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Reduced flocking by birds on islands with relaxed predation

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Adaptive hypotheses for the evolution of flocking in birds have usually focused on predation avoidance or foraging enhancement. It still remains unclear to what extent each factor has contributed to the evolution of flocking. If predation avoidance were the sole factor involved, flocking should not be prevalent when predation is relaxed. I examined flocking tendencies along with mean and maximum flock size in species living on islands where predation risk is either absent or negligible and then compared these results with matched counterparts on the mainland. The dataset consisted of 46 pairs of species from 22 different islands across the world. The tendency to flock was retained on islands in most species, but in pairs with dissimilar flocking tendencies, island species were less likely to flock. Mean and maximum flock size were smaller on islands than on the mainland. Potential confounding factors such as population density, nest predation, habitat type, food type and body mass failed to account for the results. The results suggest that predation is a significant factor in the evolution of flocking in birds. Nevertheless, predation and other factors, such as foraging enhancement, probably act together to maintain the trait in most species.

Keywords: birds; flocking; islands; relaxed predation; pairwise comparative method

1. INTRODUCTION

Although foraging in flocks is common in many species of birds, the precise adaptive value of the behaviour is not clear. As with other social systems in animals, adaptive hypotheses for the evolution of flocking usually emphasize predation avoidance or foraging enhancement (Krause & Ruxton 2002). However, it has proved difficult to disentangle the relative contribution of each factor. Comparative studies using naturally occurring variation in sociality among species represent one way to examine the role of these two ecological factors in the evolution of flocking in birds.

On many islands, animals experience little predation pressure because of a lack of natural enemies. Generally, studies have shown that living on islands with relaxed predation can have a large impact on morphological and behavioural traits (Fullard 1994; Blumstein *et al.* 2000). Willis (1972) was the first to suggest that if flocking is mostly an adaptation to reduce predation, island bird species that experience little or no predation will show little or no flocking when compared with similar mainland species that are exposed to predation. The idea is that flocking should be reduced over evolutionary times in the absence of positive selection by predation pressure (Wcislo & Danforth 1997) or adjusted opportunistically by individual birds in flocks in response to the perceived decrease in predation (Mangel 1990; Szekely *et al.* 1991).

There have been few investigations of flocking behaviour on islands. Willis (1972) reported little flocking in Hawaii, supporting his hypothesis of reduced flocking on islands with relaxed predation. Ironically, later studies found the opposite effect: flocking occurs in many Hawaiian islands, as does avian predation (Hart & Freed 2003). Reduced flocking has also been observed in several avian taxa in Jamaica when compared with their counterparts in nearby Costa Rica (Pulliam 1973). However, the existence of several avian predators on the island implies that other ecological factors must be responsible for differences in sociality. In mammals, one study documented smaller group sizes in a population of long-tailed macaques (*Macaca fascicularis*) living on a predator-free island, when compared with a nearby island with predators (Van Schaik & Van Noordwijk 1986). All of the aforementioned studies are essentially based on a sample size of one because they include only one comparison between an island and a matched mainland species. This means it is difficult to separate the effect of relaxed predation from the effect of island and species characteristics.

Here, I examine differences in flocking behaviour in matched pairs of island and mainland species from different areas around the world. I documented the general tendency to flock, along with mean and maximum group size, in island and matched mainland species. I predicted that if predation alone were responsible for the evolution of flocking, flocking should not occur in island populations exposed to relaxed predation. By contrast, if predation plus other factors were involved, flocking should occur but to a reduced degree. Changes in flocking behaviour in response to variation in predation have been documented previously. Most of these studies have focused on adjustments in group size after a temporary increase in predation risk. For instance, group size usually increases in response to the simulated presence of a predator (Caraco *et al.* 1980; Szekely *et al.* 1989). The island study provides an opportunity to examine adjustment in flocking behaviour when predation is maintained at a low level over a longer period of time.

2. METHODS

I searched the literature to identify islands where the extent of predation on bird species could be assessed. For the analysis, I considered only predation on foraging birds during the

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non-breeding season because predation on adult foraging birds is probably most relevant to the choice of foraging group size. Predation on eggs or nestlings during the breeding season was therefore noted but discounted unless the same predators targeted adult birds in the non-breeding season. In a few cases, I included islands where avian predators were considered vagrants so that predation risk was deemed negligible there. Also in a few cases, I included islands where potential predators occupied habitats that did not overlap with those of the bird prey species. The main sources of information about predation were diet analysis and accounts of predator attacks. In many cases, personal observations by researchers on predator–prey relationships confirmed and complemented this information.

On islands where the risk of predation was deemed either absent or negligible, I systematically documented the flocking behaviour of all bird species present. I classified species into one of three categories of flocking behaviour based on accounts of aggregations during the non-breeding season: (i) strictly solitary: birds forage singly; (ii) occasionally social: aggregations of more than two birds occur under some circumstances but are not common and involve few individuals; or (iii) strictly social: individuals search for food and/or feed in groups. When group size data were available, I tallied mean and maximum group size to provide quantitative estimates of flocking behaviour. I also distinguished between flocking involving conspecifics (intraspecific flocking) and flocking involving other species (mixed-species flocking).

The final step consisted of pairing each selected island species with the most closely related species on the mainland. Mainland was defined as any large adjoining body of land where predation risk was deemed non-negligible. In most cases, the mainland was the nearest continent where a fuller complement of mammalian, reptilian and avian predators could be found. The mainland species came from a mainland population of the same species, a mainland sub-species, or a sister species as identified from recent phylogenetic analyses based on traits other than flocking behaviour. In a few cases, I paired a species with a relative from the same genus living on the mainland in a similar habitat. The flocking behaviour of these mainland species was determined as described above.

I excluded from the analysis all pairs that consisted of only solitary species because lack of flocking by island species cannot be related exclusively to relaxed predation in these cases (Read & Nee 1995). In pairs of species with dissimilar flocking tendencies, I used the McNemar test with Yates' correction for continuity to determine whether the less sociable species occurred more often on islands than on the mainland. In pairs for whom I had estimates of mean or maximum group size, I used the Wilcoxon signed-ranks test to determine whether the median estimate was smaller on islands than on the mainland. When testing predictions, I used one-tailed statistical tests throughout.

Differences in flocking behaviour between the members of a pair may reflect changes in predation only if other ecological factors that influence flocking behaviour remain constant between the species. Body mass, food type, population density, food availability and habitat openness have all been discussed as potential correlates of flocking behaviour in birds. Flocking may be more common in smaller, more vulnerable species (Thiollay & Jullien 1998), in species that forage on clumped resources (Crook 1965) or in open, riskier habitats (Buskirk 1976), in species that exploit more abundant food sources (Davies 1976; Elgar 1987; Grubb 1987; Delestrade 1999) and in species where population density is sufficient to promote aggregations. If these parameters vary significantly between the island and mainland species, any differences observed cannot be attributed solely to the difference in predation pressure. I collected data on these potential confounding factors for each species except for food abundance for which estimates were not available.

3. RESULTS

I uncovered 22 islands where predation on foraging birds during the non-breeding season was deemed either absent or negligible (see electronic Appendix A). These islands are situated mostly in the tropics, e.g. the Caribbean, Indian, Atlantic and Pacific Oceans. They generally lie very far from the mainland and harbour a depauperate avifauna. Most of these islands are exploited for their resources and birds are usually confined to protected areas. I documented flocking behaviour in 46 island species from 15 different families. Limited knowledge about flocking behaviour or poorly known phylogenetic relationships precluded inclusion of additional species in the analysis.

For intraspecific flocking, I detected no differences in flocking tendencies between island and matched mainland species in 35 pairs (76.1%). In the remaining 11 cases, 10 species (90.9%) flocked to a lesser extent on islands than on the mainland ($p < 0.01$). I detected no difference in the occurrence of mixed-species flocking in 17 out of the 32 pairs with available data (53.1%). In the remaining 15 cases, mixed-species flocking occurred to a lesser extent on islands than on the mainland in 14 pairs ($p < 0.005$). Combining the available data for intra- and mixed-species flocking, seven pairs (15.2%) showed dissimilar overall flocking tendencies, and in all cases island species flocked to a lesser extent than their mainland counterparts ($p < 0.025$).

Mean flock size was smaller on islands than on the mainland ($p = 0.023$, $n = 17$; figure 1). Maximum flock size was also smaller on islands than on the mainland ($p < 0.0001$, $n = 23$; figure 1). In the 23 pairs where estimates were available, maximum flock size was smaller on islands than on the mainland in 19 pairs.

I compared ecological traits in the subset of species pairs that showed either dissimilar flocking tendencies or differences in mean or maximum group size ($n = 26$; electronic Appendix A). Male body mass was not different between the island and matched mainland species (Wilcoxon's signed-ranks test, $p = 0.82$, $n = 13$). In all but two of the 26 cases, island and matched mainland species foraged in the same type of habitat. In one exception, the island species foraged in a more open habitat than did the mainland counterpart, whereas in the other, it foraged in a more closed habitat. In all but seven cases, island and matched mainland species foraged on the same type of food. The exceptions were five island species that were more insectivorous than their mainland counterparts and two island species showing the opposite trend, a non-significant difference (McNemar's test, $p > 0.25$).

In terms of population density, 10 island species were considered either rare or uncommon, and therefore probably occurred at a lower density than on the mainland.

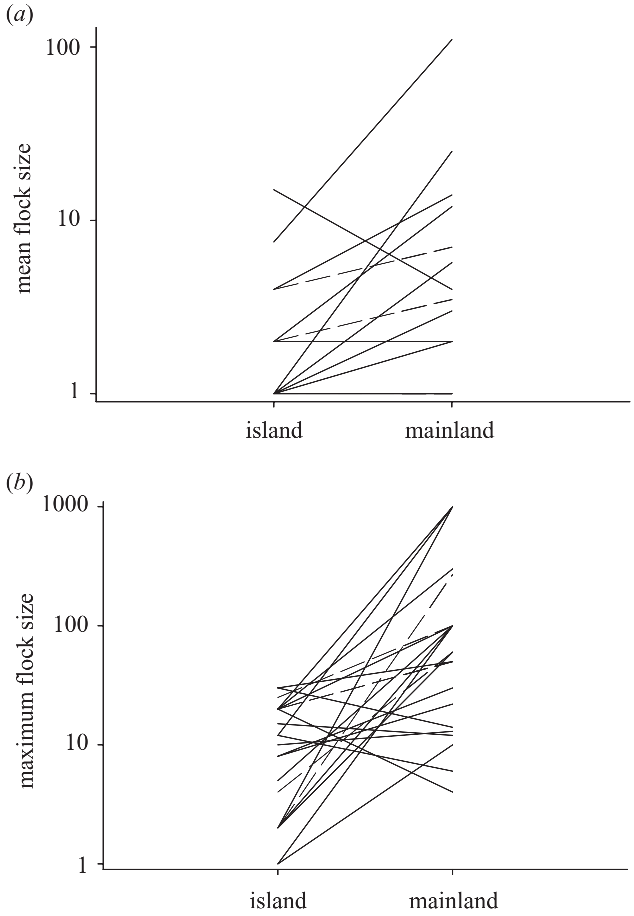

Figure 1. Comparison of (*a*) mean ($n = 17$), and (*b*) maximum ($n = 23$) flock size in island and matched mainland species counterparts. Dashed lines indicate pairs including a rare or uncommon island species.

Nevertheless, the median decrease in mean flock size was not different in the subset of island species occurring at lower densities than on the mainland (median = 0, $n = 5$) than in the subset of island species occurring at similar densities than on the mainland (median = −2, $n = 11$, Wilcoxon's two-sample test, $p = 0.42$). Similarly, the median decrease in maximum flock size was not different in the subset of island species occurring at lower densities than on the mainland (median = −56, $n = 5$) than in the subset of island species occurring at similar densities than on the mainland (median = −58, $n = 17$, Wilcoxon's two-sample test, $p = 0.82$).

Many island species experienced predation during the breeding season, usually after the introduction of predators such as rats or snakes (see electronic Appendix A). The median decrease in mean flock size was not different in the subset of island species that experience no predation (median = −3.4, $n = 2$) than in the subset of island species exposed to predation during the breeding season (median = −0.75, $n = 10$, Wilcoxon's two-sample test, $p = 0.60$). Similarly, the median decrease in maximum flock size was not different in the subset of island species that experience no predation (median = −98.5, $n = 4$) than in the subset of island species exposed to predation during the breeding season (median = −30, $n = 9$, Wilcoxon's two-sample test, $p = 0.13$).

4. DISCUSSION

The pairwise comparative analysis showed that flocking behaviour in birds is often reduced when species experience less predation. Indeed, on islands where predation on foraging birds was deemed either absent or negligible during the non-breeding season, bird species showed a lesser tendency to flock and/or occurred in smaller flocks than closely related mainland species. Nevertheless, the tendency to flock was retained in most island species.

Differences in ecological factors between island and mainland habitats appeared to have little influence on the results. Factors believed to influence flocking behaviour, such as body mass, food type and habitat openness did not differ between the island and matched mainland populations.

Some island species did occur at low densities. Low population density could conceivably place a limit on aggregation size. However, it may also be the case that low population density simply leads to the formation of fewer flocks rather than smaller flocks (Alonso *et al.* 1987). For example, mean flock size in warblers wintering in the Virgin Islands was not influenced by population density (Ewert & Askins 1991). In Hawaii, mean and maximum flock size in mixed-species groups varied little between populations of different density (Hart & Freed 2003). Furthermore, I also documented reduced flocking in island species regardless of density, suggesting that population density was not a confounding factor in the analysis.

Reduced flocking on islands might reflect low food availability. However, there is little evidence that habitat productivity is typically less on islands. In fact, islands often support much higher densities of animals than corresponding mainland habitat, suggesting that at the very least island habitats are productive enough to support large populations (Wallace 1978; Blondel 2000). For instance, groups of long-tailed macaques were smaller on an island isolated from predators than on nearby island exposed to predation, despite the fact that productivity was similar at the two locations (Van Schaik & Van Noordwijk 1986). In the present dataset, which included many islands and habitats from many different parts of the world, it also seems unlikely that productivity would be consistently lower on islands.

Reduced flocking on islands may also sometimes be the result of a depauperate avifauna. It is therefore possible that low species diversity can restrict the formation of mixed-species flocks. Here, mixed-species flocking was less common on islands, perhaps because of the lack of suitable companion species. However, the island effect on flocking was apparent even in intraspecific flocks.

It has been suggested that anti-predator behaviour in one context may be maintained by the presence of any predator even in a different context. For instance, anti-predator behaviour at night in a marsupial species was thought to be maintained after encounters with a diurnal predator (Blumstein & Daniel 2002). Here, flocking in the non-breeding season was still reduced in species known to suffer from predation during the breeding season. A larger sample size will be needed to examine this idea more fully. Nevertheless, it may be the case that birds can learn that some predators during the breeding season are innocuous during the non-breeding season.

It is unclear whether the solitary island species have lost the ability to flock. One would expect that in the absence of positive selection for flocking, random genetic drift mutations would lead to the eventual disappearance of flocking (Wcislo & Danforth 1997). However, if flocking on islands is costly to maintain, perhaps because of increased competition for food in groups, one would expect that with little predation pressure, individuals would gain an advantage as flocking behaviour is lost. It is not clear how much time would be needed for a trait such as flocking to disappear from a population through random genetic drift mutations or active selection against the behaviour. In guppies, social behaviour persisted to some extent 100 generations after a population from a high-predation site was introduced to a low-predation site (Magurran *et al.* 1992). In other cases, relaxed predation pressure has been shown to exert little influence on behaviour even thousands of years after isolation from predators (Blumstein 2002). Future work could document the responses of solitary island species to the presence of potential predators to see whether flocking behaviour has been lost or simply lays dormant.

In island species where flocking was not documented, predation probably represented the main selection pressure. In other species, where flocking persisted to some extent, predation pressure alone is insufficient to explain the maintenance of the trait. In a large-scale study of the ecological determinants of intraspecific flocking in birds, food type and dispersion explained a large amount of variation in flocking tendency among bird families (Beauchamp 2002). Presumably, the same factors play a role on islands and are responsible in part for the maintenance of the trait. It appears that generally in birds, predation pressure and other ecological factors act together to maintain flocking. The comparative study of island species with closely related mainland species can therefore be a useful tool to assess the relative contribution of predation pressure and other ecological factors to the evolution of flocking in birds.

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