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The conservation implications of mixed-species flocking in terrestrial birds, a globally-distributed species interaction network

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ABSTRACT

Conservation biologists now view species interaction networks as systems that should be targets of conservation, but there are few actual cases in which networks have formed the basis for management strategies. Terrestrial mixed-species bird flocks (hereafter, TMSF) represent one such potential system: they form throughout the world, and in most cases have an asymmetric organization in which one or a few species play 'nuclear' roles, being particularly important for flock formation or maintenance. A quantitative study on the distribution of TMSF and how they respond to anthropogenic disturbance (AD) is still, however, needed. We surveyed 201 publications on terrestrial TMSF worldwide, finding that 19% of the world's bird species participate in them, including 158 threatened species, with tropical species dominating these lists. Of 31 TMSF studies that investigated AD, 22 showed significant declines in some metric, with TMSF in more impacted areas including 1/4 fewer species, and 1/3 fewer individuals. In 13/15 studies, TMSF were more sensitive to AD than the overall bird community. We conceptualize the reasons behind this response: first, AD directly influences drivers of flocking (predation, foraging), and second, AD produces changes in community composition that affect TMSF, such as when the extirpation or reduction of nuclear species affects other species' participation. We rank nuclear species globally by their consistency of leadership and number of followers, suggesting that these species' interactive roles be considered as part of their conservation value, and further that conserving TMSF provides an efficient mechanism to ensure the protection of many species simultaneously.

1. Introduction

The consideration of species interactions can shift both the priorities and efficiency of conservation. How species interact is increasingly seen as a focus of biodiversity conservation, given that species interaction networks can be even more sensitive to anthropogenic disturbance (AD) than individual species (Valiente-Banuet et al., 2015). Mutualistic interactions are especially vulnerable (Magrach et al., 2014) because such links between species can produce co-extinction (Dunn et al., 2009). Whereas a sole focus on rare species exhibiting declining trajectories can be expensive and carry risks of failure (Joseph et al., 2009; Possingham et al., 2002), strategies that encompass coherent species interaction networks (Tylianakis et al., 2010), or that target 'strongly interacting species' that influence many other species (Simberloff, 1998; Soulé et al., 2003), can protect more species with limited conservation funds than single species approaches (McCarthy et al., 2008).

Mixed-species groups are found widely in the animal kingdom: occasionally in invertebrates, but commonly in fish, certain types of mammals, and frequently in birds, both in aquatic habitats (such as wetlands, shores, freshwater lakes and marine environments) and in terrestrial ones (Goodale et al., 2017). Here we focus on terrestrial mixed-species flocks (hereafter TMSF), the great majority of which are in forests, with the remaining systems present in savannahs and grasslands. Such systems are the most studied kind of mixed-species

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animal group, with over 340 published articles to our knowledge (Goodale et al., 2017). They are found throughout the world in the non-breeding season in temperate regions, and year-round in the tropics, although a quantitative global analysis of their distribution and characteristics is still lacking (but see regional studies Goodale et al., 2015; Goodale et al., 2009; Powell, 1985; Tubelis, 2007). TMSF are important to the fitness of their participants: flocking decreases antipredator behavior (and presumably predation risk) and increases foraging success (Morse, 1977; Sridhar et al., 2009), leading to greater survival of obligate members (Jullien and Clobert, 2000). TMSF also show repeated patterns of organization, wherein some species are 'nuclear', or important to flock formation and/or cohesion (Farley et al., 2008; Goodale and Beauchamp, 2010; Moynihan, 1962), so that it may be possible to target such nuclear species in conservation efforts.

Since mixed-species groups include many different kinds of species and affect the fitness of their members, interest in their implications for conservation has been longstanding. Several studies have already suggested that certain kinds of mixed-species groups should be conserved as communities and systems, including birds that nest near predators (Haemig, 2001), multiple species of fish that use the same spawning grounds (Kobara et al., 2013), and seabirds that associate with marine mammals and predatory fish where prey fish are concentrated (Veit and Harrison, 2017). As for TMSF, two reports in the 1990's of studies of bird communities of Amazonian forests suggested that TMSF participants may be especially sensitive to AD (Stouffer and Bierregaard Jr., 1995; Thiollay, 1992). This result was collaborated by a study that focused on mixed-species flocks in Amazonia (Van Houtan et al., 2006), and a later community-wide study in Central America (Sigel et al., 2006). A study by Sridhar and Sankar (2008) was noteworthy in pointing out how some changes in TMSF were based on changes in the pool of species that could flock. This article, and several earlier and subsequent ones (Maldonado-Coelho and Marini, 2004; Mammides et al., 2015; Stouffer and Bierregaard Jr., 1995; Zhang et al., 2013) also raised the possibility that changes to a nuclear species could reverberate onto other species that participate in TMSF. Although these results have been qualitatively reviewed (Goodale et al., 2017; Goodale et al., 2015), a quantitative review is lacking, and a framework is needed for understanding the mechanisms and drivers of TMSF degradation provoked by AD.

We have three objectives for this article. First, we investigated what proportion of the global avifauna, and of threatened bird species, has been reported as participating in TMSF, and specifically whether TMSF hold more bird families, species or individuals in particular climatic zones or biogeographical regions. Second, we ask how AD (in particular, fragmentation and land-use intensification) affects TMSF systems, comparing the response of TMSF participants to that of all species. In the discussion, we review and diagram the different kinds of mechanisms that may lead to such a response. Third, we attempt to rank the most important nuclear species to target in conservation plans, by measuring the consistency of their leadership and the number of species reported to follow them, as well as their own distribution, and arguing that these species' importance to other species should be incorporated into considerations of their conservation value.

2. Material and methods

2.1. Global participation in TMSF and geographical variation

We surveyed all articles about TMSF we could find using bibliographic search engines (Web of Science, Google Scholar), and an existing on-line bibliography (http://www.animal-ecology-guangxi.com/content/mixed-species-bird-flocks-bibliography, compiled by EG and Hari Sridhar). We excluded articles that exclusively focused on aggregations around fruiting trees, or those species that follow army ants, as that phenomenon has similarities to an aggregation. We included studies that gave a list of bird species participating in TMSF or had some figures on the size of TMSF, and found a total of 170 studies with this information (Supplemental Data 1; because sometimes the same dataset was used in multiple articles, this included 196 total papers; in addition, five review papers were relevant to the issue of geographical variation in flocks, and we used some data from these articles that was not accessible elsewhere). From these papers we then extracted the following data (although few papers had information on all these aspects): 1) the number of species that participated, 2) the number of families in that participant list, 3) the average number of species per TMSF, 4) the average number of individuals per TMSF, 5) the percentage of the bird species at the site that were reported to participate in TMSF. If papers described TMSF at multiple sites or multiple TMSF systems at one site, we averaged values between these different sites/systems. These metrics were analyzed at two hierarchical levels, i.e. three latitudinal zones (Tropical zone, North Temperate zone, and South Temperate zone) and nine geographic zones (Fig. 1), as long as sample size was greater than three. One characteristic of TMSF for which we hypothesized there might be regional differences is in the proportion of migrants; specifically, we thought the percentages would be higher in the Neotropics because of some strongly migratory systems described there (Eaton, 1953; Hutto, 1987; McDermott and Rodewald, 2014) compared to the Paleotropics. Hence, we added a separate analysis of this question, selecting 20 papers randomly from these two regions, and assessing migration through the Handbook of the Birds of the World on-line addition (www.hbw.com). All statistical tests were non-parametric, so to avoid breaking assumptions of normality and heteroschedastity. We used Kruskal-Wallis tests, followed by step-down multiple comparisons, to analyze differences of flock size, or in the percentage of migrants, across latitudinal and geographic regions, using SPSS 22.0 (IBM-SPSS Inc., Chicago, IL, USA). Bird taxonomy is based on Gill and Donsker (2014), and the information about the threatened status of species is from the IUCN Red List, Version 2013.2.

2.2. Response of TMSF systems to human-induced disturbance

We performed a meta-analysis (Koricheva et al., 2013) of how TMSF respond to human disturbance, selecting all flock articles that investigated any aspect of human disturbance (n = 31). We concentrated on two response variables that were found in the most papers: the average number of species per flock and the average number of individuals per flock. For each study, we took the site most affected by AD ("impacted site", either the most altered site or the smallest fragment) and compared this to the least disturbed site or largest fragment ("unimpacted site"; only a few studies looked at the landscape level at a spatial scale greater than the site itself and thus we did not incorporate this scale into the analysis). Several studies had multiple comparisons or two different disturbance gradients (e.g., both fragmentation and land-use intensity), and in these cases we considered each comparison as a separate study. We then evaluated the overall effect size of disturbance on the log mean ratio (which takes into account the size of flocks) for number of species (17 studies) and individuals (13 studies) in TMSF, using Restricted Maximum Likelihood Estimation in the 'metafor' package in R (Viechtbauer, 2010). We evaluated the models for violations of the assumptions of normality, reporting Wald's Z test scores, parameter means and confidence intervals. We also report back-transformed estimates of the mean ratios derived from the fitted model, for biological interpretation.

Of all these studies that investigated disturbance, 15 had information with which to compare the sensitivity of TMSF participants to all bird species. However, the types of information were various and hence not easily incorporated into the meta-analysis (e.g., five studies specifically compared TMSF species to other guilds in their response to a kind of change, whereas for the other studies one could calculate how flocks changed from one habitat to another, and then compare that to the way in which total species richness and/or abundance changed between those habitats). In this analysis we simply use a vote-counting