



Collective decision making and social interaction rules in mixed-species flocks of songbirds



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Associations in mixed-species foraging groups are common in animals, yet have rarely been explored in the context of collective behaviour. Despite many investigations into the social and ecological conditions under which individuals should form groups, we still know little about the specific behavioural rules that individuals adopt in these contexts, or whether these can be generalized to heterospecifics. Here, we studied collective behaviour in flocks in a community of five species of woodland passerine birds. We adopted an automated data collection protocol, involving visits by RFID-tagged birds to feeding stations equipped with antennae, over two winters, recording 91 576 feeding events by 1904 individuals. We demonstrated highly synchronized feeding behaviour within patches, with birds moving towards areas of the patch with the largest proportion of the flock. Using a model of collective decision making, we then explored the underlying decision rule birds may be using when foraging in mixed-species flocks. The model tested whether birds used a different decision rule for conspecifics and heterospecifics, and whether the rules used by individuals of different species varied. We found that species differed in their response to the distribution of conspecifics and heterospecifics across foraging patches. However, simulating decisions using the different rules, which reproduced our data well, suggested that the outcome of using different decision rules by each species resulted in qualitatively similar overall patterns of movement. It is possible that the decision rules each species uses may be adjusted to variation in mean species abundance in order for individuals to maintain the same overall flock-level response. This is likely to be important for maintaining coordinated behaviour across species, and to result in quick and adaptive flock responses to food resources that are patchily distributed in space and time.

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Group living is an integral part of the life history of many animals, providing benefits to individual participants by reducing predation risk (Cresswell & Quinn, 2004; Hamilton, 1971; Ioannou, Guttal, & Couzin, 2012; Krause & Ruxton, 2002), facilitating information transfer (Couzin, 2009) and improving decision making (Sumpter, Krause, James, Couzin, & Ward, 2008; Ward, Herbert-Read, Sumpter, & Krause, 2011; Ward, Krause, & Sumpter, 2012; Ward, Sumpter, Couzin, Hart, & Krause, 2008). However, social living may also be costly, as it can increase

resource competition (Dhondt, 2012; Krause & Ruxton, 2002), and exposure to parasites and disease (Krause & Ruxton, 2002). One common strategy to reduce competition while maintaining antipredation benefits is to join mixed-species groups (Greenberg, 2000; Harrison & Whitehouse, 2011; Krause & Ruxton, 2002). By associating with ecologically similar, but not identical, species, individuals may potentially be able to continue acquiring relevant benefits such as safety from shared predators (Sridhar, Beauchamp, & Shanker, 2009) and information about the environment (Seppanen, Forsman, Monkkonen, & Thomson, 2007), while reducing niche overlap (Greenberg, 2000; Harrison & Whitehouse, 2011; Krause & Ruxton, 2002). If this hypothesis is true, we predict that, given a choice of where to forage within a patch, moving individuals should choose areas of high density, regardless of species. However, the strength of

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social attraction may vary, reflecting individual and species differences in the balance of costs and benefits, or the need to maintain flock-level cohesion (Aplin, Farine, Mann, & Sheldon, 2014). To test these predictions, we investigated the flocking dynamics in a wild population of songbirds.

Studies of the social behaviour of monospecific groups have shown that strikingly complex patterns of movement and group behaviour can emerge from relatively simple social interactions between individuals (often referred to as collective animal behaviour; Ballerini et al., 2008; Buhl et al., 2006; Guttal & Couzin, 2010; Ioannou et al., 2012; Sumpter, 2006, 2010). These patterns can often be reproduced using simple algorithmic rules (Couzin & Krause, 2003; Herbert-Read et al., 2011; Katz, Tunstrom, Ioannou, Huepe, & Couzin, 2011; Sumpter, 2010). The emergence of complex grouping behaviour from simple social rules based upon attraction to, and repulsion from, nearby conspecifics (Arganda, Pérez-Escudero, & De Polavieja, 2012; Couzin & Krause, 2003; Herbert-Read et al., 2011; Katz et al., 2011; Pérez-Escudero & De Polavieja, 2011; Pérez-Escudero et al., 2013; Sumpter, 2010) could apply equally to mixed-species groups (Farine, Downing, & Downing, 2014; Jolles, King, Manica, & Thornton, 2013), such as in mixed schools of fishes (Hoare, Ruxton, Godin, & Krause, 2000), herds of ungulates (Fitzgibbon, 1990) or flocks of birds (Farine, 2013a; Farine, Garroway, & Sheldon, 2012; Farine & Milburn, 2013). As Morse (1970, p. 120) stated, '[group] formation depends upon positive responses by individuals to members of their own or other species', where the positive response separates mixed-species groups from aggregations at a locally abundant resource (such as food or water).

One approach that has successfully linked individual decision rules to the biology of social groups is a combination of empirical data with mathematical models of decision making derived from theory (Sumpter, Mann, & Perna, 2012). Fitting models to empirical data has been used in order to determine the rules that maintain synchrony in birds (Ballerini et al., 2008), fish (Herbert-Read et al., 2011; Katz et al., 2011) and invertebrates (Ame, Halloy, Rivault, Detrain, & Deneubourg, 2006). Once a predictive model is generated, simulations can be used to make predictions about the adaptive function of these rules. For example, the aggregation rule used by cockroaches (Ame et al., 2006) was found to maximize individual fitness when simulated in agent-based models. As a result, this study suggested that temporary safe patches can emerge as a by-product of the dynamic self-organization by individuals responding to the distribution of others, even in a uniform landscape (Ame et al., 2006).

We recorded the movement decisions of individually marked birds participating in mixed-species flocks to investigate the social rules that drive the formation and maintenance of animal groups. (1) We investigated within-flock dynamics in order to determine whether birds moved towards others or away from them when foraging in food patches. (2) We then compared these patterns to a null model in order to determine how the observed pattern of movement differs from random. (3) We then fitted a Bayesian decision-making model (Arganda et al., 2012) that enabled us to determine (a) whether birds had different rules for conspecifics and heterospecifics, and (b) whether species varied in their use of conspecific and heterospecific interaction rules. (4) Finally, we used an agent-based model to determine whether inferred interaction rules could quantitatively reproduce the patterns we observed and to explore the properties of the decision-making rules that we inferred. In doing so, this study provides a benchmark for understanding the nature of mixed-species flocks using some recently developed approaches from computational biology.

METHODS

Study Site and General Protocol

The study took place at Wytham Woods (51° 46'N, 1° 20'W), Oxfordshire, U.K. Great tits, *Parus major*, blue tits, *Cyanistes caeruleus*, marsh tits, *Peocile palustris*, coal tits, *Periparus ater*, and Eurasian nuthatches, *Sitta europaea*, were caught in mist nets using multi-access feeders regularly during the two winters in which the study took place. In addition, locally breeding birds and their offspring were caught in their nestboxes during the spring as part of long-term field studies in this population (Aplin, Farine, Morand-Ferron, & Sheldon, 2012; Farine & Lang, 2013). All individuals were fitted with a British Trust for Ornithology (BTO) metal leg ring and a plastic leg ring containing a uniquely coded PIT tag (IB Technology, Aylesbury, U.K.). We estimate that the proportion of the population fitted with PIT tags exceeded 90% at the time of the study (Aplin, Farine, et al., 2013), and we do not expect that untagged birds had much impact on our results. We conducted five replicates of the study in February 2011 and 15 replicates between December 2011 and February 2012. Replicates were placed throughout the woods, capturing the variation in population sizes driven by different understory habitat densities, and other habitat features. On some occasions, up to three replicates were running simultaneously; however, these were spaced at least 1 km apart and no individuals were detected at more than one replicate when replicates were operating simultaneously.

Field Observations

At each replicate, we deployed a square of four identical feeders filled with unhusked sunflower seeds (henceforth a 'patch'; Fig. 1a). Each feeder contained two access holes, both fitted with an antenna capable of reading the PIT tag fitted to birds as they land on the surface of the antenna (Francis Instruments, Cambridge, U.K.). We filled feeders with sunflower seed, which birds typically pick up by landing on the feeder and then fly to a nearby tree to process (see [Supplementary movie](#)), thereby minimizing interference competition (Aplin, Sheldon, & Morand-Ferron, 2013). Further, these feeders provide food at a constant rate thereby removing any effects of perceived resource depletion on foraging decisions (Stephens, Brown, & Ydenberg, 2007). These feeders also represented by far the most abundant food source available in the local patch, and the availability of nonfeeder options nearby were unlikely to have much impact on the behaviour of visiting birds. Eating seed in this fashion, birds did not form independent groups on each feeder, but maintained more natural flock formation in the nearby trees.

Feeders were placed 50 m apart, which is within visual and auditory range of other birds, but avoids the potential for individuals to feed on different feeders from the same perching location. To minimize differences in microhabitat features (presence of nearby habitat refuges) that are known to alter feeding behaviour (Dolby & Grubb, 2000), we moved some feeders inwards up to 5 m when setting out each patch. Patches were always contained within areas with uniform habitat density (but these could vary between patches). Each patch was set out and marked in the days preceding deployment. Feeders were then installed after dark the night before we started data logging to enable natural discovery of the patch. Patches were checked from day 2 onwards and removed once the food in any one feeder was fully depleted; if this did not happen the deployment was ended on the fourth day and data from that day were discarded. The antennae recorded the identity of all birds visiting the feeder, scanning for the presence of a tag every 1/16th of a second and logging one record per bird in each 15 s interval.

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