlier during playbacks of jackdaw calls compared to control playbacks (-8.73 ± 2.09, lower/upper CI = -13.24/-4.22, t = -4.18, p = 0.001, R^2 = 0.54; Figure S1C).

(4) SUPPLEMENTAL TABLE AND FIGURE (see next page)

Table S1. Top ten mixed-effects models from the 'top set' (Δ AICc ≤ 6) predicting **(A)** departure time relative to sunrise and **(B)** temporal coordination of departures (i.e., proportion of roost members departing together). Fixed effect headings in **(A)** refer to barometric air pressure ('Baro'), cloud coverage ('Cloud'), final calling intensity in the minute prior to departure ('Final call'), low frequency background noise in the final minute before departure ('Final noise'), whether it rained before departure ('Rain'), the rate of change in calling intensity ('Slope call') and rate of change in low frequency background noise ('Slope noise'). Summary statistics for the linear regression models using playback treatment to predict the time relative to sunrise of **(E)** the first departure and **(F)** the final departure (for cases when there were two separate departures). In the R^2 estimate column of **(C-F)**, the conditional R^2 is provided in the first row and estimates the proportion of variance explained by the fixed and random effects combined, while the marginal R^2 estimate is provided in the second row and estimates the variance explained by the fixed effects only[S25]. Thereafter, semi-partial R^2 estimates are provided for individual fixed effects and the random effect. For **(C)** and **(D)**, R^2 estimates refer to adjusted R^2. Statistically significant variables ($p < 0.050$) are denoted by the * symbol.

(A) LMMs predicting departure time														
Model	**Intercept**	**Baro**	**Cloud**	**Final call**	**Final noise**	**Rain**	**Slope call**	**Slope noise**	**DF**	**LogLik**	**AICc**	**ΔAICc**	**Retained**	**Weight**
55	**-70.08**	**NA**	**0.15**	**-0.51**	**NA**	**+**	**-13.29**	**NA**	**7**	**-86.90**	**192.88**	**0.00**	**yes**	**0.29**
51	-31.19	NA	0.13	NA	NA	+	-18.33	NA	6	-89.18	194.02	1.14	yes	0.17
119	-71.25	NA	0.15	-0.53	NA	+	-13.41	-7.44	8	-86.42	195.70	2.82	no	0.07
56	-8.87	-0.06	0.14	-0.55	NA	+	-12.01	NA	8	-86.48	195.83	2.94	no	0.07
31	-77.14	NA	0.13	-0.79	0.22	+	NA	NA	7	-88.42	195.94	3.06	yes	0.06
63	-68.32	NA	0.14	-0.55	0.07	+	-11.10	NA	8	-86.71	196.29	3.40	no	0.05
115	-30.84	NA	0.13	NA	NA	+	-18.67	-5.85	7	-88.94	196.98	4.10	no	0.04
23	-96.24	NA	0.15	-0.84	NA	+	NA	NA	6	-90.67	197.00	4.12	yes	0.04
52	-0.63	-0.03	0.12	NA	NA	+	-17.94	NA	7	-89.10	197.29	4.41	yes	0.03
59	-31.67	NA	0.13	NA	-0.01	+	-18.51	NA	7	-89.18	197.45	4.57	no	0.03

(B) Binomial GLMMs predicting temporal coordination of departures													
Model	**Intercept**	**Final call**	**Final noise**	**Rain**	**Slope call**	**Slope noise**	**Wind**	**DF**	**LogLik**	**AICc**	**ΔAICc**	**Retained**	**Weight**
2	**29.61**	**0.40**	**NA**	**NA**	**NA**	**NA**	**NA**	**3**	**-9.75**	**26.43**	**0.00**	**yes**	**0.13**
10	18.57	0.25	NA	NA	3.93	NA	NA	4	-8.81	27.21	0.79	no	0.09
26	34.55	0.47	NA	NA	6.04	-15.51	NA	5	-7.59	27.68	1.26	no	0.07
6	30.09	0.40	NA	+	NA	NA	NA	4	-9.11	27.83	1.40	no	0.06
18	38.16	0.52	NA	NA	NA	-7.92	NA	4	-9.18	27.96	1.53	no	0.06
34	29.86	0.42	NA	NA	NA	NA	0.09	4	-9.38	28.36	1.93	no	0.05
4	27.46	0.42	-0.05	NA	NA	NA	NA	4	-9.53	28.67	2.24	no	0.04
22	40.42	0.54	NA	+	NA	-10.14	NA	5	-8.22	28.93	2.51	no	0.04
9	-0.12	NA	NA	NA	7.73	NA	NA	3	-11.12	29.16	2.73	yes	0.03
14	18.27	0.24	NA	+	3.79	NA	NA	5	-8.45	29.40	2.98	no	0.03

Variable	**Estimate**	**SE**	**95% CI (lower)**	**95% CI (upper)**	**T/Z value**	**P value**	**R^2 estimate**	**Variance**	**SD**
(C) LMM predicting departure time from rate of change and final calling intensity							0.91		
Fixed effects							0.68		
Intercept	-70.41	19.56	-106.29	-34.25	-3.60	0.002*			
Rain									
No	0								
Yes	11.56	2.13	7.44	15.48	5.43	<0.001*	0.30		
Cloud	0.15	0.03	0.09	0.20	4.85	<0.001*	0.22		
Slope call	-13.25	4.96	-22.47	-4.11	-2.67	0.013*	0.16		
Final call	-0.51	0.25	-0.97	-0.05	-2.03	0.054	0.12		
Random effects							0.23		
Roost site							0.23	34.28	5.86
(D) Binomial GLMM predicting the temporal coordination of departures							0.71		
Fixed effects							0.71		
Intercept	30.26	10.20	14.61	56.84	2.97	0.003*			
Final call	0.41	0.14	0.19	0.77	2.92	0.004*			
Random effects							0.00		
Roost site							0.00	0.00	0.00
(E) Linear model predicting first departure time from playback treatment							0.20		
Intercept	-36.00	1.73	-39.60	-32.40	-20.85	<0.001*			
Playback									
Control (wind)	0								
Jackdaw calls	-6.57	2.53	-11.85	-1.30	-2.60	0.017*			
None	-1.25	2.44	-6.35	3.85	-0.51	0.614			
(F) Linear model predicting final departure time from playback treatment							0.18		
Intercept	-33.63	1.63	-37.02	-30.23	-20.69	<0.001*			
Playback									
Control (wind)	0								
Jackdaw calls	-6.09	2.38	-11.05	-1.13	-2.56	0.019*			
None	-1.63	2.30	-6.42	3.17	-0.71	0.488			

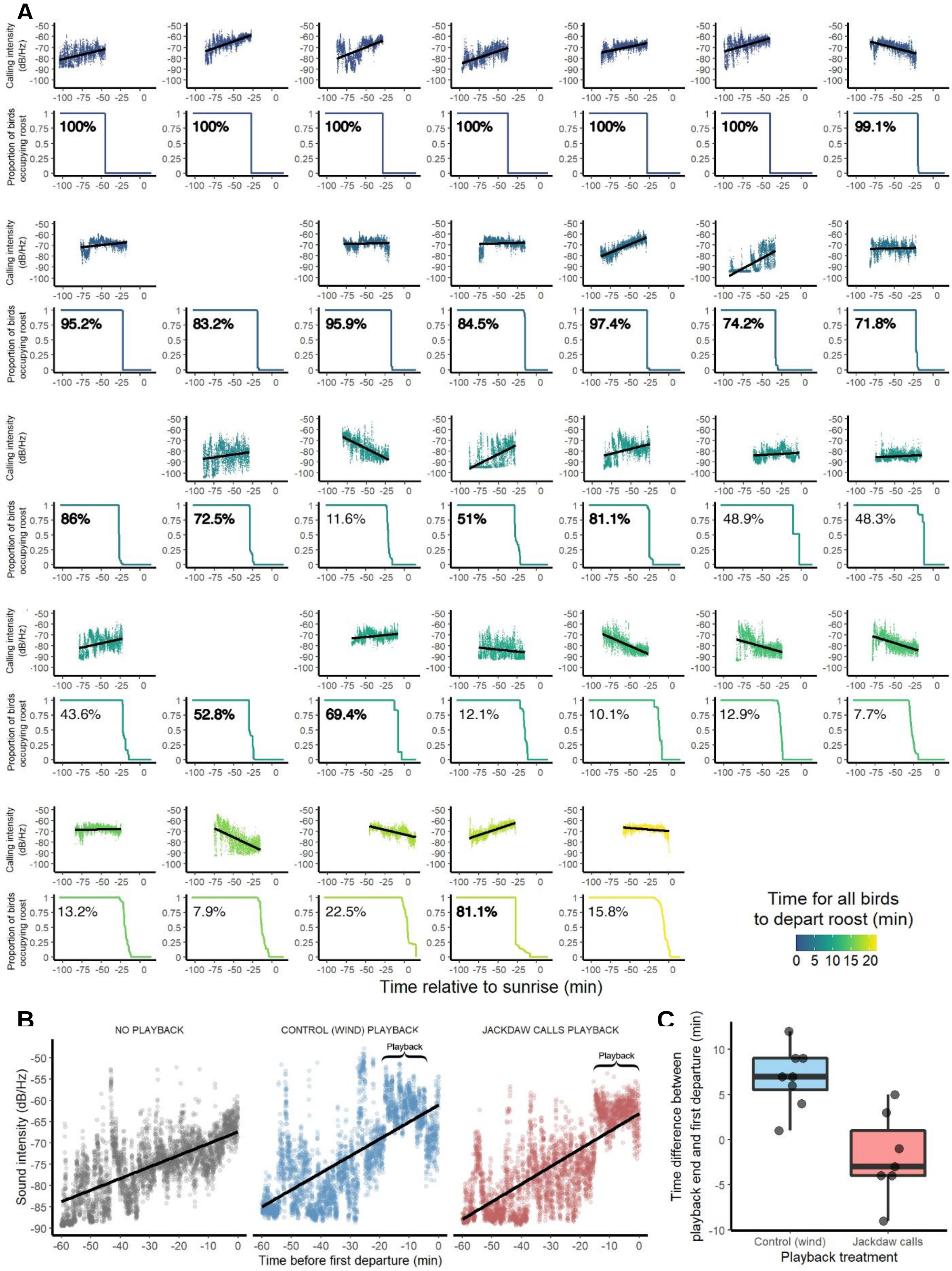

Figure S1. (A) Change in the proportion of birds occupying the roost over time relative to sunrise per morning (below plots; n = 33) paired with the change in calling intensity relative to sunrise before the largest departure for each morning with available acoustic data (above plots; n = 30). The colours indicate the time taken for all birds to leave the roost: Blue coloured lines and data points indicate mornings where the whole roost left quickly; more yellow colours indicate longer times. When the rise in calling intensity was steeper and reached a higher final intensity, birds tended to depart the roost earlier, in larger groups and more quickly. Mass group departures, where large numbers of birds leave almost simultaneously are indicated by vertical drops in the departure plots. Numbers show the percentage of the roost population in the largest departing flock. In cases where these flocks contained >50% of the roost population (indicated in bold), birds in these departing flocks left within 4.32 seconds of each other on average (range: 1.03-7.81 secs). **(B)** Examples from three mornings during our playback experiments of the relative inclines in calling intensity over the hour period before departure when there was no playback (0.27 ± 0.01, upper/lower 95% CI = 0.26/0.28, t = 55.30, p < 0.001), a control (wind) playback (0.40 ± 0.01, lower/upper CI = 0.38/0.41, t = 56.88, p < 0.001) and a playback of jackdaw calls (0.41 ± 0.01, lower/upper CI = 0.40/0.43, t = 69.62, p < 0.001). The 15-minute period when playbacks were broadcasting audio is highlighted in the second and third plots. **(C)** Time difference between the end of the broadcasted playback audio and the first departure time for control (wind) and jackdaw calling playbacks. Negative values indicate minutes before the playback end time.

AUTHOR CONTRIBUTIONS

A.T. and J.W.J. conceived the original idea. A.J.D., A.T., N.J.B., and J.E.H-R. designed the methodology, with input from G.E.M. A.J.D. collected and collated the data, with logistical field support from G.E.M. A.J.D. performed all acoustic and statistical analyses. J.E.H-R. wrote the code for the acoustic analysis. A.J.D. and J.W.J. prepared all figures. A.J.D. drafted the manuscript. All authors discussed results, contributed to drafts and gave final approval for submission. A.T. was responsible for supervision, resource and equipment access, project administration and funding acquisition.

DECLARATION OF INTERESTS

The authors declare no competing interests.

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