

Mixed-species animal groups

2021 online symposium

June 14-18, 2021, Beijing Time Zone

Co-organizers: Eben Goodale, Liping Zhou

Monday, June 14, 2021 | Day 1

09:30 pm - 09:35 pm

Eben Goodale

Symposium introduce

1. 09:35 pm - 09:55 pm

Marian Y. L. Wong

Behavioural plasticity in a native species may be related to foraging resilience in the presence of an aggressive invader

2. 09:55 pm - 10:15 pm

Anne Heloise Theo

Response of mixed-species shoaling groups to reef recovery in the Lakshadweep Islands, India

3. 10:15 pm - 10:35 pm

Alex Trillo

Who is your neighbor? Eavesdropping Parasites and the Influence of Nearby Signalers

4. 10:35 pm - 10:55 pm

Nora V Carlson

What makes a 'community informant'? Information reliability and anti-predator signal eavesdropping across mixed-species flocks of tits

5. 10:55 pm - 11:15 pm

Indrikis Krams

Alarm calling behavior of wintering crested tits and willow tits great tits depend on the groups' social structure

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Tuesday, June 15, 2021 | Day 2

1. 09:30 pm - 09:50 pm

Scott Robinson

Mimicry and patterns of species associations in birds

2. 09:50 pm - 10:10 pm

Shuang Xing

Convergence in mixed-species flocks: Insights from plumage coloration on bird community assembly

3. 10:10 pm - 10:30 pm

Kamal Raj Gosai

Evaluating plumage mimicry between the Greater Necklaced and Lesser Necklaced Laughingthrush in mixed-species bird flocks

4. 10:30 pm - 10:50 pm

Harrison H. Jones

Patch size and vegetation structure drive Andean mixed-species flock interaction strength and nuclear species roles

5. 10:50 am - 11:10 pm

Giselle Mangini

Arthropod detectability play an important role over group foraging behavior of birds: a new theoretical framework for mixed-species flocks

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Wednesday, June 16, 2021 | Day 3

1. 09:30 pm - 09:50 pm

Kathryn Sieving

Changes in attitude: Latitudinal shifts in social roles within avian mobs of North America

2. 09:50 pm - 10:10 pm

Todd M. Freeberg

Mixed-species flock variation and finding novel food: correlational and experimental studies with North American parids

3. 10:10 pm - 10:30 pm

Brittany A Coppinger

An experimental test of the effect of conspecific and heterospecific presence on individual behavior of Carolina chickadees and tufted titmice

4. 10:30 pm - 10:50 pm

Jenny Munoz

The influence of facilitation in the elevational ranges of tropical birds

5. 10:50 am - 11:10 pm

Ettore Camerlenghi

Information about Predators Varies across an Amazonian Rain Forest as a Result of Sentinel Species Distribution

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Thursday, June 17, 2021 | Day 4

1. 09:30 pm - 09:50 pm

Qiang Zhang

Trait-mediated assembly of mixed flock networks in southern China

2. 09:50 pm - 10:10 pm

Priti Bangal

Flock-species richness influences node importance and modularity in mixed-species flock networks

3. 10:10 pm - 10:30 pm

Cameron L. Rutt

Seasonal dynamics of flock interaction networks across a human-modified landscape in lowland Amazonian rain forest

4. 10:30 pm - 10:50 pm

Flavia Montaño-Centellas

Temperature and vegetation complexity structure mixed-species flocks along a gradient of elevation in the tropical Andes

5. 10:50 am - 11:10 pm

Fanjul María Elisa

Relationship among vegetation structure and mixed-species flocks composition along the latitudinal gradient of the subtropical montane forest of the Yungas, Argentina

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Friday, June 18, 2021 | Day 5

09:30 pm - 11:00 pm

All participants

Discussion

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Co-organizers: Eben Goodale, Liping Zhou

ABSTRACTS - June 14, 2021 | Day 1

Behavioural plasticity in a native species may be related to foraging resilience in the presence of an aggressive invader

Melinda L. Keiller, Laura K. Lopez, Kai C. Pajmans, Marian Y. L. Wong¹

¹ School of Earth, Atmospheric and Life Sciences, University of Wollongong

Competition between invasive and native species can result in the exploitation of resources by the invader, reducing foraging rates of natives. However, it is increasingly recognized that multiple factors can enhance the resilience of native species competing for limiting resources with invaders. Although extensively studied in terrestrial species, little research has focused on behavioural plasticity in aquatic ecosystems and how this influences native species resilience. Here, we examined the role of behavioural plasticity in interactions between a native Australian fish, *Pseudomugil signifer*, and a widespread invasive fish, *Gambusia holbrooki*. To determine whether *P. signifer* displays behavioural plasticity that may mitigate competition with *G. holbrooki*, we first quantified social behaviours (aggression, submission and affiliation) and shoal cohesion for each species in single- and mixed-species groups. Second, we compared the feeding rates of both species in these groups to ascertain if any modulation of social behaviours and cohesion related to foraging success. We found that aggressive and submissive behaviours of *G. holbrooki* and *P. signifer* showed plasticity in the presence of heterospecifics, but social affiliation, shoaling and, most importantly, foraging, remained inflexible. This variation in the degree of plasticity highlights the complexity of the behavioural response of a native species and suggests that both behavioural modulation and consistency may be related to sustaining foraging efficiency in the presence of an invader.

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ABSTRACTS - June 14, 2021 | Day 1

Response of mixed-species shoaling groups to reef recovery in the Lakshadweep Islands, India.

Anne Heloise Theo, Kartik Shanker

Herbivores play an important function in coral reef ecosystems by removing algae, making space available to coral recruits. The high abundance of herbivores in the reefs of the Lakshadweep islands has potentially aided in reef recovery, despite most areas having suffered massive losses, with live coral cover down to 5% in many sites. Mixed-species grouping in herbivores could potentially benefit both the participant species and the reef ecosystem by improving foraging efficiency. We examined the grouping propensity and species diversity within groups for the three herbivore groups; parrotfish groups, surgeonfish groups and small surgeonfish groups across three islands and three years following the 2010 mass bleaching event in the Lakshadweep islands. Both surgeonfish groups and parrotfish groups both displayed variation in species diversity and propensity measures across island and habitat. In particular, the grouping propensity and species richness of parrotfish groups varied significantly with season (year of sampling) whereas surgeonfish groups did not. Similar patterns were noted in the species assemblages participating in these groups, as both parrotfish and surgeonfish groups exhibited variation in species composition across habitat, while parrotfish groups also displayed variation across time. The number of parrotfish groups observed also declined steadily across the years, indicating that parrotfish groups may have formed in response to the changes on the reef due to the 2010 mass bleaching event, slowly diminishing as the reefs recovered, while surgeonfish groups are likely influenced by local process at the islands.

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ABSTRACTS - June 14, 2021 | Day 1

Who is your neighbor? Eavesdropping parasites and the influence of nearby Signalers

Alex Trillo¹, Christopher Benson, Michael Caldwell, Tiffany Lam, Oliver Pickering, David Logue

¹ Gettysburg College, Dept. of Biology

Males of species with similar breeding requirements often display from mixed-species aggregations. While studies have explored how signaling conspecific neighbors mediate predation and parasitism risk suffered by a focal individual, less is known about how signaling heterospecific neighbors shape these risks. Our studies demonstrate a mechanism by which interactions between heterospecific signalers can substantially influence the attraction of eavesdropping parasites, thereby altering parasitism pressure on their neighbors. We find that the species identity of, call variants produced by, and density of signaling neighbors can each strongly affect these risks. As a companion to our experimental studies, we have developed a simple model, illustrating how the relative attractiveness of neighbors can alter eavesdropper risks faced by signalers. Together, this work indicates neighbors may play an important role in the attraction of eavesdropping parasites to heterospecific signalers.

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ABSTRACTS - June 14, 2021 | Day 1

What makes a 'community informant'? Information reliability and anti-predator signal eavesdropping across mixed-species flocks of tits

Nora V Carlson^{1,2}, Susan D Healy², Christopher N Templeton³

1 Max Planck Institute of Animal Behaviour, Radolfzell, Germany

2 University of St Andrews, St Andrews, Scotland

3 Pacific University, Forest Grove, USA

Mobbing is an anti-predator behaviour characterized by prey harassing a predator, often while producing specific calls. Some species (information sources) include predator threat information in their mobbing calls, but others (information scroungers) do not (either silent, or not including information) and are thought to eavesdrop on this information. Particularly important sources of information are considered community informants. To be considered a community informant, a species must not only produce reliable information, but most importantly, that information must be used multiple species in the community. To determine if species in a community fit into their predicted 'community informant' or 'scrounger' positions based on their ecology, we conducted predator presentations with robotic taxidermy mounts and recorded the vocal responses of each species. We found that species that, at first glance, appear to fit a 'community informant' role do not always meet all the criteria due to unreliability, and that those species thought to be 'scroungers' may not rely as heavily on 'sources' as previously thought. Communities appear to be more a gradient of information across sources and scroungers rather than a division.

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ABSTRACTS - June 14, 2021 | Day 1

Alarm calling behavior of wintering crested tits and willow tits great tits depend on the groups' social structure.

Indriķis Krams^{1,2,3}, Ronalds Krams³, Tatjana Krama³

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3 Department of Biotechnology, Daugavpils University, Daugavpils 5401, Latvia

Social birds often give alarm calls when they see approaching predators. It has been shown that great tits (*Parus major*) give low-risk alarm calls when accompanied by their mates, but they rarely warn unfamiliar individuals. In this study, we tested whether alpha males of crested tits (*Lophophanes cristatus*) and willow tits (*Poecile montanus*) wintering in mixed-species flocks warn each other when in 'despotic' groups exhibiting a nearly linear dominance hierarchy and in 'egalitarian' mixed-species groups in which the hierarchy is less steep. We found that crested tit and willow tit alpha males uttered alarm calls in the presence of all flock members in 'egalitarian' groups while they warned mostly their mates and young females in 'despotic' groups. This explains improved winter survival in both tit species in 'egalitarian' groups.

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ABSTRACTS - June 15, 2021 | Day 2

Mimicry and patterns of species associations in birds

Scott Robinson¹, Rebecca Kimball¹, Ed Braun¹, Eben Goodale, Yang Liu

¹ University of Florida

Recent advances in molecular phylogeny have shown that convergent evolution, which reaches its extreme form in mimicry, is much more widespread than originally believed. Many nearly identical taxa formerly thought to be closely related are now known to have evolved their shared traits independently. Many apparent cases of convergent evolution occur in species that coexist in multi-species societies. In this talk, we first review the hypothesized ways in which multi-species bird flocks favor convergent plumage traits, which include: (a) sharing traits that promote social cohesion ("social mimicry"), (b) selection against species that differ enough in appearance from others in a flock species that they are more conspicuous to predators ("the oddity effect"), and (c) "background matching" in which species converge on color patterns that are different for predators to detect. Second, we review evidence for and against each of these hypotheses as well as alternative hypotheses for convergent plumage such as interspecific social dominance mimicry and physiological constraints (e. g., Gloger's Rule). Third, we develop the hypothesis that convergent evolution in flocks is a mechanism promoting diversification within lineages as the composition of the flocks and hence the characters shared change across the ranges of species. We conclude with a discussion of what kinds of studies are necessary to prove that shared plumage traits in birds that form multi-species flocks result from convergent evolution.

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ABSTRACTS - June 15, 2021 | Day 2

Convergence in mixed-species flocks: Insights from plumage coloration on bird community assembly

Shuang Xing, Liping Zhou, Eben Goodale, Yang Liu, Ari E. Martínez, Scott K. Robinson

The plumage coloration of birds plays an important role in species interactions and environmental adaptation. It has been hypothesized to be relevant for inter-species associations inside mixed-species bird flock communities that are facilitated by positive species interactions. Meanwhile, there may be a selection pressure for plumage convergence among species in flocks to better avoid predators. However, the similarities and differences in plumages across flocking and non-flocking species have rarely been quantitatively assessed. In this study, we compared plumage color for both flocking and non-flocking bird species across land-use gradients (agriculture, buffer and forest) in subtropical and tropical China. We obtained plumage coloration by using the species images from the Handbook of the Birds of the World for all the sampled species to test potential color convergence in bird flocks. Among 184 flocking species out of 321 bird species sampled in 10 study sites in southern China, the plumage color similarity between pairs of flocking species was higher than random pairs generated by a null model from all sampled species and such patterns remained consistent across the three sampled land-use types. Furthermore, the color similarity between species pairs within the same flocks tended to be higher than random pairs from all flocks. These similarities could be due to species in ecological time preferring to associate with other similar species, or convergent evolution. Our findings reveal how elements of sociality and species interactions may influence morphological traits of bird communities.

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ABSTRACTS - June 15, 2021 | Day 2

Evaluating plumage mimicry between the Greater Necklaced and Lesser Necklaced Laughingthrush in mixed-species bird flocks

Kamal Raj Gosai¹, Liping Zhou¹, Yang Liu², Scott Robinson³, Eben Goodale¹

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2 State Key Laboratory of Biocontrol, Department of Ecology, School of Life Sciences, Sun Yat-sen University, Guangzhou, Guangdong, China

3 Florida Museum of Natural History, University of Florida, Gainesville, Florida, United States

Over a century of observations of birds in mixed-species flocks across the world, it has been repeatedly reported that some species resemble each other in their plumage to such an extent that it suggests mimicry. Potential mechanisms of convergence in flocks include that similarities facilitate communication or confuse predators. Alternatively, examples of bird mimicry have been explained by interspecific social dominance (ISDM), in which a subordinate species mimics a dominant one to avoid aggression. We evaluated mimicry in two species of laughingthrush that are distributed from Nepal eastwards into southeast Asia and China. Once considered close relatives because of their striking resemblance in their plumage, recent phylogenies have placed the Greater Necklaced Laughingthrush (GNL, *Pterorhinus pectoralis*) and the Lesser Necklaced Laughingthrush (LNL, *Garrulax montileger*) in different genera. We measured 101 museum specimens of GNL and 75 specimens of LNL that were collected in China and Vietnam. These specimens give some evidence for convergence in color: birds in areas of allopatry tend to be more dissimilar in overall body color than those in sympatry. At the same time there appears to be divergence in body size, with GNL larger and LNL smaller when the species are sympatric. Next, we investigate patterns of co-occurrence in five mixed-species flock datasets from Nepal, Arunchal Pradesh, Myanmar, southwestern China (Yunnan), and eastern China (Zhejiang). The two species are not common (> 30% of flocks) in any dataset. In 4/5 datasets, they are positively associated, and in two datasets the association is perfect (the species are never found apart). Finally, we present some behavioral data from Nepal. In flocks, conspecific individuals tend to be closer together than heterospecifics, although the average distance between individuals of the two species was but 3.9 ± 1.7 (SD) m. Of the times in which the two species followed each other, GNL was always the leader; aggressive interactions were largely absent except for one displacement of LNL by GNL. Our observations confirm a case of mimicry that appears to be related to the spatial association of the two

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species in mixed-species flocks, but as yet we are unable to distinguish among the various explanations for its adaptive value. In addition to flock-associated mimicry and ISDM, other kinds of mimicry should be explored, including Batesian mimicry (are either of the species toxic or distasteful?) and aggressive mimicry (GNL in particular is a large and aggressive bird that might repel the attack of predators).

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ABSTRACTS - June 15, 2021 | Day 2

Patch size and vegetation structure drive Andean mixed-species flock interaction strength and nuclear species roles

Harrison H. Jones, Scott K. Robinson

Mixed-species flocks are a key facilitative interaction for tropical birds. Forest fragmentation leads to species loss and spatial turnover in these flocks, yet it is unknown how these changes to composition influence within-flock species interactions. We used network analysis to characterize flocking interactions along a fragment-size gradient in the Colombian Western Andes. We asked 1) how patch size, edge density, and vegetation structure explained network measures indicative of flock cohesion, 2) whether changes were driven by flocking species turnover or changes to the frequency of species co-occurrence, and 3) whether nuclear species, those that maintain flock stability and cohesion, changed in importance across the gradient. We constructed weighted social networks from flock compositions observed on 500-m transects, and then calculated global network measures and the centrality of six nuclear species. Patch size and edge density did not correlate with interspecific co-occurrence patterns, but interaction strength increased with canopy height. Flocks contained numerous, weak interactions, and there were no flock subtypes, suggesting flock composition was dynamic and unstructured. Several redundant nuclear species were present and varied in importance based on ecological conditions. A chlorospingus (Passerellidae) was most central in old-growth forest, whereas several tanager (Thraupidae) species became more central in smaller fragments and disturbed forest. When partitioning network dissimilarity, we found that 66% of dissimilarity resulted from species turnover, whereas only 34% resulted from changes to species co-occurrence. This finding suggests that coherence of flocking behavior itself is maintained even as extensive species turnover occurs from continuous forest to small fragments.

ABSTRACTS - June 15, 2021 | Day 2

Arthropod detectability play an important role over group foraging behavior of birds: a new theoretical framework for mixed-species flocks

Giselle Mangini¹, Karl Mokross², Facundo Gandoy¹, Juan Ignacio Areta³

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2 Departamento de Ecologia UNESP – Campus Rio Claro, Rio Claro, São Paulo, Brasil.

3 Laboratorio de Ecología, Comportamiento y sonido (ECOSON), IBIGEO – CONICET, Salta, Argentina.

Mixed-species flocks presumably provide birds with antipredator and foraging benefits. The foraging benefits hypothesis predicts that less food will trigger flocking activity; however, flocking activity may also respond to the difficulty of detecting food, which has not been evaluated. We found that flocking propensity of birds was more strongly correlated with arthropod detectability than arthropod abundance after two years in Yungas forest studying 129 mixed-species flocks, recording 1344 birds' foraging sequences, and capturing 25591 arthropods. We performed a first analysis to evaluate whether environmental traits (temperature and foliage density), or arthropod abundance, or rather the combination of both influenced the frequency of arthropod detections made by birds. We found that the combination of environmental traits and arthropod abundance explained food detection of birds. Prey detection was negatively influenced by ambient temperature and foliage density but positively by arthropod abundance. Based on these results, we define our flocking behavioral trigger model that allowed us to compare the relative importance of the difficulty in detecting prey items using a proxy latent variable, arthropod crypsis, and arthropod abundance as predictors of flocking propensity. Flocking propensity peaked when arthropod abundance was greatest but especially when the arthropod community was constituted by a higher proportion of immature and nonflying arthropods, the temperature was low and the foliage density was higher. Lastly we assessed whether birds within mixed flocks experienced increased foraging efficiency compared to birds outside such flocks. On average, individuals within mixed flocks increased their preycapture attempt rate by 40% whilst the search rate increased by 16%. Our research add a new perspective on the drivers of mixed-species flocking, showing that the capacity to find and recognize prey items may have a greater effect on sociality than prey abundance when deciding whether to join a mixed flock to obtain the associated foraging benefits.

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ABSTRACTS - June 16, 2021 | Day 3

Changes in attitude: Latitudinal shifts in social roles within avian mobs of North America

Kathryn Sieving¹, Peter Monte¹, Jeffrey Lucas², Todd Freeberg³

1 Department of Wildlife Ecology & Conservation, University of Florida, Gainesville FL USA

2 Department of Biological Sciences, Purdue University, West Lafayette IN USA

3 Department of Psychology, University of Tennessee, Knoxville TN USA

Under complexity leadership theory, the dynamics of leadership in a complex adaptive social network should respond to changes in follower dynamics. In order to test this idea, we undertook a comparison of avian mob participation by four widely distributed sympatric North American species across a wide latitudinal gradient. All four species (2 from family Paridae, 1 Sittidae, 1 Picidae) are frequently present in, and/or actively lead, mobbing aggregations in aggressive approaches toward a detected predator or stimulus. We predicted that participation in mobbing by the 4-core mob participants would vary with (a) latitude-related patterns in species richness of the overwintering bird community, and (b) participation patterns by core species. We define mob participation for each species as the (a) probability of attendance, (b) speed of arrival at a mob (given attendance), and (c) close approach during mobbing. We used a standardized predator call playback protocol at 43 independent locations across eight different sites in three states in the US (FL, TN, IN) during October to March 2016 - 2018. We conducted 162 playback trials, of which 118 were positive responses we could analyze for speed and proximity metrics.

Mob participation/presence: Mobs were more likely to form in early winter and if more non-core heterospecifics were present. Mob species richness greatly increased participation by Tufted Titmouse and Downy Woodpecker, though discouraged Carolina Chickadee attendance. Titmice were overall most likely to attend, and to be present within 5m of mob center. Titmice and the woodpecker both attended less often if White-breasted Nuthatch attended; chickadees attended significantly more often if either the nuthatch or woodpecker attended. At the highest latitude (IN), the nuthatch was the most common mobbing species (70% of mobs) while the titmouse dominated in the S (FL: 94% of mobs). In Tennessee, titmice and nuthatches were equally the most frequent mobbers (78%). In all states, Carolina Chickadees (46%) mobbed less frequently than Titmice (76%) or Nuthatches (63%) and Downy Woodpeckers (31%) mobbed least often of any species. **Speed of arrival (given participation):** Both the woodpecker and the nuthatch arrived significantly faster at higher latitudes, but overall, nuthatches arrived the quickest, then titmice, chickadees followed by woodpeckers. Findings generally confirm that more speciose mobs can foster mob leadership that is more vigorous. However, attraction and repulsion patterns and

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distributional differences among co-leader species interacts with the local community context to generate clear latitudinal differences in mob organization and social roles.

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ABSTRACTS - June 16, 2021 | Day 3

Mixed-species flock variation and finding novel food: correlational and experimental studies with North American parids

Brittany A. Coppinger¹, Shannon K. Eppert², [Todd M. Freeberg](#)³

¹ University of Tennessee & Villanova University, USA

² University of Tennessee & James Madison University, USA

³ University of Tennessee, USA

Studies of human decision-making from a wide range of disciplines indicate that diverse groups of people typically make better decisions than homogeneous groups of people. Recent studies point to the same general effect in non-human animal species. One way in which animal groups are frequently diverse is in terms of mixed-species group [MSG] composition. We assessed the role of MSG composition on behavior in groups of parids – Carolina chickadees, *Poecile carolinensis*, and tufted titmice, *Baeolophus bicolor*. In unmanipulated MSGs in natural field settings, both chickadees and titmice were more likely to solve a novel feeder task if their groups were more diverse in terms of MSG composition. In manipulated MSGs in semi-natural aviary settings, we exposed flocks to a range of novel feeder tasks from novel feeding contexts to situations in which an apparatus needed to be manipulated for the birds to obtain food. We found that titmice generally solved the novel feeder tasks more quickly than chickadees. For both chickadees and titmice, success at solving these novel feeder tasks depended upon the relative proportion of the two species in the experimental flocks. Successful chickadee flocks solved tasks faster with a higher proportion of titmice in their flocks. Successful titmouse flocks, furthermore, had a higher proportion of titmice in their flocks than did unsuccessful titmouse flocks. Taken together, our studies reveal that these two species of parid are highly sensitive to variation in MSG composition, and point to the importance of heterospecifics in behavior and decision-making of individuals.

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ABSTRACTS - June 16, 2021 | Day 3

An experimental test of the effect of conspecific and heterospecific presence on individual behavior of Carolina chickadees and tufted titmice

Brittany A Coppinger¹, Harry E. Pepper², Emily Graham³, Stephen A. Kania⁴, Kathryn E. Sieving⁵, Jeffrey R. Lucas⁶, Todd M. Freeberg⁴

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2 University of Tennessee, Knoxville

3 University of Tennessee, Knoxville & University of Maryland, Baltimore

4 University of Tennessee

5 University of Florida, Gainesville

6 Purdue University

Animals often change their behavior based on the presence, size, or composition of their social group. Many such effects have been studied in communicative contexts, called audience effects, but group composition may influence non-communicative behavior in addition to communicative behavior. Understanding heterospecific effects on behavior is important for understanding the structure of mixed-species groups. We experimentally tested for conspecific and heterospecific effects on communicative and non-communicative behavior in mixed-species groups of Carolina chickadees and tufted titmice. We sampled birds from naturally-occurring mixed-species flocks and held them in semi-natural outdoor aviaries. After the birds acclimated to the aviaries, we measured rates of calling, flying activity, and social interactions. Chickadees call less and initiate more close perches in flocks of more chickadees. Chickadees call and fly less in flocks with more titmice. There were no significant heterospecific effects on the calling, flying rates, or rates of close perches of titmice, but titmice did call and fly less and initiate more close perches in flocks with more titmice. Our experimental results reveal important sensitivities to variation in social context in these two species. Increased knowledge of heterospecific influences on communication and other behavior will be fundamental for understanding the social lives of individuals in mixed-species groups.

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ABSTRACTS - June 16, 2021 | Day 3

The influence of facilitation in the elevational ranges of tropical birds

Jill Jankowski, [Jenny Munoz](#)

Mixed-species flocks are an important social system for birds globally. These flocks are found in most terrestrial habitats across the world and reach their maximum diversity, complexity, and stability in the Neotropics. Here, species differ in the degree to which they participate in flocks, ranging from species that never join flocks to those that opportunistically join flocks, to those that stay day-long in flocks and appear incapable of foraging independently of flocks (obligate followers) with potentially life-long associations with the same heterospecific flock members. Yet, the tendency to flock is best viewed along a continuum, rather than as a set of discrete categories. Moreover, we should expect selection to shape life history traits differently in species participating in flocks to differing degrees. To date, however, little attention has been given to the evolutionary, physiological, and ecological implications of this widespread living strategy in birds. Therefore, eco-evolutionary questions on the implications of this widespread group living strategy remain unexplored. For example, studies examining whether mixed species flock participation can influence higher-level ecological patterns in communities, have rarely been conducted. We studied 223 independent flocks along an elevational gradient stretching from lowland rain forest to treeline (400-3400 m) on the eastern slope of the Andes in Manu National Park, Peru. We integrated data from demography, point counts, flock observations, occurrence within and outside of flocks and elevational ranges distributions of species to examine whether interdependency of obligate flock members can influence higher-level ecological patterns in communities. Specifically, we evaluated whether mixed-species flock participation influences range limits, range overlap and patterns of coexistence in tropical birds. We hypothesize that if facilitative interactions between flock members set range limits along environmental gradients, species with a high tendency to flock together will exhibit elevational ranges that coincide and overlap more than expected by chance. Similarly, species with a high tendency to flock will exhibit co-occurrences that coincide more than expected by chance.

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ABSTRACTS - June 16, 2021 | Day 3

Information about predators varies across an Amazonian Rain Forest as a result of sentinel species distribution

Ettore Camerlenghi, Paola Tellaroli, Matteo Griggio, Ari Martinez

Information about predation risk is of fundamental value in biological communities. Because many prey species have shared predators, eavesdropping on other species' alarms is a widely recognized mechanism underlying the formation of mixed-species groups. However, information transfer may vary both across and within groups because some species provide higher-quality information about predators than others. We tested this phenomenon in Amazonian understory mixed-species flocks of birds in which two sentinel species—the bluish-slate antshrike (*Thamnomanes schistogynus*) and the dusky-throated antshrike (*Thamnomanes ardesiacus*)—occupy different habitats and provide alarm calls that are used by eavesdropping flock mates. In a playback experiment, two associate species responded significantly more strongly to alarm calls from the same sentinel species, reflecting the greater reliability of information about predator threats that could affect survival and habitat choice. Our work provides evidence of a repeated asymmetry across space in the available information about threats.

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ABSTRACTS - June 17, 2021 | Day 4

Trait-mediated assembly of mixed flock networks in southern China

Qiang Zhang¹, Marcel Holyoak², Eben Goodale³, Yong Shen¹, Christos Mammides³, Fasheng Zou¹

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Network theory provides a flexible framework for exploring community structure through considering species composition and the interactions, but how non-trophic interaction networks (i.e., bird flocks) respond to natural environmental gradients (i.e., elevation) are poorly understood. In this study, we combined long-term monitoring of mixed-species bird flock networks, as well as data on participants' evolutionary history and species traits, and data on forest structure, to seek how flock communities respond to the changes of elevation and vegetation. Our results presented that elevation primarily affect flock communities through re-assembling interspecific associations rather than modifying species composition, in which increasing elevation had a weak impact on diversity and abundance of flocks, but enhanced interspecific associations (normalized and weighted degree), network connectivity (increasing network density) and cohesion (decreasing network modularity). Plant community also mediated the effects of elevation on flocks. Vegetation type changed from subtropical evergreen broad-leaved forest to the montane elfin (tree diversity and size decreased, density increased) with increasing elevation, which produced a more stressful environment for flocks (i.e., lack of food and refuge), consequently resulted in a more cohesive network to buffer environmental stress in high elevations. The phylogenetic and functional perspective showed that associations between close species were weakened and connections between dissimilar species were strengthened, easing competition at the stressful environments provided by high elevations. This study provides an integrative insight into the responses of bird flock communities to natural environmental gradients.

Mixed-species animal groups

2021 online symposium

June 14-18, 2021, Beijing Time Zone

ABSTRACTS - June 17, 2021 | Day 4

Flock-species richness influences node importance and modularity in mixed-species flock networks

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Interdependencies in social groups of animals are a combination of multiple pairwise interactions. Heterospecific groups are often characterized by important species that contribute more to group initiation, maintenance or function than other species. However, in large heterospecific groups, many pairwise interactions are not realised, while others may not be biologically significant, confounding inferences about species importance. In this study, we examine context dependent changes in species importance and assortment in mixed-species bird flocks from a tropical field site in Southern India using social network analysis. Specifically, we ask how species structural importance and community assortment changes when we compare flocks with different levels of species richness, starting with two-species flocks where benefits (provision or gain) are most tightly linked between the participating species. We find that different species emerge as structurally important in flocks of different richness. We also find that assortment is higher in two-species flocks and decreases with increase in number of species in the flock referred to as 'flock richness' hereafter. While our results are largely correlated in both raw and filtered networks, we believe that filtered networks can provide insights into community level importance of species in mixed-flocks while raw networks depict flock-level patterns. We argue that the structural importance of species in mixed-species flock networks is not tightly linked to their functional significance in the community. We suggest that it is important to consider context when interpreting species centrality and importance in network structure. Finally, we propose that examining species structural importance at different flock richness values provides insights into biologically meaningful functional roles of species.

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Seasonal dynamics of flock interaction networks across a human-modified landscape in lowland Amazonian rain forest

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Although lowland tropical rain forests were once widely believed to be the archetype of stability, seasonal variation exists. In these environments, seasonality is defined by rainfall, leading to a predictable pattern of biotic and abiotic changes. Only the full annual cycle reveals niche breadth, yet most studies of tropical organisms ignore seasonality, thereby underestimating realized conditions. If human-modified habitats display more seasonal stress than intact habitats, then ignoring seasonality will have particularly important repercussions for conservation. We examined the seasonal dynamics of Amazonian mixed-species flocks, an important species interaction network, across three habitats with increasing human disturbance. We quantified seasonal space use, species richness and attendance, and four ecological network metrics for flocks in primary forest, small forest fragments, and regenerating secondary forest in central Amazonia. Our results indicate that, even in intact, lowland rain forest, mixed-species flocks exhibit seasonal differences. During the dry season, flocks included more species, generally ranged over larger areas, and displayed network structures that were less complex and less cohesive. We speculate that—because most flocking species nest during the dry season, a time of reduced arthropod abundance—flocks are simultaneously constrained by these two competing pressures. Moreover, these seasonal differences were most pronounced in forest fragments and secondary forest, habitats that are less buffered from the changing seasons. Our results suggest that seasonality influences the conservation value of human-modified habitats, raising important questions about how rain forest organisms will cope with an increasingly unstable climate.

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Temperature and vegetation complexity structure mixed-species flocks along a gradient of elevation in the tropical Andes

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Mixed-species flocks constitute community modules that can help test mechanisms driving changes to community composition across environmental gradients. We examined elevational patterns of flock diversity (species richness, taxonomic diversity, species and guild composition) and asked if these patterns were reflections of the full bird community at a given elevation (open-membership hypothesis), or if they were instead structured by environmental variables. We surveyed both the overall avian community and mixed-species flocks across an undisturbed elevational gradient (~1350 – 3550 m) in the Bolivian Andes. We then tested for the role of temperature, resource diversity (arthropods, fruits) and foraging niche diversity in structuring these patterns. Patterns for the overall and flocking communities were similar, supporting our open-membership hypothesis that Andean flocks represent dynamic, unstructured aggregations. Membership openness and the resulting flock composition, however, also varied with elevation in response to temperature and vegetation complexity. We found a mid-elevation peak in flock species richness, size, and Shannon's diversity at ~2300 m. The transition of flocking behavior towards a more open-membership system at this elevation may explain a similar peak in the proportion of insectivores joining flocks. At high elevations, increasing abiotic stress and decreasing fruit diversity led more generalist, gregarious tanagers to join flocks, resulting in larger yet more even flocks alongside a loss of vegetation structure. At lower elevations, flock species richness increased with greater vegetation complexity, but a greater diversity of foraging niches resulted in flocks that were more segregated into separate canopy and understory sub-types. This segregation likely results from increased costs of interspecific competition and activity matching (i.e., constraints on movement and foraging rate) for insectivores. Mid-elevation flocks (~2300 m) seemed, therefore, to benefit from both the open-membership composition of high-elevation flocks and the high vegetation complexity of mid- and low-elevation forests.

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Relationship among vegetation structure and mixed-species flocks composition along the latitudinal gradient of the subtropical montane forest of the Yungas, Argentina.

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The structural and physiognomic characteristics of forests and montain forest are fundamental aspects that influence the richness, abundance and composition in bird communities. Mixed-species flocks (an association of different species that are formed as a strategy to increase foraging efficiency and / or reduce the risk of predation, mainly in the autumn-winter of the Yungas of Argentina) are considered an emerging property of the community of birds and as such could be directly influenced by the conditions of a given environment. The objective of the present work was to analyze how the vegetation structure could influence the species composition of mixed-species flocks, along the latitudinal gradient of the subtropical montain forest of the Yungas of Argentina. Eight sites were studied along the 700 km of distribution of the Argentine Yungas. In each site, transects visited from June to September (2006-2009) were established. Richness and abundance of mixed-species flocks were determined. In addition, 20 plots of 20x20 m were established at each site. The vegetation variables that were analyzed were: percentage of coverage of the low, medium, high and very high strata, depth of litter, total basal area, richness and abundance of woody species (DBH greater than 5 cm), and maximum height of the canopy. Multivariate analyzes indicated that vertical strata coverage and litter depth were the main variables associated with changes in the species composition of mixed-species flocks along the gradient, but not the richness and abundance of tree or shrub species. The mixed-species flocks of the Yungas presented a relationship with the physiognomy of the subtropical montain forest, which could be indicating that they are strongly linked to the conditions of the vegetation of the place.