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Heterogeneous structure in mixed-species corvid flocks in flight

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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. However, such models often assume that individuals are identical and interchangeable, and fail to 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, *Corvus monedula*, and rooks, *Corvus frugilegus*, we show that birds preferentially associated with conspecifics and that, like high-ranking members of single-species groups, the larger and more socially dominant rooks positioned themselves near the leading edge of flocks. Neighbouring birds showed closer directional alignment if they were of the same species, and neighbouring jackdaws in particular flew very close to one another. Moreover, birds of both species often flew especially close to a single same-species neighbour, probably reflecting the monogamous pair bonds that characterize 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.

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-organizing 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 (1) long-range attraction to group members, (2) short-range repulsion and (3) 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, b; Hemelrijk & Hildenbrandt 2011).

Mathematical models of self-organization 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 nonrandom organizations 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 organization for birds worldwide, and an extensive literature suggests that

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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 preroost 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 homogeneous 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 (cf. 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 preroosting sites before combining in a single large flock above the roost (sunset $\pm$ 45 min), between 19 October 2011 and 8 February 2012 in an area of approximately 0.3 km^2 in and around the village of Madingley, Cambridgeshire, U.K (see Appendix Fig. A1). Photographs were taken perpendicular to the flocks' flight direction at a distance of approximately 100–300 m, from different locations throughout each evening so as to avoid pseudoreplication from repeated shots of the same flock. The number of different flocks photographed per evening ranged from one to 11 (mean $= 3.1 \pm 0.8$). We used a Canon EOS 7D digital SLR camera with a Canon EF 100–400 mm 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 maximize distinguishability between the features of jackdaws and rooks. The drive mode was set to high-speed continuous shooting (8 frames/s), 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 maximize 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, CA, U.S.A.). 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 in which 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 data set 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 (1) this allowed us to have several representatives from each flock section but (2) 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