THE RELATIONSHIP BETWEEN BREEDING BIRD DENSITY AND VEGETATION VOLUME

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ABSTRACT.—An index of total vegetation volume was strongly correlated with breeding bird density at 31 sites in four separate studies conducted in southwestern shrub and desert habitats between 1974 and 1987. Vegetation volume was not as strongly correlated with winter bird density in two of these studies. We suggest that these correlations indicate that breeding birds respond strongly to resources associated with vegetation and that such a resource-based response may explain such well-known patterns as the edge effect and the high avian breeding densities in southwest riparian habitats. The technique we describe for measuring total vegetation volume provides a quick and accurate method of estimating this simple aspect of vegetation structure and may be useful in describing plant communities quantitatively. *Received 26 Feb. 1990, accepted 29 May 1991.*

An underlying assumption of theoretical models of avian community structure generated in the 1960s is that the number and diversity of birds in an area reflect the availability of critical resources. This linkage between community structure and resources was supported initially by MacArthur and MacArthur's (1961) demonstration of a close correlation between foliage diversity (FHD) and bird species diversity (BSD). Since then the relationship between vegetation structure and avian community parameters has been the subject of much research. Although widely accepted at first, the BSD/FHD relationship and, by association, the underlying resource assumption have come under strong criticism for two reasons. First, while some studies confirmed the empirical relationship described by MacArthur and MacArthur (MacArthur et al. 1966, Karr and Roth 1971, Terborgh 1977, Moss 1978, Dickson and Segelquist 1979, Beedy 1981, Bell 1982), others did not (e.g., Stamp 1978, Conner et al. 1979, Karr 1980, Erdelen 1984, Engstrom et al. 1984). Thus, the generality of the proposed relationship appeared questionable. Secondly, both BSD and FHD were calculated using information indices, which hide important information by combining measures of species richness and relative abundance, and may lack a direct, biologically meaningful explanation (James and Rathbun 1981). Several authors have suggested that simpler population parameters with direct biological interpretation be used to quantify both vegetation and wildlife populations (Karr 1980, James and Rathbun 1981, Erdelen 1984). We propose that to assess properly the resource

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assumption that underlies MacArthur and MacArthur's original work, the relationship between vegetation characteristics and avian community patterns should be re-examined using these simple population parameters.

In this paper, we report the relationship between two such simple population parameters for avian communities in a variety of southwestern habitats. We first describe a simple method of measuring vegetation volume in habitats where vegetation is generally under 8 m in height. We then demonstrate that an index of vegetation volume generated by our measuring technique was closely correlated with total breeding bird density in four different studies. We suggest that these strong correlations provide evidence that breeding birds respond to critical resources as estimated by vegetation volume. This resource-based hypothesis may provide a biological explanation for several well-known patterns of avian distribution, including the edge effect and the high avian densities reported from desert riparian systems. Our study suggests that the assumption that community patterns reflect a dependence on critical resources is a viable hypothesis that deserves further examination.

METHODS

We first developed our technique for measuring vegetation volumes and documented the relationship between total vegetation volume (TVV) and breeding bird density (BBD) during a 1984 study of avian habitat selection in New Mexico. Because sample sizes in this study were small, we re-examined the TVV/BBD relationship by measuring vegetation volumes and bird densities at 15 sites in southern Arizona in 1985 and 1986. In this paper, we first present the results of this larger study to demonstrate the technique by which we measured vegetation volumes and to document the TVV/BBD relationship. We then briefly describe similar TVV/BBD correlations we found in three smaller data sets, including the original New Mexico study, to establish the generality of the relationship.

1985–1986 Arizona data. — We measured vegetation using a variation of the vertical-line intercept technique (MacArthur and Horn 1969). We refer to our variation of the technique as the "pole method." A 6-m pole was constructed from 18-mm diameter electrical conduit pipe and marked in decimeter and meter sections. We used this pole to measure an index of the volume of woody perennial plants in each meter layer above the ground. Holding the pole vertically at each point where TVV was to be measured, we counted the number of decimeter sections that contained vegetation within a radius of 1 dm from the pole. We therefore sampled a series of cylinders 0.1 m tall and 0.1 m in radius.

We called each decimeter cylinder that contained vegetation a "hit." The number of possible hits in each meter layer above the ground ranged from 0–10. We also recorded the species of plant that was responsible for each hit. If two or more plant species were present in the same meter layer, the total number of hits in that layer were allotted between the plant species according to the relative dominance of each plant within the layer. By holding the pole over our heads, we could count the number of hits in layers up to 8 m above ground. We estimated the number of hits in layers >8 m for the few plants reaching that height in the habitats we studied. Total vegetation volume (TVV) was estimated from these data as: TVV = h/10p; where h = the total number of hits summed over all meter layers at all points measured, and p = the number of points at which vegetation volumes were measured. TVV

has the units of cubic meters of vegetation per square meter, and in our study ranged from 0 to 2.0 for southwestern desert and shrub habitats. This technique overestimates actual vegetation volume because each decimeter cylinder containing any vegetation, regardless of amount, was counted as full. This error could be reduced by decreasing the radius or the height of the cylinder. Because of the manner in which data were collected, indices of vegetation volumes for each plant species and each meter layer could also be calculated, as well as indices of plant height, percent cover, and FHD.

We measured TVV and censused birds at 15 study sites located in the Tucson Valley, Pima County, Arizona in 1985 and 1986. All sites were located in the Arizona Upland Subdivision of the Sonoran Desertscrub or Riparian Deciduous Woodland and Scrubland biomes (Brown 1982) and reflected the natural distribution of vegetation types found in the Tucson Valley. TVV was measured as outlined above at 4–12 random plots selected at regular intervals along a transect through each major habitat. Specific plot locations were randomly chosen from starting points located at regular intervals along, and within 30 m of, transects used to census birds. A 20-m straight-line transect was established within each of the plots along a randomly determined heading from a point close to the center of each plot. Volume measurements were taken at 2-m intervals along this transect. A second 20-m transect was established perpendicular to the first, resulting in measurements from 20 points in each plot.

We compared the amount of variation in bird density explained by TVV with the amount of variation explained by other vegetation indices such as plant species diversity, FHD, and the vegetation volumes of particular plant species. FHD was calculated from the data collected by the pole method by treating each meter of the pole as a layer, and using the standard Shannon-Weiner information index $H' = -\Sigma\, p_i \ln p_i$, where p_i = the proportion of total hits found in the ith meter layer. The meters are not "layers" as traditionally thought of in FHD studies; that is, they are not necessarily separate levels of vegetation to which the birds may be responding (MacArthur and MacArthur 1961). However, the pole method allows FHD to be calculated using up to eight layers, which provides a more accurate profile of vegetation than usual measures of FHD.

We estimated bird densities using 0.6–4.6-km long variable-width belt transects (Emlen 1971). Areas censused ranged from 12–90 ha. We conducted winter bird censuses in December 1985 and January 1986 and breeding bird censuses in July 1986. All censuses were conducted between 05:00 and 09:00 h MST during suitable weather.

During the breeding season, densities for territorial birds were based on numbers of breeding pairs per 25 ha. A single adult bird of either sex, as well as two birds of opposite sexes together, was counted as a pair. Groups of birds composed of adults with recent fledglings were counted as one pair. Densities of non-territorial species, such as House Finches (*Carpodacus mexicanus*) or Brown-headed Cowbirds (*Molothrus ater*), were estimated from total counts, as were those of all birds in winter. Breeding density estimates were also based on total counts for species where young birds had dispersed and it was not possible to identify family groups (e.g., Cactus Wrens [*Campylorhynchus brunneicapillus*], Verdins [*Auriparus flaviceps*], and Gambel's Quail [*Callipepla gambelii*]). Birds flying over transects and the few migratory or visiting species encountered were not included in analyses.

New Mexico data set.—We also had access to vegetation volumes and bird densities from three smaller studies. Although most of these data were not collected specifically for examining the TVV/BBD relationship, we present them here to document the generality of the strong correlation between TVV and BBD in southwestern habitats. Techniques for measuring vegetation and bird densities differed among the studies; therefore, we cannot make strong comparisons among the different data sets. However, measurement techniques

were used consistently within each study. Thus, each study can be examined independently for evidence supporting the TVV/BBD relationship.

We measured vegetation volumes in six different biomes in Grant County, New Mexico, in March 1984 (Mills and Carothers 1986). Study sites were located in six habitat types: cottonwood-dominated Sonoran Riparian Deciduous Forest, box-elder dominated Sonoran Riparian Deciduous Forest, mesquite-dominated Sonoran Riparian Deciduous Woodland, Madrean Evergreen Woodland, Great Basin Conifer Woodland, and Semidesert Grassland (Brown 1982). Lists of dominant plants and birds recorded in this study and studies described below are available from the authors.

We measured volumes in 1–4 plots at each study site in a manner similar to that described above except for the following details. We estimated vegetation volumes within the cylinder described by a radius of 1 dm from each meter layer of a 5-m pole. The pole was not marked in decimeters, instead volume categories of 0.0, 0.1, 0.5 and 1.0 density were estimated for each meter layer. A value of 0.1 was given to any estimate of volume ≤0.1 of the total meter layer, 0.5 was given to any estimate between 0.1 and 0.5, and 1.0 was given to any estimate between 0.5 and 1.0. For vegetation taller than could be recorded by the 5-m pole, a single estimate of the volume in all remaining layers was made.

For a number of plots, vegetation volumes were measured by both the pole method and the shapes and plots method (Balda 1969). The shapes and plots method is an alternate technique for measuring volumes in which plants are classified into general geometric shapes, and volumes are estimated from appropriate height and width measurements. To correct for variation in density within plants, we visually assigned each plant into density classes of 0.1, 0.5, or 1.0, which was then multiplied by the total volume. We censused birds in New Mexico along 2–4 km long variable-width belt transects as described above. Areas of study sites ranged from 40–80 ha. For small, well-defined, long and narrow, or irregularly shaped habitats, such as riparian forests, we estimated total bird densities based on total counts of birds and areas measured from aerial photographs with a planimeter. Breeding bird censuses in these habitats were conducted in June and July 1983, while winter censuses were conducted in January and February 1983.

1987 Arizona data.—We measured vegetation volumes and censused birds at six Sonoran Desertscrub or Riparian Deciduous Woodland sites in the Tucson Valley, Pima County, Arizona, from April through July, 1987. These sites served as native-vegetation control sites for a larger study of the relationship between vegetation volume and the densities of urban birds. Two of the six control sites had been used in the 1985–1986 Arizona study. Vegetation volumes were measured as in the 1985–1986 Arizona study. We measured vegetation volumes and recorded plant species at 10 plots per study site in May–July 1987. We censused birds using fixed-width belt transects (Emlen 1971). All transects were 800 m (½ mi) long and 49 m (160 ft) wide. This produced a total census area of 3.9 ha (10 acres) at each site. The size of the plots was dictated by limitations on plot size in the urban areas for which these plots served as controls.

All bird censuses were conducted in April and May 1987 between 05:00 and 09:00 h MST. Fledglings, visitors, and migrants were not included in density estimates. Because non-territorial birds such as doves and House Finches could be using the sites in a manner different than territorial birds (Anderson et al. 1983), we calculated the relationship between TVV and total bird density both with and without these species in this data set.

Verde River, Arizona, data.—Carothers et al. (1974) provide vegetation volumes and bird censuses for four cottonwood-dominated Sonoran Riparian Deciduous Forests along the Verde River in central Arizona. They estimated vegetation volumes with the shapes and plots method without any correction for internal foliage volume. For our analysis, we

eliminated from total bird densities both European Starlings (*Sturnus vulgaris*), which apparently used these sites only for roosts, and all bird species directly dependent on water.

Statistical analysis.—We used simple linear regression to examine the relationship between TVV and total bird density, calculating correlation coefficients (r) and examining residuals to determine the strength of the correlations. To correct for departures from normality, we applied a square-root transformation to the vegetation volume data, and a $\log_{10}$ transformation to the density, species richness, and FHD data. Although we ran all statistical tests on the transformed data, we present the untransformed data in Fig. 1 for clarity. Significance of regression coefficients was accepted at the $P < 0.05$ level for all statistical tests.

We also ran a series of simple linear regressions using bird density as the dependent variable and a number of vegetation characteristics as the independent variables. These tests were done to determine if TVV explained more variance in bird density than did FHD, plant species richness, or the volumes of the most common plant species. When a series of statistical tests are examined simultaneously in this manner, there exists a high probability of Type I error (incorrectly rejecting a true null hypothesis) (Rice 1989). Accordingly, we performed a sequential Bonferroni test to determine if all r values with $P < 0.05$ should be considered significant. Four of the seven regressions in this series yielded r values with $P < 0.05$, and all four of these results should be considered significant at a table-wide significance level of $P = 0.05$, according to the Bonferroni procedure. Finally, we also used stepwise multiple regression to see if TVV or other vegetation parameters were consistently loaded first into a regression model explaining density variance.

RESULTS

1985–1986 Arizona data.—Total vegetation volume (TVV) and total breeding bird density (BBD) for the 15 sites in southeastern Arizona were highly correlated ($r = 0.930$, $P = 0.0001$, Fig. 1). Examination of the residuals showed an extremely close fit to the linear model. TVV and wintering bird density were not significantly correlated at the eight sites where winter censuses were conducted ($r = 0.485$, $P = 0.223$). However, TVV was significantly correlated ($r = 0.787$, $P = 0.020$) with the winter density of bird species that are not primarily seedeaters (sparrows, finches, and quail).

TVV was always the first variable loaded into the stepwise multiple regression models that related variation in BBD to seven vegetation structure and floristics variables. TVV had a higher r value ($r = 0.93$) in these regression models than did FHD ($r = 0.865$, $P = 0.0001$), plant species richness ($r = 0.437$, $P = 0.103$), and the volumes of the four most widespread plant species (*Prosopis juliflora*, $r = 0.789$, $P = 0.0005$; *Larrea tridentata*, $r = -0.378$, $P = 0.164$; *Acacia constricta*, $r = 0.007$, $P = 0.979$; *Acacia greggii*, $r = 0.746$, $P = 0.0014$).

Other data.—TVV and BBD for the six New Mexico sites were also highly correlated ($r = 0.951$, $P = 0.0036$; regression equation for transformed variables: y = 0.58x + 1.91). Examination of the standardized residuals showed no significant departure from a normal distribution
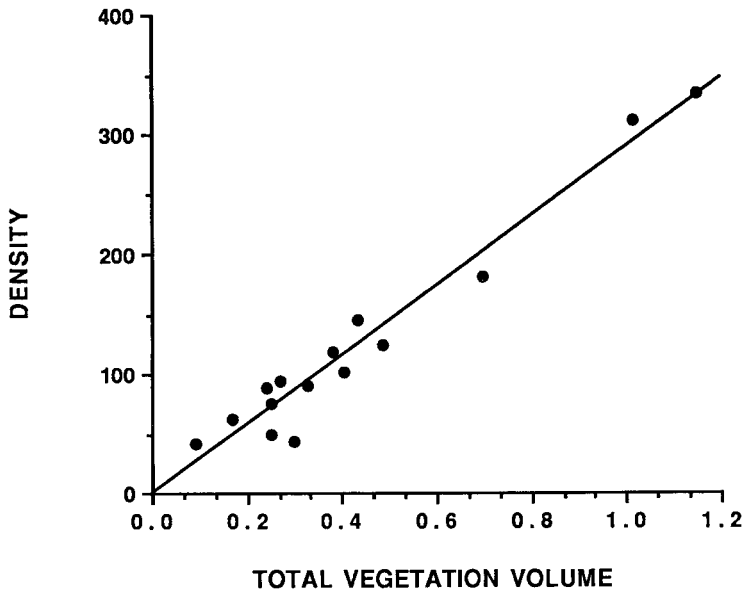
FIG. 1. Total breeding bird density (pairs per 25 ha) as a function of total vegetation volume (TVV) for the 1985–1986 Arizona study sites. Regression equation: y = 290x − 1.0.

(Kolmogorov-Smirnov test for goodness of fit, $P > 0.05$); however, sample sizes were very small. Inspection of the residuals suggested a curvilinear function might fit the data better than the linear model, but with only six data points no strong conclusion can be made. For the five study sites censused in winter, TVV was not significantly correlated with total wintering bird density ($r = 0.824$, $P = 0.086$) or with non-seedeaters ($r = 0.818$, $P = 0.090$).

Values of vegetation volumes generated with the pole method and shapes and plots method were highly correlated ($r = 0.979$, $P = 0.004$, $N = 5$). Volume estimates derived from the shapes and plots method were higher than those from the pole method (about 1.9 times higher for the four lowest points; Mills, unpubl. data).

In the 1987 Arizona data set, a significant correlation was found between TVV and BBD at the six control sites ($r = 0.866$, $P = 0.026$, regression equation: y = 0.30x + 1.37). The regression did not change substantially when non-territorial and exotic species were removed from the density data ($r = 0.873$, $P = 0.023$). In the 1987 data set, FHD correlated better with BBD than did TVV (FHD: $r = 0.947$, $P < 0.0041$). However, the

densities of non-territorial native birds (doves and finches) and the non-native House Sparrow (*Passer domesticus*) were increased at some of our 1987 Arizona sites that were close to urban areas, and we suspect that this increase masked the TVV/BBD relationship. When non-territorial birds and exotic species were removed from the density data, TVV loaded as the first variable into the stepwise regression model. None of the sites in the other studies was close to urban areas.

Finally, there was a significant correlation between TVV and BBD at the four cottonwood forest sites described by Carothers et al. (1974) ($r = 0.999$, $P = 0.0008$; regression equation: $y = 0.005x + 3.51$).

DISCUSSION

Significant correlations were found between TVV and BBD in all four studies. This result appears quite robust, since the regressions were uniformly high in spite of wide variation in the habitats sampled and variations in the methods of measuring bird density and vegetation volume. Although the habitats sampled in both of the Arizona studies were mostly from within the same biome, few dominant plant or bird species were shared between study sites. Even fewer shared species were recorded between sites in the New Mexico study because sites were mostly from different biomes. Although vegetation volume estimates were based on small sample sizes in the New Mexico study, the correlation between TVV and BBD was still high. The relationship between vegetation volume and bird density appeared to exist both within the same plant community and between different types. This suggests that, within the range of southwestern habitats we sampled, breeding bird density correlated with vegetation volume regardless of plant species composition. Additional studies from other shrubby habitats are necessary to test the generality of this empirical relationship.

Other studies that examined correlates of bird density have found that foliage volume accounted for a significant portion of the variation in bird density or species richness (Anderson et al. 1983, Meents et al. 1983, Robinson and Holmes 1984, Vander Wall and MacMahon 1984, Verner and Larson 1989). Some workers have found that other vegetation parameters such as percent foliage cover and FHD correlate significantly with bird density (Shurcliff 1980, Hino 1985); in general, these studies did not measure vegetation volume.

A number of studies suggest that measures of floristics such as densities of individual plant species are more important determinants of bird community parameters than are physiognomic (structural) measures (Kroodsma 1982; Rice et al. 1983, 1984; Rotenberry 1985). Findings of these

studies do not conflict with the TVV/BBD relationship we describe. Many of these studies used presence/absence data of individual bird species, while we examined variation in total bird density. Even though some studies include bird densities and indices of vegetation volume in their data sets (i.e., Rotenberry 1985), analyses are usually based on similarity indices, which compare proportions of various parameters and do not include total bird densities or total vegetation volume.

These studies also emphasize that individual bird species are often closely associated with individual plant species. Many such relationships are well-known (e.g., Meents et al. 1982), and some were apparent in our data sets. Floristics and physiognomy are both important in determining avian community structure. With individual bird species responding in different ways to floristics and physiognomy, the strong correlation between total vegetation volume and total breeding bird density is all the more remarkable and has some interesting implications for community ecology. In particular, our results suggest that the total number of birds in southwestern lowland habitats is dependent on some factor(s) associated with the amounts of vegetation present. If, as we argue below, these factors are the resources on which bird populations depend for successful breeding, then this would support the assumption underlying Mac-Arthurian community ecology that resource levels determine consumer levels.

Resource-based hypothesis. — Simple indices lend themselves to biologically meaningful interpretation (Karr 1980, Erdelen 1984). A reasonable hypothesis for the strong correlations between vegetation volume and breeding bird density is that bird density is proportional to available resources. Vegetation volume is an accurate estimator of plant biomass (Fonteyn 1978, Schlesinger and Jones 1984); therefore, volume could be an accurate estimator of resources associated with plant biomass. If plants provide resources in proportion to their vegetation volume (by providing more insect prey, more nest sites, or more favorable daytime roosts, for instance), then bird density should be proportional to vegetation volume.

One line of evidence supporting the resource-based hypothesis comes from the lack of significant correlations between winter bird density and TVV as measured in the summer. A high percentage of wintering birds in the southwest are flocking granivores, which feed on grass and forb seeds gleaned from the soil or from weedy annual plants (Pulliam and Brand 1975). We would not predict these groups to be heavily dependent on the foliage of woody perennials, except perhaps for roost sites; thus, their numbers should not be correlated strongly with TVV. When these seedeaters are removed from the winter bird densities, a significant cor-

relation occurred between TVV and winter bird density in the 1985–1986 Arizona data set but not the New Mexico data set.

Areas of high foliage volumes are often recognized as sites of high breeding bird densities. Riparian habitats of the southwest have long been recognized as supporting among the highest bird densities in North America (Carothers and Johnson 1975). It appears likely that high vegetation volume and the associated resource levels can account for these high bird densities. In our samples, cottonwood riparian forest had the highest TVV values we recorded.

Another well-known pattern that may be explained by vegetation volume is the edge effect, the increase in bird densities at the interface between habitat types. Many edge areas, especially where there is a large difference between habitats in canopy height, support high vegetation volumes because of the increased penetration of light to all foliage layers.

If the relationship between vegetation volume and bird density is resource-based, then fluctuations in resources should yield fluctuations in bird populations (Dunning and Brown 1982), and regions subject to disturbance should have more variable bird populations than areas with more stable resource levels. Dunning (1986) examined Breeding Bird Censuses and suggested that many North American habitats have relatively stable bird populations. We expect resources are relatively stable in these habitats and that vegetation volume might be a good estimator of bird density in these areas. Other habitats show wide density fluctuations attributable to disturbance of vegetation (e.g., flooding, Dunning 1986) and presumably, therefore, resource levels. We suggest that measurement of vegetation volume might be a useful tool in predicting changes in bird populations resulting from such disturbance-caused changes in resources. In areas where disturbance does not cause large-scale changes in vegetation, TVV will be of less use. Some shrub-steppe and grassland habitats might be examples of such areas, since Wiens (1974) proposed that bird populations in these habitats are strongly affected by unpredictable climatic instability during the breeding season.

In habitats dominated by exotic vegetation suspected to harbor low levels of insect prey (e.g., eucalyptus), bird densities are often lower than in apparently equivalent habitats dominated by native vegetation (Anderson et al. 1977). When exotic plants form a substantial proportion of an area's vegetation (such as in many urban areas), we expect lower correlations between TVV and BBD since vegetation volume will reflect available resources less accurately. In areas where these plants are native and contain significant insect faunas, we would expect higher correlations. In a simple test of these ideas, vegetation volumes were more correlated

with densities of native birds in urban neighborhoods landscaped mostly with native vegetation when compared to urban areas dominated by exotic plants (Mills et al. 1989).

We suggest that changes in vegetation volume should be considered when comparing bird communities within and between habitats. For instance, rarefaction has been suggested as a technique for standardizing species richness values within a habitat when study sites are of different sizes (James and Rathbun 1981). Rarefaction generates an expected number of species per number of individuals. Our study suggests that equal-area sites that differ widely in vegetation volume should support different numbers of individuals. Standardization of species richness values for both area effects (through rarefaction) and resource-level differences (as measured by vegetation volume) may be important for accurate comparisons between sites.

It may seem that our results merely restate the previously reported relationship between bird species diversity and foliage height diversity that has provoked such strong criticism. Our analyses are different, however. Our measure of vegetation, TVV, reflects the total amount of vegetation present in an area, not the distribution of vegetation within presumed "layers" of the environment, as does FHD. Similarly, breeding bird density is a simpler measure of avian community structure than is bird species diversity. The problems associated with diversity indices have prompted several authors (cited previously) to call for the use of simple measures of community structure. Using these simpler measures, we still find evidence consistent with the idea that the number of consumers in a community is determined by resource levels. Use of these simple community measures may allow more rigorous testing of the resource assumption than has been possible (Mills et al. 1989). We acknowledge that the data presented here do not constitute a test of the resource assumption. However, the present atmosphere in community ecology is such that we feel the value of examining resource-consumer relationships must be re-established before specific tests of such relationships can be appreciated. Mills et al. (1989) present a simple test of the resource assumption using urban bird communities in Arizona.

LITERATURE CITED

ANDERSON, B. W., A. HIGGINS, AND R. D. OHMART. 1977. Avian use of saltcedar communities in the Lower Colorado River Valley. Pp. 128–136 *in* Importance, preservation and management of riparian habitat: a symposium (R. R. Johnson, ed.). U.S. For. Serv. Gen. Tech. Rep. RM-43, Fort Collins, Colorado.

———, R. D. OHMART, AND J. RICE. 1983. Avian and vegetation community structure and their seasonal relationships in the lower Colorado River valley. Condor 85:392–405.

BALDA, R. P. 1969. Foliage use by birds of the oak-juniper woodland and ponderosa pine forest in southeastern Arizona. Condor 71:399–412.

BEEDY, E. C. 1981. Bird communities and forest structure in the Sierra Nevada of California. Condor 83:97–105.

BELL, H. L. 1982. A bird community of New Guinean lowland rainforest. 3. Vertical distribution of the avifauna. Emu 82:143–162.

BROWN, D. E. (ED.). 1982. Biotic communities of the American southwest—United States and Mexico. Desert Plants 4:1–342.

CAROTHERS, S. W. AND R. R. JOHNSON. 1975. Water management practices and their effects on nongame birds in range habitats. Pp. 210–222 *in* Proc. symposium management of forest and range habitats for nongame birds (D. R. Smith, tech. coord.). U.S. For. Serv. Gen. Tech. Rep. WO-1, Fort Collins, Colorado.

———, ———, AND S. W. AITCHISON. 1974. Population structure and social organization of southwestern riparian birds. Am. Zool. 14:97–108.

CONNER, R. N., J. W. VIA, AND I. D. PRATHER. 1979. Effects of pine-oak clearcutting on winter and breeding birds in southwestern Virginia. Wilson Bull. 91:301–316.

DICKSON, J. G. AND C. A. SEGELQUIST. 1979. Breeding bird populations in pine and pine-hardwood forests in Texas. J. Wildl. Manage. 43:549–555.

DUNNING, J. B. 1986. Shrub-steppe birds revisited: implications for community theory. Am. Nat. 128:82–98.

——— AND J. H. BROWN. 1982. Summer rainfall and winter sparrow densities: a test of the food limitation hypothesis. Auk 99:123–129.

EMLEN, J. T. 1971. Population densities of birds derived from transect counts. Auk 88:323–342.

ENGSTROM, R. T., R. L. CRAWFORD, AND W. W. BAKER. 1984. Breeding bird populations in relation to changing forest structure following fire exclusion: a 15 year study. Wilson Bull. 96:437–450.

ERDELEN, M. 1984. Bird communities and vegetation structure: I. Correlations and comparisons of simple and diversity indices. Oecologia 61:277–284.

FONTEYN, P. I. 1978. An experimental evaluation of competition among *Larrea tridentata* Cav. and *Ambrosia dumosa* (Gray) Payne. Ph.D. diss., Univ. California, Santa Barbara, California.

HINO, T. 1985. Relationships between bird community and habitat structure in shelterbelts of Hokkaido, Japan. Oecologia 65:442–448.

JAMES, F. AND S. RATHBUN. 1981. Rarefaction, relative abundance, and diversity of avian communities. Auk 98:785–800.

KARR, J. R. 1980. Geographical variation in the avifauna of tropical forest undergrowth. Auk 97:283–298.

——— AND R. R. ROTH. 1971. Vegetation structure and avian diversity in several New World areas. Am. Nat. 105:423–435.

KROODSMA, R. C. 1982. Bird community ecology in power-line corridors in east Tennessee. Biol. Conserv. 23:79–94.

MACARTHUR, R. H. AND H. S. HORN. 1969. Foliage profile by vertical measurements. Ecology 50:802–804.

———— AND J. W. MACARTHUR. 1961. On bird species diversity. Ecology 42:594–598.

————, H. RECHER, AND M. CODY. 1966. On the relation between habitat selection and species diversity. Am. Nat. 100:319–322.

MEENTS, J. K., B. W. ANDERSON, AND R. D. OHMART. 1982. Vegetation relationships and food of Sage Sparrows wintering in honey mesquite habitat. Wilson Bull. 94:129–138.

————, J. RICE, B. W. ANDERSON, AND R. D. OHMART. 1983. Nonlinear relationships between birds and vegetation. Ecology 64:1022–1027.

MILLS, G. S. AND S. W. CAROTHERS. 1986. Bird populations in Arizona residential developments. Pp. 122–127 *in* Wildlife conservation and new residential developments (K. Stenberg, and W. W. Shaw, eds.). School Renewable Nat. Resour., Univ. Arizona, Tucson, Arizona.

————, J. B. DUNNING, AND J. M. BATES. 1989. Effects of urbanization on breeding bird community structure in southwestern desert habitats. Condor 91:416–429.

MOSS, D. 1978. Diversity of woodland song-bird populations. J. Anim. Ecol. 47:521–527.

PULLIAM, H. R. AND M. R. BRAND. 1975. The production and utilization of seeds in plains grassland of southeastern Arizona. Ecology 56:1158–1166.

RICE, J., R. D. OHMART, AND B. W. ANDERSON. 1983. Habitat selection attributes of an avian community: a discriminant analysis investigation. Ecol. Monogr. 53:263–290.

————, B. W. ANDERSON, AND R. D. OHMART. 1984. Comparison of the importance of different habitat attributes to avian community organization. J. Wildl. Manage. 48:895–911.

RICE, W. R. 1989. Analyzing tables of statistical tests. Evolution 43:223–225.

ROBINSON, S. K. AND R. T. HOLMES. 1984. Effects of plant species and foliage structure on the foraging behavior of forest birds. Auk 101:672–684.

ROTENBERRY, J. T. 1985. The role of habitat in avian community composition: physiognomy or floristics? Oecologia 67:213–217.

SCHLESINGER, W. H. AND C. S. JONES. 1984. The comparative importance of overland runoff and mean annual rainfall to shrub communities of the Mojave Desert. Bot. Gaz. 145:116–124.

SHURCLIFF, K. S. 1980. Vegetation and bird community characteristics in an Australian arid mountain range. J. Arid Environ. 3:331–348.

STAMP, N. E. 1978. Breeding birds of riparian woodland in south-central Arizona. Condor 80:64–71.

TERBORGH, J. 1977. Bird species diversity on an Andean elevational gradient. Ecology 58:1007–1019.

VANDER WALL, S. B. AND J. A. MACMAHON. 1984. Avian distribution patterns along a Sonoran Desert bajada. J. Arid Environ. 7:59–74.

VERNER, J. AND T. A. LARSON. 1989. Richness of breeding bird species in mixed-conifer forests of the Sierra Nevada, California. Auk 106:447–463.

WIENS, J. A. 1974. Climatic instability and the "ecological saturation" of bird communities in North American grasslands. Condor 76:385–400.