Heterogeneous structure in mixed-species corvid flocks in flight

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Introduction

Background: Flocks of birds in flight represent a striking example of collective behaviour. Models of self-organization suggest that repeated interactions among individuals following simple rules can generate the complex patterns and coordinated movements exhibited by flocks. Such models are often based on the assumption that individuals are identical and interchangeable. However, group members often mix associatively according to a variety of morphological and physiological factors such as sex and size as well as species' social systems.

Problem: Studies of collective behaviour seldom consider the impact of **heterogeneity** on **collective behaviour** and fail to account for **individual characteristics** and **social relationships** among group members

Objective: To investigate how heterogeneity (*specifically species differences and social relationships*) can affect flock structure and dynamics. Mixed-corvid flocks of rooks and jackdaws are an ideal system to investigate this as (1) they spent a large portion of the year together in large groups; (2) both species' social system centres around long-term monogamous pair bonds; (3) rooks are larger and often dominant in foraging interactions and access to roosting sites.

Material & Methods

Flock analyses based on photos of mixed-species corvid flocks

What: front, middle and back thirds of corvid flocks (see picture)

How: Canon EOS 7D with Canon EF 100-400mm f/4.5-5.6 L IS lens (8fps)

When: sunset $\pm$ 45min between 19 Oct 2011 - 8 Feb 2012

Where: in and around the village of Madingley, Cambridgeshire

Photo selection: 115/1211 photos of 44 flocks (no duplicates, flock < 20 birds)

Analysis

- Species identification >95% certainty
- Randomly 4 focal birds selected in each flock section
- Determined species of focal and 7 nearest neighbours
- Measured distance to and relative alignment with neighbours

Results

1 Birds were closer together in larger flocks ($p=0.02$; Fig. 1b) and in the middle of flocks ($p<0.001$; Fig. 3R), which did not affect the species distribution within flocks ($p=0.28$).

2 Rooks were more likely to be at the front (Fig. 1a) and leading edge of the flock (*both*: $p<0.001$).

3 Birds preferentially associated with same species neighbours ($p<0.001$) and birds were often observed to fly in same-species dyads (Fig. 2).

4 Same-species neighbours were more aligned than mixed-species dyads ($p<0.001$; Fig. 3L).

Discussion

Models of self-organisation propose the simple rules of attraction, short-range repulsion and alignment among neighbours determine collective behaviour.

We show that these simple rules were affected by the size of and position within flocks, the relationships between group members and birds' distribution across flocks. Birds typically flew near conspecifics and in discrete dyads which may potentially reflect the monogamous pair-bonds in both species; rooks may have a dominant influence on the collective movements of the flocks.

Thus, **characteristics of individuals** and their **social systems** likely result in preferential associations that critically influence flock structure.

Future studies must consider the modulating effect of **heterogeneity** on the simple rules individuals use in **collective movements**.

Figure 1. (a) Proportion of rooks in the front, middle and back of flocks. The horizontal line indicates the average proportion of rooks across all flocks. (b) Relationship between flock size and neighbour distances.

Figure 2. Jackdaws flying in clearly identifiable, discrete dyads.

Figure 3. (left) Alignment between neighbours in jackdaw, rook and mixed dyads. (right) Distance between neighbours in the front, middle and back of flocks. Bars show means $\pm$ SE.

Selected literature

- Beauchamp, G. 2012. *Animal Behaviour* 83, 1125-1129;
Conradt, L. & Roper, T. J. 2005. *Trends in Ecology & Evolution* 20, 449-456; Coombs, C. J. F. 1961. *Bird Study* 8, 55-70; Couzin, I. D. & Krause, J. 2003. *Advances in the Study of Behavior* 32, 1-75; Krause, J. & Ruxton, G. D. 2002. Oxford: Oxford University Press; Sumpter, D. J. T. 2006. *Philosophical Transactions of the Royal Society B* 361, 5-22; Vicsek, T. & Zafeiris, A. 2012. *Physics Reports* 517, 71-140.

“Spectacular collective behaviour can be found in a large range of animal species. Our research highlights that heterogeneity plays an important role in these striking displays of group behaviour.”

Jolle Jolles