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Vocally mediated consensus decisions govern mass departures from jackdaw roosts

Alex J. Dibnah[1,*], James E. Herbert-Read[2,3], Neeltje J. Boogert[1], Guillam E. McIvor[1], Jolle W. Jolles[4], and Alex Thornton[1,*]

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 (Supplemental information). Roosting jackdaws (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 (Supplemental information and 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 (Supplemental information), 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

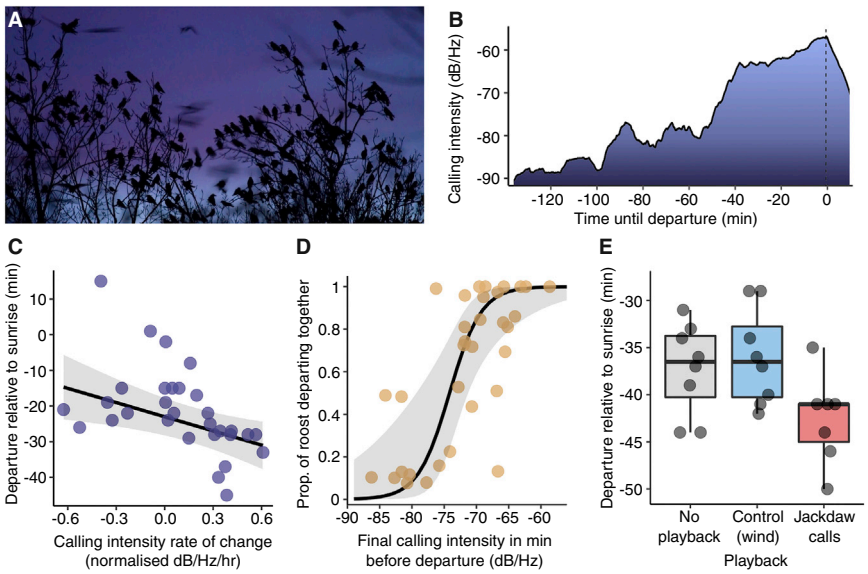

Figure 1. Vocalisations govern the timing and temporal coordination of mass departures from jackdaw roosts.

(A) A winter roost moments prior to a mass departure (photo by J.W. Jolles). (B) Example of a rise in calling intensity prior to a mass departure in one of the observed roosts. (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.

the largest group departure (Figures 1B and 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 and 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 (Supplemental information). 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[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 and Supplemental results). 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 experimental procedures: "Statistical Analyses"), 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 and 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.

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.

SUPPLEMENTAL INFORMATION

Supplemental information including one figure, one table, supplemental experimental procedures, supplemental results, acknowledgements and author contributions can be found with this article online at https://doi.org/10.1016/j.cub.2022.04.032.

DECLARATION OF INTERESTS

The authors declare no competing interests.

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[1]Centre for Ecology and Conservation, University of Exeter, Penryn, UK. [2]Department of Zoology, University of Cambridge, Cambridge, UK. [3]Aquatic Ecology, Department of Biology, Lund University, Lund, Sweden. [4]Centre for Ecological Research and Forestry Applications (CREAF), Barcelona, Spain.
*E-mail: alexdibnah01@gmail.com (A.J.D.); alex.thornton@exeter.ac.uk (A.T.)