

Research Article

Leadership of Winter Mixed-Species Flocks by Tufted Titmice (*Baeolophus bicolor*): Are Titmice Passive Nuclear Species?

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The tufted titmouse (*Baeolophus bicolor*, TUTI) is a nuclear species in winter foraging flocks whose antipredator calls are used to manage predation risk by diverse heterospecifics. We hypothesized that satellite species in mixed flocks follow TUTI (not vice versa), thereby defining the role of TUTI as a “passive” nuclear species. We followed 20 winter mixed-species flocks in North-Central Florida and assessed angular-angular correlations between overall flock, TUTI, and satellite species movement directions. We observed significant correlations between overall flock movement directions and those of TUTI, confirming our central prediction. Within flocks, however, fine-scale movement directions of satellite species were often more highly correlated with those of other satellites than with TUTI movements. We conclude that TUTI are passive nuclear species whose movements define flock paths, but within flocks, TUTI movements may have less influence on satellite movements than do other factors.

1. Introduction

Multispecies bird flocks, comprising individuals that move together in organized association with each other as they forage during daylight hours, are a common phenomenon in forested ecosystems of the world [1]. Flock participants occupy different behavioral niches, or social roles, within flocks. Flocking species are generally classified into “nuclear” and “satellite” roles [2–4]. Nuclear species are those flock participants whose conspicuous behaviors (distinctive alarm or other vocalizations and active movements) enhance flock cohesion and may stimulate flock formation. Nuclear species are typically intraspecifically social (occurring in extended family groups for some of the year), and they occur more often in flocks than outside of them when flocks occur [5, 6]. Nuclear species are thought to fall into two general categories: passive or active nuclear species [2, 3]. Passive nuclearity is hypothesized to come about when satellite species actively seek out and follow the nuclear species, thereby defining the nuclear species as the flock leader. Conversely, active nuclear species are hypothesized to seek out and join existing mixed-species flocks and are just as likely to follow the satellites as

to be followed by satellites, but active nuclear species are still able to maintain flock cohesion (see review in Farley et al. [4]). A variety of fitness benefits can accrue to satellite species as a result of flocking with nuclear species, but benefits to nuclear species are less obvious [7–12].

Parids (family Paridae) function as nuclear species in winter and nonbreeding mixed-species forest flocks in North America and elsewhere in the Holarctic [4, 7–9, 13]. As a family, parids have traits that predispose them to nuclear roles in heterospecific groups; they are intraspecifically social [1, 14, 15] and aggressive mobbers of potential predators, usually leading mobbing events; their behavior may significantly reduce predation risk for satellite species [4, 11, 13, 14, 16–19]. In the Eastern United States of America, the tufted titmouse (TUTI; *Baeolophus bicolor*) is a socially dominant parid that functions as a nuclear species in flocks even where TUTI co-occur with chickadees in flocks (chickadees may also serve as nuclear species when not participating in flocks with TUTI [14]). TUTI, like other parids, produce copious threat-related vocalizations that are thought to be signals meant for conspecifics but that are used as informational cues by numerous heterospecifics [19–22]. Some parids give

food-related cues for conspecifics [23], but their use by heterospecifics has not been documented to our knowledge.

Thus, the central known fitness benefits available to satellite species, or heterospecific associates of parids more generally, may be the reduction of predation risk during critical activities [9, 19]. Dolby and Grubb Jr. [7] demonstrated that when TUTI were removed from isolated woodlots, individuals of satellite species remaining in those woodlots in winter occupied reduced foraging niches, avoided exposed foraging sites, and declined in overall physical condition relative to individuals who were in woodlots where TUTI had not been removed. The presence of parids enhances access to resources and microhabitats within forest bird home ranges ([9]; aids heterospecifics in finding suitable breeding habitat via heterospecific attraction; [24]) and possibly increases nest success [25]. These findings suggest that the prodigious amount of information that parids produce concerning their immediate perceptions of predation risk aids their fellow prey species in many aspects of decision making including (a) increased foraging efficiency, (b) access to critical micro- and macrohabitats, and (c) an elevation of the effectiveness of antipredator defense [10, 19, 22, 25, 26].

Determination of whether nuclear species interact with heterospecifics passively or actively in mixed flocks has only received speculation at this point [10], yet this kind of information could enhance understanding of the evolutionary ecology of facilitation, parasitism, and mutualism in animal communities [27]. For example, if titmice are active nuclear species, soliciting close relationships with other species, it would suggest that they accrue benefits from associated heterospecifics [28]. In this case, it might be productive to test whether the finely tuned antipredator calls of tufted titmice may involve active signaling to heterospecifics rather than being purely intraspecific (kin) signals that are gleaned by eavesdropping heterospecifics [15]. If, however, titmice are passive flock leaders being followed by other species, then exploring aspects of heterospecific exploitation of the nuclear species would be most productive [10]. To date, we have conflicting evidence regarding what tufted titmice may gain in the presence of heterospecifics. One potential benefit is food items taken from smaller satellites (kleptoparasitism; [29]). However, we have witnessed that the only species in actively foraging mixed flocks that reliably get killed during hawk attacks are titmice (T. A. Contreras and K. E. Sieving, unpublished data), suggesting that the presence of flocks may be an important fitness cost to titmice. Here, we sought to determine whether TUTI are passive or active nuclear species in order to inform future research questions and critically assess the common assumption that mixed-species bird flocks are models of mutualism [30]. If satellite and nuclear species are not gaining fitness through association, then it would be more productive to assume that the full range of exploitative (parasitic and commensal) and mutualistic relationships are displayed in flocks [10, 27, 31]. We undertook an analysis to distinguish active from passive flock leadership by TUTI in order to clarify future steps in understanding the ecological and evolutionary relationships acting within mixed species flocks.

Studies in North-Central Florida [4, 9, 16, 17] and elsewhere in Eastern NA (see Greenberg [1]) identify TUTI as the primary nuclear species in most winter mixed-species bird flocks. While this classification of TUTI is based on their pervasive presence in winter foraging flocks and their dominating role in mixed-species mobbing flocks [7, 9], the question remains whether TUTI are functioning as passive or active nuclear species in winter foraging flocks. Accordingly, we used a correlative analysis of TUTI and satellite movements at two spatial scales of flocking behavior which we categorized as: (1) the correlation between the movement of TUTI or satellites with overall flock movement through a landscape (*flock leadership*) and (2) the correlation between the movement of TUTI or satellites with the movement of immediate flock members (*within-flock movement*).

We followed mixed-species flocks during a single winter (2004) in North-Central Florida, mapping the overall movement directions of flocks and the movement directions of randomly selected satellite species and TUTI in each flock (providing comparisons for both analyses; flock leadership, and within-flock movements). Based on Farley et al. [4], we classified individuals in the flock as nuclear species (TUTI), satellite species (species who are “regular and occasional associates” in mixed-species flocks), or nonflocking species. If TUTI are functioning as passive nuclear species and flock leaders, then we predicted that (1) overall flock movement direction should be more highly correlated with the movement direction of individual TUTI than with those of satellite species (Figure 1(a)) and (2) the within-flock movement directions of satellite species in flocks should be more highly correlated with the movement direction of the nearest TUTI than with the nearest satellite species (Figure 1(b)).

Previous observations of forest bird mobbing activity (see Sieving et al. [9]) also suggest that satellite species may be more likely to move through areas with less vegetative cover (open cover types) when TUTI are present, especially when perceived or actual risk of predation may be high. Therefore, we also predicted stronger correlations between TUTI movement direction and flock movement direction as flocks move through more open cover types.

2. Materials and Methods

2.1. Study System. To test our predictions, we observed and followed wintering mixed-species: forest passerine flocks in North-Central Florida from January to March, 2004. Flocks were observed at 3 sites: (1) the University of Florida’s Ordway-Swisher Biological Station (Putnam County; N 29° 41’ 45.6”, W 81° 58’ 56.2”), (2) the San Felasco Hammock Preserve State Park (Alachua County; N 29° 42’ 46.3”, W 82° 27’ 23.7”), and (3) Payne’s Prairie Preserve State Park (Bolen’s Bluff location; Alachua County; N 29° 33’ 24.6”, W 82° 19’ 47.5”). All 3 sites had similar vegetation and cover types. In hardwood stands (cover type: hardwood), the canopy and subcanopy layers were dominated primarily by laurel oak (*Quercus laurifolia*), live oak (*Q. virginiana*), sand live oak (*Q. geminata*), water oak (*Q. nigra*), pignut hickory (*Carla glabra*), sweetgum (*Liquidambar styraciflua*), or cabbage palm (*Sabal palmetto*), while the understory was

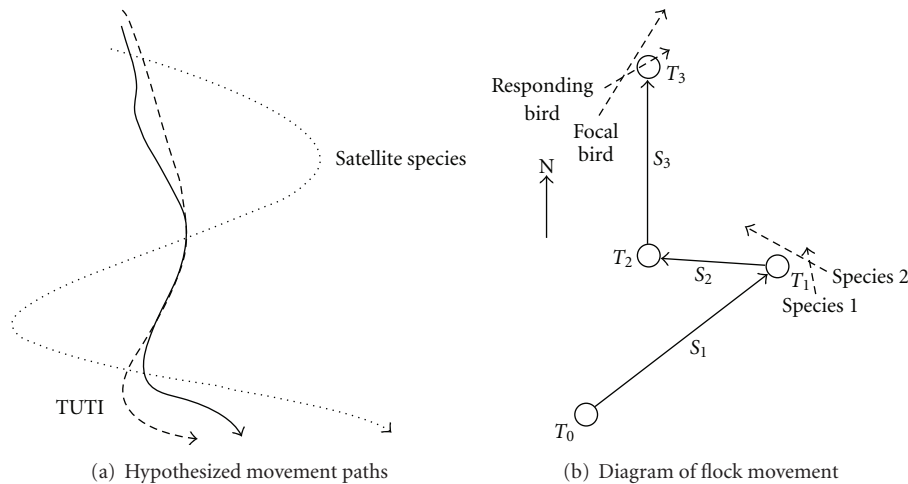


FIGURE 1: (a) Illustration of one example of the hypothesized relationships between the overall flock movement path (using successive flock centers to chart the path; black line) and the movement paths of two individual flock participants: TUTI (nuclear species; dashed line) and a satellite species (dotted line). (b) Diagram of a 15-minute portion of a flock movement path with T_0 , T_1 , T_2 , and T_3 representing estimated flock centers at 0, 5, 10, and 15 minutes respectively. Lines S_1 , S_2 , and S_3 represent “movement” segments between estimated flock centers, with the length of the line representing the movement distance of the flock and the arrow showing the overall flock movement direction (azimuth) between flock centers. Dashed lines (SPECIES 1 and SPECIES 2) represent the observed movements of 2 randomly selected birds observed while at flock center T_1 (to be correlated with flock path). Dashed lines at T_3 represent the movements of a FOCAL BIRD and a RESPONDING BIRD (an individual in the same general area that moves immediately after the focal individual moves) to be correlated with each other for within-flock analysis. These observations were made at all flock centers.

dominated by *Ilex* spp., *Lyonia* spp., and saw palmetto (*Serenoa repens*). More open habitats (cover type: open) used in the study generally had a sparse overstory of widely dispersed mature longleaf pine (*Pinus palustris*) with a patchily distributed subcanopy of *Quercus* spp. (primarily turkey oak (*Quercus laevis*) and sand live oak), and rosemary (*Ceratiola ericoides*), and understory dominated by wiregrass (*Aristida stricta*), exotic grasses, saw palmetto, and various forms. Flocks occurred throughout the woodland communities of our study areas, and we sought replicate samples in 3 major cover types that were identified as (a) hardwood and (b) pine-dominated (open) forest and (c) the boundaries between these two major forest classifications. Indeed, flock dynamics varied across these three habit designations, and we included them as predictors in our analyses (see below).

2.2. Flock Observations and Data Collection. Mixed-species flocks without TUTI are rarely observed in our study region [4]; therefore, we systematically searched each of the 3 study areas for the presence of TUTI using existing trails and roads, and then initiated observations of the associated flocks. To reduce the possibility of pseudoreplication of individual and flock movement data, we never surveyed any specific area more than once and each flock observed was at least 350 m from any other flocks observed, based on maximum reported TUTI winter home range sizes [17, 32]. Once located, flocks were followed for a minimum of 15 minutes, allowing birds to become acclimated to the observer (T. A. Contreras in all cases). Flocks were considered acclimated when birds stopped approaching the observer, and alarm calls were infrequent or directed at other bird species. After acclimation, we followed the flock for a maximum of 55 minutes.

2.2.1. Flock Leadership Data. We collected data for determining flock leadership at 5-minute intervals, and during each interval, we (1) estimated and marked the center of the flock (based on the area of the aggregation with the greatest estimated number of birds) by placing a wire flag in the ground, (2) identified the flocking species and estimated the number of individuals present in the flock, and (3) estimated the movement azimuth (degrees), of multiple randomly selected TUTI and satellite focal individuals at each flock center (azimuths of sampled individuals were estimated from the flock center using a compass; Figure 1(b)). If we lost track of a flock during the observation period, we then searched for a new flock to observe.

2.2.2. Within-Flock Movement Data. During each 5-minute interval, we estimated the direction and distance of movements made by randomly selected individuals in the flock and of the next movement made by another flock participant that was closest to the first bird, assuming that the “responding individual” was moving in response to the movement of the focal individual. These estimates were used for determining within-flock movement correlations (Figure 1(b)). To maximize the potential that the responding bird was actually responding to, or aware of, the focal bird’s movement, the second bird had to be within 5 m of the focal bird’s initial position and had to move within 60 seconds of the focal bird’s movement; otherwise, we selected a new focal bird and responding individual. And if, within a flock, we lost track of individuals under observation, we selected a new focal bird and responding individual.

To randomly select individuals for observations (both “flock leadership” and “within flock movement”), at each flock center, we started at a randomly selected azimuth and

then scanned the flock in a clockwise direction for the first focal individual that moved more than 5 m horizontally. We then estimated the movement distance (using a range-finder) and the movement direction (azimuth) of that individual. The azimuth for each individual was estimated from the initial point where the individual was observed. In some cases, this often meant marking the initial and subsequent horizontal positions with pin flags and then returning later to obtain measurements. Although individuals within flocks were not marked and could have been observed more than once within each flock, randomizing the selection of flock members for observations, and the relatively large number of individuals per flock may have reduced the probability of pseudoreplication of observations of individual flock participants.

2.2.3. Characterization of Flock Path and Habitat. After observations were completed for each flock, we determined the overall path of each flock. We returned to the first flock center observed (which had been flagged) and measured its position using a global positioning system (GPS, accuracy ± 3 m; Garmin *GPSMap 76*, Garmin International Inc., Olathe, Kan, USA). The distance and direction (azimuth) of each subsequent flock center relative to the previous flock center was measured using a compass and range finder and then plotted by connecting lines between successive flock centers (Figure 1(b)). Distances between flock centers ranged from 0–131 m with a mean distance of 32 ± 21 m (\pm SD).

At each of the flock centers, we recorded the “cover type” that the flock and individuals moved through (for each 5-min segment of movement): (1) hardwood, (2) open (generally pine sandhill or other pine stands with sparse canopy cover), and (3) boundary, for example, the flock crossed the boundary between hardwood and pine cover types during a 5-minute segment. Using the GPS to find the approximate position of the first flock center allowed us to plot the overall path using a GIS (ArcView v3.2, ESRI, Redlands, Calif, USA) to view flock centers overlaid on digital orthophoto quarter-quadrangles with 1-m resolution (1999; Land Boundary Information System (LABINS), Florida Dept. of Environmental Protection, Bureau of Survey and Mapping, Tallahassee, Fla, USA) and confirm cover types for each subsequent flock center. In addition, within a 0.05-ha circle surrounding each estimated flock center, we estimated (1) the proportions of overhead canopy (e.g., emergent, dominant, and codominant crown classes) and subcanopy cover using a densitometer, (2) the density of large stems >5 -cm diameter at breast height (DBH) using the point-quarter method [33], and (3) the number of small stems <5 -cm DBH but >1 m in height within the 0.05-ha circle. We predicted that there would be significant differences between hardwood and open cover types in one or more of the vegetation characteristics, and this might help inform our interpretations of movement patterns; that is, birds may move faster or slower through more open habitats, and this can influence flock cohesion [34].

2.3. Data Analysis. Two spatial scales of movements were analyzed to assess the prediction that satellite species primar-

ily follow TUTI and not each other. First, we asked which species are leading/directing the path of the flock (*flock leadership*) by testing whether TUTI movement paths (direction of movements during 5 min intervals) are more highly correlated with the overall flock paths than with satellite species movement directions). Second, we tested whether individual satellite species were tracking the fine-scale movements of nearby titmice more so than those of nearby satellite species (*within-flock movements*). For all analyses we used $\alpha = 0.05$ to determine statistical significance.

2.3.1. Flock Leadership. Using movement data for both flocks and individuals for each 5-minute time segment, we first calculated correlation coefficients between the azimuth for flock movement during each of the 5-minute time intervals and the azimuth for randomly selected individuals in the flock during the 5-min interval. We divided analyses between the three cover type classes where flocks were observed (hardwood, open (pine), or boundary), and for this analysis included further subdivisions of the data into two flock movement distance categories (fast, >30 m/5 minutes; slow, <30 m/5 minutes). This latter categorization was adopted, because flock movement rates varied greatly around the mean of 30 m/5 min; some flocks were sometimes stalled, whereas at other times a flock could move up to 131 m/5 min (see Section 2.2. *Flock Observations and Data Collection*), and we noted that movement dynamics appeared to differ between relatively slow and fast-moving flocks. Finally, analyses were further subdivided by flock role (nuclear (TUTI) vs. satellite species; Table 1).

2.3.2. Within-Flock Movements. To test the prediction that the within-flock movement direction and distance of individual flock members would be more highly correlated with those of the nuclear species (TUTI), we calculated correlation coefficients (r_{aa}) and associated 95% confidence intervals between the movement azimuths of randomly selected individuals within the flock (focal species) and the first individual to move after the focal individual moved (responding species). As above, the data were subdivided by focal species type (i.e., nuclear (TUTI) versus satellite species; nonflocking species were not included in this analysis) and cover type. We further subdivided the analyses by the movement distance of focal species using two distance classes: individuals moved <15 m or >15 m. These distance classes for within-flock movement are based on the mean within-flock movement of focal species (15.5 ± 21 m (\pm SD)), and were delineated to represent biologically reasonable distinctions between exploitation of a single foraging patch (within 15 m) versus changing foraging patches (moving more than 15 m in a single movement). Only movements >5 m were recorded/analyzed, since movements of less than 5 m were very frequent and probably correlated with movements of escaping prey rather than flock mates.

If only conspecifics are responding to focal individuals, then correlations of within-flock movement directions between focal and responding individuals would suggest that the movement of individuals within flocks was influenced primarily by intraspecific interactions. Therefore, we used

TABLE 1: All species encountered in mixed-species flocks during the study (classified into flock roles (nuclear, satellite, or nonflocking) based on Farley et al. [4]). Percentage of flocks is the percentage of the 20 flocks where the species was encountered at a minimum of one observation point. Max. number of individuals is the estimated maximum number of individuals in a flock observed at one time.

Common name	Scientific name	% of flocks/max. # of individuals
Nuclear		
Tufted titmouse	<i>Baeolophus bicolor</i>	100/6
Satellite		
Black-and-white warbler	<i>Mniotilta varia</i>	50/2
Blue-gray gnatcatcher	<i>Poliioptila caerulea</i>	70/6
Blue-headed vireo	<i>Vireo solitarius</i>	30/2
Carolina chickadee	<i>Poecile carolinensis</i>	20/3
Downy woodpecker	<i>Picooides pubescens</i>	40/3
(Yellow) palm warbler	<i>Dendroica palmarum</i>	15/15
Pine warbler	<i>Dendroica pinus</i>	35/2
Red-bellied woodpecker	<i>Melanerpes carolinus</i>	30/3
Ruby-crowned kinglet	<i>Regulus calendula</i>	95/15
White-eyed vireo	<i>Vireo griseus</i>	15/1
Yellow-throated warbler	<i>Dendroica dominica</i>	10/1
Nonflocking		
Blue jay	<i>Cyanocitta cristata</i>	5/3
Eastern bluebird	<i>Sialia sialis</i>	5/2
Yellow-rumped warbler	<i>Dendroica coronata</i>	15/50+
Northern parula	<i>Parula americana</i>	10/2
White-throated sparrow	<i>Zonotrichia albicollis</i>	5/20

a G -test of independence to determine if there was a lack of independence between the movement of the focal species observed and whether or not the responding individual was a conspecific or heterospecific. For the G -test we used a 3×2 contingency table with the columns being the flock role of the focal species (nuclear vs. satellite vs. nonflocking species) and the rows being whether or not the responding species was a conspecific or heterospecific. Cells within the table contained the frequency of responding individuals.

Since correlation coefficients for circular data (e.g., azimuths) should not be calculated using statistical tests for linear measurements [35], we used *Igor Pro* statistical software (v.6.2.1, Wavemetrics, Inc., Lake Oswego, Ore, USA) to calculate Angular-Angular correlation coefficients (r_{aa}), which are analogous to a Pearson's r (see methods described in Zar [35] and Fisher [36]) and the 95% confidence intervals associated with each r_{aa} . If "0" did not fall within the confidence interval calculated for an r_{aa} , then the correlation coefficient was statistically significant at $P < 0.05$ [35]. Given the lack of significance testing options for angular correlations (we found none), we relied on the 95% confidence intervals (CI) for each r_{aa} to make inferences about whether or not r_{aa} 's from comparable categories were biologically

different. If CI's for correlation coefficients (in general), and for other directional measures similar to r_{aa} 's, do not overlap, and if the CI's are similar in magnitude, then meaningful differences can safely be assumed (see Nakagawa and Cuthill [37] for discussion).

3. Results

3.1. Flock Observations. In total, 20 flocks were observed at our study sites (13 flocks at the Ordway-Swisher Preserve, 5 flocks at the San Felasco Hammock Preserve State Park, and 2 flocks at the Payne's Prairie Preserve State Park) with an average of 8 flock centers mapped per flock path recorded (range = 4–12 flock centers). There was a significant difference in flock movement rates (per segment) in different cover types ($F_{2,131} = 7.56$, $P = 0.0007$, $r^2 = 0.10$). Flock movement rates were significantly greater as flocks crossed boundaries (12.5 ± 4.0 m/minute (\pm SD)) when compared to movement rates of flocks in hardwood (6.1 ± 4.5 m/minute (\pm SD)) or open (6.1 ± 3.5 m/minute (\pm SD)) cover types. A total of 16 species were detected, and besides TUTI, only two others were present in the majority of flocks observed: Ruby-crowned Kinglets and Blue-gray Gnatcatchers which were present in 95% and 70% of the flocks, respectively (Table 1). Mean species richness for the 20 flocks was 5.6 ± 1.7 species per flock (\pm SD) with a mean maximum number of individuals in each flock of 23.8 ± 23.2 individuals (\pm SD). Five common species observed in or near flock centers, that are not flock participants (nonflocking species, Farley et al. [4]; Table 1), were excluded from all analyses except for the G -test above. Along flock paths, the proportion of overhead canopy cover was greater in hardwood than in open (pine) cover types (Figure 2(a)), whereas proportions of overhead subcanopy, small stem density, and large stem density were similar between hardwood and open cover types (using 95% confidence intervals; Figures 2(a) and 2(b)). This suggests that while canopy cover was different between the two general habitat types, subcanopy and shrub cover is similar.

3.2. Flock Leadership. We observed a total of 346 individuals (113 TUTI and 233 satellites) whose movement directions were correlated with flock movement at 117 flock centers. For all cover types (slow and fast-moving flocks pooled) and for both slow and fast-moving flocks (cover types pooled), flock movement direction was more highly correlated with the movement direction of TUTI than with the movement direction of satellites (Figures 3(a), 3(b), and 3(c)). When flocks were moving slowly across boundaries, satellite movement direction and flock movement direction were more highly correlated, whereas in open (pine) cover there was a negative correlation between flock and TUTI movement directions (Figure 3(b)). We note relatively small sample sizes for the latter two findings (Figure 3(b)). For fast-moving flocks (>30 m/5 minutes; Figure 3(c)), the movement direction of TUTI was more highly correlated with flock movement direction than with the movement direction of satellite species in all cover types. The greatest difference between correlation coefficients calculated for TUTI and satellite species with

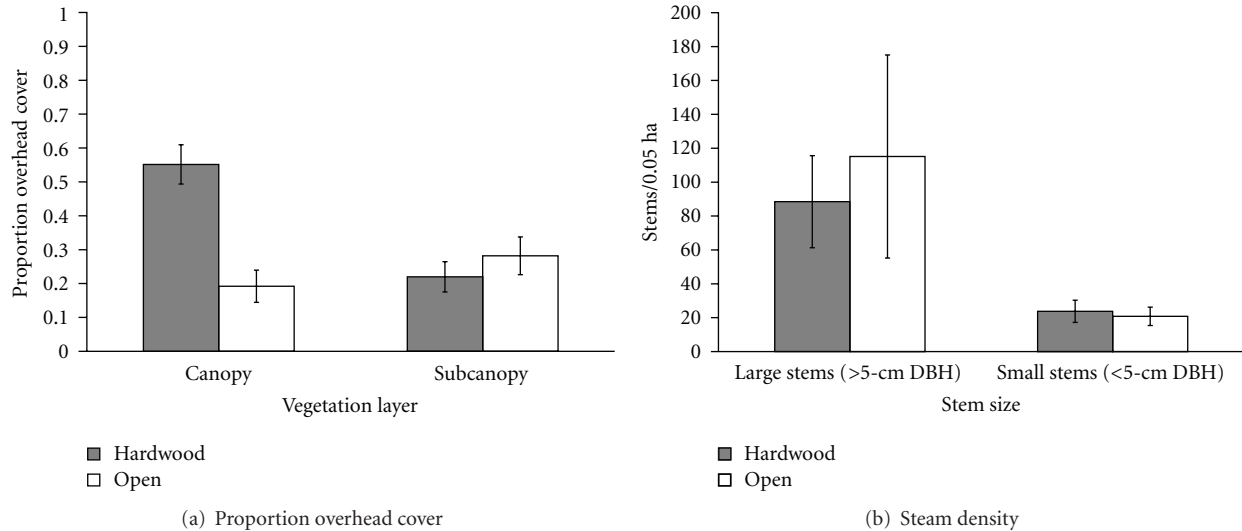


FIGURE 2: Mean overhead canopy cover (a) and mean stem density (b) for hardwood (gray bars) and open (white bars) cover types. Error bars represent 95% confidence intervals.

flock directions was when flocks moved quickly across boundaries (Figure 3(c)).

3.3. Within-Flock Movements. We were able to observe and record the movement response of birds to the initial movement of 113 focal individuals (focal species; including 3 observations of nonflocking species) across the 20 flocks observed. The flocking type of the focal species observed (nuclear, satellite, or nonflocking) was independent of whether or not the responding individual was conspecific or heterospecific ($G = 1.4$, $df = 2$, $P = 0.5$). This suggests that responding individuals did not only respond to conspecific focal individuals.

Overall, a responding individual's directionality of movement within the flock was more highly correlated with satellite focal individuals than it was with TUTI focal individuals (Table 2). For movement through different cover types, angular-angular correlations (r_{aa}) between the movement direction of focal individuals and responding individuals showed that in hardwoods and more open habitats, a responding species was more likely to move in the same direction as a TUTI than a satellite species; however, at boundaries, a responding individual's movement direction was very highly correlated with the movement direction of satellite focal individuals (Table 2).

When considering within-flock movements for the two different movement distance classes (<15 m versus >15 m), when focal individuals moved less than fifteen meters, a responding individual's movement direction was more correlated with the movement direction of satellite focal individuals and this was also the case for movement through open cover types (Table 2). In open habitat, there was a significant negative correlation between the within-flock movement direction of TUTI and responding individuals. In contrast, the correlation between the movement directions of TUTI and responding individuals was significantly greater in hardwood cover (Table 2).

For within-flock movements where focal individuals moved >15 m, a responding individual's movement direction was more correlated with satellite movements for all habitats combined (Table 2). At boundaries, correlations were greater when focal individuals were satellite species (there was no significant correlation for focal TUTI), but for open cover types, the correlation was greater when focal individuals were TUTI. In hardwood cover, there was no significant correlation for the focal TUTI, but there was a significant negative correlation with focal satellite species movement directions (Table 2).

4. Discussion

4.1. Flock Leadership by Titmice Suggests a Passive Nuclear Role. As we predicted, the movement directions of TUTI were clearly more highly correlated with overall flock paths than with the movement directions of satellite species participating in the same flock (Figure 3(a)), supporting our hypothesis that TUTI are followed by satellites in mixed-species flocks (e.g., TUTI act as a passive nuclear species). This was particularly obvious when flocks were moving fast and moving across boundaries between hardwood and open cover types (Figures 3(a) and 3(c)). When flocks were moving slowly, however, correlations were less consistent in open and boundary cover but were consistent with our predictions in hardwood habitat (Figure 3(b)). Since mean flock movement rates were greater across boundaries than mean flock movement rates in open or forest cover types, perhaps the most parsimonious explanation for the loss of TUTI leadership in slow-moving flocks in open habitat is that vegetative substrate for perching in that cover type was sparser than in the subcanopy of hardwood forests, providing fewer options for an individual to use as a destination perch during flock-following (Figure 2). Even when flocks are stalled in hardwood habitat that is dominated by large, multi-branching oaks, each flock participant will be surrounded

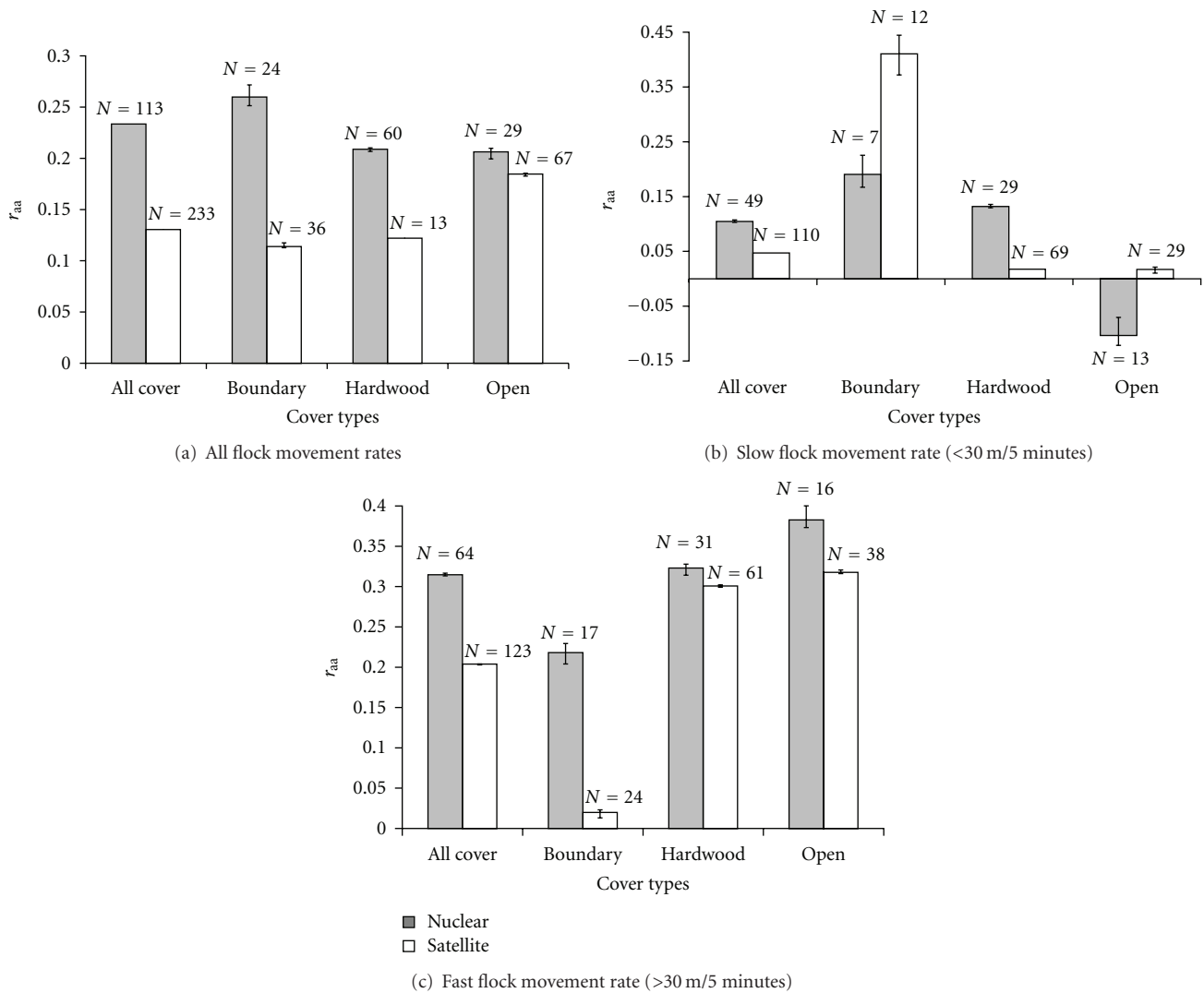


FIGURE 3: Angular-angular correlation coefficients (r_{aa}) for correlations between the movement direction of nuclear (TUTI; gray bars) or satellite (white) flock participants and flock movement direction in all cover types combined (All Cover), boundary (boundary between hardwood and open cover), hardwood, and open cover types. The sample size for each coefficient is above each bar. (a) Correlation coefficients in different cover types for all flock movement rates; (b) Correlation coefficients in different cover types for slow flock movement rates (<30 m/5 minutes); (c) Correlation coefficients in different cover types for fast flock movement rates (>30 m/5 minutes). Error bars represent 95% confidence intervals for each r_{aa} . Missing error bars represent 95% confidence intervals that were too small to be visible (CI < 0.001).

by high densities of potential perching substrates. Thus, individuals seeking to stay close to TUTI can always move in the direction of a TUTI individual in hardwood forest and have a suitable perch in a preferred location. In an open pine habitat, however, perching and foraging substrate and cover availability will all be much sparser overall. Therefore, if the TUTI are not moving then movements of individuals seeking to stay in the area with TUTI will be influenced more by feeding or other activities which, if perches are limited, may take them away from TUTI or closer to other satellite species (Figure 3(b)). Indeed, given (a) the dominant assumption that more open habitats convey higher predation risk for small birds in general [9, 34, 38], and (b) that TUTI may be especially targeted by predators attacking flocks (T. A. Contreras and K. E. Sieving, unpublished data, see above),

avoidance of stalled TUTI by flock mates in open habitats may be prudent (Figure 3(b)). However, these variations on our central prediction do not detract from the overall conclusion that when foraging flocks are moving, TUTI movements define the flock path in all wooded habitats that we studied. The only way that this pattern could reflect other than purely passive leadership on the part of the nuclear species is if TUTI were somehow compelling other species to follow or rally around them. Given that titmouse (and other parid) mobbing calls do indeed attract a high variety of species [20, 39], rallying calls directed at heterospecifics are quite possible. However, such calls are as yet undocumented despite extensive examination of parid vocal repertoires [40]; their detection was beyond our capabilities in this study.

TABLE 2: Angular-Angular correlation coefficients (r_{aa}) for correlations between a focal individual's movement direction and the movement direction of responding individuals (within-flock movement) in different cover types and for different movement distances of focal individuals. N = number of individuals observed. Confidence intervals (95% CI) for each r_{aa} are reported (L_1, L_2 ; see Zar [35]). Confidence intervals that do not include 0 indicate a significant r_{aa} (in bold print) at $P < 0.05$.

Flock role	Overall (All cover types)							Cover type					
	r_{aa}	N	95% CI (L_1, L_2)	r_{aa}	N	95% CI (L_1, L_2)	r_{aa}	Hardwood		r_{aa}	Open		
All focal individuals													
Nuclear	0.101	65	0.097, 0.101	-0.072	16	-0.101, -0.078	0.170	29	0.163, 0.174	0.267	20	0.257, 0.279	
Satellite	0.182	45	0.181, 0.187	0.918	5	0.880, 0.953	0.049	28	0.046, 0.062	0.197	12	0.169, 0.234	
Focal individual <15 m													
Nuclear	0.034	34	0.024, 0.033	-0.094	9	-0.070, 0.004	0.173	18	0.151, 0.179	-0.243	7	-0.315, -0.140	
Satellite	0.121	25	0.116, 0.129	N/A	1	N/A	0.063	19	0.056, 0.074	0.328	5	0.140, 0.650	
Focal individual >15 m													
Nuclear	0.207	31	0.201, 0.211	0.037	7	-0.041, 0.087	-0.025	11	-0.063, 0.024	0.393	13	0.369, 0.406	
Satellite	0.339	20	0.339, 0.354	0.986	4	0.983, 0.996	-0.168	9	-0.182, -0.109	0.160	7	0.070, 0.303	

4.2. *Within-Flock Movement Patterns May Reflect Social Complexity within Flocks.* We detected a great variety of patterns with respect to fine-scale movements of satellite and nuclear species (Table 2), and almost no corroboration of our central prediction of high correlations between TUTI movements and subsequent satellite movements. As mentioned above, this could be due to the rapidly shifting and complex social environment within mixed-species flocks that likely dominates participants' attention simultaneously with avoiding predators and searching for food. Increasing evidence suggests that while mixed-species foraging flocks may have evolved under selection to avoid predators while enhancing foraging efficiency (reviewed in Sridhar et al. [10]), once formed, flocks will host a wide variety of other behaviors that are equally critical to survival and reproduction. Within the permanent bird flocks that are characteristic of tropical forests (canopy, understory, and ant following), the life cycles of flock participants play out within an intensely social environment [41–43]. While engaged in facultative winter flocks, temperate forest resident and migrant birds experience a similarly complex social milieu including (in addition to antipredator vigilance and foraging) everything from information gathering [44, 45], mate assessment and status signaling [46], territorial defense [47], courtship [48], to a complex variety of conspecific and heterospecific dominance interactions and competitive conflicts over food and feeding sites [49–51]. Thus, the finding that fine-scale movements of birds in mixed flocks are not predictable based on a single factor (spatial cohesion with the nuclear species). For example, 3 of the satellite species most frequently observed in flocks (Carolina Chickadee, Ruby-crowned Kinglet, Pine Warbler; Table 1) have foraging behaviors similar to those of TUTI (e.g., lower canopy/shrub foragers or gleaners; De Graaf et al. [52]) and are subordinate to TUTI. Given TUTI's propensity to steal food, it is not surprising that satellite species often move away from TUTI when approached within 5 meters (Table 2).

While their aggression, vigilance, and gregariousness make TUTI excellent community informants [19, 53], mob

leaders [9, 20], and nuclear species in foraging flocks [1, 4], these same traits likely reduce their attractiveness at close distances. In our experience with keeping TUTI in aviaries [54], we find TUTI can be exceptionally aggressive toward unfamiliar individuals in confined spaces. Our data also suggest that satellite species are more willing to tolerate each other at close range than are TUTI (Table 2). The only high correlation between satellite and TUTI movement directions in our analysis occurred when movement distances were greater than 15 m in open cover types. At these distances, we are seeing movements that are more closely related to overall flock movement; the kinds of movements that satellites should be tracking in order to “keep up” with flocks. Both of our analyses suggest that the nuclear-satellite species relationships and social roles are indeed context dependent [12], influenced by habitat type (and associated perception of predation risk), habitat structure, flock speed, movement distances made by individuals, and spatial scales over which movements occur (e.g., within vs. between foraging patch and across habitat boundaries).

Therefore, our results suggest that within slow-moving flocks, individuals may be responding to the movement of other individuals in the flock and less attention may be paid to nuclear species. Conversely, as flocks move greater distances, and relatively faster through landscapes, TUTI act as flock leaders and passive nuclear species, particularly in cover types that may be perceived as more hostile by forest passerines, for example, open cover types and while crossing forest-open cover type boundaries; see Sieving et al. [9]. Srinivasan et al. [12] suggested that for mixed-species aggregations, acting as a nuclear species may not be a “fixed species property”, that is, species characteristics that determine species suitability as a nuclear species, or even as flock leaders, may be “context dependent”. Heterospecific interactions and the roles of mixed-species flock members may change as flocks move through landscapes and different cover types. Traits that would make TUTI suitable as flock leaders and nuclear species (e.g., socially dominant/aggressive, generalized habitat use, and high vocal

complexity; [4, 19, 20]) when flocks are moving quickly or moving long distances through potentially dangerous cover types may not make them the preferred attractant (e.g., passive nuclear species) for other flocking species as flocks engage in other activities while flocking.

5. Conservation Implications

Our findings contribute to an expanding base of information suggesting that parids serve as community-level facilitators of (potentially) a great number of heterospecifics in diverse taxa. Because parids tend to be very common where they occur, designating them as “keystone facilitators” is not technically correct (their effect on flock dynamics and community structure is not disproportionate to their abundance; [55]). Moreover, we can eliminate “mutualism” from our descriptions, because the observed passive leadership of flocks by TUTI further underscores the probable lack of fitness benefits for TUTI in mixed species flocks. Nonetheless, the facilitative effects of titmice and parids are likely to be pervasive in Holarctic woodland bird communities. Tufted titmice and other parids are habitat generalists, that are able to exploit wood and shrub lands with varied species composition and habitat structures, but species that associate with them are often more specialized in habitat use [56]. Given that spatial behavior can limit the functional connectivity of fragmented and degraded forest landscapes for vertebrates (see Crooks and Sanjayan [57]), nuclear species with broad niches and less sensitivity to changes in physical connectivity may greatly enhance flock movement and increase access to spatially constrained resources for satellites willing to follow them. For example, tufted titmice clearly expand the foraging niches of their winter satellites [7], and they increase the permeability of high contrast habitat boundaries to satellite movement [8, 9, 58]. Thus, following titmice may largely counteract the strong effects of lethal and nonlethal predation threats that constrain movement and access to resources [18, 59] for flock associates. Paridae include a high proportion of nuclear species and/or flock leaders [14] and traits that support the role of nuclear species in mixed flocks are well developed and conserved across the family, including high vocal complexity [19], bold personality [60], and high vigilance [61, 62]. Therefore, across the Holarctic, it is likely that parid-led mixed-species flocks gain similar foraging and habitat exploitation advantages on their winter home ranges.

Parid facilitation of other species is not limited to mixed flocks. Heterospecific attraction has been defined as the deliberate selection of breeding territories by migrants that are already populated by resident heterospecifics [26, 27]. Heterospecific attraction is strong between parids (as the resident attractor) and migrant forest passerines that breed sympatrically with them (experimental documentation comes from Scandinavian and North American parid species; [24, 60]). The positive benefits of using resident parids as cues for settlement are especially pronounced in high latitudes, where short nesting seasons make rapid identification of productive breeding habitat critical for long-distance migrants [63, 64]. Additionally, enhanced reproductive success may accrue to heterospecifics from nesting

near parids [65]. Thus, attraction of heterospecifics to parids occurs across scales, from foraging microhabitat to choice of breeding patch, and it enhances fitness-related measures at the level of individuals and alters species distributions within communities. Thus, our work with flocks leads us to concur with current thinking that facilitation is as important (or more so) as competition and predation in shaping selective regimes and species patterns within animal communities [66].

One clear benefit that heterospecifics gain by being close enough to parids to hear them is the exceptionally high-quality information parids produce that precisely and accurately conveys their perception of predation risks and threats [19, 21, 22, 67]. Changes in the types of titmouse calls as they move through the landscape may reflect changes in their perception of predation risk [19]. Therefore, it would be beneficial for any species that share predators with titmice to be able to interpret and respond appropriately to titmouse calls. Moreover, the number and diversity of species across the Holarctic that utilize parid information to inform their predator-avoidance decisions are apparently very large [20, 53, 68]. Thus, we argue that the facilitative role of parids may best be described as “community informants.” The use of socially derived information from parids to effectively avoid predators enables heterospecifics to achieve greater efficiency in other critical activities and provides a largely sufficient explanation for heterospecific attraction to parids, both within winter flocks or breeding bird communities [46, 69]. Therefore, we view the most important implication of our work as this: in attempts to conserve declining species that may be receiving important benefits from association with parids, consideration should be given to maintaining or strengthening those benefits in conservation strategies.

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