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# Anthropogenic disturbance and mixed-species groups

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Mixed-species groups (MSGs) are composed of individuals of two or more species with such close associations that they can be regarded as members of the same social group. MSGs are ubiquitous and are often advantageous for the individuals involved, as these groups confer benefits of exploiting food resources and increased predator detection. Individuals often suffer negative impacts from human-caused disturbances to their habitats. Types of anthropogenic disturbance include outright loss of habitat, habitat fragmentation, and noise. Anthropogenic disturbance can negatively impact behaviors such as communication, foraging, and predator detection. Unsurprisingly, anthropogenic disturbance is a key driver in biodiversity changes across the world. Many studies have focused on the impact of anthropogenic disturbance on single species, but comparatively little work has addressed the influence of anthropogenic disturbance on MSGs. Therefore, a framework is needed to explore how anthropogenic disturbance affects the behavior, composition, and function of MSGs. This brief review paper aims to start to craft such a framework to stimulate research into these questions.

KEYWORDS

**anthropogenic disturbance, mixed-species groups, habitat fragmentation, noise, species interactions, species richness**

## Introduction

Mixed-species groups (MSGs) are composed of individuals of two or more species with such close associations that they can be regarded as members of the same social group (Goodale et al., 2017). MSGs are common in fish (Lukoschek and McCormick, 2000), birds (Sridhar et al., 2009), and mammals (Stensland et al., 2003) and may be far more ubiquitous than typically appreciated (Carlson et al., 2023). MSGs are often advantageous for the individuals involved, as these groups confer benefits of exploiting food resources and increased predator detection (Goodale et al., 2017). For example, some species benefit from their involvement in MSGs by eavesdropping on the alarm and mobbing calls of Carolina chickadees (*Poecile carolinensis*) and tufted titmice (*Baeolophus bicolor*; Sullivan, 1984; Nolen and Lucas, 2009). Vigilance rates decline and foraging rates increase when different species of gazelle group together in large numbers (FitzGibbon, 1990) and when two

different species of *Cercopithecus* monkeys move together compared to when they occur in single-species groups (Wolters and Zuberbühler, 2003).

Individuals often suffer negative impacts from human-caused disturbances to their habitats. Types of anthropogenic disturbance include outright loss of habitat (e,g., forest clearcuts), habitat fragmentation, and noise. Although relatively brief exposure to human presence can influence behavior of individuals in their natural habitats (as in Metcalfe et al., 2022), we focus here on longer-term changes to the habitat due to alterations like forestry practices or sustained exposure to noise. Habitat loss, for example, is thought to negatively affect a much higher number of avian species and families than the combination of human hunting and introduced predators (Bennett and Owens, 2002). Furthermore, anthropogenic disturbance can negatively impact behaviors such as communication, foraging, and predator detection. For example, when exposed to motorboat noises, fathead minnows (*Pimephales promelas*) failed to respond to chemical alarm cues (Hasan et al., 2018).

Some prey species may respond to anthropogenic disturbance to their habitats similarly to how they respond to predator stimuli and so may suffer similar sub-lethal and stress effects (Frid and Dill, 2002). Unsurprisingly, anthropogenic disturbance is a key driver in biodiversity changes across the world (Chapin et al., 2000; Fontúrbel et al., 2015). Anthropogenic disturbance can lead to reductions in numbers and densities of single species and for MSGs it can also potentially lead to reductions in cross-species interactions (Tylianakis et al., 2010; Valiente-Banuet et al., 2015). Additionally, Van Houtan et al. (2006) found that species that had higher probabilities of joining MSGs in undisturbed habitat were less likely to be found in fragmented areas.

Many studies have focused on the impact of anthropogenic disturbance on single species, but comparatively little work has addressed the influence of anthropogenic disturbance on MSGs. Therefore, a framework is needed to explore how anthropogenic disturbance affects the behavior, composition, and function of MSGs. This brief (and nowhere near comprehensive) review paper aims to start to craft such a framework to stimulate research into these questions. In the sections that follow we highlight key questions that need addressing if we are to gain a greater understanding of associations between anthropogenic disturbance and MSGs in hopes of minimizing the negative effects of the former on the latter.

## Are species roles in MSGs influenced by anthropogenic disturbance?

The interdependence of individuals participating in MSGs has often been represented in the description of their roles (Winterbottom, 1943; Munn and Terborgh, 1979; Harrison and Whitehouse, 2011). There are two common terms used for individual species within the group: nuclear and satellite. Nuclear (often, leader) species are those that are central to the formation of the group largely because of their frequent signaling behavior that alerts flock members to predators and potentially to food resources (Goodale et al., 2017). Often, MSGs contain more than one nuclear species that may differ in their behaviors (Harrison and Whitehouse, 2011). Farley et al. (2008) found that tufted titmice in MSGs were more likely to be passive nuclear species, where their movements define flock paths, whereas birds like blue-gray gnatcatchers (*Polioptila caerulea*) and ruby crowned kinglets (*Regulus calendula*) possibly served as active nuclear species, deliberately seeking out other species. The other major category of species in MSGs are satellite (often, follower) species, those that are attracted to the presence, and take advantage, of nuclear species. Unlike nuclear species, satellite species do not actively behave in ways to form or maintain MSGs.

Whereas there are typically set nuclear/satellite roles for each species within an MSG, these can change with environmental variation. For instance, in a study of tropical forest bird communities, Mangini et al. (2022) found 35 different species that behaved like leader species with many switching between the leader and follower roles based on the flock composition (role reversals: see Zhou et al., 2019 for another avian MSG example). Goodale et al. (2015) found that habitat disturbance was associated with fewer individuals and diminished species richness in avian MSGs - including nuclear species - as well as decreased likelihood of MSG presence. Thus, changes in the physical environment of species, such as anthropogenic disturbance, can influence the presence and numbers of certain species, altering the size and composition of MSGs. *To what extent does anthropogenic disturbance affect nuclear and satellite species differently? What are the fitness consequences of role reversals, if they occur, in such disturbed environments?*

Nuclear species are often considered 'keystone' species in an ecosystem (Simberloff, 1998; Caro and Girling, 2010). In disturbed or fragmented habitats, the presence of these species can be associated with a wider range of habitat use by satellite species (Sieving et al., 2004) and perhaps better condition of satellite species (Dolby and Grubb, 1998). Some nuclear species may be more tolerant of anthropogenic disturbance but if they are negatively impacted by such disturbance the result may be diminishment or loss of the associated MSGs (Mammides et al., 2015). *Are conservation efforts aimed at protecting nuclear species more effective at maintaining robust MSGs (and overall greater species richness) than efforts aimed at protecting potentially rare satellite species?* This question has been answered in the affirmative for nesting fish assemblages (Peoples and Frimpong, 2013) but additional research is required.

## Do different types of anthropogenic disturbance have different effects on MSGs?

The effects of urbanization can cause both biotic and abiotic changes to the ecosystem, such as impoverishment of natural habitats, increases in the diversity and intensity of different channels of noise, fragmentation, and destruction (Morelli et al., 2023). Zou et al. (2018) found that in habitats with high human

disruption, there was a decline in avian MSG composition. Furthermore, some nuclear species are more sensitive to disturbance (Zou et al., 2018), particularly if the species are inherently highly gregarious (Martínez et al., 2024), and this may exacerbate the negative impacts of anthropogenic disturbances and lead to reduced MSG size. One major anthropogenic disturbance is habitat fragmentation, the process by which a large expanse of habitat is transformed into patches of a smaller total area, with patches isolated from each other by a matrix of habitats unlike the original (Wilcove et al., 1986). Habitat fragmentation is common in many ecosystems and increases discontinuity in the spatial patterning of resource availability, which can cause changes in individual fitness (Hagen et al., 2012) and negatively influence individuals' interactions with other species (Quiles and Barrientos, 2024). Many species living in areas that are impacted by urban fragmentation undergo reductions in their spatial distribution (Hagen et al., 2012).

Habitat fragmentation due to agricultural practices has been shown to constrain individual movement in crested mangabeys (*Cercocebus galeritus*; Kinnaird and O'Brien, 2000). Conversely, mixed-species groups of tamarin monkeys and marmosets were found to move together more often in areas of fragmentation (Tisovec et al., 2014; see also Martínez et al., 2023 for an avian example), suggesting a resiliency in MSGs that we touch on further in the penultimate section below. A summary of over 20 published studies found that fragmentation and intensity of land use were typically associated with lower species richness and number of individuals, as well as diminished likelihood of individuals being in MSGs (Goodale et al., 2017). However, two of those studies found a positive association between anthropogenic disturbance and species richness in MSGs (Péron and Crochet, 2009; Mokross et al., 2014). Both studies (one in the Democratic Republic of Congo and one in Brazil) were conducted in areas of alteration and fragmentation to rainforest that produced high rates of edge habitat that perhaps led to the higher overall number of the avian species detected. However, Mokross et al. (2014) used social network approaches to their analyses of MSGs in these habitats and found that actual interactions among different species declined in areas with more disturbed habitat.

In most cases, extensive habitat loss has a detrimental effect on individual numbers and that influence is particularly strong if the lost habitat is higher in quality (Sidhu et al., 2010). Avian MSGs in forested habitats tend to be more consistent in membership and tend to have more stable home ranges and territories in comparison to avian MSGs in more open habitat like grasslands (Terborgh, 1990). Greater stability in place and membership should create greater possibilities for mutual benefits of group members through social learning processes and pro-social behavior. *Do areas with increased fragmentation result in less spatially and temporally stable MSGs?* Additionally, research suggests that group composition and likelihood to form MSGs are contingent on the specific types of habitat, alteration to habitat, and successional complexity (see Stouffer and Bierregaard, 1995; Knowlton and Graham, 2011; Colorado Zuluaga and Rodewald, 2015). Some habitat types may be more sensitive to the effects of anthropogenic disturbance (such as the presence of roads: Kroeger et al., 2022) and so prioritizing conservation efforts of these areas may be crucial to maintain group persistence in MSGs. *To what extent does the specific type of habitat undergoing fragmentation affect MSG sensitivity to that disturbance?*

We would expect habitat fragmentation, but not necessarily increased levels of anthropogenic noise, to make MSG membership less consistent and territories less stable, though this possibility awaits testing (see Fort and Otter, 2004 for a single species study). Anthropogenic noise can be defined as human-generated acoustic stimuli that result in changes in soundscapes both due to an increase in sound levels and the addition of sounds that are different from those arising from natural sources (McDonald et al., 2006; Watts et al., 2007; Herbert-Read et al., 2017). Anthropogenic noise can have negative consequences for individuals in terms of both behavior and physiology. For example, such noise has been associated with a wide array of negative consequences like higher levels of stress (Anderson et al., 2011), increased vigilance (Matyjasiak et al., 2024), decreased responses to fitness-related signals like alarm or mobbing calls (Herbert-Read et al., 2017), and diminished foraging efficiency (Willems et al., 2022).

Jung et al. (2020) found that in areas with higher background noise compared to lower background noise, both tufted titmice (*Baeolophus bicolor*) and white-breasted nuthatches (*Sitta carolinensis*) called less in response to playbacks of a simulated approaching avian predator. Grade and Sieving (2016) reported that in low levels of traffic noise, northern cardinals (*Cardinalis cardinalis*) displayed predator avoidance in response to alarm calls of tufted titmice, but in high levels of traffic noise cardinals were less likely to show predator avoidance. Both studies suggest a masking effect of human-caused noise. A potential solution to masking by traffic noise is for individuals to maintain closer proximity to one another to increase the relative intensity of the signal compared to the noise. A study with captive flocks of tufted titmice found support for this idea (Owens et al., 2012), but we do not know if individuals in MSGs maintain closer proximity in contexts of higher levels of noise. *Do higher levels of anthropogenic noise drive closer proximities among individuals in MSGs, potentially affecting social networks and stability of MSGs?* As an added complication, predators themselves may abandon areas or hunt in them less often if those areas are exposed to sufficient levels of noise and other disturbance (Schueck et al., 2001). Perhaps in some systems the costs imposed on individuals in MSGs by anthropogenic disturbance are somewhat offset by benefits of reduced predation intensity.

## How does species richness relate to MSGs and how does anthropogenic disturbance influence that relationship?

In areas of minimal habitat fragmentation, the species richness detected may predict species presence in MSGs, but this species richness may not be associated with MSG composition in areas of

greater fragmentation (Brandt et al., 2009; Mokross et al., 2014). As mentioned above, there is relatively limited research focused on effects of anthropogenic disturbance on multiple species at a time, and of those studies, most use species richness as the key metric (Ibáñez-Álamo et al., 2020). Although this is essential information to know, we believe we also need to focus on the impact of anthropogenic disturbance on the behavior and interactions of individuals in MSGs. It is widely known that anthropogenic disturbance regularly impairs communication within single species (Jung et al, 2020; Halfwerk and Jerem, 2021; Tilgar et al., 2022). Although heterospecific communication is common, the extent to which anthropogenic disturbance impacts receiver detection of signals and cues of heterospecifics is little known. *Does anthropogenic disturbance influence the relationship between local species diversity and membership in MSGs? Are species less able to respond adaptively to the signals and cues of other species in MSGs in conditions of such disturbance?*

As mentioned avove, individuals in MSGs can benefit from being in those groups in terms of avoiding predation and finding food (Goodale et al., 2017). There is some recent evidence that individuals in more diverse MSGs can particularly benefit (Freeberg et al., 2017, 2024). These benefits of MSG diversity may stem from the groups' larger perceptual and cognitive 'toolkits' (e.g., the "Diversity Bonus" of Page, 2017), though this possibility awaits testing. If true, these larger 'toolkits' should result in these groups – particularly if they are stable in space and time – being more robust and resilient and perhaps better able to function in anthropogenic disturbance. *Are more diverse MSGs (whether based on species richness or feeding guild diversity or some other metric of diversity) better able to persist in areas of anthropogenic disturbance?*

Readers will likely have noticed that many of the examples we have provided here come from work on avian species. This bird-centrism is largely because this is where much of the work on anthropogenic disturbance and MSGs has focused (Goodale et al., 2017). We do believe that more work is needed in avian systems but stress the need for much more work in non-avian systems.

## Can we move into experimental studies of these questions?

Once an area has been impacted by anthropogenic disturbance, are there additional manipulations that can lessen the negative impacts on MSGs? Noise mitigation through artificial sound barriers or plantings of sound-dampening species near major roadways can help (Nilsson et al., 2008). Even small forest plots in seas of agricultural fields can support persistence of MSGs in some areas (Russo et al., 2023). In areas of forest fragmentation, the planting of fencerows or hedgerows can increase movement of certain species from one fragment to another (Gillies and St Clair, 2008) and if those species are nuclear species, this manipulation could potentially increase movement of other species in MSGs (Sieving et al., 2004). *Experimental work on efforts to remediate anthropogenic disturbance is needed to assess potential benefits to MSGs.*

Beyond that request for a specific type of experimental work, a final concluding remark is simply that more experimental science is needed on associations between anthropogenic disturbance and MSGs. There is a small but growing body of literature on the influences of anthropogenic disturbance on MSGs and we are now in a position where we should start more experimental testing to get at questions of causation. For example, *how do the presence, composition, and networks of different species in an MSG differ in the context of experimental manipulations of traffic noise or habitat structure or density?* While the body of literature on this is small, the studies that have used such methods in their exploration of these topics have been crucial to our understanding of how sensitive MSGs are to habitat degradation. Increased experimental research on these questions could be essential for developing conservation methods for both MSGs and the species that depend on them.

## Concluding remarks

The last few decades of research have made clear the largely negative impacts of human activity on the presence and number of individuals of different species in affected habitat. Increasingly, this research has addressed how different kinds of anthropogenic disturbance are associated with the presence and number of species in MSGs in affected habitat. Fundamental questions remain, however. In this brief review, we hope we have raised a sufficient 'call-to-arms' to generate increased research into key topics raised here. Boiled down to essentials, we believe increased research efforts devoted to the following could transform our understanding of the relationship between anthropogenic disturbance and MSGs:

- the extent to which species roles in MSGs change in anthropogenic disturbance.
- the roles of different types of anthropogenetic disturbance on MSG presence and composition.
- the extent to which anthropogenic disturbance affects the relationship between species richness and species presence in MSGs.
- experimental manipulations of disturbance (including habitat repair) to test impacts on MSGs.

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