1   **Heterogeneous structure in mixed-species corvid flocks in flight**

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27   **Abstract**

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29   Flocks of birds in flight represent a striking example of collective behaviour. Models of self-

30   organisation suggest that repeated interactions among individuals following simple rules can

31   generate the complex patterns and coordinated movements exhibited by flocks. However,

32   such models often assume that individuals are identical and interchangeable, and fail account

33   for individual differences and social relationships among group members. Here, we show that

34   heterogeneity resulting from species differences and social structure can affect flock spatial

35   dynamics. Using high-resolution photographs of mixed flocks of jackdaws and rooks we

36   show that birds preferentially associate with conspecifics and that, like high-ranking members

37   of single-species groups, the larger and more socially dominant rooks position themselves

38   near the leading edge of flocks. Neighbouring birds show closer directional alignment if they

39   are of the same species, and neighbouring jackdaws in particular fly in very close proximity

40   to one another. Moreover, birds of both species often fly in especially close proximity to a

41   single same-species neighbour, likely reflecting the monogamous pair-bonds which

42   characterise these corvid social systems. Together, our findings demonstrate that the

43   characteristics of individuals and their social systems are likely to result in preferential

44   associations that critically influence flock structure.

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49   **Running headline:** Heterogeneity in mixed-species flocks

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INTRODUCTION

53

54 How do large aggregations of individuals, each of which may differ in its preferred outcome,

55 coordinate their movements? The spectacular displays of flocking birds led the naturalist

56 Edmund Selous (1931) to postulate a role for "thought transference", but recent advances

57 have begun to unravel the mysteries of collective movement without appealing to the

58 supernatural (Couzin & Krause 2003; Conradt & Roper 2005; Sumpter 2006). Models of self-

59 organising systems suggest that repeated interactions among individuals following simple

60 rules can generate complex patterns and coordinated group movements. Models of agents

61 following simple rules of (i) long-range attraction to group members (ii) short-range

62 repulsion and (iii) alignment between close neighbours have generated realistic

63 representations of collective animal movements (reviewed in Sumpter 2006; Petit & Bon

64 2010). However, empirical verification of their assumptions remains scarce and largely

65 confined to model systems such as starlings, *Sturnus vulgaris* (e.g. Ballerini et al. 2008a,

66 2008b; Hemelrijk & Hildenbrandt 2011).

67

68 Mathematical models of self-organisation commonly assume that individuals are

69 identical, independently interacting agents (Vicsek & Zafeiris 2012), but this is unlikely to be

70 realistic (Sumpter 2006; Petit & Bon 2010). Group members often mix associatively

71 according to a variety of morphological and physiological factors such as sex, size and

72 energetic state (reviewed in Krause & Ruxton 2002) and species' social systems have been

73 shown to influence the spatial distribution of individuals in a variety of contexts (Krause

74 1993; King et al. 2008; Jacobs et al. 2011). However, studies of collective behaviour seldom

75 consider the impact of such heterogeneity upon the spatial dynamics of flocks, or the rules of

76 interaction underlying their coordination. Recent studies suggest that these impacts may be

77   critical. Harcourt et al. (2009), for example, demonstrated that individual differences have

78   substantial impacts on coordination rules in pairs of sticklebacks (*Gasterosteus aculeatus*),

79   while Nagy et al. (2010) identified a hierarchical structure in homing pigeon flocks (*Columba*

80   *livia domestica*), with key individuals contributing disproportionately to the group's

81   movement decisions.

82

83   Mixed-species flocks provide excellent opportunities for empirical investigations into

84   the impacts of heterogeneity on flock structure. Species differences may generate non-

85   random organisations of individuals within flocks (Latta & Wunderle 1996), while members

86   of larger or more dominant species may play a pivotal role in leading group movements

87   (Goodale & Beauchamp 2010). Mixed-species flocks are an important form of social

88   organisation for birds worldwide, and an extensive literature suggests that species differences

89   are reflected in the spatial structure and movements of foraging groups. For instance, certain

90   species may play a disproportionate role in flock formation and cohesion, while species that

91   are particularly vulnerable to predation often follow and exploit the vigilance of

92   heterospecifics (Sridhar et al. 2009; Goodale & Beauchamp 2010). However, as research has

93   focused on foraging interactions, very little is known about the structure of mixed-species

94   flocks in flight. Analyses of such aerial flocks can provide important insights into the

95   interaction rules governing group movements.

96

97   Using high-resolution photographs of jackdaws (*Corvus monedula*) and rooks

98   (*Corvus frugilegus*) in flight, we examined the effects of species differences and social

99   systems on mixed-species flocks. Jackdaws and rooks spend a large portion of the year

100   foraging and roosting together in large groups. During the winter, flocks of up to 1000 or so

101   individuals leave their foraging grounds and fly to pre-roost trees before aggregating in a

102   single flock numbering in the thousands above the roost where they spend the night (Coombs

103   1961). The social system of both species centres around long-term monogamous pair-bonds

104   (Emery et al. 2007), but rooks are larger and dominant in foraging interactions and access to

105   roosting sites (Lockie 1956; Coombs 1961). Thus, these flocks are neither homogenous nor

106   composed of anonymous individuals, and so provide an ideal system to investigate how

107   heterogeneity (specifically species differences and social relationships) can mediate the

108   movement rules that individuals adopt, and hence influence flock structure.

109

110   We assumed that flocking rooks and jackdaws would not interact in an identical

111   manner to all neighbours (c.f. Nagy et al. 2010), and that this would be reflected in flock

112   structure. Specifically, we predicted (1) that individuals would associate preferentially with

113   conspecifics, and (2) that, like high-ranking members of single-species groups (King et al.

114   2009; Nagy et al. 2010), the socially dominant rooks would position themselves near the

115   leading edge of flocks. If birds preferentially interact with specific individuals, then we

116   predicted (3) greater proximity and alignment among conspecific than heterospecific

117   neighbours. Alone, such assortment and alignment could simply reflect differing

118   aerodynamic or morphological constraints between the two species, rather than differential

119   reactions depending on neighbours' species. However, such constraints would not be

120   expected to result in the occurrence of discrete dyads of individuals within flocks.

121   Consequently, our final prediction (4) was that birds should show increased proximity to a

122   *single* same-species social partner, which is likely to reflect the monogamous pair-bonded

123   societies of these corvids (Emery et al. 2007).

124

125   **METHODS**

126   *Photography*

127   We photographed corvid flocks moving to and from pre-roosting sites before

128   combining in a single large flock above the roost (sunset ± 45 mins), between 19 October

129   2011 and 8 February 2012 in an area of approx. 0.3 km^2 in and around the village of

130   Madingley, Cambridgeshire, U.K (see Fig. A1 in Supplementary Material). Photographs were

131   taken perpendicular to the flocks' flight direction at a distance of approximately 100-300m,

132   from different locations throughout each evening so as to avoid pseudoreplication due to

133   repeated shots of the same flock. The number of different flocks photographed per evening

134   ranged from one to 11 (mean = 3.1 ± 0.8). We used a Canon EOS 7D digital SLR camera

135   with a Canon EF 100-400mm f/4.5-5.6 L IS lens. We set the camera to Auto Focus with Av

136   exposure mode, with photos taken in RAW and settings adjusted to maximise

137   distinguishability between the features of jackdaws and rooks. The drive mode was set to

138   high-speed continuous shooting (8 frames per second), allowing us to capture sets of

139   consecutive images from the front, middle and back thirds of flocks (hereafter 'flock

140   section').

141

142   *Photo Editing and Species Identification*

143   Jackdaws and rooks are visually distinctive. Jackdaws are smaller, with a short, black

144   bill, grey nape, blue/grey eyes and a wide tail in flight, while rooks are larger with entirely

145   black plumage, a long, bald beak, dark eyes, a relatively narrow tail and primary wing

146   feathers typically splayed in a finger-like fashion in flight. To maximise clarity and enable

147   species identification of as many birds as possible, we edited all photographs using the Adobe

148   Photoshop Camera Raw plugin (Adobe Systems, San Jose, California, USA). We then

149   identified rooks and jackdaws from the edited photographs based on body size, head-shape,

150   beak-shape, wing-shape and tail-shape. From a total of 1211 photographs, editing allowed us

151   to identify the species identity of >95% of birds in 144 photographs. For analysis, we

152 excluded photographs where the total flock size was less than 20 (as small flocks would not

153 permit analyses based on seven nearest neighbours in front, middle and back; see below) and

154 the few images from flocks consisting entirely of a single species. This final dataset

155 contained a total of 115 photographs from 44 flocks (N = 44 from the front and middle and N

156 = 27 from the back of flocks; each flock was assigned a unique Flock Identity). Following

157 editing, we merged all photos of front, middle and back sections to form one larger image of

158 the whole flock ("flock image"). We counted the total number of birds in each flock image as

159 a proxy for total flock size and noted the proportion of rooks in each flock. As birds were not

160 individually identifiable in flight, it is possible that the same flock may have been

161 photographed on different evenings. However, flock sizes varied substantially, from 21 to

162 638 individuals, and there were only three instances (from a total of 44 flocks) where we

163 photographed flocks of the same size over different evenings. Our collection of photographs

164 is therefore likely to represent a large sample of different flocks.

165

166 *Alignment and Proximity of Neighbours*

167   To examine the alignment and proximity of neighbours, we randomly selected four

168 focal birds from each flock section (front, middle and back), noting their species and that of

169 their nearest neighbours. We chose four focal birds because (a) this allowed us to have

170 several representatives from each flock section but (b) the number of focal birds per section

171 was sufficiently low that we could ensure focal birds would never be nearest neighbours to

172 each other, which would result in pseudoreplication. If two randomly selected birds were

173 both nearest to one other, they were only considered in the analysis once and a new bird was

174 randomly selected. We determined the distance between the midpoints of neighbouring birds

175 in jackdaw lengths (based on the average body length of seven randomly selected jackdaws in

176 the flock). To determine the directional alignment between neighbours, we used the "ruler

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177   tool" in Photoshop CS5, by dragging the tool from the midpoint of the tail and beyond the

178   midpoint of the head of each bird, thus providing the angle of the line through the body,

179   relative to horizontal in the photograph. The difference between the angles of neighbouring

180   birds was used as a measure of alignment. Our estimates of distances and alignment between

181   neighbours necessarily involve some error as they rely on two-dimensional representations of

182   the true three-dimensional structure of flocks. However, while these errors introduce some

183   noise into the data, they generate no directional biases. Our estimates are therefore likely to

184   provide robust yet conservative measures of the true degree of structure in flocks.

185

186   *Statistical Analyses*

187   Data were analysed in Genstat 14.1 using Linear Mixed Models (LMM) or

188   Generalized Linear Mixed Models (GLMM) for normal and non-normal data respectively,

189   with flock identity nested in date as a random term to control for repeated measures in all

190   cases. Initially, all probable explanatory variables were entered into the model. All possible

191   interactions between them were investigated and terms were sequentially dropped until the

192   minimal model contained only terms whose elimination would significantly reduce the

193   explanatory power of the model. Wald statistics and probability values for significant terms

194   were derived from the minimal model containing only significant terms, while values for

195   non-significant terms were obtained by adding each term individually to the minimal model

196   (Crawley 2002). The residuals for all models were visually inspected to ensure homogeneity

197   of variance, normality of error and linearity. All results with $P < 0.05$ are reported as

198   significant. Means are quoted ± s.e. throughout. Post-hoc analyses of differences between

199   levels within categorical variables (e.g. front, middle, back) were conducted by sequentially

200   excluding each level from (G)LMM analyses to enable comparisons of the remaining

201 category levels. Tables of results for all multifactorial analyses including all effect sizes and

202 standard errors are in the Appendices below.

203

204 *Preferential associations by species*

205   To test whether the birds showed preferential associations by species (prediction 1)

206 we randomly selected four focal birds per flock section and ran a GLMM with binary

207 response term (1,0) testing the probability that a focal bird's neighbour was a jackdaw.

208 Explanatory terms were focal bird species and the proportion of rooks in the flock.

209

210 *Positional differences by species*

211   To compare positional differences between the species in flocks, we randomly

212 selected one focal bird in each flock section, noting its species and that of its seven nearest

213 neighbours. We used seven neighbours because previous research indicates that individuals in

214 starling flocks interact with a fixed number of 6-7 neighbours (Ballerini et al. 2008a). Unlike

215 the analyses of associations, distances and alignments between neighbours, there was no need

216 to restrict analyses to four birds per flock section to avoid pseudoreplication. To test whether

217 rooks flew disproportionately near the leading edge of flocks (prediction 2) we used a

218 GLMM with a binomial response term (number of rooks out of the total of eight birds) and

219 flock section (front, middle or back) as an explanatory variable. Flock size, the proportion of

220 rooks, month (to control for possible seasonal variation) and time relative to sunset (because

221 individuals' motivation to reach preferred sites within the roost may increase as night

222 approaches) were fitted as additional variables.

223

224 *Proximity and alignment between neighbours*

9

225   To test whether distance and alignment differed between conspecific and

226   heterospecific neighbours (prediction 3) we noted the distance (in jackdaw lengths) and

227   directional alignment between focal birds (four per flock section) and their nearest

228   neighbours (see ESM). We then ran two LMMs with neighbour distance and neighbour

229   alignment as response terms and dyad type (jackdaws, rooks or mixed) as our variable of

230   interest, along with flock section (front, middle, back) and flock size. Distances were square-

231   root transformed and alignments were normalized for analysis using a Box-Cox power

232   transformation.

233

234   *Identification of discrete dyads within flocks*

235   Field observations and visual inspection of photographs indicated that jackdaws and

236   rooks commonly fly in discrete dyads within flocks (Coombs (1961) reported similar

237   observations). To confirm this, we used a custom-made script written in R ([www.R-](www.R-project.org)

238   [project.org](www.R-project.org)) to measure the distance between all individuals (in jackdaw or rook lengths, from

239   the midpoint of each bird) and their seven nearest same-species neighbours in a selection of

240   nine flock section photographs. In very dense flocks, even discrete dyads would tend to fly

241   near other dyads. As an illustrative sample, we therefore chose photographs of flock sections

242   in which the density was sufficiently low to allow us to identify dyads clearly. The

243   photographs used to examine jackdaw and rook dyads were not always the same, as some

244   images contained insufficient rooks. Using the neighbour-distance measurements, we

245   conducted the following analyses:

246

247   (1) Categorisation of discrete dyads and triads. We defined discrete dyads as same-

248   species neighbours whose inter-individual distance was less than half the distance to the

249   second closest neighbour. This conservative measure is likely to underestimate the true

250   frequency of discrete dyads in flocks as discrete dyads could nevertheless fly close to other

251   discrete dyads. We also investigated the occurrence of same-species triads of birds, defined

252   as cases where the nearest neighbour distances between three birds were all less than half the

253   distance to the fourth neighbour. Triads may occur among corvids when unpaired individuals

254   (either adult birds that had lost their partner or offspring from the previous breeding season)

255   associated with reproductive adult pairs, as described by Lorenz (Lorenz 1952). The results

256   are summarised in Table 1.

257

258   (2) Histograms of neighbour distances. For each of the photographs used in Table 1,

259   we plotted, for each species, histograms showing the frequency distribution of neighbour

260   distances. If birds often fly in discrete dyads one would expect frequency distributions to

261   exhibit a bimodal character, with the distribution of first neighbour distances being

262   considerably lower than that of the next six neighbours. As there is no generally accepted

263   formal test of bimodality, we present the histograms in Fig. A2 as qualitative support for the

264   presence of discrete dyads within flocks.

265

266   **RESULTS**

267   *Preferential association by species*

268   After controlling for the proportion of rooks within flocks, we found that a focal

269   bird's nearest neighbour was significantly more likely to be of the same species (GLMM: $N =$

270   454 neighbour dyads, $\chi^2 = 27.78$, $P < 0.001$; Table A1).

271

272   *Positional differences by species*

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273   Rooks made up only 21.8% ± 0.03 of flocks on average, but were disproportionately

274   likely to be positioned at the front of flocks (GLMM: N = 115 photographs; χ^2 = 26.61, P <

275   0.001; Fig. 1a; Table A2). The first bird at the leading edge was a rook in 19 out of 44 flocks

276   (= 43.2%), more than twice as often as expected by chance (binomial test: P = 0.001).

277   Species distributions within flocks were not significantly affected by flock size, month or

278   time to sunset (Table A2).

279

280   *Proximity and alignment between neighbours*

281   Neighbours flew more closely together in larger flocks (LMM: N = 454 neighbour

282   dyads; χ^2 = 6.09, P = 0.019; Fig. 1b) and in the middle of flocks relative to the front and back

283   (χ^2 = 17.35, P < 0.001; Table A3; Fig. 1c). Jackdaw dyads flew significantly closer together

284   than rook dyads or mixed dyads (LMM: χ^2 = 48.95, P < 0.001; Fig. 2a; Table A3), and the

285   directional alignment of same-species dyads was greater than that of mixed dyads (LMM: χ^2

286   = 26.93, P < 0.001; Fig. 2b; Table A4).

287

288   *Do birds fly in discrete* dyads*?*

289   An average of 41 ± 5% of jackdaws (range: 22 - 63%) and 46 ± 4% (range: 37 - 67%)

290   of rooks in the illustrative selection of photographs flew in clearly identifiable, discrete dyads

291   (Fig. 2c, Table 1). Histograms of neighbour distances commonly showed a bimodal character

292   with a peak before the average nearest neighbour distance for each species (Fig. A2),

293   suggestive of discrete dyads of birds flying in close proximity.

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295

296   **DISCUSSION**

12

297 Contrary to the assumptions of many mathematical models of single-species aggregations,

298 which treat individuals as equivalent and interchangeable, our results suggest that the

299 structure of mixed-species flocks may be critically influenced by species differences and

300 social systems. The larger and socially dominant rooks were disproportionately likely to be

301 located in the front of flocks. This effect is unlikely to result from the influence of particular

302 individual rooks, as our dataset contained photographs of numerous flocks of differing size,

303 but rather seems to represent a general property of mixed rook-jackdaw flocks. Nor is the

304 pattern readily explicable by species differences in flight velocity as rooks tend to be found

305 towards the front of flocks despite observational evidence suggesting that jackdaws can fly

306 faster (Coombs 1961). Previous work on fish schools (Krause et al. 2000), zebra herds

307 (Fischhoff et al. 2007) and small pigeon flocks (Nagy et al. 2010) suggests that individuals

308 located at the front of groups tend to assume leadership roles, initiating changes in direction

309 or pace of movement which are followed by group members. Similarly, rooks may play a

310 dominant role in influencing collective movements of mixed-species corvid flocks. It is

311 possible that rooks' preference for the front of flocks may simply reflect their motivation to

312 reach the roost first and obtain favoured positions (Coombs 1961). If this was the case, one

313 might expect rooks to move to the front as sunset approaches, but we found no such effect.

314 Moreover, roosting flocks form spectacular, swirling displays similar to starling

315 murmurations (King & Sumpter 2012) before settling, so individuals at the front of pre-

316 roosting flocks may not necessarily land first at the roost.

317

318 Thus, it thus remains unclear whether rooks derive benefits from positioning themselves

319 towards the front of flocks, whether jackdaws preferentially follow rooks or whether species'

320 relative positions reflect aerodynamic considerations Future work incorporating GPS

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321   technology to track flock members (Nagy et al. 2010) could assist in discriminating between

322   these possibilities.

323

324   The general rules of attraction, short-range repulsion and alignment among

325   neighbours proposed by models of self-organisation provide a valuable framework for

326   understanding flocking (Bajec & Heppner 2009; Petit & Bon 2010), but our results indicate

327   that their specific manifestations may be influenced by the characteristics of social systems.

328   Our measurements of neighbour distances and alignments are somewhat crude and, given the

329   noise in the data, they are likely to underestimate the true extent of spatial structure within

330   flocks. Nevertheless, a number of important patterns were apparent. First, the extent of

331   attraction and repulsion may vary depending on the position within a flock, the size of the

332   flock (see Beauchamp 2012 for similar results in semipalmated sandpipers, *Calidris pusilla*)

333   and the relationships between group members. Critically, corvids were not evenly distributed

334   across the flock but typically flew near conspecifics, with jackdaws being particularly closely

335   attracted to same-species neighbours, and birds of both species often appeared to fly in

336   discrete dyads. The occurrence of discrete dyads of birds would not be expected to emerge

337   from morphological or aerodynamic constraints alone and is likely to result from social

338   partners flying together, although further studies with identifiable individuals would be

339   needed to confirm this. Second, the alignment of neighbours was significantly higher if they

340   were of the same species, with jackdaw dyads showing near perfect parallel alignment (a

341   mean difference of only 3.8°). Both species form lifelong, monogamous pair bonds

342   characterised by high levels of affiliative behaviour and close proximity (Emery et al. 2007),

343   and our results suggest the possibility that these relationships are reflected in flock structure.

344

345   Together, our results suggest that the theoretical convenience of treating group

346   members as identical and interchangeable does not adequately reflect biological reality in

347   mixed-species flocks. Indeed, we would argue that this assumption is similarly unlikely to

348   hold in single species flocks where individuals vary and have social relationships.

349   Differences between individuals can give rise to leadership roles, which may be particularly

350   pronounced in mixed-species aggregations where larger and more dominant species may

351   commonly take the lead (King et al. 2009). Moreover, studies of both single-species and

352   mixed species-flocks must consider how the relationships between individuals may modulate

353   the degree of attraction, separation and alignment between group members. Thus, flock

354   structure cannot be fully understood without taking species' characteristics, their social

355   systems and individuals' relationships into account. Future work incorporating information

356   on the movements of known individuals will provide further empirical data which can be

357   integrated into mathematical models to better understand the influences of within-group

358   heterogeneity on collective movements.

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Table 1.

Occurrence of discrete dyads and triads of jackdaws and rooks in flocks

Flock ID	Total jackdaws	Jackdaw dyads	Jackdaw triads	Flock ID	Total rooks	Rook dyads	Rook triads
A	75	10 (27)	6 (24)	A	12	8 (67)	0
B	48	12 (50)	2 (13)	B	11	4 (36)	0
C	108	12 (22)	5 (14)	C	15	4 (27)	3 (20)
D	54	15 (56)	4 (22)	E	7	4 (57)	3 (43)
E	19	6 (63)	1 (16)	J	43	16 (37)	3 (7)
F	82	17 (41)	7 (26)	K	33	14 (42)	0
G	76	12 (32)	2 (8)	L	22	12 (55)	0
H	43	10 (47)	1 (7)	M	17	10 (59)	6 (35)
I	90	13 (29)	5 (17)	N	16	6 (38)	3 (19)
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.

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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.

470   Figure 1

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472   Figure 2
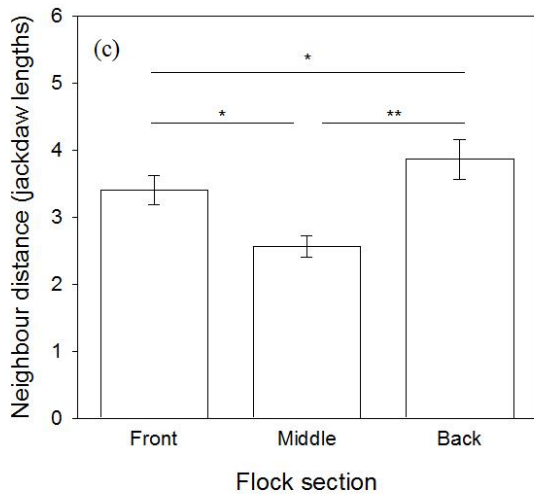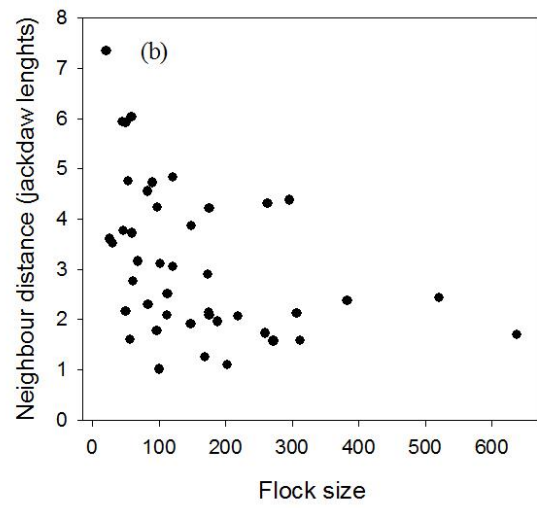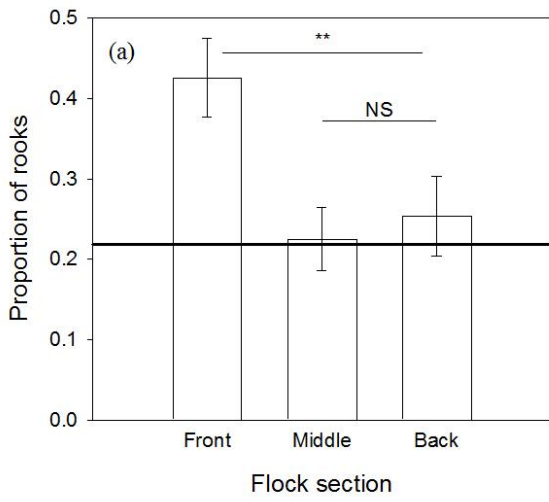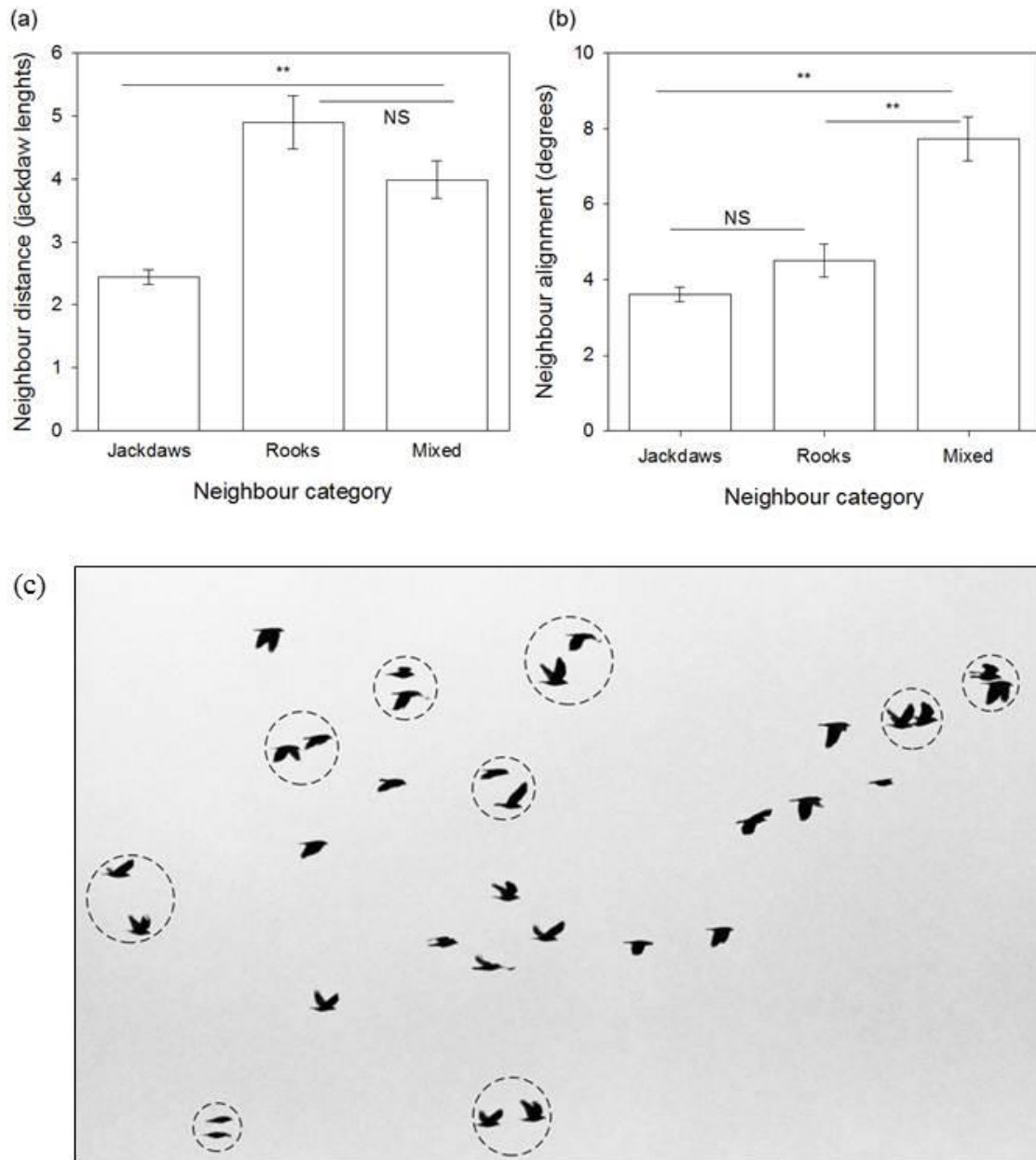
475 **APPENDIX**

476   Coefficient estimates in all tables represent the change in the dependent variable

477 relative to the baseline category and can thus be interpreted as measures of effect size.

478

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

480 jackdaw

	Wald statistic (χ^2)	d.f.	*P*
Full model			
Proportion of rooks in flock	50.27	1	<0.001
Focal species (jackdaw, rook)	27.78	1	<0.001
Minimal model	effect size	s.e.	
Constant	1.46	0.17	
Proportion of rooks in flock	-4.95	0.70	
Focal species - jackdaw	0	0	
- rook	-1.37	0.26	

481

482 This analysis used data from 454 neighbour dyads in 44 flocks. The binary response term

483 (1,0) indicated whether the neighbouring bird was a jackdaw. Flock identity nested in date

484 was fitted as a random term (estimated variance component $\pm$ SE: 0.00 $\pm$ 0.000).

485 **Table A2.** GLMM on factors affecting the proportion of rooks among focal birds and their

486 seven nearest neighbours

	Wald statistic (χ^2)	d.f.	*P*
Full model			
Proportion of rooks in flock	41.11	1	<0.001
Flock section (front, middle, back)	26.61	2	<0.001
Month (Oct, Nov, Dec, Jan, Feb)	8.84	4	0.065
Flock size	1.18	1	0.277
Time relative to sunset (min)	1.19	1	0.275
Minimal model	effect size	s.e.	
Constant	-0.29	0.20	
Proportion of rooks in flock	4.72	0.74	
Location - front	0	0	
- middle	-0.93	0.24	
- back	-0.78	0.19	

487

488 This analysis used data from 115 photographs of 44 flocks, with flock identity nested in date

489 fitted as a random term (estimated variance component ± SE: 0.201 ± 0.138). Post-hoc

490 analyses by exclusion showed that there were significantly more rooks in the front than in the

491 rest of the flock (front > middle: χ^2 = 23.67; P < 0.001; front > back: χ^2 = 11.07; *P* < 0.001;

492 middle = back: χ^2 = 0.61; *P* = 0.436).

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Table A3. LMM on factors affecting the distance between neighbours

	Wald statistic (χ^2)	d.f.	P
Full model			
Neighbour category (jackdaws, rooks, mixed)	48.95	2	<0.001
Flock section (front, middle, back)	17.35	2	<0.001
Flock size	6.09	1	0.019
Minimal model	effect size	s.e.	
Constant	1.67	0.07	
Neighbour category - Jackdaws	0	0	
- Rooks	0.51	0.09	
- Mixed	0.31	0.07	
Location - Front	0	0	
- Middle	-0.13	0.06	
- Back	0.16	0.07	
Flock size	-0.001	0.0004	

501

502 This analysis used data from 454 neighbour dyads in 44 flocks. The response term was the

503 distance between each of four focal birds per flock section and its nearest neighbour,

504 measured in jackdaw lengths, and square-root transformed for analysis. Flock identity nested

505 in date was fitted as a random term (estimated variance component ± SE: 0.065 ± 0.024).

506 Post-hoc tests by exclusion showed that jackdaw dyads flew closer together than rook dyads

507 or mixed dyads (jackdaws < rooks: $\chi^2 = 40.65$, $P < 0.001$; jackdaws < mixed dyads: $\chi^2 =$

508 27.16, $P < 0.001$; rooks = mixed: $\chi^2 = 1.64$, $P = 0.203$) and dyads in the middle of the flock

509 were closer than those in the front or back (middle < front: $\chi^2 = 5.83$, $P = 0.016$; middle <

510 back: $\chi^2 = 22.94$, $P < 0.001$; front < back: $\chi^2 = 5.19$, $P = 0.023$; Fig. 1c).

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515 **Table A4**. LMM on factors affecting the difference in alignment between neighbours

	Wald statistic (χ^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	

516

517 The analysis used data from 454 neighbour dyads in 44 flocks, with flock identity nested in

518 date fitted as a random term (estimated variance component ± SE: 0.001 ± 0.000). The

519 response term was normalized for analysis using a Box-Cox power transformation. Post-hoc

520 tests by exclusion showed that same-species dyads were more closely aligned than mixed

521 dyads (jackdaws < mixed: $\chi^2 = 25.24$, $P < 0.001$; rooks < mixed: $\chi^2 = 15.64$, $P < 0.001$;

522 jackdaws = rooks: $\chi^2 = 0.19$, $P = 0.663$).
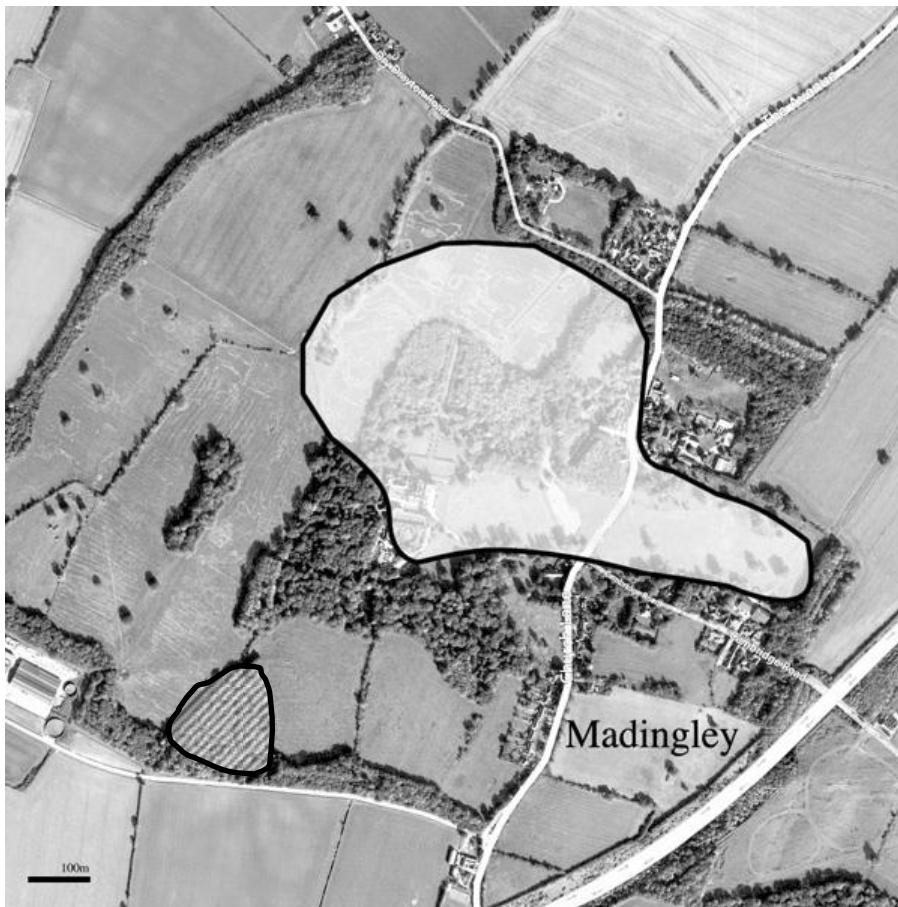
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532 **Figure A1**

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Figure A2

(a)

Distance in jackdaw lengths

(b)

Distance in rook lengths