

Characterizing complex mixed-species bird flocks using an objective method for determining species participation

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Received: 5 April 2007 / Revised: 31 December 2007 / Accepted: 28 January 2008
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Abstract We developed sampling methods to characterize the participation of bird species in foraging flocks led by the Eastern Tufted Titmouse (*Baeolophus bicolor*) in North-central Florida during winter, because standard field methods, developed primarily for permanent resident Neotropical flocks, were intractable in our system. During January–February 2004 and November 2004–March 2005, we observed 55 mixed-species flocks, recorded 40 potential flocking species [mean of 12.4 species (SD = 3.8; range 3–20), 26.3 individuals (SD = 12.2; range 8–60), and 3.1 titmice (SD = 1.4; range 1–7), per flock]. Twenty-six species were observed frequently enough (>10% of observations) to be included in analyses. We paired 60-min flock observations with 10-min point counts conducted in locations used by flocks, but after flocks had moved more than 100 m away. This method yielded a measure of flocking propensity: the ratio of the number of individuals observed in the flock versus during the point count for each species. We used regression tree (RT) analysis to classify species into groupings according to their levels of flock participation, and to investigate relationships between

flocking propensity and various environmental and social factors that we measured. Our analysis identified three clear species groups; “Nuclear/Regular Associate” (12 spp.; high/moderate), “Occasional Associate” (four spp.; moderate/low), and “Non-joiner/Accidental” (ten spp.; low/no flocking propensity). Groupings were similar to schemes produced via more time-intensive field methods. In order to contextualize grouping categories, we conducted a review of flocking group definitions and relevant autecological information (e.g., interspecific sociality) about our study species. We found this method to be useful for geographically extensive sampling of species’ participation in mixed-species flocks, despite high inter-flock variability in species composition and limited labor.

Keywords Paridae · Mixed species flocks · Regression tree · Nuclear species · Flock participation

Introduction

Morse (1970) defined “mixed-species” bird flocks (MSF) as “any group of two or more birds, whose formation depends upon positive responses by individuals to members of their own or other species.” For over a century, MSFs have provided a focal point for studies of: (1) costs and benefits of associations between species (Bates 1864; Belt 1874; Swynnerton 1915; Winterbottom 1943; Davis 1946; Morse 1970, 1977; Terborgh 1990), (2) the mechanisms underlying selection for interspecific flocking (Moynihan 1962; Greig-Smith 1978; Post 1978; Munn and Terborgh 1979; Terborgh 1990; Thiollay and Jullien 1998), and (3) the ecological consequences of these intrinsically structured aggregations for species richness and distribution patterns in natural (Lee et al. 2005; Morse 1970; Munn

Communicated by F. Bairlein.

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and Terborgh 1979) and disturbed communities (Lee et al. 2005; Maldonado-Coelho and Marini 2000, 2004). The increasingly rich literature on mixed-species flocking in birds has, to some extent, inspired similar work with other taxonomic groups (Wolf 1985; Fitzgibbon 1990; Terborgh 1990; Chapman and Chapman 1996; Frantzis and Hertzling 2002). With increasing attention to the important roles of positive interspecific interactions in ecological and evolutionary theory (Bertness and Callaway 1994; Bruno et al. 2003; Thomson et al. 2003; Crain and Bertness 2006) and conservation (Bruno et al. 2003; Crain and Bertness 2006), diverse methods for analyzing the dynamics of interspecific interactions are needed.

One of the first tasks in studying mixed-species groups is identification of group participants, or characterizing different categories (levels) of participation or association with group leaders (Winterbottom 1943, 1949; Davis 1946; Short 1961; Moynihan 1962; Morse 1970; Munn and Terborgh 1979). We encountered difficulty in characterizing participation in the complex facultative winter flocks of birds in forests of the southeastern United States using standard methods published in the avian literature. The structure of flocks here are highly variable and strongly affected by seasonal and diurnal shifts in species composition and individuals' use of space, unlike the year-round flocks of tropical forest where standard (intensive) flock characterization methods were developed (e.g., see Table 2; Winterbottom 1943, 1949; Davis 1946; Moynihan 1962; Munn and Terborgh 1979; Buskirk et al. 1972; Powell 1979). In this paper, we characterize level of participation by diverse species in facultative mixed-species flocks of North-central Florida led by the Eastern Tufted Titmouse (*Baeolophus bicolor*; Morse 1970; Gaddis 1979, 1983; Grubb and Pradosudov 1994; Sieving et al. 2004; Contreras et al., unpublished data) using a relatively low-effort field method and a more objective analysis than we typically encountered in the literature. To facilitate interpretation of our findings, we also conducted a review and summary of literature regarding both autecological traits of our study species that could influence interpretation of their level of participation, and others' definitions of flock participation.

Flock characterization methods based on tropical systems

Neotropical flocks consist of diverse permanent-resident species with a flock territory jointly held and defended year-round by “core” or obligate participants. Flocking typically occurs among forest understory species and canopy/mid-story foragers with little co-mingling of species between strata. Only a single individual, a mated pair, or a family group typically represents each species in a single

flock. Individuals or mated pairs that defend exclusive territories smaller than the flock territory may join a flock when it enters their own territory and drop out once the flock leaves. From roughly October through April, temperate migrants may join permanent tropical flocks (Davis 1946; Moynihan 1962; Buskirk et al. 1972; Munn and Terborgh 1979; Powell 1979; Gradwohl and Greenberg 1980; Hutto 1987, 1994; Gram 1998; Jullien and Thiollay 1998; Maldonado-Coelho and Marini 2000, 2004; Mathy 2005).

Among the more common methods utilized in characterizing participation in mixed-species flocks is extensive mist-netting and color-banding of individuals in the study area (Buskirk et al. 1972; Munn and Terborgh 1979; Powell 1979; Jullien and Thiollay 1998). Flocks are followed from dawn to dusk, or as long as the observer(s) can track them, and flock territories/home ranges are mapped for one or a few flocks within a study area that is often grid-based (Buskirk et al. 1972; Greig-Smith 1978; Munn and Terborgh 1979; Powell 1979; Gaddis 1983; Jullien and Thiollay 1998). During these observation periods, detailed records are kept of flock size (number of individuals), species composition and, when possible, behavioral observations (often related to which birds “lead” the flock and which ones “follow”, how long a bird stays with the flock after joining, and foraging and agonistic behaviors (Davis 1946; Moynihan 1962; Morse 1970; Buskirk et al. 1972; Greig-Smith 1978; Munn and Terborgh 1979; Powell 1979). Most early studies which initially developed these methods were based on less than two dozen independent flocks. While this system works well to characterize species behavior in regions where flocks are stable in size and species composition year-round, application of this method in locations where flock behavior is seasonal and structure is more variable could easily lead to inaccuracy or biases in generalizing about flock composition. The high amount of labor involved with intensive flock-following techniques (e.g., capture, color-marking, territory-mapping, etc.) limits sample size and, therefore, the range of conditions over which temperate flocks operate that can be studied.

Study goals

In North-central Florida, avian species diversity is higher in winter than during the summer breeding months and 35 or more species could potentially be interacting with understory forest flocks (Sieving et al. 2004) regularly or opportunistically. Moreover, winter flocks that form around Eastern Tufted Titmice (ETTI) can be encountered in a range of mixed pine and oak woodland habitats and across the wild land–urban gradient. To determine which species

are regular or obligate versus occasional flock participants against the background noise of high species richness and environmental variability of our study system, we sought a large sample size of flocks over a fairly large spatial scale. This approach would allow us to incorporate realistic system heterogeneity into our understanding of flocking aggregations while controlling the level of statistical variance in analysis. In order to achieve the sampling strategy we desired, we needed field methods less labor-intensive than mist-netting, color-marking, and dawn-to-dusk flock-following. Moreover, the usual analyses, composed of simple enumeration of species perceived to be actively “with” the flock, yielded too many ambiguous classifications, especially for rare and superabundant species. Therefore, the central goals of this study were twofold: to develop (1) a rapid field methodology that would allow extensive sampling of many flocks by one person with relatively limited time, and (2) an objective analytical method for determining which species, in a complex winter avifauna, were most highly associated with mixed-species foraging flocks organized around ETTI. In addition, in order to shed light on how to categorize flock participation, and understand both autecological and semantic sources of ambiguity in doing so, we found it necessary to (3) review and summarize key literature concerning definitions of flocking propensity and the natural history of our study species.

Methods

Study site

Mixed-species flocks were located by walking through upland forest sites where we had access (i.e., public lands) until ETTI (and associated flocks) were encountered. Areas of habitat searched for MSFs varied in terms of forest or park patch size (from small suburban parks of 10–20 ha to large wild land reserves of 10,000 ha or more) and type of matrix in adjacent non-protected areas (e.g., residential and commercial development, regenerating forest, farm lands, or wetlands). We did not use any isolated forest sites, per se, in that none of our sample sites were surrounded by matrix habitats so extensively open or otherwise hostile that titmice and other woodland birds would have restricted access due to habitat barriers (Sieving et al. 1996, 2004). In the largely forested landscapes of North-central Florida, titmice and species associated with winter flocks can be found throughout the urban to wild land gradient, and we were careful to sample only portions of apparently interconnected mosaics of forest. Furthermore, we only followed flocks that were initially contacted at least 100 m from a high-contrast edge.

Flocks were principally associated with southern hardwood forests dominated by Laurel Oak (*Quercus laurifolia*), Water Oak (*Q. nigra*), Live Oak (*Q. virginiana*), Sand Live Oak (*Q. geminata*), Pignut Hickory (*Carya glabra*), and Cabbage Palm (*Sabal palmetto*) in the canopy. Typical understory vegetation consists of Flowering Dogwood (*Cornus florida*), Red Maple (*Acer rubrum*), Saw Palmetto (*Serenoa repens*) and *Ilex* spp. Longleaf Pine (*Pinus palustris*) dominates the upland pine sandhill canopy along with the deciduous Turkey Oak (*Q. laevis*), though it is sometimes mixed with Sand Pine (*P. clausa*), Loblolly Pine (*P. taeda*), or Slash Pine (*P. elliotii*). Pine understory is characteristically open, consisting mostly of Wiregrass (*Aristida stricta*), scrubby evergreen oaks such as Chapman’s Oak (*Q. chapmanii*), Bluejack Oak (*Q. incana*), some Sand Live Oak, and Florida Rosemary (*Ceratiola ericoides*) along with various other grasses and forbs. Pines and hardwoods usually form mixed forests, with the dominant canopy and understory types varying with hydric conditions, soil type, and fire frequency (Myers and Ewel 1990).

North-central Florida has a long warm season and relatively short and mild winter (mean annual temperature 20.3°C, mean winter temperature 13.3°C, mean winter high 19.7°C and low 7.7°C; temps can drop to –8°C; based on 30-year normals; Myers and Ewel 1990), and is a transitional zone between temperate and tropical climates. Mean annual rainfall is 125.6 mm, with summers wetter than winters (Myers and Ewel 1990).

Winter forest avifauna

During the winter season (and temporarily during fall and spring migrations), the avifauna in Florida is at its most diverse due to the arrival of post-breeding individuals from the north (Kale and Maehr 1990). The study period largely excluded migrant species which join mixed flocks only temporarily during fall and spring migrations (Rodewald and Brittingham 2002) on the way to tropical wintering grounds (Davis 1946; Moynihan 1962; Buskirk et al. 1972; Powell 1979; Gradwohl and Greenberg 1980; Hutto 1987, 1994; Ewert and Askins 1991; Latta and Wunderle 1996; Gram 1998; Mathy 2005). Furthermore, titmice and other resident birds begin exhibiting breeding behavior in late January, and by mid-March, the flocks begin to disintegrate (Morse 1970; Gaddis 1983; Authors, personal observation). During the winter, birds found in forests or their edges with the potential to be included in our surveys consist of 129 species, with 42-year round residents, 39 wintering species, 39 transients, and 9 summer residents (Austin et al. 1998; see Table 3 in Appendix for species we observed). The vast majority of these are passerines, many of which may participate in mixed-species flocks.

Study design

Data were collected over two winter seasons: from January to February 2004, and November 2004 to March 2005 at several locations in Alachua, Putnam, and Columbia counties in North-central Florida. Search effort was equal for each of three diurnal time periods: Morning (0700–1000 hours), Mid-day (1000–1400 hours), and Afternoon (1400–1700 hours). However, over 50% of flocks were located in the morning, when birds tended to be most active. Birds were determined to be part of a titmouse-led mixed-species flock if at least one titmouse occurred with at least one bird of another species and all birds were moving together within 25 m of their nearest neighbor (Hutto 1987; Latta and Wunderle 1996; Rodewald and Brittingham 2002), and each bird included was with the flock for at least 5 min (Latta and Wunderle 1996; Maldonado-Coelho and Marini 2000). All individuals meeting these criteria were recorded. We followed flocks until all members had been identified and no new individuals appeared for 10 min, up to a maximum of 60 min, a time limit established in the literature (Latta and Wunderle 1996), unless the flock outran the observer before the 60-min limit was reached. One hour was a reasonable amount of time to ensure even the largest flocks were fully characterized, while reducing biases that might be caused by changes in flock composition during the observation period. Flocks that were not fully characterized before the end of the observation period, or that were lost by the observer, were not included in the analyses. We avoided areas where flocks had previously been observed in order to maintain independence of observations. Winter home ranges of ETTI flocks vary from roughly 5 to 10 ha, and may overlap other ETTI flock ranges (Grubb and Pravosudov 1994). Using this information, we assumed a circular home range with an average size of 10 ha (diameter = 356.8 m). Therefore, we attempted to observe flocks ≥ 350 m away from previously observed flocks. Neighboring flocks closer than 350 m were included, but only if we were certain it was a new flock; for example, if a flock moved due south after the observation period and another flock was encountered after walking due north, we considered the flocks to be independent.

We measured several social, seasonal, and climatic factors reflecting known influences on flock organization (Arevalo and Gosler 1994; Maldonado-Coelho and Marini 2004; Sieving et al. 2004) including: the number of individual ETTI in the flock, Julian date of observation, time of day, and mean air temperature; these were included in analyses to control/test for their possible associations with flocking propensity. Mean air temperature was calculated using measurements taken at the beginning and end of the flock observation because temperatures can shift

dramatically over an hour's observation. In addition, we included a habitat variable identifying five gross habitat categories where we encountered flocks: (1) sites within upland pine-dominated, (2) oak-dominated, or (3) mixed oak and pine forest; and either (4) mixed or (5) hardwood forest sites with high contrast (open) matrix adjacent to the site (though ≥ 100 m from initial flock observations).

Once flocks had been characterized, a 50-m-radius point count was conducted at the place the observer last watched the focal flock, after the flock moved 100 m away from that point. If the flock did not move far enough, or if it quickly circled back, the observer moved 100 m to a previous location the flock had occupied during the 1-h flock observation period before starting the point count. The observer had to move to find a point count location far enough from the flock in about 50% of cases, but all point counts were conducted within the area the focal flock had occupied during the flock observation period. Point counts lasted 10 min and, during the last minute, an area search of the count circle was conducted to detect/flush any secretive species near the observer (Bibby et al. 2000). All birds seen, heard, or flying over/through the count circle were recorded. Post hoc, we removed all observations of species recorded on point counts that we were certain never flocked with titmice (i.e.: vultures, raptors, game birds, waterfowl, and herons), and also removed from both flock and point counts those species observed on five or fewer (10%) of total flock observations (see Table 3 in Appendix, Table 1). A species was considered observed on a particular sampling occasion if it had been seen in the flock or its paired point count. All flock and point count observations were conducted by E.A.F. to eliminate inter-observer bias, though the protocol was collectively developed.

Quantifying flocking propensity

Because of the diversity of resident bird species in Florida in winter, we needed to be able to clearly separate common species that were merely coincident with passing flocks from species that were actually moving with the flocks. By comparing numbers of individuals of each species observed in flocks versus the number “left behind” once each flock moved on, we reasoned we could separate common flocking from common non-flocking species. For every species on each sampling occasion, therefore, we calculated a raw ratio of the number of individuals seen in a flock to the number of individuals seen on the paired point count, using this formula:

$$\text{Ratio} = (\#\text{individuals in flock} + 0.5) / (\#\text{of individuals in point count} + 0.5).$$

We added a nominal “half-individual” to both numerator and denominator so that ratios could be calculated when

Table 1 List of all species observed in January–February 2004 and November 2004–March 2005; the number of times a species was observed, and the number of individuals observed, in paired flock or point counts; the mean raw abundance; and the mean log-transformed flock-to-point count ratio of each species

Species code	Frequency of occurrence in flocks (%)	Number of times observed		Number of individuals observed		Mean raw abundance \pm 1 SE	Mean LogR \pm 1 SE
		Flock	Point count	Flock	Point count		
ETTI	100.0	55	9	171	11	3.11 \pm 0.19	0.74 \pm 0.04
RCKI	98.2	54	22	233	28	4.31 \pm 0.40	0.70 \pm 0.05
BGGN	80.0	44	7	171	7	3.89 \pm 0.37	0.80 \pm 0.05
PIWA	76.4	42	10	163	12	3.84 \pm 0.69	0.67 \pm 0.07
DOWO	70.9	39	4	56	4	1.41 \pm 0.11	0.49 \pm 0.04
RBWO	67.3	37	18	55	21	1.51 \pm 0.10	0.31 \pm 0.05
BHVI	58.2	32	7	43	7	1.32 \pm 0.08	0.42 \pm 0.05
YPWA	49.1	27	2	90	3	3.25 \pm 0.41	0.75 \pm 0.06
BAWW	45.5	25	1	30	1	1.20 \pm 0.10	0.50 \pm 0.03
WEVI	41.8	23	5	29	5	1.24 \pm 0.10	0.39 \pm 0.06
MYWA	34.5	19	24	101	64	4.57 \pm 0.84	-0.03 \pm 0.11
YTWA	34.5	19	1	20	1	1.05 \pm 0.05	0.44 \pm 0.05
EAPH	32.7	18	12	21	14	1.18 \pm 0.11	0.14 \pm 0.08
CARW	27.3	15	14	20	19	1.43 \pm 0.13	0.02 \pm 0.10
BLJA	25.5	14	14	27	20	1.82 \pm 0.26	0.04 \pm 0.12
CACH	20.0	11	2	17	3	1.64 \pm 0.24	0.48 \pm 0.10
NOCA	18.2	10	12	17	20	1.78 \pm 0.21	-0.06 \pm 0.14
YBSA	18.2	10	5	12	5	1.15 \pm 0.10	0.22 \pm 0.12
AMRO	16.4	9	11	23	32	2.87 \pm 0.49	-0.13 \pm 0.16
AMGO	10.9	6	10	24	21	3.17 \pm 0.64	-0.13 \pm 0.21
CHSP	10.9	6	0	50	0	8.33 \pm 3.75	1.06 \pm 0.18
HETH	10.9	6	5	8	5	1.20 \pm 0.13	0.09 \pm 0.16
GRCA	9.1	5	2	7	2	1.33 \pm 0.21	0.31 \pm 0.19
RHWO	9.1	5	6	8	12	2.00 \pm 0.22	-0.15 \pm 0.18
HOWR ^b	7.3	4	1	5	1	1.20 \pm 0.20	0.33 \pm 0.21
OCWA ^b	7.3	4	1	4	1	1.00 \pm 0.00	0.29 \pm 0.19
PIWO	7.3	4	4	4	4	1.00 \pm 0.00	0.00 \pm 0.18
PRAW ^b	7.3	4	0	4	0	1.00 \pm 0.00	0.48 \pm 0.00
EATO	5.5	3	4	5	10	2.00 \pm 0.82	-0.16 \pm 0.21
CEWA ^b	3.6	2	4	11	12	4.00 \pm 1.05	-0.25 \pm 0.41
BAOR ^b	1.8	1	0	1	0	1.00 \pm 0.00	0.48 \pm 0.00
BRTH ^b	1.8	1	0	1	0	1.00 \pm 0.00	0.48 \pm 0.00
COYE ^b	1.8	1	0	1	0	1.00 \pm 0.00	0.48 \pm 0.00
EABL ^b	1.8	1	1	2	2	2.00 \pm 0.00	0.00 \pm 0.70
HAWO ^b	1.8	1	1	1	1	1.00 \pm 0.00	0.00 \pm 0.00
MODO ^b	1.8	1	5	1	6	1.20 \pm 0.20	-0.43 \pm 0.11
NOPA ^b	1.8	1	0	1	0	1.00 \pm 0.00	0.48 \pm 0.00
OVEN ^b	1.8	1	2	1	2	1.00 \pm 0.00	-0.16 \pm 0.32
YSFL ^b	1.8	1	2	1	2	1.00 \pm 0.00	-0.24 \pm 0.24
YTVI ^b	1.8	1	0	1	0	1.00 \pm 0.00	0.48 \pm 0.00
AMCR ^a	0.0	0	6	0	8	1.33 \pm 0.21	-0.55 \pm 0.05
AMKE ^a	0.0	0	1	0	1	1.00 \pm 0.00	-0.48 \pm 0.00
BLVU ^a	0.0	0	2	0	5	2.50 \pm 1.50	-0.72 \pm 0.24
GREG ^a	0.0	0	1	0	1	1.00 \pm 0.00	-0.48 \pm 0.00
HOFI ^b	0.0	0	1	0	1	1.00 \pm 0.00	-0.48 \pm 0.00

Table 1 continued

Species code	Frequency of occurrence in flocks (%)	Number of times observed		Number of individuals observed		Mean raw abundance \pm 1 SE	Mean LogR \pm 1 SE
		Flock	Point count	Flock	Point count		
LOSH ^a	0.0	0	1	0	1	1.00 \pm 0.00	-0.48 \pm 0.00
NOMO ^b	0.0	0	2	0	2	1.00 \pm 0.00	-0.48 \pm 0.00
OSPR ^a	0.0	0	1	0	1	1.00 \pm 0.00	-0.48 \pm 0.00
RSHA ^a	0.0	0	5	0	6	1.20 \pm 0.20	0.52 \pm 0.04
RTHA ^a	0.0	0	1	0	1	1.00 \pm 0.00	0.48 \pm 0.00
TRES ^a	0.0	0	5	0	31	6.20 \pm 1.93	-1.02 \pm 0.16
TUVU ^a	0.0	0	12	0	20	1.67 \pm 0.28	-0.60 \pm 0.05
UNGU ^a	0.0	0	1	0	3	3.00 \pm 0.00	0.85 \pm 0.00
WITU ^a	0.0	0	1	0	1	1.00 \pm 0.00	-0.48 \pm 0.00
WODU ^a	0.0	0	2	0	4	2.00 \pm 0.00	-0.66 \pm 0.18

Raw abundance was defined as the greatest number of individuals observed in either a paired flock or point count. Four-letter species codes are given in Table 3 in Appendix

^a Species was not considered to be a potential flock participant, and so was excluded from analyses

^b Species was observed on <6 (<10%) of observation occasions, and so was excluded from analyses

the denominator was zero. The raw ratio was then log-transformed (as a convention to enhance magnitude estimation scaling with ratio data; Lawless 1989). Note that a log Ratio (LogR) of 0.00 indicates exactly equal numbers of individuals of a species observed on a point count as in the flock, i.e., a 1:1 raw ratio.

For each species, we calculated a weighted abundance measure using the following formula:

$$\text{(Weighted)Abundance} = \frac{(\max \text{.#times a species was observed}/55) \times (\max \text{.#individuals seen on either flock or point count})}{55}$$

where 55 is the total number of sampling occasions in this study. In effect, this weighted abundance measure reduces the calculated abundance of species that were rarely observed but only seen in large groups. In our system, several species have this type of distribution and unmanipulated abundance calculations across all of our observations seemed to overestimate a species' availability to participate in winter flocks. For example, chipping sparrows (CHSP) were only seen six times, but in groups of up to 25 individuals. A simple mean abundance for CHSP = 8.3 birds but the mean weighted abundance = 0.91 birds. In contrast, both the simple and weighted mean abundances of ETTI (from 1 to 7 individuals seen in all 55 observations) = 3.11 birds.

Data analysis

We submitted the data to a regression tree analysis (RT), using the program DTREG (Sherrod 2004) to determine if species fell into distinct categories based on flock

participation. LogR was used as the target variable, with the following ten predictor variables: Habitat Type (five categories), Location (seven different study areas), Winter Season (i.e., "1" or "2"), Flock Identification, Diurnal Time Period (as described above), Species, Julian Date of Observation, Mean Temperature, Number of ETTI per flock, and Weighted Abundance.

RT analysis takes a single continuous response, or target variable (in this case LogR) and uses a set of predictor variables to repeatedly split the data set into increasingly homogenous and mutually exclusive groups. In both classification and regression tree models (CART), each split of the target variable (e.g., branches/nodes) uses only the single most influential predictor variable (i.e., that maximizes the homogeneity within the resulting two groups) at each node (Wiles and Brodahl 2004), and this minimizes or eliminates the impact that collinearity among predictor variables can have in global regression models (Breiman et al. 1984). Moreover, CART is well-suited to ecological studies involving numerous and diverse kinds of predictor variables because it lacks assumptions about underlying distributions. Cross-validation (the process of repeatedly using one data subset to predict another subset) is conducted at each node to assess the predictive value of the model as it is built. Target variable homogeneity (or impurity) within each node is expressed as the SD around the mean of that variable—the smaller the SD relative to the mean value, the "purer" is the node and the higher its implied predictive power (Breiman et al. 1984). Variable importance (VIMP) is estimated as one of the outputs of CART procedures in DTREG, and it indicates the degree to which the variable reduces overall node impurity (on a scale from 0 to 100%; Ishwaran 2007). Because the

splitting of data can continue past the point of biological/ecological significance, rules are often used for “pruning” RT models (De’ath and Fabricius 2000). These stopping, or “pruning”, rules are based on a threshold of model error for the response variable (Scott et al. 2003). In our analysis, we used the standard pruning rule of 1 SE from the minimum model error, and a V-fold cross-validation level of 10 (Sherrod 2004).

CART models are principally descriptive rather than inferential (hypothesis-testing) and are well-suited for classifying observations into groups and identifying gradients (De’ath and Fabricius 2000). CART models imply no causal inference regarding effects of predictors on target variables, yet they achieve strong predictive power via their exhaustive cross-validation procedures used iteratively with all predictor variables during model-building (Breiman et al. 1984). In our analysis, if Species turned out to be the most important predictor of LogR, especially high values of LogR, then we would be satisfied that our method identifies the species that are maintaining close and predictable interspecific associations with ETTI in foraging flocks, despite the diversity of social and environmental conditions that reign in our study system. Alternatively, if other factors more strongly predict LogR values, then we may hypothesize that flocks form and stay tightly organized simply when conditions are conducive, but independent of the identity of species in the immediate area.

Categorizing flocking propensity

To establish the final groupings of species based on flocking propensity and select names for each category, we followed a three-step process. First, we examined RT models for the most meaningful groupings of species based on our knowledge of the system. Second, we selected the best grouping category names from the literature that were both commonly used and accurate with respect to the ecology and behavior of our study species. Finally, the latter was augmented with a review of literature about the autecology of our study species, particularly regarding winter territory defense and use of space (see Table 3 in Appendix; Poole 2005).

Results

We obtained a total of 55 flock observations paired with point counts, 22 from the first winter (13 January through 24 February 2004), and 33 from the second winter (18 November 2004 through 2 March 2005). We observed 40 species associating with mixed flocks to some degree, but only 26 species were recorded on enough occasions (>10%) to be included in RT analyses (Table 3 in Appendix, Table 1). Flocks contained an average of 12.4

species (SD = 3.8; range 3–20) and an average 26.3 individuals (SD = 12.2; range 8–60). The average number of species observed per flock was nearly twice what Gaddis (1983) found previously at one of our study locations, while the average number of individuals is similar; our results are comparable to the species richness of flocks that Hutto (1987, 1994) and Gram (1998) observed in highland pine-oak woodlands of Mexico. The number of ETTI per mixed-species flock averaged 3.1 individuals (SD = 1.4; range 1–7). Mean recorded air temperatures were 14.6°C in January and February 2004 (SD = 5.1°C; range = 5.4–25.0°C), and 18.8°C for November 2004–March 2005 (SD = 6.5°C; range 7.8–29.1°C), with an overall mean temperature across the two winters of 17.1°C (SD = 6.3°C). Eighteen flocks were observed in oak-dominated sites, 5 in hardwood sites near hard edges, 5 in mixed oak and pine sites, 19 in mixed forest sites near hard edges, and 8 in pine-dominated sites.

We ran RT analysis with and without Flock ID as a predictor variable (see below). Figure 1 shows the results of the model without Flock ID, the one most useful for our needs. In this model, only two variables were used to construct the tree: Species, VIMP = 100% and Weighted Abundance (VIMP = 35%). Three meaningful groups of species were identified (Fig. 1, Nodes 3, 4, and 5). The first group (Fig. 1, Node 3) contains 12 species that were habitually observed in flocks more often than the point counts (note the group’s mean LogR is higher than the overall model mean LogR, Node 1). This high-propensity flocking group (we called “Regular Associates”, see below) was divided into two sub-groups based upon Weighted Abundance; four species >2 birds (Fig. 1, Node 75) and eight species with mean Weighted Abundance ≤2 birds (Node 74; see Table 3 in Appendix for species codes). Note that Nodes 3, 74 and 75 all have standard deviations of half the mean or less, indicating low node impurity, or “clean” species groupings.

The other 14 species were grouped (Fig. 1, Node 2) with a much smaller (near 0.0) mean LogR than species in Node 3, indicating they were observed on point counts nearly as often as in flocks. This group was split further into a group of four species (Fig. 1, Node 5) with a mean LogR much lower than the Node 3 group, but higher than zero. The remaining ten species had a mean LogR lower than any other group (Fig. 1, Node 4) and less than 0.0, indicating they were more often observed on the point counts than in flocks. The impurity (SD relative to means) of Nodes 2, 4, and 5 are fairly high, suggesting these categories are not cleanly split.

When Flock ID was included as a predictor of LogR, Nodes 1, 2, 3, 74, and 75 appear exactly the same as in Fig. 1, but Nodes 4 and 5 are split using Flock ID instead of Species (23 flocks fall under Node 4 with mean LogR = -0.15, SD = 0.49 and 22 flocks fall under Node

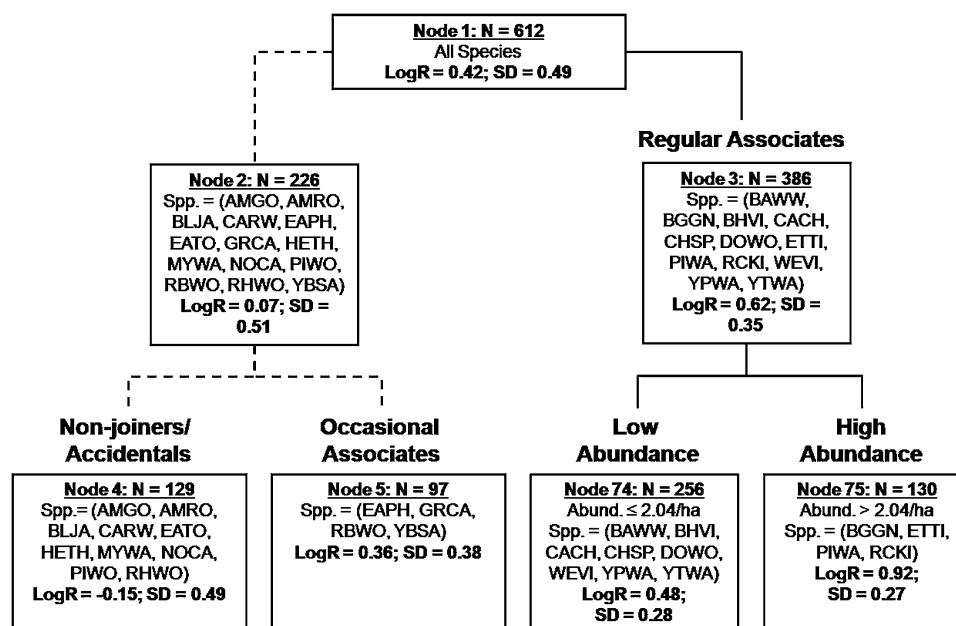


Fig. 1 Regression tree pruned to 1 SE of the mean (0.0375). The target variable is LogR, and predictor variables submitted were Habitat Type (five categories), Location (seven different study areas), Winter Season (i.e., “1” or “2”), Diurnal Time Period (as described above), Species, Julian Date of Observation, Mean Temperature, Number of ETTI per flock, and Weighted Abundance (see text). The

data set includes all 26 potential flocking species observed on >10% of sampling occasions. Four-letter species codes are given in Table 3 in Appendix. *Dotted lines* indicate groupings of birds that are less participatory in flocking aggregations than groups with *solid line* connectors

5 with mean LogR = 0.36, and SD = 0.38; VIMPs for this model: Species = 100%, Weighted Abundance = 37%, and Flock ID = 32%). The inclusion of Flock ID slightly improves model fit (unexplained residual variance after tree fitting = 0.12, and proportion of variance explained = 0.50) over the model without Flock ID (unexplained = 0.14, explained variance = 0.44). What this reflects, however, is simply that all flocks have relatively low mean LogR values. This is because flock values of LogR are based on the behavior of all individuals in the area of a given flock when it was characterized; therefore, mean flock LogR values get dragged down by species that are just in the area but not actually followers. Since our main goal was to identify species with high LogR values and both models clearly identify those species, we use the model without Flock ID in subsequent discussion because it is easier to interpret and is essentially as robust as the one with Flock ID included.

One potential source of bias in our procedure is the conduct of paired flock and point counts in different habitats. In our study system, woodland birds in winter mostly use both oak and pine-dominated and mixed habitats, thus we were not overly concerned with this source of bias, and our protocol generally tended to avoid such events. However, on three occasions, flocks were characterized in one habitat (e.g., oak) and then crossed into another habitat (e.g., pine) near the end of the sample where the point

count was then conducted. We ran the RT model without these three flocks and obtained the same tree configuration that is displayed in Fig. 1 (only minor variations in LogR were observed); therefore, we conclude that no bias resulted in our study. We caution, however, that if flock and point counts are conducted in different habitats in systems where following species exhibit greater habitat specialization than flock leaders, this could seriously bias LogR ratios.

We selected names for the three groups (see Fig. 1) that were both commonly used and did not misrepresent territorial behaviors of our study species as we could determine (Table 1). From highest to lowest flocking propensity, we used Regular Associates (high or low abundance), Occasional Associates, and Non-joiners or Accidentals; names we selected from among six major grouping categories and six sub-groups commonly used in the literature (Table 2). Additionally, we characterized the ETTI separately, identifying it as a Passive Nuclear species, and as a Leader of the flocking aggregations based on unpublished data (see below).

Discussion

We identified three nodes of the RT model that express flocking propensity in a way that clarifies our

Table 2 Compiled categorization of flocking species as developed from key papers on mixed-species flocks, with the latitude(s) where studies occurred

Flocking species category	Flocking propensity	Definition	Latitude	Key references
Nuclear	High	Species whose behavior contributes appreciably to stimulate the formation and/or maintain the cohesion of mixed flocks, and typically possessing at least the first three characteristics: (1) intraspecifically gregarious; (2) display conspicuous plumage or behavior (distinctive alarm and/or frequent contact calls; active movements); (3) are “Regular” flock participants (see below); (4) ^a are year-round residents; (5) ^a average a greater number of individuals per flock than most other flock participants; (6) ^a remain with the flock continuously or for long periods; (7) ^a are joined/followed by (i.e., lead) others more often than they join/follow others	Tropical	Moynihan (1962), Winterbottom (1943, 1949), Rand (1954), Short (1961), Vuilleumier (1967), Buskirk et al. (1972)
Passive Nuclear	High	Usually joined and/or followed by individuals of other species much more often than they join and/or follow individuals of other species (i.e., other birds seek them out to flock with, rather than vice versa)	Tropical (subtropical, south-temperate)	Moynihan (1962), Vuilleumier (1967), Hutto (1987, 1994)
Active Nuclear	High	Usually join and/or follow individuals of other species much more often than they are joined and/or followed by individuals of other species (i.e., actively seek out other birds to flock with)	Tropical	Moynihan (1962), Vuilleumier (1967)
Leader	High/moderate	Leads other birds/its followed more often than it follows other birds; roughly equivalent to a “Nuclear” species, but referring to its movement behavior within a flock, instead of its tendency to be found in a flock; not all “Nuclear” spp. are necessarily “Leader” spp., and not all “Leader” spp. may be “Nuclear” spp.	Temperate (tropical)	Morse (1970) Maldonado-Coelho and Marini (2000)
Associate/attendant	Variable	Any flocking species that is not a Nuclear species	Tropical	Moynihan (1962), Rand (1954), Short (1961), Winterbottom (1949), Vuilleumier (1967), Buskirk et al. (1972), Powell (1979)
Regular associate	High/moderate	Species nearly always in a flock when the opportunity occurs and rarely found outside of flocks; usually refers to non-Nuclear spp.	Tropical	Moynihan (1962), Davis (1946), Winterbottom (1949), Rand (1954), Short (1961), Vuilleumier (1967), Munn and Terborgh (1979), Powell (1979)
Occasional associate	Moderate/low	Species found in flocks to a lesser degree than Regular species, and often found outside of flocks; usually refers to non-Nuclear spp.	Tropical	Moynihan (1962), Short (1961), Vuilleumier (1967), Powell (1979)
Follower	Variable	Follows other birds more often than it is followed; roughly equivalent to “Associate” species, but based on the species’ movement behavior within a flock, instead of its tendency to be in a flock	Temperate (tropical, subtropical)	Morse (1970), Buskirk et al. (1972), Gram (1998)

Table 2 continued

Flocking species category	Flocking propensity	Definition	Latitude	Key references
Long-term follower	High/moderate	Species that regularly join and follow flocks over extended distances or long periods of time; roughly equivalent to a “Regular Attendant” spp., but based on the species’ movement behavior within a flock instead of its tendency to be in a flock	Tropical	Buskirk et al. (1972)
Short-term follower	Moderate/low	Accompanies mixed flocks only briefly and for short distances, or restricts their association to joining the flock without following it; roughly equivalent to an “Occasional Associate” spp., but based on the species’ movement behavior within a flock instead of its tendency to be in a flock	Tropical	Buskirk et al. (1972)
Joiner	Low/none	Species that joins a flock when it “surrounds” them, but does not follow it for any significant period; roughly equivalent to “Occasional Associate” or “Non-joiner/Accidental” spp.; based on the species’ movement behavior within a flock instead of its tendency to be in a flock	Tropical (subtropical)	Buskirk et al. (1972), Gram (1998)
Non-joiner/accidental	Low/none	Species almost never found in flocks, except coincidentally in space; do not have the calls and behaviors of flocking species	Tropical	Buskirk et al. (1972), Davis (1946), Winterbottom (1949), Rand (1954), Short (1961)

The first author or latitude listed represents the study(ies) that developed and utilized the terminology and definitions in such a way that later authors adapted them for their own uses. Parenthetical references represent key mixed-species flock studies that use similar terms and/or definitions. Studies occurring after about 1980 are generally not listed, as terminology appears to have become more standardized since then, typically using terms as outlined below with only slight modification or quantification of the definitions

^a Some authors use one or more of these characteristics in addition to the first three “universal” characteristics of Nuclear species in their definitions. It seems likely that these may gain more acceptance as characteristics of Nuclear species as more research is conducted, especially as many early studies, while not specifically outlining these characters, have Nuclear species that possess them

understanding of the system. Specifically, Nodes 3, 4, and 5 (Fig. 1) encapsulate three important groupings that facilitated our ability to characterize flock participation, and that we elected to label. Node 3 includes all species that our experience indicated would have strong flocking propensity, and some species we were not initially certain about because of their high abundance. For example, Ruby-crowned Kinglets (RCKI) are so abundant that it was difficult to tell from simple enumeration of presence of the species in the flock whether they merely coincided with flocks or were actively associated with them. The model made a clear distinction between that species and another common winter resident, the Yellow-rumped Warbler (MYWA), another superabundant winter visitor that forms large conspecific flocks, that apparently does not associate strongly with ETTI flocks (Fig. 1, Node 4). Nodes 4 and 5 identify species that may be weakly associated (Occasionals) with ETTI flocks from those that are decidedly not (Non-joiners). The Occasional Associates include Red-bellied Woodpecker (RBWO), a species that follows ETTI flocks but lags far behind at times because its foraging speed (lateral distance) is slower than the smaller foliage-gleaning species in the foraging flocks. The other three “Occasional” species seem to readily join flocks for brief periods when, for example, flocks get noisy, as when alarm calls are given by titmice (see Sieving et al. 2004). Non-joiner species (Node 4) are commonly in the same habitats as flocks, but whose movements are not influenced by flocks.

We identified groups that are very similar to those identified using more intensive methods (Morse 1970; Austin and Smith 1972; Hutto 1987; Gram 1998), suggesting that our methods are robust despite their simplicity with respect to the amount of time spent with individual flocks. In the majority of flock studies, observers note which species leave or join flocks, but typically continuously follow and characterize just the flocks, not accounting for birds using the same areas but not participating in the flock. In a few studies, individuals and species not in flocks were identified via general habitat-based surveys in addition to flock characterizations (Munn and Terborgh 1979; Powell 1979; Buskirk et al. 1972; Morse 1970). Our method allows a more direct and precise comparison of the propensity of species to be “in” versus “out” of flocks because it is essentially an individual-based measure of participation. Additionally, by conducting point counts immediately after focal flocks left the area we could control for the effects of time of day, weather, and habitat, etc., on flock participation. Moreover, since flock home ranges appear to be relatively exclusive in our system (Gaddis 1979, 1983), by conducting the point count within the focal flock’s home range, we reduce the chance another flock will intrude on that area during the point count, which

could artificially boost “out-of-flock” encounter frequencies for some species. This paired point count method also readily accounts for those birds having a personal territory/home range that restricts them in space and therefore may limit their participation in flocks.

Assigning flocking categories

In our system, the ETTI classifies readily as the main Nuclear species around which most mixed-species flocks are formed (Morse 1970; Gaddis 1979, 1983; Rodewald and Brittingham 2002), and without which the flocks quickly lose cohesion and disperse (Morse 1970; Gaddis 1983; Rodewald and Brittingham 2002). Titmice most likely act as a “Passive Nuclear” species, as they do not seem to seek out other birds; rather, other birds find a lone titmouse or titmouse group and follow them around (see Table 2). The Carolina Chickadee (CACH; *Poecile carolinensis*) is also considered a Nuclear species in our system (Morse 1970; Gaddis 1979, 1983), but it was typically much less abundant than ETTI (Table 1) in the habitats we surveyed, and is subordinate to ETTI where they do co-occur (Cimprich and Grubb 1994). In addition to being a Passive Nuclear species, we also hypothesize that titmice act as flock Leaders (see Table 2) in our system. The latter is based on unpublished data showing that the ETTI’s short-term movement paths (distance and direction) are significantly more highly correlated with the flock path than the movement paths of other species in flocks (Contreras and Sieving, unpublished data; see also Morse 1970; Gaddis 1979, 1983). Titmice clearly also fit into the high-flocking propensity group (Fig. 1, Node 3) determined by the RT model. While this inclusion is somewhat artificial, as our definition of an MSF required the presence of ETTI, we note that they were sometimes found outside MSFs (i.e., included on point counts after the flock had moved away; see Table 1).

The remainder of the species in the high flocking propensity group classified as “Regular Associates” (Table 2) because they rarely got “left behind” by flocks to be detected on point counts. Among the high-abundance Regular Associates are RCKI and Blue-gray Gnatcatchers (BGGN), two superabundant species that are nearly ubiquitous during winters in our study region. Kinglets are winter-only residents (Kale et al. 1992), and BGGN, while present year-round, have local breeding populations that migrate south and are completely replaced by conspecifics from further north (Kale et al. 1992). It has been suggested that these species may act as Nuclear species in similar systems further south (Gram 1998). It is possible they play this role in our study system, though perhaps more as Active Nuclear species (deliberately seeking out other birds; see Table 2). We have no indication, however, that

BGGN are flock Leaders in our system (Contreras and Sieving, unpublished data).

The inclusion of CHSP in the Regular Associate group is likely to be anomalous. They are known to be highly intraspecifically gregarious and nomadic in winter. In our study, they were observed just often enough to be included in analysis, but each time in very high numbers (Table 1). They were often with an MSF long enough to be included as a flocking species, but they tended to flush and fly as a conspecific group before the point count was conducted. Therefore, CHSP had high LogR values, but not because they were keeping up with ETTI. With more observations, we suspect CHSP would classify into the low/no flocking propensity (Fig. 1, Node 4) group.

Species included in the medium/low flocking propensity group (Fig. 1, Node 5) are best termed “Occasional Associates” (Table 2), but we note that this is not a behaviorally homogeneous group, and with more observations, two groups could be identified. The two woodpecker species (RBWO and Yellow-bellied Sapsuckers (YBSA)], because of their deliberate bark-foraging tactics, may actually be Regular Associates—just “slow followers”—a phenomenon described by Chen and Hsieh (2002). Conversely, some species in this group could be more like Munn and Terborgh’s (1979) “Temporary” (individual territories smaller than the flock territory) or “Patch” (patchy habitat) species: joining a flock only when it passes through its territory or habitat/resource patch. Essentially, we consider both such sub-groups as residing in the “Joiner” category (Table 2). The other two species [Eastern Phoebe (EAPH) and Gray Catbirds (GRCA)] could also be Joiner species, or they could be Non-joiner/Accidental species (Table 2). It was our perception that they approached flocks and/or the observer out of curiosity or for information-gathering (Dugatkin 1997) rather than to pursue foraging opportunities with flocks.

The species included in the low/no flocking propensity group (Fig. 1, Node 4), had a tendency to be found more often on point counts than in flocks, as indicated by their negative LogR and are accurately called Non-joiner or Accidental species. If any species in this group are misclassified, we believe none are likely to be anything more than an Occasional Associate and are not important foraging flock participants.

Territoriality and flocking propensity

In many systems in which mixed-species flocks have been studied, especially the Neotropics, territoriality can play a large role in determining which species join mixed-species aggregations, to what degree, and in what abundances they are found in flocks at various times of the year (Morse 1970; Chen and Hsieh 2002; Lee et al. 2005; MacDonald

and Henderson 1977; Hutto 1987, 1994; Gram 1998; Latta and Wunderle 1996; Bell 1980; King and Rappole 2001; Munn and Terborgh 1979; Buskirk et al. 1972; Mathy 2005). A large number of our wintering species are territorial in winter to some degree (Table 3 in Appendix). For some species, there is currently little information available regarding winter territoriality, so the notes in Table 3 in Appendix combine documented information (Poole 2005) with some speculation from our field observations. Because North-central Florida is a transitional zone in which sedentary and migratory races of a single species can co-occur in winter, we suspect that territoriality may be even more complex than we have outlined, both within and across species.

In looking at territoriality of species in the different groups (Regular Associate, Occasional Associate, and Non-joiner/Accidental), some general patterns emerge. Titmice defend an all-purpose territory as a conspecific group (Grubb and Pravosudov 1994). Since other birds seek out the Passive Nuclear titmice to flock with, it seems likely that the territory of the ETTI group may essentially be coincident with the mixed-species flock territory. When the Regular Associates are separated into high and low abundance species (Fig. 1, Nodes 75 and 74, respectively), the high-abundance Regular Associates are all intraspecifically gregarious (note, Table 1), and either have no territories (RCKI), or have a home range that is not actively defended (BGGN, PIWA). Gnatcatchers are described as holding home ranges as a male/female pair, but more than two individuals were often found within an MSF at one time, suggesting that presence of a flock may temporarily cause abandonment of their home range in order to participate.

Members of the low-abundance Regular Associate (Fig. 1, Node 74) sub-group tend to be more actively territorial. Except for CACH, which defend an all-purpose territory as a conspecific group like titmice, none of these species allow conspecifics into their winter territory, although they may tolerate a member of the opposite sex. This territorial nature makes them unlikely to be found in high abundances or densities, reducing the number of flocks they may occur in. For example, some evidence suggests that black-and-white warblers (BAWW) consider MSFs as moving foraging territories, and defend their flock membership against conspecifics (Rappole and Warner 1980). Other flocking species are known to engage in similar agonistic behaviors both within and/or between species (Morse 1970; Gaddis 1983; Ewert and Askins 1991; Latta and Wunderle 1996), which may further reduce flock participation for some species. Such a pattern is well-documented in permanent Neotropical flocks containing territorial species, where flock participation by any one species is

limited to a single individual, mated pair, or family group due to agonistic behaviors (Munn and Terborgh 1979; Powell 1979). As species such as BAWW and Yellow-throated Warblers (YTWA) were almost never found outside of flocks (Table 1), MSFs may be critical to their winter survival. Studies in which only the MSF is followed and flocking propensity is determined largely by the percentage of MSFs in which a species occurs may categorize some of these species as Occasional Associates or Non-joiner/Accidentals due to the relatively low occurrence in flocks (Gram 1998; Buskirk et al. 1972). Our methods account for this potentially serious problem; misidentification of flocking propensity for a rare species could limit understanding of its rarity (Hannon et al. 2004; Cao et al. 2001; McCoy and Mushinsky 1992; Rabinowicz et al. 1986).

Those four species we categorized as Occasional Associates (Fig. 1, Node 5) are mostly solitary territory-holders with a larger body size (20–60 g) and different foraging tactics than Regular Associates. RBWO probe and peck trees for insects, and YBSA drill “wells” into trees to collect sap and insects, and defend these created food resources. Both of these behaviors could account for them lagging behind flocks even if they were more or less following along. Both of these species are active participants in ETTI-generated mobbing aggregations (Sieving et al. 2004), and in our experience are quick to investigate flocks that become noisy (as when alarm calls are given)—suggesting they are usually not far away from flocks. We found little information in the literature regarding winter territoriality in the EAPH, except that they are typically solitary even when breeding and are known to sing occasionally in winter; specific winter data is notably lacking for this species. Rarely was more than one EAPH seen with any flock (Table 1), and “intruding” Phoebes were often vigorously pursued with much vocalization, as they do in the breeding season. This suggests they are likely territorial against conspecifics in winter as well, but as they often followed a flock for quite some time, it may or may not be fixed in space. GRCA hold exclusive all-purpose territories in winter, and are decidedly secretive in their movements in the understory, though, like the two woodpeckers (discussed above), Catbirds often investigate intrusions by human observers or alarm-calling within flocking aggregations (Sieving et al. 2004). They are likely to be more abundant than our observations suggest, but they are generally silent, reluctant to venture into the open, and are difficult to detect (E. Farley and T. Contreras, personal observation), all behaviors which would limit their participation in the highly conspicuous mixed-species flocks. More confident classification and understanding of these species’ flocking propensity will require more study.

The Non-joiner/Accidental species at first glance seem to have little in common with each other, coming from many families and possessing different habits. However, nearly all of them either hold all-purpose or foraging territories in winter, exclusively [EATO, HETH, Red-headed Woodpeckers (RHWO); Brown et al. 2000] or as a mated pair [CARW, NOCA, Pileated Woodpeckers (PIWO)], or have no territories at all (AMRO, AMGO, MYWA). Only Blue Jays (BLJA) do not have a defended territory, but conspecific groups do have home ranges. Of those species with territories, all except the Hermit Thrush are year-round residents. Species not having territories are all highly intraspecifically gregarious, abundant, and nearly ubiquitous winter residents with nomadic habits. All of the birds in the Non-joiner/Accidental group may forage in the same direction as the flock for a brief period when it “surrounds” them, but are unlikely to be participating in the flock the way Regular or Occasional Associates do. Many of these species do respond to and join mobbing aggregations (Sieving et al. 2004), however, and so may approach a flock or follow when a flock is noisy or engaged in mobbing. We noted this is especially true for BLJA. As for the two remaining woodpeckers, PIWO are very large, slow foragers with home ranges roughly 3–40 times larger than the area used by mixed-species flocks. RHWO are typically more restricted in habitat (favoring pine-dominated communities) and cache their food, aggressively and vociferously defending their caches from conspecifics and sometimes other species.

In summary, it appears that both non-territoriality and individual (family) territoriality may be correlated with high levels of flock participation. To fully understand these relationships, however, it is clear that the factors affecting territoriality must also be considered, namely, foraging behavior. Most of the Regular Associates are very similar in size and foraging tactics; both factors that limit participation in mixed-species foraging groups. Birds would not likely experience net gains by adjusting foraging to keep within a structured foraging aggregation dominated by species that forage in different strata at different rates or that do not share the same predators (Morse 1970; Munn and Terborgh 1979; Valburg 1992; Chen and Hsieh 2002; Hutto 1994; Latta and Wunderle 1996). However, serious threat of predation can force species with different foraging tactics together in mixed-species groups (Chapman and Chapman 2000).

Conclusions

The methods we developed for this study produced results comparable to those of studies utilizing more labor-intensive methods, yet better served our needs in several ways.

First, they dealt effectively with the variable nature of our study system. Our method accounted readily for variations in both abundance and the confounding of participation with mere presence in flocks. High abundance Non-joiners were identified appropriately as were low abundance species occurring in few flocks, but that were strongly associated with flocks. Therefore, our method is more objective at categorizing species' participation because it does not depend on the percentage of flocks within which a species is observed. That our method clearly identified similar groupings of species' participation to those obtained via much more labor-intensive methods was a beneficial result, suggesting that we did not sacrifice information by reducing effort (field time). Our literature review of winter territoriality in flocking species indicated that such information, in combination with foraging requirements and body sizes of species, may be sufficient to predict flocking propensity.

Finally, the large number of woodland birds associated to some degree with flocks suggests a high importance of MSFs to understanding the winter ecology of temperate forest birds. A significant proportion of non-terrestrial, small forest songbirds in the northern hemisphere join mixed-species foraging flocks in winter (Morse 1970; Hutto 1987, 1994; Gram 1998; King and Rappole 2001). Mixed-species flocks provide key benefits for participating individuals including protection from predation (Morse 1970; Gaddis 1980; MacDonald and Henderson 1977; King and Rappole 2001) and more efficient food-finding via reduced vigilance (Moynihan 1962; Morse 1970; Hutto 1994; Gram 1998; Chen and Hsieh 2002). Some potential costs are associated with participation in MSFs, e.g., the possibility of kleptoparasitism (Morse 1970; Cimprich and Grubb 1994), but, by and large, participation in winter MSFs may be essential for the survival of individuals of many species, especially those with relatively narrow foraging niches or those in harsh winter environs (Morse 1970; Vuilleumier 1967; Hutto 1987, 1994; Gram 1998; Gaddis 1979, 1983; Munn and Terborgh 1979; King and Rappole 2001; Rodewald and Brittingham 2002; Dolby and Grubb 1998). Methods presented here may serve in future studies of the nature and conservation of multi-species aggregations.

Zusammenfassung

Wir haben Stichprobenverfahren entwickelt, um die Beteiligung von Vogelarten an zur Nahrungssuche gebildeten und von östlichen Indianermeisen (*B. bicolor*) angeführten Trupps in Nord-Zentralflorida im Winter zu charakterisierung, da Standardfeldmethoden, die in erster

Linie für permanent standorttreue neotropische Trupps entwickelt wurden, in unserem System schlecht anwendbar waren. Im Januar und Februar 2004 sowie von November 2004 bis März 2005 haben wir 55 gemischte Trupps beobachtet und 40 potentiell truppbildende Arten erfasst (im Mittel 12,4 Arten (SD = 3,8; Bereich 3-20), 26,3 Individuen (SD = 12,2; Bereich 8-60), und 3,1 Meisen (SD = 1,4; Bereich 1-7) pro Trupp). Sechszwanzig Arten wurden häufig genug beobachtet (>10% der Beobachtungen), um sie in die Analysen einzuschließen. Wir haben 60-minütige Truppbeobachtungen mit zehnmütigen Punktzählungen kombiniert, die an Orten durchgeführt wurden, die von Trupps aufgesucht wurden, aber erfolgten, nachdem die Trupps sich bereits mehr als 100 m entfernt hatten. Diese Methode erbrachte für jede Art ein Maß für die Neigung zur Truppbildung (das Verhältnis der Anzahl Individuen, die im Trupp beobachtet wurden, zu denen, die während der Punktzählung erfasst wurden). Wir haben Regressionsbaumanalysen verwendet, um Arten nach dem Grad ihrer Beteiligung an Trupps in Gruppen zusammenzufassen sowie Beziehungen zwischen der Truppbildungsneigung und verschiedenen von uns gemessenen Umwelt- und sozialen Parametern zu untersuchen. Unsere Analyse identifizierte drei eindeutige Artgruppen; "Kernmitglied/reguläres Mitglied" (12 Arten; hohe/mittlere Truppbildungsneigung), "gelegentliches Mitglied" (4 Arten; mittlere/niedrige Truppbildungsneigung) und "Nicht-Mitglied/versehentliches Mitglied" (10 Arten; niedrige/keine Truppbildungsneigung). Die Gruppierungen waren vergleichbar mit Modellen, die durch zeitintensivere Feldmethoden gewonnen wurden. Um die Gruppierungskategorien im Zusammenhang zu erfassen, haben wir für unsere Untersuchungsarten eine Bewertung von Definitionen truppbildender Gruppen und relevanter autökologischer Information (z.B. zwischenartliche Vergesellschaftung) durchgeführt. Wir fanden diese Methode hilfreich, um die Beteiligung von Arten an gemischten Trupps geographisch umfassend zu beproben, trotz hoher Variabilität zwischen Trupps in der Artzusammensetzung und begrenztem Arbeitsaufwand.

Acknowledgments Funding for this study was provided through a grant from the University of Florida University Scholars Program to E.A.F. and an NSF Postdoctoral Fellowship to T.A.C. (DBI# 0309753). We also thank the Sieving lab, F. Bairlein, and anonymous reviewers for comments on previous drafts of this manuscript. This study was performed in compliance with all American laws and follows the *Guidelines to the Use of Wild Birds in Research* published by The Ornithological Council (Gaunt and Oring 1999).

Appendix

Table 3

Table 3 All species observed (listed alphabetically by species code) in January–February 2004 and November 2004–March 2005; their residency status in North-central Florida; their territoriality in winter; and the earliest and latest dates they were observed in this study

Species code ^a	Common name	Scientific name	Residency ^b	Winter territoriality ^c	Day and month observed	
					Earliest	Latest
AMCR ¹	American Crow	<i>Corvus brachyrhynchos</i>	Y	–	18 November	12 January
AMGO	American Goldfinch	<i>Carduelis tristis</i>	W	N	22 November	2 March
AMKE ¹	American Kestrel	<i>Falco sparverius</i>	Y	–	8 December	8 December
AMRO	American Robin	<i>Turdus migratorius</i>	W	N/F	18 November	2 March
BAOR ²	Baltimore Oriole	<i>Icterus galbula</i>	W	N	9 February	9 February
BAWW	Black-and-white Warbler	<i>Mniotilta varia</i>	W	Sx	18 November	24 February
BGGN	Blue-gray Gnatcatcher	<i>Poliophtila caerulea</i>	Y	Hp?	18 November	2 March
BHVI	Blue-headed Vireo	<i>Vireo solitarius</i>	W	Ax?	18 November	1 March
BLJA	Blue Jay	<i>Cyanocitta cristata</i>	Y	Hg	18 November	2 March
BLVU ¹	Black Vulture	<i>Coragyps atratus</i>	Y	–	9 February	12 February
BRTH ²	Brown Thrasher	<i>Toxostoma rufum</i>	Y	A	18 November	18 November
CACH	Carolina Chickadee	<i>Poecile carolinensis</i>	Y	Ag	18 November	19 February
CARW	Carolina Wren	<i>Thryothorus ludovicianus</i>	Y	Ap	18 November	2 March
CEWA ²	Cedar Waxwing	<i>Bombycilla cedrorum</i>	W	N	4 January	4 February
CHSP	Chipping Sparrow	<i>Spizella passerina</i>	W	N	22 November	1 March
COYE ²	Common Yellowthroat	<i>Geothlypis trichas</i>	Y	A?/N?	11 January	11 January
DOWO	Downy Woodpecker	<i>Picoides pubescens</i>	Y	Sr	18 November	2 March
EABL ²	Eastern Bluebird	<i>Sialia sialis</i>	Y	Ag/Fg	22 November	24 November
EAPH	Eastern Phoebe	<i>Sayornis phoebe</i>	W	A?x/F?x	18 November	2 March
EATO	Eastern Towhee	<i>Pipilio erythrophthalmus</i>	Y	A?x?/S?x?	18 November	2 March
ETTI	Eastern Tufted Titmouse	<i>Baeolophus bicolor</i>	Y	Ag	18 November	2 March
GRCA	Gray Catbird	<i>Dumetella carolinensis</i>	Y	Ax	18 November	4 February
GREG ¹	Great Egret	<i>Ardea alba</i>	Y	–	12 December	12 December
HAWO ²	Hairy Woodpecker	<i>Picoides villosus</i>	Y	Ap/Ax	3 February	3 February
HETH	Hermit Thrush	<i>Catharus guttatus</i>	W	Ax	18 November	1 March
HOFI ²	House Finch	<i>Carpodacus mexicanus</i>	Y	N?	9 February	9 February
HOWR ²	House Wren	<i>Troglodytes aedon</i>	W	A?x?	18 November	9 January
LOSH ¹	Loggerhead Shrike	<i>Lanius ludovicianus</i>	Y	–	12 December	12 December
MODO ²	Mourning Dove	<i>Zenaida macroura</i>	Y	Ap?	24 November	11 February
MYWA	Yellow-rumped “Myrtle” Warbler	<i>Dendroica coronata</i>	W	N/F	18 November	2 March
NOCA	Northern Cardinal	<i>Cardinalis cardinalis</i>	Y	Ap	18 November	2 March
NOMO	Northern Mockingbird	<i>Mimus polyglottos</i>	Y	Ap/Ax	22 November	8 December
NOPA ²	Northern Parula	<i>Parula americana</i>	S	N?	1 March	1 March
OCWA ²	Orange-crowned Warbler	<i>Vermivora celata</i>	W	N	18 November	19 February
OSPR ¹	Osprey	<i>Pandion haliaetus</i>	Y	–	19 February	19 February
OVEN ²	Ovenbird	<i>Seiurus aurocapillus</i>	W	A?x?	20 December	21 January
PIWA	Pine Warbler	<i>Dendroica pinus</i>	Y	H?g	18 November	2 March
PIWO	Pileated Woodpecker	<i>Dryocopus pileatus</i>	Y	Ap	18 November	11 January
PRAW ²	Prairie Warbler	<i>Dendroica discolor</i>	W	N?/H?/A?	18 November	18 January
RBWO	Red-bellied Woodpecker	<i>Melanerpes carolinus</i>	Y	Ap	18 November	2 March
RCKI	Ruby-crowned Kinglet	<i>Regulus calendula</i>	W	N/Ax	18 November	2 March
RHOW	Red-headed Woodpecker	<i>Melanerpes erythrocephalus</i>	Y	Fx?	18 November	20 January
RSHA ¹	Red-shouldered Hawk	<i>Buteo lineatus</i>	Y	–	22 November	2 March
RTHA ¹	Red-tailed Hawk	<i>Buteo jamaicensis</i>	Y	–	12 February	12 February
TRES ¹	Tree Swallow	<i>Tachycineta bicolor</i>	W	–	18 November	10 February
TUVU ¹	Turkey Vulture	<i>Cathartes aura</i>	Y	–	22 November	19 February

Table 3 continued

Species code ^a	Common name	Scientific name	Residency ^b	Winter territoriality ^c	Day and month observed	
					Earliest	Latest
UNGU ¹	Unidentified gull	<i>Larus</i> spp.	W	–	11 January	11 January
WEVI	White-eyed Vireo	<i>Vireo griseus</i>	Y	A?r?	22 November	2 March
WITU ¹	Wild Turkey	<i>Meleagris gallopavo</i>	Y	–	19 February	19 February
WODU ¹	Wood Duck	<i>Aix sponsa</i>	Y	–	18 November	6 January
YBSA	Yellow-bellied Sapsucker	<i>Sphyrapicus varius</i>	W	Fx?	18 November	24 February
YPWA ^d	Palm Warbler	<i>Dendroica palmarum</i>	W	N/F	18 November	2 March
YSFL ²	Northern “Yellow-shafted” Flicker	<i>Colaptes auratus</i>	Y	Hx?/A?x?	22 November	20 January
YTVI ²	Yellow-throated Vireo	<i>Vireo flavifrons</i>	S	A?x?	2 March	2 March
YTWA	Yellow-throated Warbler	<i>Dendroica dominica</i>	Y	N/S?x?	18 November	1 March

Residency status is based on Florida Breeding Bird Atlas data (Kale et al. 1992). Winter territoriality designations are based on information from The Birds of North America Online (Poole 2005)

^a Species excluded from analyses because: 1 = not considered to be a potential flock participant, 2 = observed on <6 (~10%) of observation occasions

^b Y Year-round resident (not necessarily the same individuals as breeding season), W =winter/non-breeding season only, S = summer/breeding season only

^c A dash (–) indicates territoriality not relevant since the species was not considered to be a potential flock participant; A slash (/) between two letters indicates there is evidence in the literature for both types of territorial behavior, and a question mark (?) indicates we suspect this territorial behavior may occur in our area based on literature and field observations, but the literature is inconclusive or insufficient. Territory types: N no established territory or home range, H established home range, but no defended territory, A all-purpose territory, F foraging territory/defends specific food resource, S defends space around itself, not tied to a set place. Territory type modifiers: p territory/home range held by a mated pair, g territory/home range held by a group of conspecifics, x excludes all conspecifics, r excludes conspecifics of same gender

^d While this code officially refers to the eastern “Yellow” *D. p. hypochrysea* subspecies, we used it to denote any Palm Warbler, regardless of subspecies (both the “Western” *D. p. palmarum* and “Yellow” subspecies regularly occur in north Florida in winter, and are sometimes difficult to differentiate quickly and reliably in the field)

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