Using foraging ecology to elucidate the role of species interactions in two contrasting mixed-species flock systems in northeastern Peru

USING FORAGING ECOLOGY TO ELUCIDATE THE ROLE OF SPECIES INTERACTIONS IN TWO CONTRASTING MIXED-SPECIES FLOCK SYSTEMS IN NORTHEASTERN PERU

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ABSTRACT.—Mixed-species flocks are formed on the basis of both positive and negative species interactions. We use foraging behavior in two different flock types to interpret the extent to which core species minimize niche overlap to reflect negative interactions. We also use the foraging behavior of alarm-calling species to infer whether their behavior is consistent with predictions for species that accrue benefits by associating with other flocking species. The foraging patterns of core species in tierra firme flocks show large differences with respect to foraging maneuvers and substrates, a finding that is consistent with niche theory. In igapó (a blackwater seasonally inundated forest), only the alarm-calling species show differences in foraging patterns among core flock members. We also show that alarm-calling species in different sites show different patterns of association with other flocking species: one species, *Thamnomanes saturninus*, shows no strong tendency to associate with any other species in the flock and the other, *Thamnomanes schistogynus*, perches close to and immediately below other species in the flock. These observations are consistent with the hypothesis that alarm-callers benefit from insects flushed from other flock members in igapó forest but not in tierra firme forest. In northeastern Peru, subtle variation in the foraging behaviors among alarm-calling species in tierra firme and igapó flocks may reflect differences in species interactions among key flock members. *Received 10 November 2014. Accepted 4 December 2015.*

Key words: foraging behavior, mixed-species flocks, species interactions.

INTRODUCTION

Mixed-species animal groups represent an evolutionary and ecological paradox. Species living in stable and permanent mixed-species groups are simultaneously subjected to intense selection for trait convergence to facilitate group living and for trait divergence to minimize competition (Boinski and Garber 2000, Hsieh and Chen 2011). One way in which morphologically similar species can coexist is through behavioral partitioning of resources (MacArthur 1958). Foraging behavior, for example, has often been used as an indirect measure of resource use (Pianka 1973), and a number of studies have used foraging behavior to evaluate niche overlap among species (Holmes et al. 1979, Robinson and Holmes 1982). The tropics provide an iconic example of the diversity of foraging behaviors exhibited by tropical birds. For example, tropical birds have long been known to have specific microhabitat preferences such as specialization on dead leaves (Remsen and Parker 1984, Remsen and Robinson 1990). Indeed, some genera such as *Epinecrophylla,* while specializing on dead-leaves, show otherwise remarkably similar

patterns of prey selection to other antwren genera such as *Myrmotherula* (Rosenberg 1993). Where coexisting flock species forage on similar substrates, such as in the genus *Myrmotherula,* species have shown vertical segregation within a flock (foraging in different strata of the forest: (Pearson 1977). Few studies have quantified foraging behavior of all core members of a mixed species flock (MSF) system in an area, or compared these collective foraging behaviors across flock types from different species pools. Core species are those that are almost always present in a mixed species flock, and that are rarely found outside of flocks (Munn and Terborgh 1979). As core members have high co-occurrence in space and time, such data may provide insights into how different flock systems cope with the costs of ecologically similar species foraging together and about assembly rules that may underlie the composition of MSFs. Comparing foraging behaviors of core flocking species across flocks from different areas may provide indirect evidence for the types of species interactions potentially underlying flock organization (Goodale et al. 2009, Srinivasan and Quader 2012). Comparing and contrasting foraging maneuvers and substrates among species can provide an assessment of niche overlap and competition interactions. Other subtle behaviors such as foraging in proximity to other species may further provide indirect evidence of the strength

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of association among different species within flocks — a potential index of interdependence (Sridhar and Shanker 2014).

In this study, we document the extent to which stable core flock members in two different flock systems differ in their foraging behavior as a means of evaluating the degrees of niche overlap and/or interdependence and consequently the hypothesized roles of competition and mutual interdependence in flock organization. In Amazonian mixed-species flocks, alarm-calling sentinel birds, which forage by sallying, are thought to have a mutualistic relationship with gleaning birds (Munn 1985): the latter benefit from alarm calls while the former benefit from either feeding on insects flushed by gleaning species or through kleptoparasitism of gleaning species. However, different habitats have different sentinel species, and if variation exists in the degree to which these birds depend on gleaning flock members, then this should be reflected in the extent to which they orient their behavior around other core flock species that glean and flush insects (Sridhar and Shanker 2014). Sallying birds that rely on gleaning species should be close to and underneath birds from which they obtain flushed insects. In addition, in order to minimize competition, species with otherwise similar foraging strategies (e.g., gleaning) within a flock type will differ in other aspects of their behavior such as substrate use (e.g., gleaning living versus dead leaves), in order to minimize niche overlap. We compare variations in foraging behavior in two flock systems to understand how processes indicative of competition and cooperation may operate differently between them.

METHODS

Study Site.—We used both tierra firme and seasonally inundated black water forests (igapó) around the Madre Selva Biological Station on the Rio Orosa, a backwater tributary of the Amazon ~100 km downriver from Iquitos, in the department of Loreto, Peru (lat 3°37′2″S, long 72°14′8″W). Tierra firme and igapó forests differ greatly in their bird species composition and forest structure (Remsen and Parker 1983). Igapó forests in Madre Selva differ structurally from tierra firme forests in having areas that are devoid of understory vegetation, lower canopies ($\bar{x} = 18m$ versus $\bar{x} = 24m$, unpubl. data), and more frequent and taller vine tangles. Associated with these differences is a high level of species turnover between understory bird communities of the two forest types. For example, *T. saturninus,* which predominantly feeds off understory vegetation, is much less abundant in igapó forests (see results). In addition, the understory vegetation in much of the igapó open understory lacks suspended dead leaves, which may explain the lack of permanent dead-leaf specialists in the flock. We collected foraging data from 20 flocks in tierra firme forest in ~100 ha in the vicinity of the station and 10 flocks in the igapó forest, ~4 km upriver of the station, in a patch of forest of ~60 ha. We chose these flocks that were readily accessible in areas of primary forest (selective logging has occurred throughout) in both sites; we present descriptive statistics on these flocks in Table 1a.

Foraging Observations.—We collected data on foraging behavior from October–December of 2009 and 2010 by following both banded and unbanded flocks present throughout the two forest sites. These flocks have very stable and predictable roosting sites, territories and membership: Individual species that are permanent members typically included a mated pair with attending juveniles during part of the year (Munn 1985). In our study site, species flocking occurrence was calculated as the mean percentage of time that each species was found across all flocks that were each followed from 6–10 hrs a day. The percentage of time a species was found in a flock was calculated as the proportion of half hour intervals in which an individual species was present over the total number of intervals a flock was followed. Species were considered in a flock if they were feeding within 15 m of another species for at least 15 mins (Martínez and Gomez 2013). We consider species with a flocking occurrence ≥80% as being core flock members and they were chosen as the focal species for evaluating overlap in foraging ecologies (Table 1b). By following a specific flock on a given date, we know that any individual adult flock member of the same sex is the same individual. We used focal animal sampling to quantify the foraging behavior of different permanent flock members found in two separate habitats: tierra firme and igapó forest. We opportunistically initiated focal scan sampling by locating an individual bird of one of the target species and quantifying foraging behavior up to a maximum time of 4 mins. We conducted focal animal sampling by observing the same individual bird through multiple foraging

TABLE 1.   Summary statistics describe in our study site: a) the mean number of individuals (flock size) and mean number of species (species richness) across all flocks where mean (+/-SE) estimates for each flock were derived across all the half hour intervals from which a flock was censused and b) the percent occurrence of core flocking species by forest type where occurrence was calculated as mean occurrence across all flocks (occurrence in each flock is derived as fraction of census intervals over total number of intervals that species was detected in a flock). See supplementary material Appendix 1, Table A1, for a list of species within each flock.

a)

Forest type	Flock size	Species richness
Tierra firme	7.9 +/- .50 (20)	5.7 +/- .32(20)
Igapó	13.3 +/- .74 (10)	9.8 +/- .40(10)

b)

Tierra firme forest species	% Occurrence	Igapó forest species	% Occurrence
Thamnomanes saturninus	93	*Thamnomanes schistogynus*	98
Epinecrophylla haematonota	88	*Microrhopias quixensis*	91
Myrmotherula axillaris	87	*Pygiptila stellaris*	86

sequences of constant observation that lasted from 30 secs to 4 mins as we followed 1–2 flocks throughout the day. Focal scans were considered a different foraging sequence if more than 5 mins lapsed between sequences, at which point we would find a different bird. From each foraging sequence, we quantified only the first observation of maneuvers, substrate, and foraging heights. Maneuvers and substrates were quantified using guidelines established in Remsen and Robinson (1990). We used 1) the following maneuvers: Glean, Sally-Hover, Sally-Strike, Hang, Flush-Chase, Flush-Pursue and 2) the following sub-strates: Green-Leaf, Dead-Leaf, Air, Live-Branch, Dead-Branch (see Table 2 for definitions). We analyzed additional behavioral differences within the genus, such as distance from perch to substrate where prey was attacked, nearest-neighbor distances, and the angle at which the foraging individual of *Thamnomanes* was perched relative to its nearest neighbor. *Thamnomanes* sp. are by far the predominant sallying birds in these flocks, and these additional variables may reflect the degree to which they depend on other flock members (Sridhar and Shanker 2014). We estimated distance to nearest neighbor in 10-cm

TABLE 2.   Definitions of different foraging maneuvers and substrates used in this study, taken from Remsen and Robinson (1990).

Maneuver	Definition	Substrate	Definition
Glean	To pick food items from a nearby substrate that can be reached without full extension of legs or neck; no acrobatic movements are involved	Green Leaf	When a bird attacks any live-leaf substrate
Sally-Strike	To fly from a perch to attack a food item in a fluid movement without gliding, hovering, or landing	Dead Leaf	Attacks directed at dead and dry leaves whether still attached to stems or suspended/accumulated within other vegetation or the forest floor.
Sally-Hover	To fly from a perch and then hover at the target substrate	Air	Attacks that are directed at prey that are in flight
Hang	All glean maneuvers where body is suspended below the feet	Live Branch	When attacks are directed at the surface or within a live branch
Flutter-Chase	To flush or dislodge prey and then chase prey, typically after prey fall from vegetation	Dead Branch	When attacks are directed at any part of a dead branch either suspended or still attached to a living tree
Flush-Pursue	Similar to flutter-chase except species deliberately flush prey from hiding places and pursue flying or falling prey		

TABLE 3.   The number of foraging sequences collected per species.

Forest type	Species	No. of individuals	No. of foraging sequences
Tierra firme	*Epinecrophylla haematonota*	12	40
Tierra firme	*Myrmotherula axillaris*	16	43
Tierra firme	*Thamnomanes saturninus*	11	67
Igapó forest	*Pygiptila stellaris*	10	19
Igapó forest	*Microrhopias quixensis*	10	23
Igapó forest	*Thamnomanes schistogynus*	10	97

increments when birds were closer than 1 m and rounded to the nearest half meter if >1 m away. If different species of *Thamnomanes* depend on flushed prey items from other birds, then they should spend much of their time in a position underneath other birds waiting for falling prey items. Our nearest-neighbor measures were not taken after *Thamnomanes* made a perch change; therefore, we don't know if the associations are of *Thamnomanes* with other species or vice-versa (Sridhar and Shanker 2014). However, our field observations suggest that it is usually *T. schistogynus* which initiates the association. *T. saturninus,* while much less active, is often isolated and any positioning next to heterospecifics appeared much more random on behalf of both species. For estimating the position of *Thamnomanes* to its nearest neighbor, we used a clock-hand orientation where *Thamnomanes* would be at the center of the clock and the neighboring species would be at the corresponding clock number position (we combined the data for the right and left clock halves given that they are symmetrical). In total, we use 290 foraging sequences over 69 individuals for six species from 26 different flocks from both habitats combined (Table 3). In a similar manner, we used only one foraging height per foraging sequence and in the case of the additional behavioral observations of the genus *Thamnomanes*, we used only one observation per foraging sequence. All observations were dictated into an Olympus voice recorder (Olympus Corp., Tokyo, Japan). Visual height estimation was periodically compared with estimates using a laser range finder (using a range finder every time, to measure each height where a foraging bird was first located while simultaneously taking foraging data was not feasible). The birds we followed were a mix of banded and unbanded birds; however, flocks roost in the same locations (Gradwohl and Greenberg 1980, Jullien and Thiollay 1998), so by following different flocks

on different days we are confident we gathered statistically independent observations from different individual birds.

Data Analysis.—In comparing foraging differences among species, we derived mean values for each series of foraging sequences for each individual and used each mean from each individual as an independent estimate. Therefore, the sample size reflects the number of independent means used to estimate differences among species for the different variables of foraging behavior. The single exception was in the case of comparing maneuvers and substrates among species, in that case we combined multiple observations from individuals of all foraging sequences. We did so after comparing individual patterns of maneuvers and substrates among individuals within species to assure that patterns were similar among individuals. In comparing foraging differences amongst the permanent flocking species, we derived contingency tables and calculated Fisher Tests to compare whether a) use of foraging maneuvers differed among species and b) use of foraging substrates differed among species. Because we were interested in which pairs of species differed along these foraging axes, we made multiple pairwise comparisons among permanent flocking species. We then used a Bonferroni correction to account for inflated type I error rates that can result from multiple pairwise comparisons (we interpreted different patterns of maneuvers or substrates at $P = 0.008$). Although number of observations was the measure used in the analyses, we use proportions in frequency histograms to standardize the results for ease of cross-species comparisons. We used either two sample t-tests or a one-way ANOVA to compare flight distances used in attacks among species within each forest. We used one-way ANOVA to evaluate whether there were foraging height differences among species within flocks within each of the two forest types, and used post-hoc

Tukey tests to identify which pairs of species differed significantly in height. To compare nearest-neighbor distances between the two species of *Thamnomanes*, we used a two-tailed *t*-test. To compare differences amongst nearest-neighbor species positions, we determined whether the position of each species of *Thamnomanes* in relation to its nearest neighbors was non-random using a Chi-Square Test, treating the left and right halves of the clock as equivalent in the analysis. Lastly, to determine if any of the species that occur within the flocks are found to be nearest neighbors to *Thamnomanes* disproportionately, we compared the observed proportion of foraging observations in which each species was the nearest neighbor of *Thamnomanes* to the proportion expected under a model of independence among species in which their frequency as a nearest neighbor was determined only by their flocking occurrence (i.e., their probability of occurrence in a flock as estimated by the empirical proportion of flocks in which they occur). Given that pairs and sometimes a juvenile bird represent almost all species, we feel variation in group sizes among species is negligible. We used Monte Carlo methods to generate a *z*-score for each species within each flock as observed minus expected value of the proportion of observations in which each species within a flock should be a nearest neighbor divided by the standard deviation of the expected. We used 10,000 iterations to generate an expected value and its standard deviation for each flock in which we collected data both on occurrence and on nearest neighbors ($n = 8$ for *T. schistogynus* flocks and $n = 9$ for *T. saturninus* flocks). We concluded that a species was disproportionately associated with *Thamnomanes* if the mean *z*-score (across all flocks) was significantly >0 using students *t*-test with degrees of freedom equal to the number of flocks - 1. Data from 2009 and 2010 were pooled together. All analyses were conducted in R version 2.14 (R Core Team 2012).

RESULTS

At the tierra firme site, our foraging results showed high overlap of the predominant foraging maneuvers among *M. axillaris* and *E. haematonota* (Table 4a, Figs. 1a,b), both of which were gleaners. As predicted, substrates used, however, differed widely with *E. haematonota* that specialized on dead leaves and *M. axillaris* that

TABLE 4. Fisher test comparisons amongst species pairs to test for similarity amongst maneuvers for species in both a) tierra firme and b) igapó forests.

a)

Pairwise comparisons	*P*-value
*E. haematonota * M. axillaris*	$P = 0.13$
*E. haematonota * T. saturninus*	$P < 0.001$
*M. axillaris * T. saturninus*	$P < 0.001$

b)

Pairwise comparisons	*P*-value
*M. quixensis * P. stellaris*	$P = 0.23$
*M. quixensis * T. schistogynus*	$P < 0.001$
*P. stellaris * T. schistogynus*	$P < 0.001$

specialized on live leaves (Table 4b, Figs. 2a,b). The other species that caught prey on live leaves, *T. saturninus*, caught most of its prey on the undersides of leaves (72.7% below and 27.2% above, $n = 22$, $\chi^2 = 4.5$, df $= 1$, $P = 0. 033$), whereas *M. axillaris* attacked prey about equally on both the upper and lower surfaces of leaves (40% above and 60% below, $n = 20$, $\chi^2 = 0.8$, df $= 1$, $P = 0.37$). In the igapó forest, permanent members of flocks showed similar patterns of foraging behaviors, with the notable exception of *T. schistogynus* (Table 4b, Figs. 1d–f). *M. quixensis* and *P. stellaris* both gleaned (and occasionally sallied) prey largely on living leaves, whereas *T. schistogynus* predominantly attacked prey in the air (Table 5a,b, Figs. 2d–f). Flight distances did not differ among species in tierra firme (*t*-test, df $= 12$, $P = 0.095$) in spite of *T. saturninus* sallying more frequently, although there was a trend for *T. saturninus* to have longer sallying distances (Fig. 3a). In igapó forest, *T. schistogynus* appeared to have sallying distances far greater than those shown by other flock members (on the rare occasion when those species used flight maneuvers (ANOVA, $F(2,18)=9.23$, $P = 0.002$, Fig. 3b).

Foraging heights of *M. axillaris* within tierra firme flocks overlapped extensively with other permanent flock members, whereas *E. haematonota* foraged significantly lower than *T. saturninus* (ANOVA, $F(2,21) = 4.14$, $P = 0.031$, TukeyHSD adjusted *P*-value $= 0.023$ for the pairwise difference between *T. saturninus* and *E. haematonota*, Fig. 4a). Amongst igapó flocks, all three permanent flocking species showed high overlap in their foraging heights, (ANOVA, $F(2,21) = 0.261$, $P = 0.77$, Fig. 4b). The distance
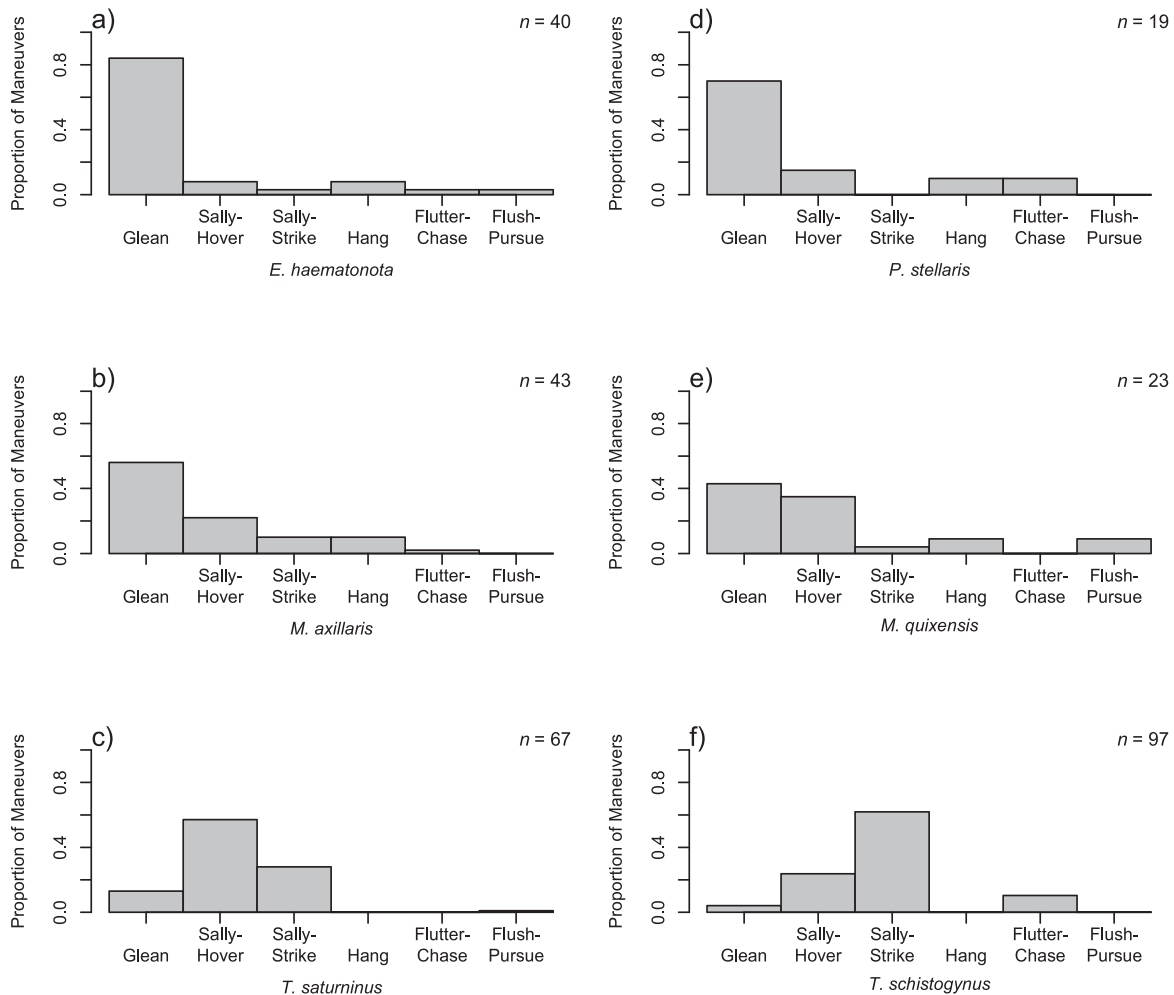
FIG. 1.   Proportion of foraging maneuvers based on first attacks of each sequence for multiple sequences for each species in *tierra firme* and *igapó* forests. n = number of sequences that we observed for each species.

to nearest neighbor was considerably closer for *T. schistogynus* in igapó flocks than it was with *T. saturninus* in tierra firme flocks (Fig. 5, *t*-test, df = 15, $P < 0.001$). *T. saturninus* appeared to have no directional bias with respect to its heterospecific neighbors (Table 6, $\chi^2 = 0.49$, df = 1, $P = 0.48$), whereas *T. schistogynus* non-randomly perched at angles below heterospecific neighbors (Table 6, $\chi^2 = 48$, df = 1, $P < 0.001$). In addition, the identity of several nearest neighbors was non-random according to their expected frequencies for both species of *Thamnomanes* (Fig. 6a,b). With respect to *T. saturninus*, one of the most common flock members, *M. axillaris* was more often its nearest neighbor than expected because of chance alone (*t*-test, df = 8, $P = 0.049$). As for *T. schistogynus*, *L. tangarinus* (*t*-test, df = 7, $P = 0.045$) and *P. genibarbis* (*t*-test, df = 7, $P = 0.049$) were observed to be

nearest neighbors more often than expected as a result of chance alone.

DISCUSSION

Our results provide partial evidence for competition and interdependence in MSFs: the foraging behavior of MSFs in Amazonia reflects both minimized overlap among the foraging axes of gleaning flock members (competition) and behaviors of *Thamnomanes* consistent with dependence on other gleaning species (cooperation). *T. schistogynus* foraged close to and below other members of the flock, which is consistent with the hypothesis that it depends upon other species to flush insects (Sridhar and Shanker 2014). Within igapó flocks, gleaning species differed relatively little in their foraging behavior, suggesting a reduced role for resource partitioning for food resources. In contrast, in tierra firme flocks, *T. saturninus* showed
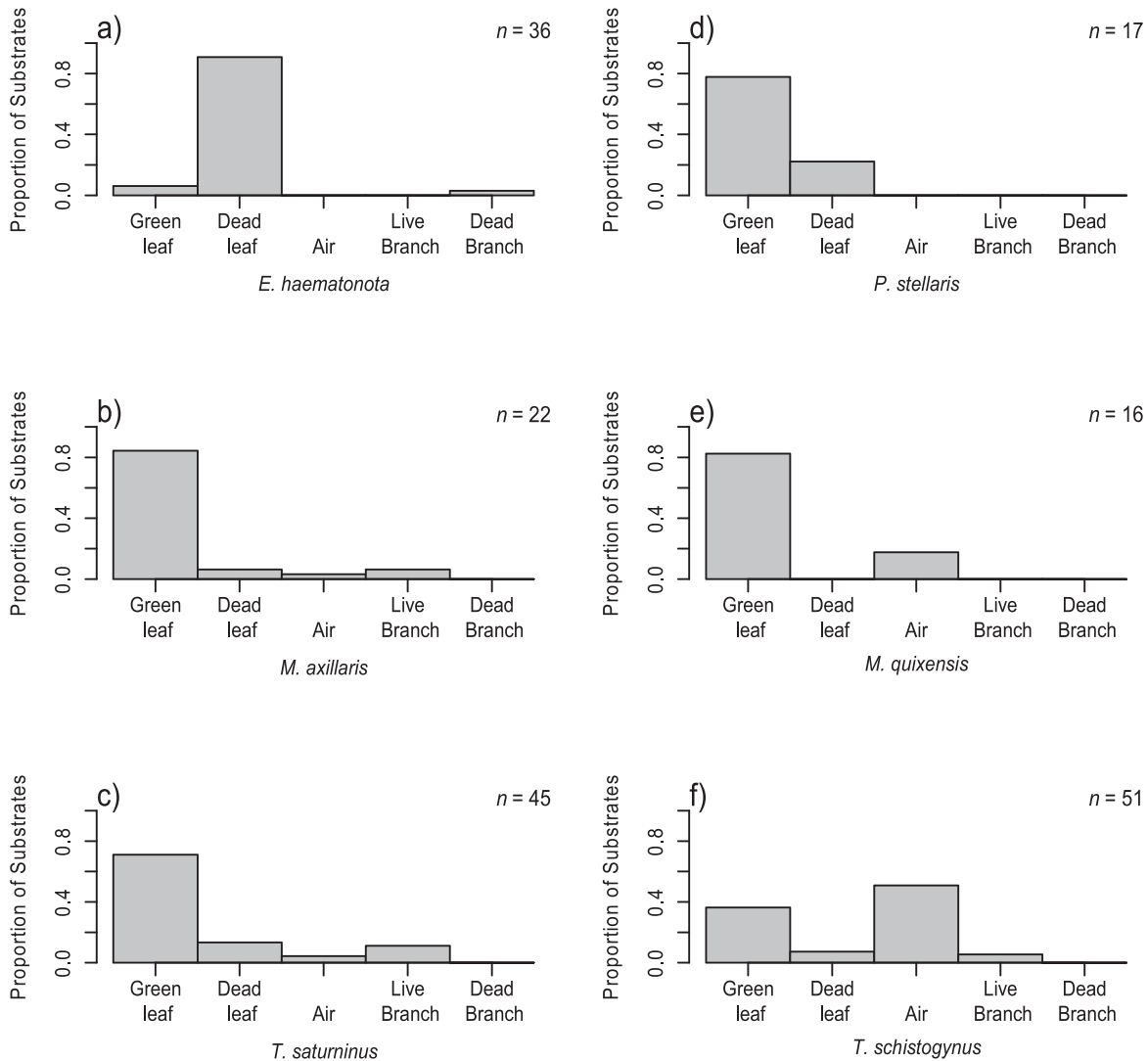
FIG. 2.   Proportion of foraging substrates based on first attacks of each sequence for multiple sequences for each species in both *tierra firme* and *igapó* forest. n = number of sequences that we observed for each species.

no tendency to change its position with respect to other flock members or to catch aerial prey that might have been flushed by other members of the flock, and the species remained much farther from other flock members than its counterpart *T. schistogynus* (Table 6 and Fig. 5). In addition, in tierra firme flocks, each species had very different foraging behaviors, a result consistent with the hypothesis that resource partitioning facilitates species coexistence (Alatalo et al. 1985, Leme 2001). The gleaning species take advantage of alarm calling by *T. ardesiacus* (Martínez and Zenil 2012) but do not provide any benefit to the latter. Thus in the igapó forest, a species of *Thamnomanes* appears to provide and receive benefits (a form of cooperation), whereas in the tierra firme forest,

species tend to follow *Thamnomanes* because it provides benefits (i.e., vigilance against predators) but do not appear to confer any benefits themselves, possibly reflecting commensalism or parasitism. Taken together, these results suggest that these two flock systems may be organized differently. In the rest of the discussion, we examine the implications of our results for the structure of MSFs and for communities in general.

While species clearly must be similar enough in some aspect of phenotype in order to flock (Sridhar et al. 2012), species that have high levels of co-occurrence must differentiate across some niche axis in order to avoid competition. Each permanent member of the tierra firme flocks had distinct foraging niches defined by foraging

TABLE 5. Fisher test comparisons amongst species pairs to test for similarity among substrates for species in both a) tierra firme and b) igapó forests.

a)

Pairwise comparisons	P-value
E. haematonota * M. axillaris	$P < 0.001$
E. haematonota * T. saturninus	$P < 0.001$
M. axillaris * T. saturninus	$P = 0.95$

b)

Pairwise comparisons	P-value
M. quixensis * P. stellaris	$P = 0.024$
M. quixensis * T. schistogynus	$P < 0.002$
P. stellaris * T. schistogynus	$P < 0.001$

maneuvers and substrates (Tables 3–4, Figs. 1–2). These differences were substantial enough that it is unlikely that these species competed strongly for the same food resources. In igapó forest, the gleaning species, *P. stellaris* and *M. quixensis*, showed some partitioning of their foraging niche through either maneuver or substrate or both, but the differences were not significant nor were their foraging heights different (Table 3b, 4b, and Figs. 1d–f, 2d–f, and 4a). They may differ sub-

stantially in diet (which we did not quantify) given their considerable difference in body mass and the much larger bills of *P. stellaris* (Alatalo and Moreno 1987). These results are consistent with previous studies that show differences in either morphological or behavioral traits of similar species coexisting in flocks, consistent with the hypothesis that competition influences the organization of mixed species flocks (Wiley 1971, Jones 1977, Newell et al. 2014). Larger scale studies have been less conclusive: Studies of mixed species flocks in both the Andes and the Amazon suggest more typical assembly rule patterns suggesting competition, although the results of the latter more likely reflected habitat segregation among flock types and did not consider the associations among species on small spatial scales (Graves and Gotelli 1993, Colorado and Rodewald 2015). A recent global meta-analysis suggests that flocks in many sites across the world are organized through positive associations among species with similar traits such as body size or foraging strategy (Sridhar et al. 2012). Such larger scale studies, however, lack the resolution provided by detailed local studies of foraging ecology of the species within flocks.
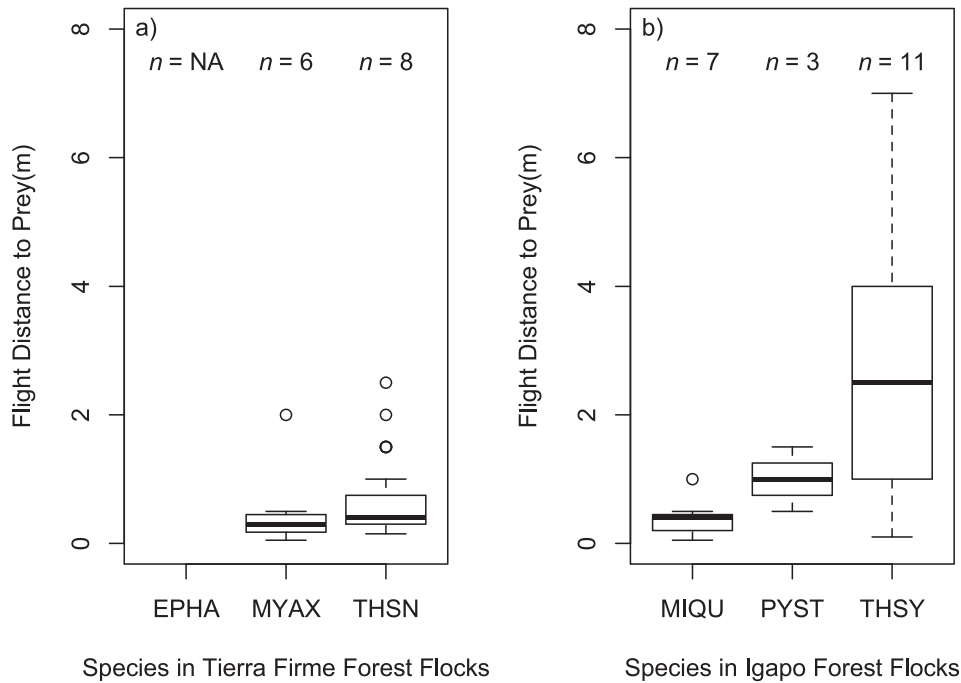

FIG. 3. Flight distances estimated from flight-based foraging maneuvers on first attacks of each sequence for multiple sequences for each species for a) tierra firme forests and b) igapó forests. *n* = number of mean foraging sequences that we observed for each species. Where EPHA = *E. haemotonota*, MYAX = *M. axillaris*, THSN = *T. ardesiacus*, MIQU = *M.quixensis*, PYST = *P. stellaris*, THSY = *T. schistogynus*.
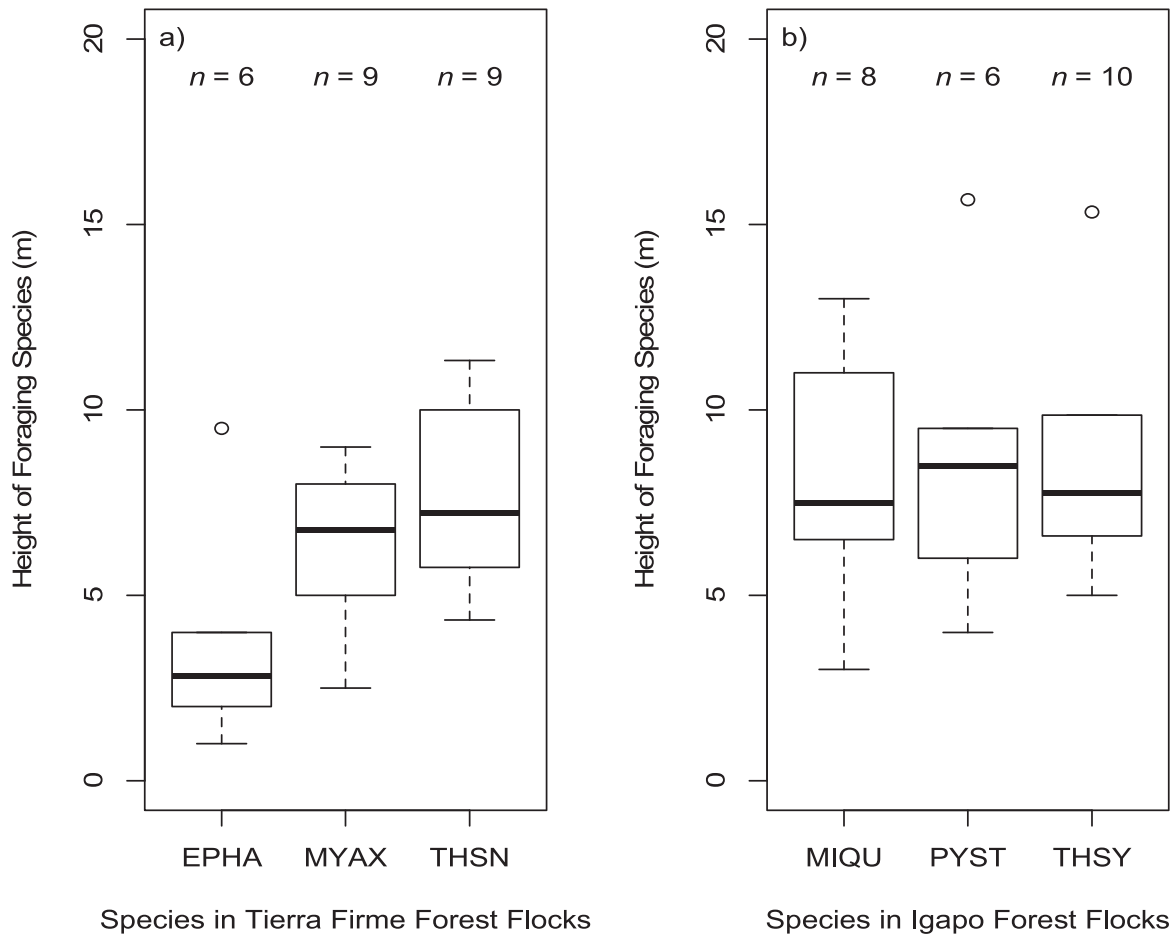
FIG. 4.   Foraging heights for each species where n = mean height of individual foraging sequences for each of 8–10 individual birds per species, for a) tierra firme and b) igapó. Where EPHA = *E. haemotonota*, MYAX = *M. axillaris*, THSN = *T. ardesiacus*, MIQU = *M.quixensis*, PYST = *P. stellaris*, THSY = *T. schistogynus*.

Details of movement rates, microhabitat use, and substrate use may provide finer-scale resolution necessary to assess the influence of competition on the coexistence of species in flocks (Jones 1977, Newell et al. 2014). The subtleties of species interactions may further be influenced by differences among individuals (Farine and Milburn 2013), i.e., age and dominance hierarchies may also influence interactions (Cresswell 1994).

The two alarm-calling species diverged dramatically in their use of foraging maneuvers and substrates as well as their tendency to orient their behavior with respect to other flocking species. While both used aerial maneuvers, *T. saturninus* predominantly hovered to catch prey on leaf surfaces, whereas *T. schistogynus* used longer sallying maneuvers and chased prey items in the air (Figs. 1–4). The maneuvers of *T. schistogynus* and its non-random association with either larger

birds such as *P. stellaris* and *L. tangarinus* or dead leafing specialists such as *P. genibarbis* (Fig. 6b) are consistent with the hypothesis that a large proportion of its prey items are flushed by other bird species or that it kleptoparasitizes these species (Munn 1986, Sridhar and Shanker 2014), whereas the behavior of *T. saturninus* is consistent with a foraging ecology that does not depend upon the activities of other surrounding birds. In tierra firme, *M. axillaris* was found to be neighbors more often than expected from chance. We suggest that this may indicate a preference on the part of this species to try and maintain a presence somewhere near *T. saturninus*, because of its dependence on alarm calls. These differences in foraging behavior also appear to have morphological correlates. *T. schistogynus* has rictal bristles consistent with other flycatching species that take prey items from the air, whereas
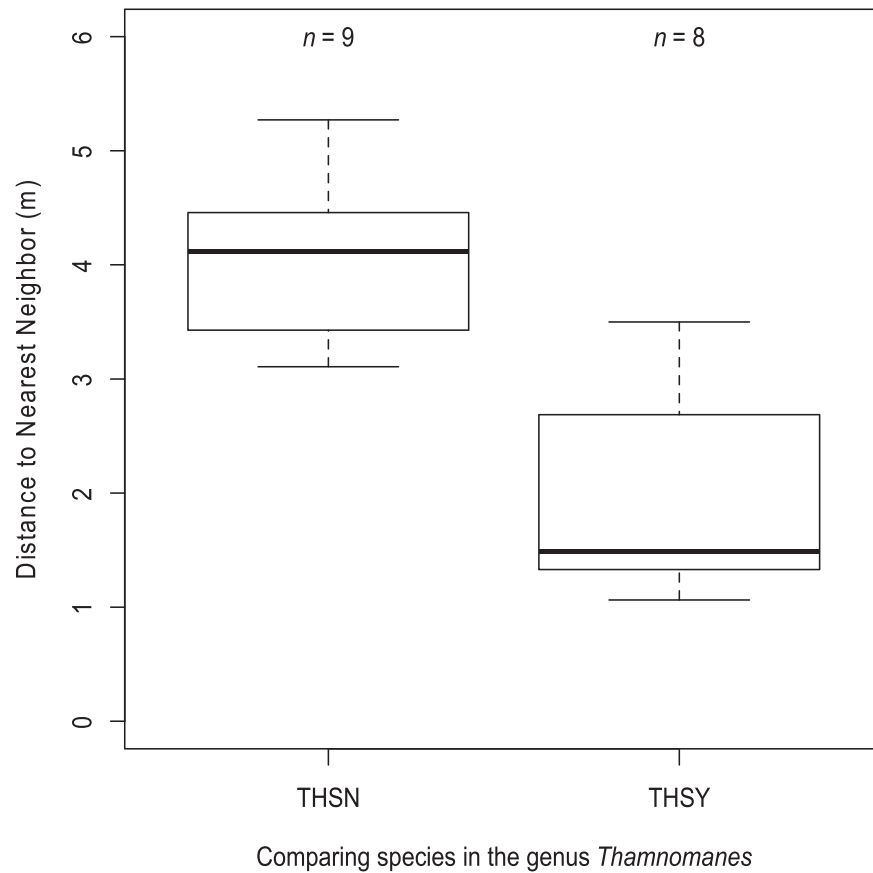
FIG. 5.   The distance to nearest-neighbor species for foraging individuals in the genus *Thamnomanes*, a) tierra firme, and b) igapó forest. *n* = number of mean foraging sequences that we observed for each species. Where THSN = *T. saturninus*, and THSY = *T. schistogynus*.

T. ardesiacus, the sister species of *T. saturninus* in this study, does not (Schulenberg 1983). Thus, differences in foraging behaviors between the alarm-calling sentinels may underlie potential differences in species interactions organizing flocks in different habitats.

From an evolutionary standpoint, these two flocks may reflect different stages in the evolution of interspecific cooperation (Axelrod and Hamilton 1981). *T. schistogynus* is a very vocal flock member that has been hypothesized to use its vocalizations to "attract" other species to the flock (Munn and Terborgh1979), and has even been observed using kleptoparasitism to steal prey items through false alarm calls. The use of false alarm calls has not been observed in *T. saturninus,* which is also a much less vocal flock member than *T. schistogynus*. Thus, flock members may be eavesdropping on *T. saturninus* strictly for their own benefit, whereas *T. schistogynus* may have evolved a strategy in which it benefits from other species through flushed insects and kleptoparasitism. We suggest that finer-scale studies can reveal how subtle differences in the behaviors of flock

TABLE 6.   Proportion of positions where the nearest-neighbor species was either above or below a foraging *Thamnomanes*. We quantified positions by using a clock reference in relation to *Thamnomanes*. Above = Positions from 10 to 2 o'clock and Side or Below = Positions from 3 to 9 o'clock.

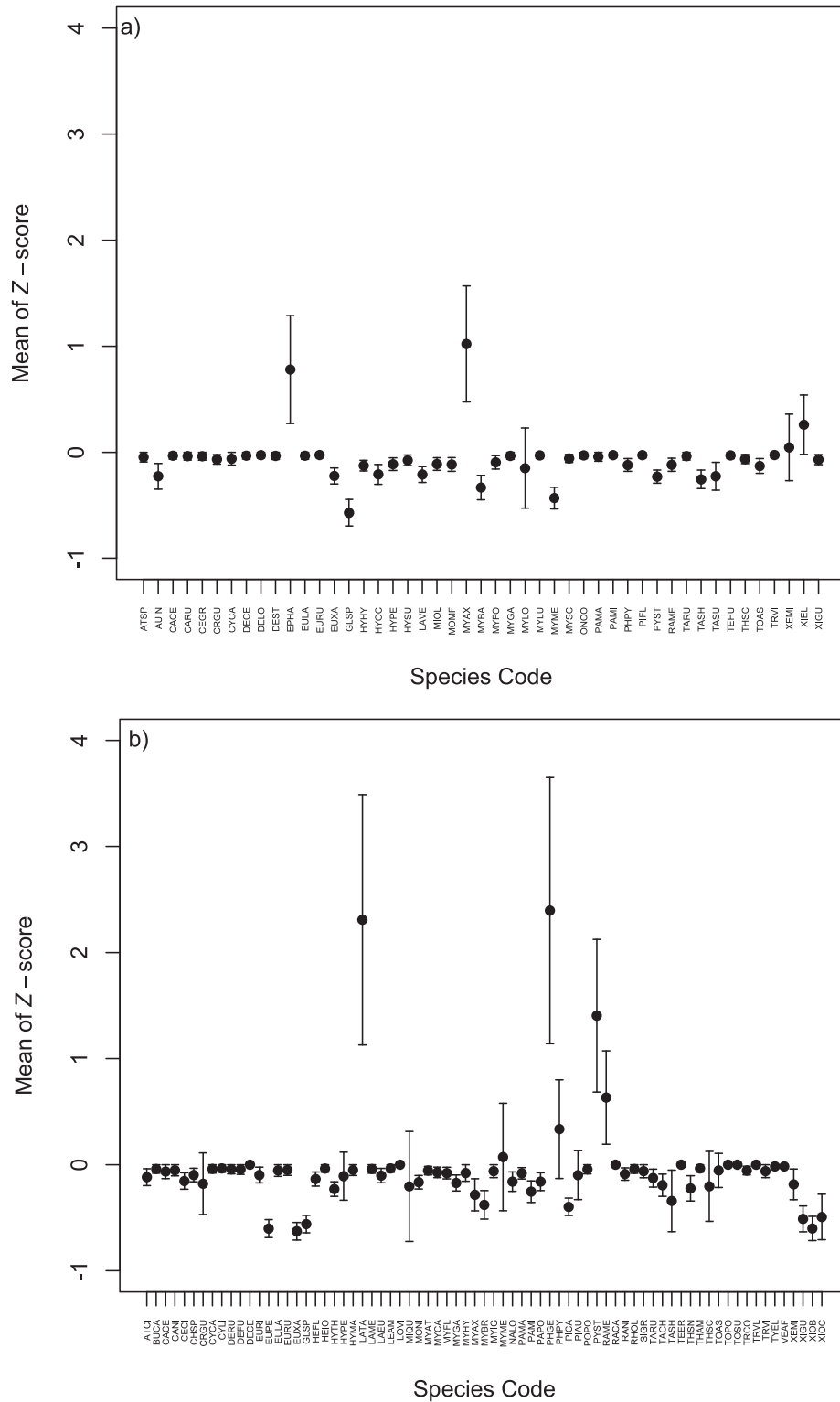| Species	Nearest neighbor above	Nearest neighbor below	*n*
T. saturninus	0.466	0.534	103
T. schistogynus	0.846	0.154	91

FIG. 6.   The mean *Z*-score of different nearest-neighbor species to a) *Thamnomanes saturninus* and b) *Thamnomanes schistogynus* based on the flocking occurrence of different species. Dark circles = mean *Z*-scores for the difference in the observed and expected proportions of nearest neighbors for each species averaged across each flock where nearest-neighbor observations were recorded ($n = 8$ for *T. saturninus* and $n = 9$ for *T. schistogynus*). Error bars=+/- 1 Standard Error. The codes on the x-axis correspond to the first two letters of the genus and first two letters of the species. See supplementary material Appendix 1, Table A1, for a full list of species names corresponding to the four letter code abbreviations on the x-axis.

members may lead to interesting insights into the relative importance of different species interactions like competition, commensalism, kleptoparasitism, and mutualism both within as well as among flock types. Quantifying the relative abundance of different behaviors, such as foraging strategy, may also provide fertile ground for theoretical explorations of the mechanisms underlying the evolution of species interactions among different flock types.

Ultimately, while morphology and behavior can provide insights about species interactions within flocks, they are best used when done in conjunction with experimental removal of species to measure responses of other flocking species (Alatalo et al. 1985, 1987; Dolby and Grubb 1999). In this way, species interactions underlying different flock types, whether they are competitive or cooperative, can be rigorously assessed. Based on the results presented in this paper we feel that future studies of the organization of mixed-species flocks should take into account foraging behaviors among flock members in conjunction with removal experiments of different flock members, to evaluate the relative contribution of different species interactions to the organization of flocks and the consequences of these behaviors for different levels of cooperation amongst heterospecific groups.

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