WINTER FORAGING ECOLOGY OF MIXED INSECTIVOROUS BIRD FLOCKS IN OAK WOODLAND IN SOUTHERN ARIZONA

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The occurrence of mixed flocks of insectivorous birds during winter in north temperate regions is widely recognized (see Morse 1970 for references). However, there have been few attempts to quantify the interspecific relationships of members of foraging flocks. Most previous studies considered foraging behavior of members of the same genus during the breeding season (see Sturman 1968 for references), although Gibb (1954, 1960) discussed the foraging ecology of several species throughout the year, and Morse (1967a, b) studied the foraging ecology of unrelated species in summer and winter, respectively. Notably, Morse (1970) presented extensive data on foraging and interactions of mixed winter flock members in eastern North America.

In southern Arizona, several species of insectivorous birds winter in oak woodland (Lee and Yensen 1969; Smith and Horn 1969, 1970; Yensen and Lee 1970) and participate in mixed foraging flocks. The low density and stature of the vegetation provide an excellent opportunity to study foraging interactions of such mixed flocks. This study attempts to describe foraging niche, spatial relations, and behavior of the wintering, insectivorous, foliage-gleaning guild of birds of oak woodland in southern Arizona.

METHODS

Studies of flocks were conducted from September through December 1969 in Molino Basin, Santa Catalina Mountains, Pima County, Arizona (4400 ft). A few additional foraging observations were obtained in Bear Canyon (5600 ft). Data on flock composition were gathered in several areas. From January onward, mixed flocks in Molino Basin lose their integrity and there is evidence of prebreeding behavior. Flocks as considered here are foraging groups of birds bound together by intrinsic attraction between members, as defined by Morse (1970).

When a foraging flock was encountered, composition and spatial distribution were noted. Flocks were followed for as long as possible, or until they dispersed. Data on foraging behavior, movements, changes in flock composition, and other interactions were recorded. Composition changes were noted by counting the number of birds present in the flock at 10–15 min intervals. From these data it was possible to deter-

mine the per cent of time a species spent with a flock ("per cent flock time" in table 1). Overt aggressive interactions are expressed as number per foraging observation; no attempt was made to quantify subtle displacements.

Foraging behavior data, modified after Sturman (1968) were recorded as follows: (1) method of foraging (glean, hover, hawk, peck, probe); (2) foraging stance (upright or hang); (3) type and height of vegetation; (4) relative position in vegetation (as per cent from top and axis); (5) perch size; (6) surface character of perch and foraging surface; and (7) foraging surface (upper or lower). Each observation included these seven points.

Observations were taken as rapidly as possible in order to obtain a continuous record of the foraging activities of the flock as it moved through the area. This was greatly facilitated by the use of tape recorders. We do not feel that this method is likely to bias the data since those birds studied are very active foragers and rarely spend more than a few seconds at a particular foraging station. It also reduces the bias for conspicuous sites introduced by the standard observation technique (Hartley 1953).

Mean per cent difference is the average difference (in per cent) of all alternatives in each category. Diversity of foraging was calculated, using the information-theoretical measure (H') of Shannon and Weaver (1949) and the tables of Lloyd et al. (1968). These are expressed as evenness ($J' = H'/H'_{max}$). Maximum generalization occurs when all alternatives are equally utilized. The smaller the value of J', the greater the specialization in the use of the several recognized alternatives. Conversely, a tendency toward generalization is indicated by greater J' values (Pielou 1966). Data are treated statistically with chi square, with significance defined as the 0.05 level.

Vegetation density was determined for the portion of the study area where most foraging data were collected, using the point-centered quarter method of Cottam and Curtis (1956). In addition, for each plant sampled, measurements of crown diameter, depth, and shape were made, from which volume of vegetation was calculated.

STUDY AREA

The study area, within the evergreen oak woodland (Lowe 1964), is dominated by Emory and Mexican blue oaks (*Quercus emoryi* and *Q. oblongifolia*) with an understory of grasses, amole (*Agave schotti*), and several chaparral species, including manzanita (*Arctostaphylos pungens*), squawbush (*Rhus trilobata*), holly-leaf buckthorn (*Rhamnus californicus*), silktassel (*Garrya wrightii*) and wait-a-minute bush (*Mimosa biuncifera*). The oaks are distributed mainly along washes and on north-facing slopes. Stands of manzanita, amole, grasses and wait-a-minute bush

TABLE 1. Some characteristics of mixed flocks in Arizona oak woodland.

Species	First encounter		Total observations of flock		
	no. individuals in flock[a] ($\bar{x} \pm$ SD)	frequency of occurrence (% flocks)	no. individuals in flock[a] ($\bar{x} \pm$ SD)	frequency of occurrence (% flocks)	% flock time
Woodpeckers[b]	1.0 ± 0.0	14.8	1.6 ± 0.7	25.9	12.2
Bridled Titmouse	4.1 ± 1.6	88.8	4.3 ± 1.6	88.8	97.0
Common Bushtit	14.1 ± 5.0	44.4	15.5 ± 4.4	44.4	98.1
Verdin	1.3 ± 0.5	66.7	1.5 ± 0.6	88.8	63.8
White-breasted Nuthatch	1.0 ± 0.0	25.9	1.1 ± 0.3	29.6	48.1
Bewick's Wren	1.4 ± 0.6	63.0	1.6 ± 0.9	74.1	66.6
Other wrens[c]	2.2 ± 1.0	18.5	1.9 ± 0.9	29.6	36.5
Ruby-crowned Kinglet	1.5 ± 0.7	66.7	1.6 ± 0.6	81.5	74.9
Vireos[d]	1.0 ± 0.0	18.5	1.1 ± 0.3	37.0	72.7
Warblers[e]	3.0 ± 1.4	18.5	2.9 ± 1.7	33.3	40.4
Others[f]	3.5 ± 0.1	7.4	2.4 ± 1.7	18.5	33.3
Total flock	14.6 ± 9.0		17.6 ± 8.3		

[a] Only when species present.
[b] Red-shafted Flicker (*Colaptes cafer*), Yellow-bellied Sapsucker (*Sphyrapicus varius*), Ladder-backed Woodpecker (*Dendrocopos scalaris*), Arizona Woodpecker (*D. arizonae*).
[c] House Wren (*Troglodytes aedon*), Rock Wren (*Salpinctes obsoletus*).
[d] Hutton's Vireo (*Vireo huttoni*), Warbling Vireo (*V. gilvus*).
[e] Orange-crowned Warbler (*Vermivora celata*), Nashville Warbler (*V. ruficapilla*), Audubon's Warbler (*Dendroica auduboni*), Black-throated Gray Warbler (*D. nigrescens*), Townsend's Warbler (*D. townsendi*), Hermit Warbler (*D. occidentalis*), Wilson's Warbler (*Wilsonia pusilla*).
[f] Broad-tailed Hummingbird (*Selasphorus platycercus*), Western Flycatcher (*Empidonax difficilis*), Western Wood Pewee (*Contopus sordidulus*), Blue-gray Gnatcatcher (*Polioptila caerulea*), Scott's Oriole (*Icterus parisorum*), Hepatic Tanager (*Piranga flava*).

form a mosaic over much of the rest of the area. Relative volume of important plants is presented in figure 2.

RESULTS

FLOCK ORGANIZATION AND BEHAVIOR

Initially, flocks appear to have little structure, but on closer inspection, a distinct organization appears. When present, Common Bushtits (*Psaltriparus minimus*) act as flock leaders. This species moves through an area almost continually (as noted by Root 1964) in contrast to other flock members which may remain in a small group of trees for several minutes before moving on. Bushtits often move ahead of the rest of the flock by as far as 50 m before the flock, generally following the same route, catches up again. Otherwise, flock behavior of bushtits was similar to that found by Miller (1921). Other flocking species appeared to be organized around a core of Bridled Titmice (*Parus wollweberi*), the whole moving more or less as a group from tree to tree, which appears typical of most *Parus* flocks (Morse 1970). Routes of flocks showed little pattern except that they followed denser vegetation and avoided areas with little cover, traversing the latter in one flight. On occasion flocks dispersed toward midday. Odum (1942) found a similar tendency in *Parus* flocks.

Very little intra- and interspecific aggression was noted during the study. We have eight records of the former and four of the latter, or 0.007 per foraging observation. This contrasts with 0.038 hostile interactions per foraging observation reported by Morse (1970). No evidence of an interspecific social hierarchy was discernible. Two of the four instances of intraspecific aggression among titmice occurred within a 5 min span. One bird entered a cavity (roost?) in an oak, another bird tried to enter twice, and was chased both times. Two intraspecific interactions between Verdins (*Auriparus flaviceps*) may have been territorial disputes; Verdins appear to be territorial in winter, generally remaining with flocks only while in their own territory. Other interactions were simple displacements.

FLOCK COMPOSITION

Flock composition (when first found), frequency of occurrence of species, mean maximum number of each species associated with flocks (as they were followed), and an indication of fidelity of each species to a flock (per cent flock time) are presented in table 1. When first encountered, flocks in Molino Basin contained an average of 14.6 birds, generally including Bridled Titmouse, Verdin, Bewick's Wren (*Thryomanes bewickii*), and Ruby-crowned Kinglet (*Regulus calendula*). Each of these species occurred in over 70 per cent of the flocks examined. Although Common Bushtits occurred in only 44 per cent of all flocks, when present they comprised an average of 60 per cent of the flock. Of the 62 flocks

found in the Santa Catalina Mountains, 53 contained a member of the genus *Parus*. Flocks containing *Parus* averaged 14.9 birds per flock; those without averaged 9.6. In oak woodland, flocks containing bushtits averaged 23.3 birds; flocks without bushtits averaged 7.8 birds.

Groups of titmice and bushtits serve as focal points; other species enter these groups and then depart. Neither of these species was seen away from flocks during the study period. Other constant flock members were Verdin, Bewick's Wren, and Ruby-crowned Kinglet (table 1). Hutton's Vireo (*Vireo huttoni*), although present in only 26 per cent of the flocks, usually remained with a flock for extended periods. Woodpeckers and nuthatches foraged alone more than with flocks and remained with flocks for only short periods, as previously indicated by Odum (1942) and Morse (1970). Warblers joined flocks but were absent from the area after late October. Various fringillid flocks (sparrows, towhees, juncos) occasionally mingled with but did not follow insectivorous bird flocks.

Size and composition varied as the flocks moved through the study area, as noted for other *Parus* flocks by Wallace (1941). Such changes were due to the entrance and departure of such irregular flock members as woodpeckers and nuthatches and the entrance of other species as they were encountered by the flock. Verdins joined a flock as it moved through their territory. Flock membership by a specific Verdin lasted only as long as the flock remained within that Verdin's territory, after which it tended to return to where the flock was first encountered. Ruby-crowned Kinglets have been reported to be territorial in winter (Rea 1970, Morse 1970) but we often observed several (as many as eight) in a foraging flock without aggression. Movement of bushtits ahead of the rest of the flock was not considered a composition change since titmice and others nearly always followed.

Flocks in oak woodland outside Molino Basin had similar composition, except for one seen in Madera Canyon, Santa Rita Mountains, which contained 20–25 titmice and eight other birds of four species. This was by far the largest number of titmice seen together and may have been the result of nearby feeding stations. Other flocks observed never contained more than six titmice.

At least three titmouse flocks were present in Molino Basin during the study period. Also present was one flock of about 20 bushtits which on occasion split into two groups. The titmouse flocks remained in definite areas (ap-
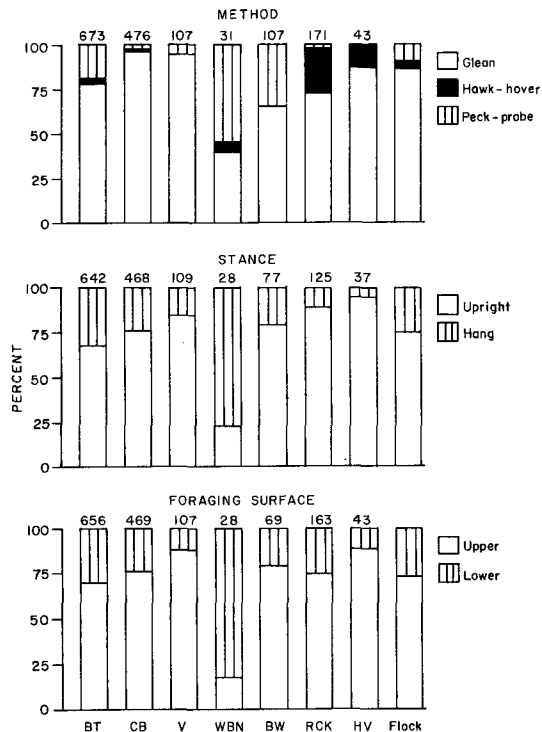

FIGURE 1. Foraging method, stance, and surface of mixed flock members in Arizona oak woodland (*n*'s indicated above each figure, BT = Bridled Titmouse, CB = Common Bushtit, V = Verdin, WBN = White-breasted Nuthatch, BW = Bewick's Wren, RCK = Ruby-crowned Kinglet, HV = Hutton's Vireo, flock = foraging of average flock).

proximately 70 acres) of the basin, while the bushtits appeared to roam throughout, joining any of the titmouse flocks. On 6 December, all three titmouse flocks were seen, two with six, and one with four titmice. The first two contained nine and ten bushtits.

FORAGING NICHE

Foraging behavior. All species studied, except White-breasted Nuthatch (*Sitta carolinensis*), foraged mainly by gleaning (fig. 1). Probing and pecking were important methods of titmice and wrens and the most important method of nuthatches. Kinglets frequently foraged on the tips and lower sides of leaves by hovering. All species except the nuthatch fed predominantly in an upright position. Titmice, bushtits, and wrens, however, utilized a hanging position more than 20 per cent of the time (fig. 1). Wrens generally hung from trunks and larger branches while probing in cracks and crevices in the bark. Titmice and bushtits hung from twigs and small branches while gleaning from lower foliage surfaces. Nuthatches hung from trunks and branches nearly 80 per cent of the time.
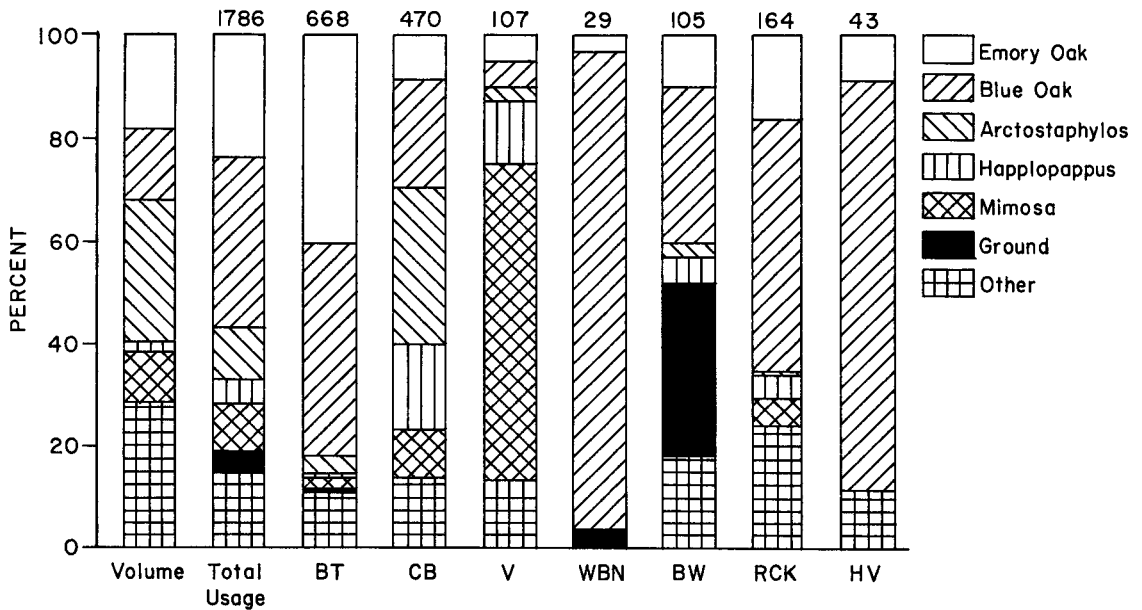
FIGURE 2.   Vegetation availability and usage by insectivorous birds in Arizona oak woodland (legend as in fig. 1).

Foraging station. The five common species foraged on different vegetation substrates (fig. 2). Both titmice and kinglets utilized oaks, but the latter used blue oak three times as often as Emory oak. The bulk of all foraging was done toward the end of branches, regardless of plant species foraged in or the bird species involved (fig. 3), the exceptions being the wren and nuthatch. Bushtits, kinglets, and vireos utilized the outer quarter of branches more than 60 per cent of the time.

Foraging height varied considerably (table 2). Bushtits, Verdins, and wrens foraged low, generally in shrubs or on the ground (fig. 2, 3). Others tended to forage higher and in trees.

All species used primarily bark surfaces and usually smaller twigs for perching (fig. 4). Bewick's Wrens and White-breasted Nuthatch, unlike the other species, tended to perch on larger limbs. The upper foliage surface was the principal foraging surface of all except the wren and nuthatch (figs. 1, 4). The three parids and the wren fed off lower surfaces mainly by hanging, while the kinglet utilized such surfaces by hovering or stretching. Foraging station and behavior were significantly different for nearly all species pairs for which a suitable sample was available (table 3).

DISCUSSION

Winter insectivorous bird flocks in temperate forests are strikingly constant in size, despite diverse habitats. Data from several sources (table 4) indicate that flocks average 10–17 birds, suggesting an optimum size, perhaps leading to maximum efficiency in utilizing resources. Interactions of such factors as crowding, cohesion, level of interaction, food

TABLE 2.   Percent utilization of foraging height by seven oak woodland species.

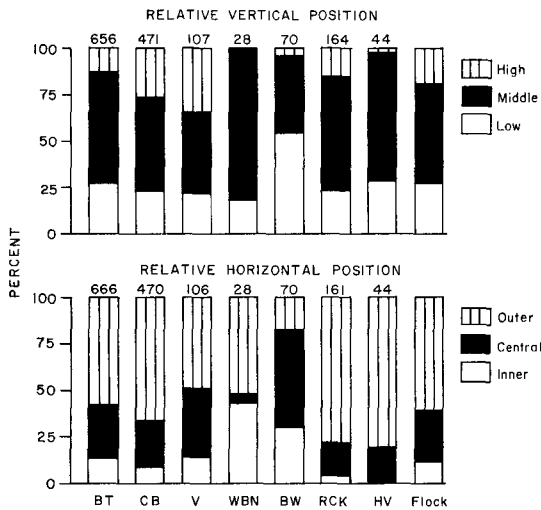| Height (m)	Bridled Titmouse	Common Bushtit	Verdin	White-breasted Nuthatch	Bewick's Wren	Ruby-crowned Kinglet	Hutton's Vireo
0–0.9	15.3	58.3	74.3	3.7	65.1	22.8	7.0
1.0–1.9	33.3	23.0	23.8	29.6	14.7	35.2	27.9
2.0–2.9	25.3	8.3	1.0	51.9	12.8	23.5	44.2
3.0–3.9	15.3	6.7	–	14.8	6.4	14.8	18.6
4.0–4.9	5.4	1.1	–	3.7	0.9	1.9	2.3
5.0–5.9	3.2	0.7	–	–	–	–	–
≥ 6.0	2.1	2.0	1.0	–	–	1.8	–
n	652	460	105	27	109	162	43

FIGURE 3. Position in vegetation of foraging insectivorous birds in Arizona oak woodland (legend as in fig. 1).
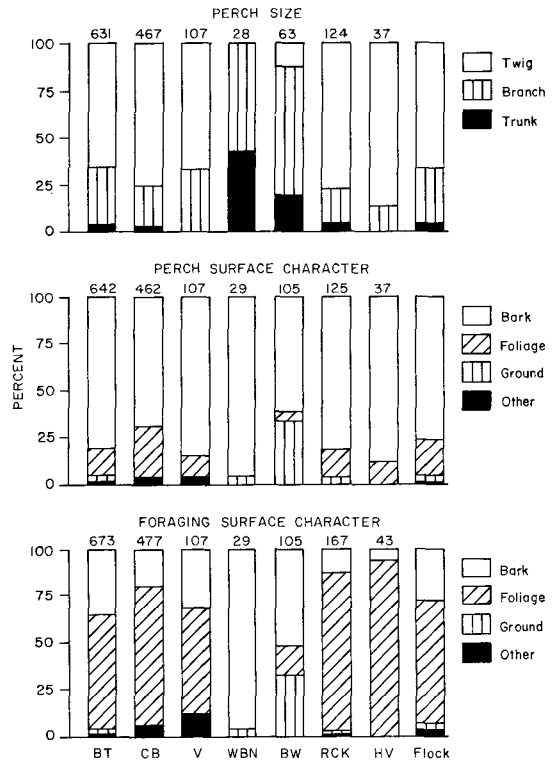

FIGURE 4. Perch size, perch surface character, and foraging surface character of insectivorous birds in Arizona oak woodland (legend as in fig. 1, other = flowers, fruits, and buds).

availability, and foraging efficiency may place an upper limit on flock size. Additionally, two genera, *Parus* and *Regulus*, dominate these flocks in numbers. The former are probably important in flock formation, and act as flock leaders (Morse 1970); mixed flocks generally do not form unless a member of this genus is present. Ninety per cent of mixed winter flocks contain *Parus* (table 4). This situation holds in southern Arizona except for flocks containing bushtits. In these, bushtits act as flock leaders with titmice taking a secondary role. Their active behavior, continuous calling, drab plumage, and, especially, their gregariousness qualify them as a nuclear species (Moynihan 1962). Tropical flocks appear to be more vari-

able in size. Davis (1946) reported flocks in Brazil averaging about nine birds; Malayan flocks average more than 35 birds per flock (McClure 1967).

Of interest in recent studies is foraging diversity (Sturman 1968, Morse 1970, Willson 1970). In this study the two larger species

TABLE 3. Mean per cent differences in foraging birds in Arizona oak woodland.

Species pair	Method	Stance	Position		Perch size		Character of		Foraging surface	Vege-tation	Mean diff.
			from top	from axis	quali-tative	quanti-tative	perch surface	foraging surface			
BT-CB[a]	7.5	7.3	4.9	3.3	6.8	8.5	3.4	4.7	5.3*	15.2	6.8
BT-V	6.9	16.4	7.8	3.5*	1.6*	8.8	2.3	3.2	9.1	21.2	7.9
BT-BW	8.0	10.8*	8.9	13.1	35.1	21.6	10.7	15.7	9.6*	14.1	14.1
BT-RCK	9.1	21.7	4.8	10.5	6.5*	5.4	0.7*	7.5	5.5*	8.0	7.2
CB-V	1.2*	9.1*	5.5	6.1	5.7*	0.5*	5.5	5.9	12.9	14.6	6.6
CB-BW	12.4	3.5*	10.3	16.1	41.9	30.1	10.7	20.3	4.3*	12.3	16.0
CB-RCK	10.0	14.4	5.0	5.5	1.2*	3.2	3.4	4.7	0.2*	12.7	6.3
V-BW	11.2	5.6	11.0	10.2	36.6	30.4	11.1*	17.0	8.6*	20.0	16.0
V-RCK	10.4*	5.3*	9.9	13.3	6.6*	3.4*	2.1*	9.6	12.7	19.0	9.9
BW-RCK	12.7	10.9	8.7	19.9	38.2	27.0	10.3	22.5	4.1*	10.5	16.1
No. of categories	5	2	6	6	3	4	6	6	2	7	47

[a] BT = Bridled Titmouse, CB = Common Bushtit, V = Verdin, BW = Bewick's Wren, RCK = Ruby-crowned Kinglet.
* P > 0.05 chi square.

TABLE 4. Flock size and abundance of major flocking species of mixed flocks in several geographical areas.

Location	$\bar{x}$ flock size	$\bar{x}$ no. Parus	% flocks with Parus	$\bar{x}$ no. Regulus	% flocks with Regulus	No. flocks	Source
Louisiana	17.0	6.5	90.7	4.5	68.2	129	Morse 1970
Maryland	14.1	8.8	95.5	4.7	77.6	223	Morse 1970
Maine (summer)	15.7	4.9	77.7	3.8	57.1	63	Morse 1970
Maine (winter)	10.2	8.2	93.9	3.0	67.3	49	Morse 1970
Massachusetts	–	6–8	–	–	–	–	Wallace 1941
New York	–	7–8	–	–	–	–	Odum 1942
Illinois	10–11	8	–	–	–	–	Johnston 1942
Arizona	14.1	3.9	85.5	2.3	71.0	62	this study
England	11.6	–	–	–	–	–	Gibb 1960
England	–	12±	–	–	–	–	Hinde 1952

(titmouse and wren) were more diverse in their foraging than were the three smaller species (table 5). There is an indication that nuclear species (or flock leaders) are more generalized than attendant species (Morse 1970). A similar indication is shown here. Bewick's Wren, although diverse in its foraging, forages quite differently from (table 3), and interacts little with, other flock members. Total foraging diversity of the titmouse is comparable to that of other parids (see table 9 in Sturman 1968). Titmouse position diversity ($J' = 0.79$) is similar to that given for *Parus* by Morse (1970, our data reanalyzed, using Morse's categories for comparison). Ruby-crowned Kinglet was more diverse than previously found for *Regulus* ($J' = 0.81$, this study, vs. $J' = 0.51 - 0.71$, Morse 1970).

We found that titmice alter their foraging in a manner which appears to reduce competition with associated species. Thus, while foraging with bushtits, which tend to forage upright and peripherally on twigs in lower vegetation, titmice forage more by hanging on larger perches, relatively higher and closer to the axis of trees than when bushtits are absent.

With wrens, titmice avoided larger branches which were used heavily by wrens. In the presence of kinglets, which often glean off lower surfaces in the peripheral vegetation by hovering, titmice foraged more by gleaning in an upright stance on upper surfaces and closer to the axis.

Presence of kinglets and wrens did not affect the foraging pattern of bushtits. Insufficient data on bushtits in the absence of Verdins and titmice prevent further comparisons. However, on one occasion bushtits, foraging alone, foraged at all levels in oaks. These stations were rarely used when titmice were present. An additional observation which indicates the plasticity of bushtit foraging stations was obtained in pine-oak woodland in Bear Canyon. Here, titmice foraged in oaks as in Molino Basin. However, bushtits foraged predominantly in pines (74 per cent of 70 observations). An analogous situation was described by Snow (1949) who found that Crested and Willow Tits (*Parus cristatus* and *P. atricapillus*) foraged low in flocks dominated by Great Tits (*P. major*). When not in Great Tit flocks, they fed at all heights.

TABLE 5. Foraging diversity (J') of five species of birds in Arizona oak woodland (n's as in figs. 1–4).

Foraging category	Bridled Titmouse	Common Bushtit	Verdin	Bewick's Wren	Ruby-crowned Kinglet
Method	0.49	0.15	0.17	0.46	0.49
Stance	0.91	0.82	0.65	0.76	0.51
Position from top	0.85	0.90	0.97	0.82	0.80
Position from axis	0.90	0.84	0.91	0.91	0.68
Perch size qualitative	0.66	0.52	0.56	0.79	0.57
Perch size quantitative	0.60	0.24	0.25	0.99	0.40
Perch surface character	0.40	0.50	0.36	0.58	0.40
Foraging surface character	0.59	0.55	0.68	0.73	0.39
Foraging surface	0.90	0.83	0.56	0.76	0.83
Vegetation	0.63	0.87	0.62	0.79	0.71
Mean	0.69	0.62	0.57	0.76	0.58

TABLE 6. Effect of associated species on the foraging diversity of Bridled Titmouse and Common Bushtit (as J' with minus J' without the species in question).

Foraging category	Species pair[a]					
	BT-CB	BT-RCK	BT-V	BT-BW	CB-RCK	CB-BW
Method	−0.16	−0.18	−0.04	0.15	0.05	0.00
Stance	0.08	−0.14	0.04	−0.02	0.19	0.11
Position from top	0.07	−0.03	0.04	0.08	0.06	0.03
Position from axis	0.06	0.04	0.04	0.17	0.03	0.08
Perch size qualitative	−0.05	−0.10	−0.09	−0.09	−0.09	0.08
Perch size quantitative	0.01	−0.13	−0.03	−0.04	−0.05	0.05
Perch surface character	0.04	0.04	0.12	0.08	−0.01	0.02
Foraging surface character	0.06	0.11	0.11	0.13	0.02	0.01
Foraging surface	0.03	0.11	−0.02	−0.02	0.16	0.11
Vegetation	−0.06	−0.04	0.06	−0.06	0.08	0.28
Net change	+0.08	−0.32	+0.23	+0.38	+0.44	+0.77
Total change	0.62	0.92	0.59	0.84	0.74	0.77

[a] CB = Common Bushtit, BT = Bridled Titmouse, RCK = Ruby-crowned Kinglet, V = Verdin, BW = Bewick's Wren.

Changes in foraging diversity of a given species when associated with others are complex. Titmice were more diverse while foraging with all species except kinglets (table 6). Bushtits were more diverse while foraging with kinglets and wrens. The changes generally involve a specialization in perch size and method and generalization in other foraging stations. Titmice tend to become more specialized in vegetation usage, while bushtits tend to become more generalized (table 6). Total change in titmouse foraging diversity is greatest while it is foraging with kinglets and Bewick's Wrens, both of which frequently utilize oaks.

Morse (1970) demonstrated that socially dominant species modify the foraging station of subordinate species, but the reciprocal was weakly developed. Data presented here suggest an alternative, with the flock leaders (also numerical dominants) modifying their foraging to increase compatibility with each other and associated species. Such behavior may reduce the selection for a social hierarchy with no increase (actually a reduction) in hostile behavior. Increased diversity when foraging with other species may be due to displacement from a specific foraging station image, occurring when a foraging bird encounters another species (or individual) in a "pre-selected" foraging station. Rather than exhibiting aggressive behavior, the foraging bird simply moves to an alternate foraging station, thus avoiding any confrontation while continuing to forage. Such strategy is adaptive if one or more of the following is true: (1) food is readily available and obtainable in an alternative site; (2) such a displacement confers some advantage on either or both birds (e.g., no aggression, thus time and energy channeled into continued foraging); and (3) the benefits of interspecific flocking offset any disadvantage of foraging site modification. This ties in well with the findings that flock leaders tend to be more diverse in their foraging. Also, they are generally more abundant in flocks than other species, and the potential for intraspecific competition is greater among the commoner species because of their numbers. Without territorial behavior in winter, the food supply is not partitioned as in summer. Greater diversity allows several individuals of the same species to forage together without increasing competition. This is somewhat analogous to morphological differences between the sexes of some birds (Selander 1966). The logical question, then, is whether or not birds are more diverse in their foraging in winter than summer and whether this is related to flocking. Some evidence is available. Golden-crowned Kinglets in Maine are more diverse in winter than in summer (J' = 0.65 and 0.59, respectively, Morse 1970). Data for several North American and European parids are presented by Sturman (1968). We calculated mean J' from those studies in Sturman's table 7 for which both summer and winter data were available. Both North American and European Parus tended to be more diverse in winter (J' = 0.72 for each) than in summer (J' = 0.65 and 0.70, respectively).

No species in flocks studied by Morse (1970) approached the numbers of bushtits present in Arizona flocks. This, coupled with the lack of hostile interactions and the changes in foraging behavior while with other species, sug-

gests that there may be basic differences between flock organization at middle elevations of the Southwest and flocks in other areas. The parallels between the Common Bushtit and the Long-tailed Tit (*Aegithalos caudatus*) in England are interesting. Both associate with mixed flocks, occur in similarly sized groups, maintain some integrity within larger flocks, move faster over the substrate than other flock members, call continuously, and forage low (Hinde 1952, Gibb 1960). The two appear to be ecological equivalents, and it would be interesting to know if the Long-tailed Tit has the same effect on mixed flocks as do bushtits.

SUMMARY

Composition, organization, and foraging behavior of mixed insectivorous bird flocks were examined in oak woodland in southern Arizona. Differences in vegetation utilized for foraging appear to be the major factor by which the several species achieve spatial separation. Significant differences were also found in method and position of foraging. Titmice and bushtits modify their behavior in the presence of each other and of other species in a way which apparently reduces interspecific contact. Such modification may be responsible for the comparatively low level of interspecific aggression and the lack of a social hierarchy. Post-breeding, mixed insectivorous bird flocks in temperate regions are remarkably similar in size, suggesting an optimum size for such flocks. It is suggested that flocks at middle elevations of the southwestern United States differ to some extent from other Temperate Zone flocks studied, possibly due to the presence of bushtits.

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