

AN ABSTRACT OF THE THESIS OF

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Title: An analysis of guild structure of avian communities, Columbia  
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Abstract approved:

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Effects of habitat and season on guild structure of avian communities were examined for islands in the estuary zone of the Columbia River, Oregon. Bird species were classified into guilds according to their major food item, typical foraging substrate, and foraging behavior. Variation in community structure indices (number of guilds, guild diversity, evenness, bird density, and biomass) among habitats and seasons were analyzed with multivariate analysis of variance and discriminant function analysis. Cluster analysis was used to examine patterns of guild distribution among habitats and seasons.

Four habitat-bird community associations (tree-shrub, upland, beach-low marsh, and high marsh) were described based on results from this study. High guild evenness within tree-shrub habitats during the breeding season (spring and summer) distinguished tree-shrub bird communities from communities within the 3 other habitats. Relatively stable bird density within tree-shrub habitats was attributed to high vegetation heterogeneity and later successional stage of tree-shrub habitats.

Seasonal variation of community structure indices was greatest within upland habitats. Comparison of seasonal patterns in number of guilds, guild evenness, bird density, and guild composition between

tree-shrub and upland habitats suggested greater stability of food resource productivity, availability, and diversity within tree-shrub habitats. Differences in avian community structure between the 2 terrestrial seral stages (tree-shrub and upland) were ascribed to differences in successional stage and vegetation complexity.

High avian biomass distinguished bird communities of beach-low marsh habitats and was probably related to high productivity typical of estuary systems. Seasonal variation of community structure, primarily a winter reduction in bird density, was least definitive in beach-low marsh habitats. Lack of winter reduction in number of guilds and seasonal changes in guild composition suggested low winter density was related to reduced availability of food resources as affected by tidal inundation, low temperatures, and ice on the river.

Bird communities associated with the high marsh habitat were characterized from all other bird community-habitat associations by greater number of guilds. Less extensive tidal inundation, greater vegetation complexity and more edge effect in the high marsh habitat than in beach-low marsh habitats seemed to affect greater occurrence of terrestrial associated guilds.

Results of this study indicated description of avian community structure on the basis of food-resource defined guilds was useful in interpreting how environmental (habitat and season) variation may affect bird communities. Validity of inferences from this study requires more detailed analysis of the bird communities and their habitats. Thus, the guild approach as used in this research is most appropriate for preliminary examination of communities, indicating areas where more specific study should increase understanding of the structure and functioning of avian communities.

An analysis of guild structure of avian  
communities, Columbia River, Oregon

by

Cecilia Lea Barham Noyes

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AN ANALYSIS OF GUILD STRUCTURE OF  
AVIAN COMMUNITIES, COLUMBIA RIVER, OREGON

INTRODUCTION

Studies of avian community structure commonly involved relating variation of species composition and/or descriptive community characteristics (eg. density, biomass, abundance, diversity, and evenness) to environmental variation (eg. MacArthur 1964, Karr 1968, Emlen 1972, Recher 1969, Kricher 1972). Composition of groups of functionally related species facilitated analysis and comparison of communities (eg. Salt 1953, 1957; Willson 1974, Anderson 1970a,b; Karr 1976, 1980, Landres and MacMahon 1980, Holmes et al. 1979) and also provided further understanding of the mechanisms that determine community structure. Root (1967) originally termed these functional classes of species, guilds, and defined them as " a group of species that exploit the same class of environmental resources in a similar way".

Classification of species according to their functional role was based primarily on food habits, foraging substrate, or foraging behavior. Differential utilization of resources and foraging substrates were considered 2 primary factors determining community structure (Cody 1974, Karr 1980, Holmes et al. 1979). Salt (1953), in an ecological analysis of different avifaunas, grouped species into major categories according to the substrate type in which they foraged (air, foliage, timber, ground). Further subdivision within each category was based on either the major component of the diet (insect, nectar,

seed) or foraging mode (searching, drilling, predator). Salt (1953) found differences in relative abundance of birds within each functional group reflected differences in vegetative structure and climate among habitats. Several researchers used modifications of Salt's (1953, 1957) system of ecological classification in comparisons of forest avifaunal structure (Bock and Lynch 1970, Anderson 1970a, b; Wiens 1975, Wiens and Nussbaum 1975).

Orians (1969) found that the number of species within guilds, classified according to diet and foraging mode, accounted for changes in the structure of bird communities that were not revealed by simple counts or relative abundance of species. Guild composition in turn indicated structural differences of vegetation among tropical forest sites that were not explicable in terms of vegetative measurements (number of tree species, foliage height profile, or productivity of habitats). Willson (1974), in a study of relationships between avian community organization and vegetative complexity, arranged guilds by food habits, foraging strata, and foraging behavior. Bird species diversity, number of guilds, and number of species per guild were examined in relation to foliage height diversity and percent vegetation coverage. Addition of a tree layer, in a series of increasing vegetative complexity, had the greatest influence on species additions. Increase in species was primarily because of the addition of guilds rather than guild expansion. Johnson (1975) and Thompson (1978) also noted the importance of a tree layer in increasing number of guilds. This observation suggested addition of species was because of increased environmental patchiness of the tree layer rather than an increase in

resource productivity. These findings supported the suggestion of Karr (1975, 1976) that number of feeding sites and resource types determined the number of species. However, Karr (1976) also suggested productivity governed the number of individuals that breed in an area. Contrariwise, Willson (1974) found abundance and biomass of birds were not related to productivity of habitats.

Seasonal variation of the environment also was considered an important factor influencing community structure (Karr 1976, 1980, Weins and Rotenberry 1980, Salt 1953). Because guild classification was based on patterns of resource use, seasonal variation of guild composition facilitated assessment of environmental factors important in affecting community structure. Karr (1976) suggested seasonal stability of species diversity within foraging guilds corresponded with seasonal stability of the selected foraging microhabitat of the guild and the stability of resources within the microhabitat.

Most studies of guild composition primarily consisted of description and analysis of the number, composition, and distribution of guilds, or species composition and organization within guilds; guild diversity and evenness were not used as indices of community structure. The objective of this study was to use guilds (guild diversity, richness, evenness, and patterns of guild occurrence) and bird density and biomass to describe avian community structure, and to analyze and interpret differences in community structure as affected by season and habitat variation. Avian data collected from a variety of habitats, during all seasons, on islands of the Columbia River, Oregon, provided a basis on which to perform the analysis of guild structure.

## METHODS

### Habitat Apportionment

Habitats on each of the 3 islands were previously described by Crawford and Dorsey (1980). Miller Sands island and spit were divided into 6 habitats: tree-shrub (MSTS), upland (MSUP), island beach (MSB), spit beach (MSSB), spit upland (MSSU), and large marsh complex (MSM) (Appendices, Fig. 9). West Sand also was divided into 6 habitats: tree-shrub (WSTS), transition<sup>1</sup> (WSTR), upland (WSUP), diked upland (WSDU), marsh (WSM), and beach (WSB) (Appendices, Fig. 10). Jim Crow Sands was apportioned into the 3 following habitats: beach (JCB), marsh (JCM), and upland (JCUP) (Appendices, Fig. 11).

### Bird Census Techniques

All birds observed within habitat boundaries (including birds flying over a habitat, under 40 m) were censused by Geoff Dorsey with the variable circular-plot method (Reynolds et al. 1980). Density estimates (birds/ha) and community parameters computed from the data were suited to comparison of bird communities among seasons or habitats because season and habitat related variation in detectability of birds was accounted for (Reynolds et al. 1980). Avian samples for each habitat consisted of the pooled results from 10 census stations, stations were placed randomly within each habitat. Morrison et al. (1981) suggested 10 replicates per sample provided an accurate

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<sup>1</sup> Transition habitat consisted of mixed upland and tree-shrub habitat.

description of a variety of bird communities. Avian censuses were conducted each month; 3 monthly censuses (replicates) were conducted each season within each habitat: summer (June, July, August), fall (September, October, November), winter (December, January, February), and spring (March, April, May). Bird species data were organized into a 15 (habitat) X 4 (season) X 3 (monthly replicate) X 126 (species) array of densities (total 180 samples). Species densities (birds/ha) were multiplied by the species' corresponding average body weight, derived from literature, to obtain a 15 X 4 X 3 X 126 array of species biomass (g/ha).

#### Guild Classification

All bird species observed on the 3 islands were apportioned into the major type of environment in which they foraged (Table 1); within these categories, species were placed into feeding guilds based on their major food item, foraging mode, and foraging substrate. Summaries of life histories (Martin et al. 1951, Bent 1919, 1921, 1922, 1923, 1925, 1926, 1927, 1929, 1937, 1938, 1939, 1940, 1942, 1946, 1948, 1950, 1953, 1958, 1968) and personal communication with G. Dorsey and D. Edwards provided the basis for guild assignments. Species that changed their feeding habits seasonally were reclassified into the appropriate guild. An identification number was assigned to each guild (Table 1) in order to simplify reporting and discussion of results. Species observed and their guild classification are listed in Appendix 2.

#### Description and Analysis of Avian Community Structure

Avian density, biomass, guild diversity, and the 2 components of

Table 1. Classification scheme for bird guilds on islands of the lower Columbia River, Oregon, 1978-1979.

Location	Major food item <sup>a</sup>	Foraging mode	Foraging substrate	Guild #	Typical species	
Terrestrial	V <sup>b</sup> /I <sup>c</sup>	Raptorial	Ground	1	Red-tailed hawk	
		Raptorial	Air	2	Cooper's hawk	
	I	Sally	Air	3	Western flycatcher	
		Glean	Foliage/Twig	4	Black-capped chickadee	
		Glean/Probe	Bark	5	Downy woodpecker	
		Glean	Ground/Foliage	7	Bewick's wren	
	Plant	Glean	Foliage	8	Cedar waxwing	
		Glean	Ground/Foliage	9	American goldfinch	
	I/Plant	Glean	Ground/Foliage	11	Song sparrow	
	Nectar	Glean	Floral	12	Rufous hummingbird	
	Aquatic	V	Raptorial	Water	13	Bald eagle
Surface dive			Water	14	Common merganser	
Aerial dive			Water	15	Caspian tern	
Wade			Water	16	Great blue heron	
I		Surface dive	Water	17	Bufflehead	
		Glean	Water	29	Northern phalarope	
		Wade	Water	18	Greater yellowlegs	
		Glean/Shallow Probe	Shore/Water	24	Western sandpiper	
		Medium/Deep Probe	Shore/Water	25	Long-billed dowitcher	
Plant		Dabble	Water	21	Mallard	
		Surface Dive	Water	20	Ruddy duck	
V/I		Glean/Scavenge	Water	19	Western gull	
I/Plant		Surface Dive	Water	27	Greater scaup	
Aquatic/Terrestrial		I	Glean/Probe	Ground/Shore	22	Killdeer
			Glean	Foliage	23	Long-billed marsh wren
			Glean	Air	6	Barn swallow
	Plant	Graze	Ground/Shore	26	Canada goose	
	V/I/Plant	Omnivorous	Arboreal/Ground/Shore	28	Common crow	

<sup>a</sup> Note that the major food item can change with season, see Appendix 4 for listing of bird species and their guild classification.

<sup>b</sup> V=Vertebrate

<sup>c</sup> I=Invertebrate

diversity, guild richness, and evenness, were used to describe community structure for each sample. Total avian density and biomass were calculated from summation of species densities and biomasses, respectively (ie. sum across 4th dimension of array of species densities and biomasses). The array of species densities was transformed into a 15 X 4 X 3 X 28 array of guild densities by summing density estimates for the constituent species of each guild. Guild diversity, richness, and evenness were derived from the data matrix of guild densities. Guild diversity was calculated with the Shannon and Weaver (1949) information index,  $H'_G = -\sum_{i=1}^n (p_i \log_e p_i)$ , where  $n$  is the number of guilds in a sample and  $p_i$  is the proportion of total density that consisted of the  $i$ th guild. Number of guilds per sample was used as an index of guild richness ( $R_G$ ). Evenness, with which bird density was apportioned among guilds, was estimated by the ratio of observed diversity index to the maximum value of diversity given the same number of guilds,  $J'_G = H'_{obs} / \log_e n$  (Pielou 1966), where  $H'_{obs}$  is the estimated Shannon-Weaver (1949) index and  $n$  is the number of guilds within the sample.

Prior to statistical analysis, all 5 community parameters were examined for normality of their distributions. Number of guilds did not require transformation; natural logarithm transformations of avian density and biomass were applied to improve normality of the data. Guild diversity was converted to its square root and evenness of guilds was transformed to the arcsin of the square root, both transformations commonly were used to improve normality of data (Zar 1974).

Two-way multivariate analysis of variance (MANOVA) (Morrison 1976) was used to test for significance of the main effects of season and



habitat on the 5 indices of community structure. The preliminary test for interactive effect between season and habitat, ie. differential seasonal variation of community structure indices among habitats, was significant ( $P < 0.01$ ), which implied tests for effects of habitats on community structure should be examined within each season category and tests for season effects should be examined within each habitat (Morrison 1976). This analytic approach was not used because the sample size (3) for each season-habitat combination was considered inadequate to indicate meaningful patterns of community structure variation among seasons and habitats. In order to minimize interactive effects and maintain a sufficient sample size, the 15 habitats were reclassified into 3 generalized habitat categories based on similarity of their physiognomy and guild assemblage: tree-shrub (TRSH), upland (UPL), and beach-marsh (BEMA). Generally, insignificant season-habitat interactive influence was indicated within the 3 generalized habitat groups with 2-way MANOVA, thus main effects of season and habitat on avian community structure (avian density, biomass, guild diversity, richness, and evenness) were examined within each habitat group. In order to examine differences in community structure among the generalized habitat groups, comparisons of habitat groups were made within each of the 4 seasons (4 tests) with 1-way MANOVA. Wilks lambda statistic was used to determine significance of all MANOVA tests. If a significant difference in community structure was indicated by MANOVA, stepwise canonical analysis of discriminance (CAD) (Pimental 1979) was used to examine the pattern and degree of variation among seasons or habitats, and to determine what community parameters were important in accounting for

differences. Canonical analysis of discriminance affords maximum separation among groups (eg. seasons or habitats) in as few canonical variables as possible (Pimental 1979). Each canonical variable is a linear function of the selected community parameters. Relative importance of canonical variables was evaluated by examination of canonical correlation coefficients ( $R_C$ ), which measure the degree to which canonical variables afforded discrimination among groups. Separation of groups with respect to canonical variables was related to differences in community structure by examining correlations between the original community parameters and canonical variables. Canonical variables that demonstrated an interpretable separation among groups were plotted in order to examine the degree and pattern of separation among groups (seasons or habitats).

Distribution of guilds among seasons was analyzed with CLUSB, an iterative clustering computer program. The CLUSB algorithm minimized within cluster variation for a specified number of clusters (McIntire 1973), thus guilds that had similar patterns of seasonal occurrence tended to form clusters. The array of guild densities was partitioned into 3 arrays, 1 for each island. Guild densities for each season were averaged over all habitats. Average density of each guild,  $\bar{y}_{ij}$ , where  $i$  is the guild subscript and  $j$  is the season subscript, was transformed by the following formula:  $\ln 1000(\bar{y}_{ij} / \sum_{i=1}^n y_{ij}) + 1$ ; where  $n$  is the number of guilds occurring in season  $j$ . This transformation equalized samples for each season and reduced the tendency of abundant guilds to cluster regardless of their seasonal occurrence. Additionally, rare guilds (those composed of less than 0.35% of the total density in each

season) were eliminated, which reduced clustering of guilds on the basis of infrequent occurrence and also reduced formation of single guild clusters. Canonical analysis of discriminance was used to relate guild clusters to their pattern of occurrence within seasons. Clustering of guilds with respect to occurrence among habitats was performed in a manner similar to that described for clustering of guilds on the basis of seasons.

## RESULTS

Patterns of Community Structure Indices

Intra-Habitat Habitat-season interaction of community parameters within the tree-shrub habitat group (MSTS, WSTS, and WSTR) was significant ( $P < 0.05$ ). Interaction was primarily because of high fall bird densities within MSTS, relative to WSTS and WSTR (Fig. 1). Because examination of the seasonal pattern of bird density within MSTS from 1976-1977 (Fig. 1) (calculated from data from Crawford and Edwards 1978) indicated the significant divergence among densities in tree-shrub habitats (1978-1979) may have been related to random sampling error, MSTS, WSTS, and WSTR were therefore maintained as a single habitat group for further analysis. Provision of sufficiently large sample sizes for multivariate analysis (Green 1979) was of additional importance in maintaining the 3 tree-shrub habitats as 1 group.

Seasonal variation of community structure within tree-shrub habitats was significant ( $P < 0.001$ ) as evidenced by separation of seasons with respect to the 1st canonical variable (CV1) (Fig. 2). The canonical structure (Table 2) indicated guild diversity ( $H'_G$ ) and its 2 components richness ( $R_G$ ) and evenness ( $J'_G$ ), and avian biomass were important in discriminating seasons. Numerical dominance of tree-shrub habitats during fall and winter by guilds 4 (insectivorous foliage/twig gleaners), 7 (insectivorous ground/foilage gleaners), and 9 (granivorous ground/foilage gleaners), which together constituted 93% of total bird density during fall and 86% during winter, was lower during spring and summer (28 and 48%, respectively). High levels of  $J'_G$  during spring and



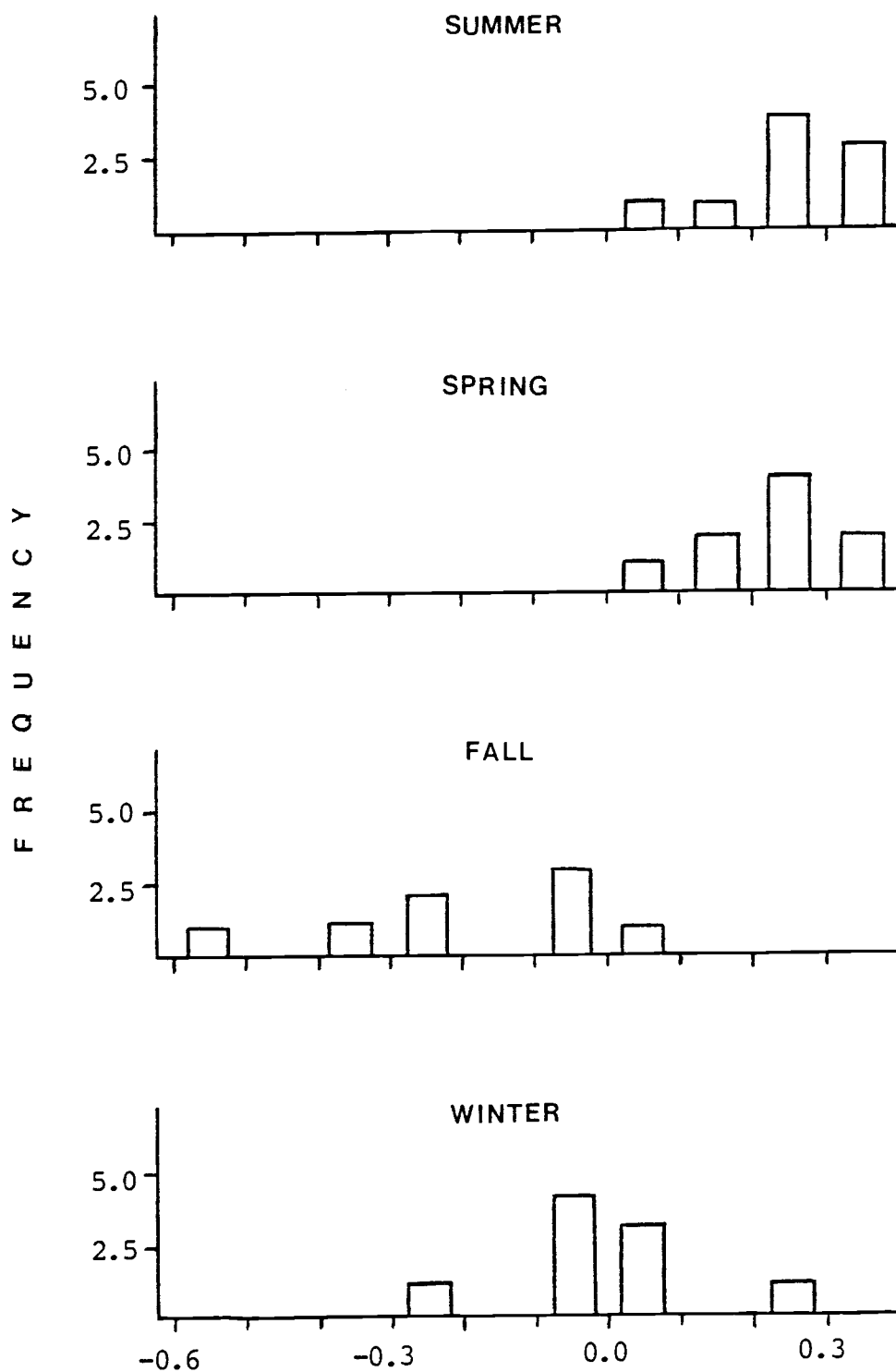


Fig. 2. Histograms of 1st canonical variable scores, demonstrating patterns of seasonal variation of community structure within tree-shrub habitats on islands of the lower Columbia River, 1978-1979.

Table 2. Mean community parameters and correlations with 1st canonical variable (canonical structure), demonstrating variation among seasons within the tree-shrub habitat group on islands of the lower Columbia River, 1978-1979.

Community parameters	Season				Canonical structure cv1 <sup>a</sup>
	Summer N=9	Spring N=9	Fall N=9	Winter N=9	
$R_G$ (# of guilds)	7.4 (1.6) <sup>b</sup>	8.4 (1.5)	5.7 (2.1)	5.7 (2.1)	0.711
Density (birds/ha)	12.19 (8.19)	12.73 (5.48)	11.73 (10.08)	9.83 (4.87)	0.213
Biomass (g/ha)	540.7 (189.5)	681.8 (755.3)	293.0 (199.2)	468.0 (491.8)	0.597
$H'_G$	1.63 (0.22)	1.57 (0.24)	0.95 (0.35)	1.06 (0.24)	1.000
$J'_G$	0.821 (0.051)	0.742 (0.104)	0.559 (0.175)	0.636 (0.109)	0.863

<sup>a</sup> Canonical correlation coefficient equals 0.742.

<sup>b</sup> Standard deviation shown in parentheses.

summer (Table 2) resulted from the change in numerical dominance of these 3 guilds. Values of  $R_G$  were high within tree-shrub habitats during spring and summer and corresponded with arrival and residence of guilds 3 (flycatchers), 6 (swallows), and 12 (hummingbirds). Seasonal patterns of guild diversity, richness, and evenness reflected changes in community structure from a breeding to a non-breeding community. Although numbers of nests were not censused in the various habitats, canopy layer of arboreal habitats was commonly used as nest sites by common crows (scientific names of bird species listed in Appendix 2) (guild 28). Downy woodpeckers (guild 5), black-capped chickadees (guild 4), tree swallows (guild 6), and members of the ground/foilage gleaning guilds 7 and 11 (Bewick's wrens, winter wrens, and starlings)

nested in tree cavities and crevices. Middle to low arboreal and shrub layers were nest sites of such species as western flycatchers (guild 3), orange-crowned warblers (guild 4), rufous hummingbirds (guild 12), and members of the ground/foilage gleaning guilds (American robins, American goldfinches, song sparrows, and Swainson's thrushes). Mallards (guild 21) nested among ground vegetation of tree-shrub habitats.

Low bird biomass in fall corresponded with increased numerical importance of guilds 4 and 7 (comprising 66.4% of total density), which primarily consisted of small species (chickadees, kinglets, warblers, and wrens). Minor seasonal variation of bird density (Table 2) was in part because of different seasonal patterns of density among tree-shrub habitats (Fig. 1), ie. season-habitat interaction. Excluding MSTs (1978-1979), some reduction in bird density during fall was indicated (Fig. 1). Comparison of community parameters among the 3 tree-shrub habitats indicated no significant difference ( $P > 0.05$ ).

No significant interaction was found between seasons and upland habitats (JCUP, MSUP, WSUP, WSDU) ( $P > 0.05$ ). Community structure indices differed among seasons within upland habitats ( $P < 0.001$ ). All 5 community parameters were important in describing seasonal differences (Table 3) with respect to CV1 (Fig. 3). Avian density and richness of guilds were elevated from low levels in winter through spring and reached highest levels in summer; figures for fall were intermediate between winter and spring (Table 3). Biomass was highest in spring, lowest in fall, and intermediate during summer and winter (Table 3). Utilization of the planted upland of Jim Crow Sands (JCSI) by guild 26 (geese) resulted in high average biomass (relative to low bird density)



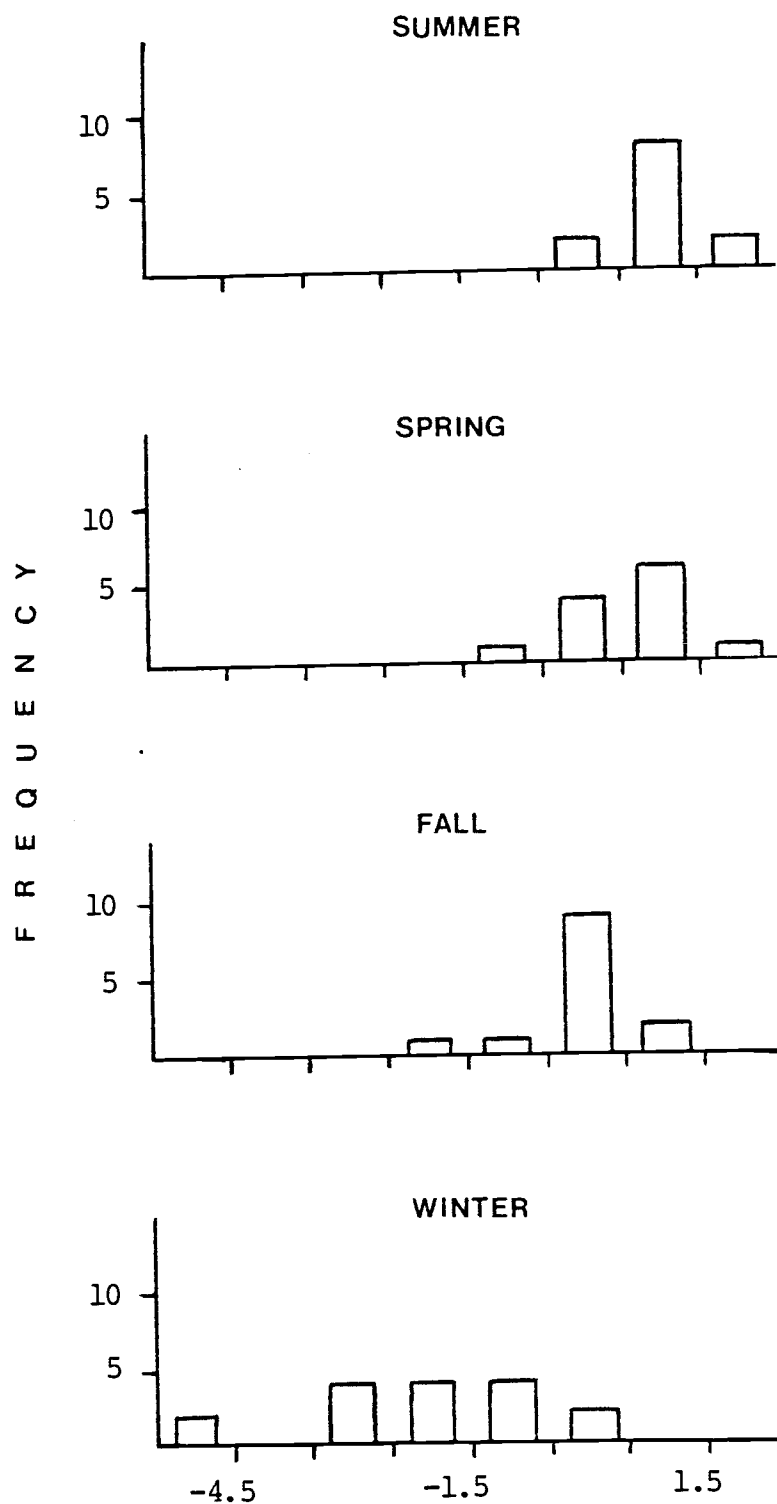


Fig. 3. Histograms of 1st canonical variable scores, demonstrating patterns of seasonal variation of community structure within upland habitats on islands of the lower Columbia River, 1978-1979.

Table 3. Mean community parameters and correlations with 1st canonical variable (canonical structure), demonstrating variation among seasons within the upland habitat group on islands of the lower Columbia River, 1978-1979.

Community parameters	Season				Canonical structure Cv1 <sup>a</sup>
	Summer N=12	Spring N=12	Fall N=12	Winter N=12	
$R_G$ (# of guilds)	8.4 (1.8) <sup>b</sup>	6.8 (2.1)	5.8 (2.0)	4.1 (1.9)	0.770
Density (birds/ha)	8.53 (3.43)	5.82 (4.80)	2.92 (2.08)	1.71 (2.35)	0.944
Biomass (g/ha)	517.3 (276.7)	636.8 (865.0)	364.3 (268.7)	586.3 (1202.0)	0.781
$H'_G$	1.20 (0.28)	1.14 (0.29)	1.04 (0.55)	0.56 (0.36)	0.741
$J'_G$	0.570 (0.128)	0.612 (0.121)	0.589 (0.274)	0.373 (0.232)	0.565

<sup>a</sup> Canonical correlation coefficient equals 0.700.

<sup>b</sup> Standard deviation shown in parentheses.

and high variability of bird biomass during winter. Average guild evenness was lowest during winter, however variability reduced the relative importance of  $J'_G$  in discriminating seasons within upland habitats (Table 3). Guild diversity demonstrated a seasonal pattern intermediate between the seasonal patterns of its 2 components, guild richness and evenness (Table 3). Less definitive contrast between breeding (spring and summer) and non-breeding (fall and winter) seasons, as compared to seasonal variation within tree-shrub habitats, may be related to the secondary importance of upland habitats to breeding birds. Upland habitats provided essentially 2 types of nesting strata, herbaceous vegetation with occasional shrubs and sparsely vegetated or bare ground. Ground/foilage gleaners (savannah sparrow, white-crowned

sparrows, horned larks, and song sparrows) were the common nesting guilds within upland habitats. Mallards (guild 21) and killdeer (guild 22) occasionally nested in upland habitats. Community parameters were compared among the 4 upland habitats and no significant differences were found ( $P > 0.05$ ).

Season-habitat interaction within the beach-marsh habitat group (JCB, JCM, MSB, MSSB, MSM, MSSU, WSB, and WSM) was not significant ( $P > 0.5$ ). Seasonal variation of community structure was significant ( $P < 0.001$ ), but was the least definitive of the 3 habitat groups (Fig. 2, 3,4). The key distinction among seasons was reduced avian density during winter (Table 4), which may be related to more rigorous weather conditions and reduced availability of food resources associated with water, because of ice on the river. Guild diversity, richness, and evenness demonstrated no distinct seasonal variation within the beach-marsh group. Small variation of these parameters among seasons may partially be related to minor use of beach, marsh, and spit upland habitats by nesting birds because of tidal inundation and/or lack of cover. Spotted sandpipers (guild 24) probably nested on isolated areas of Jim Crow Sands beach above the high tide line and violet-green swallows nested among driftwood on areas of beaches not exposed to high tides. Because of tidal inundation, species that typically used marsh habitats as nesting areas either did not nest on the islands or nested in other habitats. Mallards were the primary dabbling waterfowl species (guild 21) observed nesting on the islands; nests were placed in upland or tree-shrub habitats. Tabor (1976) considered the limited amount of non-tidal marshes as the primary cause of low breeding

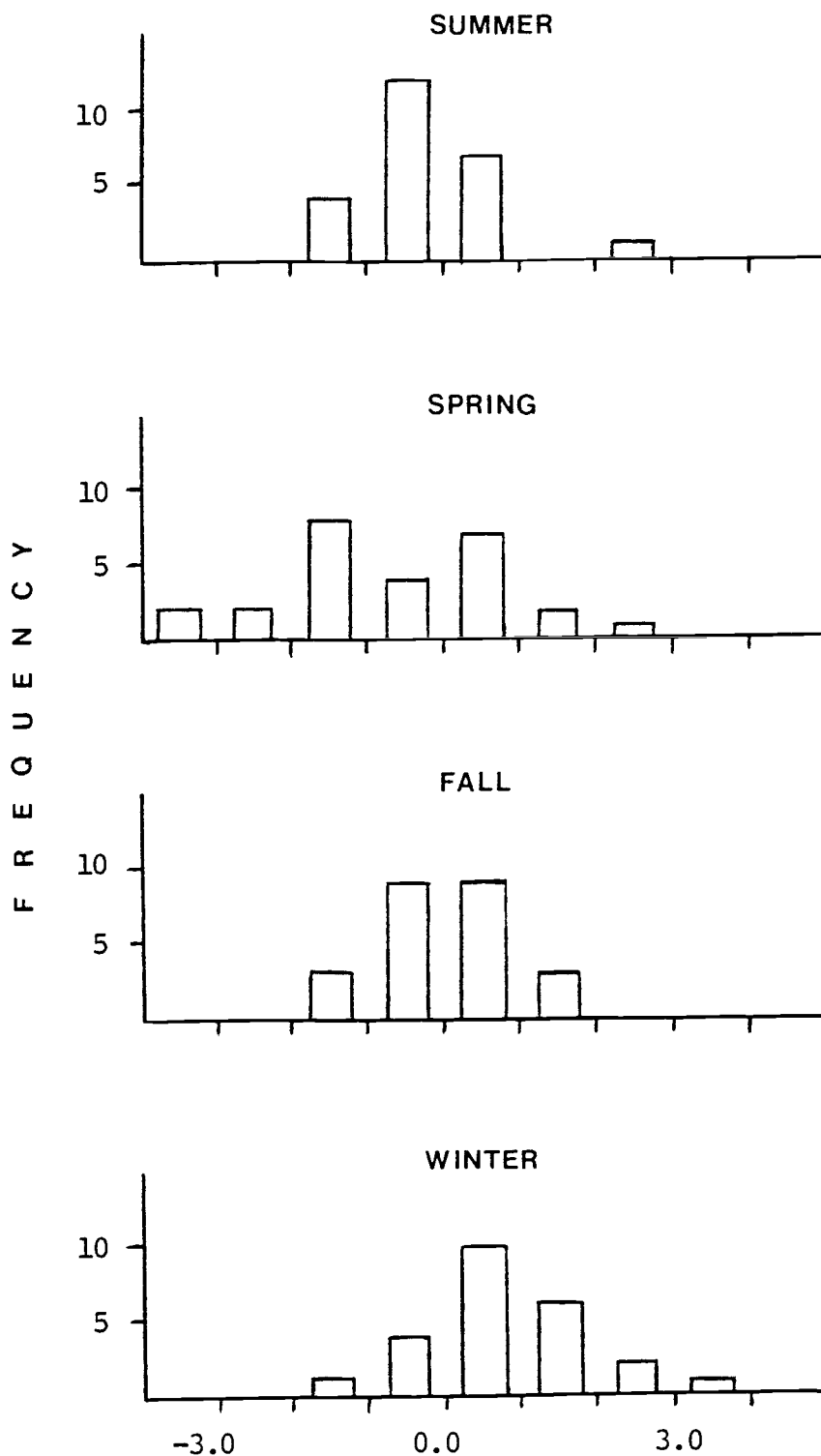


Fig. 4. Histograms of 1st canonical variable scores, demonstrating patterns of seasonal variation of community structure within beach-marsh habitats on islands of the lower Columbia River, 1978-1979.

Table 4. Mean community parameters and correlations with 1st canonical variable (canonical structure), demonstrating variation among seasons within the beach-marsh habitat group on islands of the lower Columbia River, 1978-1979.

Community parameters	Season				Canonical structure
	Summer N=21	Spring N=21	Fall N=12	Winter N=21	CV1
$R'_G$ (# of guilds)	7.0 (2.1) <sup>b</sup>	7.3 (2.8)	7.8 (2.4)	6.2 (1.7)	-0.289
Density (birds/ha)	11.38 (9.76)	29.99 (78.40)	9.20 (11.14)	3.54 (3.33)	-0.990
Biomass (g/ha)	2590.1 (2185.0)	2775.0 (4093.0)	2814.5 (2656.3)	1156.7 (879.0)	-0.551
$H'_G$	1.04 (0.33)	1.03 (0.38)	1.20 (0.45)	1.05 (0.31)	0.215
$J'_G$	0.551 (0.156)	0.532 (0.148)	0.597 (0.196)	0.586 (0.126)	0.473

<sup>a</sup> Canonical correlation coefficient equals 0.471.

<sup>b</sup> Standard deviation shown in parentheses.

densities of waterfowl on the Columbia estuary.

Comparison of community parameters among habitats within the beach-marsh habitat group indicated a significant difference ( $P < 0.005$ ) between West Sand marsh and all other habitats. Habitats were reclassified into 2 groups, beach-low marsh complex (BELM) (spit upland and all beach and marsh habitats except West Sand Island marsh) and high marsh (HM) (West Sand marsh). Greater number of guilds,  $R'_G$ , within HM was the primary distinction between the 2 groups (Table 5). More frequent occurrence within HM by the 3 ground/foilage gleaning guilds (7, 9, and 11) and rufous hummingbirds (guild 12) probably influenced higher  $R'_G$  levels. Guilds 7, 9, 11, and 12 occurred in 33, 58, 67, and 25% of the samples, respectively, within the high marsh, and on the

Table 5. Mean community parameters and correlations with 1st canonical variable (canonical structure), demonstrating variation among habitats within the beach-marsh habitat group on islands of the lower Columbia River, 1978-1979.

Community parameters	Habitat		Canonical structure
	BELM N=84	HM N=12	CV1 <sup>a</sup>
R <sub>G</sub> (# of guilds)	6.7 (1.9) <sup>b</sup>	10.1 (2.9)	-0.860
Density (birds/ha)	14.43 (43.25)	7.20 (5.65)	0.047
Biomass (g/ha)	2530.2 (2882.6)	960.8 (652.1)	0.383
H' <sub>G</sub>	1.05 (0.36)	1.31 (0.35)	-0.572
J' <sub>G</sub>	0.566 (0.163)	0.573 (0.124)	-0.195

<sup>a</sup> Canonical correlation coefficient equals 0.566.

<sup>b</sup> Standard deviation shown in parentheses.

average, 6, 20, 17, and 5% of the samples, respectively, within the beach-low marsh habitats. Greater occurrence of the 3 ground/foilage gleaning guilds was probably related to the combination of juxtaposition of high marsh to upland and tree-shrub habitats (Appendices, Fig. 10), greater vegetative cover than beach-low marsh habitats (Appendices, Table 12), and less tidal inundation than beach-low marsh habitats; whereas higher occurrence of guild 12 was probably primarily related to edge effect.

Inter-Habitat Significant variation of community structure among the 4 habitat groups (tree-shrub, upland, beach-low marsh, and high marsh) was demonstrated during all 4 seasons ( $P < 0.001$ ). During summer, biomass of birds, diversity, evenness, and number of guilds demonstrated

differences in community structure among the 4 habitat groups (Table 6). Levels of  $H'_G$  and  $J'_G$  were lowest within the beach-low marsh group (BELM), intermediate within the upland habitat group (UPL), and reached highest levels within high marsh (HM) and the tree-shrub group (TRSH). Although both HM and TRSH had relatively high guild diversities, high diversity within the tree-shrub group was primarily due to a high evenness of guilds. Guild diversity within the high marsh was related more to its high guild richness (demonstrated by separation on the 2nd canonical axis, Fig. 5). High evenness of guilds within TRSH possibly was related to the importance of this type habitat to breeding birds. The high marsh was regularly utilized by aquatic associated guilds and the 3 ground/foilage gleaning guilds (7, 9, and 11), which produced a high level of  $R_G$  (Table 6). Low evenness within upland habitats resulted from dominance by guilds 7 and 6 (constituted 39 and 25% of the bird density, respectively). Numerical dominance of BELM by guilds 19 (gulls), 24 (gleaning/shallow probing shorebirds), and 6 (swallows), which together comprised 83% of the bird density, resulted in a lowered  $J'_G$  (Table 6). Guilds 6 and 19 were less dominant within HM, thus  $J'_G$  was greater than that of BELM (Table 6). The beach-low marsh group was further discriminated from the other habitat groups by a larger biomass of birds (Table 6), which was because of greater abundance of large birds within the beach-low marsh habitats.

Relationships among community structure of the 4 habitat groups during spring were similar to that observed during summer. Relative positions of the 4 habitat groups with respect to CV1 (Fig. 6) corresponded to biomass of birds and diversity and evenness of guilds

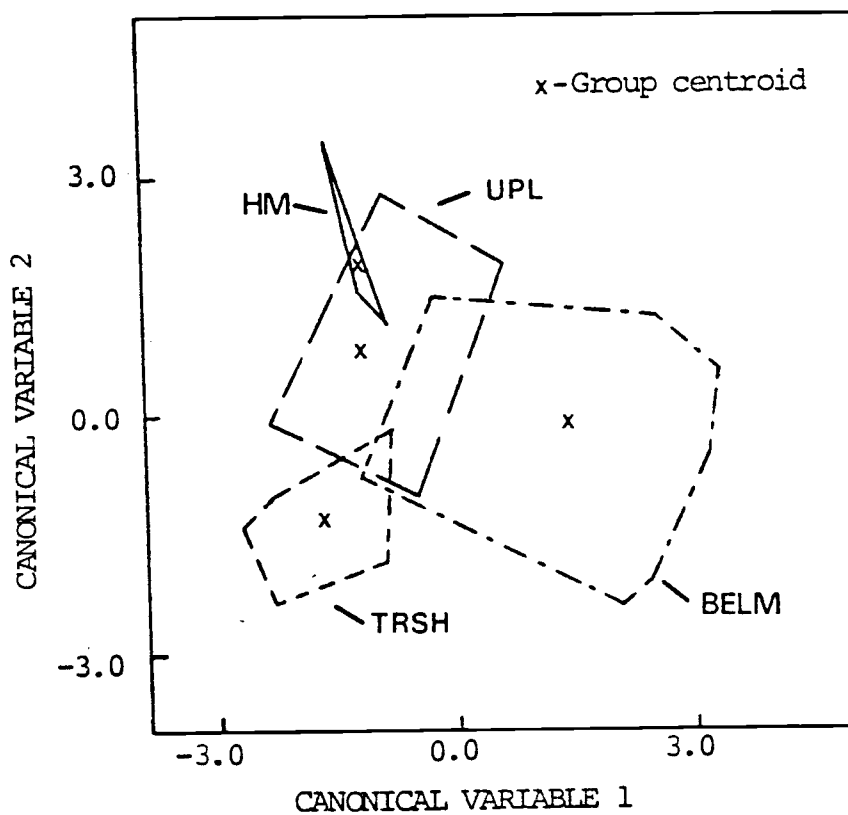


Fig. 5. Location of habitat groups in canonical discriminant space, demonstrating variation in community structure among habitats on islands of the lower Columbia River, summer 1978.



Table 6. Mean community parameters and correlations with 1st and 2nd canonical variables (canonical structure), demonstrating variation among habitat groups, tree-shrub, upland, high marsh, and beach-low marsh, on islands of the lower Columbia River, summer 1978.

Community parameters	Habitat				Canonical structure	
	TRSH N=9	UPL N=12	HM N=3	BELM N=21	CV1 <sup>a</sup>	CV2 <sup>b</sup>
$R_G$ (# of guilds)	7.4 (1.6) <sup>c</sup>	8.4 (1.8)	11.0 (1.7)	6.4 (1.5)	0.539	0.622
Density (birds/ha)	12.19 (8.19)	8.53 (3.43)	5.47 (0.23)	12.22 (10.18)	0.094	-0.340
Biomass (g/ha)	540.7 (189.5)	517.3 (276.7)	640.0 (210.3)	2868.7 (2198.6)	0.831	-0.191
$H'_G$	1.63 (0.22)	1.20 (0.28)	1.51 (0.15)	0.98 (0.29)	-0.813	0.228
$J'_G$	0.821 (0.051)	0.570 (0.128)	0.635 (0.096)	0.538 (0.161)	-0.634	-0.561

<sup>a</sup> Canonical correlation coefficient equals 0.811.

<sup>b</sup> Canonical correlation coefficient equals 0.691.

<sup>c</sup> Standard deviation shown in parentheses.

(Table 7). High average biomass of birds within BELM discriminated this habitat group from the 3 other habitat groups (Table 7). Diversity and evenness of guilds was highest within the tree-shrub group and lowest within the beach-low marsh group (Table 7). Upland habitats had low to intermediate levels of  $H'_G$  and  $J'_G$ . Guild diversity was intermediate within high marsh, but guild evenness was low, which indicated that the intermediate level of  $H'_G$  was because of high number of guilds observed within HM (Table 7). Relative position of habitats with respect to CV2 (Fig. 6) was related to a confounding of many patterns; the most evident difference was the high number of guilds within HM (Table 7).

Separation of habitat groups during fall was caused primarily by

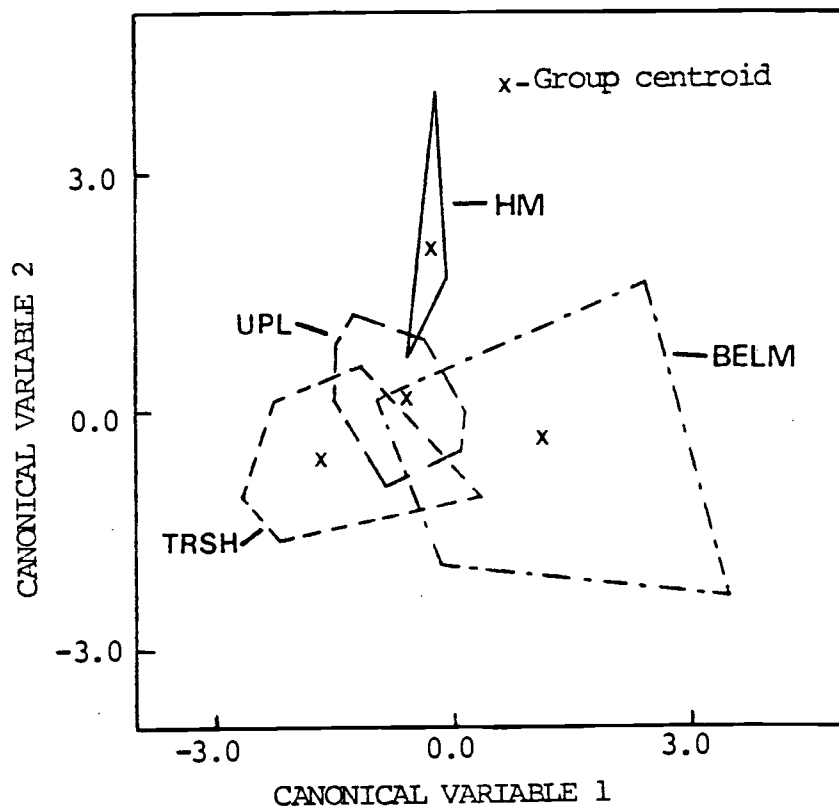


Fig. 6. Location of habitat groups in canonical discriminant space, demonstrating variation in community structure among habitats on islands of the lower Columbia River, spring 1979.

Table 7. Mean community parameters and correlations with 1st and 2nd canonical variables (canonical structure), demonstrating variation among habitat groups, tree-shrub, upland, high marsh, and beach-low marsh, on islands of the lower Columbia River, spring 1979.

Community parameters	Habitat				Canonical structure	
	TRSH N=9	UPL N=12	HM N=3	BELM N=21	CV1 <sup>a</sup>	CV2 <sup>b</sup>
$R_G$ (# of guilds)	8.4 (1.5) <sup>c</sup>	6.8 (2.1)	10.7 (4.6)	6.9 (2.3)	-0.286	0.375
Density (birds/ha)	12.73 (5.48)	5.82 (4.80)	10.38 (11.93)	32.79 (83.60)	0.123	-0.348
Biomass (g/ha)	681.8 (755.3)	636.8 (865.0)	881.0 (679.3)	3045.5 (4313.3)	0.746	-0.241
$H'_G$	1.57 (0.24)	1.14 (0.29)	1.28 (0.29)	0.99 (0.39)	-0.668	-0.072
$J'_G$	0.742 (0.104)	0.612 (0.121)	0.555 (0.096)	0.529 (0.156)	-0.639	-0.255

<sup>a</sup> Canonical correlation coefficient equals 0.768.

<sup>b</sup> Canonical correlation coefficient equals 0.574.

<sup>c</sup> Standard deviation shown in parentheses.

differences in biomass of birds and number of guilds supported (Table 8). Contrast among bird biomass within BELM, TRSH, and UPL was represented along the 1st canonical variable (CV1) (Fig. 7). HM supported an intermediate biomass of birds (Table 8) as indicated by its position along CV1 (Fig. 7). High marsh supported the greatest number of guilds, which paralleled the high guild diversity and resulted in separation from the other habitats with respect to CV2 (Fig. 7). Although tree-shrub and beach-low marsh habitat groups supported high average densities, the large variability of density minimized its importance in discriminating habitats (Table 7). No discernable pattern among habitats was demonstrated with regard to guild evenness.

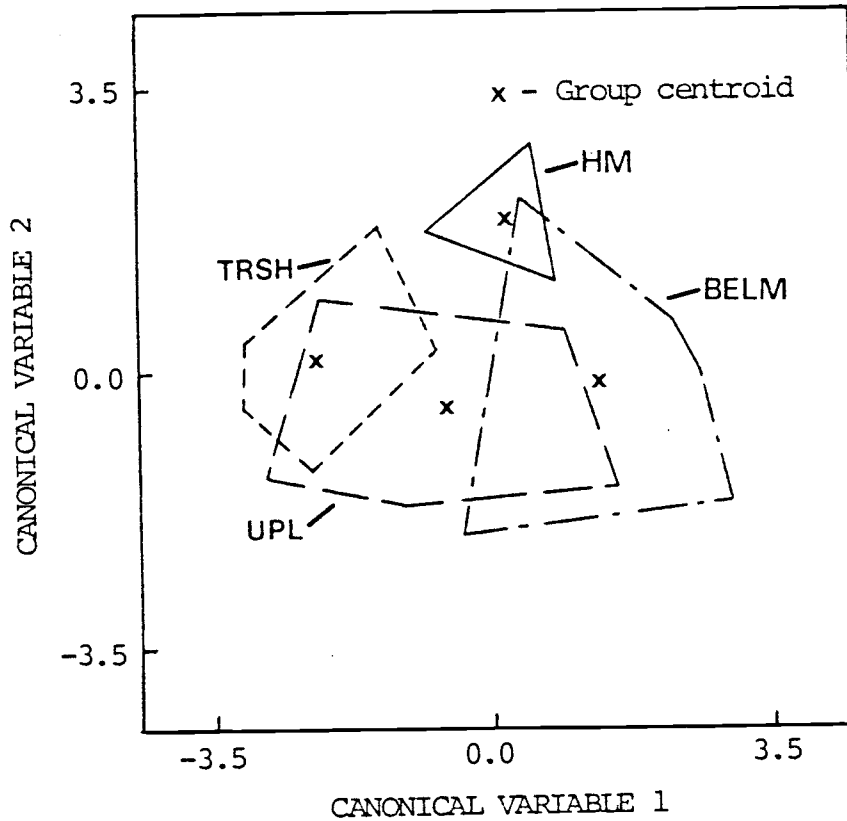


Fig. 7. Location of habitat groups in canonical discriminant space, demonstrating variation in community structure among habitats on islands of the lower Columbia River, fall 1978.

Table 8. Mean community parameters and correlations with 1st and 2nd canonical variables (canonical structure), demonstrating variation among habitat groups, tree-shrub, upland, high marsh, and beach-low marsh, on islands of the lower Columbia River, fall 1978.

Community parameters	Habitat				Canonical structure	
	TRSH N=9	UPL N=12	HM N=3	BELM N=21	CV1 <sup>a</sup>	CV2 <sup>b</sup>
R <sub>G</sub> (# of guilds)	5.7 (2.1) <sup>c</sup>	5.8 (2.0)	11.0 (1.7)	7.3 (2.1)	0.384	0.895
Density (birds/ha)	11.73 (10.09)	1.92 (2.08)	6.78 (3.02)	9.54 (11.86)	-0.073	0.500
Biomass (g/ha)	293.0 (199.2)	364.3 (268.7)	1151.6 (956.2)	2994.9 (2783.8)	0.790	0.417
H' <sub>G</sub>	0.95 (0.35)	1.04 (0.55)	1.52 (0.20)	1.15 (0.46)	0.265	0.391
J' <sub>G</sub>	0.559 (0.175)	0.589 (0.274)	0.637 (0.079)	0.592 (0.208)	0.129	0.012

<sup>a</sup> Canonical correlation coefficient equals 0.818.

<sup>b</sup> Canonical correlation coefficient equals 0.516.

<sup>c</sup> Standard deviation shown in parentheses.

Variation of community structure among habitat groups during winter primarily corresponded to avian density, biomass, guild diversity, and evenness (Table 9). Tree-shrub habitats supported the greatest density of birds, which discriminated this group from all other habitat groups (especially UPL and BELM) (Fig. 8 and Table 9). The greater vegetative complexity of tree-shrub habitats probably acted as protection from harsh weather conditions during winter and contributed to high bird density. Weather conditions during winter likely had considerable influence on densities in upland and beach-low marsh habitats. HM had intermediate bird density and continued to support the highest number of guilds. The dunlin (guild 25) numerically dominated HM during winter (comprising 58%

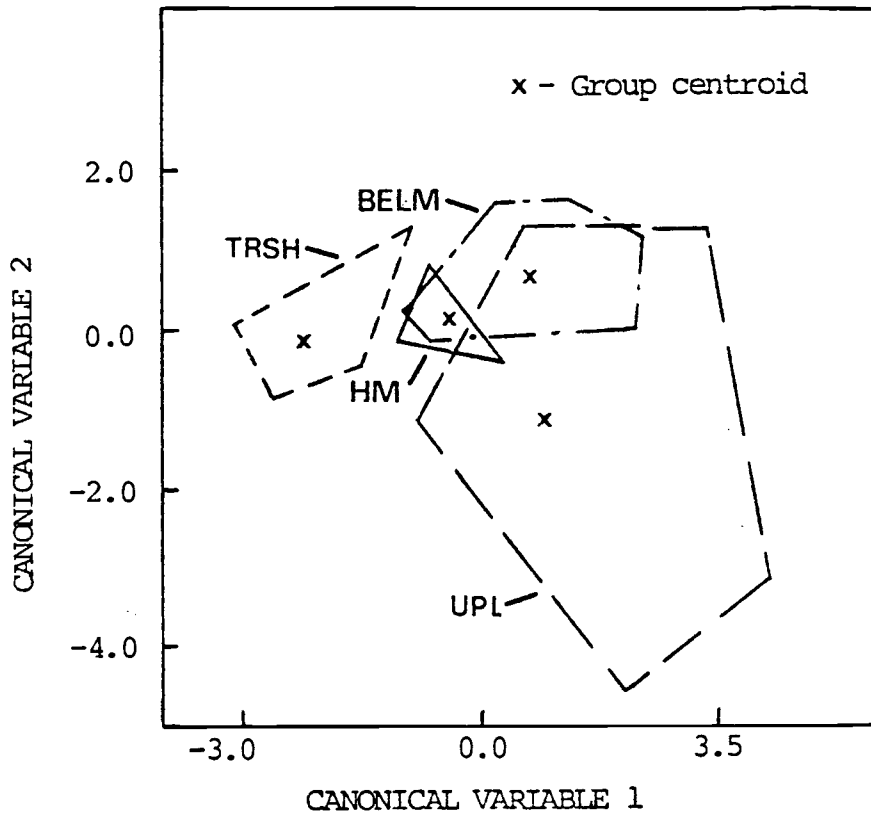


Fig. 8. Location of habitat groups in canonical discriminant space, demonstrating variation in community structure among habitats on islands of the lower Columbia River, winter 1979.

Table 9. Mean community parameters and correlations with 1st and 2nd canonical variables (canonical structure), demonstrating variation among habitat groups, tree-shrub, upland, high marsh, and beach-low marsh, on islands of the lower Columbia River, winter 1979.

Community parameters	Habitat				Canonical structure	
	TRSH N=9	UPL N=12	HM N=3	BELM N=21	CV1 <sup>a</sup>	CV2 <sup>b</sup>
$R_G$ (# of guilds)	5.7 (2.1) <sup>c</sup>	4.1 (1.9)	7.7 (2.5)	6.0 (1.6)	-0.259	0.510
Density (birds/ha)	9.83 (4.87)	1.71 (2.35)	6.18 (1.66)	3.17 (3.36)	-0.756	0.434
Biomass (g/ha)	468.0 (491.8)	586.0 (1202.0)	770.9 (421.3)	1211.8 (919.4)	-0.006	0.962
$H'_G$	1.06 (0.24)	0.56 (0.36)	0.94 (0.46)	1.07 (0.29)	-0.363	0.813
$J'_G$	0.636 (0.109)	0.373 (0.232)	0.466 (0.174)	0.603 (0.112)	-0.335	0.808

<sup>a</sup> Canonical correlation coefficient equals 0.784.

<sup>b</sup> Canonical correlation coefficient equals 0.604.

<sup>c</sup> Standard deviation shown in parentheses.

of the bird density) and resulted in a low level of guild evenness (Table 9); however, because of the relatively high number of guilds, diversity was intermediate, thus separation along CV2 was not evident. Low guild diversity and evenness occurred within upland habitats (indicated by position on CV2) (Fig. 8). Beach-low marsh habitats continued to support the highest biomass of birds (Table 9) but the separation was not as strong as during other seasons.

#### Guild Distribution among Seasons and Habitats

Cluster analysis of guilds according to seasonal occurrence on each of the 3 islands was summarized into 3 classes of residency: permanent,

breeding season, or non-breeding season residents (Table 10). In most cases more than 1 cluster of guilds composed a residency category; clusters of guilds within a category generally demonstrated similar patterns of seasonal occurrence but differed in relative abundance (high versus low densities). Although these residency classifications were not absolute, they provided a somewhat objective method for comparing seasonal occurrence of guilds among islands. Possible factors influencing inter-island differences in seasonal classification of guilds were in some cases better understood when guild cluster analysis according to distribution among habitats was examined.

Because there were differences in the complex of habitats present on each of the 3 islands, no one classification scheme of guilds according to patterns of occurrence in habitats could be applied. Guilds occurring on Miller Sands Island (MSI) were classified into 5 categories of habitat use (Table 11): guilds that generally utilized 1) all habitats but were most abundant in upland and arboreal habitats, 2) all habitats but were least abundant in arboreal habitats, 3) primarily upland and arboreal habitats, 4) and 5) beach, marsh, and spit upland habitats in medium and low densities, respectively. Four relatively consistent categories of habitat use were indicated by cluster analysis for West Sand Island (WSI): guilds that generally used 1) all habitats but were most abundant in upland and arboreal habitats, 2) primarily beach and marsh habitats, and minor use of upland habitats, 3) arboreal habitats, and 4) beach and marsh habitats (Table 11). Guilds 12 (rufous hummingbirds), 21 (dabbling waterfowl), and 23 (long-billed marsh wrens) formed a cluster but demonstrated an inconsistent pattern



Table 10. Classification of guilds into categories of residency on islands of the lower Columbia River, 1978-1979.

Island	Permanent Resident	Breeding-Season Resident	Non-Breeding-Season Resident
Miller Sands	4	3	1
	7	5	2
	11	6	9
	15	12	14
	19	22	17
	21	29	18
	24		20
	28		25
			26
			27
West Sand	1	2	17
	4	3	25
	5	6	26
	7	8	
	9	12	
	11	13	
	14	15	
	19		
	21		
	22		
	23		
	24		
28			
Jim Crow Sands	9	6	5
	14	7	20
	19	11	23
	21	12	
	24	15	
	25	22	
	26	29	
	28		

Table 11. Classification of guilds into categories of habitat use on islands of the lower Columbia River, 1978-1979.

Island	Habitat Use Pattern					
Miller Sands	H(TS)M(UP) L(M,B,SU,SB)	M(UP,TS)L(B) N(M,SU,SB)	H(UP,M,B,SU, SB),N(TS)	M(B,SU,SB) L(M)N(UP,TS)	L(M,B,SU,SB) N(TS,UP)	
	9	1	6	14	17	
	11	2	19	15	18	
	28	3	21	24	20	
		4	25		22	
		5			27	
		7			29	
		12				
	West Sand	H(UP,DU,TS,TR) L(M,B)	M(TS)L(TR) N(UP,DU,M,B)	H(B)M(M) L(UP)N(TS,TR)	M(M)L(B) N(UP,DU,TS,TR)	
		1	2	14	13	
6		3	19	15		
7		4	22	17		
9		5	24	25		
11		8		26		
28						
Jim Crow Sands	H(UP,M,B)	L(UP,B)N(M)	L(M,B)N(UP)	L(M)N(UP,B)		
	6	7	14	20		
	9	11	15	23		
	19	12	21			
	22	29	28			
	24					
	25					
26						

N = 0-1% of bird density in the specified habitat, 1% < L < 5%, 5% < M < 10%, H > 10%

TS = tree-shrub, TR = transition, UP = upland, DU = diked upland, M = marsh, B = beach, SB = spit beach, SU = spit upland

of occurrence among habitats. Guild 12 occurred in medium relative abundance on WSTS, WSTR, WSM, and WSDU. Guild 21 occurred in medium abundance in WSM and low densities in WSUP and WSDU. Guild 23 occurred in high densities in WSDU and low densities in WSM. Essentially 4 patterns of habitat use were indicated for Jim Crow Sands (JCSI): guilds which generally utilized 1) all habitats, 2) marsh and beach habitats, 3) upland and beach habitats, and 4) marsh habitats (Table 11).

Marsh, beach, and early successional upland habitats were common to all 3 islands. Jim Crow Sands lacked habitats with arboreal cover or late successional upland stages. Guilds 19 (gulls), 21 (dabbling waterfowl), 24 (gleaning/probing shorebirds), and 28 (common crows) were classified as permanent residents on all 3 islands, which indicated arborescent habitats and/or late upland seral stages were not requisites (although utilized by guilds 9, 21, and 28) for the permanent presence of these guilds. Seasonal patterns of occurrence for breeding season resident guilds 6 (insectivorous air gleaner) and 12 (nectar/insect floral gleaner) were the same on all 3 islands, which suggested habitat differences among the islands had minor influence on seasonal distribution of these guilds. Highest densities of guilds 7 (insectivorous ground/foilage gleaner) and 11 (omnivorous ground/foilage gleaner) on MSI and WSI were observed in upland and arboreal habitats (Table 11). Guilds 3 (insectivorous air sallyer), 4 (insectivorous foliage/twig gleaner), and 5 (insectivorous bark gleaner/prober) were associated with habitats with arboreal cover (Table 11). Guild 5 occurred year-round on MSI but was classified as a breeding season resident because of greater relative abundance during spring and summer.

Regular occurrence of guild 3 during the breeding season on MSI and WSI corresponded with the presence of arboreal cover on these islands. Guilds 3 (insectivorous air sallyer) and 4 (insectivorous foliage/twig gleaner) were eliminated from cluster analysis of JCSI because of absence or low relative abundance during all 4 seasons. Guild 5 (insectivorous bark gleaner/prober) was included in cluster analysis but was observed once on JCSI. Arboreal cover on MSI and WSI provided sources of food and nest sites for members of guilds 3, 4, and 5, available in sufficient amounts to support regular occurrence of these guilds. Absence of guild 7 (insectivorous ground/foilage gleaner) during winter on JCSI and within upland habitats on MSI and WSI indicated arboreal cover was requisite for year-round occurrence of this guild. Guild 11 (omnivorous ground/foilage gleaner) was absent from JCSI during fall and occurred in low densities during fall and winter within upland habitats on MSI and WSI, which may indicate upland areas were marginal habitats during fall and winter for guild 11. On MSI and WSI, guilds 7 and 11 included bird species that foraged in association with arboreal cover (eg. Bewick's wrens, winter wrens, common flickers, Swainson's thrushes, rufous-sided towhees, and American robins); these bird species were not observed on JCSI. Addition of arboreal-associated species to guilds 7 and 11 in conjunction with permanent residence of these 2 guilds on MSI and WSI may suggest greater seasonal stability of terrestrial food resources (largely invertebrates) was provided by arboreal cover. Year-round occurrence of guild 9 (herbivorous/granivorous ground/foilage gleaner) on JCSI, in contrast to seasonal absence of the other ground/foilage gleaning guilds (7 and 11) implied terrestrial

plant food resources were seasonally less variable than invertebrate food resources on JCSI. Although guild 9 was classified as a non-breeding season resident on MSI, members of guild 9 utilized MSI during the breeding season in intermediate numbers. Discrepancy in classification of guild 9 on MSI may be because of random sampling error, or established plantings in the non-censused portion of MSI upland may have influenced distribution of guild 9.

Guild 8 (frugivorous foliage gleaner) only occurred on WSI, which may be related to the later successional stage of portions of the tree-shrub habitat on WSI. Guilds 1 (vertebrate ground raptor) and 2 (vertebrate air raptor) demonstrated different seasonal patterns of distribution on MSI and WSI, however they occurred in greater relative abundance and during more seasons than on JCSI. Relatively few perch sites, depauperate rodent, amphibian, and reptilian populations, and the small size of JCSI probably reduced occurrence of terrestrial associated raptors (guilds 1 and 2). Guild 23 (insectivorous foliage/shore gleaner) only occurred as a permanent resident on WSI. Although long-billed marsh wrens (guild 23) were observed in WSM they primarily occurred in the diked upland (WSDU), a type of habitat not available on JCSI and MSI. Rare occurrence of guild 23 on JCSI and MSI indicated foraging and nesting by this guild was limited in marsh habitats because of tidal inundation, wave action, and unsuitable vegetation. Guild 23 was the only invertebrate foraging guild to occur in an upland habitat year-round. Presence of standing dead vegetation during winter (rock/litter category, Appendices, Table 12) may have provided a stable microhabitat not present in the other uplands.

In general, members of guilds 13, 14, 15, 16, 17, 18, 19, 20, 21, 22, 24, 25, 27, and 29 (see Table 1 for description of guilds) were primarily associated with aquatic habitats and did not breed on the islands. Tidal inundation of marsh habitats and large portions of beach habitats probably influenced this pattern of seasonal occurrence. A small percentage of members of guilds 19 (gulls), 21 (dabbling waterfowl), 22 (ground/shore gleaner), and 26 (ground/shore gleaner) used nest sites in upland or spit upland habitats. Some members of guild 21 (mallards) utilized habitats with arboreal cover for nest sites. Some members of guilds 14 (piscivorous surface diver), 15 (piscivorous aerial diver), and 19 nested in areas adjacent to the islands and utilized the islands for foraging. Additionally, year-round presence of guilds 14, 15, 19, 21, 24 (glean/shallow probing shorebirds), and 25 (deep probing shorebirds) on all or some of the islands was in part related to the inclusion of different species with various timing of arrival and departure during spring and fall migration. Thus a guild could be a permanent resident on an island yet not include species that breed on the island. Guilds 16 (piscivorous wader), 17 (invertebrate foraging surface diver), 18 (invertebrate foraging wader), 20 (herbivorous/granivorous surface diver), and 27 (omnivorous surface diver) were classified as non-breeding residents; the majority of species within these guilds and within guilds 21, 24, 25, and 26 either migrated north or to other areas of the Pacific Northwest to breed. The northern phalarope (guild 29) was classified as a breeding season resident on JCSI; however this species (guild) has an arctic breeding range.

## DISCUSSION

Results of this study indicated examination of guild structure of avian communities facilitated understanding of some of the effects of season and habitat variation on bird communities. Classification of species into guilds resulted in reduced dimensionality of the community components from 126 species to 28 guilds, which simplified analysis and conceptualization of avian community structure. The guild approach, as used in this study, involved circular reasoning in that bird species were classified into guilds according to their method of food resource use; then patterns of guild structure variation were related back to the food resource. Analysis of bird community structure based on categories of food resource utilization may have confounded effects related to other resource requirements (eg. nest sites, roost sites, and thermal cover). However, food resource partitioning frequently was suggested as a major mechanism influencing community structure (Cody 1974, Karr 1976, 1980, Holmes et al. 1979). Thus, the investigator felt clarification of food resource related mechanisms by guild analysis was appropriate for examining avian community structure.

From the perspective of guild structure of bird communities 4 habitat types (tree-shrub, upland, beach-low marsh, and high marsh) were described in this study. Seasonal variation of bird density was minor within tree-shrub habitats, yet number of guilds declined during fall and winter. The combination of these 2 seasonal patterns indicated 1 or more guilds had greater bird densities during fall and winter. Lowered guild evenness during fall and winter corresponded with

increased bird density within guilds 4 (insectivorous foliage/twig gleaners), 7 (insectivorous ground/foilage gleaners), and 9 (granivorous ground/foilage gleaners) during fall, and 4 and 9 during winter. Increased numerical importance of guild 9 during fall and winter, and concurrent reduction of guild 11 (omnivorous ground/foilage gleaners), reduced guild evenness. The shift in numerical importance of these guilds was in part because of dietary shifts of species from an omnivorous diet during the breeding season to a granivorous diet. This change in diet probably reflected nutritional demands of reproduction and feather molt by adults and growth and development of young of the year (Scott 1973). Changes in relative availability of plant and invertebrate food resources associated with the ground/foilage strata possibly also affected seasonal changes in diet. Rotenberry (1980) found bird species changed dietary habits in response to seasonal changes in food composition. Winter typically was an unstable period for terrestrial invertebrates associated with foliage substrates in temperate areas (Karr 1976).

Monospecific and multispecific foraging flocks of members of guilds 4 (insectivorous foliage/twig gleaners) and 9 (granivorous ground/foilage gleaners) were commonly observed during fall and winter (G. Dorsey pers. comm.). Foraging in flocks increased efficiency in locating less abundant and/or a more patchy distribution of food resources (Cody 1974, Greig-Smith 1978, Wiens 1976). Because guilds 4 and 9 supported higher densities of birds, the occurrence of foraging flocks probably was more related to changes in resource abundance. Foraging flocks were not observed for guild 7 (insectivorous



ground/foilage gleaners) during fall and winter (G. Dorsey pers. comm.) and the number of species within guild 7 declined; this suggested reduced intraspecific and/or interspecific territoriality during fall and winter was a possible factor permitting increased bird density within guild 7. Guild evenness within tree-shrub habitats was high in the breeding season (spring and summer) and low during the non-breeding season (fall and winter), which also suggested seasonal changes in territoriality. Territoriality commonly was greatest during the breeding season (Wallace and Mahan 1975). Kricher (1972) and Tramer (1969) suggested increased intraspecific territorial behavior minimized numerical dominance by the most common nesting species and resulted in higher species evenness for breeding bird communities. Because most guilds occurring within tree-shrub habitats during spring and summer consisted of breeding species, heightened intraspecific territoriality during the breeding season probably increased evenness of guilds. Increased interspecific territoriality during the breeding season (Rotenberry et al. 1979, Gorton 1977) may also increase guild evenness. Because of the similarity of resource utilization among species within the same guild, interspecific territoriality should be most evident among species within the same guild (Landres and MacMahon 1980). Greater dispersion of individuals within guilds, resulting from interspecific territoriality, may result in reduced numerical dominance of the most common nesting guilds and increased guild evenness in the same manner that intraspecific territoriality was proposed to increase species evenness. The apparent effect of heightened territoriality on increased guild evenness may indicate a generally more homogeneous

resource distribution and/or greater predictability of resources within tree-shrub habitats during spring and summer. Wiens (1976) proposed the efficiency and energetic expense of maintaining a territory for procurement of sufficient resources increased with resource aggregation (patchiness) and/or reduced resource predictability.

Seasonal variation of guild numbers within upland habitats suggested a decline in the diversity of food resources available, from peak levels in summer, to lowest levels in winter. A similar seasonal pattern was shown for density of birds, which indicated that seasonal fluctuations in bird density within upland habitats were partly related to changes in the number of guilds present. In addition there was a general decline in bird density within guilds from peak densities in summer. This pattern indicated that both diversity and abundance of food resources within upland habitats were strongly affected by season. In contrast, increased density in certain guilds compensated for reduction in the number of guilds and resulted in relatively stable bird density in tree-shrub habitats. Arboreal cover within tree-shrub habitats provided buffered microhabitats, which likely increased the ability of birds to forage during adverse weather conditions and increased seasonal stability of invertebrate food resources. Vegetation cover modified temperature extremes, wind velocity, and precipitation (Collier et al. 1973, Pianka 1974). An apparent difference between upland and tree-shrub habitats during fall, and particularly winter, was a depauperate diversity and density of terrestrial invertebrate foraging guilds present in upland habitats. Excluding observation of shorebird and gull flocks flying over uplands, ground/foliage gleaners

(granivorous and omnivorous) were the predominant birds utilizing upland habitats during winter. Seeds were probably the most available food resource within upland habitats (excluding WSDU) during winter. Quay (1947) found herbivorous/granivorous species were more numerous in early successional stages of an upland sere; Fretwell (1972) suggested this relationship was due to greater production of seeds and fruits in unstable, early successional habitats. Although omnivorous birds occurred in uplands during winter the majority of these birds also occurred in tree-shrub habitats, and thus from what habitat invertebrates were obtained was not evident. Karr (1976) suggested seasonal stability of the substrate selected for foraging was an important factor influencing the number of insectivorous species. The large amount of standing litter present in WSDU during winter probably provided a microhabitat that could sustain guild 23 (long-billed marsh wren), the only invertebrate foraging guild present in upland habitats through winter. Presence of a bark substrate within tree-shrub habitats presumably provided a relatively stable microhabitat for overwintering invertebrates, their eggs, and larvae, and thus probably was influential in maintaining invertebrate foragers year-round in relatively stable densities. Karr (1976) proposed bark microhabitats provided the most seasonally stable resource for bird communities in temperate habitats.

Another factor that was apparent in the difference between tree-shrub and upland habitats was the number of species present within the numerically dominant guilds during winter. The 3 predominant guilds within tree-shrub habitats during winter, guilds 4

(insectivorous foliage/twig gleaner), 7 (insectivorous ground/foilage gleaner), and 9 (granivorous ground/foilage gleaner), generally comprised 3, 2, and 4 to 5 species, respectively. Contrariwise, guilds most commonly observed utilizing upland habitats during winter, guilds 9, 11 (omnivorous ground/foilage gleaner), and 23 (insectivorous foliage/shore gleaner), were comprised of 1 or 2 species. Vertical segregation of foraging location increased food resource partitioning among species (Cody 1974, Landres and MacMahon 1980). Thus greater vertical heterogeneity within tree-shrub habitats (relative to upland habitats), as indicated by the number of strata (Appendices, Table 12), may have affected the greater number of species within predominant guilds of tree-shrub habitats. Additionally, the presumed greater environmental stability of tree-shrub habitats may also influence tolerance for species packing within guilds. Odum (1969) proposed that utilization of net production within early successional stages (eg. upland habitats) was predominantly through plant-herbivore-carnivore food webs, whereas, in later successional stages the majority of net production was utilized by detritivores, which slows the nutrient cycle rate between the environment and organisms and stabilizes the system against external perturbations (eg. season). Comparison of the patterns of bird density and number of guilds between upland and tree-shrub habitats may reflect differences that corresponded with stability of the 2 different successional stages.

Low guild evenness within upland habitats during winter contrasted with high relative guild evenness within tree-shrub and beach-low marsh habitats. Upland habitats were numerically dominated by 1 guild,

primarily consisting of 1 species, during winter (in 83% of winter upland samples 1 guild comprised greater than 70% of the total density, and in 75% of winter samples 1 species comprised greater than 70% of the total density). This pattern probably reflected the effect of winter climate on low abundance, predictability, and availability of food resources within upland habitats. Although birds nested within upland habitats, seasonal variation of guild evenness did not contrast the breeding and non-breeding season as indicated for tree-shrub habitats. Fewer species, within fewer guilds, nested in upland habitats than in tree-shrub habitats, and a large portion of the avifauna foraged, but did not nest, within uplands. Kricher (1972) compared breeding bird communities among herbaceous and forested habitats and found the occurrence of non-nesting species was most apparent in the herbaceous field. Kricher (1972) proposed greater utilization by opportunistic species may be a characteristic of early successional habitats. Rotenberry et al. (1979) related opportunistic foraging within shrubsteppe and grasslands to environmental (climate) instability. Although upland and tree-shrub habitats were subject to the same climatic conditions, the effect on birds and the resources they utilized was probably different because of differences in vegetation complexity. Complexity of the vegetation was in turn related to the successional stage of upland and tree-shrub habitats.

Bird communities within beach-low marsh habitats demonstrated the least seasonal variation in community structure of all habitats examined. Bird density declined during winter within beach-low marsh habitats; however, the number of guilds did not exhibit a substantial

reduction from levels within other seasons. Comparisons of these 2 seasonal patterns indicated reduction in food abundance or availability, and not diversity of food types (as indicated by relatively constant number of guilds), reduced bird density. Exposed or shallowly inundated intertidal zones provided an important foraging substrate for a large number of guilds present in beach-low marsh habitats. Low tidal amplitude during winter probably reduced the available foraging space for many birds associated with beach-low marsh habitats and reduced bird density. Shorebirds (guilds 22, 24, and 25) were most apparently dependent on food resources associated with exposed intertidal substrates. Recher (1966) proposed reduced available foraging space, as limited by tidal inundation, reduced migrant shorebird densities during winter. Peterson and Peterson (1979) found that although aerial searching birds (members of guilds 13, 15, and 19) commonly foraged by flying over water they spent a significant portion of their time foraging in shallow water within the intertidal zone. Dabbling waterfowl (guild 21) commonly foraged in shallow water within the intertidal zone (Peterson and Peterson 1979). Birds diving from the water surface for food resources (guilds 14, 18, 20, and 27) typically foraged in deeper water (Peterson and Peterson 1979). Interestingly, these surface diving guilds were most abundant during winter and fall when tidal amplitude was lowest. However, these birds were not abundant enough (comprising 15.5% of total density in beach-low marsh habitats during winter) to offset reduction of other birds during winter. Although densities of guilds 19, 24, and 25 were reduced in winter they still comprised a major portion (59.3%) of the winter bird

community in beach-low marsh habitats. Optimum area for foraging within beach-low marsh habitats for surface diving guilds probably occurred during winter when tidal amplitude was lowest. Contrariwise, foraging area was at a minimum for birds foraging in exposed tide flats, shallow water, or foraging while wading through water.

Climatic factors also may have reduced densities in beach-low marsh habitats during winter. Ice flows, which collected in the intertidal zones during winter (G. Dorsey pers. comm.), cold temperatures, and winter storms may have reduced the invertebrate fauna and/or limited access to food resources by birds searching for food from, above, or at the water substrate, versus birds searching under water. Accessibility of benthic food items may also be reduced during winter because of downward vertical migration (Reading and McGrorty 1978, Kinne 1967, Gray 1974). Reduced availability of benthic fauna directly affects birds foraging on benthic invertebrates and indirectly affects piscivorous birds foraging in intertidal zones.

Minor seasonal variation of guild evenness occurred within beach-low marsh habitats. Almost all birds occurring in beach-low marsh habitats did not nest on the islands, thus seasonal changes in intraspecific territoriality and its apparent effect on guild evenness within tree-shrub habitats was not evident in beach-low marsh habitats. Consistently low guild evenness within beach-low marsh habitats corresponded with year-round occurrence of foraging aggregations within the predominant guilds; the lack of seasonal variation of guild evenness may reflect patchy (temporal and spacial) distribution of food resources. Tidal cycles likely were an important factor influencing

distribution of food resources. Space, substrate type, vegetation cover, and moisture content, which affect distribution of benthic fauna, were directly or indirectly influenced by tidal inundation (Burger et al. 1977).

Beach-low marsh habitats consistently supported the highest bird biomass, which reflected the large average size of birds associated with aquatic habitats. Larger body size of birds in beach-low marsh habitats may be related to the high productivity characteristic of most estuary systems (Whittaker 1975). The high marsh supported avian biomass intermediate between that supported in beach-low marsh habitats and tree-shrub and upland habitats. Generally low numerical importance of gulls (guild 19) and piscivorous surface divers (guild 14) in the high marsh reduced avian biomass from high levels found in beach-low marsh habitats. Greater vegetation cover and less tidal inundation may reduce ability of these 2 guilds to forage within the high marsh.

Seasonal patterns of community structure indices were not examined within the high marsh because of the small sample size each season. The high marsh was consistently distinguished from all other habitats by its high guild richness. Frequent occurrence of ground/foilage gleaning guilds 7, 9, 11, and nectivorous guild 12, in addition to the aquatic associated guild assemblage typical of beach-low marsh habitats, caused this distinction. Greater production of grasses and sedges within the high marsh and its higher elevation from the water (thus less frequent and extensive tidal inundation) probably provided a more available and abundant resource of seeds (food item of guilds 9 and 11) and insects (food item of guilds 7 and 11). Regular tidal inundation



of the beach-low marsh habitats caused seeds to be windrowed on the edge of upland or tree-shrub habitats (G. Dorsey pers. comm.), which presumably further reduced availability of food resources of guilds 9 and 11 within beach-low marsh habitats. Juxtaposition of the high marsh to upland and tree-shrub habitats probably affected the greater occurrence of guild 12 and to some degree higher occurrence of ground/foilage gleaning guilds. Although the relative abundance of guilds 7, 9, and 11 was less than that in upland habitats, seasonal pattern of their occurrence was similar in both habitats. This may indicate seasonal stability of plant and invertebrate food resources of ground/foilage gleaning guilds was similar to upland habitats.

Although the bird assemblage of the high marsh predominantly consisted of birds obtaining food resources from the estuary system, the community structure caused me to consider the high marsh bird community as an ecotone between bird communities of terrestrial (tree-shrub and upland) and estuary (beach-low marsh) systems. Ecotones commonly support greater number of species; apparently greater number of guilds may also be indicative of an ecotone. Higher number of guilds was not indicated for WSTR, which was described as a transitional habitat between an upland and a tree-shrub habitat (Crawford and Dorsey 1980). At the level of guild classification used for this study, ecotonal effects on bird communities may only be evident when the adjoining habitats possess relatively distinct guild assemblages.

Patterns of individual and synergistic variation of number of guilds, guild evenness, guild composition, avian density, and biomass were useful in indicating season and habitat related factors affecting

avian community structure. Although guild diversity frequently was important in describing season and habitat differences, it generally was not a useful index because the 2 components of diversity, guild richness and evenness, often varied independently. More salient information was obtained when these 2 components were examined separately rather than combined into 1 index. Variation of guild evenness was possibly a function of homogeneity of food distribution within a habitat and the degree to which birds utilized a habitat for nest sites. Use of indices such as diversity and evenness to describe community structure were criticized because of their dubious biological meaning (Goodman 1975, Green 1979). I found guild evenness was useful for summarizing the pattern of distribution of birds among guilds. Additionally, guild evenness indicated differences among bird communities not demonstrated by avian density, biomass, or number of guilds. No definitive variation among habitats was found with respect to guild richness with the exception of greater numbers of guilds in the high marsh. However, comparison of seasonal patterns of guild numbers among habitats suggested seasonal variation of food resource diversity differed among habitats. Interpretation of variation in bird density varied according to the corresponding pattern of guild richness, evenness, and guild composition. Changes in food resource abundance, diversity, availability, temporal or spacial distribution likely were factors affecting bird density. Bird biomass probably reflected productivity of food resources available to the bird community.

Results of this study suggested possible factors influencing community structure. However, validity of these inferences requires

more detailed investigation of the bird communities and their habitats. In summary, the approach used for this study is most appropriate for preliminary investigations of communities, particularly diverse communities. This approach may also provide insight into particular areas where more detailed study may further understanding of the structure and functioning of communities.

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## APPENDICES

Appendix 1. Description of study islands, lower Columbia River, Oregon, 1978-1979.

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Analysis of guild structure of avian communities was conducted with data collected by Geoff Dorsey from June 1978 to May 1979 on 3 islands (Miller Sands, West Sand, and Jim Crow Sands) within the estuarine zone of the Columbia River, Oregon (Crawford and Dorsey 1980). Miller Sands (228 ha) and Jim Crow Sands (86 ha), located between River Miles 22 and 25, and 26 and 28, respectively, were formed by the deposition of dredged materials. Deposition was initiated on Miller Sands during the 1930's; during 1974 a sand spit was created by deposition. Portions of Miller Sands upland and sand spit were planted during summer 1976. The first known deposition on Jim Crow Sands occurred in 1957. The eastern portion of Jim Crow Sands had dredged material deposited within the period 1977 to 1979. Grass plantings were established on the eastern one-half of Jim Crow Sands upland during summer 1978. West Sand Island (257 ha), a natural island located in Baker Bay near the mouth of the Columbia River, was partially formed from dredged material.

Climate of the lower Columbia River was characterized by wet winters and dry summers (U.S. Army Engineers District, Portland 1975). Astoria, located centrally among the islands, had average maximum and minimum temperatures of 14.3 and 5.8°C, respectively, and an average annual precipitation of 143.8 cm per year (National Oceanic and Atmospheric Administration 1979).

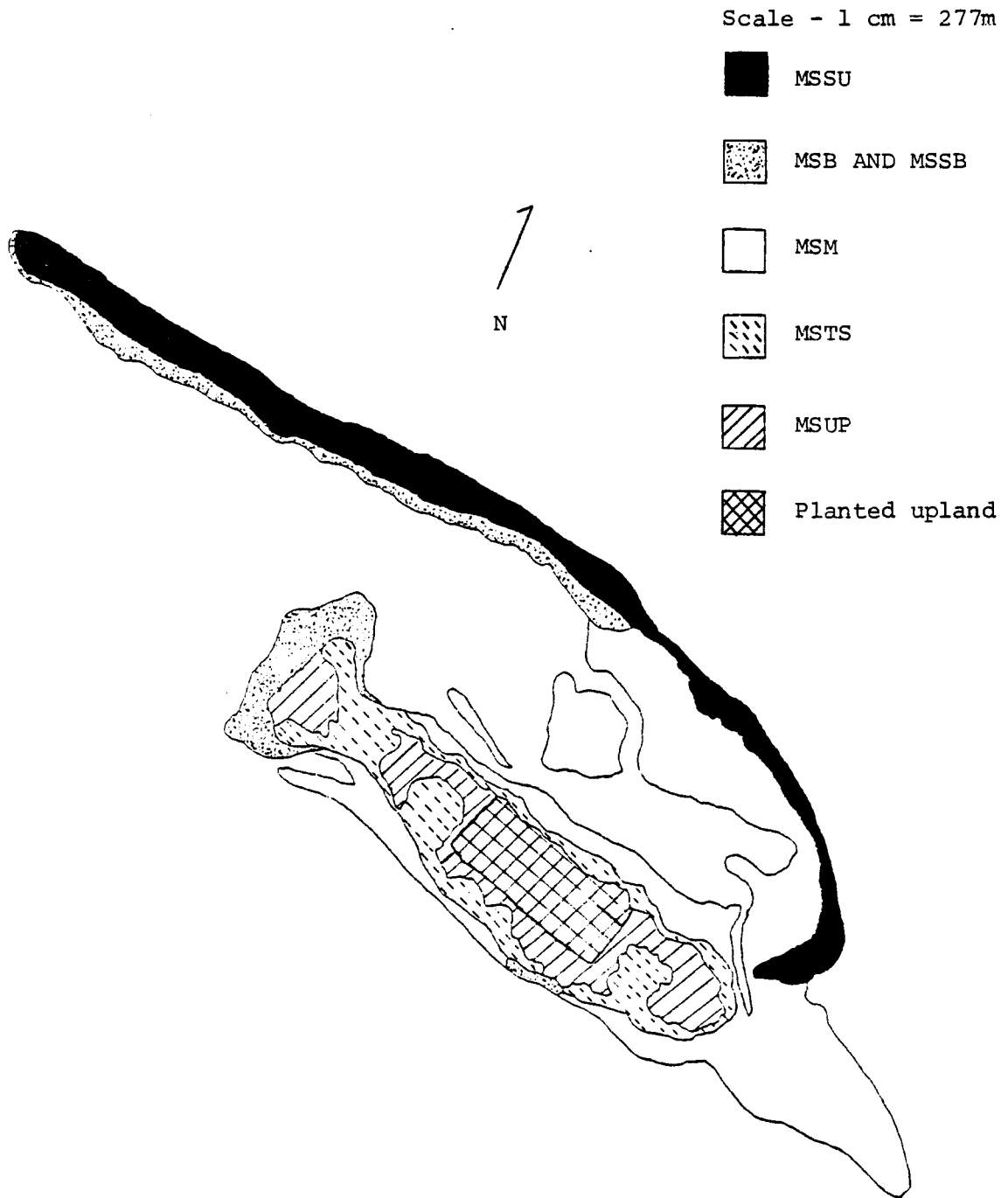


Fig. 9. Habitat locations for Miller Sands Island, Columbia River, Oregon.

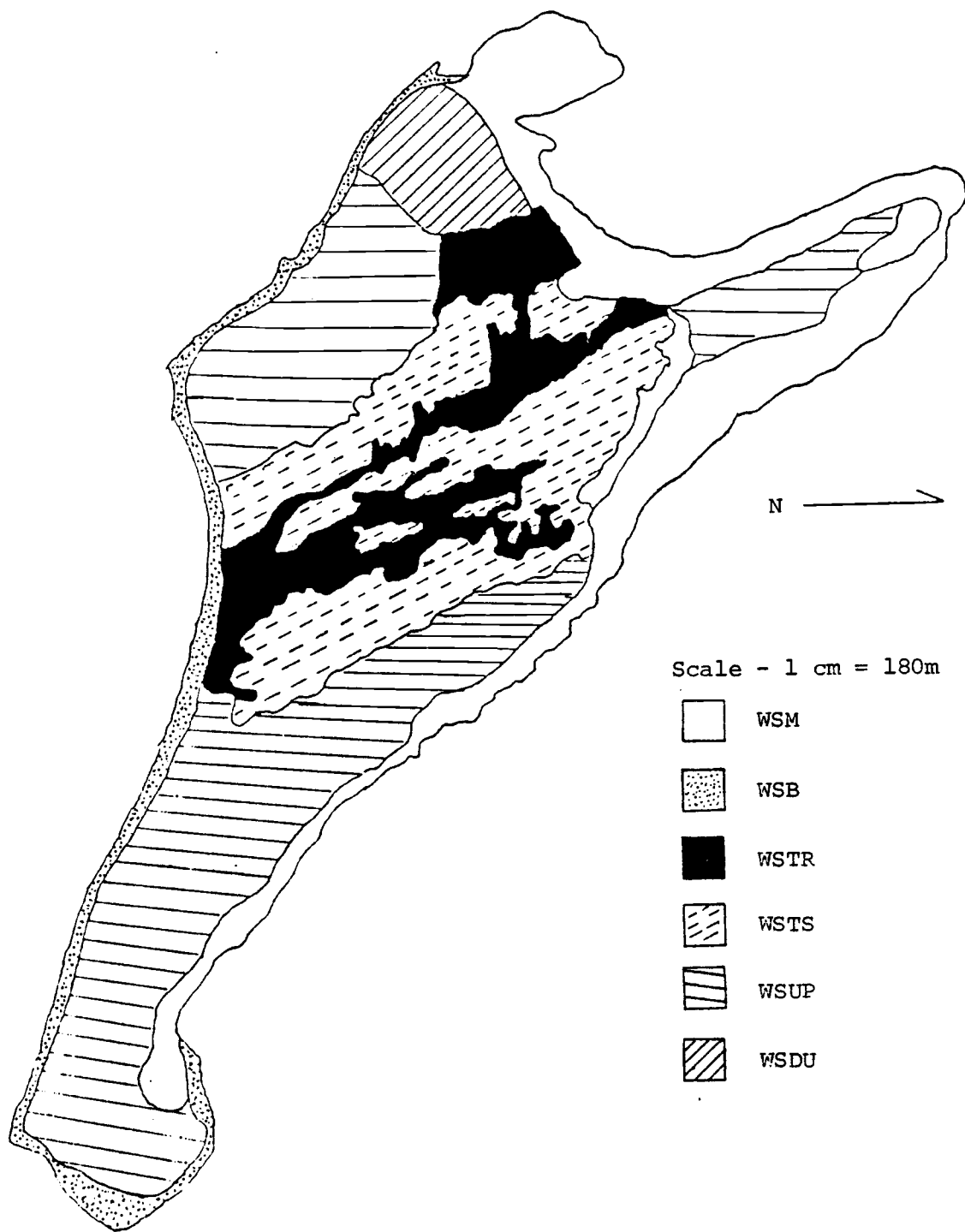


Fig. 10. Habitat locations on West Sand Island, Columbia River, Oregon.

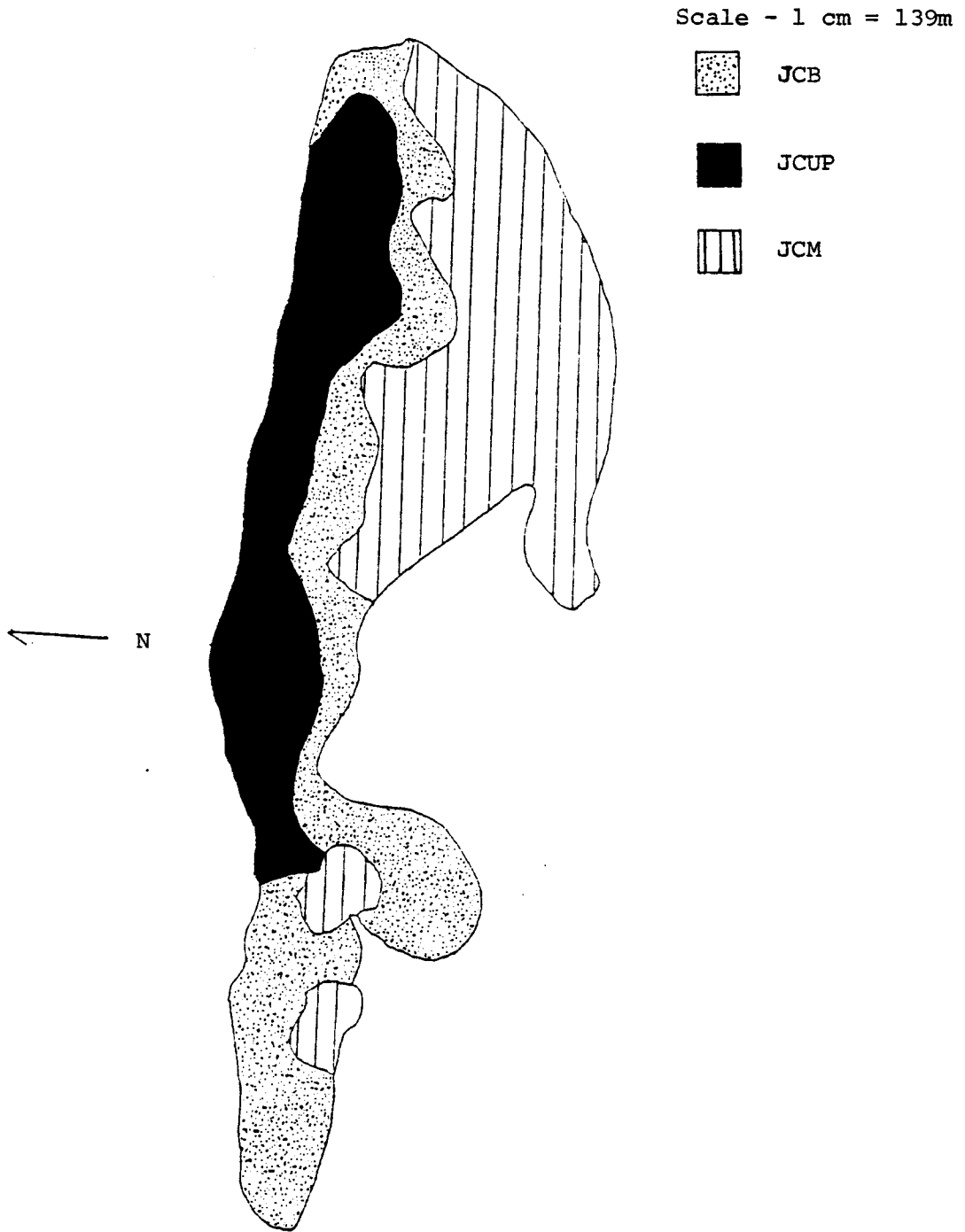


Fig. 11. Habitat locations for Jim Crow Sands Island, Columbia River, Oregon.



Table 12. Seasonal percent cover of vegetation and non-living components for habitats on Miller Sands, West Sand, and Jim Crow Sands Island, Columbia River, Oregon, 1978-1979.<sup>a</sup>

	Habitat <sup>b</sup>														
	MSM	JCM	WSM	MSSU	MSSB	MSB	JCB	WSB	MSUP	JCUP	WSDU	WSUP	MSTS	WSTS	WSTR
Summer															
Moss/lichen	0	1	0	0	0	0	0	0	37	0	0	3	11	9	1
Rock/litter	4	3	9	6	4	1	1	10	15	17	12	16	46	38	17
Bare ground	36	78	8	92	95	98	98	90	7	69	0	20	7	0	1
Forbs	9	1	10	1	1	0	1	0	24	5	12	35	11	8	23
Grass/sedge	52	17	73	1	1	0	1	0	12	2	76	26	10	41	56
Overhead cover	0	0	0	0	0	0	0	0	0	0	0	0	72	64	8
Fall															
Moss/lichen	1	5	0	0	0	0	0	0	41	1	0	6	11	9	2
Rock/litter	46	11	56	6	2	5	3	7	21	46	52	28	65	51	52
Bare ground	40	80	18	90	97	94	94	93	3	40	0	26	1	0	1
Forbs	3	1	0	3	1	1	2	0	20	3	6	20	8	9	17
Grass/sedge	10	4	26	0	0	1	0	0	10	10	42	19	6	32	28
Overhead cover	0	0	0	0	0	0	0	0	0	0	0	0	42	35	4

Table 12. (continued)

	Habitat <sup>b</sup>														
	MSM	JCM	WSM	MSSU	MSSB	MSB	JCB	WSB	MSUP	JCUP	WSDU	WSUP	MSTS	WSTS	WSTR
Winter															
Moss/lichen	1	0	2	0	0	0	0	0	50	3	0	12	9	11	4
Rock/litter	18	10	49	7	3	18	2	25	37	24	85	42	75	64	71
Bare ground	80	89	33	92	97	82	98	75	2	56	0	26	1	0	0
Forbs	0	0	0	0	0	0	0	0	5	1	2	11	1	4	8
Grass/sedge	1	1	16	0	0	0	0	0	5	13	13	8	4	22	17
Overhead cover	0	0	0	0	0	0	0	0	0	0	0	0	28	32	2
Spring															
Moss/lichen	0	0	8	0	0	0	0	0	48	1	0	10	18	11	5
Rock/litter	11	5	34	6	1	6	4	7	27	15	75	33	57	44	57
Bare ground	78	91	32	92	99	93	96	93	1	42	0	29	0	1	0
Forbs	1	1	0	1	0	0	0	0	14	4	5	18	12	6	14
Grass/sedge	10	3	27	1	0	1	0	0	7	36	20	10	5	38	22
Overhead cover	0	0	0	0	0	0	0	0	0	0	0	0	71	60	8

<sup>a</sup> Data from Crawford and Dorsey (1980); percent overhead cover, G. Dorsey pers. comm.

<sup>b</sup> Island designated by 1st 2 letters of acronym, MS=Miller Sands Island, JC=Jim Crow Sands Island, WS=West Sands Island; M=marsh, SU=spit upland, SB=spit beach, B=beach, UP=upland, DU=diked upland, TS=tree-shrub, TR=transition.

Appendix 2. Bird species occurring on islands of the lower Columbia River, and their guild classification.

Species	Guild <sup>a</sup>
Common loon ( <i>Gavia immer</i> )	14
Red-throated loon ( <i>G. stellata</i> )	14
Horned grebe ( <i>Podiceps auritus</i> )	14
Western grebe ( <i>Aechmophorus occidentalis</i> )	14
Double-crested cormorant ( <i>Phalacrocorax auritus</i> )	14
Pelagic cormorant ( <i>P. pelagicus</i> )	14
Great blue heron ( <i>Ardea herodias</i> )	16
Whistling swan ( <i>Cygnus columbianus</i> )	21
Canada goose ( <i>Branta canadensis</i> )	26
Black brant ( <i>B. bernicla</i> )	26
White-fronted goose ( <i>Anser albifrons</i> )	26
Snow goose ( <i>A. caerulescens</i> )	26
Mallard ( <i>Anas platyrhynchos</i> )	21
Gadwall ( <i>A. strepera</i> )	21
Pintail ( <i>A. acuta</i> )	21
American green-winged teal ( <i>A. crecca</i> )	21

## Appendix 2. (continued)

Species	Guild <sup>a</sup>
European wigeon ( <i>Anas penelope</i> )	26
American wigeon ( <i>A. americana</i> )	26
Northern shoveler ( <i>A. clypeata</i> )	21
Greater scaup ( <i>Aythya marila</i> )	27-fall 20-winter, spring
Lesser scaup ( <i>A. affinis</i> )	20
Common goldeneye ( <i>Bucephala clangula</i> )	17
Bufflehead ( <i>B. albeola</i> )	17
White-winged scoter ( <i>Melanitta fusca</i> )	17
Surf scoter ( <i>M. perspicillata</i> )	17
Black scoter ( <i>M. nigra</i> )	17
Ruddy duck ( <i>Oxyura jamaicensis</i> )	27
Common merganser ( <i>Mergus merganser</i> )	14
Red-breasted merganser ( <i>M. serrator</i> )	14
Sharp-shinned hawk ( <i>Accipiter striatus</i> )	2
Cooper's hawk ( <i>A. cooperii</i> )	2
Red-tailed hawk ( <i>Buteo jamaicensis</i> )	1

## Appendix 2. continued)

Species	Guild <sup>a</sup>
Rough-legged hawk ( <i>Buteo lagopus</i> )	1
Bald eagle ( <i>Haliaeetus leucocephalus</i> )	13
Marsh hawk ( <i>Circus cyaneus</i> )	1
Peregrine falcon ( <i>Falco peregrinus</i> )	2
Merlin ( <i>F. columbarius</i> )	2
American kestrel ( <i>F. sparverius</i> )	1
American coot ( <i>Fulica americana</i> )	27
Semipalmated plover ( <i>Charadrius semipalmatus</i> )	24
Killdeer ( <i>C. vociferus</i> )	22
Black-bellied plover ( <i>Pluvialis squatarola</i> )	24
Ruddy turnstone ( <i>Arenarius interpres</i> )	24
Common snipe ( <i>Capella gallinago</i> )	22
Whimbrel ( <i>Numenius phaeopus</i> )	25
Spotted sandpiper ( <i>Actitus macularia</i> )	24
Greater yellowlegs ( <i>Tringa melanoleucus</i> )	18
Lesser yellowlegs ( <i>T. flavipes</i> )	18

## Appendix 2. (continued)

Species	Guild <sup>a</sup>
Baird's sandpiper ( <i>Calidris bairdii</i> )	24
Least sandpiper ( <i>C. minutilla</i> )	24
Dunlin ( <i>C. alpina</i> )	25
Long-billed dowitcher ( <i>Limnodromus scolopaceus</i> )	25
Western sandpiper ( <i>C. mauri</i> )	24
Marbled godwit ( <i>Lymosa fedoa</i> )	25
Sanderling ( <i>C. alba</i> )	24
Northern phalarope ( <i>Lobipes lobatus</i> )	29
Glaucous gull ( <i>Larus hyperboreus</i> )	19
Glaucous-winged gull ( <i>L. glaucescens</i> )	19
Western gull ( <i>L. occidentalis</i> )	19
Herring gull ( <i>L. argentatus</i> )	19
California gull ( <i>L. californicus</i> )	19
Ring-billed gull ( <i>L. delawarensis</i> )	19
Mew gull ( <i>L. canus</i> )	19
Bonaparte's gull ( <i>L. philadelphia</i> )	19

## Appendix 2. (continued)

Species	Guild <sup>a</sup>
Heerman's gull ( <i>Larus heermani</i> )	19
Black-legged kittiwake ( <i>Rissa tridactyla</i> )	19
Common tern ( <i>Sterna hirundo</i> )	15
Caspian tern ( <i>S. caspia</i> )	15
Short-eared owl ( <i>Asio flammeus</i> )	1
Common nighthawk ( <i>Chordeiles minor</i> )	6
Vaux's swift ( <i>Chaetura vauxi</i> )	6
Rufous hummingbird ( <i>Selasphorus rufus</i> )	12
Belted kingfisher ( <i>Megaceryle alcyon</i> )	15
Common flicker ( <i>Colaptes auratus</i> )	7-spring, summer 11-fall, winter
Downy woodpecker ( <i>Dendrocopos pubescens</i> )	5
Western flycatcher ( <i>Empidonax difficilis</i> )	3
Olive-sided flycatcher ( <i>Nuttallornis borealis</i> )	3
Horned lark ( <i>Eremophila alpestris</i> )	11-spring, summer 9-fall, winter
Violet-green swallow ( <i>Tachycineta thalassina</i> )	6
Tree swallow ( <i>Iridoprocne bicolor</i> )	6

## Appendix 2. (continued)

Species	Guild <sup>a</sup>
Rough-winged swallow ( <i>stelgidopteryx ruficollis</i> )	6
Barn swallow ( <i>Hirundo rustica</i> )	6
Cliff swallow ( <i>Petrochelidon pyrrhonota</i> )	6
Purple martin ( <i>Progne subis</i> )	6
Stellar's jay ( <i>Cyanocitta stelleri</i> )	9-fall, winter, spring, 11-summer
Common raven ( <i>Corvus corax</i> )	28
Common crow ( <i>C. brachyrhynchus</i> )	28
Black-capped chickadee ( <i>Parus atricapillus</i> )	4
Winter wren ( <i>Troglodytes troglodytes</i> )	7
Bewick' wren ( <i>Thryomanes bewickii</i> )	7
Long-billed marsh wren ( <i>Cistothorus palustris</i> )	23
American robin ( <i>Turdus migratorius</i> )	7-spring 11-summer, winter
Varied thrush ( <i>Ixoreus naevius</i> )	11
Hermit thrush ( <i>Catharus guttatus</i> )	7
Swainson's thrush ( <i>C. ustulatus</i> )	7-spring 11-summer, fall
Townsend's solitaire ( <i>Myadestes townsendi</i> )	11



## Appendix 2. (continued)

Species	Guild <sup>a</sup>
Golden-crowned kinglet ( <i>Regulus satrapa</i> )	4
Ruby-crowned kinglet ( <i>R. calendula</i> )	4
Water pipit ( <i>Anthus spinoletta</i> )	22
Cedar waxwing ( <i>Bombycilla cedorum</i> )	8
Northern shrike ( <i>Lanius excubitor</i> )	1
Starling ( <i>Sturnus vulgaris</i> )	7-spring 11-summer, fall, winter
Hutton's vireo ( <i>Vireo huttoni</i> )	4
Orange-crowned warbler ( <i>Vermivora celata</i> )	4
Yellow warbler ( <i>Dendroica petechia</i> )	4
Yellow-rumped warbler ( <i>D. coronata</i> )	4
Black-throated gray warbler ( <i>D. nigrescens</i> )	4
Townsend's warbler ( <i>D. townsendi</i> )	4
Chestnut-sided warbler ( <i>D. pensylvanica</i> )	4
Common yellowthroat ( <i>Geothlypis trichas</i> )	7
Wilson's Warbler ( <i>Wilsonia pusilla</i> )	4
Western meadowlark ( <i>Sturnella neglecta</i> )	7-spring 11-fall, winter

## Appendix 2. (continued)

Species	Guild <sup>a</sup>
Red-winged blackbird ( <i>Agelaius phoeniceus</i> )	11-summer 9-winter
Northern oriole ( <i>Icterus galbula</i> )	4
Brown-headed cowbird ( <i>Molothrus ater</i> )	11
House finch ( <i>Carpodacus mexicanus</i> )	9
American goldfinch ( <i>Carduelis tristis</i> )	11-spring 9-summer, fall, winter
Rufous-sided towhee ( <i>Pipilo erythrophthalmus</i> )	9-fall, winter 11-spring
Savannah sparrow ( <i>Passerculus sandwichensis</i> )	11-spring 7-summer, fall
Dark-eyed junco ( <i>Junco hyemalis</i> )	9
White-crowned sparrow ( <i>Zonotrichia leucophrys</i> )	9-spring, fall 11-summer
Golden-crowned sparrow ( <i>Z. atricapilla</i> )	9
Fox sparrow ( <i>Passerella iliaca</i> )	9
Song sparrow ( <i>Melospiza melodia</i> )	11-spring, summer 9-fall, winter
Lapland longspur ( <i>Calcarius lapponicus</i> )	11
Snow bunting ( <i>Plectrophenax nivalis</i> )	9

<sup>a</sup> See Table 1 for description of guilds.

Table 13. Avian guild densities (birds/ha), summer 1978, within tree-shrub, upland, high marsh, and beach-low marsh habitats on islands of the lower Columbia River, Oregon.

Guild # <sup>a</sup>	Habitat			
	TS	UP	HM	BELM
1	0.08	0.02	0.01	t <sup>b</sup>
2	0.09			
3	0.33	0.01		
4	1.65	0.10		
5	0.37			
6	0.82	1.60	0.64	4.38
7	1.82	3.53	0.58	0.11
8	0.26	0.01		
9	2.20	1.21	0.30	0.13
11	3.20	0.50	0.12	0.09
12	1.06	0.80	2.12	0.13
13	t	0.01		t
14		0.04	0.10	0.05
15	0.02	0.03	0.04	0.44
16	0.02	0.01	0.01	t
18		0.01		
19	0.04	0.24	0.34	2.94
21		0.03	0.02	0.32
22		0.02	0.01	0.15
23		0.20	0.20	
24		0.08	0.92	3.55
25				t
26			0.01	t
28	0.22	0.10	0.05	0.09
29				t

<sup>a</sup> Description of guilds given in Table 1.

<sup>b</sup> Density less than 0.01 birds/ha

Table 14. Avian guild densities (birds/ha), fall 1978, within tree-shrub, upland, high marsh, and beach-low marsh habitats on islands of the lower Columbia River, Oregon.

Guild # <sup>a</sup>	Habitat			
	TS	UP	HM	BELM
1	0.03	0.02	0.03	t <sup>b</sup>
2	0.01	0.02		
4	7.11	0.11		
5	0.09	0.03		
6		0.10	0.07	0.10
7	2.02	0.08		
8	0.01			
9	2.02	1.52	0.50	0.55
11	0.23	0.16	0.16	t
13				t
14	0.01	0.04	0.02	0.22
15			0.01	0.03
16		t	0.01	t
17			0.07	0.03
18				0.03
19	t	0.16	0.42	1.66
21	0.01	0.04	0.67	0.71
22		0.16	0.03	0.22
23		0.32		
24		0.05	2.56	1.25
25		0.02	1.97	4.16
26		0.04	0.19	0.40
27			0.01	0.04
28	0.18	0.03	0.06	0.08
29				t

<sup>a</sup> Description of guilds given in Table 1.

<sup>b</sup> Density less than 0.01 birds/ha

Table 15. Avian guild densities (birds/ha), winter 1979, within tree-shrub, upland, high marsh, and beach-low marsh habitats on islands of the lower Columbia River, Oregon.

Guild # <sup>a</sup>	Habitat			
	TS	UP	HM	BELM
1	0.04	0.01	0.01	t
2	0.08	t <sup>b</sup>		t
4	3.32			0.15
5	0.10			
7	1.08			0.04
9	4.38	0.58	0.04	0.40
11	0.43	0.28	0.96	0.01
13		t		t
14		t	t	0.28
15				t
16		t	t	t
17		t		0.04
19		0.42	0.08	0.65
20				0.04
21	0.06	0.01	0.33	0.07
22	0.01		0.03	
23	0.05	0.18		0.04
24		0.01	1.22	0.40
25		0.13	3.41	0.98
26		0.05	0.09	0.02
27				t
28	0.28	0.02	0.01	0.05

<sup>a</sup> Description of guilds given in Table 1.

<sup>b</sup> Density less than 0.01 birds/ha

Table 16. Avian guild densities (birds/ha), spring 1979, within tree-shrub, upland, high marsh, and beach-low marsh habitats on islands of the lower Columbia River, Oregon.

Guild # <sup>a</sup>	Habitat			
	TS	UP	HM	BELM
1	0.02	0.02	0.04	0.01
2	0.02	0.04		
3	0.21			
4	1.43	0.02		
5	0.17			
6	1.65	1.62	1.31	2.12
7	1.32	0.17	0.03	0.02
8	0.53			
9	0.73	0.28	0.01	
11	4.74	2.09	0.41	0.34
12	1.41	0.13	1.06	0.15
13	0.02		0.27	t <sup>b</sup>
14			0.02	0.14
15		0.01		0.06
16			0.01	t
17			0.13	t
18			0.02	0.01
19	0.02	0.29	0.18	1.65
20		0.07	0.01	0.02
21	0.06	0.08	0.41	0.12
22		0.10	0.05	0.26
23		0.18		
24			4.21	7.88
25		0.61	2.05	19.74
26		0.01	0.09	0.09
28	0.37	0.10	0.06	0.09
29				0.17

<sup>a</sup> Description of guilds given in Table 1.

<sup>b</sup> Density less than 0.01 birds/ha