Condor 84:84–90

A COMPARISON OF FORAGING BEHAVIOR AMONG PERMANENT, SUMMER, AND WINTER RESIDENT BIRD GROUPS

ROBERT E. LEWKE

ABSTRACT.—Foraging behavior of permanent resident bird species in summer and winter was compared with that of summer resident and winter resident bird groups of a floodplain habitat along the lower Snake River in southeastern Washington. Ten criteria were used to compare foraging differences between seasonal groups. In summer, permanent residents differed significantly from invading summer residents in 8 of 10 foraging categories. In summer, permanent residents foraged on the forest edge, in the tree-shrub physiognomic type, and usually on the ground. Summer residents differed by feeding more frequently in trees or in the air and by gleaning insects off mulberry or willow leaves. In winter, permanent residents foraged on the ground of the forest edge, either in the tree-shrub or grass-herb physiognomic types. Winter residents fed in trees or on the ground, in the woods or forest edge, and in the tree-shrub physiognomic type. When in trees, these birds usually gleaned insects off small branches and dead leaves. Separation of foraging behavior was approximately six times greater in winter than in summer.

Many avian ecologists, including Lack (1944), Hinde (1958), MacArthur (1958), Holmes and Pitelka (1968), Willson (1971) and Sealy (1973) have believed that differences in bird foraging behavior are as important to niche segregation as differences in food items selected. Even though similar food items may be eaten, different methods of foraging expose birds to prey items in different locations and thus potentially reduce competition and allow coexistence.

Studies of niche segregation have shown separation of foraging behavior of a few closely related species (e.g., Hartley 1953, Gibb 1954, MacArthur 1958, Norris 1958, Recher 1966, Sturman 1968, and Morse 1970). Few ecologists have attempted to analyze the foraging differences among groups of less closely related species or among most species of an avian community (but see Cody 1968, Wiens 1969, Willson 1970, Pearson 1971, Austin and Smith 1972, and Emlen 1972).

Leck (1972) found that migrant frugivores in the tropics generally were attracted to superabundant fruit resources, and thus did not seriously compete with local frugivores. Karr (1976:456) summarized his and others' work: "In general, it appears that the evolutionary strategies of migrant birds are keyed to the exploitation of superabundant and/or sporadically available resources in their tropical wintering areas." Blondel (1969:312) noted that the "food niche of wintering birds is never occupied by other birds." Emlen (1972) found that winter invader granivores in Texas were primarily small-seed foragers whereas permanent residents were primarily large-seed foragers. Willson (1970:171) stated that "neither the influx of spring foods nor the distribution of spring foods changes the degree of specialization of these birds [several species of permanent residents in Illinois]." If this is true, then invading species should evolve foraging habits that differ from those of permanent residents. Foraging preferences of permanent residents might cause invading summer and winter residents to respond to this competitive group in similar ways.

Moreau (1972) reported that 65 of 90 (72%) migrant species in six African habitats appeared not to compete seriously with permanent residents. Moreau (1972) and others stated that migrants generally exploit food resources not fully used by permanent residents. Herrera (1978) found permanent residents of a Mediterranean bird community to be more specialized feeders than migrants. Finally, Holmes, Bonney, and Pacala (1979) found height, location (trunk, branch, etc.), and tree species to be the most important criteria for separating birds of a New Hampshire bird community into four foraging guilds.

The purposes of this study were to determine if summer and winter migrant birds forage in a riparian habitat in southeastern Washington so that they minimize competition for food with permanent residents and to identify the most important foraging criteria which segregate resident groups.

STUDY AREA AND METHODS

Alpowa Creek Study Area was an 11.5-ha plot located along the lower Snake River in southeastern Washington 11.3 km west of Clarks-

TABLE 1. Composition of winter and summer populations of birds in terms of residency status and general food habits. Numbers in parentheses are percentages.

Residency status	Number of species per feeding category							
	Insectivore	Granivore	Frugivore	Insectivore–Granivore	Insectivore–Frugivore	Omnivore	Piscivore	Total
PRS[a]	7 (41)	5 (29)	1 (6)	1 (6)	2 (12)	0 (0)	1 (6)	17 (100)
SR	16 (67)	0 (0)	0 (0)	5 (21)	3 (13)	0 (0)	0 (0)	24 (101)
Total	23 (56)	5 (12)	1 (2)	6 (15)	5 (12)	0 (0)	1 (2)	41 (99)
PRW	4 (24)	6 (35)	1 (6)	1 (6)	3 (18)	1 (6)	1 (6)	17 (101)
WR	5 (42)	4 (33)	0 (0)	2 (17)	1 (8)	0 (0)	0 (0)	12 (100)
Total	9 (31)	10 (34)	1 (3)	3 (10)	4 (14)	1 (3)	1 (3)	29 (98)

[a] PRS = Permanent Residents Summer; SR = Summer Residents; PRW = Permanent Residents Winter; WR = Winter Residents.

ton. The creation of Lower Granite Dam flooded the study area in February, 1975. The area included four recognized plant communities: (1) woodland dominated by mulberry (*Morus alba,* 57%), willow (*Salix* sp., 32%), and hackberry (*Celtis douglasii,* 4%); (2) willow flat composed primarily of willow trees and shrubs; (3) weed field dominated by cheatgrass (*Bromus tectorum*), lamb's quarters (*Chenopodium album*), and prickly lettuce (*Lactuca serriola*); and (4) sage flat dominated by sagebrush (*Artemisia tridentata*) and cheatgrass (Lewke 1975). Average annual precipitation of this arid site was 33 cm; 1973 and 1974 summer temperatures often exceeded 38°C; winter temperatures rarely reached −17°C.

Foraging data, recorded as observations, were obtained while conducting censuses and random "cruising" from sunrise until 10:00. No attempt was made to follow particular individuals for long periods; only one foraging observation was recorded per sighting. Data were pooled for both sexes over an entire season. For each foraging observation, I recorded the following data: (1) physiognomic type (appearance of plant community); (2) habitat (forest edge, woods, or field); (3) site (e.g., ground, herb, tree, etc.); (4) height from ground; (5) tree species used; (6) plant part used as a foraging substrate; (7) diameter of trunk or branch; (8) condition of plant used as foraging substrate (alive or dead); and (9) foraging method (e.g., drill, glean, etc.). Time spent in each physiognomic type and habitat was proportional to the amount of each subtype present. Parts of 66 days (265 h) in 1973 and 1974 were spent collecting data with approximately equal time during summer and winter months.

Species have been grouped and analyzed according to three types of residency: permanent (in summer and in winter), summer, or winter residents. Diet preferences were obtained from Bent (1946–1968) and Martin et al. (1951). Differences between the two summer groups and between the two winter groups were tested with chi-square contingency tables on the original data using the 5% level of significance.

RESULTS

Table 1 shows the composition of summer and winter populations of birds in the study area. In summer, permanent residents comprised 41% (17 of 41) of the species, while in winter, permanent residents made up 59% (17 of 29 species) of the avian community.

FOOD HABITS

Table 1 shows that permanent resident species in summer were mostly insectivores (41%) and granivores (29%). The summer resident group included 16 insectivorous (67%), but no exclusively granivorous, species. In winter, permanent and winter residents were nearly equal in their granivorous and insectivorous feeding habits. Chi-square contingency tables revealed no significant differences in species' food habits between either the two summer groups or the two winter groups. Table 2 lists the residency status and general food habits of each species studied.

Foraging behavior of each residency group for nine categories is indicated in Table 3 and summarized below. All statistical comparisons were made between permanent residents in summer and summer residents and between permanent residents in winter and winter residents.

PHYSIOGNOMIC TYPE

Summer residents differed from permanent residents primarily by their greater selection of the rocky shore physiognomic type. Winter residents chose the tree-shrub type more often than permanent residents and the grass-herb type less often than permanent residents. Although the differences between both sets of groups are significant, the permanent vs. winter resident differences were much greater than those between permanent and summer resi-

TABLE 2. Residency and food habits of birds at Alpowa Creek Study Area, Washington.

Species	Food habits[a]	
	Summer	Winter
Permanent residents		
Ring-necked Pheasant (*Phasianus colchicus*)	G	G
California Quail (*Lophortyx californicus*)	G	G
Great Blue Heron (*Ardea herodias*)	P	P
Mourning Dove (*Zenaida macroura*)	G	G
Downy Woodpecker (*Picoides pubescens*)	I	I
Hairy Woodpecker (*Picoides villosus*)	I	I
Common Flicker (*Colaptes auratus*)	I	F–I
Horned Lark (*Eremophila alpestris*)	I	I
Black-billed Magpie (*Pica pica*)	I	O
Canyon Wren (*Catherpes mexicanus*)	I	I
American Robin (*Turdus migratorius*)	F–I	F–I
Cedar Waxwing (*Bombycilla cedrorum*)	F	F
Starling (*Sturnus vulgaris*)	I–F	F–I
Western Meadowlark (*Sturnella neglecta*)	I	I–G
American Goldfinch (*Carduelis tristis*)	G	G
House Finch (*Carpodacus mexicanus*)	G	G
Song Sparrow (*Melospiza melodia*)	G–I	G
Summer residents		
Killdeer (*Charadrius vociferus*)	I	–
Spotted Sandpiper (*Actitis macularia*)	I	–
Common Nighthawk (*Chordeiles minor*)	I	–
Say's Phoebe (*Sayornis saya*)	I	–
Western Wood Pewee (*Contopus sordidulus*)	I	–
Eastern Kingbird (*Tyrannus tyrannus*)	I	–
Western Kingbird (*Tyrannus verticalis*)	I	–
Barn Swallow (*Hirundo rustica*)	I	–
Cliff Swallow (*Petrochelidon pyrrhonota*)	I	–
Rough-winged Swallow (*Stelgidopteryx ruficollis*)	I	–
House Wren (*Troglodytes aedon*)	I	–
Gray Catbird (*Dumetella carolinensis*)	F–I	–
Veery (*Catharus fuscescens*)	I–F	–
Red-eyed Vireo (*Vireo olivaceus*)	I	–
Yellow-breasted Chat (*Icteria virens*)	I	–
Yellow Warbler (*Dendroica petechia*)	I	–
Northern Oriole (*Icterus galbula*)	I	–
Brown-headed Cowbird (*Molothrus ater*)	I–G	–
Red-winged Blackbird (*Agelaius phoeniceus*)	I–G	–
Brewer's Blackbird (*Euphagus cyanocephalus*)	I	–
Rufous-sided Towhee (*Pipilo erythrophthalmus*)	G–I	–
Lazuli Bunting (*Passerina amoena*)	G–I	–
Lark Sparrow (*Chondestes grammacus*)	G–I	–
Black-headed Grosbeak (*Pheucticus melanocephalus*)	I–F	–
Winter residents		
Mountain Chickadee (*Parus gambeli*)	–	I–G
Black-capped Chickadee (*Parus atricapillus*)	–	I–G
Brown Creeper (*Certhia familiaris*)	–	I
Winter Wren (*Troglodytes troglodytes*)	–	I
Bewick's Wren (*Thryomanes bewickii*)	–	I
Varied Thrush (*Ixoreus naevius*)	–	F–I
Ruby-crowned Kinglet (*Regulus calendula*)	–	I
Golden-crowned Kinglet (*Regulus satrapa*)	–	I
Evening Grosbeak (*Hesperiphona vespertina*)	–	G
Dark-eyed Junco (*Junco hyemalis*)	–	G
White-crowned Sparrow (*Zonotrichia leucophrys*)	–	G
Tree Sparrow (*Spizella arborea*)	–	G

[a] G = Granivore; I = Insectivore; F = Frugivore; O = Omnivore; P = Piscivore.

dents (see Table 4). All four groups used the tree-shrub physiognomic type more than predicted by the percentage of that physiognomic type in the study area. Each group used the grass-herb type less than expected by chance.

FORAGING HABITAT—ECOTONE EFFECT

The forest edge was used by all but the winter residents more often than the other two subcategories. A comparison of groups showed that permanent residents in summer used for-

est edge more than summer residents, but winter permanent residents and winter residents differed primarily in their use of fields and woods. Permanent residents in winter preferred the woods habitat to the field habitat (28% vs. 19%), but winter residents greatly preferred the woods to the field (48% vs. 7%). Differences between these groups were significant.

FORAGING SITES

Foraging site subcategories included ground, herb, shrub, tree, and air. Permanent residents in summer foraged predominantly on the ground and in trees, whereas summer residents used ground, tree, and air sites evenly. In winter, permanent residents foraged predominantly on the ground, but winter residents used the ground less and the trees more than permanent residents. Differences between both groups compared were significant.

Foraging heights. In general, lower foraging levels were preferred and higher foraging levels were avoided. These data may be biased, since birds are more easily seen near the ground. Observations of birds foraging on the ground were omitted so that all data would represent foraging heights on vegetation. Although permanent residents in summer and summer residents differed significantly in selection of foraging height (Table 4), this difference was much less than that between permanent residents in winter and winter residents. In summer the highest three foraging categories (above 9 m) contributed the most to chi-square. Seven percent of the summer residents foraged above 15 m whereas only 1% of the permanent residents foraged at that height. Permanent residents in winter preferred the lowest foraging height class, whereas winter residents used the first four height classes more evenly.

Tree species used. Permanent residents in summer favored chokecherry (*Prunus virginiana*) and avoided willows (Table 3). This preference was attributed entirely to the American Robin. Also, the permanent residents foraged primarily on the ground rather than in trees. I noted only 89 instances of permanent residents in trees, yet two to three times as many records of other groups foraging in trees. Summer residents showed little preference for any particular tree species. They avoided mulberries to some extent and selected chokecherries more often than expected. The difference between summer groups was significant.

Permanent residents in winter preferred hackberry and poplar (*Populus nigra*), but avoided mulberry trees. Winter residents preferred hackberry even more than permanent winter residents but did not prefer poplars

TABLE 3. Foraging behavior (percentage of observations) of permanent resident birds in summer (PRS) and winter (PRW), summer residents (SR), and winter residents (WR).

Foraging category and frequency of occurrence	PRS	SR	PRW	WR
Physiognomic type				
Rocky shore (1%)	2	9	+	0
Grass-herb (53%)	29	29	43	20
Sagebrush (3%)	1	+	2	4
Shrub (11%)	5	4	1	2
Tree-shrub (32%)	64	58	55	74
Total observations	373	586	1,268	2,215
Habitat				
Field (59%)	15	25	19	7
Forest edge (7%)	66	49	53	45
Woods (34%)	19	26	28	48
Total observations	343	498	1,216	2,208
Foraging site				
Ground	59	32	72	37
Herb	4	4	13	4
Shrub	3	5	2	7
Tree	34	32	13	52
Air	0	27	0	+
Total observations	369	750	1,127	2,384
Foraging height (m)				
0.3–1.5	24	23	57	26
1.5–3	7	12	6	21
3–6	18	20	6	26
6–9	28	22	22	18
9–12	18	12	3	6
12–15	4	5	6	+
>15	1	7	3	2
Total observations	136	345	309	1,667
Tree species				
Mulberry (57%)	57	38	9	15
Willow (32%)	6	36	24	34
Hackberry (4%)	0	6	31	44
Maple (4%)	0	9	4	3
Box elder (2%)	0	1	0	+
Poplar (+)	2	1	29	1
Elm (+)	0	1	2	+
Chokecherry (+)	34	4	0	1
Total observations	89	216	127	1,209
Plant part				
Branch	61	24	40	44
Trunk	7	6	20	10
Leaf	25	67	6	43
Flower	7	3	20	2
Bud	0	0	14	0
Total observations	29	248	139	1,524
Diameter (cm)				
<2.5	85	67	46	73
2.5–13	15	15	27	13
>13	0	19	27	14
Total observations	20	75	78	805
Condition				
Alive	62	86	73	49
Dead	38	14	27	51
Total observations	26	231	144	1,450
Foraging method				
Drill	13	0	35	3
Glean	84	75	65	87
Hover-glean	3	18	0	10
Flycatch	0	7	0	+
Total observations	32	300	124	1,558

TABLE 4. Importance of foraging categories as segregating factors between permanent residents in summer and summer residents and between permanent residents in winter and winter residents. Chi-squares are from contingency tables.

Category (df)	Summer				Winter			
	χ^2	sig-χ^2 (0.05)	Excess	Importance rank	χ^2	sig-χ^2 (0.05)	Excess	Importance rank
Food habits (6)	12.22	12.60	0.00	10	5.34	12.60	0.00	10
Physiognomic type (4)	22.01	9.49	12.52	5	220.93	9.49	211.44	6
Habitat (2)	23.80	5.99	17.81	4	109.60	5.99	103.61	7
Foraging site (4)	143.80	9.49	134.31	1	613.85	9.49	604.36	1
Foraging height (6)	16.55	12.60	3.95	8	246.31	12.60	233.71	3
Tree species (7)	88.20	14.10	74.10	2	247.07	14.10	232.97	4
Plant part (4)	13.59	9.49	4.10	7	353.85	9.49	344.36	2
Diameter (2)	4.60	5.99	0.00	7	24.40	5.99	18.41	9
Condition (1)	11.70	3.84	7.86	6	29.70	3.84	25.86	8
Foraging method (3)	42.44	7.81	34.63	3	235.10	7.81	227.29	5
			Σ 289.28				Σ 2,002.01	

nearly as much as winter permanent residents. The difference between winter groups also was significant.

Plant parts used. Four of the five recognized subcategories—branch, trunk, leaf, and flower—were foraging substrates, whereas the fifth—bud—was a plant part eaten by birds. Permanent residents in summer significantly differed from summer residents primarily in their lesser use of leaves, and their extensive use of branches (Table 3). In winter, permanent residents rarely used leaves, but winter residents foraged on leaves most of the time. Winter leaves were nearly all dead hackberry leaves still clinging to branches. Permanent residents used flowers and buds more often than winter residents. The difference in winter usage of plant parts was significant (Table 4).

Diameter of branches and trunks. Permanent residents in summer and summer residents both foraged on branches less than 2.5 cm in diameter (Table 3). The difference between permanent residents in summer and summer residents was not significant. Permanent residents in winter foraged significantly more often on large diameter plant parts than winter residents.

Condition of plant parts used. Permanent residents in summer foraged significantly more often on dead plant parts than did summer residents. Permanent residents in winter foraged significantly more often on live plant material than did winter residents.

FORAGING METHODS

All groups foraged mainly by gleaning (picking insects off the substrate). Summer residents and winter residents hover-gleaned (gleaning a substrate while hovering over or flying past it) more frequently than permanent residents in summer and winter. However, permanent residents in both seasons were observed drilling for food more frequently than their summer and winter resident counterparts. These differences between groups in summer and winter were both significant.

DISCUSSION

Although statistical analysis showed all but three of the group comparisons within seasons to be significantly different, some segregating criteria were clearly more important than others (Table 4). The size of the calculated chi-square values of group comparisons should indicate the relative importance of a foraging category as a segregating criterion.

Excess chi-square values (Table 4) demonstrate that foraging site (ground, herb, shrub, tree, or air) was the most important segregating criterion between groups both in summer and winter. In summer the seasonal summer residents foraged in the air whereas I never saw permanent residents foraging there, although Smith (1978) reported flycatching behavior of the Song Sparrow. Permanent residents fed primarily on the ground and in trees. Because insects do not occur in the air during all seasons, permanent residents have probably evolved the habit of feeding at sites that are more productive all year (Herrera 1978). Summer residents take advantage of this unfilled niche. In fact, if I had collected more foraging data on swallows, the 27% value for summer resident utilization of air would have been higher.

Permanent residents in winter foraged primarily on the ground whereas seasonal winter residents foraged more in trees. Winter resident foraging data were influenced greatly by large populations of Black-capped Chickadees and Evening Grosbeaks. Permanent residents increased their use of the ground from summer to winter seasons while decreasing their use of trees (Table 3). The separation between per-

manent and seasonal residents' use of foraging sites in winter was 4.5 times greater than in summer (compare excess chi-squares in Table 4).

The foliage gleaning niche was filled in the summer by the Yellow Warbler and Red-eyed Vireo and in the winter by the Black-capped Chickadee, Ruby-crowned Kinglet, and Golden-crowned Kinglet. No permanent resident species could be described as a predominant foliage gleaner. The Song Sparrow was the most important resident foliage gleaner, but was neither as exclusive nor as agile and adept a foliage gleaner as the four other species mentioned. The niche nevertheless remained filled most of the year because of the closeness of arrival and departure dates for summer and winter residents.

In summer the next most important segregating categories were tree species and foraging method. When foraging in trees, permanent residents primarily used mulberry and chokecherry, whereas summer residents foraged mostly in mulberry and willow trees (Table 3). Although both permanent and summer resident insectivores foraged mainly by gleaning, the permanent residents (woodpeckers) drilled more (13%) than the summer residents (0%). On the other hand, summer residents used either hover-gleaning or flycatching foraging methods much more than permanent residents.

In winter, tree species and foraging methods were fourth and fifth in order of importance, while plant part and foraging height occupied the second and third most important categories. The plant part category shows that when trees are used as a foraging site, permanent residents used branches, trunks, dead flowers and buds, but avoided dead leaves as a foraging site. The more agile winter residents—chickadees and kinglets—fed mostly on branches and dead leaves. The foraging height category reveals that permanent residents fed close to the ground, whereas winter residents foraged quite evenly within the first four height categories. If the ground foraging observations had been included in the height categories, the separation between permanent and winter residents would have increased as 72% of the observations for permanent residents were on the ground.

Herrera (1978) described four foraging guilds in a Mediterranean bird community. Although he did not consider summer and winter migrants as separate groups, he found a good separation between permanent residents and migrants. Guild I—aerial sweepers and flycatchers—contained only migrant species, whereas guild II—bark gleaners—contained only resident species. Guild III—foliage gleaners—contained both migrants and residents, and guild IV—ground foragers—contained only resident species for 8 of 12 months. My results are strongly in agreement with these findings.

Holmes, Bonney, and Pacala (1979) supplied enough data in their guild study of a summer bird community in New Hampshire to allow comparisons of permanent resident vs. summer resident foraging behavior. Again, good separation of the two groups was found. Two guilds were composed mainly of permanent residents and two of summer residents. Statistical analysis of their data revealed a significant difference between groups in their foraging location but not in tree species utilized. Although they combined several criteria thus making direct comparisons with my study difficult, my results support theirs.

If permanent resident food supply is more stable and less seasonal as Herrera (1978) suggested, then permanent residents should have evolved efficient methods of exploiting this resource. This would make it difficult for migrants to successfully compete with residents for the same resource. The best option for migrants would be to exploit a different food source (Leck 1972, Herrera 1978) or the same food source in a different way. My data support the second option and do not rule out the first.

In winter the top seven ranked categories (see Table 4) all had high excess chi-square values. In summing the excess chi-squares for each season, the winter total (2,002) was nearly seven times greater than the summer total (289). Since winter food supplies were almost certainly smaller than summer food supplies, I would have predicted a greater separation between groups in winter than in summer. These data support Morse's (1967) suggestion that foraging patterns between two species (in this situation two groups) would be most distinct under more severe environmental conditions.

Because residency groups are composed of different proportions of species with various foraging habits, one can characterize a foraging tendency for the group as a whole. This does not mean that we can describe an average or typical winter, summer, or permanent resident bird. In summary, permanent residents in summer foraged on the forest edge, in the tree-shrub physiognomic type, and usually on the ground. When foraging in vegetation, they were usually in mulberry trees gleaning insects off living branches. Most invading summer residents were found on the forest edge, in the tree-shrub physiognomic type, on the ground, in trees, or in the air. When in vegetation, the

summer residents gleaned insects off mulberry or willow leaves usually not more than 9 m above the ground. In winter, permanent residents foraged on the ground of the forest edge, either in the tree-shrub or grass-herb physiognomic types. Invading winter residents fed in trees or on the ground, in the woods or on the forest edge, and in the tree-shrub physiognomic type. When in trees, these birds usually gleaned insects off small branches and dead leaves of hackberry and willow trees at the height of 1–9 m.

ACKNOWLEDGMENTS

Financial support for this study came from the State of Washington Water Research Center, the U.S. Department of the Interior, Office of Water Resources Research, and the Department of Zoology, Washington State University. I thank I. O. Buss, M. F. Willson, J. R. Karr and several anonymous reviewers for reading early versions of this manuscript and offering helpful suggestions. L. Glenna typed the final draft of the manuscript.

LITERATURE CITED

AUSTIN, G. T., AND E. O. SMITH. 1972. Winter foraging ecology of mixed insectivorous bird flocks in oak woodland in southern Arizona. Condor 74:17–24.

BENT, A. C. 1946–1968. Life histories of North American [birds]. U.S. Natl. Mus. Bulls. 191 (1946), 195 (1948), 196 (1949), 197 (1950), 203 (1953), 211 (1958), 237 (1968).

BLONDEL, J. 1969. Sédentarité et migration des oiseaux dans une garrigue méditerranéenne. Terre Vie 3:269–314.

CODY, M. L. 1968. On the methods of resource division in grassland bird communities. Am. Nat. 102:107–147.

EMLEN, J. T. 1972. Size and structure of a wintering avian community in southern Texas. Ecology 53:317–329.

GIBB, J. 1954. Feeding ecology of tits, with notes on Treecreeper and Goldcrest. Ibis 96:513–543.

HARTLEY, P. H. T. 1953. An ecological study of the feeding habits of the English titmice. J. Anim. Ecol. 22:261–288.

HERRERA, C. M. 1978. Ecological correlates of residence and non-residence in a mediterranean passerine bird community. J. Anim. Ecol. 47:871–890.

HINDE, R. A. 1958. Behavior and speciation. Biol. Rev. 34:85–120.

HOLMES, R. T., AND F. A. PITELKA. 1968. Food overlap among co-existing sandpipers on northern Alaskan tundra. Syst. Zool. 17:305–318.

HOLMES, R. T., T. E. BONNEY, JR., AND S. W. PACALA. 1979. Guild structure of the Hubbard Brook bird community: a multivariate approach. Ecology 60:512–520.

KARR, J. R. 1976. On the relative abundance of migrants from the north temperate zone in tropical habitats. Wilson Bull. 88:433–458.

LACK, D. 1944. Ecological aspects of species-formation in passerine birds. Ibis 86:260–286.

LECK, C. F. 1972. The impact of some North American migrants at fruiting trees in Panama. Auk 89:842–850.

LEWKE, R. E. 1975. Preimpoundment study of vertebrate populations and riparian habitat behind Lower Granite Dam on the Snake River in southeastern Washington. Ph.D. diss., Washington State Univ., Pullman.

MACARTHUR, R. H. 1958. Population ecology of some warblers of northeastern coniferous forests. Ecology 39:599–619.

MARTIN, A. C., H. S. ZIM, AND A. L. NELSON. 1951. American wildlife and plants: a guide to wildlife food habits. McGraw-Hill, New York.

MOREAU, R. E. 1972. The Palaearctic African bird migration systems. Academic Press, New York.

MORSE, D. H. 1967. Foraging relationships of Brown-headed Nuthatches and Pine Warblers. Ecology 48:94–103.

MORSE, D. H. 1970. Ecological aspects of some mixed-species foraging flocks of birds. Ecol. Monogr. 40:119–168.

NORRIS, R. A. 1958. Comparative biosystematics and life history of the nuthatches *Sitta pygmaea* and *Sitta pusilla*. Univ. Calif. Publ. Zool. 56:119–300.

PEARSON, D. L. 1971. Vertical stratification of birds in a tropical dry forest. Condor 73:46–55.

RECHER, H. F. 1966. Some aspects of the ecology of migrant shorebirds. Ecology 47:393–407.

SEALY, S. G. 1973. Interspecific feeding assemblages of marine birds of British Columbia. Auk 90:796–802.

SMITH, J. N. M. 1978. Flycatching by male Song Sparrows, *Melospiza melodia*. Can. Field-Nat. 92:195–196.

STURMAN, W. A. 1968. The foraging ecology of *Parus atricapillus* and *P. rufescens* in the breeding season, with comparisons with other species of *Parus*. Condor 70:309–322.

WIENS, J. A. 1969. An approach to the study of ecological relationships among grassland birds. Ornithol. Monogr. 8.

WILLSON, M. F. 1970. Foraging behavior of some winter birds of deciduous woods. Condor 72:169–174.

WILLSON, M. F. 1971. A note on foraging overlap in winter birds of deciduous woods. Condor 73:480.

Department of Zoology, Washington State University, Pullman, Washington 99163. Present address: District One Technical Institute, Eau Claire, Wisconsin 54701.
Accepted for publication 21 October 1980.