Composition of mixed-species flocks of migrant and resident birds in Cuba

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La Chillina *Teretistris fernandinae* y el Pechero *T. fornsi* constituyen un género endémico de aves cubanas que se caracterizan por su comportamiento de bandadas. Durante el período de invierno ciertas especies migratorias y residentes se unen a éstas especies para formar bandadas mixtas. En este trabajo documentamos el número de especies y enumeramos el total de individuos en 230 bandadas mixtas en bosques manejados del oeste de Cuba y en matorral costero del norte de la isla. Documentamos un total de 30 especies residentes y 26 especies migratorias en bandadas. Nuestros resultados resaltan la importancia que juegan las dos especies de *Teretistris* en las bandadas mixtas en Cuba. También documentamos que la participación de especies residentes es menor que la de migratorias en las bandadas mixtas. El fenómeno de bandadas mixtas es un componente importante del ciclo anual para especies migratorias, en especial los parúlidos.

Mixed-species flocks are common and obvious in Neotropical habitats. In the Caribbean islands flocks have been noted on Puerto Rico[2,5,24,29], Jamaica[4], Haiti[20], in the Dominican Republic[18], the Virgin Islands[7] and on Cuba[6,16]. Unlike other islands, however, such flocks have not been described in detail for Cuba. One previous report treated mixed-species flocks of migratory wood warblers in Cuba[16].

Cuba is an important wintering area for Nearctic–Neotropical migrant birds (hereafter 'migrants')[11,16,30,31]. With 50% of the total land area in the Caribbean, the island offers the largest wintering area for migrants. Cuban avifauna contains 24 endemic species[10], two of which, Yellow-headed Warbler *Teretistris fernandinae* and Oriente Warbler *T. fornsi*, appear to be species around which mixed-species flocks often form. The behavioural ecology of these species has been little studied[9,26], and their taxonomic relations to wood warblers (Parulidae) are also uncertain[19]. Eaton[6] did not recognise *Teretistris* spp. as flock associates. Our objectives here are to: document the composition of mixed-species flocks in Cuba; describe the contribution of migratory and resident birds to flock composition; and to assess associations among species within flocks.

Methods

Study areas

We studied flocks in Ciego de Ávila province, on the north coast of Cuba, in Matanzas province, in the south, and noted their presence in Pinar del Río province, in the west (Fig. 1). Kirkconnell counted flocks at study sites on Cayo Coco, Ciego de Ávila province. He also tallied flocks at several localities in the Península de Zapata, Matanzas province: at Bermejas, El Ojo del Roble, Guamá, Los Lechuzos, Los Sábalos, Mera, Playa Larga and Santo Tomás; and he gathered data on composition of flocks at La Güira and La Majagua, Pinar del Río province, in western Cuba.

Hamel and colleagues counted flocks at study sites in the Península de Zapata, Matanzas province: at Bermejas, Caleta Buena, Caleta del Toro, Camilo, El Cenote, El Brinco, El Ojo del Roble, La Salina, Lindero, Linea de Quintela, Los Canales, Los Gallegos, Los Lechuzos, Los Sábalos, Mera, Placencia and Santo Tomás.

Habitats

We studied flocks in several habitats, including mixed woodland and pastureland, xeric semi-deciduous forest, mesic semi-deciduous forest, moist semi-deciduous forest transitional to freshwater mangrove forest, mangrove forest, and coastal scrub. Brief observations in Pinar del Río province included also montane mixed pine–semi-deciduous forest. Habitats in the localities are described in González Alonso *et al.*[11], McNicholl[21]

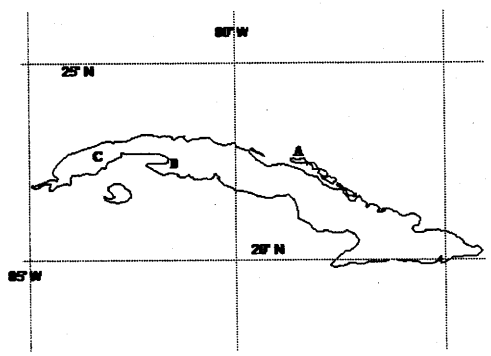

Figure 1. Location of study areas of mixed-species flocks in Cuba: A—Cayo Coco, Ciego de Ávila province; B—Península de Zapata, Matanzas province; C—La Guira, Pinar del Río province.

Table 1. Composition of 230 mixed-species flocks of birds in Cuba.

		Province and Sample size		
		Ciego de Ávila 26 flocks	Matanzas 202 flocks	Pinar del Río 2 flocks
Species		Mean number of birds/flock ± s.e., number of flocks		
American Kestrel	*Falco sparverius*	-	1 , n=1	-
White-crowned Pigeon	*Patagioenas leucocephala*	1.5±0.29, n=4	-	-
White-winged Dove	*Zenaida asiatica*	-	1 , n=1	-
Common Ground-dove	*Columbina passerina*	1±0, n=2	-	-
Cuban Parrot	*Amazona leucocephala*	-	1 , n=1	-
Great Lizard-cuckoo	*Saurothera merlini*	2 , n=1	2 , n=1	-
Cuban Pygmy-owl	*Glaucidium siju*	-	1±0, n=2	-
Cuban Emerald	*Chlorostilbon ricordii*	-	1.07±0.07, n=15	1 , n=1
Cuban Trogon	*Priotelus temnurus*	-	1.17±0.11, n=12	1 , n=1
Cuban Tody	*Todus multicolor*	1.75±0.48, n=4	1.06±0.06, n=17	-
Yellow-bellied Sapsucker	*Sphyrapicus varius*	1 , n=1	1±0, n=4	-
Cuban Green Woodpecker	*Xiphidiopicus percussus*	1.67±0.33, n=3	1±0, n=7	-
Northern Flicker	*Colaptes auratus*	-	1 , n=1	-
Cuban Pewee	*Contopus caribaeus*	1±0, n=3	1.03±0.03, n=35	-
La Sagra's Flycatcher	*Myiarchus sagrae*	1±0, n=3	1.37±0.09, n=30	1 , n=1
Loggerhead Kingbird	*Tyrannus caudifasciatus*	1.5±0.5, n=2	1.17±0.11, n=12	-
Blue-grey Gnatcatcher	*Polioptila caerulea*	-	1.45±0.09, n=92	-
Cuban Gnatcatcher	*Polioptila lembeyei*	1±0, n=2	-	-
Red-legged Thrush	*Turdus plumbeus*	1.33±0.33, n=3	1.3±0.3, n=10	1 , n=1
Grey Catbird	*Dumetella carolinensis*	1 , n=1	1.08±0.08, n=12	-
Northern Mockingbird	*Mimus polyglottos*	1 , n=1	1 , n=1	-
White-eyed Vireo	*Vireo griseus*	-	1±0, n=2	-
Cuban Vireo	*Vireo gundlachii*	1±0, n=2	1.2±0.06, n=50	-
Yellow-throated Vireo	*Vireo flavifrons*	-	1.14±0.14, n=7	-
Black-whiskered Vireo	*Vireo altiloquus*	1±0, n=2	1.14±0.14, n=7	2 , n=1
Blue-winged Warbler	*Vermivora pinus*	1 , n=1	1±0, n=2	-
Northern Parula	*Parula americana*	1.33±0.33, n=3	2.59±0.22, n=128	2±1, n=2
Yellow Warbler	*Dendroica petechia gundlachi*	-	1.67±0.67, n=3	-
Magnolia Warbler	*Dendroica magnolia*	1 , n=1	1.06±0.04, n=34	-
Cape May Warbler	*Dendroica tigrina*	1.67±0.33, n=3	1.1±0.1, n=10	-
Black-throated Blue Warbler	*Dendroica caerulescens*	1±0, n=5	1.16±0.06, n=56	1 , n=1
Black-throated Green Warbler	*Dendroica virens*	-	1.18±0.1, n=17	1 , n=1
Blackburnian Warbler	*Dendroica fusca*	-	1 , n=1	-
Yellow-throated Warbler	*Dendroica dominica*	1.5±0.5, n=2	1±0, n=8	-
Olive-capped Warbler	*Dendroica pityophila*	-	-	1 , n=1
Prairie Warbler	*Dendroica discolor*	1.5±0.5, n=2	1.12±0.07, n=41	-
Palm Warbler	*Dendroica palmarum*	2.4±0.51, n=5	3.5±0.73, n=22	3±0, n=2
Black-and-white Warbler	*Mniotilta varia*	1±0, n=4	1.37±0.09, n=87	1 , n=1
American Redstart	*Setophaga ruticilla*	1±0, n=3	1.26±0.06, n=96	-
Worm-eating Warbler	*Helmitheros vermivorum*	1±0, n=2	1±0, n=20	1 , n=1
Swainson's Warbler	*Limnothlypis swainsonii*	1 , n=1	-	-
Ovenbird	*Seiurus aurocapillus*	1±0, n=4	1±0, n=10	-
Northern Waterthrush	*Seiurus noveboracensis*	1 , n=1	1.8±0.37, n=5	-
Louisiana Waterthrush	*Seiurus motacilla*	-	2±1, n=2	-
Common Yellowthroat	*Geothlypis trichas*	1±0, n=2	1.4±0.17, n=25	-
Yellow-headed Warbler	*Teretistris fernandinae*	-	3.22±0.13, n=166	3 , n=1
Oriente Warbler	*Teretistris fornsi*	2.55±0.45, n=11	-	-
Hooded Warbler	*Wilsonia citrina*	-	1±0, n=4	-
Wilson's Warbler	*Wilsonia pusilla*	-	1 , n=1	-
Red-legged Honeycreeper	*Cyanerpes cyaneus*	-	1 , n=1	-
Western Spindalis	*Spindalis zena*	1.83±0.4, n=6	1±0, n=10	-
Cuban Bullfinch	*Melopyrrha nigra*	1.67±0.33, n=3	1.63±0.27, n=19	-
Yellow-faced Grassquit	*Tiaris olivacea*	1 , n=1	2.08±0.45, n=12	-
Tawny-shouldered Blackbird	*Agelaius humeralis*	-	4 , n=1	-
Greater Antillean Grackle	*Quiscalus niger*	1±0, n=2	2.5±0.5, n=2	-
Greater Antillean Oriole	*Icterus dominicensis*	-	1.33±0.12, n=24	-
Total Species	56	35	50	13
Mean flock size, species	5.38±0.2, n=230	3.69±0.29, n=26	5.58±0.22, n=202	7.5±2.5, n=2
Mean flock size, individuals	9.26±0.38, n=230	5.46±0.49, n=26	9.73±0.41, n=202	12±1, n=2

and Wallace *et al.*[31]. Briefly, they can be characterised as a wide variety of native, primarily second-growth forests, grazed native forests and some highly modified habitats in the vicinity of tourist resorts and inhabited areas. Prominent tree species in most localities included *Bucida burseras*, *Bursera simaruba* and *Lysiloma latisiliquum*; *Ceiba pentandra*, *Conocarpus erecta* and *Sabal parviflora* were also noticeable, among a variety of other species. Stature of the vegetation in these localities was usually less than 20 m.

Field methods

We observed mixed-species flocks while walking trails and transects, both specifically searching for flocks, and as supplementary observations during other work[11]. Observations were made primarily during the boreal winter when migrants are present on Cuba, in January 1987–89 and 1992, February 1989, 1991, 1992, and March 1989. Additional observations were made in September 1988 and April 1989. Upon encountering a flock, we followed it and observed as many constituents as possible[13]. We recorded numbers of individuals, by age and sex when possible, of each species encountered. Individuals within c.20 m of other birds were considered to be within a flock, thus our tallies indicate both active and passive participants.

Because we concentrated on flocks, we did not systematically record the occurrence of solitary individuals of *Teretistris* spp., or of other species. Our data are thus useful as a characterisation of obvious flocks, but not necessarily a characterisation of the tendency of each species to flock. To assess the latter, we compared the frequency of occurrence of species in flocks with that in point counts[15] made at the same study site, at Los Sábalos in the Ciénaga de Zapata, Matanzas province[11].

Statistical analysis

Flock composition. We summarised information on the size and species composition of flocks and the frequency of occurrence and abundance of each species within flocks. We conducted correlation analyses of abundance of the most frequent species, χ^2 contingency table analyses of occurrence of less frequent species in relation to more abundant species.

Occurrence on point counts vs flocks. Sufficient numbers of point counts[15] for statistical comparison of flock participation with occurrence on point

Table 2. Significant associations among species in mixed-species flocks in Cuba, after Bonferroni correction. Associations determined between abundance of individuals recorded in 230 flocks, measured by *r*, and frequency of occurrence in flocks, measured by χ^2_1 from 2 ↔ 2 contingency table. Values reported are those whose $P<0.0002$ for abundance and $P<0.0003$ for frequency of occurrence.

Species	Associates[a]	*r*	χ^2_1
Dumetella carolinensis	*Vireo altiloquus*	0.28	ns
Polioptila caerulea	*Contopus caribaeus*	ns	12.7
	Dendroica magnolia	ns	15.5
	Dendroica caerulescens	ns	18.1
Parula americana	*Polioptila caerulea*	0.40	24.8
	Mniotilta varia	0.47	18.4
	Setophaga ruticilla	0.26	ns
Setophaga ruticilla	*Polioptila caerulea*	0.24	ns
	Vireo gundlachii	ns	15.5
	Dendroica discolor	0.30	ns
Helmitheros vermivorus	*Dendroica caerulescens*	0.24	12.3
	Mniotilta varia	0.35	16.4
	Icterus dominicensis	ns	17.1
Teretistris fernandinae	*Polioptila caerulea*	ns	13.1
	Parula americana	0.32	17.6
	(Dendroica palmarum)	ns	(45.0)
	Mniotilta varia	0.30	ns
	Setophaga ruticilla	0.28	19.7
Teretistris fornsi	*Xiphidiopicus percussus*	0.28	ns
Icterus dominicensis	*Chlorostilbon ricordii*	0.27	ns
	Priotelus temnurus	0.24	ns
	Dendroica magnolia	ns	15.5
	Dendroica discolor	ns	13.9

[a] Parentheses indicate that the relationship between these species is negative, suggesting disassociation.

counts were taken only in semi-deciduous forest on karst substrate at Los Sábalos, Matanzas province[11]. We used χ^2 contingency table analysis to compare the relative frequency of species in flocks with their relative frequency on point counts at Los Sábalos.

All analyses were undertaken using procedures in SAS[28]. Results are presented as ± SE. We accepted statistical significance at P=0.05, after Bonferroni correction to account for the often large number of simultaneous comparisons used.

Results

We recorded 56 species in at least one flock. Of these, 30 were Cuban resident species, six were Cuban endemics and 11 were represented by endemic Cuban subspecies. Among 26 migratory species were 25 Nearctic breeders that visit Cuba in winter and Black-whiskered Vireo *Vireo altiloquus*, a Neotropical species which breeds in Cuba and winters to the south.

We observed a total 230 flocks (Table 1) comprising 2,129 birds. Kirkconnell tallied 74 flocks, including all those in Ciego de Ávila (n=26) and Pinar del Río provinces (n=2). Hamel and colleagues counted 156 flocks in Matanzas province. Mean flock size was 9.3 ± 0.4 birds (range 2–31) of 5.4 ± 0.2 species (range 1–14).

Flocks were observed during all daylight hours and all months. Flock size did not vary according to time of day (Fig. 2; Kruskall-Wallis test for number of species, χ^2=12.9, 11 d.f., P=0.30; Kruskall-Wallis test for number of birds/flock, χ^2=7.9, 11 d.f., P=0.72).

Flock composition

T. fernandinae was the most abundant and most frequent species encountered, with 537 individuals encountered in 167 (82%) of 204 flocks observed in its range, and a mean 3.2 ± 0.13 birds per flock (range 1–10). *T. fornsi* could only have been encountered in 26 flocks tallied within the species' range, at Cayo Coco, Ciego de Ávila province, where 28 individuals were observed in 11 flocks (42%), with a mean 2.5 ± 0.45 birds per flock (range 1–6). The combined occurrence of *Teretistris* spp. included 565 individuals in 178 (77%) of 230 flocks (Fig. 3). The mean number of *Teretistris* spp. was 3.1 ± 0.12 birds per flock when present. The proportion of all individuals observed in flocks that were either of these two species was 0.27.

On average, flocks included 6.8 ± 0.34 individuals of 4.6 ± 0.19 species other than *Teretistris* spp. Wood warblers are a major component of the migrant avifauna on Cuba, and 26 species appear in our dataset. Excluding *T. fernandinae* and *T. fornsi* (the only warbler species in 18 flocks), at least one wood warbler species was found in each of 210 of the 230 mixed-species flocks recorded. On average, those 210 flocks included 4.7 ± 0.27 warblers of 3.0 ± 0.12 species other than *Teretistris* spp.

Participation by resident and migrant species in flocks

Resident birds were observed in 219 flocks (95%). The mean number of residents was 4.4 ± 0.18 per flock, of 2.2 ± 0.08 species including *Teretistris* spp. Thus the average flock included 1.5 individuals of a single resident species additional to *Teretistris* spp.

Table 3. Comparison of species occurrence in flocks with occurrence on point counts at Los Sábalos, Matanzas province, Cuba. Species are included for which a combined total of 19 individuals was recorded on 34 point counts and 34 randomly selected flocks[1].

Species	χ^2_1	$P > \chi^2_1$
Group A. Species equally frequent in flocks and in point counts		
Dumetella carolinensis	3.06	0.08
Polioptila caerulea	2.43	0.12
Dendroica magnolia	0.03	0.87
Dendroica virens	0.98	0.32
Dendroica dominica	0.22	0.64
Setophaga ruticilla	2.62	0.11
Seiurus aurocapillus	0.80	0.37
Melopyrrha nigra	0.03	0.86
Tiaris olivacea	2.81	0.09
Unidentified woodpecker	2.36	0.12
Group B. Species more frequent in flocks than in counts		
Parula americana	21.38	0.000
Dendroica caerulescens	5.50	0.02
Dendroica discolor	6.80	0.01
Mniotilta varia	13.98	0.000
Teretistris fernandinae	13.89	0.000
Group C. Species more frequent in counts than in flocks		
Glaucidium siju	54.42	0.000
Todus multicolor	30.53	0.000
Priotelus temnurus	22.95	0.000
Chlorostilbon ricordii	18.54	0.000
Xiphidiopicus percussus	3.85	0.05
Sphyrapicus varius	5.83	0.02
Contopus caribaeus	44.33	0.000
Tyrannus melancholicus	25.07	0.000
Myiarchus sagrae	36.45	0.000
Turdus plumbeus	45.17	0.000
Vireo gundlachii	8.91	0.003
Dendroica palmarum	6.87	0.01
Geothlypis trichas	8.64	0.003
Spindalis zena	3.85	0.05
Icterus dominicensis	9.15	0.002

[1] Species uniquely found on point counts include *Fulica americana*, *Falco sparverius*, *Buteo platypterus*, *Bubulcus ibis*, *Columbina passerina*, *Gallinula chloropus* and *Dives atroviolacea*.

Species uniquely found in flocks include *Dendroica tigrina*, *Wilsonia citrina* and *Helmitheros vermivorum*.

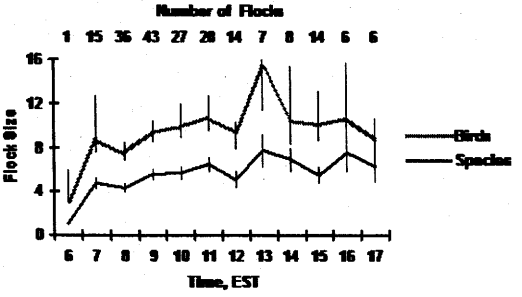

Figure 2. Occurrence of mixed-species flocks in Cuban habitats, by time of day.

Migrants were observed in 215 flocks (91%). The mean number of migrants was 5.4 ± 0.30 individuals per flock, of 3.5 ± 0.14 species.

Occurrence of individual species in flocks

Product-moment correlation and χ^2 contingency table analysis of the occurrence and abundance of 31 species that occurred in at least ten of 230 fully inventoried flocks indicated a number of strong associations between species. The number of associations where $P<0.05$ (97 of 357 pairwise comparisons of frequency; 88 of 465 pairwise comparisons of abundance) is far larger than that expected by chance, indicating that at least some species associate with each other in flocks (Table 2). Very few associations were negative. Frequency of occurrence of *T. fernandinae* and *D. palmarum* did indicate a significant disassociation (Table 2).

Occurrence of species in flocks was compared to that on point counts made in the same habitat at Los Sábalos, Matanzas province[11]. Sufficient data (19 occurrences on points/flocks) were available to compare frequencies of occurrence for 29 species. Of these, 15 species occurred more frequently on point counts than in flocks, five species occurred more frequently in flocks than on point counts, and nine species occurred at indistinguishable frequency in flocks and on point counts (Table 3). Three species of Nearctic breeding migrants occurred only in the dataset from flocks, *Dendroica tigrina*, *Helmitheros vermivorum* and *Wilsonia citrina*. Seven other species were found only on point counts (Table 3). Species more likely to be found, or only found in flocks numbered seven migrant and one resident species, whilst residents outnumbered migrants 12 to 3 amongst birds more often recorded on point counts.

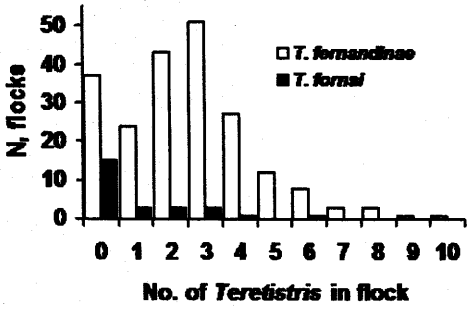

Figure 3. Frequency of group sizes of *Teretistris* spp. in mixed-species flocks observed in Cuba. In addition to sample of 230 mixed-species flocks, the occurrence of eight observations of unaccompanied single *T. fernandinae* is included.

Discussion

Clearly, *Teretistris* spp. are important participants in mixed-species flocks in Cuba. Most flocks in native forest habitats included at least one individual of one of these two species. Garrido[9] noted that they forage in a variety of ways. In this respect, as well as their flocking behaviour, they are reminiscent of mainland species of Paridae[1]. *T. fernandinae* is perhaps a more prominent member of mixed-species flocks than is *T. fornsi*. However, the small sample of flocks observed in the range of the latter species invites additional study of flocks of *T. fornsi*.

Cuban mixed-species flocks appear to be composed primarily of migrant birds in association with one or more individuals of *Teretistris* spp. Ewert & Askins[7] also noted that migrants comprised 91% of birds in 28 flocks they described in the US Virgin Islands. The much greater frequency of predators (*Glaucidium siju*) in point counts than in the vicinity of flocks suggests that flocks and their predators do not occur together. Ground-foraging birds, such as resident *Turdus plumbeus* and migratory *Seiurus* spp., are not common in flocks in Cuba, although they are in Puerto Rico (F. Vilella pers. comm.). *Seiurus aurocapillus* does associate with *Limnothlypis swainsonii*, another ground-foraging migrant[17]. Study of marked birds would assist in clarifying the question of the function of flocking in Cuban birds.

Resident species appear not to participate in mixed-species flocks to the same extent as migrants. Even such frequent flock associates as *Contopus caribaeus* and *Vireo gundlachii* occurred significantly more frequently on point counts than in flocks. The combination of these findings suggests to us that anti-predator functions may be a partial explanation for the formation of flocks by temporary residents[8,22], birds presumably less familiar with the locations and behaviour of predators in the winter grounds than are the permanent residents. Detection of predators is a difficult task, however (O. Garrido pers. comm.), reinforcing Chipley's[3] contention that predation

need not be conspicuous to be important. Without additional data on food resources and foraging behaviours of birds in and out of flocks, it is impossible to eliminate alternative explanations[12,14,23,25,27].

Our work is a first step to understanding the significance of mixed-species flocks in the Cuban avifauna. Mixed-species flocks, because they so prominently include migrants, are probably of great importance to the non-breeding biology of migrants in Cuba, particularly parulids. Further work on habitat associations, patterns of movements of flocks, changes in flock composition during different parts of the winter season, and differences in flock behaviour in the presence of various predators and predator abundance would be valuable.

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