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Diversity and Density of Shelterbelt Bird Communities

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DIVERSITY AND DENSITY OF SHELTERBELT BIRD COMMUNITIES

BY

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A thesis submitted
in partial fulfillment of the requirements for
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1978

DIVERSITY AND DENSITY OF SHELTERBELT BIRD COMMUNITIES

This thesis is approved as a creditable and independent investigation by a candidate for the Master of Science, and is acceptable as meeting the thesis requirements for this degree, but without implying that the conclusions reached by the candidate are necessarily the conclusions of the major department.

Thesis Advisor

Head, Dept. of Wildlife and
Fisheries Sciences

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DIVERSITY AND DENSITY OF SHELTERBELT BIRD COMMUNITIES

Abstract

THOMAS E. MARTIN

The number of bird species and the density of each species were monitored in 69 shelterbelts in eastern South Dakota during spring migration and breeding seasons in 1976 and 1977. A total of 44 different species of birds were found during breeding and 68 species during spring migration. Approximately 60 to 80% of the species in a shelterbelt eat insects as part or all of their diet. Most of these bird species are territorial. Usually only 1 - 2 pairs of a territorial species will reside in any one shelterbelt. This low density is caused by the limited habitat area that shelterbelts provide. Shelterbelts are, essentially, forest islands surrounded by cultivated and natural grasses.

Area of the shelterbelt accounted for approximately 60% of the variation in the number of species and density of the bird communities in both seasons as a result of the "island effect". The limited food space provided by these forest islands makes ecological isolation among coexisting species necessary for birds to replenish energy stores lost due to migrational flight.

The importance of shelterbelt area on species numbers during the breeding season can be partly attributed to the minimum area requirement of territorial pairs during breeding. Some species will not reside in shelterbelts below a minimum size due to the large territory size these birds require. However, minimum area does not explain the upper limit placed on the number of species that will coexist in shelterbelts.

Diffuse utilization of the limited food supplies was postulated as setting the upper limit. Bird species that coexisted tended to exhibit different foraging strategies, thus reducing overlap in use of food resources. Implied increases in territory size with increases in the number of coexisting species were found.

Theories on species-area models were re-evaluated in terms of competitive saturation. Ability of the species source pool to supply enough competitively different species to saturate the available food space for the smallest islands was postulated as the reason for the high species-area slope found. All species-area relationships were evaluated in terms of one general curve and were considered a sub-section of that curve. Placement on the curve, and consequently, the slope of the species-area relationship, was related to immigration and extinction rates, based on the effective source pool size. The effective source pool size was related to the actual source pool size, the distance of the archipelago from the source pool, and the overall vagility of the species comprising the source pool.

The idea of diffuse competition influencing the territory size of bird species was further investigated by mapping territories of yellowthroats, house wrens, and brown thrashers in 2 large shelterbelts. Results indicated that territory size of these species was larger in belts with a greater number of coexisting species than in the smallest shelterbelt size colonized by one pair of each species.

The variation in community diversity and density unexplained by area was attributed to environmental factors and sampling error. The effect of area was removed. The transformed data were analyzed to provide management alternatives using multiple regression to delineate the environmental factors influencing community diversity and density during both migratory and breeding seasons. A shelterbelt that is subjected to light grazing to eliminate a heavy shrub understory and enhance development of a lush herbaceous layer is considered optimal for both diversity and density. Dense rows of shrubs along the borders of the belts also contributed to an increase in the bird population. Heavy grazing or mowing of the belt after the belt was well established reduced bird diversity. Utilization of tree species that provide open foliage conditions, such as Siberian elm, led to increased bird diversity and density.

Multiple regression analyses of the environmental factors influencing 14 of the bird species commonly inhabiting shelterbelts were performed. In general, the 14 species preferred a shelterbelt configuration similar to that described for the diversity and density measures. In addition, specific preferences of each species suggested ways of modifying the bird community composition. Removal of eastern red cedar may lead to a reduction in noxious species. Planting of green ash, due to its infection by heartrot, and retaining snags enhances the presence of hole nesting species such as house wrens and woodpeckers. Other species preferences are discussed.

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Section I

INTRODUCTION

This study was initiated to quantify the diversity and density of avian species utilizing shelterbelts in eastern South Dakota. Objectives were to describe the relationship of the vegetative structure of the shelterbelts to bird density and diversity, and to provide management suggestions for maximizing attractiveness of the belts for those bird species compatible with farming operations, yet minimize the attractiveness to noxious species. There has been no comprehensive quantitative study reported in the literature on the utilization of shelterbelts and windbreaks by birds relative to age of stand, understory density, canopy coverage, canopy volume, and numerous other quantitative features of these forest islands.

Farming and ranching practices are intensive in the prairie areas of South Dakota and the surrounding Great Plains. Farms and ranches occupy 94% of the land area of the Great Plains (Griffith 1976). The establishment of wooded areas by man in this intensively managed agricultural environment has been minimal in relation to total land area available. Only 3% of the land area of the Great Plains is forested (Griffith 1976). Shelterbelts occupy 1.1% of the land area of eastern South Dakota (Walker and Suedkamp 1977). Shelterbelts are, therefore, present as a series of isolated forest habitats in a sea of cultivated fields and natural grasses. The "woodland islands" supply habitat for breeding birds which include elevated song and display perches used by both grassland and woodland birds. Shelterbelts also provide resting and feeding stations utilized by many spring and fall transient birds.

Distribution of birds between and within vegetative communities is determined by their selection of specific habitats. Management of the distribution of birds among habitats, therefore, is contingent on understanding the process by which habitat selection occurs. Selection for a specific habitat by a bird is believed to be a behavioral response to proximate and ultimate environmental stimuli causing an innate settling response (Lack 1933, Svardson 1949, Hilden 1965). Recognition of proximate cues is believed brought about by evolution and early experience. Imprinting of the habitat features in which birds are raised influences their selection of habitats (Klopfer 1963, Klopfer and Hailman 1965). Natural selection tends to "select" those birds settling in habitats providing the ultimate factors necessary for maximal survival and reproductive success, and the birds, therefore, should evolve to be more selective of habitats maximizing fitness (Svardson 1949, Hilden 1965, Fretwell and Lucas 1969, Orians 1971, Verner 1975).

Maximizing the attractiveness of shelterbelts to birds is dependent on determining the proximate factors recognized by birds in this habitat type. Bird species diversity in other forest and grassland habitats is related to the structural complexity of the vegetation (MacArthur and MacArthur 1961, MacArthur 1964, MacArthur et al. 1966, Ficken and Ficken 1966, Recher 1969, Austin 1970, James 1971, Anderson and Shugart 1974). Inferences reached from these studies suggest that manipulation to increase the complexity of the habitat structure should result in an increase in the density and diversity of birds.

Just the presence of shelterbelts allows an increase in birds on the prairies. Orendurff (1940, 1941) qualitatively demonstrated an increase in the numbers of birds over the 10 years following establishment of windbreaks and shelterbelts. Emerson (1940) provided a quantitative estimate of the number of birds utilizing shelterbelts in Nebraska for food and cover and related his estimates to the total plantings in Nebraska. However, neither Emerson nor Orendurff attempted to quantify the relationship between specific vegetation characteristics of the habitat and the diversity and density of the avifauna.

Rotzien (1966) counted birds in 8 shelterbelts in North Dakota during 3 winter periods. He named the 1 or 2 most common bird species and the dominant trees in each belt, but did not quantitatively relate the density and diversity of birds to vegetative structure. Rotzien did conclude, in the absence of tabular data, that density of cover was not related to density and diversity of birds. Field (1971) quantified the number and distribution of bird nests present in a single shelterbelt, but did not correlate her findings with vegetative characteristics.

The importance of shelterbelts to increased crop production due to reduced soil erosion (Goldsmith 1976, Lyles 1976), soil moisture distribution (Frank et al. 1976, Rosenberg 1976), and microclimatic modification (Rosenberg 1976, Skidmore 1976), and livestock protection (Aitchison 1976, Fewin 1976) has been documented. Researchers believe that 10 times as many shelterbelts are needed than are now planted to stop decimation of the prairies through soil erosion (Goldsmith 1976, Griffith 1976). Delineation of the environmental factors influencing the diversity of birds utilizing shelterbelts provides opportunity for management suggestions to benefit shelterbelt bird communities in the

Great Plains. Shelterbelts can be designed to benefit both birds and humans.

Section 2

STUDY AREA

South Dakota, located in the eastern portion of the northern Great Plains, is divided by the Missouri River into 2 similarly sized east-west segments. This study was conducted in the eastern half of the state, between 42 and 46° latitude and 96 and 101° longitude. During the study, average monthly temperatures for May, June, and July were 57, 70, and 76°F, respectively (NOAA 1976). The average annual temperature was 46°F, which was 1°F above normal. The average annual precipitation was 12.5 inches; 10.4 inches below normal.

Eastern South Dakota varies in topography from flat to undulating, and the majority of the land is farmed for small grains. Establishment of shelterbelts to reduce wind erosion of topsoil has been sponsored by governmental and private agencies from the 1930's to date. Shelterbelts established near farmsteads improve appearance of the farmstead, provide shade in summer, reduce wind speed and snow accumulation around the home and other buildings, and shield cattle and other livestock. Walker and Suedkamp (1977) determined that 56.9% of the shelterbelts in South Dakota were directly related to farmsteads.

A shelterbelt was defined for this study as a homogeneous stand of trees and/or shrubs planted in linear rows. Shelterbelts vary considerably in size, shape, and composition of plant species (Table 1). Many young belts are cultivated for the first 4 to 5 years to reduce competition for water with trees and shrubs. Some belts established near farmsteads are mowed and lack an understory. Many belts are grazed, and

Table 1. Maximum, minimum, and mean values of selected characteristics of shelterbelts, demonstrating the variability among the 69 shelterbelts studied in eastern South Dakota.

VARIABLE[1]	MAXIMUM	MINIMUM	MEAN	± SE
LENGTH	877.8m	72.9m	261.7	19.5m
WIDTH	65.9m	6.6m	27.8	1.6m
AREA	29230.7m^2	984.2m^2	7532.8	778.4m^2
AGE	61yrs	3yrs	20.5	1.3yrs
NTR	11	0	5.3	0.3
NSR	9	0	1.7	0.2
TNR	20	3	7.0	0.4
NTRSPP	7	0	2.8	0.2
NSHSPP	4	0	1.5	0.2
CANHT	14.2m	6.3m	9.6	1.0m

[1] Explanation of mnemonics are given in Appendix J.

the understory density is modified by the intensity and duration of the grazing.

There are 2.5 shelterbelts per square mile in eastern South Dakota, representing 1.1% of the land area (Walker and Suedkamp 1977). The 69 belts evaluated in this study included 14 shrub and 14 tree species. Mean canopy height (9.60 ± 0.99m) and mean shrub row height (2.00 ± 0.17m) provide an average measure of height of the belts. Siberian elm *(Ulmus pumila)* was the most common tree species, while American elm *(Ulmus americana),* green ash *(Fraxanus pennsylvanica),* hackberry *(Celtis occidentalis),* and Russian-olive *(Elaeagnus angustifolia)* were common. Honeysuckle *(Lonicera tatarica),* lilac *(Syringa vulgaris),* wild plum *(Prunus americana),* and chokecherry *(Prunus virginiana)* were the most common shrubs.

Section 3

METHODS AND MATERIALS

Plot Selection

Study plots were selected from throughout the eastern half of South Dakota to encompass substantial geographic variation. Selection of shelterbelts was accomplished by utilizing a 2-stage cluster sampling of quarter-sections (65 hectares) (Brewster et al. 1976). Counties were divided into 8 similarly-sized groups to insure an even distribution of study plots throughout the study area. Eight townships were selected at random from each group of counties. A circle (scale radius of 4 miles) was drawn using the northwestern corner of each selected township as the pivot point and encompassing parts of the 4 townships adjacent to that corner. The resulting circle was quartered using the township boundaries. All quarter-sections within each of the township segments encompassed by the respective circle were numbered, and 1 quarter-section was selected at random from each of the 4 areas. The resulting randomly selected 288 quarter-sections were clustered in groups of 4 to minimize travel time between sample areas.

Names and addresses of the landowners of all selected quarter-sections were obtained through the cooperation of the local offices of the Agricultural Stabilization and Conservation Service. Each landowner was mailed a letter of explanation of the project, a pre-addressed and stamped envelope, and a questionnaire (Appendix A) requesting information concerning presence or absence of shelterbelts on the selected quarter-sections. The landowner was requested to state yes or no concerning the presence of shelterbelts and, if presence was affirmed, to complete information concerning the description and history of the shelterbelt.

Of the 288 questionnaires mailed, 186 were returned. Sixty-four landowners indicated presence of 97 shelterbelts and granted permission for study. A large sample size was believed essential to allow the study to evaluate the range of variability existing in shelterbelts within the large geographical region. All 97 potential belts were visited during the initial winter bird counting period. A number of shelterbelts were not on the selected quarter-section and some did not fulfill the definition of a shelterbelt. Removal of the non-conforming plots reduced the sample size to 69 shelterbelts.

Vegetation measurements

Shelterbelts provide a unique situation because their unusual homogeneity allowed specific description of the habitat features. Techniques for sampling vegetation allowed measurements to be obtained in conjunction with the breeding season censuses. Vegetation was evaluated during a fairly uniform phenological period and, as Lack (1970) noted, coinciding with the time of peak food requirement for most bird species.

Habitat variables were measured in discrete or continuous units. Variables measured on a continuous scale included length; width; number of tree rows; number of shrub rows; age; height of herb layer; height of shrub layer; height of shrub rows; height of tree rows; canopy coverage; ground coverage; understory density; snag density; density of the various shrub and tree species; and volume of all shrub and tree species. Age was obtained from the landowner or by aid of an increment borer. Measurement of percent slope by a Brunton compass determined vegetation height. Ground and canopy coverages were measured by observing the presence-absence of green vegetation through an ocular tube (James and Shugart 1970).

Understory density was measured using a density board (Giles 1971) 6 ft in height and divided into 1 ft alternately painted black and white sections numbered 1 to 6 from bottom to top. At a distance of 21.5 m, the investigator recorded the numbers of sections obscured by the vegetation between each planted row at 3 locations in each belt.

The number of snags and all shrub and tree species were counted in each of 2, 50m long transects. The average of these 2 transects was used as the density for each species. This was deemed sufficient due to the uniform planting of the vegetation in a belt. Species diversity of vegetation was based on the Shannon information index (Shannon and Weaver 1963).

Canopy and shrub volumes were calculated using a computer program written by Mawson, Thomas and DeGraff (1973). Calculation of canopy volume followed classification of the trees into 1 of 15 geometric forms. The program was developed for studies in which all trees within the plot were measured. It was not feasible to measure every tree in each of the 69 shelterbelts. Because of the homogeneity within shelterbelts, 10 individuals of each tree species present in a belt were measured. The program was modified to calculate volumes based on the ratio of the number of trees measured against the actual number of trees of the species in each belt.

Two additional modifications were incorporated into the program. One allowed calculation of the average volume of each species and the other modified the volume in relation to foliage density. Previous Investigators calculating canopy volumes (e.g. Sturman 1968, Balda 1969, Thomas et al. 1973) have made the invalid assumption that all trees having the same geometric form have the same foliage density. Individual trees of a given species vary decidedly in the amount of foliage per unit area. Trees utilized for volume estimates were separated into 5 density classes. A tree classified in density class 1 was considered to have sufficient foliage to completely occupy the volume of space predicted by the geometric form selected for it. A density class rating of 2 indicated the foliage only "filled" 80% of the volume of the form selected for that tree. Density classes 3, 4 and 5 were considered 60%, 40%, and 20% "full" respectively.

Variables measured as discrete included orientation of the belt; proximity of the belt to other woody cover, roads, water, human residence, and livestock feedlot; mowing; and grazing. Belt orientation was classified as east-west, north-south, or, if L-shaped, both. Proximity of the belt to various influencing factors was classified into 1 of 5 categories: less than 200 m, 200-400 m, 400-600 m, 600-1000 m, and greater than 1000 m. Mowing was recorded as yes or no, and grazing was classified as light, medium, or severe.

Bird census

The transect method of Emlen (1971) was used during spring migration and summer resident periods because it allows rapid censusing of all individuals during any season. Censuses were conducted within 2 hours of sunrise and sunset.

Transects extending 61 m on both sides of the observer were established perpendicular to the belt. Transects were repeated at 122 m intervals to provide maximum possible accuracy. Some species went undetected during the transect counts if they were present as only 1 or 2 individuals and were near the edges of the transects. The isolated and restricted nature of the shelterbelts allowed walking the length of the belts upon completion of all transects and tallying any species unrepresented in the transects. These species were then assigned the abundance value equivalent to the number of individuals counted.

A computer program written in PL/I calculated the abundance of each bird species from the lateral counts following Emlens' (1971) derivations. The program calculated the peak inflexion of the lateral counts by comparing each 3 m strip to the subsequent 2 strips. If the number of individuals observed in the lateral strip being compared was greater than both of the following 2, then the strip immediately following that peak was considered to be the end of the plateau. However, to reduce overestimation of species due to chance or clumped observations near the observer, a minimum peak of 12 m was established. This distance was selected because it was felt all birds within 12 m were being detected. Based on these calculated densities, the program then computed the overall bird species diversity, species richness, and equitability for each belt.

Upon completion of these calculations, the program adjusted the densities of all species to a common plot size.

Statistics

The Shannon information index (Shannon and Weaver 1963) was used because it incorporates both species richness (McIntosh 1967) and equitability (Lloyd and Ghelardi 1964). All paired comparisons were based on Student's T-test (Steele and Torrie 1960) unless noted as being analyzed through analysis of variance or least-squares regression. Analysis of the environmental variables was accomplished through step-wise, multiple regression. The 90% confidence interval was used in all statistics.

Section 4

EFFECT OF AREA ON THE COMPOSITION AND DIVERSITY OF MIGRANTS

INTRODUCTION

The effect of area on the number of breeding bird species occupying both real and virtual islands has been studied in an increasing number of island groups in recent years (e.g. MacArthur and Wilson 1963, 1967, Abbot 1974, Johnson 1975, Diamond and Mayr 1976, Schoener 1976, Galli et al. 1976). However, the role of area in modifying the composition and diversity of transients utilizing habitat islands as resting and feeding stations during their northerly migration in the spring has not been reported.

Censuses of avian migrants were initiated on 8 May in the 69 study shelterbelts during spring migration in 1976 and 1977. Censuses of study plots were initiated in the southern portion of the state and continued northward to minimize the temporal dynamics of migration. Nineteen and 13 days were required to complete the censuses in 1976 and 1977, respectively. In 1976, the first 3 - 4 days were utilized to accomplish duplicate counts to test differences between morning and evening censuses and reliability of the counts. T-tests illustrated no significant differences ($p > .10$) between counts; duplicate counts were not conducted in 1977. Efficiency in counting and fewer days lost to rainfall reduced the duration of counts in 1977.

RESULTS

Between-years comparison

The shortened circuit time in 1977, especially in the initial few days, resulted in the 1977 censuses being completed at an earlier stage of migration than in 1976. Consequently, the 69 study shelterbelts illustrated lower ($p<0.01$) mean species richness, diversity, and density during 1977 as compared to the 1976 migratory season (Table 2).

Black-billed cuckoos are late migrants and were observed near the end of the 1976 migratory census period. No black-billed cuckoos were observed during the 1977 migratory count, although many were observed during breeding. This species illustrates the effect earlier completion of the 1977 counts had on the bird community composition. Of the species represented in 2 or more plots, 77.8% were found in fewer plots in 1977 than in 1976 (Appendix C). The mean number of species during the 1977 migratory count (9.59) was still slightly higher ($p<0.10$) than the mean (8.49) for the subsequent 1977 breeding count.

Species richness in 1977 was lower than in 1976, but varied among belts in a similar manner both years, as indicated by the correlation ($r = 0.802$) of 1976 species richness with 1977 species richness. Density, though 52.2% lower ($p<0.01$) in 1977 than 1976, also varied similarly between years ($r = 0.868$). Diversity provided the lowest correlation ($r = 0.616$) between years. Since the diversity index is comprised of 2 components, species richness and equitability, and species richness exhibits a much higher correlation between years, the lower correlation of diversity is due to the low correlation ($r = 0.307$) of equitability

Table 2. Means and standard errors of all study shelterbelts (N = 69) for 1976 and 1977 migratory seasons. a) Community species richness, diversity, and density. b) Number of species per food habits group. c) Density of each food habits group. d) Percent species composition.

		1976		1977	
	Variable	Mean	± SE	Mean	± SE
a)	Species richness	12.536	0.742	9.594	0.499
	Species diversity	1.967	0.065	1.706	0.047
	Density	66.109	4.366	35.487	3.049
b)	Granivores	2.681	0.102	2.565	0.093
	Omnivores	3.638	0.254	2.971	0.166
	Insectivores	6.203	0.493	4.058	0.343
c)	Granivores	26.130	2.117	16.116	1.269
	Omnivores	17.067	1.384	11.983	1.318
	Insectivores	22.790	2.400	7.580	0.795
d)	Granivores	0.255	0.017	0.299	0.014
	Omnivores	0.298	0.017	0.315	0.012
	Insectivores	0.447	0.020	0.386	0.019

between years. Further insight into the differences between years is provided by grouping the species of each plot into their primary food habits as granivores, omnivores, or insectivores (Appendix B). The mean number of species found for each classification in both years (Table 2b) illustrates no difference ($p>0.10$) in the number of granivore species between years. There are fewer omnivore ($p<0.05$) and insectivore ($p<0.001$) species in 1977 than 1976.

The mean densities of granivores and of insectivores averaged over all plots (Table 2c) are not significantly different ($p>0.10$). However, if these means are divided by the mean number of species for their respective group to approximate the number of individuals per species, the result is 9.83 granivores per granivore species and only 3.67 insectivores per insectivore species in 1976, and 6.42 and 1.85 for 1977, respectively. Granivore species such as common grackles and house sparrows are more social as compared to the more solitary insectivores.

The resultant decrease in number of insectivore species as compared to granivore species in 1977 as compared to 1976 (Table 2b) is clearer when represented as the proportion of species in the community representing each food habits group (Table 2d). The mean percentage of total species in a plot classified as granivores is higher ($p<0.10$) in 1977 even though the mean number of granivore species illustrates no difference. The difference in proportional representation of granivore species between years can be attributed mainly to the reduced ($p<0.05$) representation of insectivores.

Analysis of primary food habits with area

The shelterbelts were divided into 3 size classes to facilitate analysis of the changes in the representation of each food habits group with changes in plot size. Size class 1 represents the smallest 23 (984 to 3,682 m^2), size class 2 the intermediate 23 (3,770 to 7,430 m^2), and size class 3 the largest 23 (7,451 to 29,230 m^2) shelterbelts studied. Mean plot size and standard error for each size class is given in Table 3b. The number of species (Figs. 1,2) and density (Figs. 3,4) of each food habits group increased with plot size in both years (Appendix C). Two factor analysis of variance was utilized to describe the changes in food habits groups relative to each other and with respect to plot size (Appendix D). The increase in number of species with plot size is highly significant ($p<0.001$) in both years (F=12.129 in 1976, F=52.972 in 1977). The number of species of each food habits group differs significantly ($p<0.001$) from each other (F=51.984 in 1976, F=14.604 in 1977) because the number of insectivore species is greater than the number of omnivore species and omnivore species exceed the number of granivore species.

The interaction between food habits and size class is also highly significant ($p<0.001$) in both years (F=7.636 in 1976, F=11.774 in 1977). The significant interaction indicates that differential rates of increase of the 3 food habits groups occur with changing plot size. For both years the number of species of insectivores increases faster than omnivores and omnivores increase faster than granivores as plot size increases. Insectivores comprise an increasing proportion of the species as plot size increases. Conversely, granivores comprise a decreasing proportion of the species (Figs. 1,2). Relatively little change in the proportional

Figure 1. Mean number of species of granivores (G), omnivores (O), and insectivores (I) censused during spring migration 1976 in each of 3 shelterbelt size classes. Size classes 1, 2, and 3 represent the smallest, intermediate, and largest 23 shelterbelts, respectively. The regression equations are based on all 69 shelterbelts and all are highly significant ($p<0.001$). The numbers indicate the mean percent representation of each food habits group for each size class.

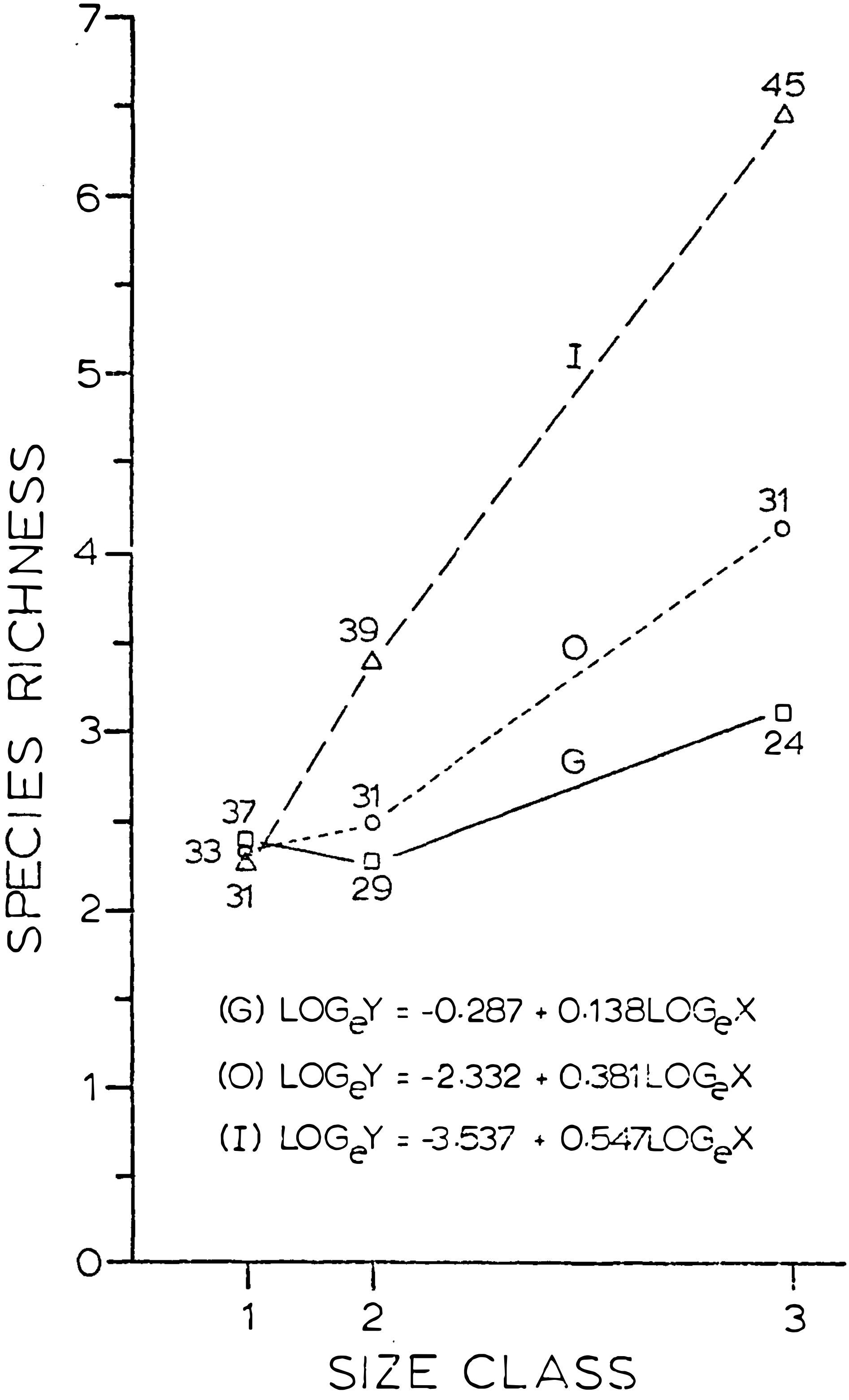

SPECIES RICHNESS
SIZE CLASS
0
1
2
3
4
5
6
7
1
2
3
I
O
G
45
39
31
31
24
37
33
31
29
(G) LOG$_e$Y = -0·287 + 0·138LOG$_e$X
(O) LOG$_e$Y = -2·332 + 0·381LOG$_e$X
(I) LOG$_e$Y = -3·537 + 0·547LOG$_e$X

Figure 2. Mean number of species of granivores (G), omnivores (O), and insectivores (I) censused during spring migration 1977 in each of 3 shelterbelt size classes. The regression equations are based on all 69 study shelterbelts and all are highly significant ($p<0.001$). The numbers indicate the mean percent representation of each food habits group for each size class.

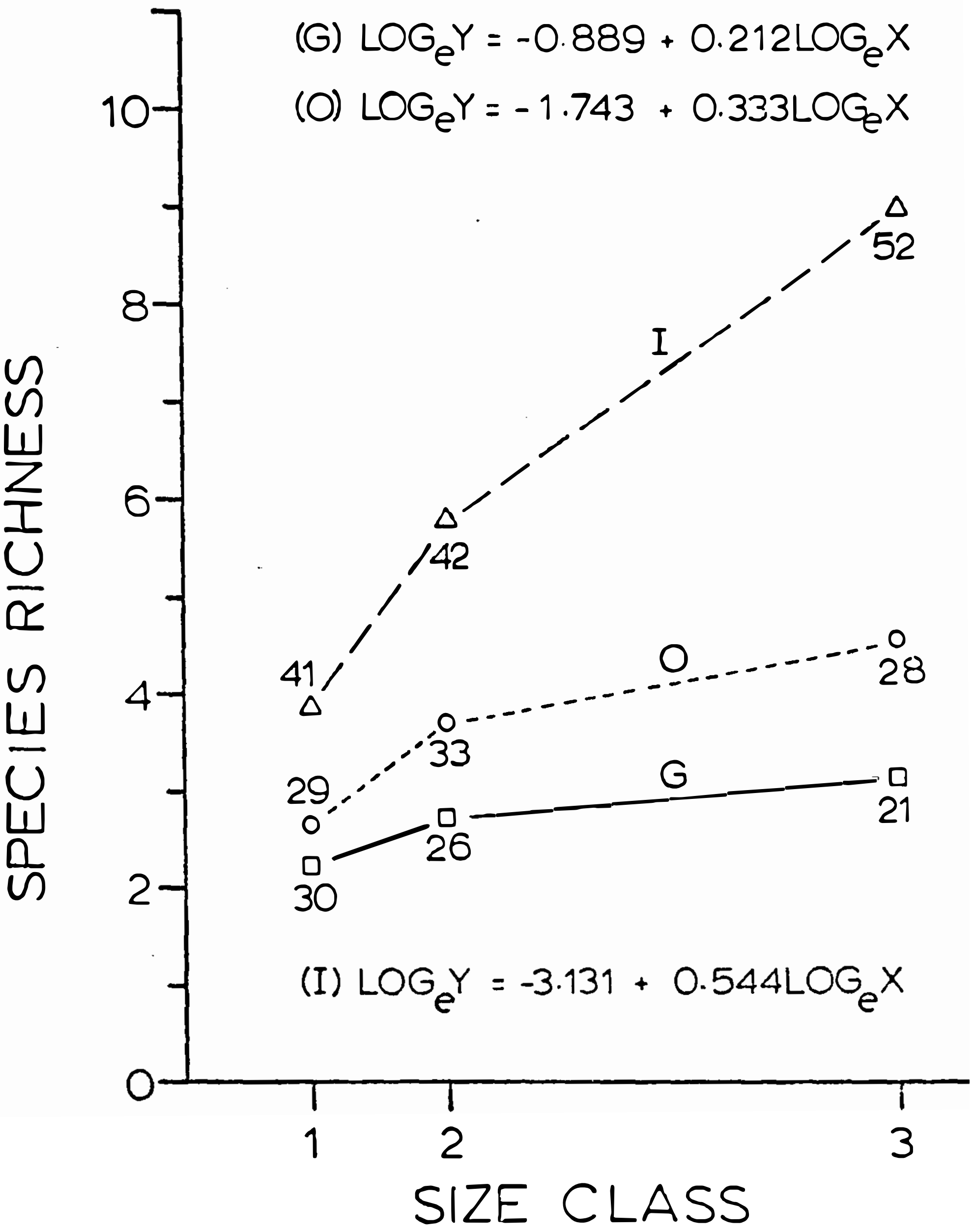

(G) LOG$_e$Y = -0.889 + 0.212LOG$_e$X
(O) LOG$_e$Y = -1.743 + 0.333LOG$_e$X
(I) LOG$_e$Y = -3.131 + 0.544LOG$_e$X
SPECIES RICHNESS
0
2
4
6
8
10
SIZE CLASS
1
2
3
I
O
G
41
42
52
29
33
28
30
26
21

Figure 3. Mean density of granivores (G), omnivores (o), and insectivores (I) censused during spring migration 1976 in each of 3 shelterbett size classes. The regression equations are based on all 69 study shelterbelts and all are highly significant ($p<0.001$). The numbers indicate the mean percent representation of each food habits group for each size class.

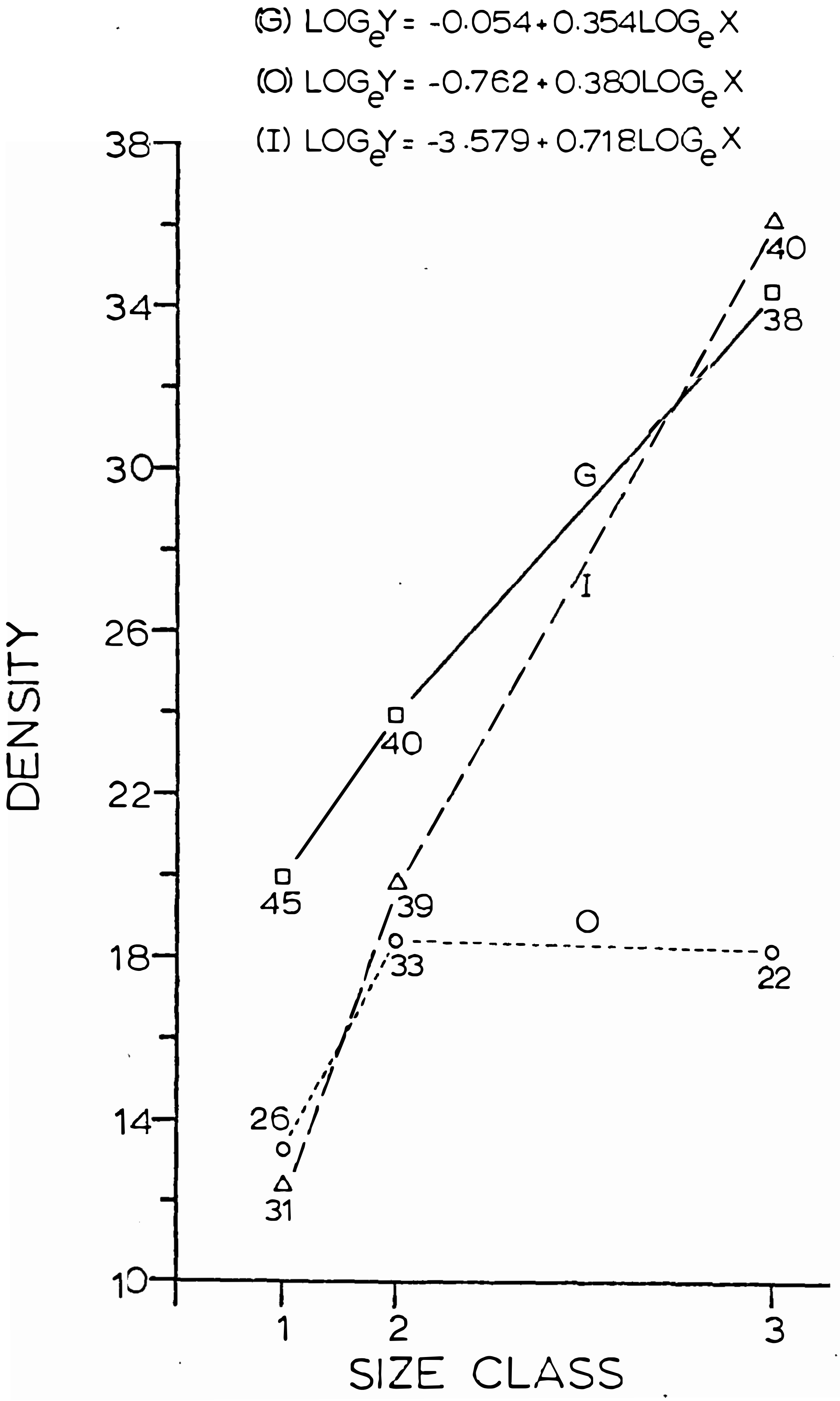
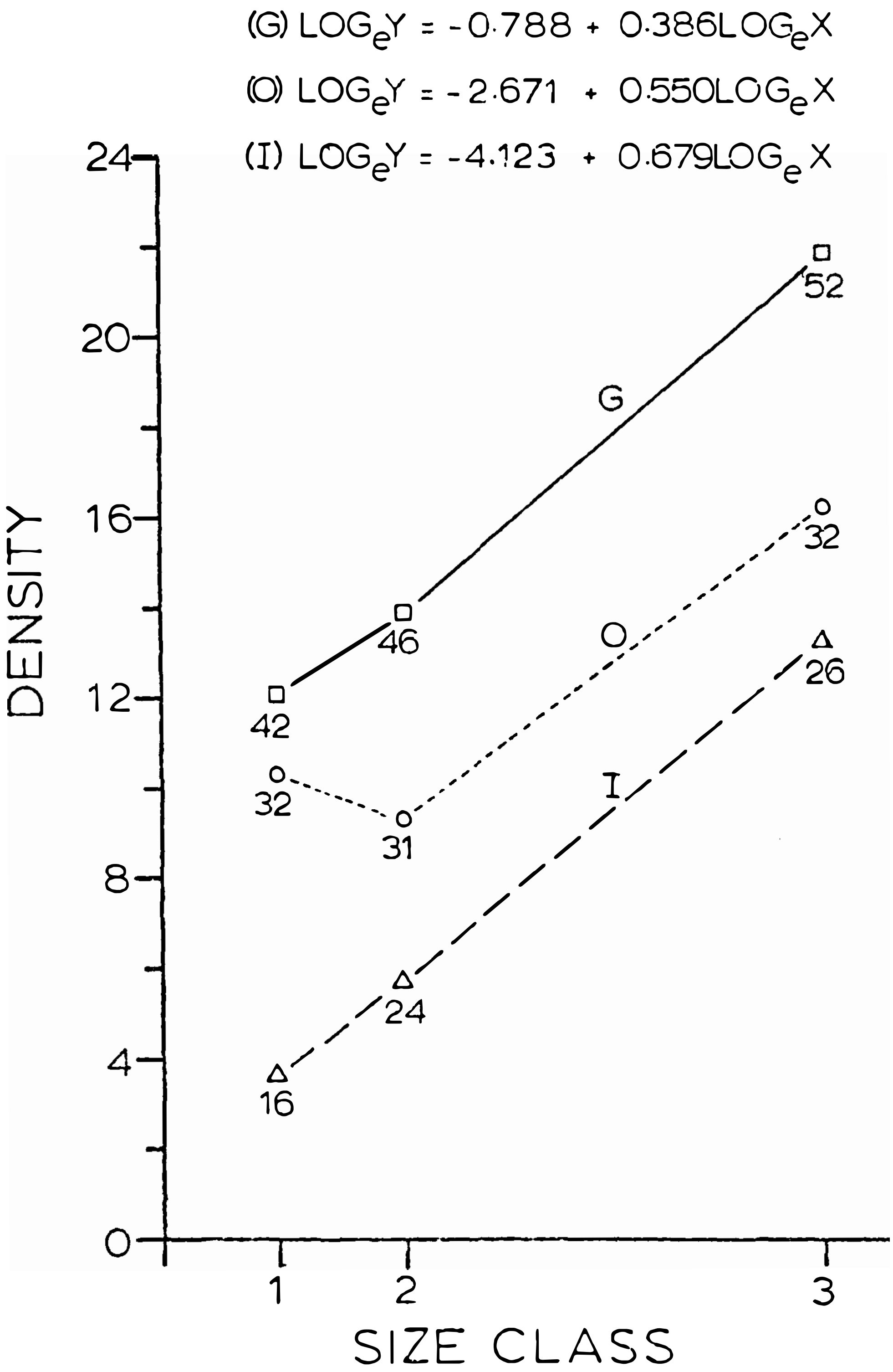

(G) LOG$_e$Y = -0.054 + 0.354LOG$_e$X
(O) LOG$_e$Y = -0.762 + 0.380LOG$_e$X
(I) LOG$_e$Y = -3.579 + 0.718LOG$_e$X
DENSITY
38
34
30
26
22
18
14
10
SIZE CLASS
1
2
3
G
I
O
45
40
38
39
40
31
26
33
22

Figure 4. Mean density of granivores (G), omnivores (O), and insectivores (I) censused during spring migration 1977 in each of 3 increasing shelterbelt size classes. The regression equations are based on all 69 study shelterbelts and all are highly significant ($p<0.001$). The numbers indicate the mean percent representation of each food habits group for each size class.


(G) LOG$_e$Y = -0·788 + 0·386LOG$_e$X
(O) LOG$_e$Y = -2·671 + 0·550LOG$_e$X
(I) LOG$_e$Y = -4·123 + 0·679LOG$_e$X
DENSITY
0
4
8
12
16
20
24
SIZE CLASS
1
2
3
G
O
I
42
46
52
32
31
32
16
24
26

representation of omnivores occurs as plot size increases.

Although insectivores dominate community species composition, granivores comprise the greatest proportion of individuals in the communities. Highly significant ($p<0.001$) increases in density of all 3 food habits occur with increases in plot size ($F=12.254$ in 1976, $F=14.918$ in 1977). The differences between food habits groups are less marked in 1976 ($F=5.597$, $p<0.010$) than in 1977 ($F=18.265$, $p<0.001$). There was a greater similarity in density of insectivores and granivores in 1976 as compared to 1977 (Figs. 3,4). The regression slopes illustrate there is a larger increase in number of insectivore individuals than omnivores and a larger increase in number of omnivore individuals than granivores with increasing plot size. However, the increase in number of insectivore individuals is not sufficient to change the dominant status of granivores (Figs. 3,4).

Effect of area on community species richness

The increase in the number of species of each of the 3 component food habits groups of the community with increases in size class implies that composite community richness increases with area (Table 3a). Regression of species richness on area provides a strong correlation in both years ($r = 0.774$ in 1976, $r = 0.821$ in 1977). Previous studies on the species-area relationship during the breeding season have illustrated the relationship to be a power ($S = CA^z$) or exponential ($\exp(S) = A$) function, where S is the number of species and A is the area (MacArthur and Wilson 1963, 1967, Hamilton et al. 1964, Hamilton and Armstrong 1965, Vuilleumier 1970, Diamond 1973). The data collected during the breeding

Table 3. Means and standard errors by size class (N = 23 shelterbelts per size class) for the 1976 and 1977 migratory seasons. a) Species richness. b) Plot size (in m^2). c) Species diversity. d) Equitability. e) Unstandardized density. f) Standardized density.

	1976		1977	
Size Class	Mean	± SE	Mean	± SE
a) 1	8.743	0.753	6.966	0.394
2	12.178	1.264	8.132	0.528
3	16.700	1.224	13.700	0.838
b) 1	2553.023	162.216		
2	5416.742	247.988		
3	14616.243	1323.649		
c) 1	1.683	0.098	1.425	0.051
2	1.921	0.108	1.621	0.060
3	2.297	0.098	2.071	0.067
d) 1	0.627	0.045	0.606	0.043
2	0.691	0.026	0.714	0.017
3	0.746	0.020	0.723	0.023
e) 1	45.692	4.962	25.981	3.607
2	62.591	7.204	28.944	3.080
3	90.066	7.389	51.543	4.585
f) 1	19.854	3.434	11.283	3.201
2	12.011	1.384	5.200	0.519
3	6.793	0.669	3.711	0.300

season in this study demonstrate a power function (Section 5). Both exponential (r = 0.725 in 1976, r = 0.776 in 1977) and power (r = 0.651 in 1976, r = 0.729 in 1977) functions illustrate declines in the correlation of species richness with area during migration. This suggests the relationship is nearly linear. However, if the relationship was truly linear, the slope, z, should equal 1 (i.e. $S = CA^1$). The slopes were actually 0.439 and 0.406 for 1976 and 1977, respectively.

Due to the high correlation of species richness between years, the data were pooled over years. The resulting regression of species richness on area illustrates a similarly high linear correlation (r = 0.818) with an intermediate slope (z = 0.409). However, the regression equation underestimates the tail of the relationship (Fig. 5), indicating the regression estimate of the slope is too low.

Community density

Total community density increases as a function of area (Table 3e). The linear function (r = 0.811) illustrates a higher correlation than either the exponential (r = 0.775) or power (r = 0.712) functions. The slope (z = 0.597) also suggests the relationship is approaching linearity. Removal of the social common grackles, American robins, and house sparrows from the data produces an even greater slope (z = 0.891). The density of less social species increases linearly with area (Fig. 6).

Community density does not increase at the same proportional rate as area. A 100% increase in density usually follows an approximate 500% increase in area. Thus when density is standardized to the smallest shelterbelt (984.m^2), it shows a significant decrease ($p<0.001$) as area

Figure 5. Species richness of each of the 69 study shelterbelts plotted against the area of those shelterbelts. The species richness of each plot is based on the average of 1976 and 1977 migratory season censuses. Correlations exhibited are highly significant ($p<0.001$).

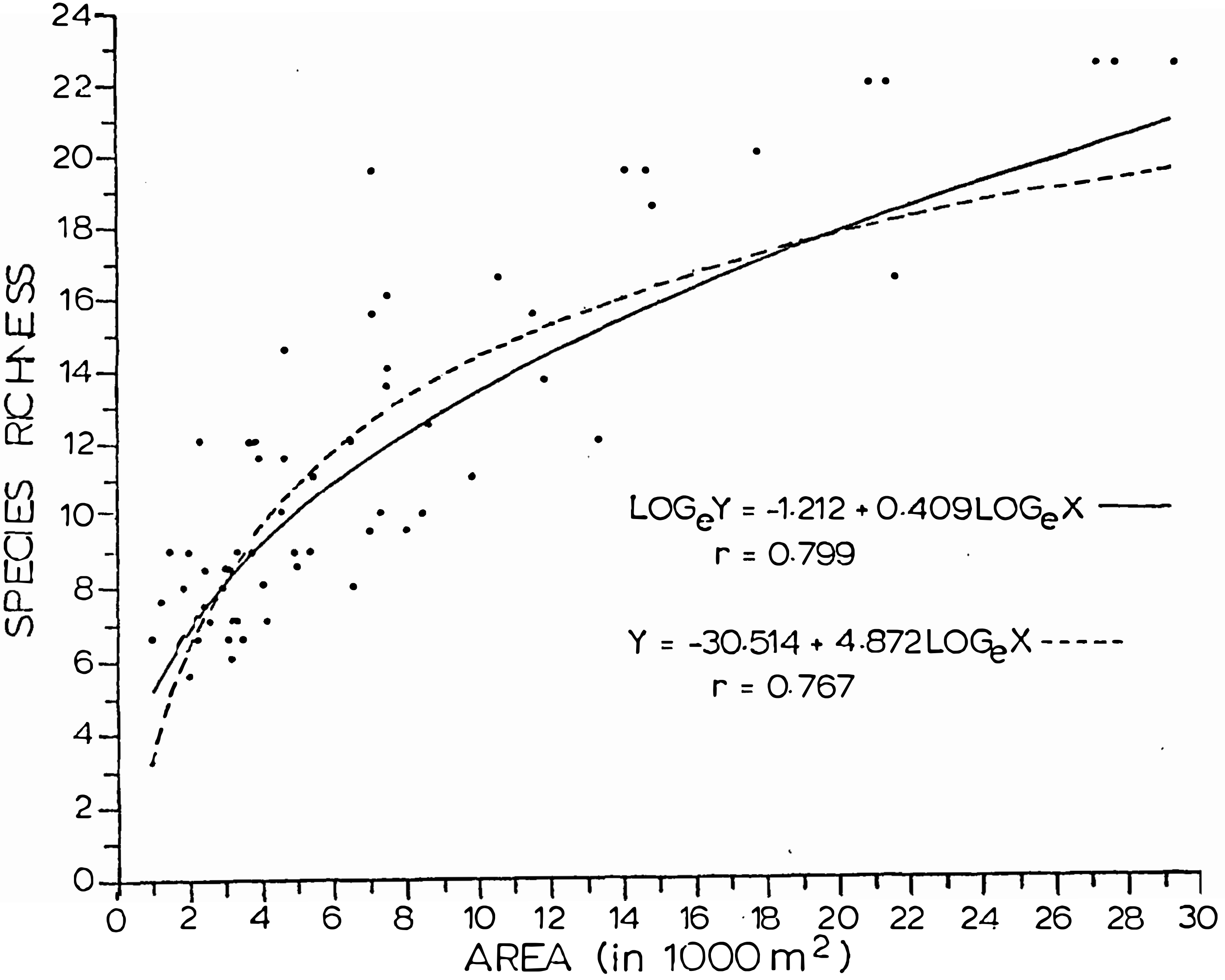
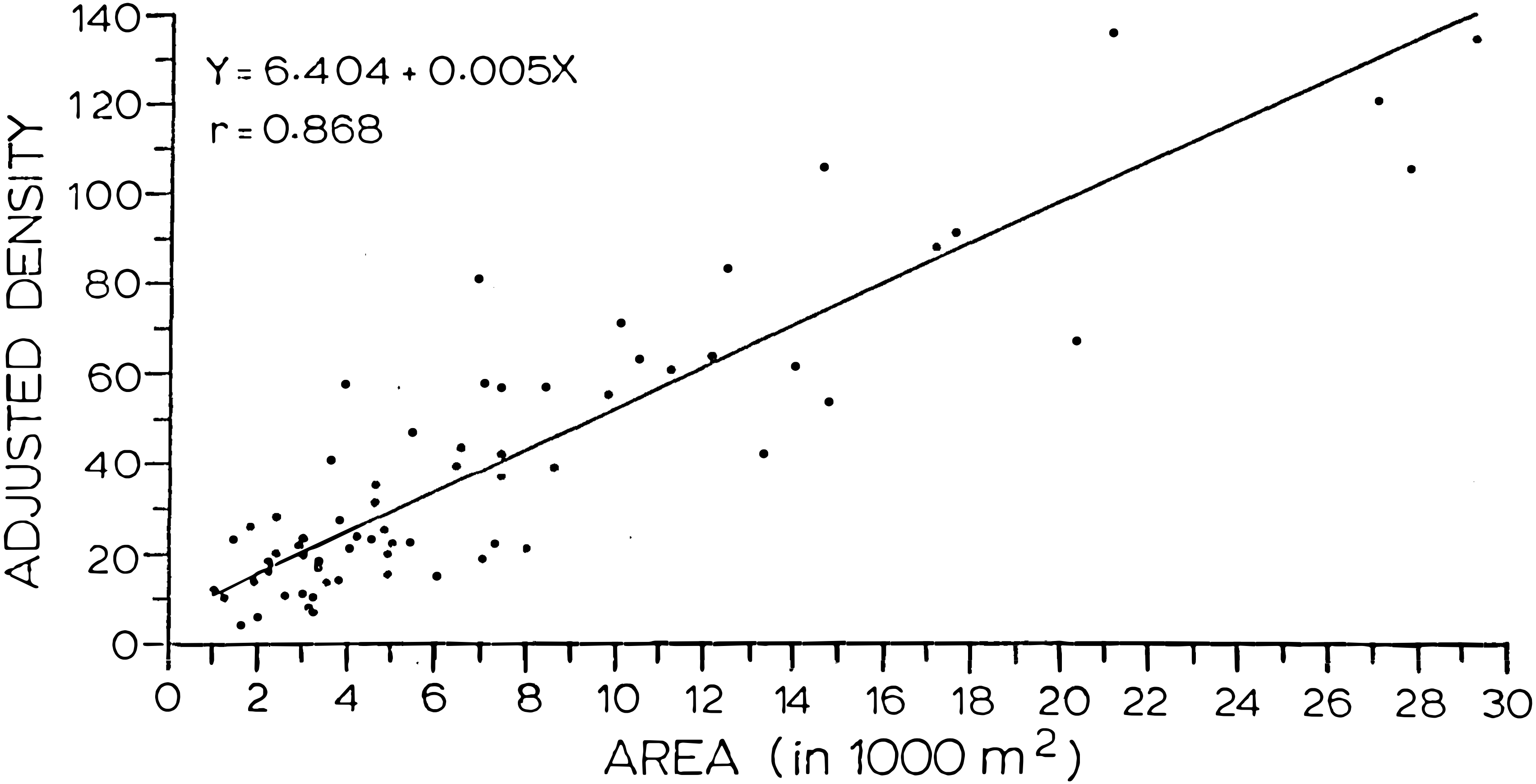

SPECIES RICHNESS
0
2
4
6
8
10
12
14
16
18
20
22
24
AREA (in 1000 m²)
0
2
4
6
8
10
12
14
16
18
20
22
24
26
28
30
LOGeY = -1·212 + 0·409LOGeX
r = 0·799
Y = -30·514 + 4·872LOGeX
r = 0·767

Figure 6. Total community density adjusted by subtraction of the densities of common grackles, house sparrows, and American robins and plotted against the area of those shelterbelts. All densities are based on the average of 1976 and 1977 migratory season censuses. The regression equation is highly significant ($p<0.001$).


Y = 6.404 + 0.005X
r = 0.868
ADJUSTED DENSITY
0
20
40
60
80
100
120
140
AREA (in 1000 m²)
0
2
4
6
8
10
12
14
16
18
20
22
24
26
28
30

increases from size class 1 to 3 (Table 3f). Standardized density produces a curvilinear (backward J) relation with area (Fig. 7), as is typical of density compensation in islands.

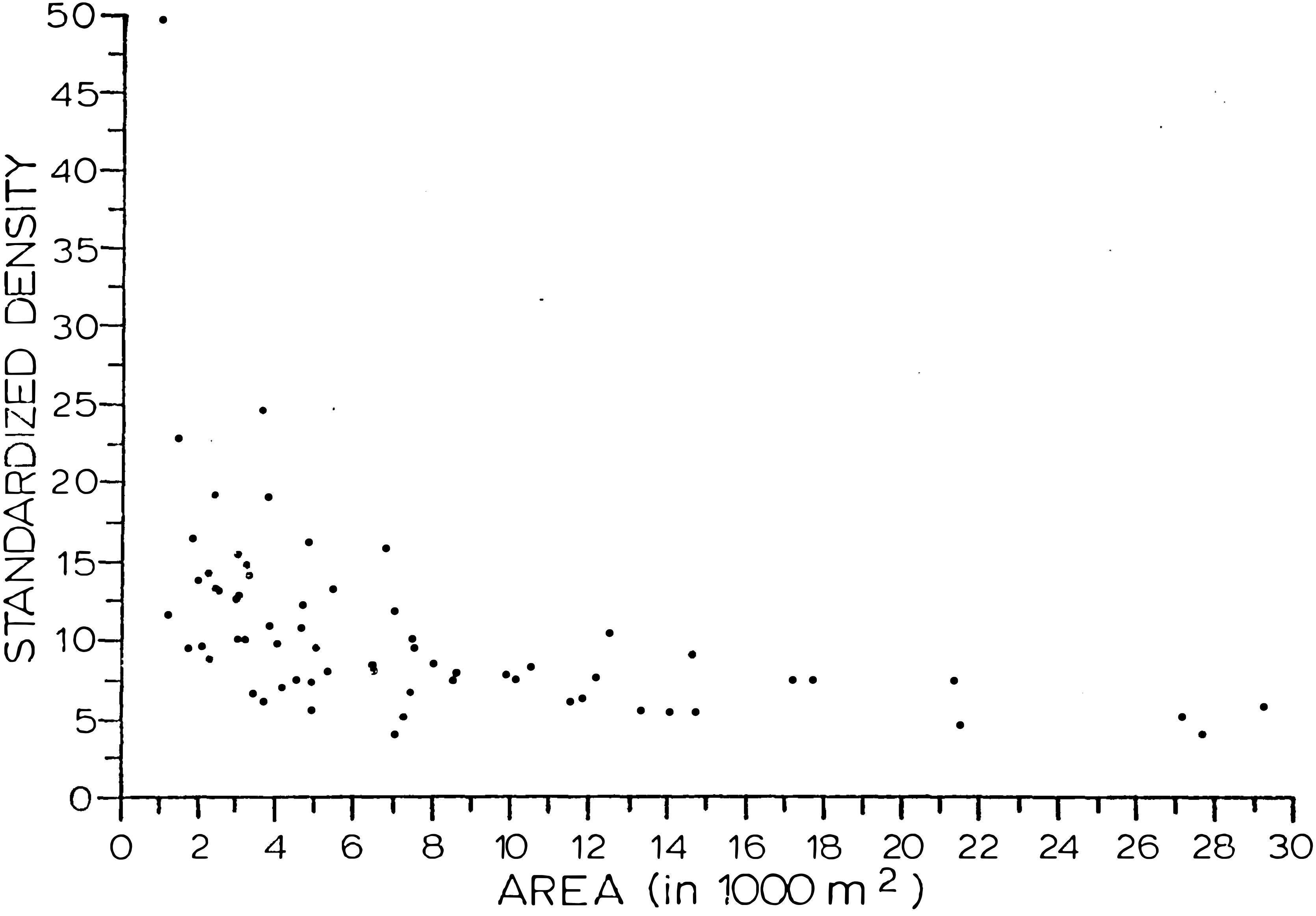
Species richness is a better predictor of community density than is area. Regression analysis between community density and species richness produces a high correlation (r = 0.859). Species richness can be viewed as an index of both the area and the suitability of food resources and habitat structure of a plot. A plot which has an area large enough to support 18 species but which only supports 12 due to poor food or habitat tends to have a lower density than that predicted by area. Thus the species richness and density of a plot tend to vary closely together.

DISCUSSION AND CONCLUSIONS

Species richness demonstrates a correlation with area during spring migration that is almost as high as during breeding season (r = 0.818 and 0.830 for species richness and area during migration and breeding respectively). Density is more highly correlated with area during migration (r = 0.811) than during breeding (r = 0.789). Since the "island effect" is as strong during migration as during breeding, similar factors may be operating in both seasons to place upper limits on the number of species and individuals which coexist in a shelterbelt.

Species numbers and density of all 3 food habits groupings increased with increases in plot size. Insectivores, because they comprise the greatest proportion of species of most of the shelterbelt bird communities, exhibit the highest correlation with area. However,

Figure 7. Standardized community density of each of the 69 study shelterbelts plotted against the area of those shelterbelts. Standardized density represents the community density of birds per 984.2 m^2, the smallest shelterbett studied.


STANDARDIZED DENSITY
50
45
40
35
30
25
20
15
10
5
0
0
2
4
6
8
10
12
14
16
18
20
22
24
26
28
30
AREA (in 1000 m 2)

the correlations of the number of species in each food habits group with the community species richness are higher by year or pooled over years, than is the number of species in each food habits group correlated with area. These conditions indicate the high inter-dependency among food habits groups. Community species richness is an index of the area and the environmental suitability of a plot, and both of these influence the community composition.

The correlation of area with all 3 food habits groups combined is stronger than the correlation of each group with area. A decrease in the number of species of 1 food habits group is compensated by an increase in another. The inter-compensation is probably due to: 1) habitat and food resources being optimal for 1 group and sub-optimal for another; or 2) competitive interactions; or 3) a combination of 1 and 2.

Migrants are less stringent in their selection of habitats as resting and feeding stations during migration than of their breeding habitat. Their migratory mode of existence forcing them to encounter and utilize a wide variety of habitats necessitates plasticity. However, several investigators have demonstrated that migrants do utilize habitats that are at least superficially similar to their breeding habitat outside of the reproductive period (MacArthur 1958, Morse 1968, Parnell 1969, Power 1971, Lack and Lack 1972, Lack 1976, Hamilton and Noble 1975).

Multiple regression analyses were performed to determine which habitat and environmental variables were responsible, or associated with the variables responsible for the residual variation unexplained by area. These results will be considered in detail in sections 7 and 8, but 1 of the significant variables to be considered here was the diversity of vegetation.

The significance of vegetation diversity is important from 2 standpoints. First, habitat factors are important to migrants, and the differential responses of migrant species to the habitat modifies species numbers and composition. Second, several investigators have shown vegetation diversity to be a better predictor of bird species diversity than area, although vegetation diversity is related to area (Power 1972, 1975, 1976, Harris 1973, Lack 1973, Amerson 1975, Johnson 1975).

Vegetation diversity is not as important as area to the number and species composition of avian migrants utilizing shelterbelts. The correlations of vegetation diversity with species richness (r = 0.238) is clearly less than the correlations of the same indices with area. However, shelterbelts are considerably more homogeneous with respect to vegetation than most other habitat islands studied. The correlation between vegetation diversity and area (r = 0.302) is comparatively low.

The significance of vegetation diversity, in spite of the minor role it plays in the habitat configuration of shelterbelts, suggests that avian migrants may rely on more readily visable proximate cues than do breeding individuals. A comparison of the 3 largest shelterbelts during migration versus breeding seasons provides information to support this concept. The largest 3 shelterbelts (48, 62, 29) have areas of 27138, 27629, and 29231 m^2, respectively. During migration these 3 plots held 24 species in 1976 and 21 species in 1977. However, during the breeding season, these 3 plots of similar size held 18 and 13 species, respectively. The differences in species richness between seasons in these plots can be attributed to the differential responses to environmental factors of migrants to the more visable proximate cues and will be discussed in greater detail in section 7.

The existence of a relationship between species number and area during migration could be due, at least, to 2 reasons. One possibility is that larger wooded areas attract more species. If larger belts provide a better target for temporary colonization, then a disproportionate number of species would be expected in the larger belts. The power function distribution of species among belts suggests that target size does not present a satisfactory answer.

I have suggested that limits on the number of coexisting species during breeding are placed by the limited food space characteristic of habitat islands. Competition for the food resources within the boundaries of the islands is reduced through territorial spacing and ecological isolation (Section 5). Competition for the limited food resources of habitat islands could arise during migration. Seventy to 80% of the migrants utilizing shelterbelts are insectivores and omnivores. Many migrants are insectivorous due to the seasonality of the food source of insectivores in the temperate zones (MacArthur 1959, Anderson 1970, Karr 1971, 1976a,b, Morse 1971, Welty 1975). It, therefore, is logical that the major portion of the migratory communities is species which are wholly, or partly, insectivorous, but the overlapping food habits may also result in competitive interactions. Spring migration occurs when insect hatches and seed production have just begun. Thus while migrant individuals require much less food than they require during the breeding season, the greater number of individuals exploiting a smaller food supply can create a competitive situation.

A competitive situation during migration may be enforced by the energy demands of migrants. The demand for energy placed on the physiological system by migration is high, and energy appears to require daily replenishment where possible. Graber and Graber (1962), studying birds killed at a television tower near Champaign, Illinois, estimated the birds to have lost between 2.6 and 4.4% of their gross body weight per hour while flying. Hussell (1969) suggested that veeries lost 1.3% of their gross body weight per hour and ovenbirds 1.0% per hour. The continual nightly losses require migrants to feed and replenish their energy stores during the day (Berthold 1975, Rappole 1976).

Any behavior which optimizes an individual's ability to replenish its energy and to successfully migrate and breed would tend to be selected. Thus ecological isolation and individual spacing, through mutual avoidance wherever possible, could arise due to the competitive advantage it confers on obtaining a suitable food source in areas such as habitat islands where the food space has definite boundaries.

Maintenance of individual spacing by migrants is suggested by a review of the literature. The vast majority of nocturnally migrating birds migrate as solitary individuals (Lowery and Newman 1955, Eastwood and Rider 1966, Schaefer 1968, Bellrose 1971, Gauthreaux 1972, Balcomb 1977). Hebrard (1971) also noted that woodland passerine migrants individually initiate their nightly flights. The solitary nature of migrants in flight might suggest similar behavior during the day while feeding. Territoriality and ecological separation among North American migrants on their tropical wintering grounds has been commonly observed

(Eaton 1953, Willis 1966, Schwartz 1964, Karr 1971, 1975, Lack 1971, 1976, Lack and Lack 1972, Leck 1972a, Moreau 1972, Rappole 1976). Spacing behavior is characteristic of species which feed on dispersed food, such as insects (Rand 1954, Brown 1964, Horn 1968, Orians 1971, Karr 1971, Wiens 1976). Since migrants display ecological isolation and spacing behavior during both breeding and winter season (whenever dispersed food is available), it seems logical that they continue to maintain such behavior during migration if dispersed food is available but total food resources are limited. By exploiting a uniformly dispersed food source which they isolate intra-specifically through individual spacing and inter-specifically through foraging strategies, food availability is then predictable and search time and energy is minimized.

The values Power (1971) calculated in a re-evaluation of the data of Parnell (1969) illustrate that the ecological distance of migrants is 88.1% of breeding individuals in foliage types and 85.5% in habitat zones. These high percentages demonstrate that the ecological distance among species is not as great during migration as during breeding, but ecological isolation still exists.

Part of the individual distance maintained between spring migrants may be due to the onset of breeding territorial behavior. Stewart (1953:99) indicated that some of the resident yellowthroat males he studied arrived "at least as soon as, if not before, the transient males that nest farther north." There were many instances in which I observed males of a particular species giving their territorial song during migration, but by breeding season I would find only 1 or 2 breeding pairs.

Rappole (1976) has documented the establishment of individual territories of transient northern waterthrushes around a pond where they do not breed. A pond, like shelterbelts, represents a resource space of definite boundaries and individuals which could not establish a territory around the pond did not attempt to establish territories in the surrounding less suitable habitat. Transient waterthrushes that established territories while migrating through Rappole's (1976) study area in Texas showed weight gains, while birds unable to obtain territories did not gain weight. Thus individual spacing in transients does appear to confer an advantage in obtaining food, at least in areas of limited resource space.

The amount of food resources diminishes as the number of birds coexisting increases due to increasing use of the resources. Increasing density also implies decreasing ecological space due to an increase in number of species with density. Thus numbers eventually reach a point, whereupon the suitability of the shelterbelt as a habitat for resting and feeding begins to decline (see Fretwell and Lucas 1969) and subsequent individuals entering the belt find encounters of other birds too frequent to remain.

That the number of species is modified by the available food space is also supported by the analysis of the food habits groups. Insectivores, which would be expected to be the most territorial, illustrate the greatest increase in number of species with increasing area, implying they are restricted the most by ecological space. Omnivores, which are less territorial than insectivores, and granivores, which are less territorial than omnivores, show intermediate and low influences of area on species numbers, respectively, as would be predicted if resource space is modifying density and the resultant species numbers.

I have suggested that species which are ecologically and spatially isolated during the breeding and winter seasons should continue to maintain such isolation during their transitory migrant stage, if food space is limited and the food resource dispersion warrants such behavior. In the temperate zone where this isolating behavior is commonly profitable, limited ecological space as provided by habitat islands, places an upper limit on the density and correlated number of species which can coexist at one time. Habitat islands are important to many species crossing otherwise unsuitable areas during migration. Those individuals that maintain an isolated area feed better and, hypothetically, reach their breeding grounds in better shape than individuals which do not try to isolate a food source. Those individuals arriving on the breeding ground in good physiological condition should be able to procure good breeding territories and optimize their reproductive success, so there is a greater recruitment of their genes in the next generation.

Direct data supporting the above postulation are weak, but not lacking. The postulation is supplied as a plausible explanation of the observed species-area relationship during migration in the hope that it will stimulate further research into the behavior of migrants.

Section 5

COMPETITION AND THE SPECIES-AREA RELATIONSHIP

INTRODUCTION

Islands have definite and abrupt boundaries and, whether they are real or habitat islands, are ideal for the study of competitive interactions and adaptations that allow coexistence of species. The number of species that can successfully coexist and the relationship between this number and area of islands has been explored in numerous studies (e.g. MacArthur and Wilson 1963, 1967, Hamilton et al. 1964, Hamilton and Armstrong 1965, Vuilleumier 1970, Diamond 1973, Diamond and Mayr 1976, Galli et al. 1976, Schoener 1976).

Studies were initiated in 1976 to monitor the variance in bird species numbers and densities among 69 shelterbelts in eastern South Dakota to identify environmental factors that might be responsible for this variance. Complete censuses of all belts were made in 1976, and 2 sets of censuses were conducted in 1977.

It was apparent early in this study that the isolated nature of shelterbelts resulted in a species-area relationship characteristic of island biotas. The data were analyzed to determine why the species-area relationship exists for habitat islands and how these results relate to real island situations.

RESULTS

Species richness

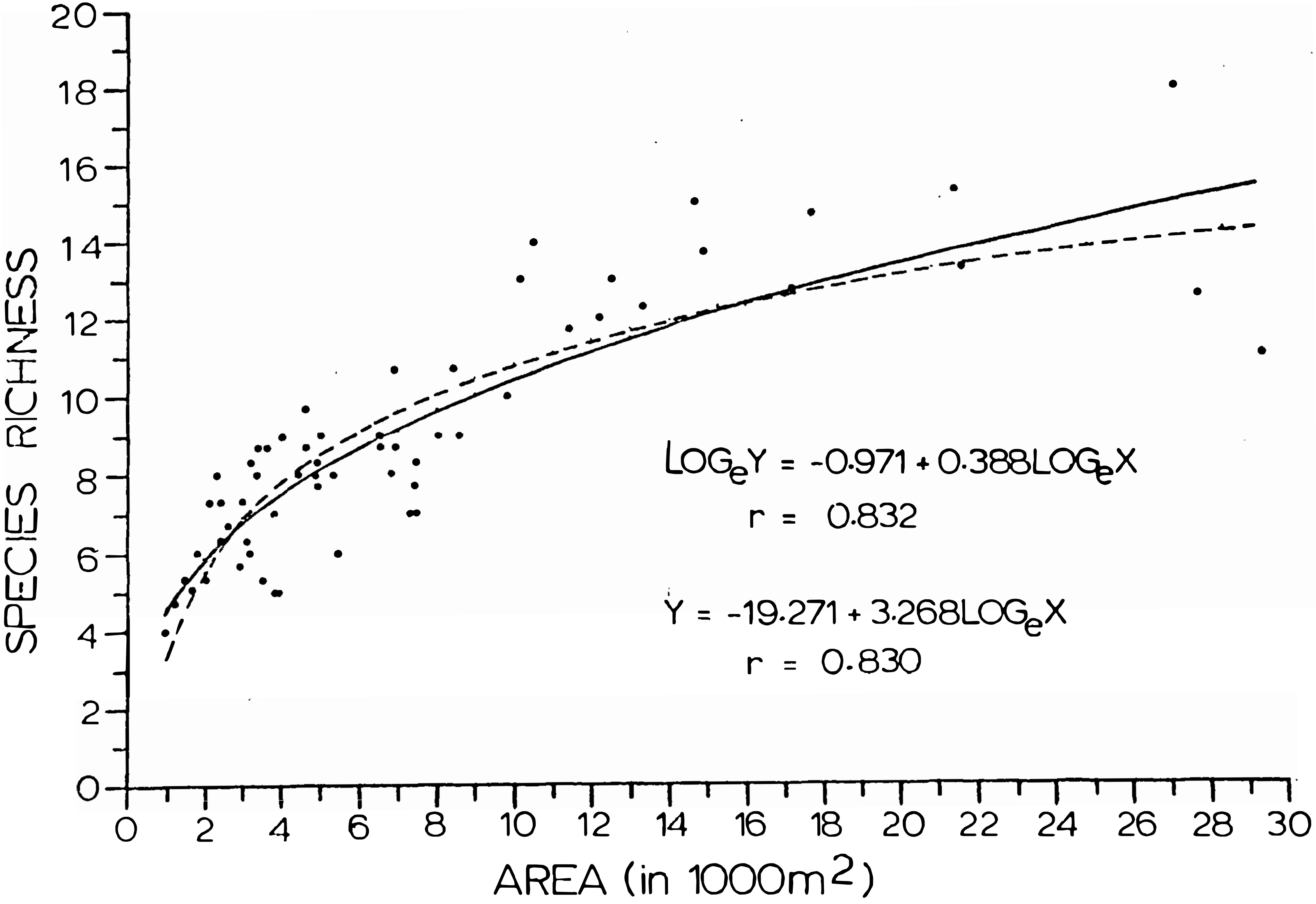
Species richness, when averaged over the smallest, medium and largest 23 shelterbelts, shows an increase with the 3 size classes during all 3 censuses (Table 4). Analyses indicated no significant differences ($p>0.10$) between any of the 3 overall means. There were no differences ($p>0.10$) found among means within a size class with 1 exception; within the smallest size class the mean for 1976 is higher ($p<0.10$) than the mean of the second census of 1977. Data were pooled over all censuses due to the homogeneity found (Table 4a).

Regression of species richness on area produced similar correlation coefficients among the power ($r = 0.832$), exponential ($r = 0.830$), and linear ($r = 0.805$) functions, although the former 2 are slightly higher than the latter. The slope ($z = 0.388$) implies that the power function best fits the relationship. However, the true form and slope is slightly obscured due to the variance in the date being inflated by environmental variation in the plots (Fig. 8). Part of the variance exhibited in Table 4 is due to the variance in plot size within a size class (Table 3b). The influence of environmental variation in obscuring the true relationship is exhibited by the underestimation of the regression equation of the data at the larger shelterbelt areas (Fig. 8). This indicates the slope predicted by regression is low.

Table 4. Means and standard errors for each size class (N = 23 shelterbelts per size class) and for all plots (N = 69 shelterbelts) for the 1976 and both 1977 breeding censuses, and the composite average of the three censuses. a) Species richness. b) Species diversity. c) Equitability. d) Density.

	1976		1977-1		1977-2		COMPOSITE	
Size Class	Mean ± SE		Mean ± SE		Mean ± SE		Mean ± SE	
a) 1	7.43	.56	6.39	.35	6.13	.33	6.65	.44
2	7.61	.43	7.26	.38	7.74	.39	7.54	.40
3	11.61	.77	11.83	.62	12.22	.63	11.97	.63
ALL	8.97	.40	8.49	.38	8.70	.41	8.72	.38
b) 1	1.575	.095	1.437	.058	1.441	.048	1.484	.070
2	1.684	.055	1.597	.054	1.663	.050	1.648	.053
3	2.126	.075	2.041	.058	2.065	.057	2.077	.063
ALL	1.795	.052	1.692	.045	1.723	.043	1.737	.046
c) 1	0.753	.043	0.713	.045	0.743	.040	0.736	.042
2	0.812	.019	0.791	.018	0.795	.016	0.799	.018
3	0.845	.021	0.800	.012	0.800	.011	0.815	.016
ALL	0.803	.018	0.768	.017	0.779	.015	0.783	.015
d) 1	33.56	3.69	30.29	3.61	30.57	3.53	31.48	3.57
2	31.70	2.66	37.08	4.06	40.54	4.08	36.45	3.69
3	54.96	5.04	58.14	5.09	62.00	4.54	58.38	4.87
ALL	40.07	2.57	41.83	2.84	44.37	2.81	42.09	2.67

Figure 8. Species richness of each of the 69 study shelterbelts plotted against the area of those shelterbelts. The species richness of each plot is based on the average of the 1976 and 1977 breeding season censuses. Correlations exhibited are highly significant ($p<0.001$).


SPECIES RICHNESS
0
2
4
6
8
10
12
14
16
18
20
AREA (in 1000m²)
0
2
4
6
8
10
12
14
16
18
20
22
24
26
28
30
LOGeY = -0.971 + 0.388LOGeX
r = 0.832
Y = -19.271 + 3.268LOGeX
r = 0.830

Analysis of primary food habits relationships

Insight into coarse changes in bird species composition of shelterbelts with increases in shelterbelt area can be obtained by grouping birds by primary food habits. To facilitate statistical analyses, plots were grouped into 3 size classes (Figs. 9,10). Two factor analysis of variance was performed on the relationship between plot size classes and food habits. However, regressions were based on the continuous range of study plots (Figs. 9,10). Analysis of the mean number of species per food habits group per size class (Appendix I) indicated a highly significant difference (F=35.062, $p<0.001$) among food habits groups and a highly significant increase (F=57.305, $p<0.001$) in the mean number of species with an increase in size class (Fig. 9).

The interaction between food habits groups and size classes is also highly significant (F=13.768, $p<0.001$). This interaction can be attributed to the differential rates of increase in the number of species of each food habits classification with plot size. The regression slopes (Fig. 9) illustrate that the number of species of insectivores increases faster with plot size than omnivores, and omnivores increase faster than granivores. These differential rates of increase lead to insectivores representing an increasing proportion of the species of the larger avifaunal communities, while granivores decrease in proportional representation as plot size increases (Fig. 9). Omnivores remain relatively unchanged in porportional representation.

Two factor analysis of variance illustrates highly significant differences (F=30.710, $p<0.001$) among densities of food habits groups. Density of all 3 groups illustrates a highly significant increase

Figure 9. Mean number of species of granivores (G), omnivores (O), and insectivores (I) censused during 1976 and 1977 breeding seasons in each of 3 increasing shelterbelt size classes. The regression equations are based on all 69 study shelterbelts and all are highly significant ($p<0.001$). The numbers indicate the mean percent representation of each food habits group for each size class.

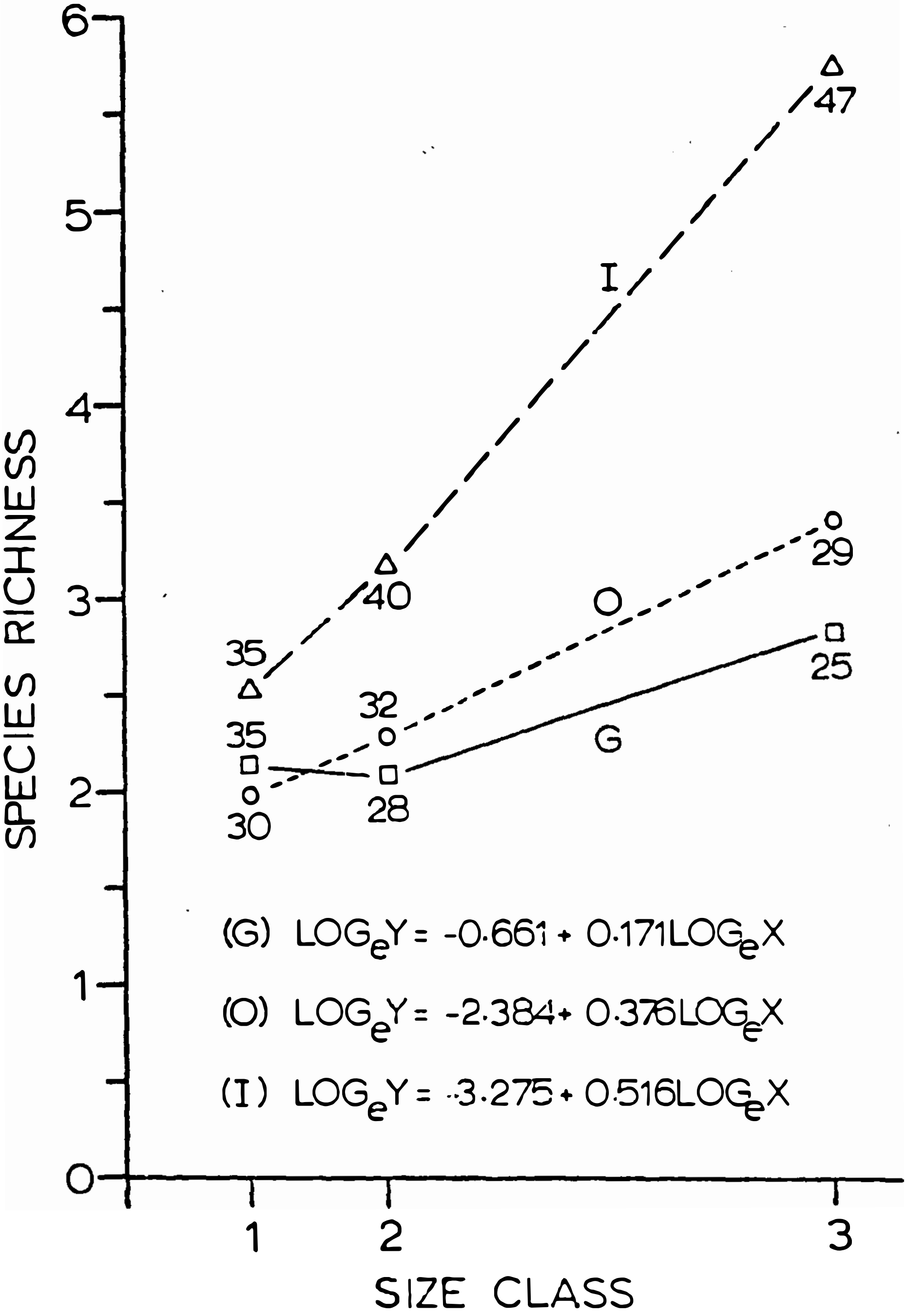
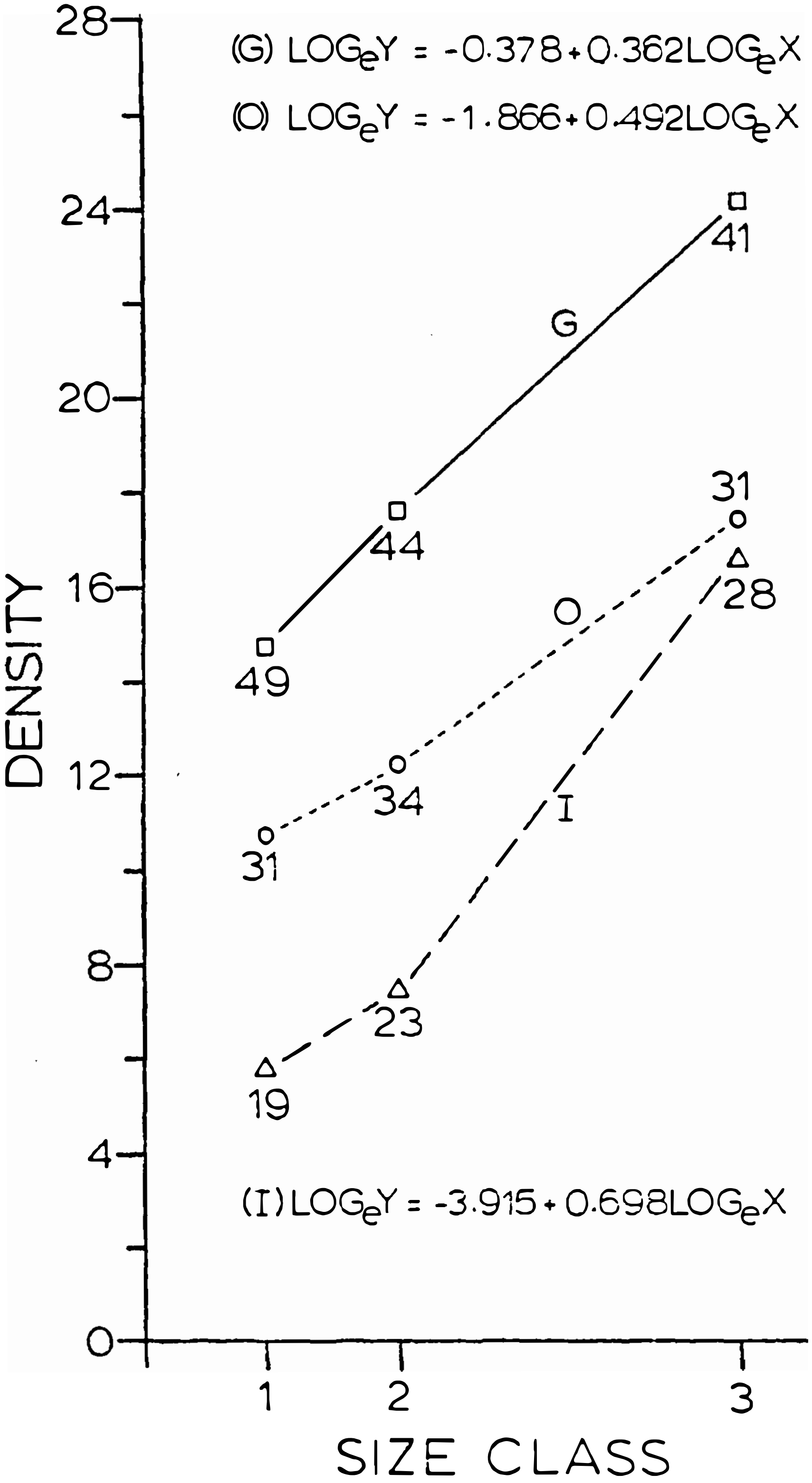

SPECIES RICHNESS
0
1
2
3
4
5
6
SIZE CLASS
1
2
3
I
O
G
35
35
30
40
32
28
47
29
25
(G) LOG$_e$Y = -0.661 + 0.171LOG$_e$X
(O) LOG$_e$Y = -2.384+ 0.376LOG$_e$X
(I) LOG$_e$Y = -3.275 + 0.516LOG$_e$X

Figure 10. Mean density of granivores (G), omnivores (O), and insectivores (I) censused during 1976 and 1977 breeding seasons in each of 3 increasing shelterbelt size classes. The regression equations are based on all 69 study shelterbelts and all are highly significant ($p<0.001$). The numbers indicate the mean percent representation of each food habits group for each size class.


(G) LOG$_e$Y = -0.378 + 0.362LOG$_e$X
(O) LOG$_e$Y = -1.866 + 0.492LOG$_e$X
(I) LOG$_e$Y = -3.915 + 0.698LOG$_e$X
G
O
I
49
44
41
31
34
31
19
23
28
DENSITY
0
4
8
12
16
20
24
28
SIZE CLASS
1
2
3

(F=14.974, $p<0.001$) with plot size (Fig. 10). The proportional density representation of insectivores increases and granivores decreases as was the case for proportional species representation. However, granivores represent the greatest proportion of individuals in the avifaunal communities (Fig. 10) in contrast to insectivores which represent the dominant proportion of species (Fig. 9).

Community density

Community density, or the total number of individuals in a shelterbelt, increases with plot size. Investigators of island theories have postulated that the relationship between community density and area should be linear (e.g. May 1975, Diamond and Mayr 1976), although I know of no reported study that illustrates linearity. Regression analysis of community density with area indicates that the linear relationship produces a higher correlation (r = 0.802) than either the exponential (r = 0.750) or power (r = 0.681) functions (Fig. 11).

If density is increasing linearly with area (increasing at a constant rate), and the number of species is increasing logarithmically (increasing at a decreasing rate), then the relationship between density and species richness is curvilinear because density increases at a faster rate at the larger plot sizes than does species richness. Plotting of density against species richness (Fig. 12) illustrates a slight upswing in the tail. This curvilinearity suggests the relationship is logarithmic. Regression illustrates that the linear relationship (r = 0.879) and the power function (r = 0.870) are very close and both are slightly higher than the exponential function (r = 0.843). In all cases the correlation is higher

Figure 11. Total community density of each of the 69 study shelterbelts plotted against the area of those shelterbelts. Density represents the total number of individuals censused in each shelterbelt averaged over 1976 and 1977 breeding seasons. The correlation exhibited is highly significant ($p<0.001$).

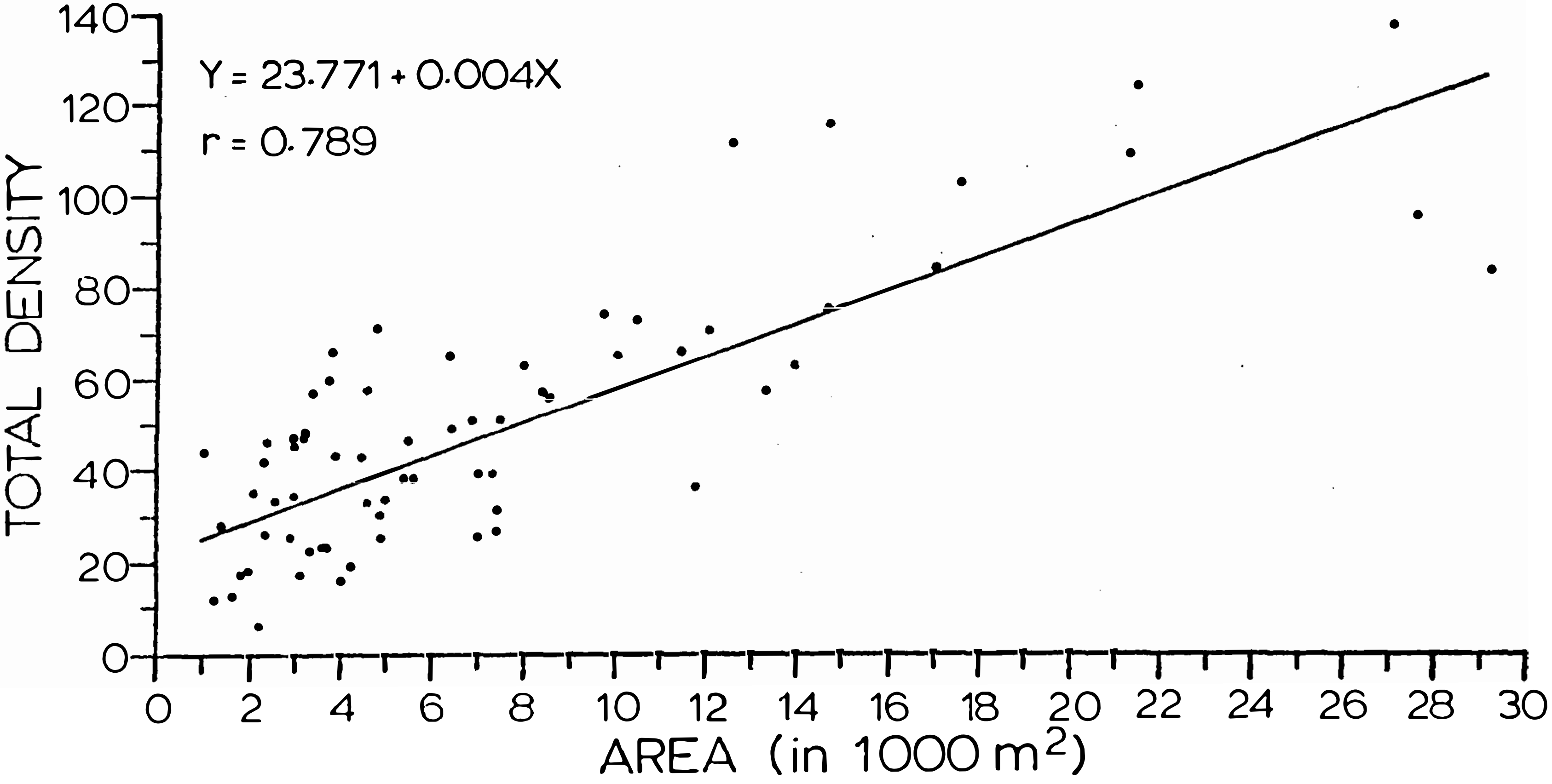
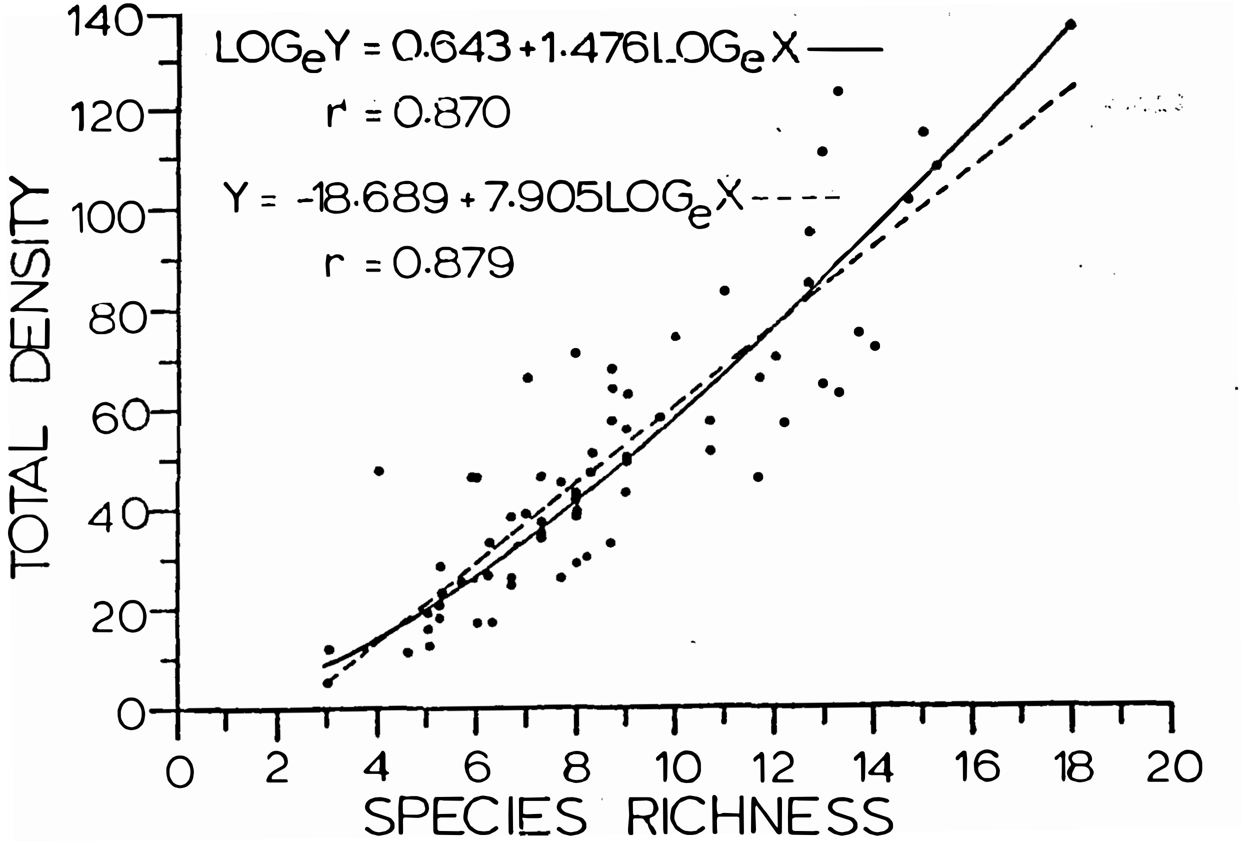

Y = 23.771 + 0.004X
r = 0.789
TOTAL DENSITY
0
20
40
60
80
100
120
140
AREA (in 1000 m²)
0
2
4
6
8
10
12
14
16
18
20
22
24
26
28
30

Figure 12. Total community density of each of the 69 study shelterbelts plotted against the species richness of those shelterbelts. The density and species richness of each plot is based on the average of 1976 and 1977 breeding season censuses. Correlations exhibited are highly significant ($p<0.001$).


$\log_e Y = 0.643 + 1.476 \log_e X$ ——
r = 0.870
$Y = -18.689 + 7.905 \log_e X$ ----
r = 0.879
TOTAL DENSITY
0
20
40
60
80
100
120
140
0
2
4
6
8
10
12
14
16
18
20
SPECIES RICHNESS

than found for the density-area relationship, indicating species richness is a better predictor of density than is area.

The true relationship between density with area and species richness is partly obscured due to the high scatter of points. Part of this scattering can be attributed to the more sporadic densities of the most abundant social species which rely on food sources outside of the belt. If the densities of the common grackle, house sparrow, and American robin are subtracted from the total community density and this new adjusted density regressed against area (Fig. 13), the correlation is increased in all cases and the linear relation ($r = 0.889$) still produces a higher correlation than either the power ($r = 0.853$) or the exponential ($r = 0.830$) functions. Linear increase of density with area is further supported by the slope of the power function. If the relationship is linear the slope should equal 1 (e.g. $S = CA^1$) and the value calculated by log-log regression of density against area showed the slope ($z = 0.864$) to be very close to 1.0.

Regression of the adjusted density against species richness (Fig. 14) demonstrates that the power ($r = 0.925$) and the exponential ($r = 0.924$) functions have similar correlation coefficients, and both are slightly higher than the linear function ($r = 0.901$). The density-species richness relationship is curvilinear and illustrates that at the higher ranges of species richness there is an increase in the number of individuals per species.

Figure 13. Total community density adjusted by subtraction of the densities of common grackles, house sparrows, and American robins of each of hte 69 study shelterbelts plotted against the area of those shelterbelts. All densities are based on the average of 1976 and 1977 breeding season censuses. The correlation exhibited is highly significant ($p<0.001$).

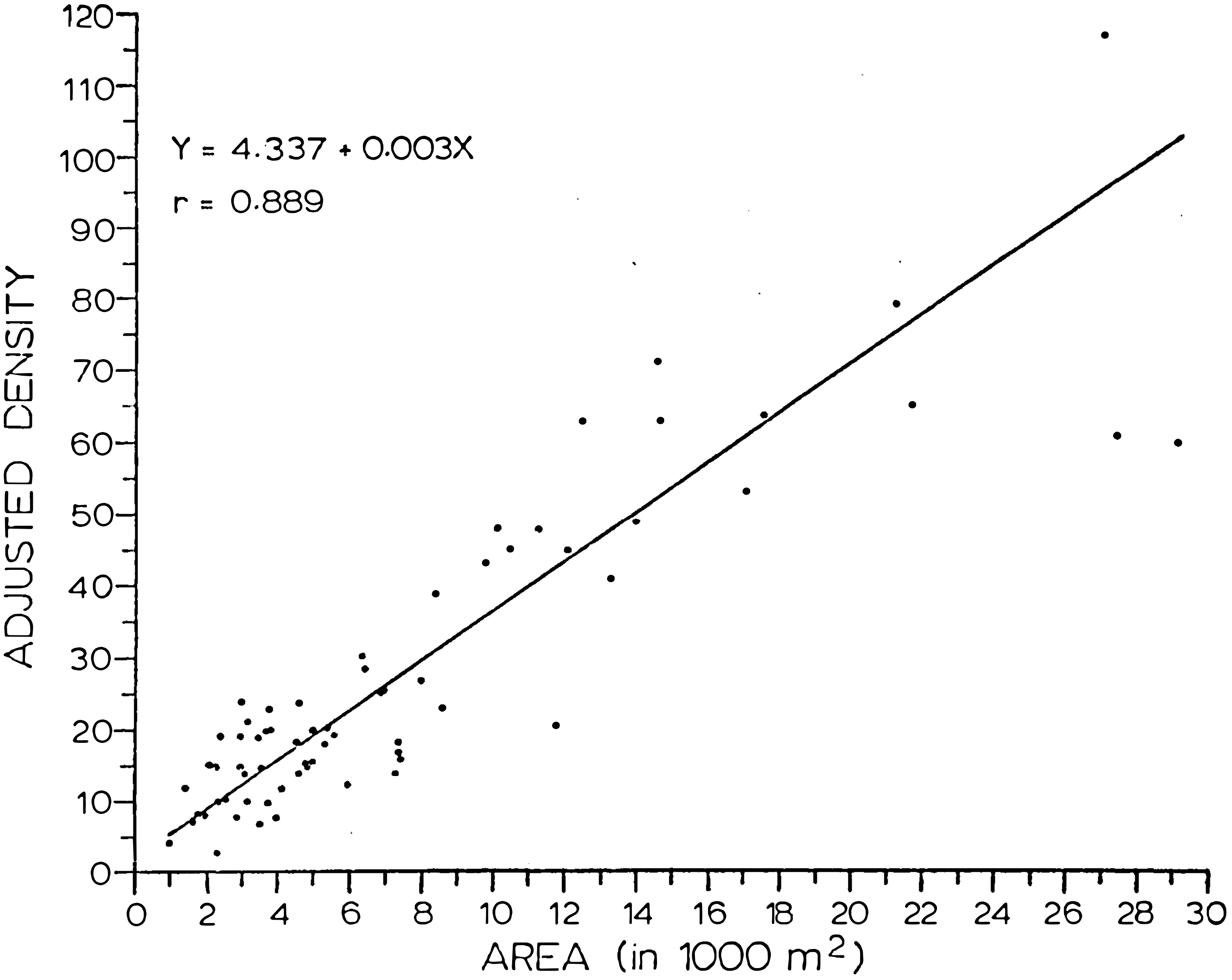
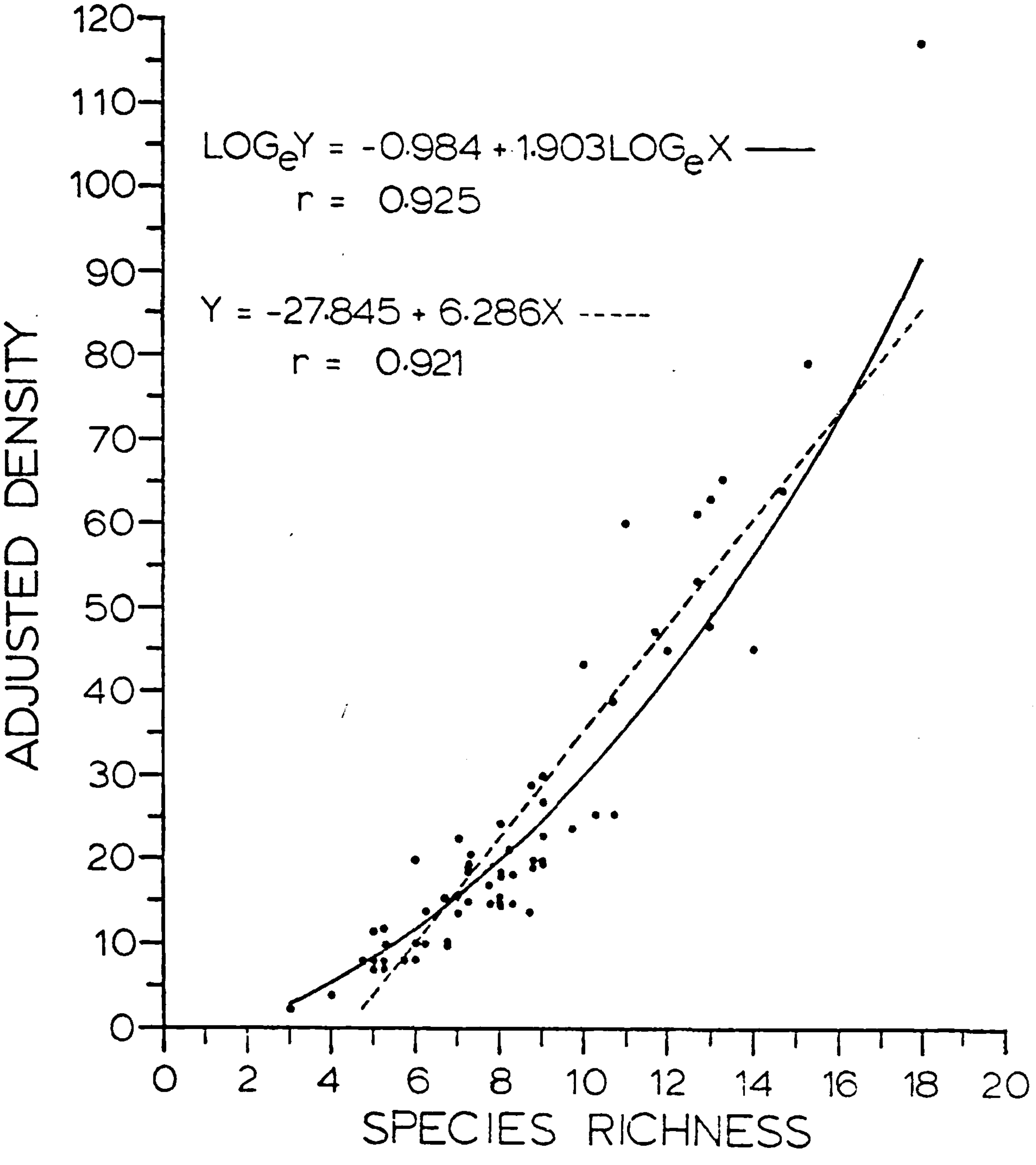

Y = 4.337 + 0.003X
r = 0.889
ADJUSTED DENSITY
0
10
20
30
40
50
60
70
80
90
100
110
120
AREA (in 1000 m2)
0
2
4
6
8
10
12
14
16
18
20
22
24
26
28
30

Figure 14. Total community density adjusted by subtraction of the densities of common grackles, house sparrows, and American robins of each of the 69 study shelterbelts plotted against the species richness of those shelterbelts. All densities and species richness are based on the average of 1976 and 1977 breeding season censuses. Both correlations exhibited are highly significant ($p<0.001$).


$\log_e Y = -0.984 + 1.903 \log_e X$ ——
r = 0.925
$Y = -27.845 + 6.286X$ -----
r = 0.921
ADJUSTED DENSITY
SPECIES RICHNESS
0
10
20
30
40
50
60
70
80
90
100
110
120
0
2
4
6
8
10
12
14
16
18
20

Species relations

Subtraction of the densities of the 3 bird species from the overall community density improves the fit of density with area since none of these species show any propensity to respond to changes in area in a predictive fashion (Table 5). Of the remaining 14 common species, only 2, western kingbird and redwing blackbird, do not show significant correlations with area. The strong relationship with area exhibited by many species can be attributed to their territorial nature. Some species require a certain minimum size (Table 6) before they will reside in a particular belt. The proportion of belts in which territorial species reside increases as belt size increases. However, in all cases, the size at which 2 pairs are found is always more than double the size at which 1 pair was initially found. Mapping of the territories of house wrens, yellowthroats, and brown thrashers in 2 large shelterbelts demonstrates the territory size of specific pairs in these larger belts to be 2 - 3 times as large as the total area of the belts which these 3 species colonize initially as 1 pair (Section 6).

DISCUSSION AND CONCLUSIONS

Some recent studies have illustrated environmental diversity, rather than island area, as the main factor accounting for bird species diversity in some island situations (Power 1972, 1975, 1976, Harris 1973, Lack 1973, Amerson 1975, Johnson 1975), although these investigators point out that environmental diversity is a consequence of island area. Multiple regression analysis of the environmental variables influencing variation in the number of bird species in shelterbelts allows the

Table 5. Correlation coefficients and the significance from regression of 18 resident species on area, length, and community species richness.

SPECIES	AREA	p	LENGTH	p	RICHNESS	p
COMMON GRACKLE	0.149	.100	0.090	.100	0.312	.010
MOURNING DOVE	0.487	.001	0.418	.001	0.624	.001
AMERICAN ROBIN	0.227	.100	0.259	.050	0.306	.025
HOUSE SPARROW	0.004	.100	0.001	.100	0.033	.100
ORCHARD ORIOLE	0.533	.001	0.511	.001	0.724	.001
BROWN THRASHER	0.653	.001	0.525	.001	0.587	.001
WESTERN KINGBIRD	0.218	.100	0.227	.100	0.329	.010
EASTERN KINGBIRD	0.553	.001	0.630	.001	0.650	.001
AMERICAN GOLDFINCH	0.645	.001	0.555	.001	0.680	.001
YELLOWTHROAT	0.365	.005	0.380	.002	0.521	.001
RED-WINGED BLACKBIRD	0.189	.100	0.181	.100	0.315	.010
HOUSE WREN	0.455	.001	0.415	.001	0.506	.001
BROWN-HEADED COWBIRD	0.403	.001	0.485	.001	0.430	.001
BLACK-BILLED CUCKOO	0.680	.001	0.566	.001	0.640	.001
SONG SPARROW	0.629	.001	0.586	.001	0.685	.001
EASTERN WOOD PEWEE	0.288	.025	0.181	.100	0.470	.001
COMMON FLICKER	0.535	.001	0.404	.001	0.530	.001
BLUE JAY	0.732	.001	0.671	.001	0.522	.001

Table 6. Density of bird species, which illustrate significant correlations with area (see Table 5), exhibited for each of the 69 shelterbelts arranged in order of increasing area (See Appendix L for listing of the area of each shelterbelt).

	PLOT NUMBERS																						
BIRD SPECIES	07	06	69	47	27	43	15	33	05	13	34	03	30	44	02	48	08	17	45	49	09	36	55
ORCHARD ORIOLE							2			2	2		2		2			2	2	2	2		2
BROWN THRASHER										2		2			2	2		2		2	1		2
WESTERN KINGBIRD			2	2			2				2		2		2			2	2	2			2
EASTERN KINGBIRD			2				2						2	2		2			1	1	1		2
AMERICAN GOLDFINCH					2		2								2	2		1		1		1	1
YELLOWTHROAT															2				2		2		2
HOUSE WREN								2		1		2					2				2		
BLACK-BILLED CUCKOO																							
SONG SPARROW								2		2					2								
EASTERN WOOD PEWEE															2			2		1			
COMMON FLICKER								2						2							2		
BLUE JAY																							

	PLOT NUMBERS																						
BIRD SPECIES	31	42	01	32	22	37	24	46	18	20	21	12	64	57	16	10	58	11	19	56	60	28	39
ORCHARD ORIOLE		2	2	2	2	2	2	2	2	2	2	2	2	2	4		4	4	2	2	2	2	2
BROWN THRASHER						2	2			2		2	2	2		2	2	4	2	2	2	1	2
WESTERN KINGBIRD		4	2					2	2	2	2			2	4		5		2	2	2		2
EASTERN KINGBIRD				2		2			2	2	2						2		2				2
AMERICAN GOLDFINCH	1								1	1	2		1					1	2				2
YELLOWTHROAT									2									2	2	2		2	2
HOUSE WREN			2				2	2				2			2								
BLACK-BILLED CUCKOO						2																	
SONG SPARROW					2	2																	
EASTERN WOOD PEWEE						2				2									4				
COMMON FLICKER				2								2											
BLUE JAY																							

	PLOT NUMBERS																						
BIRD SPECIES	35	04	66	59	65	14	40	41	23	50	54	67	61	25	53	52	38	51	26	63	62	68	29
ORCHARD ORIOLE		2	2	2	3	4	4	4	2	4	4	2		2	4	2	4	4	6	4	2	6	
BROWN THRASHER	2	2	2			2	2	2	2	4	4	2	2	2	6	4	2	4	2	6	4	2	2
WESTERN KINGBIRD			2	2	6					2	6		2		4	2		2		6	2	4	
EASTERN KINGBIRD			4		2		2	2	2	4	4	2	2	4	4	2	2	3	4	2	2	6	2
AMERICAN GOLDFINCH		1	3	2	4	3	3	2	2	1	4	4		3	4	4	4	3	1	2	4	4	3
YELLOWTHROAT		2	2		2	2	2				2			2	4	2	2	2	6			2	
HOUSE WREN				2		2	2	4				2		4				2	6	2		4	4
BLACK-BILLED CUCKOO		2		2		2		2			2	2				2	2	2	2	2	2	2	2
SONG SPARROW		2					2		2	2	2	2		2	4	4	3	3	6			6	3
EASTERN WOOD PEWEE			2		2					2	4				6	2		4			2	2	
COMMON FLICKER	2					2	2	2				2		2				2	4	2		2	2
BLUE JAY				2		2								2					4	2	2	4	2

conclusion that vegetation diversity is not a significant factor ($p<0.10$) and that the correlation with vegetation diversity is negative (Section 7). My studies demonstrate that the primary determinant of species richness and density for shelterbelts is area. The importance of area in influencing species numbers on islands has been observed by many investigators (e.g. MacArthur and Wilson 1963, 1967, Hamilton et al. 1964, Hamilton and Armstrong 1965, Vuilleumier 1970, Diamond 1973, Galli et al. 1976, Mayr and Diamond 1976).

Area of shelterbelts is a result of 2 factors, length and number of rows of vegetation (width). Unlike other real or habitat islands, increase in area does not necessarily result in an increase in botanical diversity. In natural island situations, an increase in area increases the probability of propagule immigration and increases diversity of sites for establishment. This relationship of area and plant diversity (Kilburn 1966, Power 1972, Johnson 1975, Harner and Harper 1976) and the added effect of elevation in combination with area to further increase site diversity and hence plant diversity has been documented (Power 1975, 1976, Amerson 1975). In shelterbelts, overstory composition is determined by the planting strategy, and the understory plant diversity is modified by care of the belt.

Cultivation of shelterbelts in their first 5 years to reduce competition for water between the planted trees and natural weeds allows little natural diversity in the understory. Subsequent mowing or severe grazing tends to maintain the original planted diversity. If belts are not grazed or mowed, a shrub understory develops in some cases, but the lack of woody species propagules and/or suitable micro-environment for their establishment usually results in a tall grass understory. The low correlations of area with understory density (r = 0.033), shrub layer height (r = 0.040), canopy height (r = 0.022), canopy coverage (r = 0.139), and ground coverage (r = 0.090) further support the lack of a relationship between area and environmental diversity. The low confounding of area and environmental factors therefore allows easier interpretation of the absolute importance of area in affecting bird species numbers.

Isolation

The degree of isolation of the islands under study is another factor which has been recognized as affecting insular equilibrium levels (MacArthur and Wilson 1967, Power 1975, 1976, Diamond et al. 1976, Gilpin and Diamond 1976, Johnson 1975, Schoener 1976). Isolation of shelterbelts was measured in 2 ways, distance to nearest other woody cover, and whether or not the shelterbelt bordered a tree claim. A tree claim represents a large, rectangular, 10 acre or larger block of trees. Other woody cover included any other woody habitat, such as other shelterbelts, tree claims, and riparian areas. The inclusion of the second measure, presence-absence of tree claims, was due to the presence of tree claims adjacent to 7 of the study belts and the field observations of a resultant depressing effect on species numbers.

Multiple regression analysis of environmental factors showed the presence of tree claims causes a significant reduction ($p<0.01$) in both species richness and diversity. Distance to nearest other woody cover exhibited a significant positive correlation ($p<0.10$) with species richness. This relationship can be explained as due to increasing use of more than 1 island by 1 pair as distance between islands decreases. The curvilinear relationship between species richness and area indicates a decrease in number of species per unit area with an increase in area. Therefore, if birds are viewing belts in close proximity as 1 large belt, the number of species of birds in 1 of these belts would only be a subset of the total number of species and would be less than if the belt was isolated. The close and constant scattering of shelterbelts in conjunction with the high vagility of temperate bird species reduces isolation as an inhibitor of colonization.

Minimum area

Galli et al. (1976) studied forest islands in New Jersey similar in size to shelterbelts. It was their contention that the increase in bird species numbers with an increase in area was due mainly to the meeting of progressively more and more minimum area requirements for species, and that an increase in habitat patchiness with area provided specific requirements for other species.

The data collected in shelterbelts also illustrate minimum area restrictions for some species (Table 6) that partly explains the increase in species richness with area. However, the conclusions of Galli et al. (1976) do not totally explain the increase in either their study or mine. The data presented indicate that plot 68, which is 3100 m^2, is of sufficient area to support 20 common or relatively common species (Table 6). Yet there are only 7 species, on the average, actually coexisting at this area. The data of Galli et al. (1976) similarly show only 6 coexisting species on a plot size of 0.8 ha (8000 m^2), where 20 common or relatively common species would be expected to exist if area was the major determinant. Clearly, other restrictions limit the upper number of coexisting species in a given habitat island. I suggest that diffuse competition is a major factor in setting this upper limit (see Diamond 1970a,b, MacArthur 1972, Planka 1974).

Diffuse competition

Economic defensibility of the food resource has been suggested as 1 of the major determinants of the social behavior of birds (Rand 1954, Brown 1964, Horn 1968, Orians 1971, Wiens 1976). Brown (1964), Crook (1965), and Morse (1971a) suggested, while Horn (1968) demonstrated mathematically, that evolution of the large territories of birds that include both feeding and nesting (Nice's (1941, 1943) type A) should be favored for those species which feed on randomly dispersed food. If food is randomly dispersed then its density would be proportionate to space, and an increase in space would then be equivalent to an increase of food. Therefore, territorial defense of a given space is equivalent to defense of a proportional density of food.

A direct relationship between territory size and food density has been documented for the great tit (Kluijver 1951), ovenbird (Stenger 1958, Stenger and Falls 1959), dunlin (Holmes 1970), winter wren (Cody and Cody 1972), and several species of Sylviid warblers (Cody and Walter 1976). Schoener (1968:132) in his review of factors influencing territory size noted several studies which documented expanded territory sizes in habitats that were seemingly less rich in preferred food (e.g. Howell 1952, Erickson 1938, Miller 1931, Odum 1941, Pitelka et al. 1955). Zimmerman (1971), Hertz et al. (1976), and Best (1977) also relate territory size to habitat condition.

The territory size must be large enough to compensate for the normal temporal dynamics of the resource base plus the added dampening influence of the pair feeding on it. The continual exploitation of prey by a pair will result in a declining prey base within the breeding territory if the range over which the pair forages is too small. The declining prey base results in an increase in the energy expended searching for, finding, and eating a suitable prey item and results in a declining net energy gain (Schoener 1971, Krebs et al. 1974, Pyke et al. 1977). Further reduction of the prey of a species occurs through utilization by other coexisting species.

As food resources or habitat structure become suitable for more species to coexist, the increasing number of coexisting species should result in each species being increasingly restricted to exploiting that portion of the environment to which it is best adapted, becoming habitat and foraging specialists, but remaining food generalists (MacArthur and Wilson 1967, MacArthur 1972, Yeaton and Cody 1974, Hespenheide 1975). Thus as the number of species increases and because the food spectrum remains constant, there should be an increasing overlap in food obtained (diffuse competition). This overlap decreases the available food to any I species and leads to the prediction that with increasing number of coexisting species there should be a correlated increase in territory size required to obtain sufficient food.

I have documented increases in territory sizes with increases in number of coexisting species in the yellowthroat, house wren, and brown thrasher (Section 6). Increases in territory size with increases in species richness can also be implied by comparing the minimum size of shelterbelts within which a species will reside to the minimum size shelterbelt in which 2 pairs will occur divided by 2 (Table 6). The difference is large in most cases. Yeaton and Cody (1974) documented increases in territory size with increases in number of coexisting species and further documented the decrease in niche width with increased species diversity. Abnormally small territories that increase with increasing island area, and, consequently, the number of coexisting species has been documented by Beer et al. (1956), Schnell (1963), and Nilsson (1977). Diffuse competition can explain the increase in territory size through the reduction in available food supply and restricted niche width. On a small island, niches can be expanded due to competitive release. Expansion of foraging height (Yeaton 1974, MacArthur et al. 1972), habitat breadth (Crowell 1961, 1962, Diamond 1970, Morse 1971, Terborgh 1971, MacArthur 1972, Lack 1976), and elevation residence (Terborgh and Weske 1975) due to competitive release has been documented.

Density should increase linearly with area if birds spaced themselves to obtain their food requirements. Food demands of individuals will not change so increases in food space (island area) should result in proportional increases in number of individuals. As island area increases, the resultant increase in species numbers should lead to an increase in the territory size of any particular species, but the overall community density should increase proportionally (linearly) with area because there are more species overlapping spatially. Density does increase linearly with area in shelterbelts, and the fit is considerably improved when species which feed outside of the belts are subtracted. However, if more species are coexisting in a given area of space, then selection should be for species that exploit different microhabitats, and, hence, different food resources. This selection is due to the greater food availability in unexploited microhabitats.

Assignment of all species into guild classifications following Root (1967), Karr (1971), and Willson (1974) indicates the manner in which each species generally partitions the habitat space. If division of the habitat space is such that each species in a given community does partition the space differently, the number of guilds divided by the number of species represented in the community should approach 100%. This percentage for each of the 69 shelterbelts showed that 93.7% of the species in each community were in different guilds. Most species present in a community and sharing a guild classification were highly divergent in body size. MacArthur (1972) suggested a difference in body weight by a factor of 2 or more indicates separate food resources are being utilized. Therefore, recalculation of the percentage of species per guild with the added separation by body size within guilds demonstrated the overall percent species per guild to be 99.4%. This high percentage supports the above postulation that species composition should tend to maximize resource partitioning differences between species. However, the small overlap in guilds may be due simply to the small number of species present in a shelterbelt. The number of species existing in a given shelterbelt is so small that random distribution of species might provide similar results. Moreau (1966) and Grant (1966, 1968, 1969) and Simberloff (1970) considered a similar reduction in number of congeneric species which coexist on islands, and Simberloff (1970) presented a simple method for testing the reality of this situation. Cox and Ricklefs (1977) provided a similar method.

Simberloff (1970) and Cox and Ricklefs (1977) concluded that coexistence of congenerics on islands could be explained as random occurrences. However, both studies utilized large source pools. As the source pool increases, the number of congenerics randomly drawn to coexist will decrease. Cox and Ricklefs (1977) used 375 genera as the source pool size in a study of Caribbean island fauna. They indicated there are 205 and 144 genera of birds on Panama and Trinidad, respectively, which represent their continental and large continental island situations, respectively. The continental situation has only slightly more than one-half the number of genera used as the source pool size. Further, all genera do not have the flight capability to fly to an island. Thus the source pool size is probably too large. All species known to have colonized the islands of an archipelago at some point in time would make a more justifiable source pool. One further assumption made by both studies is that congeneric species are highly competitive. The data of Lack (1976) illustrates the divergence in body size, or other competition-reducing characteristics in various congeneric bird species coexisting on islands.

I used Simberloff's (1970) random generation model on the 3 largest shelterbelts studied to reduce the effect of size restriction. For my source pool I utilized all woodland bird species known to have nested in South Dakota and which should be able to utilize shelterbelts for nesting (excluding species which are restricted to riparian areas, for example). Instead of using genera as a criteria of competition, guild classifications were used. The largest belt contained 11 species and met the random criteria ($p > 0.05$). The other 2 belts, with 17 and 18 species respectively, illustrated significantly ($p < 0.05$) more guilds per species than predicted by random distribution.

The data presented illustrating a linear increase in density with area, an upper limit on the total number of species in a community not set by a minimum size restrictions, an increase in territory size with number of coexisting species, and selection for divergence of resource partitioning all support the contention that diffuse competition is an operative factor affecting community bird species composition and restriction of total numbers which can coexist. Terborgh and Weske (1975) documented the existence of diffuse competition in restricting elevational presence of several bird species. Diamond (1975) documented the existence of diffuse competition in restricting the presence of some bird species by particular combinations of other species in several different archipelagos, causing a checkerboard distribution pattern. The checkerboard pattern has also been reported by Lack (1971, 1972, 1976), and MacArthur et al. (1972). One of the approaches to documenting diffuse competition is correlation of the variance in incidence, niche, or abundance of a given species with variation in total number of species (Diamond 1975:345). The data I presented in Table 5 illustrated the higher correlation with species numbers than with area exhibited by many species. Thus the concept that diffuse competition modifies the community bird species composition and sets an upper limit to the total number present is a reasonable explanation.

Species-area models

Schoener (1976) and Diamond and Mayr (1976) placed heavy emphasis on the ecological evaluation of dlog S/dlog A, where S is the equilibrial number of species and A is the island area, for analyzing differences in the species-area relationship among archipelagos. The species-area relationship has been documented as a curvilinear relationship and has had either an exponential (exp (S) = A) or a power ($S = CA^z$, where $z = \mathrm{dlog}\ S/\mathrm{dlog}\ A$) function ascribed to it (Preston 1962a,b, Hamilton et al. 1964, Kilburn 1966, MacArthur and Wilson 1967).

Preston (1948, 1962a,b), May (1975), and Diamond and Mayr (1976) postulate that if the islands under study are considered isolated universes with large or heterogeneous species assemblies with independent niche requirements then statistical rules predict that the species-abundance relations should approximate a lognormal distribution. Further, when density increases proportionally with area, the species-area relationship should be a power function with a slope between 0.15-0.39. If the relationships are constructed for a nested series of sample areas on a single land mass or for a community which is dominated by some single factor and division of this niche volume proceeds in a strongly hierarchical fashion with successive species pre-empting successive fractions of the niche volume, the species-abundance relation is predicted to be logseries (May 1975:83) and the form of the species-area relations should follow an exponential function with a lower slope than for isolated universes (Preston 1962a,b, May 1975, Diamond and Mayr 1976). If, on the other hand, the limited resource is divided evenly among a taxonomically homogeneous set of species then MacArthur's (1957, 1960) "broken-stick" distribution is predicted, with a species-area slope steeper than for isolated universes (May 1975).

My data appear to approximate the lognormal distribution (Table 7). Shelterbelts are not isolated universes, or a nested set of sample areas, or comprised of a taxonomically homogeneous set of species. I have postulated that there is I major limiting factor, food, the division of which cannot be even among species due to the different energetic requirements of the heterogeneous species assemblies. I have illustrated that species tend to be added to the community at a fairly constant rate due to selection for different partitioning strategies. Up to a certain area, most species are represented equally as I pair due to minimum area requirements. Some species increase in density as area continues to increase, while other species are first colonizing due to different minimum size requirements. This differential response results in an increasing divergence in species abundances. At the largest shelterbelt sizes, 2-4 pairs of house wrens and yellowthroats may exist, but minimum area requirements allow only I pair of black-capped chickadees. Further increases in area would continue to meet the requirements of other species for the first time. Thus the lognormal distribution, as compared to the logseries or other distributions, would be enhanced by sampling shelterbelts beyond the largest sizes evaluated in this study. Enhancement of the lognormal distribution would also occur by increasing the number of shelterbelts sampled. An increase in the number of shelterbelts sampled should result in greater separation of the densities of the common species and, at the same time, tend to raise the entire curve, equivalent to shifting the curve to the left, (shifting Preston's

Table 7. Distribution of the number of species among abundance classes arranged in octaves.

ABUNDANCE CLASSES	NUMBER SPECIES
1-2	2 1/2
2-4	2 1/2
4-8	5 1/2
8-16	6
16-32	6 1/2
32-64	6 1/2
64-128	5
128-256	3
256-512	2
512-1024	1
1024-2048	1

(1948)veil line to the right). Thus the lognormal distribution found, and the division of resources postulated, suggests a combination between the isolated universe model and MacArthur's model. The results, illustrating a slope of 0.388, near the upper extreme indicated for power functions, also suggest the relationship may be intermediated in form, yet shelterbelts do not really fit either model definition.

The discrepancy between model definitions found here may be attributed to the propensity that investigators have exhibited in slighting the importance of small islands. The smallest islands have a greater limitation of space (food and habitat) than larger islands. Thus the number of species that can coexist on small islands may be less, due to competitive saturation, than the actual number the source pool can provide. The upper limit on the number of species which can coexist, in comparison to the number the source pool can supply, found for shelterbelts and habitat islands in New Jersey (Galli et al. 1976) of a given size is evidence of competitive saturation. By competitive saturation I refer to the situation where the available food space is saturated by the number of species coexisting. No more species from the existing source pool can be added to the community because the available food space will not support them. Whether the source pool is large enough to saturate the smallest islands (or conversely whether the smallest island is small enough to be saturated by the source pool) and the range of island areas over which saturation can exist are important determinants of the species-area relationship of an archipelago.

Diamond and Mayr (1976) indicate the Solomon archipelago as an exponential species-area relationship. They then calculate the slope for those islands greater than l mi^2 to be 0.087 and concluded that colonization was by highly vagile species. Inclusion of islands less than l mi^2 would have increased the slope. The slope for islands below l mi^2 ($z = 0.385$) indicates a power function very similar to the slope exhibited by shelterbelts. This illustrates that z changes with area (Schoener 1976), a fact that needs further exploration.

Schoener (1976) presented a model for interactive species that predicted the slope of the species-area relationship should never exceed 0.5. Since the assumption that no more species can be added to the community is implicit in the definition of competitive saturation, then z should be maximized and approach 0.5 for these communities. The slopes for shelterbelts and for islands of the Solomon archipelago under l mi^2 are approximately 0.4, which is approaching 0.5. The slope of habitat islands studied by Galli et al. (1976) is actually set at 0.5 (square root function). Re-evaluation of Galli's (1975) data through regression found the slope ($z = 0.395$) to be similar to that found for shelterbelts and the small islands of the Solomon archipelago. However, if Galli's (1975) data from the 8 censuses at each plot size are averaged to reduce sampling variance, regression produces a slope ($z = 0.516$) very close to the square root function used by Galli et al. (1976). The biological validity of such averaging is questionnable, but the tendency of the slope to approach 0.5 is documented.

Evaluation of the relationship of area of shelterbelts and the 3 primary food habits groups can explain why the slope of the species-area curve does not actually reach 0.5. Granivores and some omnivores feed outside of the shelterbelt. Food space is not as restrictive as it is for species which rely on food inside the belt. The low and intermediate number of source species of granivores and omnivores, respectively, coupled with the low and intermediate tendencies of these 2 groups to rely on food within the belt explains the low (z = 0.171) and intermediate (z = 0.376) slopes.

Insectivores tend to be territorial and rely on food within the belt. The source number of insectivore species is high enough to result in competitive saturation and the slope (z = 0.526) is indicative of such a situation. Thus the species-area slope does reach 0.5 if just the species that feed within the belt are considered. However, the slope of the species-area relationship for all species in shelterbelts is lower than 0.5 due to the influence of species which feed outside of the belts.

The species source pool size is considerably increased during migration. The proportion and significance of species which feed outside of the belt is reduced. Thus the depressing effect of such species on the slope is reduced and the slope comes much closer to reaching 0.5 (z = 0.483 in 1976). However the species-area slope for insectivores is still only 0.544 even with the much greater source pool size. These data support the postulation that competitive saturation of the smallest belts should result in a constant slope of 0.5 following Schoener's (1976) interactive model.

General model definition

A general model of the species-area curve can be described and used to relate most findings relative to island effects. The general species-area curve begins on the left side by increasing at a constant slope of 0.5. As long as the source pool is large enough to supply competitively different species, the species-area relationship will remain constant at 0.5. The point at which the source pool can no longer keep up at the same rate as area is the point at which the slope begins to decline from 0.5. Continued increases in area leads to continued decreases in the number of competitively different species left in the source pool which have not yet colonized. As a result, larger and larger increases in area are necessary to get equivalent increases in species numbers (the species-area slope is declining faster and faster). Theoretically the area of the islands reach a limit where an increase in area does not elicit an increase in species numbers. Thus at the far right the slope of the general curve becomes 0. Any archipelago is simply a subset of the general curve and where it exists on the general curve depends on the size of the source pool, distance from the source pool immigration and extinction rates, and environmental diversity.

Support for the above general curve is supplied by the species richness-density relationship. I demonstrated earlier that because density increases linearly with area and species richness increases curvilinearly with area, there exists a curvilinear relationship between density and species richness, i.e. density increases at an increasing rate at the upper end of species richness. This relationship was also noted by Diamond (1970b). The point at which density begins to curve upward with species richness is the point at which the species-area relationship begins to depart curvilinearly from a constant relationship. The linear relation between density and area indicates the continually proportional increase in niche space with area. The point at which the slope of the species-area curve starts to depart negatively from a constant z = 0.5 relationship is the point at which the species source pool can no longer keep up with the increase in area with an increase in competitively different species. This is also the point at which the density-richness relationship curves upward indicating the increase in niche space cannot be filled by a new species, so it is instead filled by more individuals of already existing species. The upward curve of the density-richness relationship reflects this increase in density per species at the upper ranges of species richness.

The range of areas over which the z = 0.5 increases in species numbers can exist is dependent on the size of the source pool and the dispersal ability of the species in the pool. Therefore, near archipelagos have a larger source pool than far archipelagos simply because the chance of being found is much greater for near archipelagos, but also because less vagile species will colonize near archipelagos more readily than far. Because the species source pool is effectively larger for near archipelagos, the range of island areas over which the constant relationship exists is extended over that of far archipelagos and moves the archipelago to the left on the general curve in relation to a far archipelago of similar island sizes.

Tropical near archipelagos show a larger z than temperate near archipelagos because tropical archipelagos of similar distance have a larger source pool. Tropical archipelagos are therefore moved to the left relative to temperate archipelagos as tropical archipelagos can continue to add competitively different species over a larger range of island areas. The magnitude of z for an archipelago is therefore much dependent on the smallest islands within it, but it also is dependent on the vagility of these species. If the smallest islands are large enough to allow coexistence of all the species within the archipelago, as may be the case for far archipelagos where the effective source pool is small or archipelagos where the smallest island is large, then z would be small, especially if the species are highly vagile. The entire relationship would fit in the right-most part of the general curve, where z is low and approaching zero, as Diamond and Mayr (1976) found for islands greater than 1 mi^2 of the Solomon archipelago. If the smaller islands are included, z increases because the range of areas is increased toward the left side of the general curve.

There is a decrease in z with isolation because the effective species source pool is decreasing and the vagility of the resident species is increasing. Thus most species in isolated archipelagos can competitively coexist due to the low number of coexisting species present allowing horizontal separation and niche divergences. Thus the species-area relationship starts farther and farther to the right as similar sized archipelagos become more and more isolated. The farther to the right the curve is analyzed, the smaller the differences that exist due to the slope approaching zero. On the other hand, study of the left side of the curve illustrates maximum differences as the slope of small islands demonstrates whether the source pool is large enough to saturate the smallest island (z is high) or if the smallest island can support nearly equal numbers of species as the larger islands (z is low).

Schoener (1976:638) illustrated that z is larger for archipelagos where the largest island is small (<800 mi^2) than for archipelagos where the largest island is large (>1500 mi^2) and explains this as being due to the proportion of unestablished species immigrating per unit time decreasing with area. I suggest it is also due to the above explanation that archipelagos made up of small islands have greater competitive interactions which increases z. Archipelagos with large islands include a larger range of areas, which lowers z, but in addition, large islands can support most of the immigrating species, thereby enhancing a decrease in the slope.

Another factor modifying the position of an archipelago on the general curve is the environmental diversity of that archipelago. As the diversity of habitat increases, the number of species which can coexist increases due to the increase in number of realized niches. In shelterbelt islands having relatively homogeneous vegetation, selection is for species which are ecologically isolated from each through foraging means because differences in habitat are not available. The small number of congeners found by Grant (1965) might also be attributed to this fact as he noted the habitat of the Tres Marias Islands is fairly uniform. As habitat diversity increases, I would expect an increase in number of congeners and species which forage similarly, as they can isolate themselves through habitat differences. Thus area would be expected to be the best predictor of species numbers on islands with uniform habitat while both area and habitat diversity would be expected to be good predictors of the number of species of birds on islands with high habitat diversity. Increased habitat diversity increases the number of realized niches thereby moving an archipelago to the right on the general curve.

Increasing endemism would also be expected with increasing habitat diversity. Endemism has been noted as increasing with isolation (Diamond 1975). The ratio of realized to utilized niches would increase with archipelago isolation due to a decreasing number of species colonizing. Thus there is increased niche space available for divergence of species in increasingly isolated archipelagos, allowing evolution of endemic forms. Since increased habitat diversity also increases the number of realized niches, increasing habitat diversity interacts with increasing isolation to result in increasing endemism.

Saturation can occur on small islands in an archipelago. Small islands are important in determining the actual form of the species-area relationship for an archipelago because of this potential for saturation. The range of island areas that can continue to be saturated is dependent on the effective source pool size. The range of island areas that allows continuation of saturation is also dependent on the number of realized niches available. The number of realized niches would increase with increased environmental diversity, thus decreasing the sizes at which saturation can be reached.

Section 6

COMPETITION AND TERRITORY SIZE IN HABITAT ISLANDS

Decreasing island area is often accompanied by increasing density of birds per unit area (Diamond 1970a,b, 1973, Crowell 1962, Grant 1966, MacArthur et al. 1972, Nilsson 1977). Such density compensation also implies increasing territory size with island area. Nesting of bird species on islands smaller than the normal territory sizes of those species on the mainland and increasing territory size with increasing island area has been documented (Beer et al. 1956, Schnell 1963, Cody and Cody 1972, Yeaton and Cody 1974, Nilsson 1977). Decreasing territory size (increasing density compensation) with decreasing island area has been attributed to competitive release (Yeaton and Cody 1974, Nilsson 1977). Smaller islands have fewer coexisting species, and a greater range of microhabitats may be available for exploitation by the species on small islands due to the absence of species with similar foraging strategies. An expansion in the foraging height of bird species on islands has been documented (Yeaton 1974, MacArthur et al. 1972). An expansion in number of microhabitats exploited increases the effective food supply and thus allows a decrease in territory size. Yeaton and Cody (1974) presented a strong correlation between increasing species numbers and the territory size of song sparrows.

Increasing numbers of coexisting species leads to increasing restriction of each species to the microhabitat for which each is best adapted (MacArthur and Wilson 1967, MacArthur 1972, Hespenheide 1975). However, prey selection should remain diverse within the microhabitat

(MacArthur 1972, Hespenheide 1975). Maintenance of diverse prey selection leads to overlap in food consumed among species. This overlap logically increases with increasing similarity of species. Thus, such overlaps may also result in compensatory increases in territory size.

RESULTS AND DISCUSSION

Diversity and density of birds utilizing shelterbelts in eastern South Dakota were determined by censusing 69 shelterbelts in 1976 and 1977. These censuses indicated that yellowthroats and house wrens, 2 species of similar size and foraging ecology, did not coexist in small belts but did coexist in large shelterbelts (Table 6). House wrens did not occur in belts smaller than 2264 m^2, and yellowthroats required a minimum size of 3004 m^2 for residence. Coexistence occurred when shelterbelt size of 9895 m^2 was attained and was accomplished through horizontal separation. The smallest shelterbelt in which the 2 species coexisted, 14, was the widest of the 69 belts censused. The house wren pair was located near the southern boundary and toward the western edge. The yellowthroat pair was observed to the north and near the eastern edge of the belt. House wrens and yellowthroats had horizontal separation in shelterbelt 40 where pairs were established at opposite ends of the belt. The smallest belt in which spatial overlap probably occurred was belt 25 that was 14,028 m^2 in area.

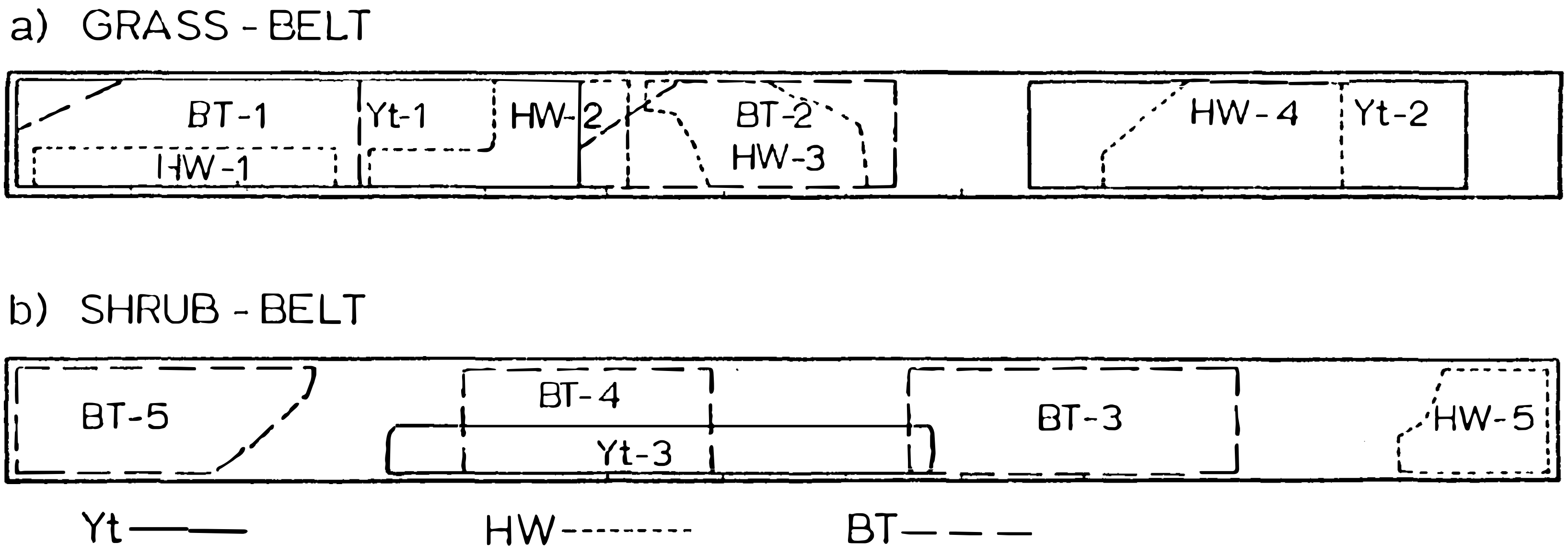
Territories of house wrens, yellowthroats, and brown thrashers were mapped in 2 large shelterbelts in 1977. Mapping was accomplished from 24 May to 18 June. The shelterbelts were visited daily, weather permitting, for 1 to 4 hours starting at sunrise. The 2 shelterbelts were of equal size (24,329 m^2) and overstory composition but differed in understory. One belt (Fig. 15a) had a grass understory resulting from grazing, while the other belt (Fig. 15b) had a thick, shrub understory. The grass-belt contained 17 bird species while the shrub-belt had only 13. Further, the grass-belt has several pairs of house wrens and yellowthroats, while the shrub-belt had 1 of each. Thus spatial overlap between house wrens and yellowthroats occurred only in the grass-belt.

Territories mapped in these large belts were larger than the area of the smallest belts inhabited by house wrens (2264 m^2), yellowthroats (3004 m^2), and brown thrashers (3004 m^2). The brown thrasher was found in 2 belts smaller than 3004 m^2 (Table 6), but in both cases another shelterbelt was nearby and could have been used in conjunction with each of the censused belts. The minimum size, 3004 m^2, indicated for the brown thrasher represents the smallest, isolated shelterbelt inhabited.

Kendiegh (1941) indicated the average territory size of house wrens to be approximately 4350 m^2 in unrestricted woodland communities. The mapped territories of house wrens in the 2 shelterbelts were similar in size to that reported by Kendeigh (1941) (Table 8), with the exception of HW-5. Stewart (1953) documented yellowthroat territories to average 5652 m^2. All 3 yellowthroat territories mapped in the shelterbelts were larger than 5652 m^2.

The territory of Yt-1 does not spatially overlap the territory of any house wrens. The territory of Yt-3 overlaps 1 house wren territory and the territory of Yt-2 overlaps 2 house wren territories (Fig. 15). The size of the yellowthroat territories increases with increasing numbers of overlapping house wren territories. If birds maintain

Figure 15. Territories of yellowthroats (Yt), house wrens (HW), and brown thrashers (Bt) mapped in 2 shelterbelts of equal size and overstory composition. One belt, a) has a heavy grass understory. The other belt, b) has a thick shrub understory.


a) GRASS - BELT
BT-1
HW-1
Yt-1
HW-2
BT-2
HW-3
HW-4
Yt-2
b) SHRUB - BELT
BT-5
BT-4
Yt-3
BT-3
HW-5
Yt
HW
BT

diverse prey selection, as MacArthur (1972) and Hespenheide (1975) postulate, then some overlap in prey types taken is expected among bird species. This overlap should increase with increasing similarity between species and leads to the prediction that territory size would be expanded when similar species coexist. Yellowthroats appear to fit this postulation as they demonstrated a constant increase in territory size with increasing numbers of house wrens spatially overlapping. House wrens, on the other hand, do not show as clear a relationship. The territory of HW-5 is not overlapping the territories of any yellowthroats, and this territory is the smallest of the mapped house wren territories. The territory of HW-3, which also does not appear to overlap with yellowthroats, is similar in size to HW-1 which does exhibit spatial overlap with a yellowthroat pair (Yt-1). Both of these house wren territories are smaller than the territories of the other 2 house wrens which spatially overlap yellowthroat territories. There are at least 2 possible explanations. HW-1 is on the eastern border of the territory of Yt-1, which was not as intensively utilized by Yt-1 as the western half. Also house wrens may be more generalized in their foraging than yellowthroats. In this case, house wrens would overlap the food habits of yellowthroats more than the converse.

Field observations indicated that yellowthroats forage mainly through foliage gleaning off leaves of shrubs and grasses and by hawking among the grasses. House wrens were observed gleaning mainly off the bark of trunks and branches, but occasionally foliage gleaning. The foliage gleaning habit of house wrens suggests that house wrens overlap the food habits of the yellowthroat more than the converse.

Table 8. Territory sizes (in m^2) of yellowthroats, house wrens, and brown thrashers in 1 shelterbelt with a grass understory and 1 shelterbelt with a shrub understory.

YELLOWTHROAT	SIZE	HOUSE WREN	SIZE	BROWN THRASHER	SIZE
GRASS UNDERSTORY					
Yt-1	9865	HW-1	3752	BT-1	5160
Yt-2	6992	HW-2	4202	BT-2	5374
		HW-3	3693		
		HW-4	3914		
SHRUB UNDERSTORY					
Yt-3	6536	HW-5	2860	BT-3	5232
				BT-4	4463
				BT-5	4818

The differences in territory size between house wrens and yellowthroats may also be due to differences in habitat preference. The results of Kroodsma (1973) and Whitmore (1977) indicate the house wren prefers a habitat where shrub density is moderate to open and a grass substrate is present. Multiple regression analysis of house wrens in shelterbelts provided similar results (Section 8). The habitat preferences of the yellowthroat are less clear. Stewart (1953:100) found yellowthroats breeding in habitats varying from an "open savana-like type with scattered groups of shrubs or trees from 3 to 15 ft in height to a fairly dense thicket of small woody plants, usually less than 3 ft in height". Kendeigh (1945) suggested yellowthroats prefer areas of dense, low vegetation. Yeaton and Cody (1974) also suggested yellowthroats prefer habitats with dense vegetation at the 0 - 2 ft level. I detected separation (Section 8) for some habitat characteristics, but overlap in others between house wrens and yellowthroats. The lack of spatial overlap in belts smaller than 14,028 m^2 and the large, mapped territory sizes may be partially due to habitat preferences. However the large difference in the territory sizes of the 2 yellowthroat pairs nesting within the same belt (Fig. 15a) indicate that differences in habitat preferences does not offer an adequate explanation.

Diffuse utilization of the food resources and restriction of foraging niche dimensions due to the greater number of coexisting species found in the mapped belts versus the smallest belts inhabited may also explain the large territory sizes. The brown thrasher does not have a close ecological associate in these belts, but the mapped territory sizes were still much larger than the smallest, isolated belt it inhabited.

Yeaton and Cody (1974) and Nilsson (1977) also documented increasing territory sizes with increasing numbers of coexisting species and attributed this compensation to increasing restriction of niche dimensions.

All 3 species studied here demonstrated substantial increases in territory size in more diverse communities as compared to more depauperate communities. The minimum shelterbelt size at which each species first colonizes, (and the actual territory size within this belt could be smaller if the pair did not use the entire belt), was considerably smaller, in all cases, than the mapped territories in communities with a greater number of coexisting species. This supports the contention that an increased number of coexisting species causes decreased niche width and results in a compensatory increase in territory size. The data also suggest that diffuse overlap in food utilization, which increases with increasing ecological similarity of species, leads to decreased available food for a species and results in compensatory increases in territory size as well.

ENVIRONMENTAL INFLUENCES OF AVIAN DIVERSITY AND DENSITY DURING MIGRATORY AND BREEDING SEASONS

INTRODUCTION

The number of species of birds which cohabit an area has been related to the foliage height distribution (MacArthur and MacArthur 1961, MacArthur et al. 1962, MacArthur et al. 1966, Recher 1969, Karr 1971, Karr and Roth 1971), percentage vegetation cover (Karr 1968, Karr and Roth 1971, Willson 1974), foliage volume (Sturman 1968, Balda 1969, 1975, Laudenslayer and Balda 1976, Szaro 1976), and various multivariable measurements of the habitat structural complexity (James 1971, Anderson and Shugart 1974, Whitmore 1975, 1977, Smith 1977). Different species must differ by range, habitat, or feeding ecology to coexist. Since birds coexisting within a given habitat are not separated by range or habitat, they must be separated by differential foraging behavior.

Some of the ways in which differences in foraging behavior can be manifested is through differences in foraging strata (Root 1967, Karr 1971, Willson 1974) and differences in vertical and interior versus exterior foliage zones (Colquhoun and Morley 1943, Hartley 1953, Gibb 1954, MacArthur 1958, Pearson 1971, Edington and Edington 1972). Thus increases in the structural complexity and patchiness (Roth 1976) of a habitat increases the number of ways in which species can partition the habitat space and leads to the prediction of increased species diversity.

Area accounts for approximately 60% of the variation in bird species number in shelterbelts during migration and breeding seasons (see Sections 4,5). Part of the residual variation unexplained by area is due to sampling error, and the remainder can be ascribed to environmental variability of the plots. Delineation of the multivariable set of environmental factors accounting for the variation in species diversity and density can be accomplished through multiple regression analyses. However, the variation in species numbers is confounded by area. An area that is large enough to accommodate twice as many species as a smaller area, but that does not have twice as many, can be assumed to be environmentally inferior to the smaller plot. However, regression analysis assumes the larger plot is actually environmentally superior because it has a greater diversity and density of birds.

By determining the relationship between area and the diversity and density measures, these measures can be predicted for a shelterbelt based on its area. Subtraction of this predicted value from the actual values results in the residual variation, due to sampling error and environmental variability, varying around zero, thus removing the increasing effect due to area. Multiple regression analyses of these transformed values allows delineation of the environmental variables accounting for the residual variation unexplained by area.

The dependent variables used for both seasons included species richness, species diversity, community density, and layer diversity. Species richness is the number of species in the community. Species diversity is the Shannon index (Shannon and Weaver 1963), which is an index of both the number of species and the evenness of distribution of those species. Community density is the number of individuals in a community, and layer diversity is the Shannon diversity based on the proportion of the community density which is in each of the herb, shrub, and tree layers during censuses. Area was the primary factor accounting for variation in the first 3 variables; richness, diversity, and density, and these were transformed by the method described above. Area was not the major determinant of the variation in layer diversity and layer diversity was not transformed.

RESULTS AND DISCUSSION

Approximately 60% of the residual variation of species richness and diversity was explained by environmental variables during both seasons (Tables 9,10). The variables important to species richness and diversity within a season were similar. The similarity may be expected since species richness is the major component of species diversity. The variables important to species richness and diversity are different between seasons. Community density (Table 11) and layer diversity (Table 12) also illustrate significant differences between seasons.

Two variables, presence of tree claims and presence of light grazing, are important for species richness and diversity during both seasons. The negative influence of tree claims on species richness and diversity in both seasons can be attributed to the species-area effect. As area increases, the number of species per unit area decreases. A tree claim bordering a shelterbelt is used by birds in conjunction with the shelterbelt. The shelterbelt is, therefore, a subset of a larger area, and the number of birds for that subset is smaller than if it had been completely isolated.

Table 9. Species richness. Environmental variables, delineated through multiple regression, that cooperatively explain the variance in species richness, and, other environmental variables that are significantly correlated with species richness during spring migration and breeding seasons.

VARIABLE[a]	MULTIPLE R[b]	RSQ[c]	SIMPLE R[d]
BREEDING			
MOWED	0.395	0.116	-0.395
GRLI****	0.493	0.243	0.310
ULPU	0.543	0.295	0.365
TRCLAIM	0.575	0.330	-0.159
LOTA	0.607	0.369	-0.344
CAAR	0.641	0.411	-0.093
GRZ	0.667	0.445	-0.026
WATER	0.692	0.479	-0.050
AGE**	0.721	0.519	0.318
ELAN	0.741	0.549	-0.124
PRAM	0.758	0.574	0.161
WOODY*	0.772	0.596	0.195
OTHER SIGNIFICANT VARIABLES (SIMPLE CORRELATION) VEGDIV (-0.235**) CC (0.251**) TRVOL (0.305***)			
MIGRATION			
AGE	0.428	0.183	0.428
HUMAN****	0.508	0.258	0.262
TRCLAIM	0.583	0.339	-0.192
RSHAR	0.611	0.373	0.128
TOTUND	0.646	0.417	0.210
JUVI	0.685	0.469	-0.189
VEGDIV	0.703	0.501	0.016
NL	0.736	0.541	0.043
GRLI**	0.758	0.575	0.213
OTHER SIGNIFICANT VARIABLES (SIMPLE CORRELATION) TRVOL (0.214*) SHRLHT (0.225*) NTRSPP (0.236**) CC (0.354***)			

Table 10. Species diversity. Environmental variables, delineated through multiple regression, that cooperatively explain the variance in species diversity, and, other environmental variables that are significantly correlated with species diversity during spring migration and breeding seasons.

VARIABLE^a	MULTIPLE R^b	RSQ^c	SIMPLE R^d
BREEDING			
ULPU	0.435	0.189	0.435
TRCLAIM	0.522	0.273	-0.271
GRLI	0.585	0.343	0.282
CAAR	0.639	0.408	-0.159
PRVI****	0.695	0.482	-0.226
JUVI	0.722	0.521	-0.233
ELAN	0.743	0.552	-0.174
NSR	0.759	0.576	0.249
LOTA**	0.779	0.606	-0.254
MORU*	0.791	0.626	0.022
OTHER SIGNIFICANT VARIABLES (SIMPLE CORRELATION) TRVOL (0.220*) VEGDIV (-0.259**) MOWED (-0.321***)			
MIGRATION			
AGE	0.339	0.115	0.339
HUMAN	0.467	0.218	0.312
TRCLAIM	0.542	0.294	-0.188
RPIPO****	0.597	0.357	0.203
CEOC***	0.641	0.411	0.205
VEGDIV	0.674	0.455	0.060
GRLI	0.696	0.485	0.193
RSHAR	0.714	0.509	0.123
SYVU	0.730	0.534	0.136
SHRLHT	0.750	0.562	0.142
NL**	0.769	0.591	0.132
OTHER SIGNIFICANT VARIABLES (SIMPLE CORRELATION) NTRSPP (0.230**) CC (0.239**)			

Table 11. Community density. Environmental variables, delineated through multiple regression, that cooperatively explain the variance in community density, and, other environmental variables that are significantly correlated with community density during spring migration and breeding seasons.

VARIABLE[a]	MULTIPLE R[b]	RSQ[c]	SIMPLE R[d]
BREEDING			
RFRPE	0.396	0.157	-0.396
SHRRHT****	0.499	0.249	0.306
FRPES***	0.555	0.308	-0.216
SHRLHT	0.597	0.356	-0.224
ROADS	0.627	0.394	-0.199
RELAN	0.648	0.420	-0.131
PRPU	0.668	0.446	-0.121
PSME	0.685	0.469	0.131
WATER	0.721	0.520	0.291
RJUVI	0.738	0.545	0.247
RULAM**	0.758	0.575	-0.068
OTHER SIGNIFICANT VARIABLES (SIMPLE CORRELATION)			
MOWED (-0.269**) ULPU (0.305***)			
MIGRATION			
SYVU	0.412	0.169	0.412
GC	0.520	0.270	0.297
SHRRHT****	0.592	0.351	0.290
HUMAN	0.626	0.392	-0.294
UNDSHR	0.660	0.436	-0.135
TNR**	0.684	0.468	0.012
PLDEN	0.700	0.489	0.106
FHT	0.713	0.508	0.056
PODE	0.730	0.533	-0.043
RLOTA	0.744	0.553	-0.043
WATER	0.764	0.584	0.273
RPRVI	0.779	0.606	0.077
RPIPU*	0.795	0.633	-0.251

Table 12. Layer diversity. Environmental variables, delineated through multiple regression, that cooperatively explain the variance in layer diversity, and, other environmental variables that are significantly correlated with layer diversity during spring migration and breeding seasons.

VARIABLE^a	MULTIPLE R^b	RSQ^c	SIMPLE R^d
BREEDING			
TOTUND	0.416	0.173	0.416
MOWED	0.540	0.292	-0.183
AREA	0.600	0.360	0.271
RELAN	0.639	0.408	-0.179
RJUVI	0.684	0.468	-0.273
HUMAN****	0.727	0.529	0.067
PRAM	0.747	0.559	0.282
PSME	0.768	0.589	-0.225
RCEOC	0.780	0.608	0.058
RPRPU	0.792	0.627	0.045
RROPS	0.803	0.645	0.160
NSR	0.813	0.662	0.219
GC	0.824	0.629	0.001
RPIPO	0.833	0.694	-0.153
GRLI*	0.841	0.710	0.126

OTHER SIGNIFICANT VARIABLES (SIMPLE CORRELATION)
FHT (0.267**) SHRLHT (0.274**) NL (0.283**) GRZ (-0.310***)
UNDSHR (0.319***)

VARIABLE^a	MULTIPLE R^b	RSQ^c	SIMPLE R^d
MIGRATION			
AREA	0.503	0.253	0.503
LOTA	0.598	0.358	0.300
LIVESTOCK****	0.657	0.432	0.265
PLDEN***	0.682	0.466	0.250
SHRLHT	0.702	0.493	0.075
PRAM	0.716	0.512	0.339
GRSE	0.727	0.529	-0.030
CANHT	0.738	0.545	0.154
TRCLAIM	0.747	0.559	-0.206
TOTUND	0.759	0.576	0.050
VEGDIV	0.776	0.602	0.420

Table 12. continued.

VARIABLE[a]	MULTIPLE R[b]	RSQ[c]	SIMPLE R[d]
MIGRATION (cont.)			
ACSA	0.790	0.625	0.044
RPRPU	0.805	0.648	0.037
CONVOL	0.813	0.661	0.185
RPRTO	0.822	0.676	-0.207
RELAN	0.830	0.689	0.033
RCEOC	0.844	0.713	0.172
PODE**	0.856	0.733	-0.096

OTHER SIGNIFICANT VARIABLES (SIMPLE CORRELATION)
FRPE (0.236**)

[a] Mnemonics are defined in Appendix J. Asterisks indicate significance levels. $*p<0.100$ $**p<0.050$ $***p<0.010$ $****p<0.005$ All variables listed above any asterisk-marked variables are significant at least at the level the asterisks indicate.

[b] Multiple correlation coefficient.

[c] Coefficient of determination

[d] Simple correlation of dependent variable with the independent variable.

Grazing was registered as the presence - absence of light, medium, or severe grazing, and as a 0-3 cumulative index of light to severe grazing. While light grazing illustrated a positive relationship with diversity and richness in both seasons, the cumulative grazing index illustrated a negative effect on species richness during breeding. The effects of grazing on the diversity and richness of bird species in shelterbelts can be interpreted in terms of the effect of grazing on the structure of the shelterbelt habitat. Increased grazing pressure produces an increasing negative correlation with herb height, shrub row height, number of layers (not counting shrub rows as a shrub layer), and understory density (Table 13).

Light grazing tends to restrict the growth of an understory shrub layer, but seems to stimulate growth of a thick herb layer (pers. obs.). The correlation matrix (Table 13) illustrates a positive correlation between light grazing and both herb height and shrub row height. A slight negative correlation existed between number of layers and light grazing, as would be expected if grazing eliminates the shrub layer. This elimination would also explain the slight negative correlation of light grazing with understory density, as restriction of the shrub layer would decrease understory density at the higher heights of measurement. Medium and severe grazing illustrate much higher negative correlations with all 4 habitat measures, indicating that increasing intense grazing increasingly restricts growth of the herb layer, shrub layer, and shrub rows, and has an overall strong inhibitory effect on the lower 6 feet of the habitat.

The cumulative grazing index illustrates the greatest negative

Table 13. Correlation matrix of the 4 grazing indicies against 4 habitat measures.

	GRLI	GRME	GRSE	GRZ
FHT	0.129	-0.354***	-0.407****	-0.562****
SHRRHT	0.042	-0.125	-0.369***	-0.392****
NL	-0.079	-0.426****	-0.504****	-0.708****
TOTUND	-0.016	-0.314***	-0.282**	-0.439****

* p<.100   **p<.020   ***p<.010   ****p<.001

correlation for the 4 measures. The higher negative correlation of the cumulative measure as compared to severe grazing can be attributed to the cumulative negative effects of both medium and severe grazing. The positive effects of light grazing is overridden in the cumulative index because the existence of light grazing is not as common as more intense grazing. The mean for light grazing (0.015 ± 0.120) indicates it is approximately .14 as common as medium grazing (0.101 ± 0.304) and .20 as common as severe grazing (0.073 ± 0.261). Thus, intense grazing tends to inhibit understory while light grazing leads to stimulation of the herb layer and opening of the middle canopy.

The increase in bird species richness and diversity with light grazing during the breeding season can be credited to the species composition of shelterbelts. The majority of bird species inhabiting shelterbelts is open-foliage species, and the opening of the shrub layer by light grazing enhances the habitat for them. I illustrated in a previous section (Section 6) the decrease in the overall number of coexisting species in a shelterbelt with a heavy shrub understory and a belt without the shrub understory, due to the absence and presence of a grazing history, respectively. Light grazing enhances conditions during breeding season for increased diversity and richness, while more intense grazing, as indicated by the cumulative index, causes a reduction in habitat suitability for species richness during breeding.

The presence of species which prefer open conditions in shelterbelts during breeding can partly be explained by the common practice of intensively grazing of shelterbelts and the resulting paucity of shelterbelts with a shrub understory. Thus establishment of a viable population of bird species which prefer a heavy shrub understory is difficult as there are not enough such habitats available. On the other hand, during migration, species which prefer heavy shrubs pass through the area, and vegetation structural characteristics such as understory density results in increasing ($p<0.025$) migratory species richness (Table 9). The number of layers is positive ($p<0.050$) for both migratory species richness and diversity, and the height of the shrub layer is important in increasing ($p<0.050$) species diversity (Tables 9,10).

The shrub layer has been postulated as being inhibitory during breeding season, and the height of the shrub layer illustrates a significant negative correlation ($p<0.025$) with breeding density, while shrub row height indicates a positive effect ($p<0.005$) during both seasons (Table 11). Herb height also indicates a positive relationship ($p<0.100$) with migratory density. Thus it can be concluded that migrants exhibit preferences for shelterbelts with no grazing, as these shelterbelts provide a shrub layer, but migrants also prefer lightly grazed shelterbelts that have an openness of the shrub rows and a thick herb layer.

The differences in preference between seasons of shelterbelts with no grazing and those that are lightly grazed are illustrated by shelterbelts 48 and 29. These 2 belts are of similar size, approximately 29,000 m^2, but 48 is lightly grazed and 29 is not grazed. A thick shrub layer occurs in 29 but is absent in 48. During migration, these 2 belts had an equal number of species in each year of study, but during breeding, in both years, 48 had 18 species, while 29 had only 11 bird species.

Migrants seem to rely more heavily on readily visable proximate habitat structural cues than do summer residents. The primary environmental factor accounting for variation in both species richness and diversity during migration is age of the shelterbelt (Tables 9,10). Age of the belt is highly correlated with many structural features of shelterbelts: shrub layer height ($r = 0.461$, $p<0.001$), shrub volume ($r = 0.266$, $p<0.050$), tree volume ($r = 0.408$, $p<0.001$), and canopy coverage ($r = 0.461$, $p<0.001$). Age is negatively correlated with mowing ($r = -0.460$, $p<0.001$), and mowing is negatively correlated with herb height ($r = -0.354$, $p<0.010$). Thus age is related to the suitability of all 3 vegetation layers. Age is related to the density of snags ($r = 0.303$, $p<0.010$) that provide nest holes, and correlated with the proximity of water ($r = 0.318$, $p<0.010$). Both nesting holes and water were indicated by MacArthur (1964) as being important additions, along with the structure of a habitat, for influencing the suitability of that habitat.

The importance of structural complexity is continually exhibited in the variables which are significant in explaining the variation in species richness and diversity. In addition to those factors discussed above, vegetation diversity and understory density are significant (Tables 9,10). Vegetation diversity is related to the patchiness of the foliage configuration, and understory density is related to the structure of the understory. Understory density is strongly correlated with herb height ($r = 0.640$, $p<0.001$), but also correlated with the presence of understory shrubs ($r = 0.538$, $p<0.001$) and the height of the shrub layer ($r = 0.536$, $p<0.001$).

Shrub layer height ($r = 0.225$, $p<0.100$), tree volume ($r = 0.214$, $p<0.100$), canopy coverage ($r = 0.354$, $p<0.010$), and the number of tree species ($r = 0.230$, $p<0.100$) are significantly correlated with migratory species diversity. Due to inter-correlations with the other variables which are significant in explaining the variation in species richness and diversity, these variables were dropped from significance by the step-wise procedure of multiple regression. However, their significant correlations with the dependent variables attest to their importance. In fact, canopy coverage exhibits the second largest correlation with species richness, indicating that if age was dropped from the analysis, canopy coverage would be the most important environmental factor explaining variance in species richness.

Habitat structure is similarly important during breeding. Age of the belts, which is important during migration, is also important in explaining increased breeding species richness. Mowing, which eliminates the understory habitat component, has the greatest depressing effect on breeding species richness, while the number of shrub rows has a positive effect on breeding species diversity (Tables 9,10).

Canopy coverage ($r = 0.251$, $p<0.050$) and tree volume ($r = 0.305$, $p<0.010$) are also positively correlated with breeding species richness. Tree volume ($r = 0.220$, $p<0.100$) is positively, while mowing ($r = -0.321$, $p<0.010$) is negatively, correlated with breeding species diversity. Mowing is also negatively correlated with breeding density $r = -0.269$, $p<0.050$). These factors were not significant in explaining variation in the dependent variables due to inter-correlations.

Another variable which did not enter into significance but which is significantly correlated with breeding species richness ($r = -0.235$, $p<0.050$) and diversity ($r = -0.259$, $p<0.050$) is vegetation diversity. The negative relationship with vegetation diversity is believed due to the confounding of vegetation diversity with other variables, and the greater importance of these variables led to the negative correlation found.

Vegetation diversity is significantly correlated with Siberian elm ($r = -0.373$, $p<0.010$), Russian-olive ($r = 0.335$, $p<0.010$), eastern redcedar ($r = 0.211$, $p<0.100$, caragana ($r = 0.201$, $p<0.100$) and tatarian honeysuckle ($r = 0.267$, $p<0.050$). All of the above correlations of vegetation species with vegetation diversity are opposite the correlations of the same species with breeding species richness and diversity.

The negative relationship with vegetation diversity is believed due to the overriding importance of other variables. Vegetation diversity is negatively correlated with the proximity of water ($r = -0.261$, $p\ 0.050$), and proximity to water is an important factor to bird species richness (Table 9) and density (Table 11) in both seasons. Vegetation diversity is also insignificantly associated with mowing ($r = 0.123$, $p>0.100$) and negatively associated with age ($r = -0.178$, $p>0.100$) both of which indicate association with decreased structural complexity. Thus migrants which are positively associated with vegetation diversity select structurally complex shelterbelts, but also key on the readily visable proximate cue of vegetation diversity. Breeding species, which are negatively associated with vegetation diversity, appear to rely on habitat structure and place more emphasis on primary factors such as the proximity of water.

Migrants are also affected by the readily visible cue of the proximity of a human residence (Tables 9,10). Human residences are associated with both water and supplementary food sources. Proximity of human residences is significantly correlated with proximity of water ($r = 0.351$, $p<0.010$), and it is also highly correlated with the proximity of livestock feedlots ($r = 0.495$, $p<0.001$). Livestock feedlots, in turn, are correlated with water ($r = 0.664$, $p<0.001$) and are associated with granivorous food supplies.

One other variable which significantly explained part of the variation in breeding density was the proximity of roads to the study belts. The importance of this factor is probably not direct, but an indirect consequence of the significant counfounding with herb height ($r = 0.345$, $p<0.010$) and tree volume ($r = 0.308$, $p<0.010$). Proximity of roads is insignificantly, positively related ($r = 0.126$, $p>0.100$) with shrub row height, which was entered as a significant variable previous to the proximity of roads. Thus shrub row height and proximity of roads provide measures of all 3 vegetation layers with little redundancy between these 2 factors.

Analysis of the proportion of individuals distributed throughout the 3 vegetation layers (Table 12) further supports the relationships found above. Factors influencing habitat structures including understory density, mowing, number of shrub rows, ground coverage, and light grazing were all important during breeding. Diversity increased with area, and was associated with an increase in number of species utilizing each of the 3 layers. During migration, significant habitat structural factors included shrub layer height, severe grazing, canopy height, understory density, vegetation diversity, and coniferous tree volume.

Proximity of livestock feedlots associated with supplementary food and water was also significant for the layer diversity index during migration.

Vegetation species

The actual and relative densities of all vegetative species were included in the multiple regression analyses because these species represent major components subject to modification. Siberian elm, the most common shelterbelt tree species, was a significant factor during the breeding season for both richness (Table 9) and diversity (Table 10) and was significantly correlated with breeding density ($r = 0.305$, $p<0.010$). Since Siberian elm is the most common shelterbelt tree species, it would be expected that many of the common bird species would be adapted to a habitat structure similar to that provided by Siberian elm. It was illustrated earlier that many of the bird species in shelterbelts tend to be open canopy species. Siberian elm grows in a semi-open canopy as the very low correlations with deciduous tree volume ($r = 0.017$, $p>0.100$) and canopy coverage ($r = -0.014$, $p>0.100$) indicate. Siberian elm branches laterally and provides many suitable nest sites. Of the nests of birds observed, 71.6% (n=88) of the doves, 92.6% (n=27) of the grackles, 88.5% (n=26) of the western kingbirds, 33.3% (n=15) of the brown thrashers, 86.7% (n=15) of the robins, 55.6% (n=9) of the eastern kingbirds, 100% (n=4) of the blue jays, and 66.7% of the orchard orioles were found in Siberian elm, although some bias is introduced due to the ease of observing nests in the open canopy of Siberian elm.

The importance of Siberian elm may also be related to its infestation by insects, most notably the elm leaf beetle (<u>Pyrrhalta</u>

luteola Muller) and spring cankerworms (Paleacrita vernata Peck). The larvae of both of these species are prominent from May to July (Stein and Kennedy 1972) and are therefore available as food to both spring migrants and breeding individuals.

Eastern redcedar was positively significant for breeding diversity, density, and negatively significant for layer diversity, and migratory richness. Many of the shelterbelts planted with eastern redcedar were ungrazed ($r = -0.146$, $p>0.100$) and had a shrub understory ($r = 0.218$, $p<0.100$) with a correlated dense understory ($r = 315$, $p<0.010$). Both factors exhibited negative influences on diversity and richness.

Eastern redcedar is used heavily for nesting by doves and grackles. Multiple regression indicated that the density of eastern redcedar was highly significant ($p<0.001$) in explaining the variance in the density of both bird species. The positive relationship between breeding density and eastern redcedar is related to the abundance of these 2 bird species.

Russian-olive was negatively associated with breeding richness and diversity. Russian-olive was selected for shelterbelt plantings because of its rapid growth even though it tends to be short-lived (Read 1964). The average survival rate of Russian-olive in 384 windbreaks averaging 15 years of age was only 57% (Read 1958). The mean age of shelterbelts in this study was 21.5 years. Most of the Russian-olive observed in the study belts was dead or in a severely decadent condition, thus accounting for the negative relations. The value of Russian-olive as an attractant for birds during its early years has not been determined.

Russian mulberry was a positive influence, while caragana was a negative influence on breeding diversity. Mulberry is a tall shrub and provides a large volume of foliage as the correlation with shrub volume ($r = 0.268$, $p<0.050$) indicates. Caragana also provided a substantial degree of foliage volume ($r = 0.230$, $p<0.050$) due to the dense nature of the foliage. However, its growth form was shorter than mulberry.

The opposite influences of these 2 shrub species may be due partly to the differences in shrub height because the height of the shrub rows has been demonstrated to exhibit a positive influence. Another factor may be the difference in limb structure. Caragana tends to grow in a clump of limbs, all thin and rising from the base of the plant, and providing no forks or lateral branches for nest placement. Species which can weave their nest around vertical branches, such as the yellow warbler, are the only ones that can consistently utilize caragana for nesting. Mulberry grows similarly to a small tree and provides many forks for available nest sites. Further, the foliage of mulberry is spread over a larger area and is therefore less dense than the foliage of the compact caragana.

American plum, similar to mulberry, positively influences breeding richness and provides many forks for potential nesting sites. It was used for nesting by several species (i.e. yellow warbler, brown thrasher, mourning dove, redwing blackbird, American robin, western kingbird). American plum is a medium-tall shrub and thus is correlated with shrub row height ($r = 0.233$, $p<0.050$). Plum also tends to be infested by webworms (Hyphantia cunea Drury). The webworms are used for food by birds, and the webs are used for constructing nests (the sole component of several yellow warbler nests).

Tatarian honeysuckle provides few forks for potential nest placement. However, the negative influence of honeysuckle may be due to the young status of most shelterbelts sampled in which honeysuckle was a component. The strong negative correlation ($r = -0.402$, $p<0.001$) between honeysuckle and age of the belt indicates this relationship. Honeysuckle also was a component in many belts which were mowed ($r = 0.367$, $p<0.010$). Thus both of these confounding factors could be partial causes of the negative relations of honeysuckle and breeding richness and diversity.

Bird species composition changes from migratory to breeding seasons and, as a result, different vegetation species are important in both seasons. One species which illustrates a highly significant positive influence on migratory species diversity is ponderosa pine. The importance of this conifer can be attributed to the migrant bird species which reside and breed in conifer forests farther north.

Hackberry also illustrates a positive effect on migratory diversity, as well as migratory and breeding layer diversity. Hackberry is slower growing but tends to live longer than most other shelterbelt tree species. Hackberry grows a large and well developed crown, as the correlations with tree volume ($r = 0.237$, $p<0.050$) and canopy coverage ($r = 0.211$, $p<0.100$) illustrate. However, hackberry was also highly associated with herb height ($r = 0.425$, $p<0.001$) and shrub row height ($r = 0.283$, $p<0.020$), both of which have been demonstrated as positive influences.

The 2 shrub species significant for migratory richness and diversity, lilac and silver buffaloberry, sucker and tend to form thickets which are used readily by birds for foraging during migration and for breeding.

CONCLUSIONS AND MANAGEMENT ALTERNATIVES

The results support the findings of previous authors that the diversity of bird species is related to the structure of the habitat. The majority of bird species which breed in shelterbelts appears to prefer semi-open foliage conditions. Thus periodic light grazing to eliminate understory shrubs, enhance herb growth, and open up the lower tree canopy, enhances shelterbelt conditions for birds. Overgrazing, however, leads not only to elimination of understory shrubs but also to a reduction in the condition of the herb layer. Further, overgrazing results in compaction of the soil. Trees on the Great Plains characteristically have problems in obtaining sufficient water for survival. Compaction of the soil by livestock intensifies this problem. This is probably the reason for the high negative correlation between grazing and shrub row height ($r = -0.392$, $p<0.001$). Mowing also negatively influences most birds because it eliminates both shrub and herb layers.

While a shrub understory is not preferred, a shrub component, as provided by shrub rows, is conducive to increased bird diversity. Both height and number of shrub rows illustrate positive influences on bird diversity. American plum, common lilac and silver buffaloberry appear especially suitable for migratory and breeding birds in South Dakota. These shrubs sucker, form thickets, and reduce wind. Survival and longevity of these 3 species relative to other shrub species used for windbreaks are favorable (Read 1958).

Russian-olive has been used as a plant species intermediate in height between shrubs and trees. Russian-olive is short-lived and is dead or decadent in many of the shelterbelts studied. Another species of similar size which appears to be utilized more by birds is Russian mulberry. Russian mulberry is recommended as a good replacement for Russian-olive.

Siberian elm appears to be the tree species most utilized by birds common to shelterbelts. The lateral branching and semi-open foliage provide good nesting and foraging sites. Efficient utilization of the limited water is also an essential component of shelterbelt trees. In a recent study on several windbreak tree and shrub species, Woodruff et al. (1976) found that Siberian elm provided the most growth per unit water used in comparison to all other tree species studied.

Hackberry, similar to Siberian elm, tends to branch laterally and also exerts a positive influence on bird diversity. Hackberry would be a good companion species to use with Siberian elm as it tends to grow more slowly and to live longer. The combination of Siberian elm, a rapidly growing species with a short life span, and hackberry, a slower growing and longer lived species, provide the quick return benefit to the farmer for taking land from production and longevity to reduce maintenance and replanting.

Shrub species which sucker and thus form a thicket of many stems are beneficial in wind-and-snow stopping power of shelterbelts in winter, but inclusion of a conifer species greatly facilitates the winter protection of a shelterbelt. Eastern redcedar and ponderosa pine are the common conifer species planted. Ponderosa pine appears more suitable for birds. Eastern redcedar tends to be used extensively by mourning doves, and 2 nuisance species (redwing blackbirds and common grackles). Removal of this plant species may lead to a reduction in nesting by all 3 bird species. Ponderosa pine is important during migration, and the more open conditions it provides relative to eastern redcedar, undoubtedly leads to greater utilization by a wider variety of breeding bird species. Insufficient sample size or confounding of variables makes conclusions hard to reach on other plant species studied.

Other environmental factors that appear to influence bird diversity are proximity of water, proximity of human residence, proximity of other woody cover, and area of the belt. The results indicate placement of belts proximal to both water and human residences enhances them for birds. Proximity of other woody cover illustrated negative influences, but this is related to area of the belt. Area of the belt is a critical factor for many species and is a limiting factor for some of the birds using shelterbelts. Species, such as the black-capped chickadee, require a shelterbelt size which is not often reached. Thus placement of shelterbelts close together and planting of large shelterbelts is critical for presence of some species. Replacement of large, multirow belts with single-row shelterbelts and/or planting of many small shelterbelts would eliminate many species requiring a minimum area and could lead to an overall reduced bird species diversity on the Great Plains.

Section 8

ENVIRONMENTAL INFLUENCES OF BIRD SPECIES BREEDING IN SHELTERBELTS

INTRODUCTION

The purpose of this section is to discuss the environmental factors influencing each of 14 of the bird species common to shelterbelts in eastern South Dakota. Optimization of a habitat for bird communities necessitates consideration of specific requirements of the component bird species in addition to the factors optimizing the overall community diversity. The environmental factors influencing community diversity were considered previously (Section 7). However, knowledge of species requirements allows habitat manipulation to select for, or against, desirable, or undesirable, species. Knowledge also allows appraisal of availability of nest cavities or other potential limiting factors that may not be emphasized in overall analysis of community diversity.

Studies of bird communities have emphasized structural components of the habitat because bird species ecologically isolate themselves from other species by differential partitioning of the foraging stratum (Root 1967, Karr 1971, Willson 1974), and vertical and horizontal spatial differences in the foliage (Colquhoun and Morley 1943, MacArthur 1958, Pearson 1971, 1975, James 1976, Laudenslayer and Balda 1976). Thus measures of the foliage height distribution (MacArthur and MacArthur 1961, MacArthur et al. 1962, MacArthur 1965, Recher 1969), percent vegetation cover (Karr 1968, Karr and Roth 1971, Willson 1974), and foliage volume (Balda 1969, 1975, Laudenslayer and Balda 1976, Szaro 1976) may be used to predict bird species diversity.

Variation in area of the shelterbelts presented a problem in application of multivariant analyses. The presence and density of many of the bird species are dependent on the area of the belt (Section 5). This relationship with area obscures the importance of habitat variables to the bird species, and all plots smaller than the minimum size requirement of a species were dropped from analyses. Thus the differential minimum areas for different species provided varying sample sizes that precluded analyses through principal components or discriminant function methods. Therefore, step-wise, multiple regression analysis was utilized.

Application of regression analysis assumes a habitat with a greater density for a given species to be better than another habitat with a lower density for that species. If the difference in densities is directly attributable to differences in area of the 2 habitats, then the larger habitat is not necessarily better. Multiple regression can partially correct for difference in area by ascribing part of the variance in density to area. However, this relationship would only be accurate if density increases as a linear function of area.

Density can not increase in perfect linearity with area because density is a discrete measure and, therefore, must increase in a step-wise manner. Further, density of many of the species appears to increase semi-logarithmically with area. I presented evidence earlier to illustrate that territory size of many birds tends to increase as area increases (Section 6). Thus the density of any I bird species increases curvilinearly with area.

The confounding effect of area was corrected by arranging shelterbelts in order of ascending size. The smallest plot in which I pair of each species resided was delineated as the minimum area required by each species. That plot and all larger plots were divided into sections with each section representing an array of plot sizes for a given density. Thus all plots up to the plot size in which a density of 2 pairs were found represented the first group. All plots up to the size in which 3 pair were found represented the second group. All plots up to the size in which 4 pair were found represented the third group, and the remaining plots represented the fourth group. All plots within a group were then adjusted relative to the density that section was considered large enough to sustain. For example, group 2 represented plots considered large enough to sustain 2 pairs. All plots within a section were adjusted relative to 8 because no species with minimum area requirements exceeded this density. If a plot in this section, 2, had a density of 4 individuals, it was classified as 8. If a plot in this section had 3 individuals, it was considered to have I less individual than the area of the plot could actually sustain. Such a plot was classed as 7. If a plot in this group had only 2 individuals, it was considered to be 2 under the number the plot could sustain based on size restrictions. Such a plot was classed as 6. These transformations were performed for all plots for each species individually. Thus the plots were adjusted relative to each other.

The environmental variables measured exhibit many inter-correlations, as is true of any multivariable data set. In some cases the correlations are coincidental and lead to confounding of variables, and in other cases the correlations represent actual associations between variables. To reduce redundancy in the text, I will first discuss those variables commonly important throughout the species regressions and, inter-correlations of those variables.

RESULTS AND DISCUSSION

Inter-correlations of environmental variables

The habitat features within a given vegetation layer tend to be highly inter-correlated (Table 14). Thus herb height is related to ground coverage. The density of the understory is highly correlated with herb height and shrub layer height. The presence or absence of understory shrubs is correlated with both shrub layer height and understory density. Shrub foliage volume is correlated with shrub layer height and shrub row height. Similarly, tree foliage volume is associated with canopy height and both are correlated with canopy coverage.

The age of the shelterbelt is positively related to the habitat structure, as the correlations between age and shrub layer height, canopy coverage, shrub volume, tree volume and the density of snags indicate. Age of the belt is associated negatively to the number of planted shrub species and positively to the number of tree species. An index of the diversity of the planted tree and shrub species based on Shannon's information theory (Shannon and Weaver 1963) is correlated with the number of shrub ($r = 0.557$, $p<0.001$) and tree ($r = 0.588$, $p<0.001$) species.

The results of the regression analyses (Table 15) illustrate many similarities to other community studies. One difference found was a significant negative relationship between vegetation diversity and orchard

Table 14. Inter-correlations of selected structural habitat features of shelterbelts. Mnemonics are defined in Appendix J.

	HHT	UNDDEN	SHRLHT	AGE	SHRRHT	TRVOL	CANHT
GC	0.325**						
HHT		0.604***					
UNDSHR		0.538***	0.641***				
SHRLHT		0.536***		0.261*			
SHRVOL			0.367**	0.261*	0.494***		
NSHSPP				-0.511***		0.463***	0.257*
CC				0.461***			
TRVOL				0.408***			0.321**
NTRSPP				0.308**			
SNAGS				0.303**			

*p<0.050, **p<0.010, ***p<0.001

Table 15. Environmental variables, delineated through multiple regression, that cooperatively explain the variance in the density of 14 breeding bird species common to shelterbelts, and, other environmental variables that are significantly correlated with these species.

VARIABLE^a	MULTIPLE R^b	RSQ^c	SIMPLE R^e
a) COMMON FLICKER			
NTRSPP****	0.598	0.358	0.598
RELAN	0.647	0.419	-0.229
WATER	0.697	0.486	0.159
RJUVIS	0.713	0.508	-0.125
CULTIVATION	0.731	0.534	0.236
CC	0.747	0.558	0.382
CANHT	0.761	0.579	0.052
SNAG	0.767	0.589	0.336
ULAM**	0.800	0.641	0.443

OTHER SIGNIFICANT VARIABLES (SIMPLE CORRELATION)
NTR (0.299**) FRPE (0.321***) SHRLHT (0.206*)

b) HOUSE WREN			
NTRSPP	0.589	0.347	0.589
FHT	0.660	0.436	0.353
RPRPU****	0.719	0.517	-0.080
RMORU***	0.752	0.566	-0.006
RELAN	0.778	0.605	-0.202
WOODY	0.800	0.640	0.283
GRLI	0.821	0.674	0.080
TRVOL	0.839	0.704	0.295
SHRVOL	0.851	0.725	0.234
AGE	0.866	0.749	0.375
PRAM**	0.880	0.775	-0.082
RPIPO*	0.889	0.790	-0.065

OTHER SIGNIFICANT VARIALBES (SIMPLE CORRELATION)
NTR (0.399****) CC (0.376***) SNAG (0.368***) MOWED (-0.204*)

Table 15. continued.

VARIABLE	MULTIPLE R	RSQ	SIMPLE R
c) ORCHARD ORIOLE			
ROADS****	0.319	0.102	0.319
RULPU***	0.429	0.184	0.251
WOODY	0.493	0.243	-0.247
GC	0.530	0.281	0.238
PRVI	0.573	0.329	0.041
RFRPE	0.607	0.369	-0.284
TOTUND	0.641	0.411	-0.175
GRZ	0.658	0.433	-0.054
CEOC	0.672	0.452	-0.177
CANHT**	0.689	0.475	-0.067
RELAN	0.711	0.506	-0.191
RJUVIS	0.728	0.531	0.014
RSHAR	0.742	0.551	-0.098
SHRRHT	0.757	0.573	0.112
CC	0.770	0.593	-0.075
JUVI*	0.784	0.614	-0.110

OTHER SIGNIFICANT VARIABLES (SIMPLE CORRELATION)
UNDSHR (-0.256**) VEGDIV (-0.244**) WATER (0.206*)

Table 15. continued.

VARIABLE[a]	MULTIPLE R	RSQ	SIMPLE R
d) WESTERN KINGBIRD			
VEGDIV	0.519	0.269	-0.519
SHRLHT	0.595	0.354	-0.237
CULTIVATION	0.652	0.425	-0.241
NTR****	0.691	0.477	-0.243
RLOTA***	0.737	0.543	-0.391
RJUVI**	0.763	0.582	0.114
RSYVU	0.777	0.603	0.051
MOWED	0.788	0.621	-0.193
RCEOC	0.800	0.641	-0.232
FHT	0.808	0.654	0.272
ULPU	0.818	0.670	0.058
PASTURE	0.828	0.686	0.135
RSHAR	0.838	0.702	0.026
RPRAR	0.844	0.713	-0.096
GRME	0.850	0.723	-0.335
CC	0.856	0.732	-0.156
GC	0.864	0.746	0.191
NSHSPP	0.867	0.752	0.236
NSR	0.879	0.773	0.121
PRAM*	0.890	0.792	0.038

OTHER SIGNIFICANT VARIABLES (SIMPLE CORRELATION)
GRZ (-0.330***) SHRRHT (0.231**)

Table 15. continued.

VARIABLE[a]	MULTIPLE R[b]	RSQ[c]	SIMPLE R[d]
e) BROWN THRASHER			
NTRSPP	0.292	0.085	-0.292
WOODY	0.410	0.168	-0.239
TOTUND***	0.513	0.263	-0.252
RULPU	0.572	0.327	0.197
LIVESTOCK	0.610	0.372	0.197
RELAN**	0.646	0.418	-0.184
RCAAR	0.672	0.452	0.142
RFRPE	0.687	0.472	-0.262
NSHSPP	0.706	0.499	0.135
GRZ	0.726	0.527	-0.074
FHT*	0.751	0.564	0.228

OTHER SIGNIFICANT VARIABLES (SIMPLE CORRELATION)
RCEOC (-0.253**) CANHT (-0.240**)

f) EASTERN KINGBIRD			
UNDSHR****	0.340	0.116	-0.340
RPRTO***	0.418	0.175	0.238
RULPU	0.489	0.239	0.279
LIVESTOCK	0.527	0.277	0.225
GC	0.562	0.316	0.198
SNAG**	0.592	0.351	-0.100
RELAN	0.611	0.373	-0.087
VEGDIV	0.627	0.394	0.030
RPODE	0.642	0.412	-0.176
NTR	0.650	0.432	-0.105
LOTA	0.670	0.449	-0.061
GRLI*	0.686	0.470	0.021

OTHER SIGNIFICANT VARIABLES (SIMPLE CORRELATION)
SHRLHT (-0.311***)

Table 15. continued.

VARIABLE[a]	MULTIPLE R[b]	RSQ[c]	SIMPLE R[d]
g) YELLOWTHROAT			
ROADS	0.419	0.175	0.419
UNDSHR****	0.537	0.289	-0.389
RROPS***	0.612	0.375	0.246
SHRRHT	0.656	0.430	0.127
RJUVI**	0.688	0.473	0.255
RSYVU	0.714	0.510	0.249
RSAAL	0.733	0.537	0.110
NTR	0.752	0.565	-0.363
HUMAN	0.770	0.593	0.292
RFRPE*	0.790	0.624	0.002

OTHER SIGNIFICANT VARIABLES (SIMPLE CORRELATION)
AGE (-0.227**) WATER (0.252**)

VARIABLE[a]	MULTIPLE R[b]	RSQ[c]	SIMPLE R[d]
h) SONG SPARROW			
CULTIVATION	0.421	0.177	0.421
ROADS****	0.540	0.292	0.400
ELAN	0.582	0.339	-0.336
LIVESTOCK	0.606	0.367	-0.052
CAAR	0.629	0.395	-0.362
GRLI	0.655	0.429	0.166
HUMAN	0.679	0.461	-0.059
RPRAR**	0.704	0.495	0.166
CANHT	0.717	0.514	-0.007
FHT	0.734	0.539	0.225
RPRPU	0.745	0.556	0.010
ACNE	0.755	0.570	0.071
RJUVI	0.762	0.581	0.036
TRCLAIM	0.771	0.594	-0.017
NSR	0.777	0.603	0.358
VEGDIV	0.792	0.627	-0.069
ULPU*	0.809	0.654	0.140

OTHER SIGNIFICANT VARIABLES (SIMPLE CORRELATION)
TRVOL (0.260**) UNDSHR (-0.254**)

Table 15. continued.

VARIABLE^a	MULTIPLE R^b	RSQ^c	SIMPLE R^d
i) REDWING BLACKBIRD			
PRAM	0.439	0.192	0.439
TOTUND	0.555	0.308	-0.229
GRZ	0.635	0.403	-0.186
TNR****	0.709	0.502	0.105
RSHAR	0.728	0.529	-0.233
FRPE	0.748	0.559	-0.155
GC	0.761	0.578	0.175
AGE**	0.782	0.612	-0.140
TRCLAIM*	0.798	0.638	-0.199

OTHER SIGNIFICANT VARIABLES (SIMPLE CORRELATION)
RULPU (0.315***) NTRSPP (-0.297**) ULAM (-0.279**) NSR (0.264**)
NSHSPP (0.264**) SHRLHT (-0.256**)

j) EASTERN WOOD PEWEE

UNDSHR	0.552	0.305	-0.552
RSYVU****	0.654	0.428	0.319
NTRSPP	0.722	0.521	-0.498
ROADS***	0.779	0.607	0.312
RPRPU	0.796	0.634	0.076
SNAG	0.813	0.661	-0.274
GRZ	0.830	0.689	0.116
NSHSPP**	0.854	0.729	0.176
RPRVI*	0.870	0.756	-0.011

OTHER SIGNIFICANT VARIABLES (SIMPLE CORRELATION)
SHRLHT (-0.332***) RULPU (0.328***) CC (0.304***) RFRPE (-0.296**)
TOTUND (-0.247**)

Table 15. continued.

VARIABLE[a]	MULTIPLE R[b]	RSQ[c]	SIMPLE R[d]
k) COMMON GRACKLE			
SNAG	0.377	0.142	0.377
RJUVIS	0.504	0.254	0.312
ULPU	0.571	0.326	0.242
MOWED****	0.616	0.379	-0.273
SHRRHT	0.648	0.419	0.353
GRME***	0.682	0.465	0.235
RCEOC	0.707	0.500	0.177
PSME	0.727	0.529	0.160
RJUVI	0.740	0.548	0.018
WATER	0.755	0.569	0.225
SHRVOL**	0.778	0.605	0.156
PASTURE	0.788	0.621	0.090
HUMAN	0.802	0.644	0.107
GRSE	0.814	0.663	-0.120
CULTIVATION	0.823	0.677	0.027
ROADS*	0.834	0.695	0.169
OTHER SIGNIFICANT VARIABLES (SIMPLE CORRELATION) NTR (0.322***) TNR (0.264**)			
l) AMERICAN ROBIN			
RJUVI	0.446	0.199	0.446
TRVOL	0.570	0.325	0.363
CULTIVATION	0.625	0.391	0.257
HUMAN****	0.672	0.452	-0.206
TRCLAIM	0.705	0.498	-0.187
SNAG***	0.745	0.554	0.278
RPRAR	0.769	0.591	0.131
RPRTO	0.790	0.625	-0.192
RSAAL**	0.808	0.654	0.217
RELANS	0.824	0.678	0.100
CC	0.838	0.702	0.212
RELAN*	0.849	0.721	-0.147
OTHER SIGNIFICANT VARIABLES (SIMPLE CORRELATION) LIVESTOCK (0.295**)			

Table 15. continued.

VARIABLE [a]	MULTIPLE R[b]	RSQ[c]	SIMPLE R[d]
m) HOUSE SPARROW			
RELAN	0.515	0.265	0.515
HUMAN	0.613	0.376	0.388
RPIPU****	0.663	0.440	0.191
CAAR***	0.693	0.481	0.322
RJUVI	0.718	0.515	0.182
CULTIVATION	0.739	0.545	-0.252
RACNE	0.756	0.571	-0.135
GC	0.777	0.604	-0.200
MOWED	0.793	0.629	-0.144
WATER	0.808	0.652	0.269
CEOC	0.820	0.672	0.124
VEGDIV	0.839	0.704	0.030
SNAG	0.850	0.722	-0.039
TNR	0.860	0.739	0.154
SHRRHT	0.868	0.753	0.284
NSHSPP	0.874	0.765	0.031
CC**	0.889	0.789	0.058
OTHER SIGNIFICANT VARIABLES (SIMPLE CORRELATION) LIVESTOCK (0.295**)			
n) MOURNING DOVE			
SHRRHT	0.296	0.088	0.296
VEGDIV	0.408	0.166	-0.150
RJUVI	0.507	0.258	0.273
UNDSHR****	0.562	0.316	-0.154
RELANS	0.609	0.371	0.232
ELAN	0.649	0.421	-0.202
ACNE	0.676	0.457	0.136
LIVESTOCK	0.698	0.487	0.188
HUMAN	0.721	0.519	0.239
PSME***	0.754	0.569	0.182
WOODY	0.772	0.596	0.013
FRPE**	0.796	0.633	-0.257

Table 15. continued.

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[a] Mnemonics are defined in Appendix J. Asterisks indicate significance levels. *p<0.100 **p<0.050 ***p<0.010 ****p<0.005 All variables listed above any asterisk-marked variables are significant at least at the level the asterisks indicate.

[b] Multiple correlation coefficient.

[c] Coefficient of determination.

[d] Simple correlation of dependent variable with the independent variable.

orioles, western kingbirds, mourning doves, and song sparrows. A significant negative relationship was also found between the number of tree species and redwing blackbirds and brown thrashers. These negative relationships may be explained largely as a result of the inter-correlations between the 2 diversity measures and the density of Siberian elm and green ash. Both vegetation diversity and number of tree species are negatively related to Siberian elm ($r = -0.373$, $p<0.010$; $r = -0.353$, $p<0.010$, respectively) and positively related to green ash ($r = 0.496$, $p<0.001$; $r = 0.412$, p 0.001, respectively). In all cases in which a species exhibits negative associations with vegetation diversity or number of tree species, that species exhibits a positive relationship with Siberian elm, a negative relationship with green ash, or both. Siberian elm is a positive factor for 8 of the 14 bird species (Table 15). The data on bird nests found in shelterbelts (Appendix I) also indicate the importance of Siberian elm as a component of the nesting habitat for several species.

Common flicker and house wren

Two bird species demonstrating a positive relationship with the number of tree species were common flicker (Table 15a) and house wren (Table 15b). The number of tree species was the most important variable in both cases and can be attributed to the high correlation of the number of tree species with snag density ($r = 0.488$, $p<0.001$) and with density of American elm ($r = 0.599$, $p<0.001$). Both birds are cavity nesting species and would be expected to respond to the density of snags. The importance of American elm is similarly related. Originally American elm was commonly planted in shelterbelts. The susceptibility to Dutch Elm disease

(Ceratocystis ulmi) has eliminated planting of this tree species in recently established South Dakota shelterbelts. However, some living and many dead American elm trees still exist in many belts, and American elm is associated with the presence of snags. Snags of American elm provided sufficient girth to provide sites for nest hole construction by common flickers.

Several bird species were negatively related to the density of green ash. The common flicker exhibited a positive relationship that may be attributed to heartrot disease (Fomes fraxinaphilus), commonly afflicting green ash. This disease causes rotting of the heartwood and provides for easy excavation of nest holes by common flickers and other woodpecker species (Conner et al. 1975, Conner et al. 1976).

The reduced longevity of Russian-olive and the negative association with common flickers and house wrens may be due to the reduced longevity of this plant species. The majority of Russian-olive plants present in the study belts were dead or decadent. Many of the dead Russian-olive stems were slightly over 3 inches in diameter and were included in the measure of snag density. The majority of the dead Russian-olives were large enough to be included as snags but were too small for excavation for use as nesting cavities.

The significance of a proximal source of water and cultivated fields (Table 15a) can be explained as supplementary water and food sources. Corn often provides supplemental food for flickers. Common flickers have been observed feeding on insects present on, or within, cornstalks, as well as feeding directly on corn kernels.

The significant effects of canopy height, canopy cover, and shrub layer height (Table 15a) appear to correspond to the results found by Anderson and Shugart (1974:831) who noted common flickers "are found in habitats where there are many large trees and a well-developed canopy and subcanopy." The house wren also appears to prefer the presence of a well-developed canopy and subcanopy. The house wren is correlated with tree volume, canopy cover, and shrub volume (Table 15b). The correlation between house wrens and age of shelterbelts may be due to the significant inter-correlations between age and both snag density and canopy cover.

The positive correlations of house wrens and common flickers with foliage measures imply that as foliage increases, the density of both species increases. This relationship could suggest these 2 species prefer dense foliage conditions. However, the shelterbelts studied in eastern South Dakota never achieved dense conditions due to the plant species utilized and the spacing provided when planted. The mean percent canopy cover (54.42) indicates the openness of the study shelterbelts. Dennis (1969) and Conner and Adkisson (1977) reported that flickers prefer to nest in or near open conditions, but both studies reported the versatility of the flicker in selecting nest sites. Kroodsma (1973) and Whitmore (1977) indicated semi-open canopy cover is preferred by the house wren. These 2 species appear well adapted to the semi-open conditions of shelterbelts. The shelterbelts with the densest foliage are still sufficiently open to be utilized and even preferred by the common flicker and house wren.

One major difference between habitats of house wrens and common flickers is the association of the house wren with the herb layer. Kroodsma (1973) and Whitmore (1977) noted the strong association of house wrens with grasses. My results (Table 15b) illustrate the positive effect of light grazing and negative effect of mowing and support their findings. Light grazing reduces the shrub understory and enhances the grass layer, while mowing eliminates both.

Orchard oriole, western kingbird, brown thrasher, eastern kingbird, and yellowthroat

Orchard orioles, western kingbirds, brown thrashers, eastern kingbirds, and yellowthroats exhibit a similar preference for habitat conditions of low canopy cover and high ground cover with few understory shrubs. The ordinations of James (1971) and Whitmore (1977) also suggest an association of these 5 species in their habitat preferences.

Orchard orioles (Table 15c) and western kingbirds (Table 15d) illustrate significant positive relationships with ground cover and significant negative relationships with canopy cover. Brown thrashers (Table 15e) provide a significant positive relationship with herb height, which is correlated with ground cover, and a negative association with canopy height, which is related to canopy cover. All 3 species illustrate significant negative correlations with development of a shrub understory and its resultant increase in understory density.

The eastern kingbird (Table 15f), characteristic of the above group, exhibits a strong negative relationship with the presence of understory and a positive relationship with ground cover. The correlations of canopy cover with other variables that are negatively associated with the eastern kingbird implies a negative association between canopy cover and eastern kingbirds. Number of tree rows is highly correlated ($r = 0.369$, $p<0.010$) with canopy cover and is negatively related to eastern kingbirds. Siberian elm is frequently used by eastern kingbirds for nesting (Appendix I), partially explaining its positive influence, but it is also negatively related to canopy cover ($r = -0.158$, $p>0.100$) and understory shrubs ($r = -0.139$, $p>0.100$).

The yellowthroat (Table 15g) exhibits a negative relationship with the presence of understory shrubs. The negative influence of canopy cover is implied by the negative associations with number of tree rows and age. The latter 2 factors have been demonstrated to be positively correlated with canopy cover. Proximity of roads is highly correlated with herb height ($r = 0.445$, $p<0.001$).

All 5 species show preference for well developed shrub rows along the outside of the belt. The orchard oriole, yellowthroat, and western kingbird exhibit clear correlations with shrub row height. In addition, the western kingbird exhibits positive relations with the number of shrub species in the shrub rows and the number of shrub rows. These latter 2 variables are highly correlated ($r = 0.846$, $p<0.001$). The brown thrasher also exhibits a preference for a wide diversity of shrub species and correlated number of shrub rows. The number of shrub species is correlated with shrub row height ($r = 0.299$, $p<0.020$).

The eastern kingbird illustrates a positive relationship with vegetation diversity. This may be explained by the high positive correlations of vegetation diversity with number of shrub species ($r = 0.557$, $p<0.001$), shrub row height ($r = 0.303$, $p<0.010$), and number of shrub rows ($r = 0.472$, $p<0.001$).

Song sparrow and redwing blackbird

Whitmore's (1977) principal components ordination indicates 2 other bird species in close association with the yellowthroat; the song sparrow (Table 15h) and redwing blackbird (Table 15i). Current results indicate that the latter 2 species are similar to the previous group of 5 species in their habitat requirements. The song sparrow illustrates strong relationships with the herb layer. It is significantly associated with herb height, proximity of roads which is correlated with herb height, and light grazing which is related to herb height. The song sparrow is negatively related to understory shrubs, although the song sparrow also exhibits positive correlations with the number of shrub rows. It prefers a lower canopy as the negative correlation with canopy height indicates, but the positive correlation with tree volume indicates a preference for a developed canopy.

The redwing blackbird is strongly associated with the development of the shrub rows. The major factor predicting the density of redwings, American plum, is highly correlated with the number of shrub rows ($r = 0.610$, $p<0.001$) and the number of shrub species ($r = 0.318$, $p<0.010$), and both of these factors are also significantly correlated with the redwing blackbird (Table 15i). The association of the redwing blackbird with the total number of rows can be explained on the basis of the correlation of this factor with the number of shrub rows ($r = 0.548$, $p<0.001$), shrub row height ($r = 0.332$, $p<0.010$), and number of shrub species ($r = 0.324$, $p<0.010$). However, the redwing still exhibits negative relationships with the development of the shrub understory, as the significant negative correlations with understory density and shrub layer height indicate. The negative influence of tree claims may be partly ascribed to its association with volunteer shrubs as correlations with shrub layer height ($r = 0.347$, $p<0.010$) and the presence of understory shrubs ($r = 0.276$, $p<0.050$) demonstrate.

The redwing blackbird, closely paralleling the previously discussed group of 5 species, exhibits a positive association with ground cover and a negative association with grazing that reduces the herb layer and ground cover. The significance of green ash may be partly related to the negative relationship of green ash with ground cover ($r = -0.317$, $p<0.010$). Similarly, silver buffaloberry is correlated with mowing ($r = 0.393$, $p<0.001$) and negatively correlated with ground cover ($r = -0.226$, $p<0.050$). The negative association of the redwing with age and understory density may be due to the high correlation of age with canopy cover ($r = 0.461$, $p<0.001$) and understory density with canopy cover ($r = 0.342$, $p<0.001$).

Whitmore (1977) indicates that yellowthroats, redwing blackbirds, and song sparrows are similar in their habitat requirements. This study indicates all 3 do prefer heavy shrub rows, but prefer an open understory. The data of James (1971) indicate the yellowthroat prefers conditions similar to those I describe. However, the data of Whitmore (1977) indicate they prefer a heavy shrub understory. If the redwing blackbird and song sparrow are associated with the yellowthroat, as my data and Whitmore's (1975, 1977) data suggest, then my data suggest the habitat preferences are more similar to those described by James (1971) than the habitat preferences delineated by Whitmore (1977) for Virgin River Valley birds.

Eastern wood pewee

The main factor predicting the presence of the eastern wood pewee (Table 15j) is the absence of understory shrubs. Presence is also significantly, negatively correlated with shrub layer height and understory density. The significant correlations with grazing, which is inversely related to herb height ($r = -0.562$, $p<0.001$), indicate the marked preference for a completely open understory. The significance of canopy cover indicates the preference of eastern wood pewees for a more developed canopy. Further, the significance of the proximity of roads may also be related to the tree crown as it is significantly correlated with tree volume ($r = 0.308$, $p<0.010$). The ordinations of James (1971) supports these results as they indicate the eastern wood pewee prefers open understory conditions but a more developed canopy.

Common grackle, American robin, house sparrow, and mourning dove

James (1971) indicates the common grackle (Table 15k) and American robin (Table 15l) prefer a greater canopy cover than many of the previously discussed species. The significance of tree volume and canopy cover indicates such a situation for the American robin. However, the common grackle illustrates no significant correlations with tree crown measurements, although it is positively related to shrub foliage volume. The importance of snags is due to the habit grackles have of perching and roosting on snags, suggesting they like a slightly more open canopy for this activity.

The house sparrow (Table 15m) shows a slight preference for higher canopy cover, while the mourning dove (Table 15n), like the grackle, exhibits little correlation with tree crown development. The mourning dove, common grackle, and house sparrow exhibit significant, positive relationships with shrub row height. Shrub row height was important to many of the species previously discussed. The mourning dove and most other species exhibit a negative association with the development of a shrub understory. The house sparrow does not follow the pattern of the other species and indicates no such tendencies.

The common grackle is positively related with medium grazing and negatively associated with severe grazing and mowing, suggesting it also prefers an open understory. James (1971) reported that common grackles prefer an open understory.

All 4 species exhibit a significant positive correlation with eastern redcedar and use eastern redcedar for nesting. All 4 indicate significant positive correlations with the proximity of human residences and its associated supplemental food and water. Both house sparrows and common grackles exhibit positive relationships with the proximity of water, as well. However, proximity of water is also highly correlated with the proximity of livestock feedlots and its grain sources. House sparrows, common grackles, and mourning doves show positive associations with the proximity of livestock feedlots.

The common grackle and American robin indicate positive associations while the house sparrow is negatively associated with cultivated fields. Cultivated fields adjacent to the shelterbelt indicate, in most cases, that the belt is a field windbreak. Field windbreaks are utilized less by house sparrows than shelterbelts proximal to human establishments.

CONCLUSIONS

The preferred shelterbelt configuration suggested by the results of this study is one that has a well developed internal grass layer with few or no understory shrubs present, but with well developed shrub rows along the outside edge of the belt. The use of shrubs that sucker along the outside would be beneficial as shrubs provide a dense thicket than can be used by species preferring this life form. The dense shrub row thicket that would develop is preferrable for reducing wind velocity. Development of thick shrub rows adjacent to an open understory with a dense herb layer but with few shrubs allows utilization of the belts by the house wren, yellowthroat, and song sparrow.

Maintenance of the semi-open foliage conditions characteristic of shelterbelts in eastern South Dakota through utilization of spacing strategies and use of open foliage tree species would meet the preferred requirements of most species common to shelterbelts. Siberian elm appears to meet the criteria for an open foliage tree species and is used for nesting by many bird species. Green ash provides easy excavation of nest holes for common flickers and house wrens due to the heartrot (Fomes fraxanaphilus). Open foliage patches and snags in the belts produced by dead and decadent trees provide additional diversity of nesting and foraging sites.

Selection and planting of plant species should be kept as diverse as possible for several reasons. First, a strong correlation between number of vegetation species and bird species has been shown in a number of studies (e.g. James 1971, Power 1972, 1976, Amerson 1975). An increase in number of plant species can increase the patchiness of the vegetation by providing different plant heights and life forms (James 1971) and by supplying a diverse set of substrates and resources to be partitioned by birds (Pearson 1977a). An increase in habitat heterogeneity has been related to increases in bird species diversity (MacArthur et al. 1962, MacArthur and Pianka 1966, Roth 1976, Wiens 1976). Further, the planting of several species allows the possible negative value of 1 species to be offset by the presence of alternative vegetation species for use by birds. For example, by incorporating 1 and only 1 row of green ash, the probability of nest hole sites being available is increased for hole nesting species, but the negative influence green ash exhibits for many bird species is minimized due to the presence of the other tree and shrub species. Also, by incorporating a diverse set of plant species, the possibility of a disease, such as the Dutch Elm disease, destroying an entire shelterbelt is minimized. Finally, different tree species with their different survival rates and longevity supply a more versatile shelterbelt. Plant species that die early can be removed and replaced. The longer-lived species continue to provide protection while the short-lived species are being replaced.

Delineation of the specific requirements of the individual species within the bird community suggest ways for modifying the bird community composition. Removal of eastern redcedar may lead to a reduction in the number of grackles by deleting a preferred nesting site. Retention of snags, which provide available nest hole sites for flickers and house wrens, enhances the probability of these 2 species inhabiting the shelterbelt community.

Total area of the shelterbelt can also influence the bird community composition due to the minimum area requirements of some species (Section 6). Thus species which require a large area, such as blue jays, black-capped chickadees, and black-billed cuckoos, are precluded from nesting the smaller shelterbelts. While area of a shelterbelt may restrict some species, the absolute importance of shelterbelts to birds on the prairies is clearly indicated by the high diversity of migratory (68 spp.) and breeding (44 spp.) birds found in the 69 study belts during the 2 year study. Thus maintenance of established shelterbelts and planting of new shelterbelts planned to include the suggestions presented will maintain the preset diversity of woodland birds on the prairies and may allow an increase in bird species numbers.

LITERATURE CITED

Abbot, I. 1974. Numbers of plant, insect, and land bird species on nineteen remote islands in the Southern Hemisphere. Biol. J. Linn. Soc. 6:143-152.

Amerson, A. B., Jr. 1975. Species richness on the nondisturbed northwestern Hawaiian islands. Ecology 56:435-444.

Anderson, S. H. 1970. Water balance of the Oregon junco. Auk 87: 161-163.

Anderson, S. H., and H. H. Shugart, Jr. 1974. Habitat selection of breeding birds in an east Tennessee deciduous forest. Ecology 55: 828-837.

Atchison, F. D. 1976. Windbreaks for livestock protection in the central Great Plains, p. 101-103. *In* R. W. Tinus (ed.) Proc. symp. shelterbelts on the Great Plains. Great Plains Agric. Council Publ. No. 78.

Austin, G. T. 1970. Breeding birds of desert riparian habitats in southern Nevada. Condor 72:431-436.

Balcomb, R. 1977. The grouping of nocturnal passerine migrants. Auk 94:479-488.

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

_____. 1975. Vegetation structure and breeding bird diversity, p. 59-80. *In* Proc. symp. on manage. of forest and range habitats for non-game birds. USDA Forest Service, GTR WO-1.

Beer, J. R., L. D. Frenzel, and N. Hansen. 1956. Minimum space requirements of some nesting passerine birds. Wilson Bull. 68: 200-209.

Bellrose, F. C. 1971. The distribution of nocturnal migrants in air space. Auk 88:397-424.

Berthold, P. 1975. Migration: control and metabolic physiology, p. 77-128. *In* D. S. Farner and J. R. King (eds.) Avian Biology, Vol. V. Academic Press, New York.

Best, L. B. 1977. Territory quality and mating success in the field sparrow (*Spizella pusilla*). Condor 79:192-204.

Brewster, W. G., J. M. Gates, and L. D. Flake. 1976. Breeding waterfowl populations and their distribution in South Dakota. J. Wildl. Manage. 40:50-59.

Brown, J. L. 1964. The evolution of diversity in avian territorial systems. Wilson Bull. 76:160-169.

Cody, M. L., and C. B. J. Cody. 1972. Territory size, clutch size, and food in populations of wrens. Condor 74:473-477.

Cody, M. L., and H. Walters. 1976. Habitat selection and interspecific interactions among Mediteranean sylviid warblers. Oikos 27:210-238.

Colquhoun, M. K., and A. Morley. 1943. Vertical zonation in woodland bird communities. J. Anim. Ecol. 12:75-81.

Conner, R. N., and C. S. Adkisson. 1977. Principal component analysis of woodpecker nesting habitat. Wilson Bull. 89:122-129.

Conner, R. N., R. G. Hooper, H. S. Crawford, and H. S. Mosby. 1975. Woodpecker nesting habitat in cut and uncut woodlands in Virginia. J. Wildl. Manage. 39:144-150.

Conner, R. N., O. K. Miller, Jr., and C. S. Adkisson. 1976. Woodpecker dependence on trees infected by fungal heart rots. Wilson Bull. 88: 575-581.

Cox, G. W., and R. E. Ricklefs. 1977. Species diversity and ecological release in Caribbean land bird faunas. Oikos 28:113-122.

Crook, J. N. 1965. The adaptive significance of avian social organizations. Symp. Zool. Soc. Lond. 14:181-218.

Crowell, K. L. 1961. The effects of reduced competition in birds. Proc. Natl. Acad. Sci. 47:240-243.

_____. 1962. Reduced interspecific competition among the birds of Bermuda. Ecology 43:75-88.

Dennis, J. V. 1969. The yellow-shafted flicker (*Colaptes auratus*) on Nantucket Island, Massachusetts. Bird-banding 40:290-308.

Diamond, J. M. 1970a. Ecological consequences of island colonization by southwest Pacific birds. I. Types of niche shifts. Proc. Natl. Acad. Sci. 67:529-536.

_____. 1970b. Ecological consequences of island colonization by southwest Pacific birds. II. The effects of species diversity on total population density. Proc. Natl. Acad. Sci. 67:1715-1721.

_____. 1973. Distribution ecology of New Guinea birds. Science 179: 759-769.

_____. 1975. Assembly of species communities, p. 342-444. *In* M. L. Cody and J. M. Diamond (eds.) Ecology and evolution of communities. Harvard Univ. Press, Cambridge, Massachusetts.

Diamond, J. M., and E. Mayr. 1976. Species-area relation for birds of the Solomon Archipelago. Proc. Natl. Acad. Sci. 73:262-266.

Diamond, J. M., M. E. Gilpin, and E. Mayr. 1976. Species-distance relation for birds of the Solomon Archipelago, and the paradox of the great speciators. Proc. Natl. Acad. Sci. 73:2160-2164.

Eastwood, E., and G. C. Rider. 1966. Grouping of nocturnal migrants. Nature 211:1143-1146.

Eaton, S. W. 1953. Wood warblers wintering in Cuba. Wilson Bull. 65: 169-175.

Edington, J. M., and M. A. Edington. 1972. Spatial patterns and habitat partition in the breeding birds of an upland wood. J. Anim. Ecol. 41:331-357.

Emerson, L. 1940. The relation of Nebraska shelterbelt plantings to the state's wildlife. Nebr. Bird Review 8:30.

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

Erickson, M. M. 1938. Territory, annual cycle, and numbers in a population of wren-tits (*Chamaea fasciata*). Univ. Calif. Publ. Zool. 42:247-334.

Fewin, R. J. 1976. Windbreaks for livestock protection in southern Great Plains, p. 104-106. *In* R. W. Tinus (ed.) Proc. symp. shelterbelts on the Great Plains. Great Plains Agric. Council Publ. No. 78.

Ficken, M., and R. W. Ficken. 1966. Notes on mate and habitat selection in the yellow warbler. Wilson Bull. 78:232-233.

Field, N. H. 1971. Use of an eastern South Dakota shelterbelt by nesting birds. S. Dak. Bird Notes 23:43-45.

Frank, A. B., D. G. Harris, and W. O. Willis. 1976. Influence of windbreaks on crop performance and snow management in North Dakota, p. 41-48. *In* R. W. Tinus (ed.) Proc. symp. shelterbelts on the Great Plains. Great Plains Agric. Council Publ. No. 78.

Fretwell, S. D., and H. L. Lucas, Jr. 1969. On territorial behavior and other factors influencing habitat distribution in birds. L. Theoretical development. Acta Biotheor. 19:16-36.

Galli, A. E., C. F. Leck, and R. T. Forman. 1976. Avian distribution patterns in forest islands of different sizes in central New Jersey. Auk 93:356-365.

Gauthreaux, S. A., Jr. 1972. Behavioral responses of migrating birds to daylight and darkness: A radar and direct visual study. Wilson Bull. 84:136-148.

Gibb, J. 1954. Feeding ecology of tits, with notes on treecreeper and goldcrest. Ibis 96:513-543.

_____. 1956. Territory in the genus *Parus*. Ibis 98:420-429.

Giles, R. H. (ed.) 1971. Wildlife management techniques. Wildlife Society. 633p.

Gilpin, M. E., and J. M. Diamond. 1976. Calculation of immigration and extinction curves from the species-area-distance relation. Proc. Natl. Acad. Sci. 73:4130-4134.

Goldsmith, L. 1976. Action needed to discourage removal of trees that shelter cropland in the Great Plains, p. 12-18. *In* R. W. Tinus (ed.) Proc. symp. shelterbelts on the Great Plains. Great Plains Agric. Council Publ. No. 78.

Graber, R. R., and J. W. Graber. 1962. Weight characteristics of birds killed in nocturnal migration. Wilson Bull. 74:74-78.

Grant, P. R. 1965. The adaptive significance of some size trends in island birds. Evolution 19:355-367.

_____. 1966. Ecological compatability of bird species on islands. Amer. Natur. 100:451-462.

_____. 1968. Bill size, body size and the ecological adaptations of bird species to the competitive situations on islands. Syst. Zool. 17:319-333.

_____. 1969. Colonization of islands by ecologically dissimilar species of birds. Can. J. Zool. 47:41-43.

_____. 1971. Variation in the tarsus length of birds in island and mainland regions. Evolution 25:599-614.

Griffith, P. W. 1976. Introduction of the problems, p. 3-7. *In* R. W. Tinus (ed.) Proc. symp. shelterbelts on the Great Plains. Great Plains Agric. Council Publ. No. 78.

Hamilton, R. B., and R. E. Noble. 1975. Plant succession and interactions with fauna, p. 96-114. *In* Proc. symp. on manage. forest and range habitats for non-game birds. USDA Forest Service, GTR WO-1.

Hamilton, T. H., and N. E. Armstrong. 1965. Environmental determination of insular variation in bird species abundance in the Gulf of Guinea. Natur 207:148-151.

Hamilton, T. H., R. H. Barth, and J. Rubinoff. 1964. The environmental control of insular variation in bird species abundance. Proc. Natl. Acad. Sci. 52:132-140.

Harner, R. F., and K. T. Harper. 1976. The role of area, heterogeneity, and favorability in plant species diversity of pinyon-juniper ecosystems. Ecology 57:1254-1263.

Harris, M. P. 1973. The Galapagos aviafauna. Condor 75:265-278.

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

Hebrard, J. J. 1971. The nightly initiation of passerine migration in spring: A direct visual study. Ibis 113:8-18.

Hertz, P. E., J. V. Remsen, Jr., and S. I. Jones. 1976. Ecological complementarity of three sympatric parids in a California oak woodland. Condor 78:307-316.

Hespenheide, H. A. 1975. Prey characteristics and predator niche width, p. 158-180. *In* M. L. Cody and J. M. Diamond (eds.) Ecology and evolution of communities. Harvard Univ. Press, Cambridge, Massachusetts.

Hilden, O. 1965. Habitat selection in birds. Ann. Zool. Fenn. 2:53-75.

Holmes, R. T. 1970. Differences in population density, territoriality, and food supply of dunlin on arctic and subarctic tundra, p. 303-319. *In* A. Watson (ed.) Animal populations in relation to their food resources. Blackwell Sci. Publ. Ltd., Oxford.

Horn, H. S. 1968. The adaptive significance of colonial nesting in the Brewer's blackbird (*Euphagus cyanocephalus*). Ecology 49:682-694.

Howell, T. R. 1952. Natural history and differentiation in the yellow-bellied sapsucker. Condor 54:237-282.

Hussel, D. J. T. 1969. Weight loss of birds during nocturnal migration. Auk 86:75-83.

James, F. C. 1971. Ordinations of habitat relationships among breeding birds. Wilson Bull. 83:215-236.

James, F. C., and H. H. Shugart, Jr. 1970. A quantitative method of habitat description. Aud. Field Notes 24:727-736.

James, R. D. 1976. Foraging behavior and habitat selection of three species of vireos in southern Ontario. Wilson Bull. 88:62-75.

Johnson, N. K. 1975. Controls of number of bird species on montane islands in the Great Basin. Evolution 29:348-357.

Karr, J. R. 1968.. Habitat and avian diversity on strip-mined land in east central Illinois. Condor 70:348-357.

_____. 1971. Structure of avian communities on selected Panama and Illinois habitats. Ecol. Monogr. 41:207-229.

_____. 1975. Production, energy pathways, and community diversity in forest birds, p. 161-176. *In* F. B. Golley and E. Medina (eds.) Tropical ecological systems: Trends in terrestrial and aquatic research. Springer-Verlag, New York.

_____. 1976a. On the relative abundance of migrants from the north temperate zone in tropcial habitats. Wilson Bull. 88:433-458.

_____. 1976b. Within- and between-habitat avian diversity in African and Neotropical lowland habitats. Ecol. Monogr. 46:457-481.

Karr, J. R., and F. C. James. 1975. Eco-morphological configurations and convergent evolution in species and communities, p. 258-291. *In* M. L. Cody and J. M. Diamond (eds.) Ecology and evolution of communities. Harvard Univ. Press, Cambridge, Massachusetts.

Karr, J. R., and R. R. Roth. 1971. Vegetation structure and avian diversity in several new world areas. Amer. Natur. 105:423-435.

Kendeigh, S. C. 1941. Territorial and mating behavior of the house wren. Illinois Biol. Monogr. 18:1-120.

_____. 1944. Measurement of bird populations. Ecol. Mongor. 14:67-106.

Kilburn, P. D. 1966. Analysis of the species-area relation. Ecology 47:831-843.

Klopfer, P. H. 1963. Behavioral aspects of habitat selection: the role of early experience. Wilson Bull. 75:15-22.

Klopfer, P. H., and J. P. Hailman. 1965. Habitat selection in birds. *In* Advances in the study of behavior. Hinde, Leheman, and Shaw (eds.) Academic Press, New York.

Kluijver, H. N. 1951. The population ecology of the great tit, *Parus m. major* L. Ardea 39:1-135.

Kluijver, H. N., and L. Tinbergen. 1953. Territory and the regulation of density in titmice. Arch. Neerl. Zool. 10:265-289.

Krebs, J. R., J. Ryan, and E. L. Charnov. 1974. Hunting by expectation or optimal foraging? A study of patch use by chickadees. Anim. Behav. 22:953-964.

Kroodsma, D. E. 1973. Coexistence of bewick's wrens and house wrens in Oregon. Auk 90:341-352.

Lack, D. 1933. Habitat selection in birds with special reference to the effects of the afforestation in the Breckland avifauna. J. Anim. Ecol. 2:239-263.

_____. 1970. The natural regulation of animal numbers. Oxford Univ. Press, Ely House, London. 633 p.

_____. 1971. Ecological isolation in birds. Harvard Univ. Press, Cambridge, Massachusetts. 404 p.

_____. 1973. The numbers of species of hummingbirds in the West Indies. Evolution 27:326-337.

_____. 1976. Island biology illustrated by the land birds of Jamaica. Univ. of California Press, Berkeley, California. 455 p.

Lack, D., and P. Lack. 1972. Wintering warblers in Jamaica. Living Bird 11:129-153.

Laudenslayer, W. P., and R. P. Balda. 1976. Breeding bird use of pinyon-juniper-ponderosa pine ecotone. Auk 93:571-586.

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

_____. 1972b. Seasonal changes in feeding pressures of fruit- and nectar-eating birds in Panama. Condor 74:54-60.

Lloyd, M., and R. J. Ghelardi. 1964. A table for calculating the 'equitability' component of species diversity. J. Anim. Ecol. 33:217-225.

Lowery, G. H., Jr., and R. J. Newman. 1955. Direct studies of nocturnal bird migration, p. 238-263. *In* A. Wolfson (ed.) Recent studies in avian biology. Univ. Illinois Press, Urbana, Illinois.

Lyles, L. 1976. Wind patterns and soil erosion on the Great Plains, p. 22-30. *In* R. W. Tinus (ed.) Proc. symp. shelterbelts on the Great Plains. Great Plains Agric. Council Publ. No. 78.

MacArthur, R. H. 1957. On the relatie abundance of bird species. Proc. Natl. Acad. Sci. 43:293-295.

_____. 1958. Population ecology of some warblers of northeastern coniferous forests. Ecology 39:599-519.

_____. 1959. On the breeding distribution pattern of North American migrant birds. Auk 76:318-325.

_____. 1964. Environmental factors affecting bird species diversity. Amer. Natur. 98:387-397.

_____. 1965. Patterns of species diversity. Biol. Rev. 40:510-533.

_____. 1972. Geographical ecology - patterns on the distribution of species. Harper and Row Publ., New York.

MacArthur, R. H., and J. W. MacArthur. 1961. On bird species diversity. Ecology 42:594-598.

MacArthur, R. H., and E. R. Pianka. 1966. On optimal use of a patchy environment. Amer. Natur. 100:603-609.

MacArthur, R. H., and E. O. Wilson. 1963. An equilibrium theory of insular zoogeography. Evolution 17:373-387.

MacArthur, R. H., and E. O. Wilson. 1967. The theory of island biogeography. Princeton Univ. Press, Princeton, New Jersey. 203 p.

MacArthur, R. H., J. M. Diamond, and J. R. Karr. 1972. Density compensation in island faundas. Ecology 53:330-342.

MacArthur, R. H., J. W. MacArthur, and J. Preer. 1962. On bird species diversity. II. Prediction of bird census from habitat measurements. Amer. Natur. 96:167-174.

MacArthur, R. H., H. Recher, and M. Cody. 1966. On the relation between habitat selection and species diversity. Amer. Natur. 100: 319-332.

Mawson, J. C., J. W. Thomas, and R. M. DeGraaf. 1973. Progarm HTVOL - The determination of tree crown volume by layers. manuscript. 41 p.

May, R. M. 1975. Patterns of species abundance and diversity, p. 81-120. *In* M. L. Cody and J. M. Diamond (eds.) Ecology and evolution of communities. Harvard Univ. Press, Cambridge, Massachusetts.

Mayr, E., and J. M. Diamond. 1976. Birds on islands in the sky: Origin of the montane avifauna of Northern Melanesia. Proc. Natl. Acad. Sci. 73:1765-1769.

McIntosh, R. R. 1967. An index of diversity and the relation of certain concepts to diversity. Ecology 48:392-404.

Miller, A. H. 1931. Systematic revision and natural history of the American shrikes (*Lanius*). Univ. Calif. Publ. Zool. 38:11-242.

Moreau, R. E. 1966. The bird faunas of African and its islands. Academic Press, New York.

Morse, D. H. 1968. A quantitative study of foraging of male and female spruce-woods warblers. Ecology 49:779-789.

_____. 1971. The insectivorous bird as an adaptive strategy. Ann. Rev. Ecol. Syst. 2:177-200.

Nice, M. M. 1941. The role of territory in bird life. Amer. Midl. Natur. 26:441-487.

_____. 1943. Studies on the life history of the song sparrow. II. Trans. Linn. Soc. New York 8:1-211.

Nilsson, S. G. 1977. Density compensation and competition among birds breeding on small islands in a south Swedish lake. Oikos 28:170-176.

NOAA. 1976. Climatological data. Annual summary of South Dakota. Vol. 81, No. 13. 16 p.

Odum, E. P. 1941. Annual cycle of the black-capped chickadee. Auk 58: 314-333.

Orendurff, C. F. 1940. The relation of the farm shelterbelt to wildlife. Nebr. Bird Rev. 8:1-4.

_____. 1941. The first wildlife inventory of Nebraska shelterbelts. Nebr. Bird Rev. 9:7-8.

Orians, G. H. 1971. Ecological aspects of behavior, p. 531-546. *In* D. S. Farner and J. R. King (eds.) Avian Biology. Vol. I. Academic Press, New York.

Orians, G. H., and M. F. Willson. 1964. Interspecific territories of birds. Ecology 45:736-745.

Parnell, J. F. 1969. Habitat relations of the Parulidae during spring migration. Auk 86:505-521.

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

_____. 1975. The relation of foliage complexity to ecological diversity of three Amazonian bird communities. Condor 77:453-466.

_____. 1977. Ecological relationships of small antbirds in Amazonian bird communities. Auk 94:283-292.

Pitelka, F. A., P. Q. Tomich, and G. W. Treichel. 1955. Ecological relations of jaegars and owls as lemming predators near Barrow, Alaska. Ecol. Monogr. 25:85-117.

Power, D. M. 1971. Warbler ecology: diversity, similarity, and seasonal differences in habitat segregation. Ecology 52:434-443.

_____. 1972. Number of bird species on the California Islands. Evolution 26:451-463.

_____. 1975. Similarity among avifaunas of the Galapagos Islands. Ecology 56:616-626.

_____. 1976. Avifauna richness on the California Channel Islands. Condor 78:394-398.

Preston, R. W. 1948. The commonness, and rarity, of species. Ecology 29:254-283.

_____. 1962a. The canonical distribution of commonness and rarity: part I. Ecology 43:185-215.

_____. 1962b. The canonical distribution of commonness and rarity: part II. Ecology 43:410-432.

Pyke, G. H., H. R. Pulliam, and E. L. Charnov. 1977. Optimal foraging: A selective review of theory and tests. Quart. Rev. Biol. 52: 137-154.

Rand, A. S. 1954. Social feeding behavior of birds. Rieldiana: Zool. 36:1-71.

Rappole, J. H. 1976. A study of evolutionary tactics in populations of solitary avian migrants. Ph.D. Dissertation, Univ. Minnesota. 243 p.

Read, R. A. 1958. The Great Plains shelterbelt in 1954. Nebr. Agric. Expt. Sta. Bull. 441, Great Plains Agric. Council Publ. No. 16.

_____. 1964. Tree windbreaks for the central Great Plains. US Dept. Agric., Agric. Handbook No. 250. 68 p.

Recher, H. 1969. Bird species diversity and habitat diversity in Australia and North America. Amer. Natur. 103:75-80.

Root, R. B. 1967. The niche exploitation pattern of the blue-gray gnatcatcher. Ecol. Monogr. 37:317-350.

Rosenberg, N. J. 1976. Effects of windbreaks on the microclimate, energy balance, and water use efficiency of crops growing on the Great Plains, p. 49-56. *In* R. W. Tinus (ed.) Proc. symp. shelterbelts on the Great Plains. Great Plains Agric. Council Publ. No. 78.

Roth, R. R. 1976. Spatial heterogeneity and bird species diversity. Ecology 57:773-782.

Rotzien, C. L. 1963. A cumulative report on winter bird population studies in eight deciduous shelterbelts of the Red River Valley, North Dakota. Proc. N. Dak. Acad. Sci. 17:19-23.

Schaefer, G. W. 1968. Bird recognition by radar. A study in quantitative radar ornithology. *In* The problems of birds as pests. Academic Press, New York.

Schnell, J. H. 1963. Prairie warbler nests on a 0.6 acre island. Wilson Bull. 75:280-281.

Schoener, T. W. 1968. Sizes of feeding territories among birds. Ecology 49:123-141.

_____. 1971. Theory of feeding strategies. Ann. Rev. Ecol. Syst. 2: 369-404.

_____. 1976. The species-area relation within archipelagos: models and evidence from island land birds. Proc. Intern. Ornith. Congr. 16: 629-642.

Schwartz, P. 1964. The northern waterthrush in Venezuela. Living Bird 3:169-184.

Shannon, C. E., and W. Weaver. 1963. The mathematical theory of communication. Univ. Illinois Press, Urbana. 117 p.

Simberloff, D. S. 1970. Taxonomic diversity of island biotas. Evolution 24:23-47.

Skidmore, E. L. 1976. Barrier-induced microclimate and its influence on growth and yield of winter wheat, p. 57-63. *In* R. W. Tinus (ed.) Proc. symp. shelterbelts on the Great Plains. Great Plains Agric. Council Publ. No. 78.

Smith, K. G. 1977. Distribution of summer birds along a forest moisture gradient in an Ozark watershed. Ecology 58:810-819.

Steele, R. G. D., and J. H. Torrie. 1960. Principles and procedures of statistics. McGraw-Hill, New York. 481 p.

Stein, J. D., and P. C. Kennedy. 1972. Key to shelterbelt insects in the northern Great Plains. USDA Forest Serv. Res. Pap. RM-85. 153 p.

Stenger, J. 1958. Food habits and available food of ovenbirds in relation to territory size. Auk 75:335-346.

Stenger, J., and J. B. Falls. 1959. The utilized territory of the ovenbird. Wilson Bull. 71:125-140.

Stewart, R. E. 1953. A life history study of the yellowthroat. Wilson Bull. 65:99-123.

Sturman, W. A. 1968. Description and analysis of breeding habitats of the chickadees, *Parus atricapillus* and *Parus rufescens*. Ecology 49:418-431.

Svardson, G. 1949. Competition and habitat selection in birds. Oikos 1:157-174.

Szaro, R. C. 1976. Population densities, habitat selection, and foliage use by birds of selected ponderosa pine forest areas in the Beaver Creek Watershed, Arizona. Ph.D. Diss., Northern Ariz. Univ., Flagstaff, Arizona. 264 p.

Terborgh, J. 1971. Distribution on environmental gradients: theory and a preliminary interpretation of distributional patterns in the avifauna of the Cordillera Vilcamba, Peru. Ecology 52:23-40.

Terborgh, J., and J. S. Weske. 1975. The role of competition in the distribution of Andean birds. Ecology 56:562-576.

Thomas, J. W., R. M. DeGraff, and J. C. Mawson. 1973. Determination of habitat requirements for birds in suburban areas. USDA Conserv. Res. Rep. 79 p.

Tompa, F. S. 1962. Territorial behavior: the main controlling factor of a local song sparrow population. Auk 79:687-698.

_____. 1964. Factors determining the numbers of song sparrows *Melospiza melodia* (Wilson), on Mandarte Island, B. C., Canada. Acta. Zool. Fenn. 109:1-68.

Verner, J. 1975. Avian behavior and habitat management, p. 39-58. *In* Proc. symp. on manage. of forest and range habitats for non-game birds. USDA Forest Service, GTR WO-1.

Vuilleumier, F. 1970. Insular biogeography in continental regions. I. The northern Andes of South America. Amer. Natur. 104:373-388.

Walker, R. E., and J. F. Suedkamp. 1977. Status of shelterbelts in South Dakota. South Dakota Dept. Game, Fish, and Parks Publ. 29 p.

Welty, J. C. 1975. The life of birds. W. B. Saunders, Philadelphia. 546 p.

Whitmore, R. C. 1975. Habitat ordination of passerine birds of the Virgin River Valley, southwestern Utah. Wilson Bull. 87:65-74.

_____. 1977. Habitat partitioning in a community of passerine birds. Wilson Bull. 89:253-265.

Wiens, J. A. 1976. Population responses to patchy environments. Ann. Rev. Ecol. Syst. 7:81-120.

Williams, A. B. 1936. The composition and dynamics of a beech-maple climax community. Ecol. Monogr. 6:317-408.

Williamson, K. 1964. Bird census work on woodland. Bird Study 11:1-22.

Willis, E. O. 1966. The role of migrant birds at swarms of army ants. Living Bird 5:187-231.

Willson, M. F. 1974. Avian community organization and habitat structure. Ecology 55:1017-1029.

Woodruff, N. P., J. D. Dickerson, E. E. Banbury, A. B. Erhart, and M. C. Lundquist. 1976. Selected trees and shrubs evaluated for single-row windbreaks in the central Great Plains. USDA, Agric. Res. Serv. NC-37. 15 p.

Yeaton, R. I. 1974. An ecological analysis of chaparral and pine forest bird communities on Santa Cruz Island and mainland California. Ecology 55:959-973.

Yeaton, R. I., and M. L. Cody. 1974. Competitive release in island song sparrow populations. Theor. Pop. Biol. 5:42-50.

Zimmerman, J. L. 1971. The territory and its density-dependent effect in *Spiza americana*. Auk 88:591-612.

Appendix A. Questionnaire mailed to landowners.

QUESTIONNAIRE

County

1. Do you have any shelterbelt or windbreak plantings on the property described in the attached letter? Yes_____ No______
2. If so, will you allow my representatives to enter and study these belts during late December, middle May, and early July, for the purpose of gathering research data only? Yes_____ No______
3. Do you wish them to contact you before they enter? Yes_____ No_____
4. Location of residence where you may be contacted (legal description if possible please):____.
5. Telephone number:__________________
6. When was the belt or belts planted?_______________
7. Was the belt cultivated when planted? Yes______ No______ How many years?____________
8. Has the belt ever been grazed? Yes_____ No______ How many years?_________ How many months out of the year?__________
9. Do you wish a final report from the project? Yes______ No_______
10. Your name and mailing address:

____

____

____

Appendix B. Common and scientific names, food habits classification, and the number of plots in which the bird species censused during 1976 and 1977 spring migration seasons were found.

COMMON NAME	SCIENTIFIC NAME	F[a]	TOTAL	1976	1977
Common grackle	*Quiscalus quiscula*	G	129	64	65
Mourning dove	*Zenaidura macroura*	G	118	51	67
American robin	*Turdus migratorius*	O	113	56	57
Brown thrasher	*Toxostoma rufum*	I	93	51	42
House sparrow	*Passer domesticus*	O	82	38	44
American goldfinch	*Carduelis tristis*	G	60	31	29
Western kingbird	*Tyrannus verticalis*	I	58	28	30
House wren	*Troglodytes aedon*	I	52	28	24
Empidonax flycatchers	*Empidonax spp.*	I	52	34	18
Orchard oriole	*Icterus spurius*	I	46	22	24
Clay-colored sparrow	*Spizella pallida*	G	45	29	16
Chipping sparrow	*Spizella passerina*	O	44	21	23
Swainson's thrush	*Catharus ustulata*	I	44	29	15
Redwing blackbird	*Agelaius phoeniceus*	O	39	22	17
Eastern kingbird	*Tyrannus tyrannus*	I	37	24	13
Yellow warbler	*Dendroica petechia*	I	37	20	17
Brown-headed cowbird	*Molothrus ater*	O	34	17	17
Song sparrow	*Melospiza melodia*	O	33	16	17
Yellowthroat	*Geothlypis trichas*	I	32	18	14
Blue jay	*Cyanocitta cristata*	O	27	14	13
Common flicker	*Colaptes auratus*	I	27	19	8
Tennessee warbler	*Vermivora peregrina*	I	26	15	11
Northern oriole	*Icterus galbula*	I	20	15	5
Starling	*Sturnus vulgaris*	O	17	12	5
Yellow-rumped warbler	*Dendroica coronata*	I	17	10	7
Gray catbird	*Dumetella carolinensis*	I	16	11	5
American redstart	*Setophaga ruticilla*	I	16	13	3
Rose-breasted grosbeak	*Pheucticus ludovicianus*	O	15	11	4
Black-capped chickadee	*Parus atricapillus*	I	14	12	2
Red-headed woodpecker	*Melanerpes erythrocephalus*	I	14	7	7
Harris' sparrow	*Zonotrichia querula*	O	13	11	2
Eastern meadowlark	*Sturnella magna*	O	13	8	5
Eastern wood pewee	*Contopus virens*	I	12	10	2
Wilsons' warbler	*Wilsonia pusilla*	I	12	10	2
White-crowned sparrow	*Zonotrichia leucophrys*	O	9	7	2
Downy woodpecker	*Picoides pubescens*	I	8	6	2
Ruby-crowned kinglet	*Regulus calendula*	I	8	6	2
Black-and-white warbler	*Mniotila varia*	I	8	6	2
Gray-cheeked thrush	*Catharus minima*	I	8	5	3
Common crow	*Corvus brachyrynchos*	O	7	4	3
Blackpoll warbler	*Dendroica striata*	I	6	5	1

Appendix B. continued.

COMMON NAME	SCIENTIFIC NAME	F[a]	TOTAL	1976	1977
Black-headed grosbeak	*Pheucticus melanocephalus*	O	6	4	2
Rufous-sided towhee	*Pipilo erythrophthalmus*	O	4	3	1
Ovenbird	*Sciurus aurocapillus*	I	4	3	1
Orange-crowned warbler	*Vermivora celata*	I	4	4	-
Magnolia warbler	*Dendroica magnolia*	I	4	4	-
Black-billed cuckoo	*Coccyzus erythropthalmus*	I	4	4	-
Warbling vireo	*Vireo gilvus*	I	3	2	1
Chestnut-sided warbler	*Dendroica pennsylvanica*	I	3	2	1
Solitary vireo	*Vireo solitarius*	I	2	1	1
Mockingbird	*Mimus polyglottos*	O	2	1	1
Yellow-headed blackbird	*Xanthocephalus x.*	O	2	2	-
White-throated sparrow	*Zonotrichia albicollis*	O	2	-	2
Hairy woodpecker	*Picoides villosus*	I	2	-	2
Lincoln sparrow	*Melospiza lincolnii*	O	1	1	-
Palm warbler	*Dendroica palmarum*	I	1	1	-
Bay-breasted warbler	*Dendroica castanea*	I	1	1	-
Philadelphia vireo	*Vireo philadelphicus*	I	1	1	-
Indigo bunting	*Passerina cyanea*	I	1	1	-
Yellow-breasted chat	*Icteria virens*	I	1	1	-
American magpie	*Pica pica*	O	1	1	-
Cape may warbler	*Dendroica tigrina*	I	1	-	1
Canada warbler	*Wilsonia canadensis*	I	1	-	1
Black-throated green warbler	*Dendroica virens*	I	1	-	1
Nashville warbler	*Vermivora ruficapilla*	I	1	-	1

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[a] F = Food habits classification, G = granivores, O = omnivores, adn I = insectivores.

Appendix C. Means and standard errors for each food habits group by size class (N = 23 shelterbelts per size class). a) 1976 species richness. b) 1976 density. c) 1977 species richness. d) 1977 density.

	GRANIVORES		OMNIVORES		INSECTIVORES	
Size Class	Mean	± SE	Mean	± SE	Mean	± SE
a) 1	2.217	0.125	2.652	0.324	3.870	0.500
2	2.696	0.203	3.696	0.460	5.783	0.887
3	3.130	0.145	4.565	0.448	8.957	0.784
b) 1	20.017	2.522	13.265	2.383	12.426	2.291
2	24.009	3.290	18.439	2.640	19.796	4.339
3	34.365	4.402	18.009	1.951	36.148	3.991
c) 1	2.348	0.135	2.304	0.222	2.304	0.304
2	2.261	0.144	2.478	0.226	3.391	0.439
3	3.087	0.153	4.130	0.254	6.478	0.617
d) 1	12.096	1.545	10.309	2.775	3.565	0.466
2	13.944	2.093	9.344	1.775	5.652	0.676
3	21.917	2.405	16.296	1.990	13.304	1.704

Appendix D. F-ratios and significance obtained through two factor analysis of variance of the number of species and density of each food habits group by plot size as summarized in Table 2. a) 1976 species richness. b) 1976 density. c) 1977 species richness. d) 1977 density.

	FACTOR	F-RATIO	SIGNIFICANCE
a)	Food habits	51.984	p .001
	Size	12.129	p .001
	Food habits by size interaction	7.636	p .001
	Food habits nested within size	24.082	p .001
	Size nested within food habits	10.203	p .001
b)	Food habits	5.597	p .010
	Size	12.254	p .001
	Food habits by size interaction	3.479	p .025
	Food habits nested within size	4.449	p .001
	Size nested within food habits	7.951	p .001
c)	Food habits	14.604	p .001
	Size	52.972	p .001
	Food habits by size interaction	11.774	p .001
	Food habits nested within size	13.112	p .001
	Size nested within food habits	27.264	p .001
d)	Food habits	18.265	p .001
	Size	14.918	p .001
	Food habits by size interaction	0.428	p .100
	Food habits nested within size	7.009	p .001
	Size nested within food habits	6.859	p .001

ppendix E. Means and standard errors of the proportional representation of each food habits group by size class (N = 23 shelterbelts per size class). a) 1976 species richness. b) 1976 density. c) 1977 species richness. d) 1977 density.

	GRANIVORES		OMNIVORES		INSECTIVORES	
Size Class	Mean	± SE	Mean	± SE	Mean	± SE
a) 1	0.301	0.034	0.287	0.025	0.412	0.029
2	0.256	0.033	0.330	0.040	0.415	0.041
3	0.207	0.014	0.277	0.021	0.515	0.030
b) 1	0.446	0.046	0.259	0.034	0.279	0.036
2	0.399	0.046	0.331	0.051	0.264	0.037
3	0.379	0.035	0.221	0.020	0.399	0.035
c) 1	0.366	0.032	0.326	0.023	0.308	0.036
2	0.290	0.016	0.312	0.025	0.393	0.034
3	0.240	0.016	0.306	0.014	0.453	0.021
d) 1	0.518	0.042	0.320	0.041	0.162	0.029
2	0.457	0.036	0.308	0.038	0.236	0.029
3	0.416	0.029	0.320	0.022	0.264	0.024

ppendix F. F-ratios and significance obtained through two factor analysis of variance of the proportional representation of each food habits group by plot size as summarized in Table 4. a) 1976 species richness. b) 1976 density. c) 1977 species richness. d) 1977 density.

	FACTOR	F-RATIO	SIGNIFICANCE
a)	Food habits	24.910	p .001
	Size	1.308	p .100
	Food habits by size interaction	3.048	p .025
	Food habits nested within size	11.550	p .001
	Size nested within food habits	2.870	p .025
b)	Food habits	6.224	p .001
	Size	0.081	p .100
	Food habits by size interaction	2.744	p .050
	Food habits nested within size	4.083	p .001
	Size nested within food habits	2.644	p .025
c)	Food habits	5.435	p .010
	Size	0.822	p .100
	Food habits by size interaction	6.240	p .001
	Food habits nested within size	5.882	p .001
	Size nested within food habits	5.898	p .001
d)	Food habits	24.957	p .001
	Size	1.286	p .100
	Food habits by size interaction	1.363	p .100
	Food habits nested within size	9.244	p .001
	Size nested within food habits	1.344	p .100

Appendix G. Common and scientific names, guild classification, and the number of plots in which the bird species censused during 1976 and both 1977 breeding season counts were found.

COMMON NAME	SCIENTIFIC NAME	G[a]	TOT[b]	76[c]	771[d]	772[e]
Mourning dove	*Zenaidura macroura*	123	196	61	67	68
Common grackle	*Quiscalus quiscula*	134	191	62	64	65
American robin	*Turdus migratorius*	323	154	56	49	49
House sparrow	*Passer domesticus*	354	144	51	45	48
Orchard oriole	*Icterus spurius*	254	133	41	46	46
Brown thrasher	*Toxostoma rufum*	223	114	39	38	37
Western kingbird	*Tyrannus verticalis*	255	103	36	33	34
Eastern kingbird	*Tyrannus tyrannus*	245	103	37	33	33
American goldfinch	*Carduelis tristis*	144	93	35	28	30
Redwing blackbird	*Agelaius phoeniceus*	334	80	27	27	26
Yellowthroat	*Geothlypis trichas*	234	68	24	22	22
House wren	*Troglodytes aedon*	234	58	18	20	20
Brown-headed cowbird	*Molothrus ater*	144	54	14	20	20
Song sparrow	*Melospiza melodia*	334	45	12	16	17
Common flicker	*Colaptes auratus*	211	39	12	13	14
Eastern wood pewee	*Contopus virens*	245	38	13	12	13
Black-billed cuckoo	*Coccyzus erythrophthalmus*	244	27	12	6	9
Northern oriole	*Icterus galbula*	244	25	6	11	8
Blue jay	*Cyanocitta cristata*	344	20	8	6	6
Warbling vireo	*Vireo gilvus*	254	19	3	8	8
Red-headed woodpecker	*Melanerpes erythrocephalus*	211	15	7	4	4
Starling	*Sturnus vulgaris*	354	14	11	1	2
Yellow warbler	*Dendroica petechia*	244	11	3	4	4
Vesper sparrow	*Pooecetes gramineus*	334	8	4	2	2
Black-capped chickadee	*Parus atricapillus*	242	8	3	2	3
Clay-colored sparrow	*Spizella pallida*	134	7	2	2	3
Chipping sparrow	*Spizella passerina*	344	7	2	2	3
Downy woodpecker	*Picoides pubescens*	211	7	2	2	3
Swainson's thrush	*Catharus ustulata*	223	7	3	2	2
Ring-necked pheasant	*Phasianus colchicus*	122	7	3	2	2
Gray catbird	*Dumetella carolinensis*	234	6	1	3	2
Black-headed grosbeak	*Pheucticus melanocephalus*	344	6	2	2	2
Common crow	*Corvus brachyrynchos*		5	2	1	2
Eastern meadowlark	*Sturnella magna*		4	2	1	1
Swainson's hawk	*Buteo swainsoni*		4	2	1	1
Great-horned owl	*Bubo virginianus*		3	1	1	1
Rose-breasted grosbeak	*Pheucticus ludovicianus*	334	3	1	1	1
American magpie	*Pica pica*		3	1	1	1
Dickcissel	*Spiza americana*	334	2	2	-	-
Blue grosbeak	*Guiraca caerulea*	334	2	2	-	-

Appendix G. cont.

COMMON NAME	SCIENTIFIC NAME	G[a]	TOT[b]	76[c]	771[d]	772[e]
Lark sparrow	*Chondestes grammacus*	323	2	1	-	1
Solitary vireo	*Vireo solitarius*	254	1	-	-	1
Harris' sparrow	*Zonotricha leucophrys*	334	1	1	-	-
Common nighthawk	*Chordeiles minor*		1	1	-	-

[a] Guild classification:
First number = primary food habits; 1 = granivore, 2 = omnivo
2 = insectivore, 3 = omnivore.
Second number = foraging stratum most commonly used; 1 = bark,
2 = ground, 3 = low, 4 = middle, 5 = high canopy.
Third number = foraging method; 1 = bark drill, 2 = bark glean,
3 = ground glean, 4 = foliage glean, 5 = sally.

[b] Total number of plots each species was found for all three censuses.

[c] 1976 census.

[d] First 1977 census.

[e] Second 1977 census.

pendix H. Means and standard errors for each food habits group by size class (N = 23 shelterbelts per size class). a) Species richness. b) Density. c) Proportional species representation. d) Proportional density representation.

	GRANIVORES		OMNIVORES		INSECTIVORES	
Size Class	Mean	± SE	Mean	± SE	Mean	± SE
a) 1	2.142	0.123	1.986	0.192	2.520	0.279
2	2.089	0.138	2.288	0.195	3.159	0.331
3	2.826	0.113	3.405	0.239	5.755	0.441
b) 1	14.739	1.895	10.698	1.997	5.732	0.701
2	17.631	2.342	12.201	1.482	7.433	0.899
3	24.157	2.298	17.464	1.797	16.558	2.056
c) 1	0.350	0.021	0.296	0.023	0.354	0.028
2	0.283	0.023	0.317	0.027	0.397	0.030
3	0.247	0.015	0.285	0.015	0.468	0.019
d) 1	0.488	0.032	0.312	0.034	0.190	0.024
2	0.435	0.028	0.340	0.028	0.225	0.029
3	0.410	0.020	0.306	0.019	0.282	0.019

Appendix I. F-ratios and significance obtained through two factor analysis of variance of food habits groups and plot sizes, as summarized in Table 3. a) Species richness. b) Density. c) Proportional species representation. d) Proportional density representation.

	FACTOR	F-RATIO	PROBABILITY
a)	Food habits	35.062	.001
	Size	57.305	.001
	Food habits by size interaction	13.768	.001
	Food habits nested within size	22.927	.001
	Size nested within food habits	31.196	.001
b)	Food habits	30.710	.001
	Size	14.974	.001
	Food habits by size interaction	0.891	.100
	Food habits nested within size	11.887	.001
	Size nested within food habits	9.038	.001
c)	Food habits	14.835	.001
	Size	0.000	.100
	Food habits by size interaction	5.768	.001
	Food habits nested within size	9.863	.001
	Size nested within food habits	5.759	.001
d)	Food habits	34.843	.001
	Size	0.724	.100
	Food habits by size interaction	1.991	.100
	Food habits nested within size	12.906	.001
	Size nested within food habits	1.982	.100

Appendix J. Explanation of variable mnemonics and the mean and standard error for those variables for the 69 study shelterbelts.

MNEMONIC	MEAN	SE	DEFINITION
ACSA	0.007	0.007	*Acer saccharinum* L. - Silver maple
ACNE	2.413	0.808	*Acer negundo* L. - Box elder
AGE	21.536	1.290	Age of the shelterbelt
AREA	7532.835	778.708	Area of the shelterbelt (in m^2)
CAAR	7.448	1.626	*Caragana arborescens* Lam. - Caragana
CANHT	9.597	0.994	Canopy height (in m)
CC	54.420	2.124	Canopy coverage
CEOC	1.855	0.674	*Celtis occidentalis* L. - Hackberry
CONVOL	31.744	11.267	Coniferous foliage volume (in m^3)
ELAN	6.826	1.244	*Elaeagnus angustifolia* L. - Russian-olive
CULTIVAT	0.739	0.053	Presence-absence of an adjacent cultivated field.
FRPE	11.828	1.954	*Fraxanus pennsylvanica* Marsh. - Green ash
GC	81.015	2.667	Ground coverage
GRLI	0.015	0.014	Light grazing
GRME	0.101	0.037	Medium grazing
GRSE	0.073	0.031	Severe grazing
GRZ	0.464	0.116	Cumulative grazing index
HHT	0.513	0.033	Herb height (in m)
HUMAN	1.290	0.099	Proximity of a human residence
JUVI	1.874	0.566	*Juniperus virginiana* L. - Eastern redcedar
LIVESTOCK	1.841	0.183	Proximity of a livestock feedlot
LOTA	7.828	1.670	*Lonicera tatarica* L. - Tatarian honeysuckle
MORU	0.203	0.193	*Morus alba tatarica* L. - Russian mulberry
MOWED	0.087	0.034	Presence-absence of mowing
NL	2.029	0.080	Number of layers - herb, shrub, or tree
NSHSPP	1.536	0.173	Number of shrub species
NSR	1.667	0.208	Number of shrub rows
NTR	5.290	0.291	Number of tree rows
NTRSPP	2.341	0.212	Number of tree species
PASTURE	0.507	0.061	Presence-absence of an adjacent pasture
PIPO	0.507	0.292	*Pinus ponderosa* Laws. - Ponderosa pine
PIPU	0.406	0.405	*Picea pungens* Engelm. - Blue spruce
PLDEN	85.942	4.537	Density of trees and shrubs combined
PODE	2.007	1.035	*Populus deltoides* Bartr. - Eastern cottonwood
PRAM	10.475	2.756	*Prunus americana* Marsh. - American plum
PRAR	0.261	0.261	*Prunus armeniaca sibiriea* - Siberian apricot
PRPU	0.668	0.412	*Prunus pumila besseyi* L. - Western sandcherry
PRTO	1.757	0.810	*Prunus tomentosa* L. - Nanking cherry
PRVI	1.194	0.617	*Prunus virginiana* L. - Common chokecherry
PSME	0.225	0.225	*Pseudotsuga mensiesii* glauca Franco - Douglas-fir

Appendix J. cont.

MNEMONIC	MEAN	SE	DEFINITION
R[1]			
ROADS	1.290	0.075	Proximity of a road
ROPS	1.309	0.585	*Robinia pseudoacacia* L. - Black locust
SHAR	0.391	0.391	*Sheperdia argentea* Nutt. - Silver buffaloberry
SHRLHT	0.317	0.077	Shrub layer height (in m)
SHRRHT	2.001	0.173	Shrub row height (in m)
SHRVOL	142.204	24.028	Shrub foliage volume (in m^3)
SNAG	8.542	1.107	Snag density
SYVU	2.012	0.823	*Syringa vulgaris* L. - Common lilac
TNR	6.957	0.348	Total number of rows
TOTUND	6.739	0.689	Total understory density
TRCLAIM	0.101	0.037	Presence-absence of an adjacent tree claim
TRVOL	872.468	69.104	Tree foliage volume (in m^3)
ULAM	8.036	1.435	*Ulmus americana* L. - American elm
ULPU	38.646	4.211	*Ulmus pumila* L. - Siberian elm
UNDSHR	0.449	0.102	Presence-absence of understory shrubs
VEGDIV	1.140	0.063	Shannon index of vegetation diversity
WATER	1.478	0.125	Proximity of an open water source
WOODY	1.188	0.081	Proximity of the nearest other woody cover

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[1] Any mnemonic starting with the letter "R", except roads and rops, indicates the relative density of a vegetation species identified by the rest of the mnemonic following the "R".

Appendix K. Data on tree species selection and nest height placement by bird species found nesting in shelterbelts.

TRSP[a]	HT[b]	LD[c]	DT[d]	TRSP	HT	LD	DT	TRSP	HT	LD	DT
Mourning dove											
ULPU	8	1	20	ULPU	7	1	20	ULPU	6	1	20
ULPU	5	3	20	ULPU	8	0	15	ULPU	6	1	10
ULPU	7	0	10	ULPU	15	0	7	ULPU	9	0	10
ULPU	12	0	25	ACNE	8	0	8	ULAM	13	0	25
JUVI	4	1	12	CEOC	4	0	30	ELAN	12	0	20
ULPU	8	4	25	ULPU	8	2	25	ELAN	9	0	20
JUVI	3	2	8	JUVI	6	0	5	JUVI	6	0	3
JUVI	4	0	10	ELAN	8	0	20	ELAN	3	0	25
LOTA	5	0	6	ELAN	6	0	20	ELAN	12	0	15
ULPU	5	0	30	ULPU	18	0	3	ULPU	10	2	30
ULPU	15	5	15	ULPU	10	0	20	ULPU	10	0	15
ULPU	20	0	10	ULPU	5	0	20	ULPU	12	4	20
ULPU	4	0	30	ACNE	4	6	12	ACNE	3	10	4
CEOC	20	0	30	ULPU	20	0	20	ULPU	5	3	30
ULPU	4	2	30	ULPU	5	1	30	ULPU	5	0	10
ULPU	4	2	35	PRAM	3	0	3	ULPU	6	0	20
ULPU	7	0	15	PRAM	5	3	7	ULPU	5	2	35
ULPU	3	1	35	ULPU	7	3	30	ULPU	6	3	35
ULPU	12	1	20	ULPU	5	3	50	ULPU	5	5	50
ULPU	6	1	15	ULPU	6	2	10	ULPU	10	0	40
ULPU	12	0	35	ULPU	12	4	20	ACNE	12	0	30
JUVI	7	4	25	PRAM	4	0	10	ULPU	5	1	8
ULPU	3	1	10	ULPU	5	1	20	ULPU	6	1	15
ULPU	5	0	30	PODE	12	0	3	ULPU	6	1	25
ULPU	6	2	25	PRAM	5	0	3	PRAM	2	0	10
PRAM	5	0	5	ULPU	7	3	25	ULPU	5	3	20
ULPU	5	2	20	ULPU	5	3	20	ULPU	8	3	15
ULPU	6	3	20	ULPU	6	3	20	ULPU	6	3	30
ULPU	6	3	35	ULPU	8	1	25	ULPU	7	2	20
ULPU	10	0	20								
Common grackle											
ULPU	15	0	15	ULPU	18	0	12	ELAN	20	0	4
ULPU	4	0	20	ULPU	10	10	0	ULPU	12	0	15
ULPU	9	0	20	ULPU	20	0	10	ULPU	6	0	25
ULPU	6	0	25	ULPU	22	0	8	ULPU	6	0	12
PRAM	5	0	6	ULPU	4	0	20	ULPU	30	0	5
ULPU	25	0	10	ULPU	25	0	15	ULPU	30	4	15
ULPU	35	0	10	ULPU	20	0	25	ULPU	30	0	15

Appendix K. continued.

TRSP[a]	HT[b]	LD[c]	DT[d]	TRSP	HT	LD	DT	TRSP	HT	LD	DT
Common grackle (cont.)											
ULPU	35	0	10	ULPU	15	2	30	ULPU	20	0	20
ULPU	25	0	20	ULPU	30	3	15	ULPU	30	4	10
Western kingbird											
ULPU	15	4	25	ULPU	22	0	45	PODE	30	0	5
PODE	25	0	10	ULPU	30	0	20	ULPU	22	0	25
ULPU	15	0	15	ULPU	8	2	20	ULPU	7	0	25
ULPU	8	0	20	ULPU	15	0	25	ULPU	12	0	25
PODE	25	0	5	ULPU	14	2	28	ULPU	7	0	20
ULPU	17	0	30	ULPU	15	0	25	ULPU	8	0	25
ULPU	10	0	20	ULPU	6	0	30	ULPU	3	0	15
ULPU	6	0	25	ULPU	9	0	25	ULPU	20	0	22
ULPU	8	0	15	ULPU	25	0	15				
Brown thrasher											
ULPU	8	0	15	PRAM	3	0	10	ULPU	6	0	20
PRAM	8	0	5	PRAM	6	0	12	PRAM	6	0	8
PRAM	5	0	7	PRAM	3	0	12	PRAM	3	0	9
ELAN	4	0	15	PRAM	5	0	6	ULPU	6	0	18
ULPU	3	0	20	ULPU	12	0	15	PRAM	4	0	8
American robin											
ACNE	6	0	15	JUVI	6	0	5	ULPU	6	0	20
ULPU	8	12	0	ULPU	12	0	2	ULPU	9	0	20
ULPU	4	0	15	ULPU	25	0	8	ULPU	5	2	15
ULPU	8	3	15	ULPU	8	1	25	ULPU	6	0	20
ULPU	10	1	15	ULPU	4	0	20	ULPU	6	0	15
Eastern kingbird											
ULPU	22	0	25	PODE	25	0	0	PODE	11	0	15
ULPU	11	0	15	ULPU	14	1	10	ULPU	25	0	10
ULPU	18	0	15	PRAM	9	0	7	PRAM	6	0	9

Appendix K. continued.

TRSP[a]	HT[b]	LD[c]	DT[d]	TRSP	HT	LD	DT	TRSP	HT	LD	DT
Blue jay											
ULPU	8	0	25	ULPU	10	1	25	ULPU	10	0	30
ULPU	9	0	25								
Orchard oriole											
ACNE	18	0	15	ULPU	30	0	5	ULPU	25	0	10

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[a] Tree species - mnemonic defined in Appendix J.

[b] Height above ground (in ft).

[c] Lateral distance out from main stem.

[d] Distance to the top of the tree above the nest.

Appendix L. Area, in m^2, of all shelterbelts studied.

PLOT	AREA
07	984.2
06	1205.0
69	1454.6
47	1672.0
27	1801.8
45	1956.2
15	2094.2
33	2264.4
05	2266.3
13	2406.7
34	2411.1
03	2580.2
30	2914.6
44	3000.4
02	3004.3
68	3009.6
08	3100.8
17	3208.2
43	3218.6
49	3356.2
09	3371.8
36	3534.0
55	3682.2
31	3770.6
42	3309.3
01	3888.0
32	4006.0
22	4183.8
37	4555.4
24	4623.8
46	4643.3
18	4847.1
20	4887.0
21	4931.6
12	5006.5
64	5381.6
57	5476.9
16	5626.2
10	6031.4
58	6446.7
11	6487.4
19	6917.9
56	7003.3
60	7046.9
28	7289.2
39	7430.0
35	7451.0
04	7462.1
66	8002.2
59	8456.0
65	8591.0
14	9826.8
40	10174.5
41	10533.6
23	11491.2
50	11838.9
54	12184.3
67	12523.3
61	13338.0
25	14027.7
53	14656.6
52	14723.1
38	17168.4
51	17665.4
26	21331.0
63	21536.1
62	27137.5
48	27629.0
29	29230.7