

SEASONAL VARIATION IN AVIAN COMMUNITY STRUCTURE: DIFFERENCES IN MECHANISMS REGULATING DIVERSITY

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ABSTRACT.—Thirty avian censuses were conducted over 2 yr along a wooded streamside in southcentral Washington. Avian species diversity and richness show temporal periodicity (summer maxima and winter minima), but evenness does not. Comparison with contemporaneous censuses in adjoining shrubsteppe shows substantially greater diversity and richness along the streamside, while community evenness is greater in the shrubsteppe. We infer these conditions to be a result of the arboreal physiognomy of the streamside plant community.

Comparing winter censuses to spring censuses, we observed statistically significant differences in avian community structure: in winter, species diversity is correlated with evenness but not richness, while in the breeding season, diversity varies as a function of richness, not evenness. Following a model proposed by Tramer (1969), we suggest that community organization during the spring breeding season may reflect elements of resource-based interspecific competition, while winter assemblages of birds are regulated by a harsh and variable climate. *Received 3 April 1978, accepted 21 February 1979.*

THE relationship between species diversity and its components, richness and evenness, has been receiving increased attention (Peet 1974). Tramer (1969) has proposed that changes in diversity may be mediated by changes in one or the other component and that these changes reflect alternative environmental conditions. He suggests that diversity changes with richness in relatively stable, benign environments and varies with evenness under unstable, rigorous conditions. The former occurs when most populations are near equilibrium, which is possible because the physical environment and resource levels remain stable over time. Fluctuations in relative abundance are minimized, and variation depends on the addition or subtraction of species. Populations in variable, rigorous environments, on the other hand, are often held below equilibria by unfavorable conditions and may expand when conditions are alleviated. Such growth may be achieved by a variety of mechanisms (e.g. increased survival, immigration) and is likely to vary according to species. Tramer expects this variability in population numbers to influence consistently the distribution of relative abundances and, hence, community evenness. Tramer's hypothesis has been tested by Rotenberry (1978) and has been found to hold for a large set of bird census data ordered along a multidimensional gradient of climatic variability and harshness.

Tramer's hypothesis explains long-term yearly and/or large-scale geographic variation in avian community structure. Therefore, it seems reasonable to try to extend the same principles to account for observed seasonal variations in local community organization. It is in this framework that we report the results of a series of bird censuses taken over a period of 2 yr in contrasting vegetation.

STUDY AREA AND METHODS

Avifaunal censuses were conducted in Snively Canyon, located on the Department of Energy's Arid Land Ecology (ALE) Reserve, Benton County, Washington, about 25 km northwest of Richland, Wash-

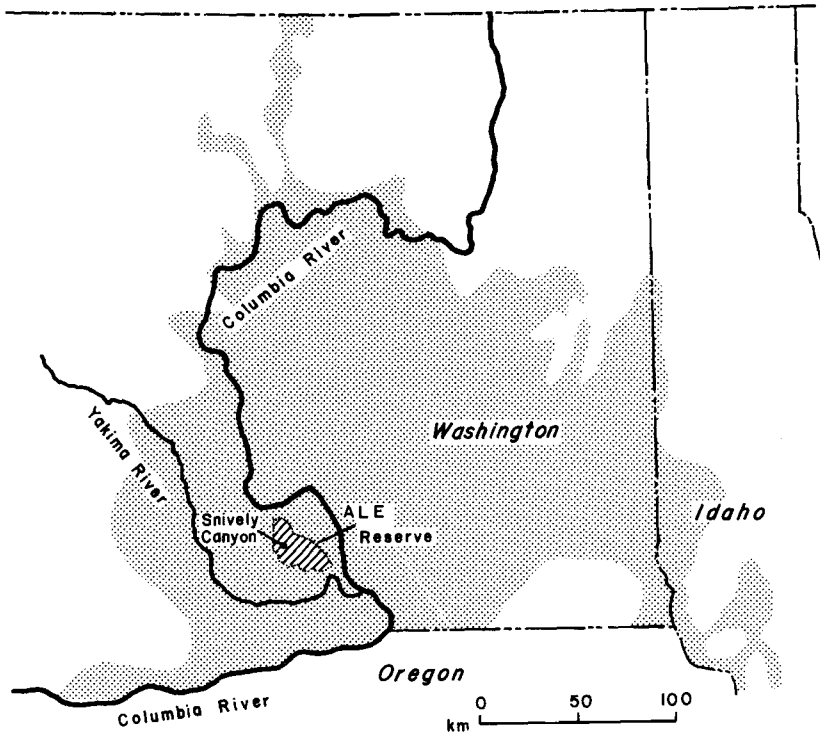


Fig. 1. Map of southeastern Washington showing the location of the Snively Canyon survey area and the extent of shrubsteppe vegetation (stippled) throughout the region (modified from Daubenmire 1970).

ington (Fig. 1). The gulch is approximately 2 km long, varying from 10–75 m wide, and up to 100 m deep. The small stream within the canyon is permanent and is closely bordered by trees, *Populus* sp. and *Salix* sp., and deciduous shrubs, *Prunus*, *Sambucus*, *Amelanchier*, *Rhus*, *Philadelphus*, and others. Snively is isolated from similar arboreal vegetation by a surrounding matrix of shrubsteppe vegetation (*Artemisia-Agropyron*) (Daubenmire 1970) (Fig. 1). The nearest similar vegetation is found along the Yakima River, ~25 km distant.

A census route was run in the morning (0700–0800 start) at intervals of 2–6 weeks from 19 July 1974 to 4 August 1976. It consisted of 12 census stops about 200 m apart along the stream. At each stop all birds identified or heard in a 3-min period were recorded. Because of the short distances between stops, care was taken to avoid any double-counting of individuals.

A companion route was set up in typical shrubsteppe vegetation in April 1976 in conjunction with another study. This route was censused as a typical cooperative breeding bird survey (Robbins and Van Velzen 1968): 3-min stops, 0.8 km (0.5 mi) apart, each sampled within a 0.4-km (0.25 mi) radius. Unlike the cooperative surveys, however, our route contained 25 instead of the usual 50 stops. Four such surveys were made in spring 1976 and three in spring 1977. Although these samples obviously counted more individuals than Snively surveys because of their substantially greater area of coverage, reduction of the data to relative abundance allows a comparison between the two types.

Species diversity was calculated according to Simpson (1949), then converted to the equivalent number of equally common species by applying a reciprocal transformation. Thus,

$$\text{Diversity} = 1 / \sum p_i^2,$$

where p_i is the relative abundance of the i^{th} species in the sample. This represents diversity as the number of equally abundant species occurring in a sample that would produce the untransformed index previously calculated for that sample. This has the advantages of retaining "number of species" as its basic unit, while including the evenness component (Peet 1974).

The richness component is simply the number of species in the sample. Evenness (the distribution of relative abundances among the species sampled) was calculated using a ratio proposed by Hill (1973):

$$\text{Evenness} = \text{Diversity} / \exp(-\sum p_i \log p_i).$$

The denominator is essentially the equivalent number of equally common species derived from the information theory measure for species diversity (Hill 1973).

Equality of means was tested using the t' -test (Sokal and Rohlf 1969: 374), which makes no assumptions concerning the homogeneity of sample variances nor requires equal sample sizes.

Partial coefficients of determination (R^2_{part}) were used to assess the separate contributions of richness and evenness to "explaining" variation in diversity (Steel and Torrie 1960). Because the calculation of diversity is mathematically not independent of values of richness and evenness, correlation analysis of variation in diversity with respect to those two variables is inappropriate.

RESULTS

The results of 21 of the 30 Snively Canyon surveys are summarized in Table 1 and include only those species that averaged at least one individual per count on either 11 breeding-season (May–August) or 10 wintering-season (November–March) counts. These species comprise 91.4% of all individuals seen during the breeding season and 82.7% of all seen during the winter. Breeding-season surveys averaged 148 individuals of 19.5 species per count, while winter surveys averaged 59 individuals of 11.3 species. Altogether, 81 species were recorded from all 30 counts combined. Similarly, the results of 7 breeding season shrubsteppe transects are given in Table 1. An average of 10.3 species and 385 individuals was seen, with 29 species recorded altogether.

Community statistics for the Snively Canyon surveys (separated by season) and the shrubsteppe transects are summarized and compared in Table 2. Substantially more individuals were seen per shrubsteppe transect compared to Snively, most likely a function of the substantially larger area covered. Nevertheless, the average number of species seen was only ~ 10 , significantly less than that observed on spring season canyon surveys. Likewise, diversity was significantly lower in the shrubsteppe than in the canyon, although evenness was significantly higher. Within the canyon, the winter bird assemblage consists of significantly fewer individuals and species at a lower diversity than does the breeding-season assemblage, although evenness does not appear to differ between the two samples.

Figure 2 summarizes the descriptive statistics of the Snively Canyon bird community as sampled through time. The periodicity of both richness and diversity is quite apparent (Fig. 2A); both achieve maximum values during the breeding season and minima during mid-winter. Community evenness shows a substantially different pattern (Fig. 2B); periodicity is undetectable, with maxima being attained between mid-November and early March 1975–76. Minimum values, however, occurred in the same time period the previous winter.

DISCUSSION

Arboreal/shrubsteppe comparisons.—Although it is often difficult to make new uses of data collected for other purposes, comparison of the Snively Canyon censuses with those conducted in the nearby shrubsteppe does allow us to make several points concerning the mechanisms we think are important in structuring the Snively bird community. For example, Table 2 clearly shows the greater richness and diversity of Snively Canyon breeding avifauna compared to that of the adjacent shrubsteppe.

TABLE 1. Dominant species of birds recorded on Snively Canyon and shrubsteppe surveys. Values are average number of individuals seen for 11 breeding-season (May–August) and 10 wintering-season (November–March) counts in the canyon, and 7 breeding-season counts in the shrubsteppe. Actual number of counts on which each species was observed is in parentheses.

Snively Canyon, breeding			Snively Canyon, wintering		
Kestrel (<i>Falco sparverius</i>)	1.0	(7)	California Quail (<i>Lophortyx californicus</i>)	1.5	(1)
Sage Grouse (<i>Centrocercus urophasianus</i>)	1.4	(2)	Ring-necked Pheasant (<i>Phasianus colchicus</i>)	1.7	(5)
California Quail (<i>Lophortyx californicus</i>)	1.8	(6)	Horned Lark (<i>Eremophila alpestris</i>)	1.1	(4)
Chukar (<i>Alectoris chukar</i>)	20.7	(9)	Black-billed Magpie (<i>Pica pica</i>)	2.2	(8)
Mourning Dove (<i>Zenaida macroura</i>)	28.5	(11)	American Robin (<i>Turdus migratorius</i>)	2.6	(6)
Eastern Kingbird (<i>Tyrannus tyrannus</i>)	1.9	(5)	Ruby-crowned Kinglet (<i>Regulus calendula</i>)	1.2	(6)
Barn Swallow (<i>Hirundo rustica</i>)	8.9	(11)	Yellow-rumped Warbler (<i>Dendroica coronata</i>)	4.7	(2)
Black-billed Magpie (<i>Pica pica</i>)	5.2	(10)	Western Meadowlark (<i>Sturnella neglecta</i>)	3.7	(5)
Rock Wren (<i>Salpinctes obsoletus</i>)	1.0	(7)	Dark-eyed Junco (<i>Junco hyemalis</i>)	26.5	(9)
Starling (<i>Sturnus vulgaris</i>)	5.6	(5)	White-crowned Sparrow (<i>Zonotrichia leucophrys</i>)	1.8	(5)
Yellow-breasted Chat (<i>Icteria virens</i>)	1.1	(6)	Song Sparrow (<i>Melospiza melodia</i>)	1.6	(7)
Wilson's Warbler (<i>Wilsonia pusilla</i>)	3.7	(4)	20 other species	10.2	
Western Meadowlark (<i>Sturnella neglecta</i>)	19.4	(11)	Shrubsteppe, breeding		
Brewer's Blackbird (<i>Euphagus cyanocephalus</i>)	2.8	(6)	Grey Partridge (<i>Perdix perdix</i>)	1.0	(2)
Brown-headed Cowbird (<i>Molothrus ater</i>)	1.1	(3)	Mourning Dove (<i>Zenaida macroura</i>)	2.1	(7)
Northern Oriole (<i>Icterus galbula</i>)	7.6	(10)	Horned Lark (<i>Eremophila alpestris</i>)	150.1	(7)
Western Tanager (<i>Piranga ludoviciana</i>)	1.5	(5)	Western Meadowlark (<i>Sturnella neglecta</i>)	144.1	(7)
Lazuli Bunting (<i>Passerina amoena</i>)	5.5	(10)	Vester Sparrow (<i>Poocetes gramineus</i>)	9.6	(7)
Vesper Sparrow (<i>Poocetes gramineus</i>)	7.4	(7)	Sage Sparrow (<i>Amphispiza belli</i>)	65.5	(7)
White-crowned Sparrow (<i>Zonotrichia leucophrys</i>)	1.0	(1)	White-crowned Sparrow (<i>Zonotrichia leucophrys</i>)	5.6	(2)
Song Sparrow (<i>Melospiza melodia</i>)	1.4	(7)	22 other species	7.0	
38 other species	12.1				

This is most likely a reflection of the well established relationship between vegetation structure and bird species diversity. Studies encompassing a wide range of habitat types (e.g. MacArthur 1964, Karr and Roth 1971) have demonstrated and discussed this correlation, and Willson (1974) has suggested that it reflects the addition of new species through the accumulation of new guilds in a stepwise fashion as vegetation complexity increases.

Although it seems intuitively likely that the wooded streamside permits the existence of a greater number of structurally-oriented guilds than the physiognomically simpler shrubsteppe, that the mechanism suggested by Willson (1974) is apparently operating here is substantiated by the observation that while diversity and richness are greater in arboreal vegetation, evenness is not (Table 2), and that increased diversity is associated with increased richness (i.e. the addition of new species), not increased evenness.

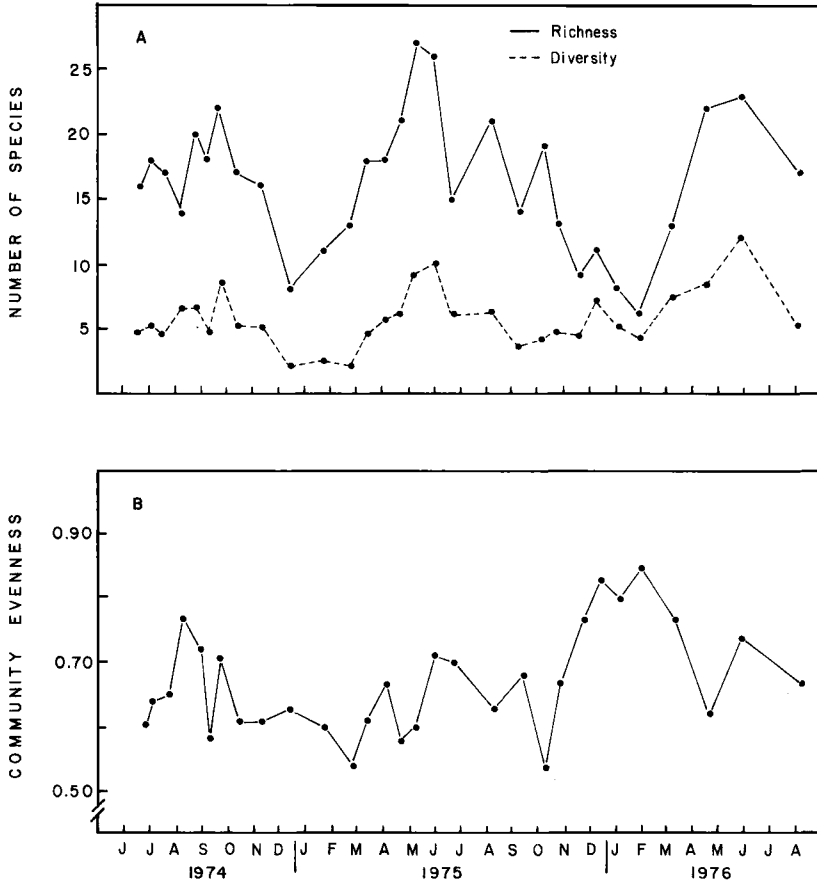


Fig. 2. Seasonal variation in bird community attributes of Snively Canyon: A—richness and diversity; B—evenness.

Seasonal dynamics.—The lack of periodicity in the evenness data (Fig. 2B), particularly when considered in conjunction with the distinct seasonality evidenced by richness and diversity, leads to some tentative conclusions regarding factors that may regulate community diversity. We observed that while the difference in evenness between both sets of winter counts (November–March 1974–75 and 1975–76) is highly significant ($P < 0.001$), it is not reflected in diversity ($P > 0.05$). Neither is there a significant difference in richness between the two years.

Examination of the partial coefficients of determination shows that during the winter, diversity clearly varies as a function of evenness ($R^2_{\text{part}} = .91$) and is quite independent of changes in richness ($R^2_{\text{part}} = .17$). A distinctly different pattern, however, is evidenced during the breeding season: diversity becomes much more highly associated with richness ($R^2_{\text{part}} = .87$) and is less so with evenness ($R^2_{\text{part}} = .72$). This strongly suggests that we are observing different methods of “regulation” of community structure at the same site, which may vary according to season.

Comparing the two seasons, resources during the breeding season are likely to be more stable than they are in winter, the vegetation structure more complex, and the climate more benign. Winter weather in the arid interior regions of the northwest

TABLE 2. Comparison of mean avian community attributes of Snively Canyon breeding and wintering season surveys and adjacent shrubsteppe breeding season surveys. Asterisks denote the probability that two adjacent means in a column are different (* = $P \geq 0.95$; ** = $P \geq 0.99$; *** = $P \geq 0.999$).

Area	Season	Number of individuals	Richness	Evenness	Diversity
Snively Canyon	Winter (n = 10)	59	11.3	0.70	4.4
	Breeding (n = 11)	148	19.5	0.67	6.8
Shrubsteppe	Breeding (n = 7)	385	10.3	0.82	2.9

can vary considerably and is often rigorous. For example, long-term weather data collected within 15 km of Snively Canyon show that winter minimum temperatures are more variable than summer maxima (a range of 27°C versus 8°C) and have never failed to drop to at least -6°C during the 60+ yr of record (Thorp and Hinds 1977). Under summer conditions it is not unreasonable to expect that populations are nearer their local equilibrium values (determined by resource states, vegetation complexity, etc.) than in winter and that the community organization might then be more likely to reflect elements of resource-based interspecific competition. Indeed, such competition and subsequent habitat partitioning is generally assumed to be the driving force behind the relationship between bird species diversity and vegetation complexity (MacArthur 1964, Karr and Roth 1971). Again, we suggest that this diversity/complexity relationship accounts for the greater variety of breeding birds in Snively Canyon compared to the shrubsteppe.

Kricher (1975) found in the simple system he observed that winter diversity [as well as summer diversity (Kricher 1972)] varied with richness rather than evenness. He concluded from this that severe weather, rather than exerting direct effects on bird species, worked indirectly by reducing food supplies. Conversely, the diversity patterns we observed certainly suggest that bird populations have the potential for regulation of their numbers outside those determined by their resource base.

The difference between Kricher's observations and ours is likely related to differences in the scale of sampling. His data were gathered in two separate successional stages that differed in vegetation structure as well as microclimate. Additionally, it seems probable that winter weather variation between his plots (separated by ~1 km) was much less extreme than the difference between summer and winter in our samples.

In any event, the patterns we have observed are statistically valid and logically consistent with Tramer's hypothesis. They point out the likelihood, often ignored, that examination of a community through its seasonal changes might easily suggest variation in the causal mechanisms that structure that community.

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