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Mixed-Species Flock Diversity and Habitat Density Are Associated with Antipredator Behavior in Songbirds

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Abstract: Human-caused changes to habitats like forestry practices and traffic noise can negatively influence antipredator and foraging behavior in animals. These behavior patterns are also frequently positively influenced by individuals being part of mixed-species groups. However, we know little about how such human-induced changes impact these behaviors in individuals of mixed-species groups. To address this gap, we examined the effects of mixed-species group composition, traffic noise, and vegetation density on antipredator and foraging behavior. We used feeders to attract mixed-species flocks of Carolina chickadees (*Poecile carolinensis*), tufted titmice (*Baeolophus bicolor*), and white-breasted nuthatches (*Sitta carolinensis*). Once we detected a flock at a feeder, we presented a Cooper's hawk model and recorded flocks' seed-taking and calling behaviors. Titmice avoided feeders more when hawk models were presented at sites with greater vegetation density. Nuthatches called more quickly with more conspecifics in their flocks, and they tended to take seed more quickly with greater diversity of species in their flocks. We did not detect the effects of physical or social environmental variables on chickadee behavior. Our results reveal individual sensitivity to environmental variation in contexts involving visual predator stimuli. More work is needed to investigate how various predator stimulus modalities affect antipredator behaviors of mixed-species flock members.



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1. Introduction

Many environmental factors can influence communicative and foraging behavior in animals. One major factor is social environmental variation such as changes in group size and group composition. The proportion of conspecifics and heterospecifics within a group can influence individual behavior. For example, Adams et al. [1] reported that for Carolina chickadees (*Poecile carolinensis*) at feeders, seed-taking latency in response to predator stimuli decreased when their mixed-species flocks had more conspecifics. Mixed-species groups provide substantial benefits to individuals in those groups, including finding food and avoiding predation while also reducing levels of competition in comparison to similar-sized single-species groups [2–5]. Another study of Carolina chickadees showed that individuals solved novel feeder tasks quicker in mixed-species flocks with greater flock composition diversity [6,7]. Although the mechanism of this “diversity bonus” in

mixed-species flocks is not yet known, it seems likely that the different behavioral and perceptual propensities of different species are involved [6,8].

In addition to being influenced by the size and diversity of their social groups, individuals' behavior can be strongly influenced by physical environmental factors like anthropogenic disturbance and variation in habitat features. Anthropogenic noise can mask important acoustic stimuli and can distract prey animals, thus negatively influencing their abilities to detect predators [9,10]. Jung et al. [11] found that mixed-species flocks of Carolina chickadees, tufted titmice (*Baeolophus bicolor*), and white-breasted nuthatches (*Sitta carolinensis*) were generally less likely to respond to acoustic predator cues masked by anthropogenic noise. Alternatively, environmental variation can also have an impact on foraging behavior. Senzaki et al. [12] found that the effectiveness of foraging by long-eared owls (*Asio otus*), short-eared owls (*Asio flammeus*), and Urial owls (*Strix uralensis*) declined with greater levels of traffic noise due to masking and aversion.

Variation in vegetation density is another human-induced environmental change that can influence group cohesion and individual membership in social groups [13]. Variations in vegetation density can also influence a group's social structure by constraining the identities of, and rates of encounters among, individuals [14]. Structural changes such as forest cutting may influence the way individuals move, such as aggregating into shelters or directly choosing to interact with others to avoid predation [15]. For example, after alarm call playbacks chickadees and nuthatches took longer to resume normal seed-taking rates if vegetation (influenced by forestry practices) near the feeder was denser [1]. Given that vegetation density and general habitat structure can vary considerably across different areas within the home range of an individual, it is reasonable to expect that variation in vegetation density plays a role in mixed-species group foraging and antipredator behavior.

This study used mixed-species groups of Carolina chickadees, tufted titmice, and white-breasted nuthatches. These mixed-species flocks are common in the southeastern United States. During the winter, a lack of food resources and increased predation risks are thought to be the key reasons these mixed-species groups aggregate during this time [13]. Chickadees and titmice serve as the nuclear species within these groups, the core species that attract and are followed by satellite species, such as nuthatches [16,17]. Nuclear species in diverse taxa are typically the leaders in group movement and are often more vigilant against predators whereas satellite species often follow and attend to those nuclear species [18–20].

Chickadees and titmice both regularly use *chick-a-dee* calls throughout the year to influence conspecific and heterospecific behavior and cohesion in these flocks [21]. These calls are composed of a combination of distinct note types that can each be absent, present, or used repeatedly to generate an open-ended number of call types [22]. Calls vary in note composition depending upon the size and level of threat of avian predators [23–26]. Additionally, *chick-a-dee* call structure and use vary with the number of conspecifics and the proportion of heterospecifics in their flocks [1,27–29].

Both physical and social environmental variation affect the behavior of individuals in mixed-species flocks in response to predator stimuli. Adams et al. [1] examined the impact of flock composition and environmental context on calling and antipredator behavior for these three species. In one experiment, an alarm call of tufted titmice was played back at feeders that Carolina chickadees, tufted titmice, and white-breasted nuthatches were using. Following the playback, chickadees took seeds more quickly from the feeder the greater the number of chickadees in the flock, and the less dense the nearby forest habitat was. Titmice were found to call more quickly in response to the alarm call playback when in larger and less diverse flocks. In a second experiment, a screech owl model was placed directly on the feeders. Chickadees called more quickly in response to the model when there were more

chickadees in the flocks and the duration of mobbing by the entire flock was greater than more nuthatches in the flocks [1].

One limitation of the Adams et al. [1] study was that they placed a predator model directly on the feeders, eliminating the possibility of foraging behavior. Our present study sought to address this limitation by presenting a predator model at a distance from the feeders to assess whether variation in social and physical environments has an impact on the mixed-species flock's behavioral responses. For our study, we used a Cooper's hawk model (*Accipiter cooperii*: a known predator of chickadees, titmice, and nuthatches). Unlike the Adams et al. [1] study, we placed the model 3 m away from the feeders being used by mixed-species flocks. Latency to call and to take a seed as well as calling and seed-taking rates were examined for the three focal species in these flocks. Based on the finding of the Adams et al. [1] study, we expected: (1) Individuals in flocks with a greater number of conspecifics will increase calling rate and decrease seed-taking latency and calling latency in comparison to those in flocks with fewer conspecifics; (2) In flocks with a greater number of total birds, regardless of species, there will be shorter latencies to call and longer latencies to take seed in comparison to smaller flocks; (3) For all three focal species, there will be greater calling and seed-taking latencies at feeders with higher levels of anthropogenic noise; and (4) In areas with higher vegetation density, calling latencies and seed-taking latencies should increase and calling rates and seed-taking rates should decrease.

2. Materials and Methods

2.1. Study Site

We studied the antipredator behavior of our mixed-species flocks of chickadees, titmice, and nuthatches at the University of Tennessee Forest Resources, AgResearch, and Education Center (UTFRREC; 36.11° N, 84.20° W) in eastern Tennessee. Data were collected in January and February 2024 between 0800 and 1500 EST. Overwintering mixed-species flocks of chickadees, titmice, and nuthatches typically form and persist throughout these months [16,30,31]. We conducted experiments at 36 feeder sites. These feeder sites were separated by at least 375 m from one another to ensure that each feeder site was independent and in a different flock's territory (previous studies have shown that birds at this field site rarely travel across feeders [32]). This UTFRREC location is part of the mixed chestnut and oak forest of the southern hardwood forest region [33] of the United States. UTFRREC is dominated by tulip trees (*Liriodendron tulipifera*), oaks (*Quercus* spp.), hickories (*Carya* spp.), and pines (*Pinus* spp.).

Each site consisted of a feeding station that was a steel pole with a wooden platform (25 cm × 40 cm × 2 cm) mounted on top. The pole was placed into the ground such that the platform was about 1.5 m off the ground. Beginning in early October 2023 and continuing through the end of this study, feeding stations were stocked every 10 to 14 days with roughly 50 g of bird seed. We used a mix of black oil sunflower seed and safflower seed that reliably attracted our three focal species [7].

We measured levels of traffic noise at all 36 feeder sites from late fall 2021 through spring 2022 using a Quest Technology 2100 Sound Level Meter (Quest Technologies, a 3M Company, Oconomowoc, WI, USA) set at C weighting and slow (1 sec) response to measure sound pressure level (dB) 5 to 6 times at each site with at least a week between consecutive recordings. The recordings were collected every day except for Sundays, between 10:00 and 13:00 EST. At our feeder sites at UTFRREC, the main source of noise is from traffic on Highway 62 (Illinois Avenue) and Union Valley Road. Traffic noise varied substantially across our 36 feeder sites and is known to influence the antipredator behavior of individuals in the flocks we study [1,11,34]. Average noise levels ranged from ~50 dB to ~70 dB. Because these noise level measures were collected two years before this study

was conducted, we repeated the noise level measures during the late fall of 2024. We re-recorded SPL measures at all 36 sites between October and November 2024. Average SPL measurements at each site from three years ago correlated strongly and positively with recent dB measurements at each site (first measurements, Spearman's $\rho = +0.811$, $N = 36$, $p < 0.001$; second measurements, $\rho = +0.905$, $N = 36$, $p < 0.001$).

All of our feeder sites were within a forest habitat, and all had vegetation on which birds could perch within 2 m of the feeders. Additionally, all feeders were in mixed forests dominated by deciduous trees or, in two cases, in pine tree plantations (planted in the 1970s) within 10 m of the edge of the mixed forest. Areas in UTRREC have undergone modification over the decades (though not in the past 5 years) ranging from clearcuts to thinning and our 36 feeder sites span secondary succession stages to undisturbed forest. As such, forest habitat density varies greatly across UTRREC and this might, in turn, affect the behavior of the birds in our study (see also [35]). To measure forest habitat density around each of our feeder sites, A FARO Focus S 350 HDR scanner (FARO Technologies, Lake Mary, FL, USA) was used to perform terrestrial Light Detection And Ranging (LiDAR) scans at each site in the first three months of 2022. The composition and density of trees and shrubs vary considerably across our 36 feeder sites and may influence antipredator behavior of individuals in our mixed-species flocks [1,36]. We mounted the FARO LiDAR scanner on a large tripod to position it directly above each feeding station. Each scan assessed vegetation at a scan distance of 50 m, at 360 degrees horizontal and 300 degrees vertical. With each LiDAR scan, the total number of points collected represents a raw metric of vegetation density. All LiDAR scans (point clouds) were processed in FARO SCENE software (Version 2019.2; FARO Technologies, Lake Mary, FL, USA). For additional analyses, we saved each scan as a .las file in the 3D point cloud and mesh processing software package CloudCompare (V2.13.alpha, Open Source Project).

To remove outliers, we cropped each point cloud with statistical outlier and noise removal. We separated vegetation (non-ground) from ground points using a cloth simulation filter for each scan. Cleaned scans that included only vegetation points were saved as new .las files that were then batch-processed in MATLAB R2023a (MathWorks Inc., Natick, MA, USA). To estimate vegetation volume (m^3) and area (m^2) from LiDAR scans we used alpha shapes. Alpha shapes are geometric objects created by lines that connect the points falling within a certain radius of one another [37]. Using this process, we created surfaces and volumes that could be compared across collections of points from each feeder site. For each feeder site, we created an alpha volume for each point cloud using an alpha radius of 1 m and standard algorithms available within the MATLAB programming environment (alphaShape). These forest alpha volumes represented our metric of vegetation density for each feeder site (after [1,6]).

2.2. Baseline and Predator Stimulus

We stocked feeding stations with 50 g of seed on the day of the trials. Once we observed a flock actively using a feeder (birds were present and regularly taking seed from the feeding station) and at least one Carolina chickadee and one tufted titmouse (our core species) were seen at the feeding station, we set up a Sennheiser (Wedemark, Germany) ME-66 microphone mounted on a desktop microphone stand connected with a 15 m microphone cable to a Marantz (Tokyo, Japan; D&M Professional) PMD-660 digital audio recorder (16-bit and 44.1 kHz sampling rate). We saved recordings as uncompressed WAV files. The microphone was positioned roughly 1.5 m away from the feeding station and was angled directly towards the platform. The observer sat at least 15 m away from the feeding station and was partially obscured by vegetation (after [32]). After we finished setting

up the recording equipment and the observer was in position, we began our trial. Each trial was split into a pre-stimulus/baseline and predator model stimulus presentation period.

A realistic plastic model of a Cooper's hawk was our predator stimulus, as the focal species of our study responded strongly to models of this species [32]. During the set up of the recording equipment the observer also installed a mount 3 m from the feeding station on which we could present the predator model. The predator model mount was placed in a direct line with the feeding station and the microphone (Figure 1). During the pre-stimulus/baseline period, we aimed to determine the number of individuals of each species present. We assessed the maximum number of individuals of each species detected within 20 m of the feeder at any one time, which is strongly positively correlated with the actual number of individuals present near the feeder [32]. This earlier study involved color-marked flocks of these three species at 15 different feeder sites, allowing the assessment of both the 'maximum number detected at any one time' and the actual number of observed individuals at the feeder during trials [32].



Figure 1. Photo depicting the audio recording set up at a feeder. The microphone is pictured in the lower left corner and is aimed at the feeder platform where the seed is located. The Cooper's hawk predator model (upper right corner) is mounted on a tree-like structure in line with the feeding platform and microphone. Photo by Todd M. Freeberg.

Following the 15 min pre-stimulus period, the observer walked to the model mount to place the hawk model. We made sure that the hawk's eyes were directly facing the feeder as the avian predator's head orientation relative to a feeder is important to antipredator and foraging behavior in these flocks [38,39]. The observer then quickly returned to the ~15 m observation distance and resumed recording the mixed-species flock activity for another 15 min. This act of walking up to place a stimulus on or near the feeder has minimal influence on birds' behavior in our mixed-species flocks; birds typically return to taking seeds within seconds of our returning to our observation site 10 to 15 m away from the feeder [32,38,39].

2.3. Data Coding and Analysis

We used one-zero sampling to assess the calling rates of the three focal species [40]. The 15 min predator model trials were broken up into ninety 10-sec bins. At the end of each 10-sec bin following the start of the trial, we coded a '1' for that species if at least one individual of that species called and a '0' for that species if no individual of that species

called. For chickadees and titmice, we coded only *chick-a-dee* calls as these have been the calls of interest in studies of antipredator and mobbing behavior in these species [21]. For nuthatches, we coded both their ‘quank’ calls and their ‘hit-tuck’ calls as, similarly to *chick-a-dee* calls, these two call types are used by both sexes in a wide range of contexts throughout the year [41].

Due to researcher errors or equipment malfunction, calls could not be coded from 6 of the 36 feeder sites, so we analyzed 30 flocks for calling behavior for chickadees and titmice and 27 flocks for nuthatches (nuthatches were not present at all sites). TMF conducted one-zero coding of calls. To assess the validity of our one-zero coding approach, ZES independently coded actual calling rates—the number of calls for each species in the 15 min predator model trials—from 8 randomly chosen flocks. Actual calling rates were highly correlated with one-zero coding of calling for those flocks: chickadees $r = +0.972$, titmice $r = +0.939$, and nuthatches $r = +0.851$; all $N = 8$).

EKF coded seed-taking rates from the observer commentary on the audio recordings. To assess inter-observer reliability [42] of seed-taking behavior, we video-recorded feeders during 12 of the predator trials. Trials were recorded using a Canon Vixia HF G70 camera. TMF independently coded seed-taking rates from those video files, and inter-observer reliabilities were high: chickadees $r = +0.996$, titmice $r = +0.998$, nuthatches $r = +0.996$; all $N = 12$.

We ran linear regression models following [1] to test our hypotheses. For each species, predictor variables for the regression models were the number of conspecifics (e.g., number of chickadees for the chickadee analysis), the total mixed-species flock size, mixed-species flock diversity, vegetation density (forest alpha volume, in m^3), and traffic noise (average dB level). We used the inverse Simpson index [43] to determine mixed-species flock diversity (Diversity Index), calculated as $1/[(P_{\text{chickadees}})^2 + (P_{\text{titmice}})^2 + (P_{\text{nuthatches}})^2 + (P_{\text{species "x"}})^2 + (P_{\text{species "y"}})^2]$. In this Equation, P is the proportion of each flock comprising chickadees, titmice, nuthatches, and each additional species, respectively [7].

Our dependent variables were calling latencies and rates and seed-taking latencies and rates. To reduce the dimensionality of the data set given latency and rate measures can covary with one another, we ran Principal Components Analyses using Varimax Rotation. We ran PCAs separately for each species. For Carolina chickadees only one PC score emerged, explaining 53.2% of the variance. Latencies for calling and seed-taking loaded positively (0.825 and 0.710, respectively) and rates for calling (−0.821) and seed-taking (−0.518) loaded negatively on this single PC score. For both tufted titmice and white-breasted nuthatches, two PC scores emerged. For titmice, PC1 explained 43.2% of the variance with seed-taking latencies loading positively (0.907) and seed-taking rates loading negatively (−0.868). PC2 explained an additional 35.1% of the variance with calling rates loading positively (0.884) and calling latencies loading negatively (−0.785). For nuthatches, PC1 explained 36.4% of the variance with calling latencies loading positively (0.842) and calling rates loading negatively (−0.780). PC2 explained an additional 35.5% of the variance with seed-taking rates loading positively (0.854) and seed-taking latencies loading negatively (−0.807).

We used the single PC score for chickadees and the two PC scores each for titmice and nuthatches in subsequent linear regression analyses for each species. We report the standardized beta coefficients (β) along with t statistics below. To estimate effect sizes for significant findings, we determined the correlation between the particular predictor variable and the relevant PC score (after [1]). All statistical analyses were performed using IBM SPSS Statistics Version 27. The normality of the residuals of the regression models was confirmed by visual inspection of P-P residual plots and by one-sample Kolmogorov–Smirnov tests. We conducted this field experiment under approved protocol #1248 of the University of Tennessee Institutional Animal Care and Use Committee.

3. Results

3.1. Tufted Titmice

For tufted titmice, forest alpha volume was positively associated with PC1 ($\beta = 0.432$, $t_1 = 2.386$, $p = 0.025$, $r^2 = 0.165$; Table 1). At feeder sites with greater forest density, titmice took longer to visit the feeder and took fewer seeds in comparison to sites with lower forest density (Figure 2). No other variable (traffic noise, number of conspecifics, flock size and flock diversity index) predicted PC1 scores and no variables predicted PC2 scores for titmice.

Table 1. Linear regression models for Principal Component scores related to calling and seed taking in the three main species of mixed-species flocks studied (dB refers to dB SPL).

Species	PC Score	Predictor Variable	β	t	p
Carolina chickadees	1	Alpha volume	0.232	1.164	0.255
		Traffic noise (dB)	0.170	0.825	0.417
		N. chickadees	−0.213	−0.814	0.423
		Flock size	0.102	0.360	0.722
		Flock diversity index	−0.185	−0.739	0.467
Tufted titmice	1	Alpha volume	0.432	2.368	0.025
		Traffic noise (dB)	0.304	1.557	0.133
		N. titmice	−0.227	−0.916	0.369
		Flock size	0.132	0.458	0.651
		Flock diversity index	−0.180	−0.759	0.455
	2	Alpha volume	0.266	1.341	0.192
		Traffic noise (dB)	0.143	0.667	0.511
		N. titmice	0.216	0.794	0.435
		Flock size	−0.013	−0.042	0.967
		Flock diversity index	−0.109	−0.419	0.679
White-breasted nuthatches	1	Alpha volume	−0.176	−0.909	0.374
		Traffic noise (dB)	0.150	0.789	0.439
		N. nuthatches	−0.408	−2.105	0.047
		Flock size	−0.030	−0.143	0.888
		Flock diversity index	−0.305	−1.517	0.144
	2	Alpha volume	−0.097	−0.480	0.636
		Traffic noise (dB)	−0.218	−1.097	0.285
		N. nuthatches	−0.276	−1.372	0.185
		Flock size	0.151	0.696	0.494
		Flock diversity index	0.425	2.036	0.055

3.2. White-Breasted Nuthatches

For white-breasted nuthatches, the number of nuthatches in a flock was negatively associated with PC1 ($\beta = -0.408$, $t_1 = -2.105$, $p = 0.047$, $r^2 = 0.253$; Table 1). At feeder sites with more nuthatches, nuthatches called more rapidly and produced more calls in comparison to feeder sites with fewer nuthatches (Figure 3). No other variable was associated with PC1 scores for nuthatches. Additionally, there was a tendency for the flock diversity index to be positively associated with PC2 scores for nuthatches ($\beta = 0.425$, $t_1 = 2.036$, $p = 0.055$, $r^2 = 0.144$). At feeder sites with a greater diversity of species in the mixed-species flocks, there was a tendency for nuthatches to visit feeders more quickly and

to take seeds at higher rates in comparison with less diverse flocks (Figure 4). No other variable was associated with nuthatch PC2 scores.

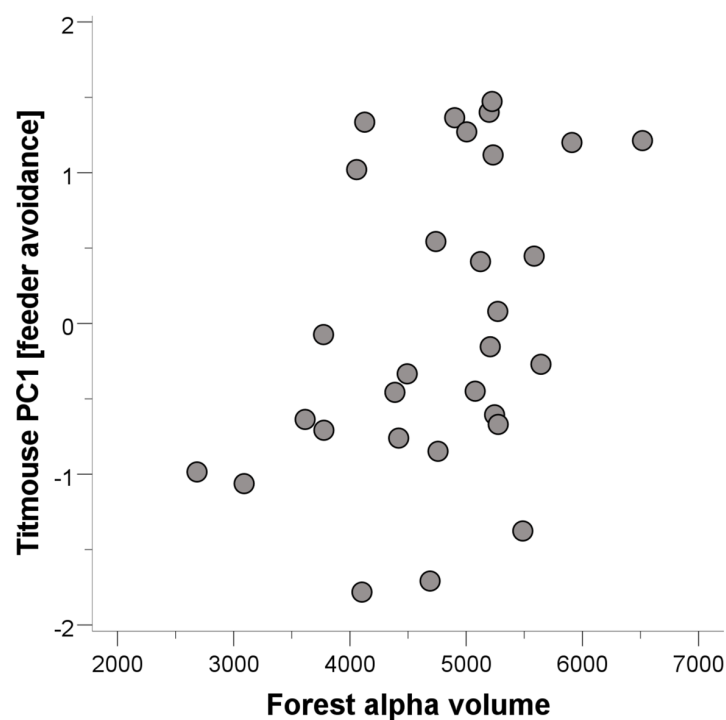


Figure 2. The positive relationship between feeder avoidance (+ seed-taking latencies and – seed-taking rates) for tufted titmice and the forest alpha-volume (vegetation density) immediately surrounding the flocks' feeders. Each gray circle represents a single flock.

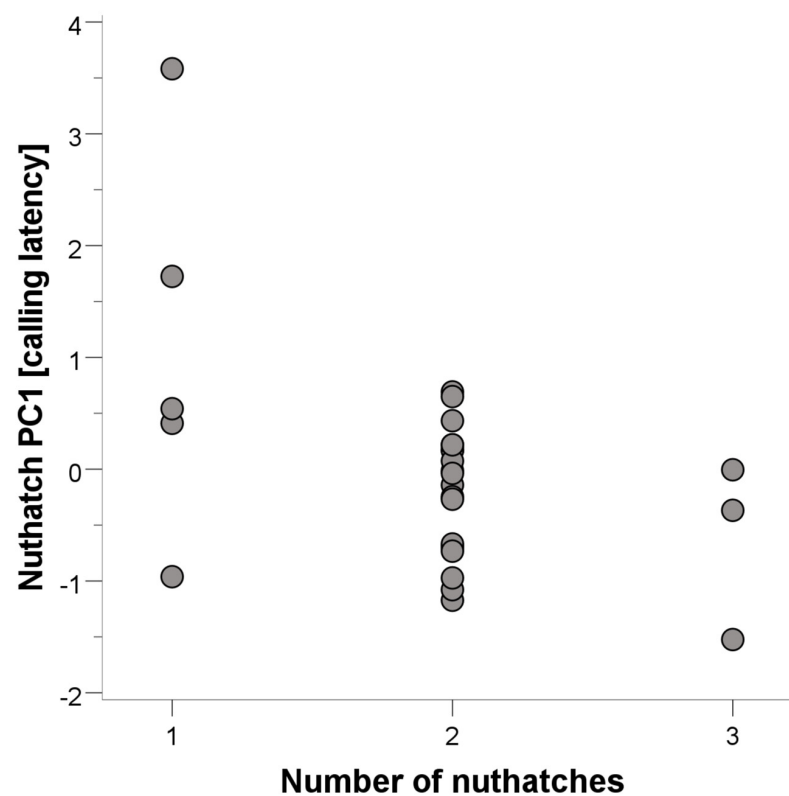


Figure 3. The negative relationship between call latency (+ calling latency and – calling rate) for white-breasted nuthatches and the number of nuthatches in their flocks. Each gray circle represents a single flock.

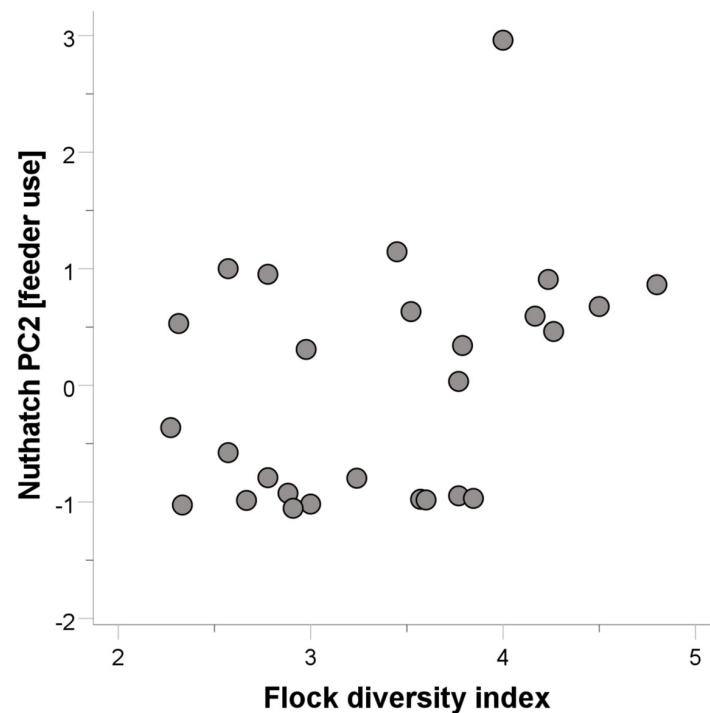


Figure 4. Tendency for an association between feeder use (+ seed-taking rates and – seed-taking latencies) for white-breasted nuthatches and the mixed-species diversity of their flocks. Each gray circle represents a single flock.

3.3. Carolina Chickadees

No variables were significantly associated with the single PC score for Carolina chickadees (Table 1).

4. Discussion

An earlier study of mixed-species flock responses to predator and risk-related stimuli found that variation in habitat density (forest alpha volume) was associated with foraging behavior in Carolina chickadees and white-breasted nuthatches [1]. In the current study, we detected an effect of forest alpha volume on seed taking in tufted titmice—titmice avoided feeders longer in the presence of the hawk model the denser the habitat was near the feeder. In terms of variation in social environmental variables, we detected an effect of the number of conspecifics on call latency in white-breasted nuthatches and also noted a tendency for nuthatches to take more seeds in more diverse flocks. Unlike the two recent studies at our bird feeders (predator-related stimuli [1]; novel feeders [6]), we did not detect any effects of our five predictor variables on Carolina chickadees' latencies and rates of seed-taking and calling.

4.1. Social Variables

Changes in social metrics can impact the response to predator stimuli. For nuthatches, the number of conspecifics was associated with the latency to call in response to the hawk model. The more nuthatches that were present at a feeder site, the shorter the latency to call during the predator stimulus period. The latency to call is likely affected by a diversity of social and physical variables in the environments of these species. White-breasted nuthatches tend to stay in the same pairs year-round rather than in larger groups, and protection of mates may be a strong incentive for exhibiting antipredator behavior [44].

As mentioned earlier, nuthatches can gain foraging and antipredator benefits by following nuclear chickadee and titmouse mixed-species flocks [45]. Although nuthatches

are satellite species, their behavior may be important in mixed-species flocks' responses to predator stimuli and mobbing contexts. Both Nolen & Lucas [46] and Jung et al. [11] found that white-breasted nuthatches called more and showed stronger antipredator behavior to avian predator stimuli than tufted titmice (a nuclear species). Although Adams et al. [1] found that the number of conspecifics did not seem to affect antipredator behavior of nuthatches, others have found the number of conspecifics to drive antipredator behavior for several species (amphipods (*Hyalella azteca*): [47]; several bird species: [1,48]). For nuthatches generally, the number of conspecifics may influence their boldness and therefore how quickly they call in risky situations, and this may be the reason that greater numbers of nuthatches result in longer mobbing events [1].

Nuthatches' foraging behavior in the context of predator stimuli may have tended to increase in more diverse flocks because of their ability to take advantage of benefits obtained from the mixed-species group—the ability to attend to the vocal signals of chickadees and titmice when a predator is detected [25,32]. Mangini et al. [49] investigated how the behavior of different species in mixed-species flocks affects which species are identified as leaders/nuclear and which foraging strategies have the most benefits. They found 35 different species that behaved like leader species, with most of them switching between the leader and follower role based on the flock composition. In our mixed-species flocks, more work is needed to test whether certain mixed-species flock compositions cause nuthatches to take more of a leader role and display stronger antipredator behavior.

A limitation of our study is that almost none of the birds in our mixed-species flocks were color-banded so individual identification was not possible. Individuals vary enormously in how they respond to predator stimuli (e.g., “shy-bold” continua) and so future work would benefit greatly from being able to assess how variation in personality within these mixed-species flocks might influence larger group-level responses to situations of risk [50–52].

4.2. Physical Environmental Variables

Variations in the physical environment can also impact mixed-species flocks' responses to predator stimuli. Adams et al. [1] compared the differences in antipredator behavior of mixed-species flocks in response to predator-related visual and acoustic stimuli. Like our findings for chickadees and nuthatches, they found that vegetation density did not affect the birds' calling or seed-taking rates. In our study, we found that titmice took fewer seeds and took longer to approach the feeders at sites that were surrounded by higher densities of vegetation. Perhaps in denser vegetation titmice are more cautious during times of risk and reduce foraging due to lower visibility.

In the mixed-species groups studied here, titmice (along with chickadees) are the core species that satellite species like nuthatches follow. It is believed that these satellite species take advantage of the diverse broadcast vocal signals produced by the core species, especially because variation in their signals is associated with important environmental variables like predator risk [25,53,54]. The ‘leader’ role of chickadees and titmice in communicating about environmental changes (e.g., changes in predation risk) and the added protection of dense vegetation could partially explain why we found that increased vegetation density was linked to decreased foraging and delayed feeder visits for titmice [13]. Although this reasoning supports the lack of response from nuthatches, it is unclear why vegetation density did not affect chickadees' alarm calling rates as well. The social contexts of the flock cannot be ruled out—perhaps individuals in mixed-species flocks stay in closer proximity to one another in conditions of high vegetation density (or higher rates of traffic noise: [34]). Meaux et al. [55] found that vegetation density did not affect the contact (social call) call rates of aviary-housed Swinhoe's White-eyes, *Zosterops simplex*, but the presence of

like individuals (dominant/subordinate status and sex) resulted in asymmetries in calling. Future research should investigate potential changes in the role of core/satellite species in the context of vegetation density in mixed-species flocks by manipulating group size, group composition, and predator context (visual, acoustic, in-flight, stationary) across a variety of species. Additionally, assessing these questions in a wider range of habitat variation than we were able to conduct at UTFRREC would allow strong tests of the intermediate disturbance hypothesis, which argues that species richness is greater in areas of intermediate habitat disturbance [56,57]. Variation in species richness across gradients of habitat disturbance could, in turn, be associated with variation in mixed-species flock size and composition.

Surprisingly, we were unable to detect any influence of variation in traffic noise on any of the behavior we measured here. Our earlier studies of these mixed-species flocks likewise found no effect of traffic noise on behavior in predator contexts [1] or novel feeder contexts [6]. However, traffic noise is associated with antipredator contexts in these flocks [11], including satellite species' responses to alarm calls of nuclear species [58]. Perhaps the feeder site context we used in these studies brings individuals into close enough proximity that any effects of traffic noise are minimized—future work in our lab will aim to assess the potential effects of traffic noise away from feeders.

5. Conclusions

Our study found that individual species' sensitivity to predator presence was impacted by aspects of both social and physical environmental variation. Tufted titmice showed higher feeder avoidance (higher latencies to take seeds and lower rates of seed taking) at sites with higher vegetation density. This may be because denser vegetation can obscure the visibility of predators, causing titmice to be more cautious and forage less during times of risk. Given this finding, as well as similar findings in our earlier study with stimuli related to risk [1], for the birds in these mixed-species flocks, we would expect increased vigilance, decreased foraging behavior, and decreased foraging efficiency in areas of very high density of vegetation, such as in primary succession following practices like clearcuts or selective logging. As many species might join mixed-species flocks primarily for the antipredator benefits these groups can provide [5], we would then also expect to find reductions in mixed-species flock species richness in areas of major disturbance following forestry practices like this.

Our study also highlighted the relationship between flock composition and foraging and calling behavior within mixed-species flocks. White-breasted nuthatches had lower latencies to call and exhibited higher call rates in response to the predator model when there were more conspecifics present. In mixed-species flocks, some satellite species may produce signaling behavior more characteristic of nuclear/leader species depending on the behavior (or lack thereof) of normal leader species in the group (see also [46]). Future studies could seek to examine the role of group composition on possible 'role reversals' within mixed-species groups and how such changes in roles can impact the sensitivity to environmental variation in individual species within the group.

Supplementary Materials: The following supporting information can be downloaded at <https://www.mdpi.com/article/10.3390/d17050363/s1>, Data Spreadsheet.

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