Heterogeneous structure in mixed-species corvid flocks in flight

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Word count of text: 4519
Abstract

Flocks of birds in flight represent a striking example of collective behaviour. Models of self-organisation suggest that repeated interactions among individuals following simple rules can generate the complex patterns and coordinated movements exhibited by flocks. However, such models often assume that individuals are identical and interchangeable, and fail account for individual differences and social relationships among group members. Here, we show that heterogeneity resulting from species differences and social structure can affect flock spatial dynamics. Using high-resolution photographs of mixed flocks of jackdaws and rooks we show that birds preferentially associate with conspecifics and that, like high-ranking members of single-species groups, the larger and more socially dominant rooks position themselves near the leading edge of flocks. Neighbouring birds show closer directional alignment if they are of the same species, and neighbouring jackdaws in particular fly in very close proximity to one another. Moreover, birds of both species often fly in especially close proximity to a single same-species neighbour, likely reflecting the monogamous pair-bonds which characterise these corvid social systems. Together, our findings demonstrate that the characteristics of individuals and their social systems are likely to result in preferential associations that critically influence flock structure.

Keywords: Collective behaviour; Corvidae; *Corvus monedula; Corvus frugilegus*; flocking; jackdaw; mixed-species; rook; social system

Running headline: Heterogeneity in mixed-species flocks
INTRODUCTION

How do large aggregations of individuals, each of which may differ in its preferred outcome, coordinate their movements? The spectacular displays of flocking birds led the naturalist Edmund Selous (1931) to postulate a role for “thought transference”, but recent advances have begun to unravel the mysteries of collective movement without appealing to the supernatural (Couzin & Krause 2003; Conradt & Roper 2005; Sumpter 2006). Models of self-organising systems suggest that repeated interactions among individuals following simple rules can generate complex patterns and coordinated group movements. Models of agents following simple rules of (i) long-range attraction to group members (ii) short-range repulsion and (iii) alignment between close neighbours have generated realistic representations of collective animal movements (reviewed in Sumpter 2006; Petit & Bon 2010). However, empirical verification of their assumptions remains scarce and largely confined to model systems such as starlings, Sturnus vulgaris (e.g. Ballerini et al. 2008a, 2008b; Hemelrijk & Hildenbrandt 2011).

Mathematical models of self-organisation commonly assume that individuals are identical, independently interacting agents (Vicsek & Zafeiris 2012), but this is unlikely to be realistic (Sumpter 2006; Petit & Bon 2010). Group members often mix associatively according to a variety of morphological and physiological factors such as sex, size and energetic state (reviewed in Krause & Ruxton 2002) and species’ social systems have been shown to influence the spatial distribution of individuals in a variety of contexts (Krause 1993; King et al. 2008; Jacobs et al. 2011). However, studies of collective behaviour seldom consider the impact of such heterogeneity upon the spatial dynamics of flocks, or the rules of interaction underlying their coordination. Recent studies suggest that these impacts may be
critical. Harcourt et al. (2009), for example, demonstrated that individual differences have substantial impacts on coordination rules in pairs of sticklebacks (*Gasterosteus aculeatus*), while Nagy et al. (2010) identified a hierarchical structure in homing pigeon flocks (*Columba livia domestica*), with key individuals contributing disproportionately to the group’s movement decisions.

Mixed-species flocks provide excellent opportunities for empirical investigations into the impacts of heterogeneity on flock structure. Species differences may generate non-random organisations of individuals within flocks (Latta & Wunderle 1996), while members of larger or more dominant species may play a pivotal role in leading group movements (Goodale & Beauchamp 2010). Mixed-species flocks are an important form of social organisation for birds worldwide, and an extensive literature suggests that species differences are reflected in the spatial structure and movements of foraging groups. For instance, certain species may play a disproportionate role in flock formation and cohesion, while species that are particularly vulnerable to predation often follow and exploit the vigilance of heterospecifics (Sridhar et al. 2009; Goodale & Beauchamp 2010). However, as research has focused on foraging interactions, very little is known about the structure of mixed-species flocks in flight. Analyses of such aerial flocks can provide important insights into the interaction rules governing group movements.

Using high-resolution photographs of jackdaws (*Corvus monedula*) and rooks (*Corvus frugilegus*) in flight, we examined the effects of species differences and social systems on mixed-species flocks. Jackdaws and rooks spend a large portion of the year foraging and roosting together in large groups. During the winter, flocks of up to 1000 or so individuals leave their foraging grounds and fly to pre-roost trees before aggregating in a
single flock numbering in the thousands above the roost where they spend the night (Coombs 1961). The social system of both species centres around long-term monogamous pair-bonds (Emery et al. 2007), but rooks are larger and dominant in foraging interactions and access to roosting sites (Lockie 1956; Coombs 1961). Thus, these flocks are neither homogenous nor composed of anonymous individuals, and so provide an ideal system to investigate how heterogeneity (specifically species differences and social relationships) can mediate the movement rules that individuals adopt, and hence influence flock structure.

We assumed that flocking rooks and jackdaws would not interact in an identical manner to all neighbours (c.f. Nagy et al. 2010), and that this would be reflected in flock structure. Specifically, we predicted (1) that individuals would associate preferentially with conspecifics, and (2) that, like high-ranking members of single-species groups (King et al. 2009; Nagy et al. 2010), the socially dominant rooks would position themselves near the leading edge of flocks. If birds preferentially interact with specific individuals, then we predicted (3) greater proximity and alignment among conspecific than heterospecific neighbours. Alone, such assortment and alignment could simply reflect differing aerodynamic or morphological constraints between the two species, rather than differential reactions depending on neighbours’ species. However, such constraints would not be expected to result in the occurrence of discrete dyads of individuals within flocks. Consequently, our final prediction (4) was that birds should show increased proximity to a single same-species social partner, which is likely to reflect the monogamous pair-bonded societies of these corvids (Emery et al. 2007).

METHODS

Photography
We photographed corvid flocks moving to and from pre-roosting sites before combining in a single large flock above the roost (sunset ± 45 mins), between 19 October 2011 and 8 February 2012 in an area of approx. 0.3 km² in and around the village of Madingley, Cambridgeshire, U.K (see Fig. A1 in Supplementary Material). Photographs were taken perpendicular to the flocks’ flight direction at a distance of approximately 100-300m, from different locations throughout each evening so as to avoid pseudoreplication due to repeated shots of the same flock. The number of different flocks photographed per evening ranged from one to 11 (mean = 3.1 ± 0.8). We used a Canon EOS 7D digital SLR camera with a Canon EF 100-400mm f/4.5-5.6 L IS lens. We set the camera to Auto Focus with Av exposure mode, with photos taken in RAW and settings adjusted to maximise distinguishability between the features of jackdaws and rooks. The drive mode was set to high-speed continuous shooting (8 frames per second), allowing us to capture sets of consecutive images from the front, middle and back thirds of flocks (hereafter ‘flock section’).

Photo Editing and Species Identification

Jackdaws and rooks are visually distinctive. Jackdaws are smaller, with a short, black bill, grey nape, blue/grey eyes and a wide tail in flight, while rooks are larger with entirely black plumage, a long, bald beak, dark eyes, a relatively narrow tail and primary wing feathers typically splayed in a finger-like fashion in flight. To maximise clarity and enable species identification of as many birds as possible, we edited all photographs using the Adobe Photoshop Camera Raw plugin (Adobe Systems, San Jose, California, USA). We then identified rooks and jackdaws from the edited photographs based on body size, head-shape, beak-shape, wing-shape and tail-shape. From a total of 1211 photographs, editing allowed us to identify the species identity of >95% of birds in 144 photographs. For analysis, we
excluded photographs where the total flock size was less than 20 (as small flocks would not
permit analyses based on seven nearest neighbours in front, middle and back; see below) and
the few images from flocks consisting entirely of a single species. This final dataset
contained a total of 115 photographs from 44 flocks (N = 44 from the front and middle and N
= 27 from the back of flocks; each flock was assigned a unique Flock Identity). Following
editing, we merged all photos of front, middle and back sections to form one larger image of
the whole flock (“flock image”). We counted the total number of birds in each flock image as
a proxy for total flock size and noted the proportion of rooks in each flock. As birds were not
individually identifiable in flight, it is possible that the same flock may have been
photographed on different evenings. However, flock sizes varied substantially, from 21 to
638 individuals, and there were only three instances (from a total of 44 flocks) where we
photographed flocks of the same size over different evenings. Our collection of photographs
is therefore likely to represent a large sample of different flocks.

Alignment and Proximity of Neighbours

To examine the alignment and proximity of neighbours, we randomly selected four
focal birds from each flock section (front, middle and back), noting their species and that of
their nearest neighbours. We chose four focal birds because (a) this allowed us to have
several representatives from each flock section but (b) the number of focal birds per section
was sufficiently low that we could ensure focal birds would never be nearest neighbours to
each other, which would result in pseudoreplication. If two randomly selected birds were
both nearest to one other, they were only considered in the analysis once and a new bird was
randomly selected. We determined the distance between the midpoints of neighbouring birds
in jackdaw lengths (based on the average body length of seven randomly selected jackdaws in
the flock). To determine the directional alignment between neighbours, we used the “ruler
“tool” in Photoshop CS5, by dragging the tool from the midpoint of the tail and beyond the midpoint of the head of each bird, thus providing the angle of the line through the body, relative to horizontal in the photograph. The difference between the angles of neighbouring birds was used as a measure of alignment. Our estimates of distances and alignment between neighbours necessarily involve some error as they rely on two-dimensional representations of the true three-dimensional structure of flocks. However, while these errors introduce some noise into the data, they generate no directional biases. Our estimates are therefore likely to provide robust yet conservative measures of the true degree of structure in flocks.

Statistical Analyses

Data were analysed in Genstat 14.1 using Linear Mixed Models (LMM) or Generalized Linear Mixed Models (GLMM) for normal and non-normal data respectively, with flock identity nested in date as a random term to control for repeated measures in all cases. Initially, all probable explanatory variables were entered into the model. All possible interactions between them were investigated and terms were sequentially dropped until the minimal model contained only terms whose elimination would significantly reduce the explanatory power of the model. Wald statistics and probability values for significant terms were derived from the minimal model containing only significant terms, while values for non-significant terms were obtained by adding each term individually to the minimal model (Crawley 2002). The residuals for all models were visually inspected to ensure homogeneity of variance, normality of error and linearity. All results with $P < 0.05$ are reported as significant. Means are quoted ± s.e. throughout. Post-hoc analyses of differences between levels within categorical variables (e.g. front, middle, back) were conducted by sequentially excluding each level from (G)LMM analyses to enable comparisons of the remaining
category levels. Tables of results for all multifactorial analyses including all effect sizes and
standard errors are in the Appendices below.

Preferential associations by species

To test whether the birds showed preferential associations by species (prediction 1) we randomly selected four focal birds per flock section and ran a GLMM with binary response term (1,0) testing the probability that a focal bird’s neighbour was a jackdaw. Explanatory terms were focal bird species and the proportion of rooks in the flock.

Positional differences by species

To compare positional differences between the species in flocks, we randomly selected one focal bird in each flock section, noting its species and that of its seven nearest neighbours. We used seven neighbours because previous research indicates that individuals in starling flocks interact with a fixed number of 6-7 neighbours (Ballerini et al. 2008a). Unlike the analyses of associations, distances and alignments between neighbours, there was no need to restrict analyses to four birds per flock section to avoid pseudoreplication. To test whether rooks flew disproportionately near the leading edge of flocks (prediction 2) we used a GLMM with a binomial response term (number of rooks out of the total of eight birds) and flock section (front, middle or back) as an explanatory variable. Flock size, the proportion of rooks, month (to control for possible seasonal variation) and time relative to sunset (because individuals’ motivation to reach preferred sites within the roost may increase as night approaches) were fitted as additional variables.

Proximity and alignment between neighbours
To test whether distance and alignment differed between conspecific and heterospecific neighbours (prediction 3) we noted the distance (in jackdaw lengths) and directional alignment between focal birds (four per flock section) and their nearest neighbours (see ESM). We then ran two LMMs with neighbour distance and neighbour alignment as response terms and dyad type (jackdaws, rooks or mixed) as our variable of interest, along with flock section (front, middle, back) and flock size. Distances were square-root transformed and alignments were normalized for analysis using a Box-Cox power transformation.

**Identification of discrete dyads within flocks**

Field observations and visual inspection of photographs indicated that jackdaws and rooks commonly fly in discrete dyads within flocks (Coombs (1961) reported similar observations). To confirm this, we used a custom-made script written in R ([www.R-project.org](http://www.R-project.org)) to measure the distance between all individuals (in jackdaw or rook lengths, from the midpoint of each bird) and their seven nearest same-species neighbours in a selection of nine flock section photographs. In very dense flocks, even discrete dyads would tend to fly near other dyads. As an illustrative sample, we therefore chose photographs of flock sections in which the density was sufficiently low to allow us to identify dyads clearly. The photographs used to examine jackdaw and rook dyads were not always the same, as some images contained insufficient rooks. Using the neighbour-distance measurements, we conducted the following analyses:

(1) Categorisation of discrete dyads and triads. We defined discrete dyads as same-species neighbours whose inter-individual distance was less than half the distance to the second closest neighbour. This conservative measure is likely to underestimate the true
frequency of discrete dyads in flocks as discrete dyads could nevertheless fly close to other
discrete dyads. We also investigated the occurrence of same-species triads of birds, defined
as cases where the nearest neighbour distances between three birds were all less than half the
distance to the fourth neighbour. Triads may occur among corvids when unpaired individuals
(either adult birds that had lost their partner or offspring from the previous breeding season)
associated with reproductive adult pairs, as described by Lorenz (Lorenz 1952). The results
are summarised in Table 1.

(2) Histograms of neighbour distances. For each of the photographs used in Table 1, we plotted, for each species, histograms showing the frequency distribution of neighbour
distances. If birds often fly in discrete dyads one would expect frequency distributions to
exhibit a bimodal character, with the distribution of first neighbour distances being
considerably lower than that of the next six neighbours. As there is no generally accepted
formal test of bimodality, we present the histograms in Fig. A2 as qualitative support for the
presence of discrete dyads within flocks.

RESULTS

Preferential association by species

After controlling for the proportion of rooks within flocks, we found that a focal
bird’s nearest neighbour was significantly more likely to be of the same species (GLMM: \( N = 
454 \) neighbour dyads, \( \chi^2 = 27.78, P < 0.001; \) Table A1).

Positional differences by species
Rooks made up only 21.8% ± 0.03 of flocks on average, but were disproportionately likely to be positioned at the front of flocks (GLMM: $N = 115$ photographs; $\chi^2 = 26.61$, $P < 0.001$; Fig. 1a; Table A2). The first bird at the leading edge was a rook in 19 out of 44 flocks (43.2%), more than twice as often as expected by chance (binomial test: $P = 0.001$).

Species distributions within flocks were not significantly affected by flock size, month or time to sunset (Table A2).

Proximity and alignment between neighbours

Neighbours flew more closely together in larger flocks (LMM: $N = 454$ neighbour dyads; $\chi^2 = 6.09$, $P = 0.019$; Fig. 1b) and in the middle of flocks relative to the front and back ($\chi^2 = 17.35$, $P < 0.001$; Table A3; Fig. 1c). Jackdaw dyads flew significantly closer together than rook dyads or mixed dyads (LMM: $\chi^2 = 48.95$, $P < 0.001$; Fig. 2a; Table A3), and the directional alignment of same-species dyads was greater than that of mixed dyads (LMM: $\chi^2 = 26.93$, $P < 0.001$; Fig. 2b; Table A4).

Do birds fly in discrete dyads?

An average of 41 ± 5% of jackdaws (range: 22 - 63%) and 46 ± 4% (range: 37 - 67%) of rooks in the illustrative selection of photographs flew in clearly identifiable, discrete dyads (Fig. 2c, Table 1). Histograms of neighbour distances commonly showed a bimodal character with a peak before the average nearest neighbour distance for each species (Fig. A2), suggestive of discrete dyads of birds flying in close proximity.

DISCUSSION
Contrary to the assumptions of many mathematical models of single-species aggregations, which treat individuals as equivalent and interchangeable, our results suggest that the structure of mixed-species flocks may be critically influenced by species differences and social systems. The larger and socially dominant rooks were disproportionately likely to be located in the front of flocks. This effect is unlikely to result from the influence of particular individual rooks, as our dataset contained photographs of numerous flocks of differing size, but rather seems to represent a general property of mixed rook-jackdaw flocks. Nor is the pattern readily explicable by species differences in flight velocity as rooks tend to be found towards the front of flocks despite observational evidence suggesting that jackdaws can fly faster (Coombs 1961). Previous work on fish schools (Krause et al. 2000), zebra herds (Fischhoff et al. 2007) and small pigeon flocks (Nagy et al. 2010) suggests that individuals located at the front of groups tend to assume leadership roles, initiating changes in direction or pace of movement which are followed by group members. Similarly, rooks may play a dominant role in influencing collective movements of mixed-species corvid flocks. It is possible that rooks’ preference for the front of flocks may simply reflect their motivation to reach the roost first and obtain favoured positions (Coombs 1961). If this was the case, one might expect rooks to move to the front as sunset approaches, but we found no such effect. Moreover, roosting flocks form spectacular, swirling displays similar to starling murmurations (King & Sumpter 2012) before settling, so individuals at the front of pre-roosting flocks may not necessarily land first at the roost.

Thus, it thus remains unclear whether rooks derive benefits from positioning themselves towards the front of flocks, whether jackdaws preferentially follow rooks or whether species’ relative positions reflect aerodynamic considerations. Future work incorporating GPS
technology to track flock members (Nagy et al. 2010) could assist in discriminating between these possibilities.

The general rules of attraction, short-range repulsion and alignment among neighbours proposed by models of self-organisation provide a valuable framework for understanding flocking (Bajec & Heppner 2009; Petit & Bon 2010), but our results indicate that their specific manifestations may be influenced by the characteristics of social systems. Our measurements of neighbour distances and alignments are somewhat crude and, given the noise in the data, they are likely to underestimate the true extent of spatial structure within flocks. Nevertheless, a number of important patterns were apparent. First, the extent of attraction and repulsion may vary depending on the position within a flock, the size of the flock (see Beauchamp 2012 for similar results in semipalmated sandpipers, *Calidris pusilla*) and the relationships between group members. Critically, corvids were not evenly distributed across the flock but typically flew near conspecifics, with jackdaws being particularly closely attracted to same-species neighbours, and birds of both species often appeared to fly in discrete dyads. The occurrence of discrete dyads of birds would not be expected to emerge from morphological or aerodynamic constraints alone and is likely to result from social partners flying together, although further studies with identifiable individuals would be needed to confirm this. Second, the alignment of neighbours was significantly higher if they were of the same species, with jackdaw dyads showing near perfect parallel alignment (a mean difference of only 3.8°). Both species form lifelong, monogamous pair bonds characterised by high levels of affiliative behaviour and close proximity (Emery et al. 2007), and our results suggest the possibility that these relationships are reflected in flock structure.
Together, our results suggest that the theoretical convenience of treating group members as identical and interchangeable does not adequately reflect biological reality in mixed-species flocks. Indeed, we would argue that this assumption is similarly unlikely to hold in single species flocks where individuals vary and have social relationships. Differences between individuals can give rise to leadership roles, which may be particularly pronounced in mixed-species aggregations where larger and more dominant species may commonly take the lead (King et al. 2009). Moreover, studies of both single-species and mixed species-flocks must consider how the relationships between individuals may modulate the degree of attraction, separation and alignment between group members. Thus, flock structure cannot be fully understood without taking species’ characteristics, their social systems and individuals’ relationships into account. Future work incorporating information on the movements of known individuals will provide further empirical data which can be integrated into mathematical models to better understand the influences of within-group heterogeneity on collective movements.

Acknowledgements

We thank Neeltje Boogert for her friendship, help and valuable comments. This work was funded a British Ecological Society grant and a BBSRC David Phillips Fellowship to A.T. A.J.K was supported by a NERC Fellowship.
REFERENCES


Table 1.
Occurrence of discrete dyads and triads of jackdaws and rooks in flocks

<table>
<thead>
<tr>
<th>Flock ID</th>
<th>Total jackdaws</th>
<th>Jackdaw dyads</th>
<th>Jackdaw triads</th>
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<th>Total rooks</th>
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<td>12 (50)</td>
<td>2 (13)</td>
<td>B</td>
<td>11</td>
<td>4 (36)</td>
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<tr>
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<td>12 (22)</td>
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<td>4 (27)</td>
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<td>16</td>
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</table>

Mean percentages (±SE): 41 ± 5%, 17 ± 2%, 46 ± 4%, 14 ± 6%

Numbers in brackets indicate the percentage of birds of each species flying in discrete dyads or triads.
FIGURE LEGENDS

Figure 1. (a) Proportion of rooks in the front, middle and back of flocks. The line indicates average proportion of rooks across all flocks. (b) Relationship between flock size and neighbour distances. (c) Distance between neighbours in the front, middle and back of flocks. Bars show means ± SE. Asterisks indicate significance levels between categories in post-hoc analyses: ** $P < 0.001$; * $P < 0.05$, NS: $P > 0.05$.

Figure 2. (a) Distance and (b) alignment between neighbours in jackdaw, rook and mixed dyads. (c) Jackdaws flying in clearly identifiable, discrete dyads.

Figure A1. Map of Madingley and surroundings. Photographs were taken within the large shaded area. To avoid pseudoreplication, photographs taken within a given evening were shot from different locations within this area. The hatched area shows the roost, where flocks would combine into a single large flock and spend the night.

Figure A2. Histograms of neighbour distances for (a) jackdaws and (b) rooks. Panels show the frequency distribution for the flocks in Table 1. There was considerable variation in neighbour distances within and between flocks, resulting in part from variation in flock shape and density. Nevertheless, a number of flocks exhibit a binomial character, with the frequency distribution of first neighbours (dark bars) showing a distinct peak. Critically, these peaks are lower than the mean nearest-neighbour distances of 2.4 jackdaw lengths or 3.4 rook lengths, indicating the presence of discrete same-species dyads of birds flying in close proximity to one another.
Figure 1

(a) Proportion of rooks

(b) Neighbour distance (jackdaw lengths)

(c) Neighbour distance (jackdaw lengths)
Figure 2

(a) Neighbour distance (jackdaw lengths)

(b) Neighbour alignment (degrees)

(c) Image of birds with circles indicating individual positions.
Coefficient estimates in all tables represent the change in the dependent variable relative to the baseline category and can thus be interpreted as measures of effect size.

Table A1. GLMM on the probability that the nearest neighbour of the focal bird was a jackdaw

<table>
<thead>
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<td>Proportion of rooks in flock</td>
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<tr>
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<td>Proportion of rooks in flock</td>
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<tr>
<td>- rook</td>
<td>-1.37</td>
<td>0.26</td>
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This analysis used data from 454 neighbour dyads in 44 flocks. The binary response term (1,0) indicated whether the neighbouring bird was a jackdaw. Flock identity nested in date was fitted as a random term (estimated variance component ± SE: 0.00 ± 0.000).
Table A2. GLMM on factors affecting the proportion of rooks among focal birds and their seven nearest neighbours

<table>
<thead>
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<th></th>
<th>Wald statistic ($\chi^2$)</th>
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<th>$P$</th>
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<td>Proportion of rooks in flock</td>
<td>4.72</td>
<td>0.74</td>
<td></td>
</tr>
<tr>
<td>Location - front</td>
<td>0</td>
<td>0</td>
<td></td>
</tr>
<tr>
<td>- middle</td>
<td>-0.93</td>
<td>0.24</td>
<td></td>
</tr>
<tr>
<td>- back</td>
<td>-0.78</td>
<td>0.19</td>
<td></td>
</tr>
</tbody>
</table>

This analysis used data from 115 photographs of 44 flocks, with flock identity nested in date fitted as a random term (estimated variance component ± SE: 0.201 ± 0.138). Post-hoc analyses by exclusion showed that there were significantly more rooks in the front than in the rest of the flock (front > middle: $\chi^2 = 23.67; P < 0.001$; front > back: $\chi^2 = 11.07; P < 0.001$; middle = back: $\chi^2 = 0.61; P = 0.436$).
### Table A3. LMM on factors affecting the distance between neighbours

<table>
<thead>
<tr>
<th></th>
<th>Wald statistic ($\chi^2$)</th>
<th>d.f.</th>
<th>$P$</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Full model</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Neighbour category (jackdaws, rooks, mixed)</td>
<td>48.95</td>
<td>2</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Flock section (front, middle, back)</td>
<td>17.35</td>
<td>2</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Flock size</td>
<td>6.09</td>
<td>1</td>
<td>0.019</td>
</tr>
<tr>
<td><strong>Minimal model</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Constant</td>
<td>1.67</td>
<td>0.07</td>
<td></td>
</tr>
<tr>
<td>Neighbour category</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>- Jackdaws</td>
<td>0</td>
<td>0</td>
<td></td>
</tr>
<tr>
<td>- Rooks</td>
<td>0.51</td>
<td>0.09</td>
<td></td>
</tr>
<tr>
<td>- Mixed</td>
<td>0.31</td>
<td>0.07</td>
<td></td>
</tr>
<tr>
<td>Location</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>- Front</td>
<td>0</td>
<td>0</td>
<td></td>
</tr>
<tr>
<td>- Middle</td>
<td>-0.13</td>
<td>0.06</td>
<td></td>
</tr>
<tr>
<td>- Back</td>
<td>0.16</td>
<td>0.07</td>
<td></td>
</tr>
<tr>
<td>Flock size</td>
<td>-0.001</td>
<td>0.0004</td>
<td></td>
</tr>
</tbody>
</table>

This analysis used data from 454 neighbour dyads in 44 flocks. The response term was the distance between each of four focal birds per flock section and its nearest neighbour, measured in jackdaw lengths, and square-root transformed for analysis. Flock identity nested in date was fitted as a random term (estimated variance component ± SE: 0.065 ± 0.024).

Post-hoc tests by exclusion showed that jackdaw dyads flew closer together than rook dyads or mixed dyads (jackdaws < rooks: $\chi^2 = 40.65, P < 0.001$; jackdaws < mixed dyads: $\chi^2 = 27.16, P < 0.001$; rooks = mixed: $\chi^2 = 1.64, P = 0.203$) and dyads in the middle of the flock were closer than those in the front or back (middle < front: $\chi^2 = 5.83, P = 0.016$; middle < back: $\chi^2 = 22.94, P < 0.001$; front < back: $\chi^2 = 5.19, P = 0.023$; Fig. 1c).
Table A4. LMM on factors affecting the difference in alignment between neighbours

| Table A4. LMM on factors affecting the difference in alignment between neighbours |
|---------------------------------|---------|-------|
|                                 | Wald statistic ($\chi^2$) | d.f.  | $P$       |
| **Full model**                  |                     |       |           |
| Neighbour category (jackdaws, rooks, mixed) | 26.93   | 2     | <0.001   |
| Flock section (front, middle, back)  | 1.05   | 2     | 0.592    |
| Flock size                       | 0.05   | 1     | 0.821    |
| Neighbour distance (jackdaw lengths) | 0.01   | 1     | 0.919    |
| **Minimal model**                | effect size | s.e.  |           |
| Constant                         | 1.09   | 0.01  |           |
| Neighbour category - Jackdaws    | 0      | 0     |           |
| - Rooks                          | 0.01   | 0.01  |           |
| - Mixed                          | 0.06   | 0.01  |           |

The analysis used data from 454 neighbour dyads in 44 flocks, with flock identity nested in date fitted as a random term (estimated variance component ± SE: 0.001 ± 0.000). The response term was normalized for analysis using a Box-Cox power transformation. Post-hoc tests by exclusion showed that same-species dyads were more closely aligned than mixed dyads (jackdaws < mixed: $\chi^2 = 25.24, P < 0.001$; rooks < mixed: $\chi^2 = 15.64, P < 0.001$; jackdaws = rooks: $\chi^2 = 0.19, P = 0.663$).
Figure A1
Figure A2