

Long-distance migrating species of birds travel in larger groups

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How individuals migrate over long distances is an enduring mystery of animal migration. Strong selection pressure for travelling in groups has been suggested in long-distance migrating species. Travelling in groups can reduce the energetic demands of long migration, increase navigational accuracy and favour group foraging at migratory halts. Nevertheless, this hypothesis has received scant attention. I examined evolutionary transitions in migration distance in all North American breeding species of birds. I documented 72 evolutionary shifts in migration distance in the pool of 409 species. In contrasting clades, long-distance migration, as opposed to short-distance migration, was associated with a larger travelling group size. No other transitions occurred alongside in other traits such as group size in the non-breeding season or body mass. The results suggest that larger group sizes have been beneficial in the evolution of long-distance migration in a large clade of birds.

Keywords: birds; flight formation; group size; migration; navigation accuracy

1. INTRODUCTION

Migration in many species of animals, ranging from insects to birds and large mammals, often involves movements across large distances, including spectacular trips of upwards of 20 000 km in some bird species [1]. How individuals migrate over such long distances is an enduring mystery in animal migration. Long-distance migration is energetically costly [2], requires considerable navigational skills to reach distant destinations [3] and forces animals to make halts in habitats whose inherent quality in terms of predation risk and foraging opportunities is often little known [4].

In birds, travelling in flocks has been thought to counteract the negative consequences of long-distance migration through three distinct mechanisms. First, flight formation in flocks can increase aerodynamic performances thus yielding considerable energy savings over long distances, especially for larger species [5]. Flocking can also enhance the ability to locate patchily distributed thermals that alleviate travelling costs in soaring species [6].

Second, by pooling information about headings, flocking may allow birds to head in the right direction more often [7] and may also assist in locating limited or obscured landmarks while flying [8]. Flocking may

also allow inexperienced individuals the opportunity to follow more knowledgeable companions to the distant target [9,10].

Third, travelling in flocks can facilitate flock formation during migratory halts as the birds are already in flocks when they stop [11]. Flocking while foraging has been shown to increase foraging efficiency and decrease predation risk [12], and may be particularly useful in stopover habitats that are at best visited only infrequently [13].

Given these benefits, strong selection pressure for travelling in flocks should exist in long-distance migrating species [14,15]. Nevertheless, I am aware of only one test of the hypothesis in one clade of birds [16]. However, this study did not consider the fact that repeated instances of flocking in long-distance migrating species may not be independent evolutionary events and instead reflect inheritance from a common ancestor. Here, I examined evolutionary transitions in migration distance in all North American breeding species of birds. I hypothesized that travelling flock size, in the clades involving a transition in migration distance, would be larger in long-distance migrating species, and thus partly explain how species can migrate over such long distances.

Evolutionary transitions in migration distance may be accompanied by other transitions that may on their own explain any relationship with flocking. For instance, long-distance migrating species may be more sociable in the non-breeding season to increase foraging efficiency or reduce predation risk. Travelling in flocks would then simply reflect the more sociable nature of such species, which has evolved to provide benefits not primarily during migration but during the non-breeding season. I thus examined whether long-distance migrating species foraged in larger groups during the non-breeding season. Similarly, I determined whether long-distance migrating species are generally smaller, which would increase their relative predation risk [17] and also favour more sociality in the non-breeding season. I also considered transitions to nocturnal migration, which may hinder the formation of flocks [18].

2. MATERIAL AND METHODS

I searched the avian literature to determine the migration propensity of all species of North American birds nesting on the continent. Migration was defined as regular return movements year after year between breeding and wintering sites. I excluded species with insufficient information about migration, irruptive species (moving irregularly after breeding over varying distances), dispersive species (moving in any direction, including altitudinal migrants) and non-native species.

I distinguished between short- and long-distance migrating species, depending on whether one leg of the migration journey covered at most 15° of latitude or more. This was adequate in North America, as most species move on a north–south axis. I noted for each species male body mass (BM) (preferably during the non-breeding season), maximum group size while foraging during the non-breeding season and maximum group size while flying during the migration. I tallied maximum group size while foraging, including or excluding members of other species, as many species foraged in mixed-species groups. This distinction rarely applied to group size while flying and was not noted. Maximum group size is more commonly reported than other statistics of grouping and has been related earlier to ecological features [19]. I determined whether migration took place primarily during the day as opposed to the day and night.

All quantitative data were log₁₀-transformed prior to statistical analysis. A phylogenetic analysis of these quantitative traits relied on independent contrasts calculated using the PDAP module [20] within MESQUITE [21], assigning all branch lengths to 1. The phylogeny was based on recent papers describing phylogenetic

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relationships among and within avian families (electronic supplementary material, appendix 1). I relied on the ancestral state reconstruction within MESQUITE to establish the most parsimonious distribution of categorical traits along the phylogeny lineages. This reconstruction allowed me to determine all evolutionary transitions in migration distance. None of the paths that joined two lineages with such a transition overlapped each other in order to ensure statistical independence [22]. I used the Wilcoxon-signed rank test for quantitative variables to establish whether the distribution of contrast values for these evolutionary transitions differed significantly from zero. I used the McNemar Test [23] to determine whether transitions between states of the timing of migration were more likely in one direction or another as migration distance shifted.

3. RESULTS

I uncovered 72 evolutionary transitions in migration distance among the 409 species of North American birds included in the dataset (electronic supplementary material, appendix 2). Evolutionary transitions spanned a large range of families from ducks to sparrows. Parsimonious state reconstruction revealed that migration distance was short at the base of the tree, and that evolutionary transitions in migration distance involved about equally frequently shifts from short- to long-distance migration, or vice versa (electronic supplementary material, appendix 2).

In clades with an evolutionary transition in migration distance, maximum group sizes while flying were larger in the long-distance migrating species ($S = -112.5$, $p < 0.0001$; figure 1) with no concomitant changes in BM ($S = 216.5$, $p = 0.17$), maximum conspecific group size while foraging ($S = -177.5$, $p = 0.17$) or maximum total group size while foraging ($S = -128.5$, $p = 0.27$). Alongside evolutionary transitions in migration distance, the timing of migration shifted five times with no preferential direction ($\chi^2 = 0.8$, $p = 0.37$).

4. DISCUSSION

Independent evolutionary transitions in migration distance were common in the large pool of North American species. A similar finding was made in two genera of European passerine birds [24], suggesting that long-distance migration has evolved independently several time in birds [25]. As expected, long-distance migration, as opposed to short-distance migration in contrasting clades, was associated with a larger travelling group size.

The alternative hypothesis that other evolutionary transitions, which occurred alongside the shift in migration distance, accounted for the increase in travelling flock size appears unlikely. The shift in migration distance was not related to a change in non-breeding group size or BM, which could both account for changes in flocking propensity while travelling. Flocking in the non-breeding season was also unrelated to migration distance in one clade of birds [26]. Similarly, few transitions occurred in the timing of migration, which has been known to influence flocking [18].

Recent studies imply that species that are sedentary rather than migratory have a larger relative brain size, which would facilitate innovation in the harsher conditions faced by non-migratory species [27]. It could be argued that long-distance migrating species would also benefit from greater behavioural flexibility, because of the greater challenges faced by species

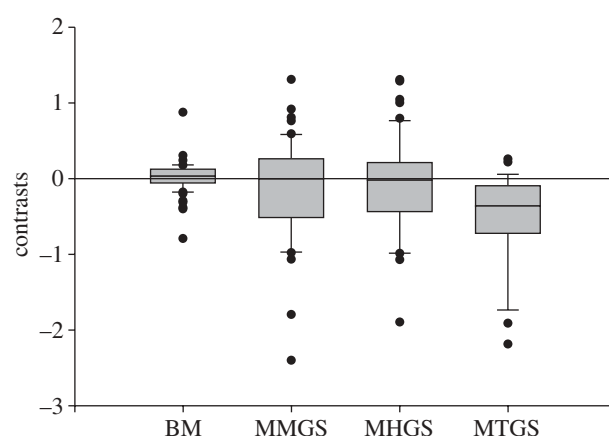


Figure 1. Box plots of the phylogenetically independent contrasts for body mass (BM), maximum group size in the non-reproductive season (monospecific (MMGS) and heterospecific (MHGS)) and travelling group size (MTGS) for migrating species of North American birds. Negative contrast values indicate that short-distance migrating species have lower values than long-distance migrating species.

forced to forage in a vast array of habitats along the route [4]. It would therefore be interesting in the future to link relative brain size to migration distance and not only to the propensity to migrate at all, and to uncover whether some individuals specialize in acquiring directional information while others use the information provided by others [15].

The implication of this study is that evolutionary changes in flock size while travelling were associated with shifts in migration distance. It is not clear whether initially larger flock sizes allowed longer migration or if longer migration favoured the evolution of larger flock sizes. Mapping of flocking propensity and migration distance on a phylogenetic tree could be used to assess causality, as has been done for other traits that have co-evolved with migration distance [28].

These findings confirm the earlier finding in raptors that travelling in flocks is more common in species migrating further [16]. Here, I extend these results to all North American breeding species of birds, using an evolutionary framework where I identified independent evolutionary transitions in migration distance. This finding could be examined in other areas, such as in the western Palaearctic, where migration distance and flocking tendencies are well documented [29].

Migration is also known in other taxa such as mammals, reptiles, insects and fishes. Migration over large distances can occur alone [30] or in large groups [31] and a challenge for future studies will be to determine when the evolution of migration in groups is more likely to occur. Obviously, travelling in groups is not necessary for long-distance migration, but the results of this study indicate that there is strong selection pressure to travel in larger groups when migration occurs over longer distances in a large clade of bird species.

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