

## DIVERSITY AND ABUNDANCE OF SPRING MIGRATORY BIRDS USING HABITAT ISLANDS ON THE GREAT PLAINS

THOMAS E. MARTIN

**ABSTRACT.**—Relationships of area with numbers of species and individuals of spring migrants were examined for 69 shelterbelts (forest islands) in eastern South Dakota. Total abundance and number of species were as highly correlated with area during spring migration as during the breeding season. The relationships of area with total abundance and number of species were highly similar between two years of study. Area was more important in determining abundance and number of species than either diversity of plant species or isolation of the islands. The dispersion of migrants among islands, indicated by the relationships of area with total abundance and species numbers, could have been a result of passive dispersal, selection for larger area, or behavioral interactions. Passive dispersal was unlikely because the isolation of an island had no significant influence on abundance or diversity. Also, the diversity and abundance of migrants were modified by habitat conditions (i.e., vegetation diversity), indicating that migrants select the forest islands they inhabit. Migrants may select large areas but they should then have increased with area at an increasing rate, but this did not occur. Dispersion among islands may be the best way for migrants to replenish their energy reserves when food is scarce. Two facts suggest that migrants may interact to disperse themselves relative to food. First, application of a model for interacting species provided increasingly better fits to ecological groups that increasingly confined their foraging within shelterbelts. Second, the density of birds was greater in smaller islands than in larger islands owing to species that did not feed solely within the islands. The density of birds that did feed primarily within the islands remained more or less constant with changing area.

Shelterbelts consist of rows of trees and shrubs forming long and narrow island configurations. Shelterbelt plantings began largely in the mid-1930's under the auspices of the Shelterbelt Project and the Prairie State Forestry Project directed by the U.S. Forest Service, Department of Agriculture (Read 1958), in order to reduce wind erosion and protect homes and livestock on the Great Plains. These islands of planted trees supplied potential habitat for many species of woodland birds. The vegetation structure of a particular shelterbelt modifies the composition, diversity, and abundance of bird species using that shelterbelt during spring migration and the summer breeding season (Martin and Vohs 1978).

A strong relationship between numbers of breeding bird species and island area has been found for many real and habitat island systems (MacArthur and Wilson 1963, 1967; Abbot 1974, Johnson 1975, Diamond and Mayr 1976, Galli et al. 1976). With the exception of a recent study by Willson and Carothers (1979) in Arizona, the influence of area on the number of transient bird species and individuals using habitat islands during migration has not been report-

ed. I examine here the influence of area of shelterbelts in eastern South Dakota on the diversity, abundance, and ecological structure of transient bird communities during the spring migrations of 1976 and 1977.

### STUDY AREA AND METHODS

The 69 shelterbelts examined in this study were scattered throughout South Dakota between its eastern border and the Missouri River. There is approximately one shelterbelt per 115 ha in this area of the state, representing 1.1% of the land area (Walker and Suedkamp 1977). These small forests represented true habitat islands, being isolated from one another by fields of natural and planted grasses. The floral diversity was low and included only 15 tree and 14 shrub species. The most common tree species were Siberian elm (*Ulmus pumila*), American elm (*U. americana*), green ash (*Fraxinus pennsylvanica*), and hackberry (*Celtis occidentalis*), while the most common shrubs were honeysuckle (*Lonicera tatarica*), lilac (*Syringa vulgaris*), American plum (*Prunus americana*), and chokecherry (*Prunus virginiana*).

I quantified the structural complexity of the vegetation for each shelterbelt. Ground and canopy coverages were measured by noting the presence or absence of vegetation through an ocular tube (James and Shugart 1970). Density of understory vegetation was measured using a density board (Giles 1971). Readings were taken between each planted row at three locations in each belt. Measurement of percent slope, from a fixed distance, estimated vegetation height.

TABLE 1. Means and standard errors of census results on 69 shelterbelts for 1976 and 1977 migratory seasons. A) Total species numbers, diversity, and abundance. B) Number of species per food habits group. C) Percent species composition. D) Number of individuals in each food habits group.

Variable	1976			1977		
	Mean	±	SE	Mean	±	SE
A) All birds						
Species numbers	12.54		0.74	9.59		0.50
Species diversity	1.967		0.065	1.706		0.047
Abundance	66.11		4.37	35.49		3.05
B) Number of species						
Granivores	2.68		0.10	2.57		0.09
Omnivores	3.64		0.25	2.97		0.17
Insectivores	6.20		0.49	4.09		0.34
C) Percent composition						
Granivores	0.26		0.017	0.30		0.014
Omnivores	0.30		0.017	0.32		0.012
Insectivores	0.45		0.020	0.39		0.019
D) Abundance						
Granivores	26.13		2.12	16.12		1.27
Omnivores	17.07		1.38	11.98		1.32
Insectivores	22.79		2.40	7.58		0.80

I determined bird species numbers and abundances by the Emlen (1971) transect method and by direct counts. Censuses were conducted within two hours of sunrise and sunset. Transects extending 61 m on both sides of the observer were established perpendicular to the belts to census abundant species, such as Common Grackle, House Sparrow, American Robin, Mourning Dove, Red-winged Blackbird, Clay-colored Sparrow, and Chipping Sparrow. Less abundant species were assigned abundance values based on the number of individuals directly counted by walking the length of the belt upon completion of the transects.

I began censusing study plots in the south on 8 May in both years and proceeded northward to minimize phenological variation among sites. Censuses were completed in 19 and 13 days in 1976 and 1977, respectively. Two observers conducted two morning and two evening censuses on four shelterbelts in 1976 to test count reliability. One observer censused a particular belt both morning and evening on one day and the other observer censused the same belt on the following day. Numbers of species did not differ significantly between days ( $P > .995$ ,  $\chi^2 = 0.078$ ) or between morning and evening ( $P > .995$ ,  $\chi^2 = 0.069$ ). In addition, total abundance did not differ significantly between days ( $P > .990$ ,  $\chi^2 = 1.03$ ) or between morning and evening ( $P > .975$ ,  $\chi^2 = 1.43$ ). Subsequent shelterbelts were censused once each year. Greater efficiency of counting and fewer rain-caused delays reduced the census period in 1977.

I grouped birds by their primary food habits (Appendix) based on my observations and the literature (Martin et al. 1951, Willson 1974), to study changes in community structure with changes in shelterbelt area. Shelterbelts were grouped into three size classes for these analyses. Size class 1 included the smallest 23 shelterbelts ( $\bar{x} \pm SE = 2,553 \pm 162 \text{ m}^2$ ), class 2 the next largest 23 shelterbelts ( $5,417 \pm 248 \text{ m}^2$ ) and class 3 the largest 23 shelterbelts ( $14,616 \pm 1,324 \text{ m}^2$ ). This grouping allowed comparative analyses of changes in the number of individuals and species representing each food habits group with changes in shelterbelt area. Analysis of variance and *t*-tests were used to test differences among size class groupings. However, regression equations were based on the continuous range of the 69 study shelterbelts.

The Shannon and Weaver (1963) index ( $H' = -\sum p_i \log_e p_i$ , where  $p_i$  represents the proportion of a community represented by species  $i$ ) was used to calculate species diversity. Equitability was calculated by  $J = H'/\log_e S$ , where  $S$  is the number of species in the community. In the following discussion, "abundance" refers to the number of individuals in a community. "Density" refers to the number of individuals per  $984.2 \text{ m}^2$  (the size of the smallest shelterbelt). "Adjusted abundance" refers to the total number of individuals in a community minus the abundances of the Common Grackle, American Robin, and House Sparrow. I examined species-area and abundance-area relationships by three regression functions: log-log (power), semi-log (exponential), and untransformed (linear). The best-fit function was determined from correlation coefficients. It is misleading to directly compare the correlation of the power function with the correlations of the other two functions because the dependent variable for the power function was transformed. Thus, the correlation coefficient for the power function was based on a second regression of arithmetic species numbers on area raised to the exponent calculated by the log-log regression.

The data in the next section are compared in various ways. First, the number of individuals and species of each food habits group are compared among groups and between years to demonstrate differences. Census results for the communities are, however, correlated between years to show that the number of individuals and species varied among communities in a similar manner both years. Next, the number of species and abundance of food habits groups are compared among groups and with area through analysis of variance. Log-log regressions were computed to compare the rate of increase (slope) of species numbers and abundance of each food habits group with area among groups and with the rate of increase of total abundance and total species numbers. The relationship between total species numbers and area is analyzed by the three regression functions to determine the curvilinearity of the relationship. Total abundance is similarly examined. Total abundance is adjusted by subtracting the abundances of the three most common vagrant species that do not rely on food within shelterbelts to examine the relationship between area and those individuals

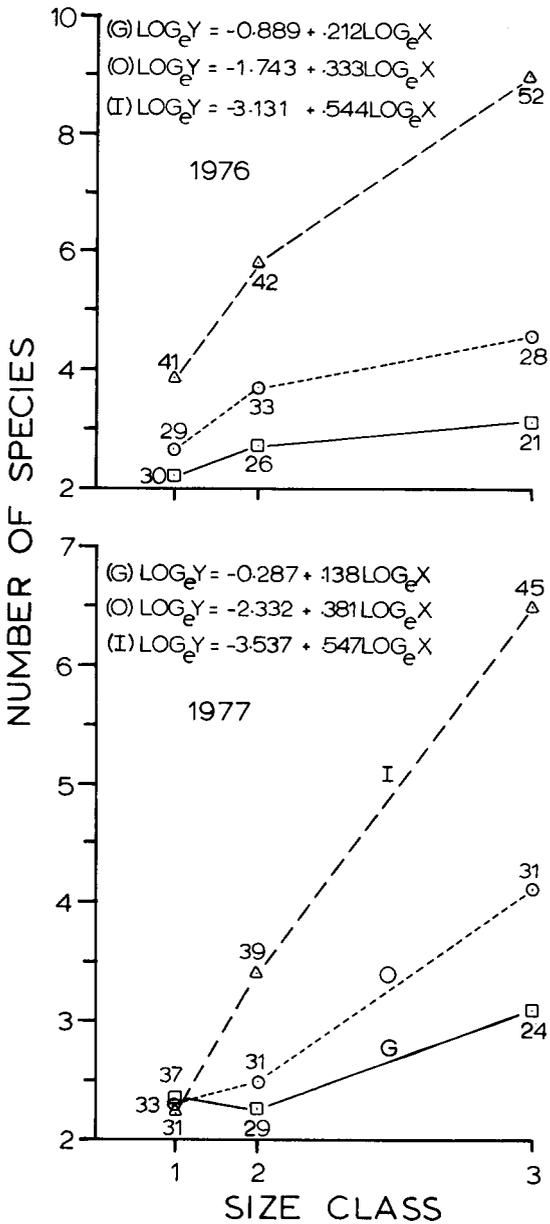


FIGURE 1. Mean number of species of granivorous (G), omnivorous (O), and insectivorous (I) birds censused during spring migrations of 1976 and 1977 in each of three classes of shelterbelts of increasing size. Numbers indicate the mean percent representation of each food habits group for each size class. Regression equations based on all 69 shelterbelts are highly significant ( $P < .001$ ).

that concentrated their feeding within shelterbelts. Finally, abundance is converted to density to illustrate the density-area relationship.

**RESULTS**

**COMPARISON BETWEEN YEARS**

The census period ended earlier in 1977 than in 1976 with the result that I missed some late migrants in 1977, such as the Black-billed Cuckoo. In addition, 77.8% of

the species represented in two or more shelterbelts were observed in fewer belts in 1977 than in 1976 (Appendix). Mean numbers of species, species diversity, and total abundance were lower in 1977 than in 1976 (Table 1A,  $P < .01$ ) owing to the earlier censusing plus possible differences in phenology between years. The mean number of granivorous species did not differ significantly ( $P > .10$ ) but there were significantly fewer omnivorous ( $P < .05$ ) and insectivorous ( $P < .01$ ) species in 1977 than 1976 (Table 1B). The lower representation of insectivores in 1977 relative to 1976 raised the proportion ( $P < .01$ ) of granivorous species per shelterbelt in 1977 (Table 1C).

All three food habits groups were less abundant ( $P < .01$ ) in 1977 than 1976 (Table 1D), but the decrease was most dramatic for insectivores. Abundance of insectivores and granivores did not significantly differ ( $P > .10$ ) in 1976, while granivores were much more abundant ( $P < .001$ ) than insectivores in 1977. Individuals per species were more numerous for granivores than insectivores in both 1976 (9.8 vs. 3.7) and 1977 (6.4 vs. 1.8).

While relationships among food habits groups differed among years, the number of species and individuals of the total avian community varied among belts in a similar manner both years. I compared years by correlating census results between years for total abundance, number of species, and species diversity. If the variation among belts were similar between years then the correlation should be high and the slope should equal 1.0. Examination of species numbers in 1976 relative to 1977 yielded a high correlation ( $r = 0.802$ ,  $P < .001$ ) and a slope (1.021) that did not differ ( $P > .10$ ) from 1.0. Comparison of abundance between years also produced a high correlation ( $r = .868$ ,  $P < .001$ ) and a slope (1.124) that did not differ ( $P > .10$ ) from 1.0. Thus, species numbers and abundance varied with area in a similar manner both years. The slope for species diversity (0.783) was less ( $P < .05$ ) than 1.0 and the correlation ( $r = .616$ ,  $P < .001$ ) was lower than for species numbers or abundance, indicating that species diversity was less constant between years. The diversity index has two components: species numbers and equitability. The reduced correlation of diversity between years can be attributed to the equitability component. The correlation of equitability between years ( $r = .307$ ,  $P < .01$ ) was much less ( $P < .001$ ) than the correlation of species numbers ( $r = .802$ ) between

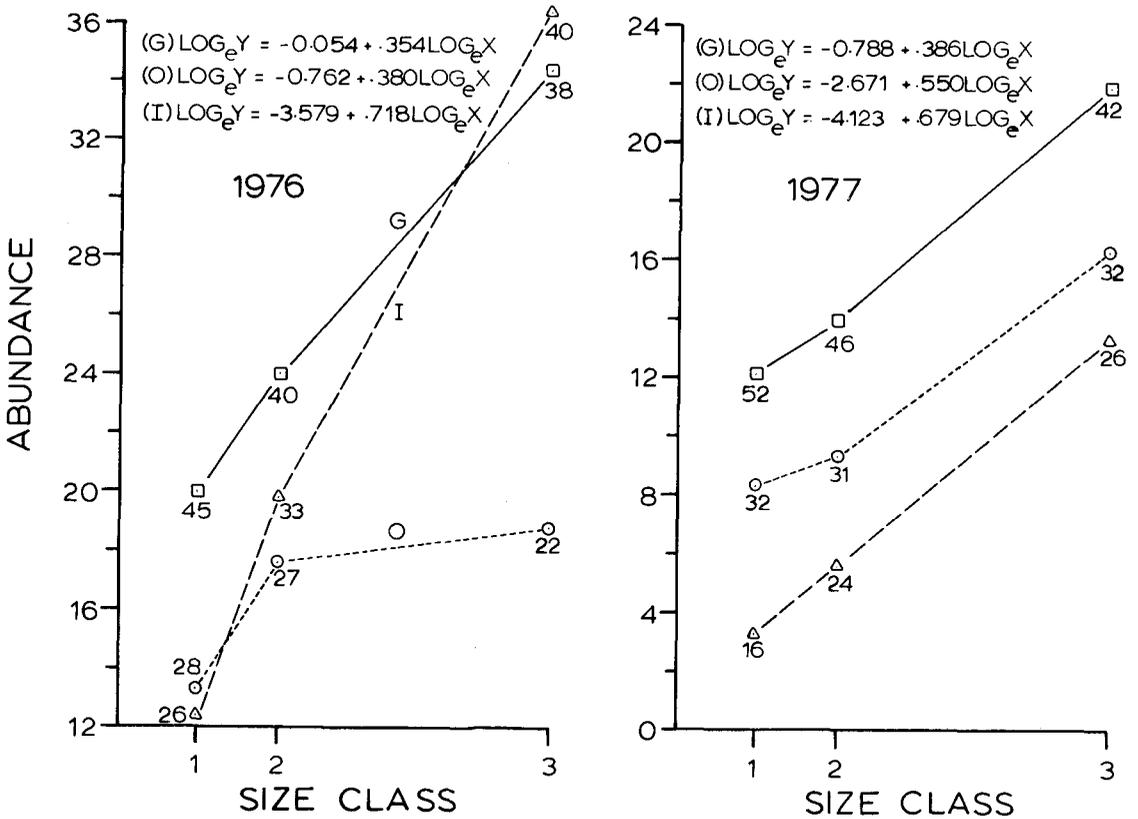


FIGURE 2. Mean abundance of granivorous (G), omnivorous (O), and insectivorous (I) birds censused during spring migrations of 1976 and 1977 in each of three classes of shelterbelts of increasing size. Numbers indicate the mean percent representation of each food habits group for each size class. Regression equations based on all 69 shelterbelts are highly significant ( $P < .001$ ).

years. The low correlation of equitability between years can be attributed to the differences in representation of food habits groups. The gregarious granivores were more dominant in 1977 and, hence, had a greater effect on equitability.

**SPECIES NUMBERS AND ABUNDANCE OF FOOD HABITS GROUPS: EFFECTS OF SHELTERBELT AREA**

Number of species (Fig. 1) of each food habits group increased with plot size in both years ( $P < .001$ ,  $F = 12.13$  in 1976,  $F = 52.97$  in 1977), and the number of species differed among food habits groups ( $P < .001$ ,  $F = 51.98$  in 1976,  $F = 14.90$  in 1977). There was a significant interaction between food habits group and shelterbelt size class ( $P < .001$ ,  $F = 7.64$  in 1976,  $F = 11.77$  in 1977); insectivorous species numbers increased faster than omnivores, which in turn increased faster than granivores, as plot size increased (compare regression slopes). These differences in rate of increase caused differences in the proportional representa-

tion of the food habits groups with changes in area (Fig. 1).

All three food habits groups (Fig. 2) became more abundant as plot size increased ( $P < .001$ ,  $F = 12.25$  in 1976,  $F = 14.92$  in 1977). Differences among food habits groups were less marked in 1976 ( $P < .01$ ,  $F = 5.60$ ) than in 1977 ( $P < .001$ ,  $F = 18.27$ ) due to a greater similarity in the abundance of insectivores and granivores in 1976 (Fig. 2). Numbers of insectivorous individuals increased faster than omnivores and granivores with increasing plot size (compare regression slopes). The greater number of insectivorous individuals in 1976 led to their constituting the greatest share of individuals in large shelterbelts in 1976; granivorous birds predominated in small plots in that year and in all plot sizes in 1977 (Fig. 2).

**EFFECT OF AREA ON TOTAL SPECIES NUMBERS AND DIVERSITY**

Total number of species and species diversity increased with area (Table 2A, B). Pre-

TABLE 2. Characteristics of avian communities censused in shelterbelts of three size classes (n = 23 shelterbelts per size class).

Size class	1976			1977		
	Mean	±	SE	Mean	±	SE
<b>Species numbers</b>						
1	8.74	0.75		6.97	0.39	
2	12.18	1.26		8.13	0.53	
3	16.70	1.22		13.70	0.84	
<b>Species diversity</b>						
1	1.683	0.098		1.424	0.051	
2	1.921	0.108		1.621	0.060	
3	2.297	0.098		2.071	0.067	
<b>Abundance</b>						
1	45.69	4.96		25.98	3.61	
2	62.59	7.20		28.94	3.08	
3	90.07	7.39		51.54	4.59	
<b>Standardized density</b>						
1	19.85	3.43		11.28	3.20	
2	12.01	1.38		5.20	0.52	
3	6.79	0.67		3.71	0.30	

vious studies of island species-area curves during the breeding season have found the relationship to be a power ( $S = CA^z$ ) or exponential ( $\exp(S) = CA$ ) function, where  $S$  is the number of species,  $A$  is area, and  $C$  and  $z$  are fitted constants (Hamilton et al. 1964, Hamilton and Armstrong 1965, MacArthur and Wilson 1967, Vuilleumier 1970, Diamond 1973). The species-area curve for shelterbelts during breeding season provided similar fits to the power and exponential functions (Martin 1980), but during spring migration (Figs. 3, 4) correlations of the power ( $r = .753$  in 1976,  $r = .851$  in 1977) and linear ( $r = .774$  in 1976,  $r = .821$  in 1977) functions were similar and

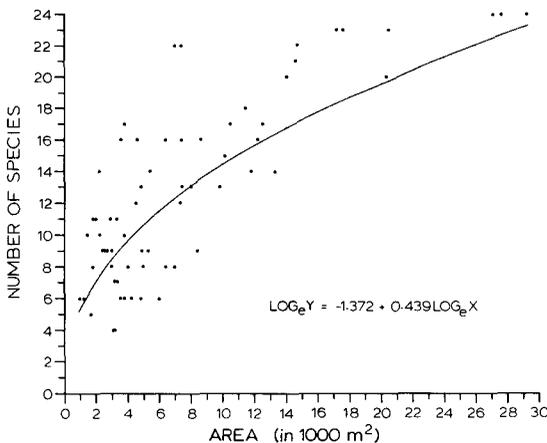


FIGURE 3. Number of species of spring migrants in relation to the area of 69 shelterbelts in 1976. The fitted line represents the power function equation displayed. The correlation is highly significant ( $P < .001$ ).

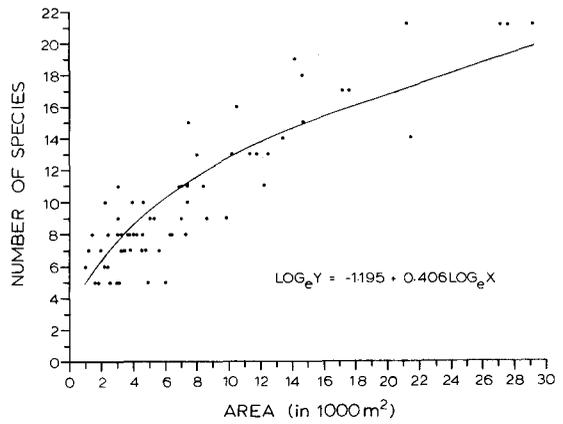


FIGURE 4. Number of species of spring migrants in relation to the area of 69 shelterbelts in 1977. The fitted line represents the power function equation displayed. The correlation is highly significant ( $P < .001$ ).

correlations of the exponential function ( $r = .725$  in 1976,  $r = .776$  in 1977) were slightly lower. The exponential model provides a better fit for asymptotic data, while the power function provides a better fit for curvilinear data that have not reached an asymptote. Thus, the results suggest that the relationship is linear or sublinear, but not asymptotic.

In a proportional relationship the slope of the power function,  $z$ , should equal 1.0 (i.e.,  $S = CA^1$ ) and the intercept of the arithmetic plot should be 0. The slopes were 0.439 (Fig. 3) and 0.406 (Fig. 4) for 1976 and 1977, respectively. Both slopes were significantly less ( $P < .001$ ) than 1.0, indicating that species numbers increased with area at a much slower rate than proportional.

TOTAL ABUNDANCE

The number of individuals in a community increased as a function of area (Table 2C) in a linear manner; correlation of the linear function ( $r = .811$ ,  $P < .001$ ) was slightly higher than for the power function ( $r = .798$ ,  $P < .001$ ) and both exhibited higher correlations than the exponential function ( $r = .775$ ,  $P < .001$ ). While the relationship was linear, the slope ( $z = .597$ ) showed that it was not proportional; a 200% increase in area yielded a 100% increase in abundance. Thus, density decreased ( $P < .001$ ) as area increased (Table 2D) in a curvilinear manner (Fig. 5), indicating that there were more individuals per unit area in smaller shelterbelts.

Subtraction of the abundances of the three most common vagrant species (Common Grackle, House Sparrow, American Robin) from total abundance produced a lin-

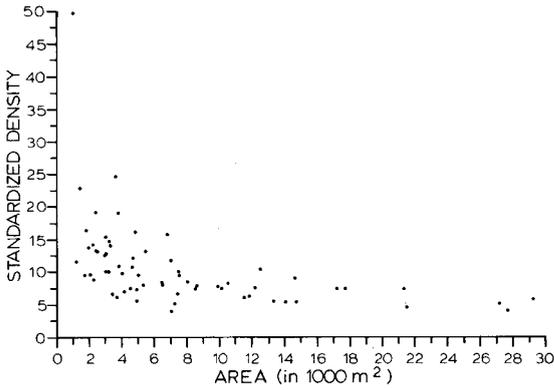


FIGURE 5. Standardized community density of the 69 shelterbelts plotted against the area of those shelterbelts. Standardized density represents the number of birds per 984.2 m<sup>2</sup>, the smallest shelterbelt studied.

ear relationship (Fig. 6) with a power function slope ( $z = .923$ ) that was not significantly different ( $P > .10$ ) from 1.0. This suggests that abundance increased proportionally to area, but the arithmetic intercept (6.404; Fig. 6) was marginally different ( $P < .10$ ) from the origin, demonstrating that the relationship was close, but not quite proportional; there still existed a very slight decrease in density with increasing area.

#### HABITAT DIVERSITY AND ISOLATION

Vegetation diversity, or other measures of habitat diversity, have been suggested as better predictors of species numbers than area, although habitat diversity and area usually are confounded (Power 1972, 1975, 1976, Harris 1973, Lack 1973, Amerson 1975, Johnson 1975). The insignificant ( $P > .10$ ) correlations of area with understory density ( $r = .033$ ), shrub layer height ( $r = .040$ ), canopy height ( $r = .022$ ), canopy coverage ( $r = .139$ ), and ground coverage ( $r = .090$ ) demonstrate the essential independence of area and habitat structure in shelterbelts. Habitat factors did explain additional variation in species numbers once the effect of area was removed (Martin and Vohs 1978). However, area was more important than habitat. For instance, vegetation diversity was correlated with species numbers ( $r = .238$ ,  $P < .05$ ) but the correlation was much less ( $P < .001$ ) than the correlation of species numbers with area ( $r = .774$ ).

Degree of isolation of an island also has been suggested as a determinant of the diversity and abundance of species present (Johnson 1975, Diamond et al. 1976, Gilpin and Diamond 1976). Distance to nearest

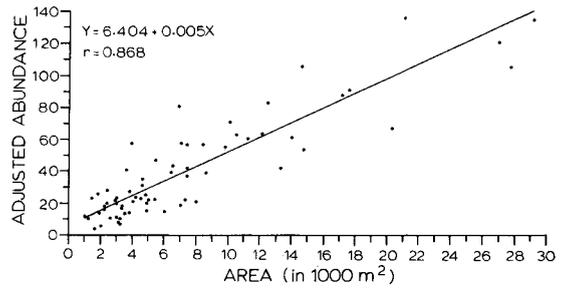


FIGURE 6. Total community abundance (less the abundances of Common Grackles, House Sparrows, and American Robins) from each of the 69 shelterbelts plotted against area. All abundances are based on the average of 1976 and 1977 spring migration censuses. The correlation is highly significant ( $P < .001$ ).

other forest island was measured for each shelterbelt and multiple regression analysis indicated this measure did not explain any additional ( $P > .10$ ) variation in abundance, species numbers or diversity.

#### DISCUSSION AND CONCLUSIONS

Transients are less selective in their habitat choice than residents (Laursen 1976) because migration causes them to encounter and use a wider variety of habitats. Migrants, however, often select habitats that superficially resemble their breeding habitat (MacArthur 1958, Morse 1968, Parnell 1969, Power 1971, Lack and Lack 1972, Lack 1976, Hamilton and Noble 1975). In other studies of islands, habitat diversity has been suggested as a better predictor of species numbers than area, but the two variables usually are confounded. The homogeneous nature of shelterbelt vegetation caused a low association between area and habitat structure, allowing the importance of area to be isolated. Habitat structure influenced migrant diversity and abundance in shelterbelts (Martin and Vohs 1978), but area was the most important determinant.

Area was as important during migration as during breeding. The correlation between species numbers and area during spring migration ( $r = .818$ ) was as high as during the breeding season ( $r = .830$ ; Martin 1980). Correlations between abundance and area also were similar during migration ( $r = .811$ ) and breeding ( $r = .789$ ; Martin 1980). Species and individuals may be expected to disperse themselves within and among stands of habitat during breeding owing to the need for spatial and ecological isolation of food resources for the family (Kluyver and Tinbergen 1953, Glas 1960, Cody 1974, Saitou 1976). It is less clear,

however, why migrants might be dispersed since they generally are considered to be more social than during breeding (Morse 1970). The observed species-area and abundance-area relationships which occurred in South Dakota shelterbelts could be a result of random (passive) processes (Simberloff 1970, Cox and Ricklefs 1977), visual selection, or behavioral interactions.

#### PASSIVE DISPERSAL

Migrants could be passively dispersed across the plains landscape; if so, belts that are more isolated should contain more birds than those which are close to other islands. Conversely, migrants may select areas where forest islands are in close proximity. In this case, abundance should be lower in isolated belts. The fact that the distance to the nearest other forest island did not explain any additional variation in abundance, species numbers, or diversity suggests that the even dispersion of birds among belts must be a direct response to area or some factor related to area.

Migrants could be passively dispersed relative to area of shelterbelts; larger shelterbelts simply accumulate more individuals and species. This possibility is hard to prove or disprove. However, the regular (linear) increase of abundance with area, regardless of proximity of other islands, makes the dispersion seem too even to occur completely by passive means. In addition, the modification of migrant diversity and abundance due to vegetation diversity and other habitat factors (Martin and Vohs 1980) shows that migrants are selecting the islands they use for resting and feeding.

#### VISUAL EFFECTS

Selection of an island could be based partly on the visual effect of area. Large wooded tracts are more conspicuous than smaller tracts and, therefore, may attract more birds. However, if birds select large islands, then a disproportionate number of individuals and species would colonize the larger islands and superlinear relationships would be predicted. The visual effect of area is undoubtedly a causal factor for the observed area relationships. However, the linear abundance-area function and the sublinear species-area function indicate that the visual cue of area does not fully explain the area relationships.

#### BEHAVIORAL INTERACTIONS

Even dispersion among belts could be caused by behavioral interactions among

the birds. As more individuals colonize a shelterbelt, they encounter each other more frequently and the habitat may become less suitable (Fretwell and Lucas 1969) if food is limited.

*Species numbers.* Schoener (1976) suggested that if conspecific individuals interact to share resource quantities that are a function of area, then they should follow a model in which the slope of the species-area relationship,  $z$ , is derived by the equation:  $z = 1 - (1/(2 - S/P))$ , where  $S$  is species number and  $P$  is the source pool size of potential colonists. This equation shows that  $z$  should approach, but not exceed, 0.5 when the numbers of coexisting species ( $S$ ) are limited to some small size relative to the number of species available to colonize ( $P$ ).

Slopes of the species-area relationship for 1976 and 1977 were slightly below 0.5. These slopes should have been lowered somewhat due to the presence of species that did not rely on food within belts. If species are not limited by food within the belt, then nearly equal numbers of species could be expected at all shelterbelt sizes; for these birds the species-area slope would approach 0. Granivores and omnivores doubtless were able to feed in surrounding grasslands, more than insectivores, and did show lower slopes. In addition, the slope for the entire community was lower in 1977 when granivores and omnivores comprised a greater proportion of the avifauna. Insectivores were the most restricted to feeding within shelterbelts and the slope of their species-area relationship did not differ ( $P > .10$ ) from 0.5 (Fig. 1).

Calculation of the species-area slopes through regression provides an estimate of the average value throughout the range of island areas. This assumes that the slope is constant throughout the range of areas, which may not be a valid assumption (Schoener 1976). Since the range of areas of shelterbelts is small, however, this bias may be minimized. If the average number of species of a food habits group found in all study belts is used as an estimate of  $S$  and the total number of species of that food habits group found during this study as an estimate of  $P$ , the equation derived by Schoener (1976) can be used to predict  $z$ . Values of 0.46 and 0.48 were predicted for insectivores in 1976 and 1977, respectively, and these are not significantly different ( $P > .10$ ) from observed values (Fig. 1).

Predicted slopes for granivores were 0.25 and 0.26 in 1976 and 1977, respectively.

These predictions are higher ( $P < .01$ ) than the observed values (Fig. 1). These data illustrate that granivores, which presumably were limited the least to foraging within shelterbelts, fitted the model for interacting species very poorly. Insectivores presumably were restricted the most to feeding within shelterbelts and they showed a close fit to the interactive model. Furthermore, slopes for insectivores during migration were not different ( $P > .10$ ) from the slope (0.515; Martin 1980) found during the breeding season, even though the source pool was much larger in spring (41 species) than during breeding (18 species; Martin 1980).

*Total abundance and density.* If migrants interact to disperse themselves relative to food supply, then abundance should increase proportionally with area, if food supply is proportional to area. Total abundance did not increase proportionally to area, resulting in a curvilinear decrease in density with increasing area (Fig. 5). However, most of the excess density of birds in small shelterbelts resulted from vagrant species that did not feed within the confines of the shelterbelts. Subtraction of the abundances of the most common vagrant species resulted in a linear relationship between abundance and area (Fig. 6) that was nearly proportional. This suggests that migrants were dispersed among shelterbelts as a function of food supply.

*Causes of food resource limitation.* Food supply could be limited during migration because food space is limited by island size and because of a great demand for food, a small supply, and overlapping food habits. The demand for food in an area is high because the number of transient individuals is high and because migrants strongly need to replenish lost fat stores during the day (Berthold 1975, Rappole 1976). Food habits of migrants may overlap because 70–80% of the birds in shelterbelts are insectivorous or omnivorous. Finally, little food is available during spring because its production has just begun. Dispersion of migrants among belts may thus represent the best means for replenishing their energy reserves.

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*Department of Wildlife and Fisheries Sciences, South Dakota State University, Brookings, South Dakota 57007. Present Address: Department of Ecology, Ethology and Evolution, University of Illinois, Vivarium Building, Champaign IL 61820. Accepted for publication 19 February 1980.*

APPENDIX. Food habits classification and the number of plots in which each bird species was found during 1976 and 1977 spring migration seasons in 69 eastern South Dakota shelterbelts.

Species	F <sup>a</sup>	Total	1976	1977
Common Grackle ( <i>Quiscalus quiscula</i> )	G	129	64	65
Mourning Dove ( <i>Zenaida macroura</i> )	G	118	51	67
American Robin ( <i>Turdus migratorius</i> )	O	113	56	57
Brown Thrasher ( <i>Toxostoma rufum</i> )	I	93	51	42
House Sparrow ( <i>Passer domesticus</i> )	O	82	38	44
American Goldfinch ( <i>Carduelis tristis</i> )	G	60	31	29
Western Kingbird ( <i>Tyrannus verticalis</i> )	I	58	28	30
House Wren ( <i>Troglodytes aedon</i> )	I	52	28	24
Empidonax flycatchers ( <i>Empidonax</i> spp.)	I	52	34	18
Orchard Oriole ( <i>Icterus spurius</i> )	I	46	22	24
Clay-colored Sparrow ( <i>Spizella pallida</i> )	G	45	29	16
Chipping Sparrow ( <i>Spizella passerina</i> )	O	44	21	23
Swainson's Thrush ( <i>Catharus ustulatus</i> )	I	44	49	15
Red-winged Blackbird ( <i>Agelaius phoeniceus</i> )	O	39	22	17
Eastern Kingbird ( <i>Tyrannus tyrannus</i> )	I	37	24	13
Yellow Warbler ( <i>Dendroica petechia</i> )	I	37	20	17
Brown-headed Cowbird ( <i>Molothrus ater</i> )	O	34	17	17
Song Sparrow ( <i>Melospiza melodia</i> )	O	33	16	17
Common Yellowthroat ( <i>Geothlypis trichas</i> )	I	32	18	14
Blue Jay ( <i>Cyanocitta cristata</i> )	O	27	14	13
Common Flicker ( <i>Colaptes auratus</i> )	I	27	19	8
Tennessee Warbler ( <i>Vermivora peregrina</i> )	I	26	15	11
Northern Oriole ( <i>Icterus galbula</i> )	I	20	15	5
Starling ( <i>Sturnus vulgaris</i> )	O	17	12	5
Yellow-rumped Warbler ( <i>Dendroica coronata</i> )	I	17	10	7
Gray Catbird ( <i>Dumetella carolinensis</i> )	I	16	11	5
American Redstart ( <i>Setophaga ruticilla</i> )	I	16	13	3
Rose-breasted Grosbeak ( <i>Pheucticus ludovicianus</i> )	O	15	11	4
Black-capped Chickadee ( <i>Parus atricapillus</i> )	I	14	12	2
Red-headed Woodpecker ( <i>Melanerpes erythrocephalus</i> )	I	14	7	7
Harris' Sparrow ( <i>Zonotrichia querula</i> )	O	13	11	2
Eastern Meadowlark ( <i>Sturnella magna</i> )	O	13	8	5
Eastern Wood Pewee ( <i>Contopus virens</i> )	I	12	10	2
Wilson's Warbler ( <i>Wilsonia pusilla</i> )	I	12	10	2
White-crowned Sparrow ( <i>Zonotrichia leucophrys</i> )	O	9	7	2
Downy Woodpecker ( <i>Picoides pubescens</i> )	I	8	6	2
Ruby-crowned Kinglet ( <i>Regulus calendula</i> )	I	8	6	2
Black-and-white Warbler ( <i>Mniotilta varia</i> )	I	8	6	2
Gray-cheeked Thrush ( <i>Catharus minimus</i> )	I	8	5	3
Common Crow ( <i>Corvus brachyrhynchos</i> )	O	7	4	3
Blackpoll Warbler ( <i>Dendroica striata</i> )	I	6	5	1
Black-headed Grosbeak ( <i>Pheucticus melanocephalus</i> )	O	6	4	2
Rufous-sided Towhee ( <i>Pipilo erythrophthalmus</i> )	O	4	3	1
Ovenbird ( <i>Seiurus aurocapillus</i> )	I	4	3	1
Orange-crowned Warbler ( <i>Vermivora celata</i> )	I	4	4	—
Magnolia Warbler ( <i>Dendroica magnolia</i> )	I	4	4	—
Black-billed Cuckoo ( <i>Coccyzus erythrophthalmus</i> )	I	4	4	—
Warbling Vireo ( <i>Vireo gilvus</i> )	I	3	2	1
Chestnut-sided Warbler ( <i>Dendroica pensylvanica</i> )	I	3	2	1
Solitary Vireo ( <i>Vireo solitarius</i> )	I	2	1	1
Mockingbird ( <i>Mimus polyglottos</i> )	O	2	1	1
Yellow-headed Blackbird ( <i>Xanthocephalus xanthocephalus</i> )	O	2	2	—
White-throated Sparrow ( <i>Zonotrichia albicollis</i> )	O	2	—	2
Hairy Woodpecker ( <i>Picoides villosus</i> )	I	2	—	2
Lincoln's Sparrow ( <i>Melospiza lincolni</i> )	O	1	1	—
Palm Warbler ( <i>Dendroica palmarum</i> )	I	1	1	—
Bay-breasted Warbler ( <i>Dendroica castanea</i> )	I	1	1	—
Philadelphia Vireo ( <i>Vireo philadelphicus</i> )	I	1	1	—
Indigo Bunting ( <i>Passerina cyanea</i> )	I	1	1	—
Yellow-breasted Chat ( <i>Icteria virens</i> )	I	1	1	—
Black-billed Magpie ( <i>Pica pica</i> )	O	1	1	—
Cape May Warbler ( <i>Dendroica tigrina</i> )	I	1	—	1
Canada Warbler ( <i>Wilsonia canadensis</i> )	I	1	—	1
Black-throated Green Warbler ( <i>Dendroica virens</i> )	I	1	—	1
Nashville Warbler ( <i>Vermivora ruficapilla</i> )	I	1	—	1

<sup>a</sup> G = granivorous, O = omnivorous, I = insectivorous.