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## **In Search of a Diversity Ethic For Wildlife Management**

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### **Introduction**

As the century nears its end and demand for food and competition for land escalate, a most important issue facing conservationists will be the preservation of a mosaic of habitats in which can be preserved a representative cross-section of native species. The need to resolve this issue is emphasized in the *Global 2000 Report to the President* (Council on Environmental Quality 1980) which predicts that, worldwide, 500,000 to 2 million species will become extinct by the year 2000 and that the rate will increase from one per day in 1980 to one per hour by century's end (Myers 1979). Although these extinctions will largely occur in developing countries (Norman 1981), over 500 species and subspecies of flora and fauna have become extinct in North America since the Puritans arrived at Plymouth Rock in 1620 (Spinks 1979). This most critical need, to preserve habitat so that floral and faunal diversity can be maintained, rests not only on the loss of genetic diversity and scientific-medical properties, but on the long term consumptive, nonconsumptive, and social values of plants and wildlife to mankind.

Historically, formulating principles of conservation worldwide, and particularly in North America (Leopold 1933), has to a great extent rested on the concept of diversity. Even recently, the National Forest Management Act (1976) has required land managers to provide for a diversity of plant and animal communities in order to meet overall multiple-use objectives. Other federal, state, and private agencies use biotic diversity as a measure of ecosystem quality and assume diversity is an ecologically sound concept applicable to land management. In spite of its popularity, diversity has often been sharply criticized owing to the ambiguity of definitions and indices (Peet 1974, Routledge 1979). This has led Hurlbert (1971) to recommend that we abandon the concept and concentrate on other aspects of species-abundance patterns. Nevertheless, diversity continues to occupy the attention of wildlife and land managers, and the concept will almost surely continue to play a role in future management of wildlife.

Resource managers have emphasized principally alpha, or within-habitat, diversity; few have acknowledged the importance of beta, or between-habitats, diversity. Gamma diversity, a measure of all species in a geographic area, has been largely ignored. Though not new concepts, beta and gamma diversity are highly relevant to wildlife conservation. This paper reviews these diversity measures with the objective of establishing the timeliness of incorporating beta and gamma diversity as integral parts of the comprehensive planning process in resource manage-

ment. Two criteria are used: (1) the ecological, geographical, and organizational level of resolution and (2) the current, long-range, and biotic usefulness of each measure of diversity. Thus, the emphasis is on the use of diversity in management situations rather than in a theoretical or mathematical framework. The lack of mathematical support for diversity indices and the unavailability of acceptable statistical procedures to compare indices are addressed elsewhere (Routledge 1980, Alatalo 1981, Wolda 1981).

## Definitions

Of particular importance to the concept of alpha diversity are species richness, the number of species in a community, and the equitability or evenness with which importance is distributed among the species. The measure of alpha diversity rests on an estimate of the number of species within a community and where each species is weighted by its abundance.  $H'$ , the Shannon Weaver index (Peet 1974), or a plethora of alternatives ( $h'$ ,  $H$ ,  $O^{H'}$ ,  $D$ ,  $1/d$ , and others) are then computed to provide an index to local diversity. Evenness is generally measured by dividing  $H'$  by the maximum possible diversity for a given number of species.

The amount of species turnover between habitat types or the change in species composition along environmental gradients exemplify beta diversity. Whittaker (1970) approaches the measurement of  $\beta$  diversity by estimating the relative similarity of samples drawn from adjacent, but different communities. An increase in beta diversity is attributable to an increase in ecological distance between samples drawn from two communities. Calculations of the degree by which the samples differ from one another include Coefficient of Community (CC), the ratio of species shared by Sample A and B to the total number of species occurring in Sample A plus Sample B (similarity index) or Euclidean Distance (ED).

Gamma diversity is the total number of species to be found in all the available habitats in a fairly large geographic area (Whittaker 1970).

## Review of Diversity

Alpha diversity reflects the number and relative abundance of species populations in a habitat type. The popularity of the classic relationship (MacArthur and MacArthur 1961) between bird species diversity and foliage height diversity has reinforced the extensive and widespread use of alpha diversity in wildlife management, particularly for nongame wildlife. With respect to nongame birds and alpha diversity, the rationale of "if it works, use it" may be misleading in terms of biology and ecological properties. The biological and ecological flaws are at least four. First, the relationship does not hold in all forest communities (Balda 1975), appearing confounded by floristics (Franzreb 1978, Holmes and Robinson 1981) and the availability of food resources (Karr 1971). Second, ignored are differences attributable to the increase in species number with increasing area, and "many combinations of species richness and relative abundance can produce the same value of the index" (James and Rathbun 1981:785). Third, the diversity of breeding populations between consecutive years on a site may reflect events during the nonbreeding season (Lack 1954, Fretwell 1972) and/or weather related phenomena that influence the availability of resources in spring (Cody 1981). Fourth, an emphasis on alpha diversity in habitat management favors the "edge" species, the

common, widespread species. Ignored are those species that require large, contiguous habitat units (Robbins 1979). All problems in use of alpha diversity cannot be highlighted in this review. Other papers in recent books by Cody and Diamond (1975), Soule and Wilcox (1980), and Keast and Morton (1980) give further biological background to reconsider alpha diversity in wildlife management whether for birds, mammals, invertebrates, or plants.

Most measures of alpha diversity ignore the spatial distribution of individuals and the composition dynamics of communities. Although two communities may exhibit the same species diversity, one could be composed of species that intermingle at random and the second of monospecific patches (Peterson 1976). Further, two communities may possess identical alpha diversity values yet not have a species in common. The importance of spatial patterns of individuals and species has long been recognized as important by ecologists and is a focal point in the consideration of within- and between-habitat diversity. Few will argue from an ecological viewpoint the fact that total number of species increases along an ecocline, desert to dry grassland to prairie to oak woodland to oak-hickory forest to mesophytic forest, for example. Importantly, some habitats along an ecocline may have low alpha diversity—dry grassland, prairies, mature woodlands—yet make a substantial contribution to the beta diversity of a habitat gradient. If alpha habitat diversity were maximized through management along an entire ecocline, you would achieve a uniformly high alpha diversity, but this would reduce beta diversity by excluding species adversely affected by diminished habitat size and/or habitat heterogeneity (Faaborg 1980).

A number of plausible ecological concepts—climatic instability, productivity of ecosystems, or the interaction of the two—exist that may determine patterns in gamma diversity. Unfortunately, studies of wildlife distribution and abundance and habitat characteristics on a regional-continental scale are few. Of those available, biogeographic and evolutionary influences are particularly important and clear habitat associations are often lacking. For example, habitat size, a biogeographic feature, is most important to the distribution of big game (Picton 1979) and birds (Thompson 1978) in the northern Rocky Mountains, to mammals and birds of the Inter-mountain Region (Brown 1978), and to the birds of the eastern forest (Robbins 1979) and northern forest/bog habitat (Anderson and Robbins 1981). There is, moreover, information from an evolutionary viewpoint that bird populations of the grassland-steppe habitat vary largely independently of one another; responses of birds to habitat characteristics differ at levels of local, regional or continental scales, and some species apparently occur independent of most habitat features (Weins and Rotenberry 1981).

### **Relevance to Management**

Table 1 summarizes the level of resolution and potential for use of each diversity type in management. The points with respect to alpha and beta diversity are illustrated in two case studies of nongame bird habitats.

#### *Case Study: Tallgrass Prairie Community*

The first is of an ecologically simplistic system, the tallgrass prairie of the east central Great Plains. Four prairie relicts in each of four size categories, 0–10 ha,

Table 1. Selected characteristics of alpha, beta, and gamma diversity.

	Diversity		
	Alpha	Beta	Gamma
Resolution			
organismal	population/communities	communities	communities/ecosystems
geographic	local	ecocline	regional/continental
ecological	questionable	good	good
Management Use			
current	extensive	limited	limited
long-range	negative	useful	useful
biotic	uncertain	excellent	excellent

>10–30 ha, >30–100 ha, and >100 ha, and located in central and southwest Missouri served as study sites. Each relict was visited during the breeding seasons of 1978–80; at each location the surveys were taken within a few days of the same date each year. Number of breeding bird species for all relicts less than 30 ha and in 20 ha blocks located at random in the >30–100 ha ( $n = 2$ ) and >100 ha ( $n = 3$ ) were surveyed using the flush method (Wiens 1969) or spotmap method (Williams 1936). The minimum criteria for breeding was satisfied if a territorial male was seen on four or more of the five censuses and if a female was detected. Because of the lek behavior in early spring of the greater prairie chicken (*Tympanuchus cupido*), supporting census information was obtained from unpublished Pittman-Robertson reports of the Missouri Department of Conservation. An index ( $D'$ ) of local grassland-shrub diversity (Wiens 1974, Roth 1976) was calculated each year along a transect extending the longest axis of each relict. Other measurements included size of relict, isolation from similar habitat (Sullivan and Schaffer 1976), and shape (Lind 1974) as an index to edge.

Using stepwise multiple regression, the four variables, area, habitat heterogeneity, edge, and isolation, were tested for their relationship to number of species that colonized the 16 prairie relicts. Of the four, size of relict contributed significantly to the annual number of bird species, 1978–80 (Table 2). Vegetation, heterogeneity, edge, and isolation made a contribution to annual number of species, but the effect was minor. The pattern of prairie or forest edge birds differed somewhat from that of the prairie birds. Again, prairie size made the major contribution, but the effect of within habitat heterogeneity and edge increased.

The striking feature in species use of prairie relicts is the high frequency of nonprairie birds, the brown-headed cowbird (*Molothrus ater*), field sparrow (*Spizella pusilla*), bobwhite (*Colinus virginianus*), red-winged blackbird (*Agelaius phoeniceus*), common grackle (*Quiscalus quiscula*), brown thrasher (*Toxostoma rufum*), bluejay (*Cyanocitta cristata*), on small prairies (Table 3). Although within habitat diversity or total bird species diversity varied little across the size range of prairie relicts, number of prairie species did increase ( $R^2 = 0.88$ ,  $P < 0.05$ ) with size of prairie. The ability of relict size to explain species distribution rests on the habitat size-dependency of selected prairie species (Samson 1980). The second prominent characteristic of small prairie relicts is the high rate of species turnover.

Table 2. Relative contributions of independent variables to the multiple correlation coefficient,  $R^2$ , for the annual number of bird species.

	Annual species list					
	Prairie birds			Prairie-forest edge birds		
	1978	1979	1980	1978	1979	1980
Area	0.8641 <sup>a,b</sup>	0.8000 <sup>b</sup>	0.8081 <sup>b</sup>	0.3667	0.3223	0.4076 <sup>c</sup>
Habitat heterogeneity	0.0358	0.0453	0.0519	0.1949	0.2313	0.0681
Edge	0.0013	0.0009	0.0050	0.1033	0.1129	0.0681
Isolation	0.0001	0.0000	0.0001	0.0003	0.0009	0.0121

<sup>a</sup>Multiple correlation coefficient( $R^2$ ).

<sup>b</sup>Significant at 0.01 level.

<sup>c</sup>Significant at 0.05 level.

Table 3. Mean values of bird community characteristics of the study prairies during the breeding seasons 1978–1980. (Species codes in footnotes follow Klimkiewicz and Robbins [1978]).

	0–10 ha ( <i>n</i> = 4)	>10–30 ha ( <i>n</i> = 4)	>30– 100 ha ( <i>n</i> = 4)	>100 ha ( <i>n</i> = 4)
Prairie birds <sup>a</sup>				
Number	2.2	3.8	5.3	6.0
Species diversity ( $H'$ )	0.371	0.98	1.698	1.19
Evenness ( $J$ )	0.535	0.81	0.95	0.66
Annual turnover (%)	33.0	21.0	12.0	0.0
Prairie-forest edge birds <sup>b</sup>				
Number	10.8	15.2	16.0	16.0
Species diversity ( $H'$ )	2.53	2.44	2.40	2.64
Evenness ( $J$ )	0.89	0.88	0.88	0.80
Annual turnover (%)	12.0	3.4	0.0	0.0

<sup>a</sup>GPCH, UPSA, WEME, DICK, GRSP, HESP.

<sup>b</sup>GOBW, MODO, YSFL, EAKI, HOLA, BLJA, MOEK, BRTH, AMRO, YELL, RWBL, COGR, BHCO, INBU, AMGO, FISP.

These rates ranged from 0 to 45 percent on relicts of 0–10 ha, 5 to 33 percent on relicts of >10–30 ha, 5 to 15 percent on relicts of >30–100 ha; only relicts of about 160 ha were able to maintain stable prairie bird communities from year to year.

Thus, management solely by within-habitat bird species diversity may not be an appropriate strategy since: (1) diversity indices often reflect a greater change in the distribution of individuals among the species versus a change in species composition as may exist along a habitat-size gradient, (2) assuming that a stable bird community is an acceptable management goal, knowledge beyond species numbers and the distribution of individuals is required, and (3) critical habitat size requirements of certain species are not addressed. Lastly, analysis of variance revealed no significant differences in the vegetation heterogeneity between the four size

categories of prairie relicts. Clearly, management to maximize alpha, or within-habitat, diversity holds little potential for increasing or stabilizing the distribution of native prairie birds. Rather, it provided new habitats for cowbirds, blackbirds, and other non-prairie species that may adversely affect the abundance of prairie species. Alpha diversity management of prairies would only have adverse impacts upon native prairie species by promoting community and ecosystemic instability, and if carried to the extreme (tree plantings, brush invasion, etc. to maximize prairie edge) would represent management for extinction of those species. Gamma diversity management would favor greatest regional diversity through the management of some small units for prairie margin species while promoting native prairie species through community and ecosystemic stability by keeping most land in large, generally undisturbed blocks. Already, virtually all remaining populations of prairie chickens occur on large blocks of (often privately owned) native rangeland (Cannon and Knopf 1980, Samson 1980).

### *Case Study: Western Forest Communities*

The second case study is of a more complex system ecologically: the forest communities of Jackson Hole, Wyoming. In 1952 and 1954, Salt (1957) surveyed the avifauna of this region for comparison to ecological counterparts of the Sierra Nevada. Six plant communities were identified based upon physiognomy. These included lodgepole pine (*Pinus contorta*) forest, lodgepole-spruce-fir ecological interface, spruce-fir forest, willow-sedge swamp, scrub meadow, and flatland aspen (*Populus tremuloides*) stand. Each site was surveyed for birds repeatedly using standard strip-transect techniques. See Salt (1957) for details of the study sites and methodology.

The six study sites represented three basic vegetative types: coniferous forest, deciduous forest, wetland communities. Salt (1957:375) compared the foraging niches of birds in these three communities schematically along foliage profiles. The spruce-fir and aspen communities had 19 species each, while the willow-sedge community comprised 15. We calculated a simple alpha diversity coefficient for each (Table 4) using the Simpson Index ( $D$ ). The riparian, willow-sedge community and spruce-fir community had comparable alpha diversities that were higher than the aspen sites. The standard conclusion drawn in practice is that the coniferous and riparian sites should receive management priority due to the greater diversity

Table 4. Comparison of species richness, alpha and beta diversity for three major vegetative communities, Jackson Hole, Wyoming 1952–1954 based on data in Salt (1957).

	Species richness	Alpha diversity ( $D$ ) <sup>a</sup>	Beta diversity	
			Comparison	(CC) <sup>b</sup>
1. Spruce-Fir	19	0.91	1::2	0.12
2. Willow-Sedge	15	0.88	2::3	0.65
3. Aspen-Flatland	19	0.77	3::1	0.11

<sup>a</sup> $D$  = Simpson index  $(1 - \sum(p_i)^2)$

<sup>b</sup>CC = Community coefficient  $(2 S_{ab}/(S_a + S_b))$

of nongame birds found in these vegetative types. However, simple Community Coefficient (CC) calculations demonstrated dramatic similarity between the riparian and aspen sites, and markedly greater beta diversity (decreased similarity) when either was compared to the coniferous type. This pattern of similarity, dissimilarity is visually illustrated in Figure 1.

We expanded the analysis (Table 5) to identify any unique components within the conifer community. Alpha diversity calculations were comparable for the lodgepole forest, spruce-fir forest, and the ecotone of the two. Beta diversity calculations, however, revealed that the ecotone alpha diversity was derived primarily from the spruce-fir component, the lodgepole community showed much greater beta diversity (i.e., decreased similarity) when compared to the other two conifer stands. The expanded analysis of the deciduous community showed no clear pattern of beta diversity between sites.

From these comparisons we conclude that forests in the Jackson Hole area should be managed to assure the maintenance of stands of lodgepole pine and spruce-fir, at least from a nongame bird perspective. We would recommend minimization of ecotones (edge) in an area—*not a single species was unique to the ecotone*. The suggestion to intensify lodgepole pine emphasis may be received skeptically since the pine forest contained the lowest species richness of the sites. When one examines the continental distribution of species in each, however, five of the eight species in lodgepole pine are restricted to the western half of North America, while 13 of the 19 species recorded in spruce-fir range continent-wide. Management for lodgepole pine sites would favor management of a western-derived avifauna while management towards spruce-fir could result, ultimately, in a single coniferous avifauna across North America comprised of many ecological generalists. Thus, the beta diversity analysis has led to gamma diversity considerations in management.

Further, beta diversity analysis revealed little need to narrow management of deciduous communities to a single vegetative type. Of the 25 species recorded in deciduous sites, 17 are continent-wide in distribution—being derived from eastern deciduous forests. Of the remaining eight species, one was also present in the coniferous stands, leaving only seven species tied specifically to western deciduous communities: 4/7 occur in willow-sedge, 5/7 in scrub-meadow, and 6/7 in aspen stands. No deciduous site was dominated by a western avifauna. Aspen showed the greatest number of western representatives, and probably should receive primary management consideration. The current emphasis on riparian habitats in the western states has been from an alpha diversity perspective, not beta or gamma. Whereas riparian communities support a somewhat unique avifauna within the Jackson Hole vicinity, the Jackson Hole riparian avifauna is really tangential to the deciduous eastern forest and, secondarily, aspen from which it is derived. A more intensive analysis of riparian avifaunas (Knopf, in prep.) will address patterns of beta diversity for such *Salix-Populus* communities.

## Conclusions

An ethic is defined as the “discipline dealing with what is good and bad. . . [leading to] principles of conduct governing individuals or groups of professionals” (Woolf 1974:393). If the ultimate goal of wildlife management is for the optimal mainte-

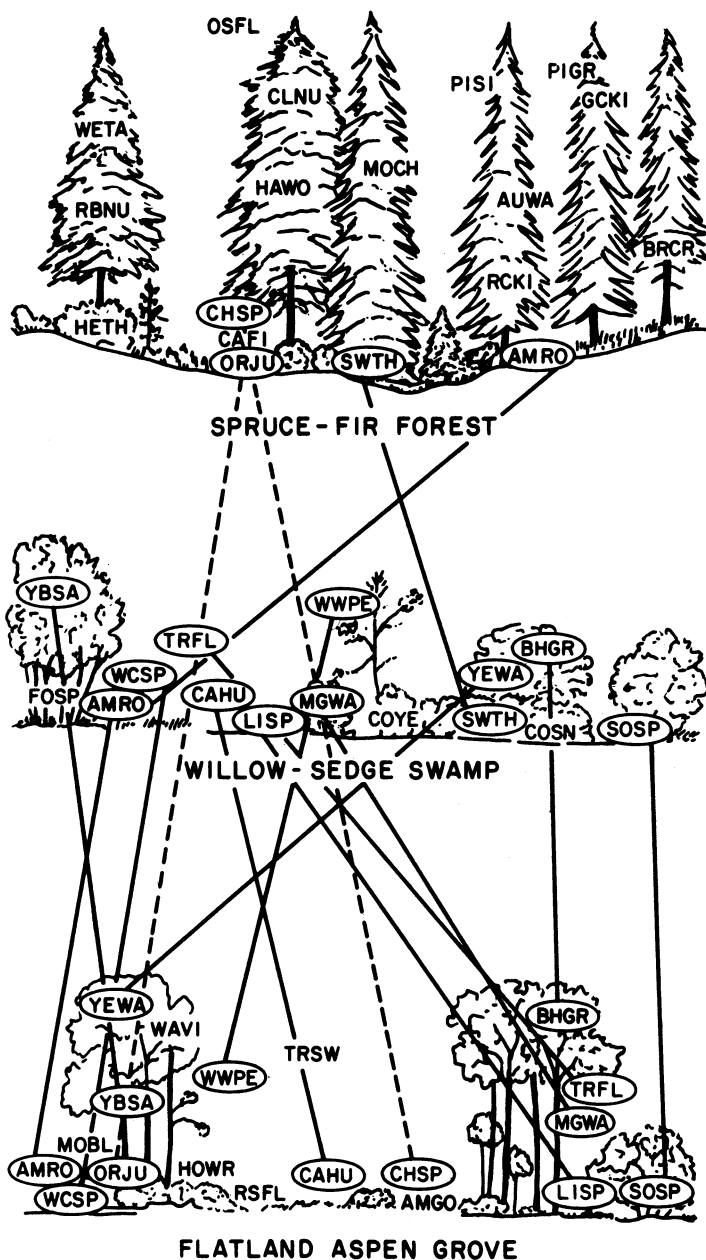


Figure 1. Vegetative community affinities of birds at Jackson Hole, Wyoming demonstrating similarity of riparian and aspen avifaunas, and the greater uniqueness of the conifer avifauna. (After Salt 1957:375). For legend of bird species codes see Klimkiewicz and Robbins (1978).

Table 5. Alpha and beta diversity comparison of 3 coniferous and 3 deciduous habitat types at Jackson Hole, Wyoming 1952–1954 based on data in Salt (1957).

	Species richness	Alpha diversity ( <i>D</i> ) <sup>a</sup>	Beta diversity	
			Comparison	CC <sup>b</sup>
<i>Coniferous</i>				
1. Lodgepole pine	8	0.82	1::2	0.55
2. Lodgepole-spruce-fir	14	0.89	2::3	0.79
3. Spruce-fir	19	0.91	3::1	0.52
<i>Deciduous</i>				
1. Willow-sedge swamp	15	0.88	1::2	0.48
2. Scrub-meadow	14	0.91	2::3	0.61
3. Flatland-aspen	19	0.77	3::1	0.65

<sup>a</sup> $D$  = Simpson Index ( $1 - \sum(p_i)^2$ )

<sup>b</sup>CC = Community Coefficient ( $2S_{ab}/(S_a + S_b)$ )

nance of the total resource, including consumptive, nonconsumptive, and esthetic values, the conduct of management should emphasize the type of ecological community mix that will provide assurance of system maintenance.

Thus, in conclusion, we propose a direction and methodology for future wildlife management based on current ecological knowledge within the context of the three levels of diversity:

1. *Minimize practices promoting site-specific diversity.* An aggregate community (plants, animals, or the interaction of the two) is not simply predictable by alpha diversity but depends to a great extent on the geographic scale of definition.
2. *Emphasize between-habitat diversity at the management unit level.* The distribution, abundance, and stability of a community or ecosystem cannot be approached piecemeal, overlooking the interaction of habitat types and associated wildlife communities. The potential for species richness is ordinarily much higher between than within vegetative communities, even when the within-habitat wildlife community may be depauperate. In practical terms, it is critical that land/wildlife managers understand within-versus between-habitat diversity in any resource system being managed.
3. *Implement a "top down" or gamma-beta-alpha diversity approach at the regional/national decision-making levels.* This approach should emphasize the economic/ecological/esthetic values of ecosystems, followed by an internal analysis of between-habitat species associations. Although local demands for alpha diversity often emerge, the current state of scientific/ecological knowledge suggests that continuation of alpha diversity management may have dire ecological consequences for the native wildlife of North America.

The most likely future approach to wildlife management rests with (1) identifying important resources within an area, (2) determining the extent and ecological value of each resource and (3) the incorporation of a resource-based diversity index into regional and local planning procedures. The extent to which diversity and its applications are developed in the next few years will play a major role in preserving North American and worldwide biotic diversity. Unfortunately, the emergence of

diversity as a respectable cornerstone for wildlife management has been slowed by an emphasis on alpha rather than higher (beta and gamma) diversity. The purpose of this paper was to identify this handicap.

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