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Review

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Studying individual-level interactions can transform our understanding of avian mixed-species flocks

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ABSTRACT

Avian mixed-species flocks are ubiquitous across habitats and a model for studying how heterospecific sociality influences the behavior and composition of animal communities. Here, we review the literature on mixed-species flocks and argue that a renewed focus on individual-level interactions among flock members can transform our understanding of this iconic, avian social system. Specifically, we suggest that an individual perspective will further our understanding of (1) how inter- and intraspecific variation in flock participation links to fitness costs and benefits, (2) the implications of familiarity between individuals in structuring mixed-species flock communities, and (3) how social roles within mixed-species flocks are related to social behavior within and across species. We summarize studies that use an individual perspective in each of these areas and discuss knowledge from conspecific social behavior to posit more broadly how individuals may shape mixed-species flocks. We encourage research approaches that incorporate individual variation in traits, relationships, and social roles in their assessment of mixed-species flocking dynamics. We propose that the analysis of individual variation in behavior will be particularly important for explicitly identifying fitness outcomes that led to the evolution of mixed-species flocks, which in turn affect community structure and resilience.

Keywords: avian mixed-species flocks, familiarity, heterospecific sociality, individual variation, social networks, species interactions

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LAY SUMMARY

- Across the world, many birds form mixed-species flocks that serve as information centers, facilitating foraging, and anti-predation behaviors for multiple species. Such social groups provide a prime example of how sociality can extend beyond species boundaries.
- Most research on this topic focuses on species-level questions (e.g., how different species fill different roles in the flock) without accounting for the importance of individual-level traits and relationships in mixed-species flocks.
- We argue that an increased focus on the individuals in mixed-species flocks is needed to understand how flock participation is linked to the evolution of traits and behaviors, how social relationships matter in interactions between species, and to reveal hidden social structure at the level of ecological communities.
- We demonstrate how techniques such as social network analysis can be used in conjunction with experiments and observations of individuals to explore the importance of individual variation and social recognition in the social dynamics of mixed-species flocks.

El estudio de las interacciones a nivel individual puede transformar nuestro entendimiento de las bandadas de aves de especies mixtas

RESUMEN

Las bandadas de aves de especies mixtas son omnipresentes en todos los hábitats y un modelo para estudiar cómo la sociabilidad heteroespecífica influye en el comportamiento y la composición de las comunidades animales. Aquí revisamos la literatura sobre bandadas de especies mixtas y argumentamos que un enfoque renovado en las interacciones a nivel individual entre los miembros de la bandada puede transformar nuestro entendimiento de este icónico sistema social aviar. Específicamente, sugerimos que una perspectiva individual mejorará nuestra comprensión de (1) cómo la variación interespecífica e intraespecífica en la participación de la bandada se relaciona con los costos y beneficios de la aptitud biológica, (2) las implicaciones de las relaciones familiares entre individuos en la estructuración de las comunidades de bandadas de especies mixtas y (3) cómo los roles sociales dentro de las bandadas de especies mixtas están relacionados con el comportamiento social dentro y entre especies. Resumimos los estudios que utilizan una perspectiva individual en cada una de estas áreas y analizamos el conocimiento del comportamiento social conespecífico para postular de manera más amplia cómo los individuos pueden formar bandadas de especies mixtas. Alentamos los enfoques de investigación que incorporan la variación individual en los rasgos, las

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relaciones y los roles sociales en su evaluación de la dinámica de las bandadas de especies mixtas. Proponemos que el análisis de la variación individual en el comportamiento será particularmente importante para identificar explícitamente los resultados a nivel de aptitud biológica que condujeron a la evolución de las bandadas de especies mixtas, que a su vez afectan la estructura y la resiliencia de la comunidad.

Palabras clave: bandadas de aves de especies mixtas, interacciones entre especies, redes sociales, relaciones familiares, sociabilidad heteroespecífica, variación individual

INTRODUCTION

Mixed-species groups are formed of animals of multiple species, typically of the same trophic level, interacting with one another (Goodale et al. 2017, 2020). Such groups are found globally in a variety of taxa including fish, mammals, and insects (Mallet 1986, Lukoschek and McCormick 2000, Stensland et al. 2003), but have been particularly well studied in birds. Mixed-species groups of birds, or mixed-species flocks, are hypothesized to form in large part for anti-predation or foraging benefits (Thiollay and Jullien 1998, Sridhar et al. 2009). Associating with other species with different behaviors, preferences, and sensory systems are thought to provide individuals with novel foraging information, niche expansion benefits, novel predator information, and reduced vigilance load (Goodale and Kotagama 2005a, Harrison and Whitehouse 2011, Goodale et al. 2020). Collectively, these associations can shape community assembly through ecological enhancement and heterospecific attraction making mixed-species flocking behavior an important aspect of community ecology (Obst and Hunt 1990, Mönkkönen et al 1996, Lukoschek and McCormick 2000). Thus, understanding what benefits are gained through participation in mixed-species flocks, how benefits are shared among flock participants, and how associations in flocks are initiated and maintained has been of long interest to ecologists.

Mixed-species flocks can be studied at the level of species or the level of individuals participating in flocks. Species-level approaches are more common, and they have typically focused on species-average traits and behaviors to reveal important details of the structure and dynamics of mixed-species flocks, including which species initiate and which species follow within communities (Sridhar et al. 2009), how different species fill different social roles (Winterbottom 1943, Davis 1946, Hutto 1994, Goodale and Kotagama 2005b, Farley et al. 2008), and how relationships between species vary across environments (Sridhar and Shankar 2008, Thomson and Ferguson 2009, Zhang et al. 2013). Individual-level studies, in contrast, can only be conducted when individuals can be reliably identified, often requiring individuals to be captured and tagged. However, when possible, an individual-level perspective on flocking communities provides a more powerful, nuanced framework for understanding the social associations between species by capturing and addressing how variation in individual traits and relationships shapes the patterns of flock participation and the behaviors exhibited in mixed-species flocks.

The stark difference between these two approaches to mixed-species flocking studies can be seen in Figure 1, which uses network analyses to illustrate both species-level (Figure 1A) and individual-level (Figure 1B) relationships in a North American winter mixed-species flock community based on data collected at radio-frequency identification (RFID) feeders. In the species-level network, nodes represent species and edges represent the strength of association between species, or the rate of species co-occurrence irrespective of the individuals observed together. In contrast, nodes in the individual-level social network represent individuals, the different colors represent species identity, and edges represent the association strength between each pair of individuals. While relatively little detail can be gleaned from the species-level network (Figure 1A), the individual-level network (Figure 1B) reveals not only complexity in heterospecific patterns of association, but also captures how conspecific social structure varies within and among species. For example, most of the Black-capped Chickadees (*Poecile atricapillus*) form one tight-knit conspecific social group, which collectively has many weak ties to heterospecific individuals, whereas no Red-bellied Woodpeckers (*Melanerpes carolinus*) forage with conspecifics. In contrast, Downy Woodpeckers (*Picoides pubescens*) and White-breasted Nuthatches (*Sitta carolinensis*) maintain a mix of strong and weak associations with different conspecific and heterospecific individuals. Thus, the individual-level network supports the widespread observation that "nuclear" species, like Black-capped Chickadees, often exhibit high levels of conspecific social cohesion, which may be linked to high production of social information (Sridhar et al. 2009, Goodale and Beauchamp 2010). This pattern cannot be observed from the species-level network. Moreover, the individual-level network also captures individual variations in types of relationships. For example, one Black-capped Chickadee has strong heterospecific associations but no conspecific associations, an unexpected pattern that might represent an alternative foraging strategy or recent loss of conspecific partners. It also illustrates that social relationships can vary between pairs, both within and across species, with some Downy Woodpecker and White-breasted Nuthatch pairs forming tighter relationships with particular conspecific individuals (likely a social pair) compared to heterospecific relationships, while others do not. Such contrasts between patterns of variation among conspecific and heterospecific relationships are not possible with species-level networks. With the incorporation of additional data, these observations can offer insight into other processes that may be contributing to the occurrence and structure of mixed-species flocks, such as individual trait differences, preferences among social partner identity, or spatial home range or territory overlap.

Observations of individuals in mixed-species flocks is not new. Some of the earliest studies of mixed-species flocks used color banding and resighting of individuals to illustrate that some Neotropical mixed-species flocks can involve stable, lifelong associations of heterospecific social partners (Davis 1946, Moynihan 1962, Willis 1967, Buskirk et al. 1972, Munn and Terborgh 1979, Gradwohl and Greenberg 1980, Jullien and Thiollay 1998, Martínez and Gomez 2013). More recently, individual-based studies using color bands or RFID tags, in combination with social network approaches, have illustrated the presence of intraspecific variance in heterospecific sociality in mixed-species flocks (Aplin et al. 2012, Farine et al. 2012, Farine and Milburn 2013, Farine et al. 2015). Further, such studies have shown that individual-specific attributes, such as social dominance, may influence these heterospecific associations (Farine et al. 2012). These individual-level studies of mixed-species flocks demonstrate that individual-level interactions are the building blocks of the patterns we see at the species level and can critically shape mixed-species flocking

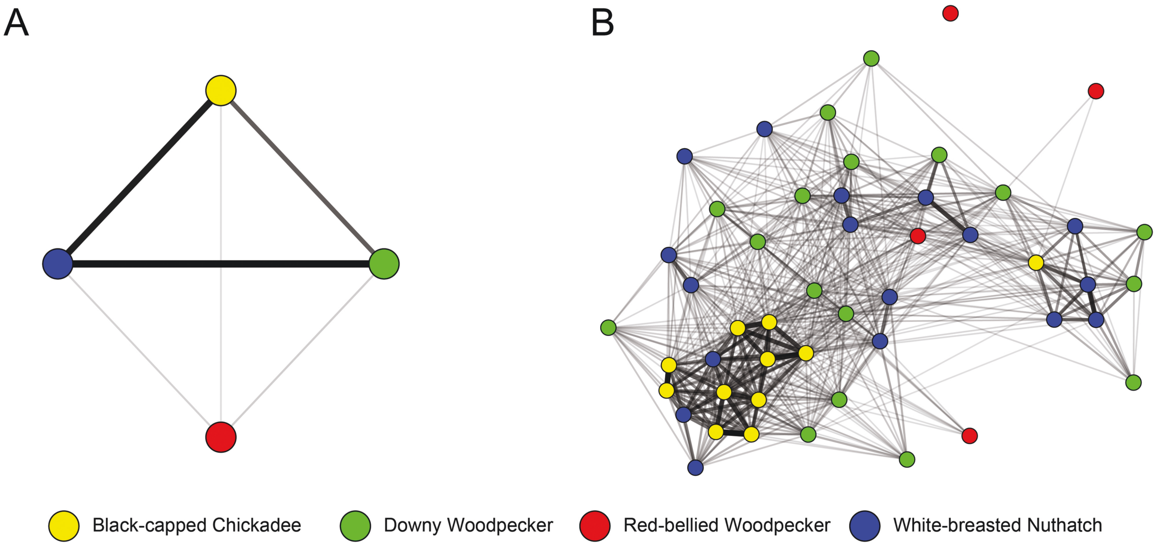

FIGURE 1. Mixed-species flocks can be described using a species-level network (**A**) or an individual-level social network (**B**). The individual-level social network illustrates much more detail of the interspecific variation the in interplay between social structure of conspecific and heterospecific interactions. These two networks illustrate social foraging dynamics of 4 resident woodland species in Nebraska: Black-capped Chickadee, Downy Woodpecker, Red-bellied Woodpecker (*Melanerpes carolinus*), and White-breasted Nuthatch in Nebraska over 3 days in January 2021. We identified membership of flocks based on temporal clusters (Psorakis et al. 2012) of feeder visitations from data streams of visitations at an array of radio-frequency identification-enabled feeders, with "flocks" defined as birds visiting a given feeder in a temporal cluster. The individual-level social network uses a force-directed layout, which places nodes closer together when they are more tightly connected. Methods are described in Supplementary Materials.

behavior. These studies confirm that processes common in conspecific social behavior are playing out in a heterospecific context, suggesting there is even more to be gained from considering individual-level social dynamics in a heterospecific context (Oliveira and Bshary 2021).

Here, we discuss the importance of an individual-level perspective on mixed-species flocks to augment the historical emphasis on species-level studies and consider how such an approach will continue to reshape our understanding of heterospecific social behavior. We examine how consideration of (1) individual variation in the costs and benefits of flocking behavior and participation, (2) individual recognition and familiarity, and (3) individual-level processes underlying social roles and information flow can add depth to our current interpretations of flocking behavior. First, measuring variation among individuals in flock participation allows us to probe how the costs and benefits of mixed-species flocks are accrued by individuals. Second, individual-level social relationships—primarily driven by familiarity—have the potential to influence behavioral dynamics and heterospecific attraction observed in mixed-species flocks. Third, considering how individual-level variation in social connections (i.e. the social network) within and across species influences flock dynamics and information transfer is key to understanding classic concepts such as species roles in mixed-species flocks. We focus our review on flocks of individuals as defined by coordinated foraging behavior involving two or more species and include some discussion of mixed-species mobbing flocks wherein birds are recruited to the joint mobbing of predators. Throughout, we explore further questions that may be answered through individual-based observations or experimentation, the potential need for reinterpretations of classic studies through the lens of the individual and discuss techniques and technologies that can aid in the methodology of individual-based studies.

Individual Variation in the Costs and Benefits of Flock Behavior and Participation

Variation in flock participation has been well characterized across species in many mixed-species flock communities. Some species are obligate participants in mixed-species flocks, some species never join flocks even when they are present in the habitat, and many others are facultative participants that join in some contexts but not others (Munn and Terborgh 1979, Gradwohl and Greenberg 1980, Wiley 1980, Thiollay and Jullien 1998, Jullien and Clobert 2000, Farley et al. 2008). A key question for understanding the evolution of mixed-species flocks is, what drives such variation in participation within and across facultatively flocking species? Here we focus on follower species, given that nuclear (or leader) species are typically joined and thus may not control when they are in a flock (Goodale and Kotagama 2005b, Contreras and Sieving 2011).

A classic assumption is that all individuals of a follower species participate in flocks at similar rates in similar contexts. However, the few studies that have taken an individual perspective have illustrated the existence of intraspecific variation in the strength of relationships between mixed-species flocking individuals as well as in foraging behavior within flocks. For example, a study of individual participants in mixed-species flocks in Australia showed that variation in social connections among individual Buff-rumped Thornbills (*Acanthiza reguloides*) showed nearly as much variation as across all participating species and that females in particular had high levels of heterospecific connections (Farine and Milburn 2013). Individual variation in mixed-species flock participation may be affected by traits that are related to variation in foraging behavior. Outside of mixed-species flocks, evidence for intraspecific variation in foraging behavior is widespread and is affected by phenotypic traits such as sex and body size (Holmes et al. 1978, Gustafsson 1988), as well as behavioral traits including personality (Aplin et al. 2014, Öst et al. 2015, Serrano-Davies et al. 2017), dominance status (Pöysä 1988), prey preferences (Estes et al. 2003), microhabitat use (Bolnick et al. 2009), and risk tolerance (Eklöv and Svanbäck 2006). Further, individuals may adjust their social foraging behavior based on dynamic factors such as body condition (Öst et al. 2015, Crino et al. 2017, Moiron et al. 2019), age (Diamond and Bond 1991, Franks et al. 2020), and breeding stage (Bell and Ford 1986, Helm et al. 2006). There is some evidence that some of these same traits affect rates of participation in mixed-species flocks. Farine et al. (2012) found that intraspecific and interspecific variation in social behavior in mixed-species tit flocks (*Paridae* sp.) was strongly related to body size.

Traits that affect variation in foraging behavior may influence an individual's participation in mixed-species flocks because they can change the balance of costs and benefits an individual receives from joining. For example, individuals with lower body condition, a trait associated with higher boldness or risk-taking behavior (Crino et al. 2017, Moiron et al. 2019), may eschew the anti-predation benefits flock participation provides in favor of foraging alone or with conspecifics. Conversely, individuals with low body condition may prioritize reduced competition in mixed-species flocks over conspecific flocks despite the likelihood of more relevant alarm calls in conspecific flocks. Birds may be selective in which flocks they join to maximally reduce overlap with flockmates in prey or microhabitat preferences and may be less likely to join flocks that contain competitors. Such avoidance can be seen at the species level, where species that exhibit tightly overlapping foraging niches are likely to be found in flocks, but not with one another (Graves and Gotelli 1993). Intraspecific variation in social position or dominance status may also impact the degree of benefits received by an individual in a flock and may increase or reduce an individual's propensity to join. For example, female White-breasted Nuthatches experience smaller reductions in rates of vigilance than males when foraging in conspecific groups (Waite 1987), and Great Tits (*Parus major*) with higher dominance status tend to show higher feeding successes at artificial feeders (Pöysä 1988). Both of these species are common flock participants, and these differences in flocking and foraging benefits may be important factors impacting the composition of individuals found within mixed-species flocks.

Evolution of mixed-species flocks requires individual variation

Understanding individual variation in flock participation opens the door for us to consider how this social behavior evolves. The classic view is that the formation of mixed-species flocks is driven by reduced competition compared to conspecific flocks with the benefits of foraging in a group. Goodale et al. (2017) implicitly assume that flocking confers the same costs and benefits to all individuals within a species. However, if individuals vary in their flock participation, either through individual differences, behavioral plasticity, or both, we must then consider whether flocking is a general behavioral response to the presence of heterospecific or represents an alternative behavioral strategy. To do this, we must begin by accounting for how and why individuals vary in foraging behavior and flock participation.

While many studies have shown shifts in a species' foraging behavior when engaging in mixed-species flocks as compared to foraging in conspecific flocks or alone (Valburg 1992, Latta and Wunderle 1996, Zou et al. 2011), these foraging shifts could occur in two different ways. First, changes in foraging behavior may be driven by social facilitation in which copying the foraging style of heterospecific or expanding one's foraging niche is equally beneficial to all individuals (Krebs 1973). For example, Farine and Milburn (2013) found that individuals in Australian mixed-species flocks actively shifted their foraging niches towards those of their individual flockmates. Alternatively, foraging shifts may result from different subsets of individuals within species that do or do not engage in flocks due to variations in foraging behaviors and strategies exhibited by these different individuals (Hutto 1988). This may occur if a subset of individuals consistently benefits from participating in mixed-species flocks, for example when individual variation in foraging strategy affects the rates of competition or facilitative information transfer in flocks. Foraging observations of marked individuals in and out of flocks can help us determine whether the contexts in which individuals participate in flocks are the same for all individuals of a species, or if individual variation results in alternative social foraging strategies (i.e. joining mixed-species flocks or not).

Elucidating the evolution of heterospecific sociality requires linking individual variation in heterospecific social behaviors to direct fitness measures such as survival and reproductive success. Many studies have used comparisons of foraging rates (Sullivan 1984, Sridhar et al, 2009), niche utilization (Zou et al. 2011, Farine and Milburn 2013), and vigilance rates (Sullivan 1984, Dolby and Grubb 1998, Sridhar et al. 2009) in and out of mixed-species flocks as proxies for fitness benefits gained through flock participation. Yet evidence linking variation among individual flocking behavior and direct fitness consequences remains rare. There are, however, several examples in which within-species variation in heterospecific interactions is linked to direct fitness consequences in non-flocking contexts. For example, Johnson et al. (2018) showed that heterospecific coresidence in joint territories among two species of fairywrens (*Malurus* sp.) influenced nest survival. Similarly, Forsman et al. (2002) showed that Pied Flycatchers (*Ficedula hypoleuca*) that nested close to nests of heterospecific (titmice: *Parus* spp.) had larger broods and heavier offspring. These examples provide tantalizing evidence that heterospecific associations are not just contextually beneficial, but have quantifiable fitness consequences for individuals that engage in them. By combining studies of individual variation in flock participation with explicit measurements of fitness, such as longevity or fledging success, we can begin to directly quantify flocking benefits and move closer to an understanding of the evolution of these heterospecific associations.

Individual Recognition and Familiarity

Social recognition at different levels is key to social behavior in birds, but studies of mixed-species flocks and conspecific flocks have generally focused on different levels of recognition. Recognition of species identity is known to be a critical component of mixed-species flocks. For example, calls of nuclear species attract other flocking species inducing flock formation (Mönkkönen et al. 1996, Goodale and Kotagama

2005b, Williams and Lindell 2018), and birds are more likely to respond to mobbing calls from species found within their community (Magrath et al. 2012). Some species even take advantage of this attention to species identity to deceive flock participants and steal food by mimicking the alarm calls of other species (Flower 2011, Igic et al. 2015). Meanwhile, within conspecific groups, identity of individuals often plays a critical role in social dynamics. For example, recognition of individuals can promote group cohesion and selection of preferred social partners (Nowicki 1983, Aubin and Jouventin 1998, Hopp et al. 2001, Clark et al. 2006, Tibbetts and Dale 2007, Buhrman-Deever et al. 2008; Chaine et al. 2018). Familiarity may impact the production of or response to an alarm or mobbing calls (Kern and Radford 2016, Coppinger et al. 2018, Coppinger et al. 2019). Repeated interactions between individuals can also promote reciprocity of cooperative behaviors such as anti-predator defense (Grabowska-Zhang et al. 2012a, Krama et al. 2012, Massen et al. 2015, Asakawa-Hass et al. 2016). However, comparatively little is known about if and how individual-level recognition influences patterns of heterospecific interactions.

A few studies provide evidence that recognition of individual social partners is an important component of mixed-species associations. Johnson et al. (2018) illustrated that recognition of social partners and selective aggression towards unfamiliar individuals occurs in Splendid and Purple-backed Fairywrens (*Malurus splendens* and *Maluru assimilis,* respectively), which co-defend joint territories against extra-group members of both species. Relationships among individuals of these species can cross generations, and recognition provides a way that long-term associations and joint territories may be maintained (Johnson et al. 2018). These two species are common participants in a larger mixed-species flocking community (Vander Meiden and Johnson personal observation), suggesting similar patterns of recognition and coordination may be widespread, potentially having implications for community structure and behavior. How recognition shapes heterospecific social partner choice has also been studied in other taxa. For example, individual chubs *(Leuciscus cephalus*) preferentially shoal with familiar heterospecific individuals rather than shoaling with unfamiliar conspecific individuals (Ward et al. 2003). Outside of mixed-species groups, such recognition has been shown to shape territorial interactions. For example, the "dear enemy" effect, where familiar, neighboring individuals receive lower rates of aggression than unknown individuals (Fisher 1954, Tumulty 2018), has been shown in a heterospecific context in crabs (Fogo et al. 2019), cichlids (Lehtonen et al. 2010), ants (Tanner and Adler 2009), and birds (Jedlikowski et al. 2022). However, we currently lack a cohesive understanding of when such familiarity effects may be important in mixed-species flocking contexts. We address two questions in turn: under what scenarios should recognition occur or be important for individual behavior, and how might the consideration of familiarity and recognition shape our research approaches?

Structure of interspecific associations and recognition emerge from spatio-temporal overlap

A key component of recognition is spatio-temporal overlap, which fundamentally affects the probability that individuals re-encounter and become familiar with one another. Thus, the spatial distribution of flocking individuals may play a critical role in the patterns of associations within mixed-species flocks. To illustrate this, we simulated different configurations of territories and home ranges of four hypothetical flocking species (Figure 2; Supplementary Material). First, we simulated a scenario in which mixed-species associations occur among breeding pairs of each species in spatially bound flocks that form in tightly overlapping heterospecific territories (e.g., Munn and Terborgh 1979, Jullien and Thiollay 1998, Farine and Milburn 2013, Johnson et al. 2018; Figure 2A, column 1). Second, we simulated flocks that arise among species with territories that are discrete within species but that variably overlap between social pairs of different species (Figure 2B, column 1). In this case, mixed-species flocks may exhibit "wave-like" properties in which individuals join or drop out as the flock moves across territories (e.g., Moynihan 1962, Powell 1979, Poulsen 1996, Davis and Recher 2002, Kotogama and Goodale 2004). Finally, we simulated flocks that occur among non-territorial members that move within home ranges that can overlap and vary between individuals within and across species (e.g., Bell and Ford 1986; Figure 1C, column 1). The differences in spatial dynamics within and across species in these different scenarios can be captured in individual-level social networks. When mixed-species flocks arise from joint territoriality among heterospecific, coresidents of territories are clustered together into discrete, strongly interconnected modules in the social network (Figure 2A, column 2). In contrast, when mixed-species flock composition is influenced by less tightly coordinated patterns of overlap among territories or home ranges, then the social network can exhibit complex patterns that include both strong and weak connections between heterospecific individuals (Figure 2B–C, column 2). Importantly, the contribution of spatio-temporal overlap to patterns of association cannot be resolved when aggregating data from individuals of the same species together (Figures 2A–C, column 3).

Our examples demonstrate how the utility of individual recognition will differ among flocking communities with different spatial relationships. The importance of individual identity should be high when heterospecific territories strongly overlap, forming discrete clusters of heterospecific individuals (Figure 2A). In such cases, the relevance of information such as the intensity of predator threat or location of novel food sources within the territory will be highest when coming from a heterospecific signaler within the same home territory, rather than a heterospecific or conspecific signaler in a different territory. In contrast, when individuals do not form discrete territories (Figure 2C) individual identity is not necessarily tied to the relevance of the information they may share, reducing the benefit of individual recognition between heterospecific. Thus, the role of individuals in production of relevant information, which may affect patterns of connections within the mixed-species social network (Aplin et al. 2012) is also affected by patterns of spatio-temporal overlap among flock members in addition to individual variation in information production.

We suggest that aspects of life history influencing spatio-temporal overlap among community members will facilitate the evolution of individual recognition across species in mixed-species flocks. For example, familiarity between flockmates may be extremely important in sedentary communities where individuals remain year-round and among species that form highly coincident territories (Munn and Terborgh

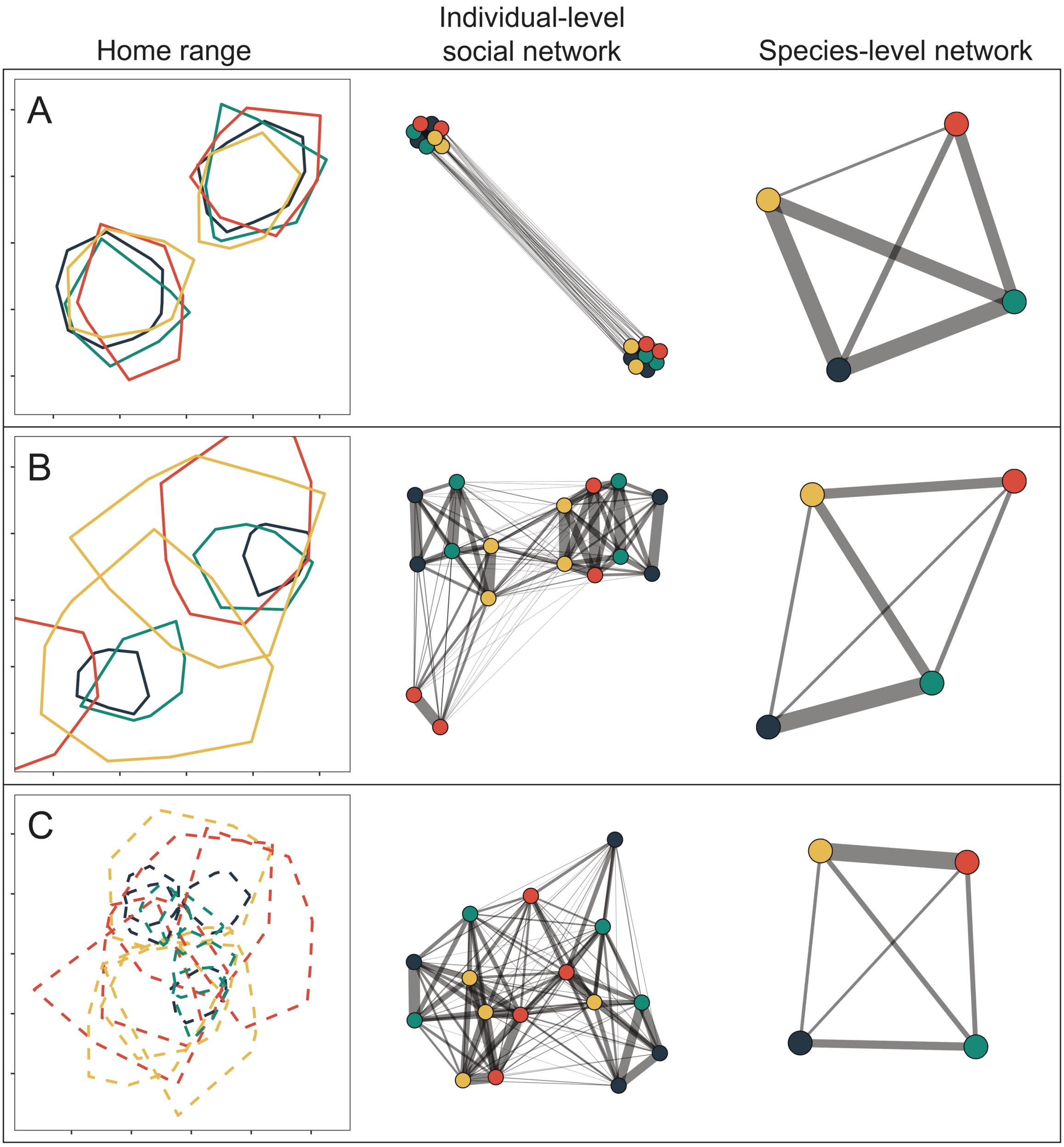

FIGURE 2. Spatial dynamics of individuals shape patterns of associations in mixed-species flocks. We simulated different configurations of territories (**A, B,** column 1) or home ranges (**C,** column 1) as represented by minimum convex polygons, and constructed corresponding individual-level social networks (**A–C**, column 2) and species-level networks (**A–C**, column 3). In each panel, different colors represent each of 4 different species, with 4 individuals per species. For territories (solid lines in **A, B,** column 1), social mates are assumed to have highly overlapping territories, and only one territory per pair is shown. For home ranges (dashed lines in **C,** column 1), each individual home range is shown. When individuals of different species co-defend joint territories (**A,** column 1), then individual-level networks exhibit clustering, with each cluster composed of the coresident individuals of each species. In the individual-level social networks (**A–C,** column 2), nodes represent unique individuals, and edges are proportional to the degree of home range overlap. Thus, our model makes the simple assumption that all individuals are equally likely to join a flock, given it is inside its territory or home range. In the species-level networks (**A–C,** column 3), each node represents a species, and the edges represent the average association between any pair of individuals of different species in the same simulation. Methods are described in Supplementary Material.

1979, Jullien and Thiollay 1998, Johnson et al. 2018). Meanwhile, the importance of the identity of flockmates and familiarity may be seasonal in migratory flocking communities (Ewert and Askins 1991, Gram 1998, Sieving et al. 2004), with weaker individual recognition during spring and fall migration when membership in the community is more dynamic. Flockmate familiarity may be least important to nomadic species that participate in flocks in many communities (Hutto 1987, Ewert and Askins 1991, Farley et al. 2008, Areta et al. 2013), or when flocks form during migration (Rodewald and Brittingham 2002).

Accounting for social recognition in study design

Failure to take into account individual-level patterns of association may cause ambiguity in how the results of studies of heterospecific interactions are interpreted. This may be particularly important for acoustic playback experiments, which have helped develop our understanding of species roles

(Sullivan 1985, Goodale and Kotagama 2005b, Williams and Lindell 2018), heterospecific attraction (Mönkkönen et al. 1996, Zhou et al. 2021), and information flow (Jiang et al. 2020) in mixed-species flocks. Individual identity can impact responses to playbacks through recognition of acoustic signatures or through stimulus location. For example, broadcasting calls of unknown individuals could cause heterospecific attraction because the call is an effective recruitment signal or because heterospecific individuals approach to investigate or contest the presence of unknown individuals. Conversely, broadcasting calls of unknown heterospecific individuals may cause little or no heterospecific attraction in contexts where foreign individuals are less likely to generate useful social information, such as during seasonal dispersal of young. Heterospecific attraction may also depend on stimulus location when birds attend to territory boundaries and locations of rivals, as in heterospecific "dear-enemy" effects (e.g., Jedlikowski et al. 2022). Similarly, response to recruitment calls in mixed-species flock contexts may vary between territorial and non-territorial species, with the response of territorial species being more likely to depend on the precise location of the playback experiment (i.e. inside or outside their territory).

Responses to the absence or loss of other flocking species may similarly be shaped by individual community structure and familiarity. Turnover of individuals through demographic processes such as deaths, births, and immigration, has significant consequences for social behavior within species (Shizuka and Johnson 2020). For example, in Great Tits, conspecific flock members that lost close associates through experimental removal studies tended to increase the number of individuals they associated with, ultimately forming stronger associations (Firth et al. 2017). Other evidence suggests that the loss of heterospecific partners may have a different community effect. In a series of field experiments, Dolby and Grubb (1998, 1999) showed that removing all parid individuals from a forest patch causes a reduction in associations in remaining flocking species and changes in their vigilance behavior. While these studies have been interpreted to illustrate the importance of nuclear species on satellite flockmate participation, the study design does not account for the impact of the sudden loss of familiar flockmates. Importantly, the removal of parid individuals impacted males and females differently (Dolby and Grubb 1998, Dolby and Grubb 2000), implying that the loss of group members or functional social roles may have differential effects on different individuals.

Accounting for individual identity in playback experiment design can be potentially difficult, often requiring time-intensive techniques such as color banding and territory mapping. However, some of the following methods may facilitate experiment design. Planning where playbacks will be conducted and recording individuals of species to be used as stimuli from that location prior to playback presentation can ensure stimuli are from familiar individuals. To examine whether such measures are needed for the full experiment, trial comparisons between local individuals, nearby individuals, and unknown individuals can also be performed as a way to illustrate that identity either does or does not need to be considered in subsequent studies. When color-banded individuals are available, repeated trials using multiple stimuli, similar to the methods employed by Johnson et al. (2018), may illuminate how different stimuli are perceived by individuals of one species even if the entire mixed-species flocking community are not individually marked. While not a minor feat, research that focuses on integrating individual recognition into mixed-species flock research questions may uncover many interesting aspects of heterospecific sociality that are impossible to address when individual observations are aggregated by species.

Individual-Level Processes Underlying Social Roles and Information Flow

Decades of work have described how different species play different roles in flock formation and function, such as "nuclear" species that lead flock movement or promote cohesion (Winterbottom 1943, 1949, Moynihan 1962), "satellite" or "follower" species that join flocks but rarely lead, and "sentinel" species that detect and transmit graded information about predators (Alves and Cavalcanti 1996, Goodale and Kotagama 2005b). Historically, these species roles have been identified via both observational and experimental studies including assessment of the frequency with which a species was seen in a flock (Hutto 1994), species' spatial positions within flocks (Morse 1970, Zhou et al. 2019), or how strongly flocking communities' responded to the vocalizations of one species over another (Mönkkönen et al. 1996, Goodale and Kotagama 2005b, Williams and Lindell 2018). More recently, the use of species-level network analysis has ushered in a new wave of studies that identify social roles through how central, or highly connected, species are within mixed-species flocking communities (Sridhar et al. 2013, Jones and Robinson 2021). However, factors like individual variation, familiarity, and spatial proximity are likely to influence the identity of and benefits provided by nuclear or central roles within flocks and how information from these species or individuals spreads throughout a flocking community.

Combining studies on individually marked communities with social network analysis provides a useful way to fill in details about how such social functions structure associations in the wild. Particularly important is to address whether social roles vary between individuals within species. For example, individual Great Tits vary in exploratory behavior which affects probability of patch discovery (Aplin et al. 2014). This in turn may affect how individual members of this species act as leaders or information transmitters in mixed-species flocks. In conspecific Willow Tit (*Parus montanus*) flocks, dominant individuals are less vigilant (Ekman 1987), a quality that could spill over into mixed-species flocks and influence which individuals are more likely to fill sentinel roles by detecting predators. The degree to which these and other types of individual trait variation discussed in Section 1 affect social roles in mixed-species flocks has rarely been studied. However, one may be able to test these ideas by looking at correlations between individual variation in relevant behaviors, such as alarm call, and variation in strength and quantity of heterospecific connections in multispecies social networks.

Another key advantage of an individual-level approach to mixed-species flocks is the ability to directly study the dynamics of information flow through a mixed-species flock community. Many hypotheses for the formation of mixed-species flocks invoke the benefits of social information that can flow through a "communication network," in which multiple signalers, receivers, and eavesdroppers interact across space and time (Sieving et al. 2010, Jones and Sieving 2019, Martínez et al. 2022). Careful study of the impact of such communication networks requires individual-level studies because the dynamics of social transmission of information are, at their core, an emergent property of interacting individuals. Emerging analytical methods such as multi-network-based diffusion models can estimate the relative tendency for information to flow between individuals within and between species, but these methods require knowledge of individual-level associations. For example, Aplin et al. (2012) and Farine et al. (2015) studied the dynamics of novel food patch discovery in a mixed-species flock community of individually tagged parid species to quantify the degree to which individuals of different species discovered novel food patches a socially, or by following conspecific or heterospecific individuals. They found that individual-level social connections to both conspecific and heterospecific substantially increased a bird's propensity to discover new food patches. They were also able to identify differences in species roles in patch discovery. Marsh Tits (*Poecile palustris*) are suspected to play a keystone role in this community because they had high per-capita rates of social discovery which then contributed to an increase in rates of other species discovering the food patch (Farine et al. 2015). Importantly, differences in the fit of models between forest patches indicated that spatial relationships between individuals may impact the method by which information spreads (Aplin et al. 2012).

DISCUSSION

Participation in mixed-species groups alters the way that animals interact with their environment, shaping microhabitat use, shifting foraging strategies, increasing safety from predators, and altering the local social community (Goodale et al. 2017). Even for species that do not participate in flocks, mixed-species groups can alter the local information landscape (Seppänen et al. 2007, Harrison and Whitehouse 2011, Martínez et al. 2022). Despite these clear implications of mixed-species groups on animal behavior, the analysis of mixed-species groups has taken a primarily species-level approach. While the species-level approach is an effective way to understand broad patterns of ecological communities, it inevitably limits the information that can be gleaned from patterns of association and behavior we observe. Without accounting for variation in how individuals engage in mixed-species flocks, we make an implicit assumption that all members of a species participate in groups at the same rate and shift their patterns of behavior in the same manner. Yet variation at the individual level has long been acknowledged as a critical aspect of both ecology and evolution, not only shaping demography, population processes, and community structure (Hawkes 2009, Shizuka and Johnson 2020), but also providing the foundation upon selective processes can act (Brodie et al. 1995).

Critically, by considering individual variation in flock participation, we can also begin to measure fitness consequences of heterospecific sociality, a key step to understanding its evolution. An individual-level perspective on mixed-species flocks thus opens the doors to new, exciting avenues of research that probe the effects heterospecific flocking relationships may have on other aspects of participants' lives. To what extent do associations impact breeding strategies, such as nest placement, territoriality, and provisioning rates? Does participation in flocks increase longevity or interannual survival? Does this vary among individuals or species? For these reasons, we hope other researchers will recognize both the need and opportunity to prioritize the integration of an individual-level focus with broader flock and species-level patterns.

Early efforts to examine the individual-level relationships between members of mixed-species bird flocks relied on study of individually color-banded populations in species-rich tropical communities with as many as 75 participating species (Willis 1967, Buskirk et al. 1972, Munn and Terborgh 1979, Gradwohl and Greenberg 1980, Jullien and Thiollay 1998, Arbeláez-Cortés et al. 2011, Farine and Milburn 2013, Johnson et al. 2018). This poses major logistical challenges, making it difficult to replicate these efforts. Observations of individually marked birds in smaller, less complex communities such as the parid-led flocks in North America and Europe (Morse 1970, Morse 1978) and the vastly understudied flocks of Australia (Bell 1980, Bell 1986, Vanderduys et al. 2012, Farine and Milburn 2013) and Africa (Gordon and Harrison 2010) or in subsets of specific, targeted species, may allow researchers to better disentangle heterospecific sociality in the context of mixed-species flocks. Modern monitoring technologies such as RFID, automated telemetry, and miniature GPS units can greatly augment the potential for studies (Smith and Pinter-Wollman 2021). This is exemplified by recent studies of heterospecific associations of two parid species in Wytham Woods (Farine et al. 2012, Farine et al. 2015). Use of RFID feeder arrays in conjunction with automated weighing devices, video cameras, weather stations, or sound recording devices (among other technologies), provides further potential to link changes in behavior to changes in patterns of association, condition, or environment (Bonter and Bridge 2011, Madsen et al. 2021). However, the use of RFID-based systems, which rely on drawing birds to resource patches where they can be monitored, may not be appropriate for asking questions about behaviors away from foraging sites or for studying species that are not drawn to artificial feeders. An alternative technique may be to use automated radio-telemetry, which has emerged as a way to monitor rapid, complex changes in associations and movement patterns within species (Shizuka et al. 2022) and could be used to great effect in flocking communities that do not aggregate at feeders. As illustrated in our case studies, these data sources can also be analyzed using social networks to capture nuanced differences in patterns of association between specific individuals.

The ubiquity of mixed-species groups within avian and non-avian taxa means that understanding the formation, structure, and maintenance of heterospecific associations and their implications for both individuals and communities is an important aspect of ecology in general (Harrison and Whitehouse 2011, Goodale et al. 2017). We believe a renewed focus on the individuals that make up mixed-species groups will not only clarify existing information on heterospecific social interactions but also provide new avenues of research that can elucidate the evolution of heterospecific sociality and inform the role of individuals in the resilience of these flocking communities. Such a perspective will become even more critical in the future as animal communities are put under greater stress from anthropogenic environmental changes that reshape animal communities and alter the information and fitness landscapes animals must navigate.

Supplementary material

Supplementary material is available at *Ornithology* online.

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Ethics statement

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Author contributions

L.V.M. and A.E.J. conceived the initial idea for the review. L.V.M. developed the idea and wrote the paper with feedback and edits from A.E.J. and D.S.

Conflict of interest statement

The authors declare that we have no competing interests.

Data availability

Data associated with this manuscript is included in Supplementary Material and is available at Vander Meiden et al. (2023).

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