Causes and Consequences of Hetrospecific Foraging Associations in Terrestrial Bird Communities

The question of group-living in animals has attracted a lot of research attention. Today, we have a nuanced understanding of ultimate explanations and proximate mechanisms for group-living, as well as the genetic basis for seemingly puzzling aspects of sociality such as altruism. However, our current view of sociality has been obtained almost entirely in an intraspecific context, i.e. based on groups consisting of individuals of a single species. On the other hand, heterospecific sociality, i.e. groups formed by individuals of multiple species, has been largely ignored in group-living theory and empirical research. This is despite the fact that heterospecific sociality is widely prevalent in nature and is known to occur in many different contexts, in a variety of taxa and in both marine and terrestrial habitats. My dissertation focuses on one of the best-known examples of heterospecific sociality, namely heterospecific foraging associations of terrestrial insectivorous birds (commonly called mixed-species flocks; flocks hereon). Flocks are found all over the world, in a variety of habitats, and include a unique suite of species in each area. Although flocks are the best-studied among different types of heterospecific associations known, most of the research has been descriptive. In other words, while we have descriptions of the richness, size and composition of flocks from many areas, we know little about why and how flocks form. Therefore, one broad objective of this dissertation was to better understand the causes of flock formation. Birds are thought to join flocks either to obtain direct foraging benefits or better protection from predators. I used different approaches to understand which of these two reasons is likely to be more important. Additionally, to situate heterospecific sociality within sociality in general, I also examined whether the mechanisms underlying flocks are similar to single-species groups or unique to a mixed-species condition. In other words, are flocks a different route to obtain the same benefits as single-species groups, or a route to obtain benefits that conspecifics cannot provide? In the previous section, I described why understanding flocks is important from the point of view of sociality. Flocks are also important for the consequences they might have on community organization. While each flock is a collection of interacting individuals of different species, populations of species are linked in a network of interactions across multiple flocks in an area. The theoretical framework guiding our understanding of community organization is currently dominated by the idea of interspecific competition. Mutualisms or positive interactions, if any, are only expected to occur between members of different trophic levels. Only recently has the need to incorporate positive interactions between members of the same trophic level into ecological theory been emphasized. Flocks and other heterospecific associations present an important example of within-trophic level positive interactions. Therefore, the second broad objective of this dissertation was to examine the consequences of flock formation on community organization. The objectives described above were addressed using multiple approaches in this dissertation. “Why” questions in ecology and evolution are generally tackled using manipulative experiments. Given that experiments are neither feasible nor ethical in the case of multispecies flocks in the wild, I addressed the “why” question by focusing on “who” instead. To understand “why” flocks form, I examined what kinds of species participate in flocks, who associates with whom, and who provides and who receives the benefits. This dissertation uses a combination of methods and data, including questions addressed at a global scale using descriptive information on flocks available from across the world. For other questions that were based on entirely new approaches developed in this dissertation, data were collected in a field site in the Western Ghats. In general, given the two broad objectives of this dissertation, the approaches I used were drawn from both behavioural and community ecology. The dissertation is organized in the following way: Chapter 1: General Introduction The first chapter provides the background to the two broad objectives of this thesis, namely understanding the causes and consequences of heterospecific foraging associations in terrestrial bird communities. Chapter 2 (published in The American Naturalist) Based on a global dataset (55 presence-absence matrices from 24 locations in multiple continents) on the composition of flocks, I asked if flocks largely consist of ecologically similar or dissimilar species. Using null models and randomization tests followed by meta-analysis, I found that the association strength of species in flocks was strongly related to similarity in body size and foraging behaviour, and higher for congeneric compared with non-congeneric species pairs. In other words, flocks seem to consist largely of similar species. Extending group-living and social information use theory to a heterospecific context, I discuss potential behavioral mechanisms leading to positive interactions among similar species in flocks as well as ways in which competition costs are reduced. These findings highlight the need to consider positive interactions along with competition when seeking to explain community organisation. Chapter 3 (published in Animal Behaviour) Two kinds of participants are recognized in flocks: those that join other species (‘followers’) and are therefore likely to be the recipients of the benefits of flock participation and those that are joined (‘leaders’). Through comparative analyses, using a large sample of flocks from around the world, I found (1) ‘followers’ tend to be smaller, more insectivorous, and feed in higher strata than matched species that participate in flocks to a lesser extent and (2) ‘leaders’ tend to be cooperative breeders (which are known to have well-developed anti-predatory systems) more often than matched species that are not known to lead flocks. Furthermore, meta-analyses of published results from across the world showed that bird species in terrestrial mixed-species flocks increased foraging rates and reduced vigilance compared to when they were solitary or in conspecific groups. Moreover, the increase in foraging rates was seen only in the case of flock followers and not flock leaders. These findings suggest a role for predation in the evolution of mixed-species flocking. Species that are vulnerable to predation follow species whose vigilance they can exploit. By doing so, they are able to reduce their own vigilance and forage at higher rates. Chapter 4 (to be submitted to Behavioural Ecology and Sociobiology) In this study, conducted in a tropical evergreen forest in the Western Ghats of India, I used intraflock association patterns to generate a community-wide assessment of benefits of flock participation for different species. I assumed that individuals needed to be physically proximate to particular heterospecific individuals within flocks to obtain any direct foraging benefit (flushed prey, kleptoparasitism, copying foraging locations). Alternatively, for all anti-predation benefits, physical proximity to particular heterospecifics is not required, i.e. just being in the flock vicinity will suffice. Therefore, I used the choice of locations within flocks to infer whether individual species are obtaining direct foraging or antipredation benefits. A small subset of the bird community (5/29 species), composed of all members of the sallying guild, showed non-random physical proximity to heterospecifics within flocks. All preferred associates were from non-sallying guilds, suggesting that the sallying species were likely obtaining direct foraging benefits, either in the form of flushed or snatched prey. The majority of species (24/29) chose locations randomly with respect to heterospecifics within flocks, and thus were likely obtaining anti-predation benefits. In summary, my study indicates that direct foraging benefits are important for only a small proportion of species in flocks and therefore that predation is likely to be the main driver of flocking. Chapter 5 (to be submitted to Oecologia) Two types of species – intraspecifically gregarious and sallying species – are thought to play important roles in flocks because studies have shown they attract other flock participants. However, it is not clear why these types of species are attractive, i.e. are they cues for flocks or do they directly provide benefits to other species? It is also not known whether these types are essential for flock formation. In this study, in a tropical evergreen forest in the Western Ghats of India, I used a novel approach to address these questions. Flocks contain anywhere between two and tens of species. My approach focused on the simplest, i.e. two-species, flocks. In two-species flocks, attraction between species must be based on direct benefit to at least one of the species. Therefore, only species combinations that result in benefit to at least one species will occur as two species flocks. Further, by examining leading and following behaviour in these combinations, I could also determine the direction of benefit-flow. Finally, given that all flocks pass through a two-species step, examining which two-species combinations are joined by other species helped understand species roles in flock formation. I found that intraspecifically gregarious species, but not sallying species, were disproportionately represented in two-species flocks, always provided the benefits when present, and that flocks containing them were joined significantly more often. Therefore, intraspecifically gregarious species, but not sallying species, play a role in providing flock benefits and flock formation. Moreover, given that most (7/8) intraspecifically gregarious species in my study site played these roles, the intraspecifically gregarious species guild can be considered an example of a within-trophic level “keystone”. Chapter 6 (“in press” in Oikos) There is a growing recognition of the need to integrate non-trophic interactions into ecological networks for a better understanding of whole-community organization. To achieve this, the first step is to build networks of individual non-trophic interactions. In this study, I analyzed the network of interdependencies among bird species that participated in flocks in an evergreen forest site in the Western Ghats, India. I found that flock networks contain a small core of highly important species that other species are strongly dependent on, a pattern seen in many other biological networks. Further, I found that structural importance of species in the network was strongly correlated to functional importance of species at the individual flock level. Finally, comparisons with flock networks from other Asian forests showed that the same taxonomic groups were important in general, suggesting that species importance was an intrinsic trait and not dependent on local ecological conditions. Hence, given a list of species in an area, it may be possible to predict which ones are likely to be important. Chapter 7: Conclusions In this section, I provide a summary of the main findings of this dissertation, discuss the main conclusions with regard to each of the two broad objectives and finally suggest future lines of investigation to further understand the causes and consequences of flock formation and heterospecific sociality in general. In summary, the work presented in this dissertation provides a picture of how and why flocks form and their likely consequences for community organization. The main driver of flock formation seems to be protection from predators, although a few species do obtain direct foraging benefits. Additionally, given that I found flocks to largely be groupings of similar species, the mechanisms through which benefits are obtained are likely to be similar to those in single-species groups. In other words, flocks are possibly a way for species that are unable to group with conspecifics, to obtain group-living benefits. My finding, that flocks largely consisted of similar species, also questions the stereotyping of interactions between similar species in communities as competitive. Other results from this study demonstrate the importance of intraspecifically gregarious species in flocks. Such species are the main providers of benefits to other flock participants and seem essential for flock formation. Finally, network analysis showed that a small core of species, mainly including species known to provide benefits at the individual flock level, are disproportionately important in the emergent community-level network of interdependencies. Such species are possibly one of the first examples of within-trophic level “keystones” discovered. Apart from the findings, this study also provides a set of new approaches and analytical frameworks that can be used to examine other multispecies foraging groups and heterospecific foraging associations in other contexts.