LIMITATION IN SMALL HABITAT ISLANDS:
CHANCE OR COMPETITION?[1]

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ABSTRACT.—Relationships between area and number of species and individuals of birds were examined for 69 forest islands (shelterbelts) in eastern South Dakota for 2 yr. The relatively homogeneous habitat of shelterbelts allowed assessment of area effects with minimal bias due to habitat heterogeneity. The number of species increased with area with a steep slope ($z = 0.39$). The total numbers of individuals increased linearly with area but not proportionally; density decreased with increasing area. The total numbers of individuals increased proportionally with area (constant density with increasing area) when abundances of three common species that foraged outside of shelterbelts were excluded. This suggested that individuals interacted to distribute themselves among shelterbelts relative to resources. A model developed for interacting species was applied to three ecological (primary food habits) groups; the group (insectivores) that was most restricted to feeding within shelterbelts provided a good fit to the model, while the group (granivores) that was least restricted to feeding within shelterbelts provided a poor fit. Minimum area requirements restricted colonization for some species in smaller shelterbelts, but species often were absent from shelterbelts larger than their minimum size requirements. The number of species that coexisted in a moderately small ($3,100\ m^2$) shelterbelt represented approximately one-third of the number of common species for which minimum size requirements were exceeded. Absences were not due simply to habitat preferences or isolation.

The total numbers of species and individuals that coexisted within a shelterbelt were limited. Limitation led to community compositions that minimized coexistence of species belonging to the same guild; the number of species per guild was less than that predicted by chance. In addition, species that belonged to guilds with many members were absent from a greater proportion of communities than species that belonged to guilds with fewer members. Occurrence among communities also was a strong function of chance (i.e. which species arrives first or accidentally missing communities), because species were absent from at least a proportion of communities predicted by chance. Finally, presence and absence of species among communities was attributed partly to habitat conditions. In short, the numbers of individuals and species within a community and the ecological structure of the community were dictated by competitive interactions, while distribution patterns of individual species among communities were a function of the combined effects of habitat, chance, and competitive interactions. *Received 8 February 1980, accepted 17 March 1981.*

THE number of species inhabiting islands increases with island area (Preston 1962a, b; Vuilleumier 1970; Diamond 1973; Juvik and Austring 1979; Martin 1980). Some have suggested that area *per se* is an important determinant of species numbers because of its effect on immigration and extinction rates (MacArthur and Wilson 1963, 1967; Simberloff 1972, 1976; Schoener 1976). Others have pointed out that environmental heterogeneity increases with area and have argued that the species-area relationship is a result of increasing area providing environmental requirements of increasing numbers of species (Power 1972, 1975, 1976; Harris 1973; Amerson 1975; Johnson 1975). The absolute importance of area is difficult to assess, because it is often confounded with environmental variables such as elevation and habitat

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diversity. Untangling these variables is arduous, because islands that differ in size generally differ in degree of environmental heterogeneity as well. Simberloff (1976) circumvented this problem, however, by experimentally altering the area of the same island and documenting that area alone could determine species numbers.

Increased species numbers on larger islands may reflect limitation, due to a reduced carrying capacity, on smaller islands. No one, however, has examined whether or not species numbers are in fact limited relative to area. Limitation of island populations by carrying capacity provides a theoretical foundation for invoking competition as a factor structuring island communities. Many authors have argued that the composition of species on islands is structured by competitive interactions (Grant 1966, 1968, 1969; Moreau 1966; Diamond 1975). Further, Diamond (1975) suggested that some species are competitively excluded by combinations of other species, causing specific distribution patterns among islands. Others have challenged these views and have suggested that species distribution patterns and community compositions can be explained by random processes (Simberloff 1970, Cox and Ricklefs 1977, Strong et al. 1979; but see Grant and Abbott 1980). The controversey is unresolved as yet, partly because these views have tended to be one-sided; little regard has been given to the possible interaction of competition and chance. An integration of the effects of chance, competition, and habitat is needed in examinations of island patterns. Here I attempt such an integration for birds of 69 shelterbelts (forest islands) in eastern South Dakota.

Shelterbelts provide a unique opportunity to evaluate these factors for two reasons. First, shelterbelts are man-made habitats with similar structural configurations (Martin and Vohs 1978). While habitats of these islands are not entirely homogeneous, several measures of habitat structure exhibit no consistent trend with area (see below). Thus, the importance of area in influencing species numbers and abundances can be assessed with minimal bias due to habitat heterogeneity. Second, shelterbelts represent very small (0.1–2.9 ha) forest islands. Small islands provide a unique situation, because some bird species can be precluded from successful colonization simply because islands are smaller than territory size requirements. This fact led Galli et al. (1976) and Rusterholz and Howe (1979) to suggest that the increase in the number of bird species with increasing area of small islands is caused by the progressive encounter of minimum size requirements for increasing numbers of species. While this explanation accounts for absences from islands smaller than minimum size requirements, however, it does not explain why species are often absent from islands larger than minimum size requirements. Again, the roles of habitat, chance, and competition must be assessed to answer this question. In this paper, I will examine the roles that area, isolation, habitat, chance, and competition play in explaining patterns of species distributions among, and composition of species within, small forest islands in South Dakota.

STUDY AREA AND METHODS

Shelterbelts are rows of planted trees and shrubs established on prairies to reduce wind erosion. These small islands of forest are surrounded by fields of cultivated and natural grasses and thus represent true habitat islands. There is approximately one shelterbelt per 115 ha in eastern South Dakota, representing 1.1% of the land area (Walker and Suedkamp 1977). The 69 shelterbelts examined in this study were scattered throughout South Dakota east of the Missouri River. Average interisland distance was 554 m. Vegetation diversity of these shelterbelts was low and included only 15 tree and 14 shrub species.

The structural complexity of the vegetation was quantified for each shelterbelt. Ground and canopy

TABLE 1. Mean number of species (± standard error) for each size class ($n = 23$ shelterbelts per size class) and for all plots ($n = 69$) for the 1976 and both 1977 breeding season censuses, and the composite average of the 3 censuses.

Size class	1976	1977-1	1977-2	Composite
1	7.43 ± 0.56	6.39 ± 0.39	6.13 ± 0.33	6.65 ± 0.44
2	7.61 ± 0.43	7.26 ± 0.38	7.74 ± 0.39	7.54 ± 0.40
3	11.61 ± 0.77	11.83 ± 0.62	12.22 ± 0.63	11.97 ± 0.63
All	8.97 ± 0.40	8.49 ± 0.38	8.70 ± 0.41	8.72 ± 0.83

coverages were measured by observing presence or absence of vegetation through an ocular tube for 50 sightings (James and Shugart 1970). The density of understory vegetation cover was measured using a density board (Giles 1971). Readings were taken between each planted row at three locations in each belt. Thus, the number of readings $= 3(n - 1)$, where n is the number of rows. The measurement of percentage slope, from a fixed distance, allowed an estimation of canopy height. Grass and shrub layer heights were measured directly. Due to the even spacing of vegetation in shelterbelts, stem densities of planted tree and shrub species and of snags were determined by counting all trees and shrubs in each of two transects 50 m in length and spanning the entire width of each belt. Finally, distances to nearest other forest islands, water, livestock feedlots, human residences, and roads were quantified. Stepwise multiple regression was applied to these habitat features to delineate the subsets of features that best predicted presence and abundances of the 14 most common bird species. Results of these analyses are presented elsewhere (Martin 1978, Martin and Vohs 1978).

Bird species abundances were monitored during the 1976 and 1977 breeding seasons using the Emlen (1971) transect method, supplemented by direct counts (see Martin 1980 for a more detailed description). The long, narrow configuration of shelterbelts allowed the determination of the absolute number of species by walking the length of the belt upon completion of the transects and tallying any species unrepresented in the transects. The presence of a territorial male was taken as evidence of residence of a breeding pair and tallied as two individuals. Censuses were conducted during a brief time period (the last week in May to the last week in June) to determine abundances prior to recruitment of young and to minimize temporal shifts in community composition. All 69 shelterbelts were censused once in 1976 and twice in 1977.

Birds were categorized by primary food habits (insectivores, omnivores, and granivores; Martin et al. 1951, Willson 1974, pers. obs.) to evaluate shifts in ecological structure with shelterbelt area. Two-factor analysis of variance was used to analyze changes in abundance and species numbers among food habits groups and with changes in area. Shelterbelts were grouped into three size classes to allow these analyses. Class 1 included the 23 smallest shelterbelts ($\bar{x} \pm \text{SE} = 2,553 \pm 162$ m²), class 2 the 23 intermediate shelterbelts ($5,417 \pm 248$ m²), and class 3 the largest 23 shelterbelts ($14,616 \pm 1,324$ m²). All analyses of differences among size class groupings were based on analysis of variance or t-tests. All regressions were based on the continuous range of the 69 shelterbelts.

Species-area and abundance-area relationships were examined by three regression functions: log-log (power), semi-log (exponential), and untransformed (linear). Determination of the best-fit function was based on correlation coefficients. It is misleading to compare the correlation of the power function with correlations of the other two functions directly, 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. All correlations are significant at $P < 0.001$ unless otherwise noted. The additive importance of edge (length plus width) relative to area was examined through stepwise multiple regression by forcing edge after area and then forcing area after edge to compare respective amounts of additional variation explained. Finally, I use the term "community" synonymously with "island" or "shelterbelt," and a proportional relationship is synonomous with isometric.

RESULTS AND DISCUSSION

Species numbers.—Mean numbers of species were not different ($P < 0.05$) among censuses within size classes (Table 1). Thus, data were pooled over all censuses.
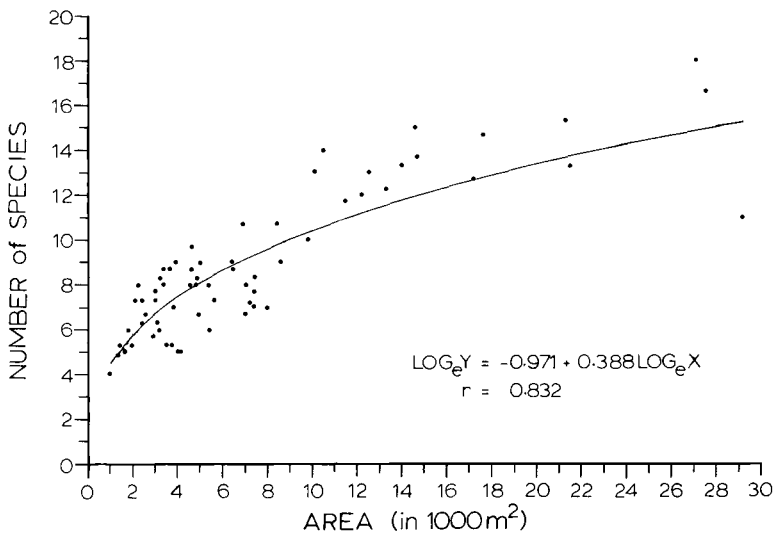
Fig. 1.   The number of bird species plotted against area for 69 shelterbelts. The number of species in each shelterbelt is based on the average of 1976 and 1977 breeding season censuses. The correlation exhibited is highly significant ($P < 0.001$).

Species numbers increased ($P < 0.001$) with area (Fig. 1) with a steep slope ($z = 0.388$), although fits of power ($r = 0.844$) and exponential ($r = 0.820$) functions were similar. The slope represents the average rate of increase in species number over all plots. Variation in species number caused by factors unrelated to area may modify the species-area slope and determination of the appropriate function. There were three possible sources of variation: sampling error, variation in habitat quality, and uneven representation of plot sizes. An analysis of species numbers between both censuses of all plots during 1977 produced a high correlation ($r = 0.959$), with a slope of 1.000 and an intercept (0.219) that was not different ($P < 0.001$) from 0, indicating that sampling error was low or at least consistent. The homogeneity of shelterbelt vegetation (see below) suggests that error from habitat variation is minimal. Under-representation of large plots relative to smaller plots slightly modified the slope and fit of functions. The slope for plots less than 1 ha ($z = 0.404$, $n = 52$) is similar to the slope for all plots, while the slope for plots greater than 1 ha ($n = 17$) is considerably lower ($z = 0.290$). The power function provides a better fit ($P < 0.02$) than the exponential function ($r = 0.793$) for plots less than 1 ha.

Many bird species inhabiting shelterbelts are edge species, and, as a result, the amount of edge may be important. The long, narrow configuration of shelterbelts results in a strong correlation between edge and area ($r = 0.855$). Edge increases more slowly than area, however, because larger belts tend to be wider ($r = 0.626$). Species numbers were highly correlated with edge ($r = 0.685$), but the correlation was less ($P < 0.02$) than with area. Further, edge explained an insignificant ($P = 0.306$) amount of additional variation (0.7%) when added after area, but area explained a significant ($P < 0.001$) amount of additional variation (11.8%) when added after edge. Thus, area appears to be more important than edge in determining species numbers.

Relationships of food habits groups.—The number of species within each food
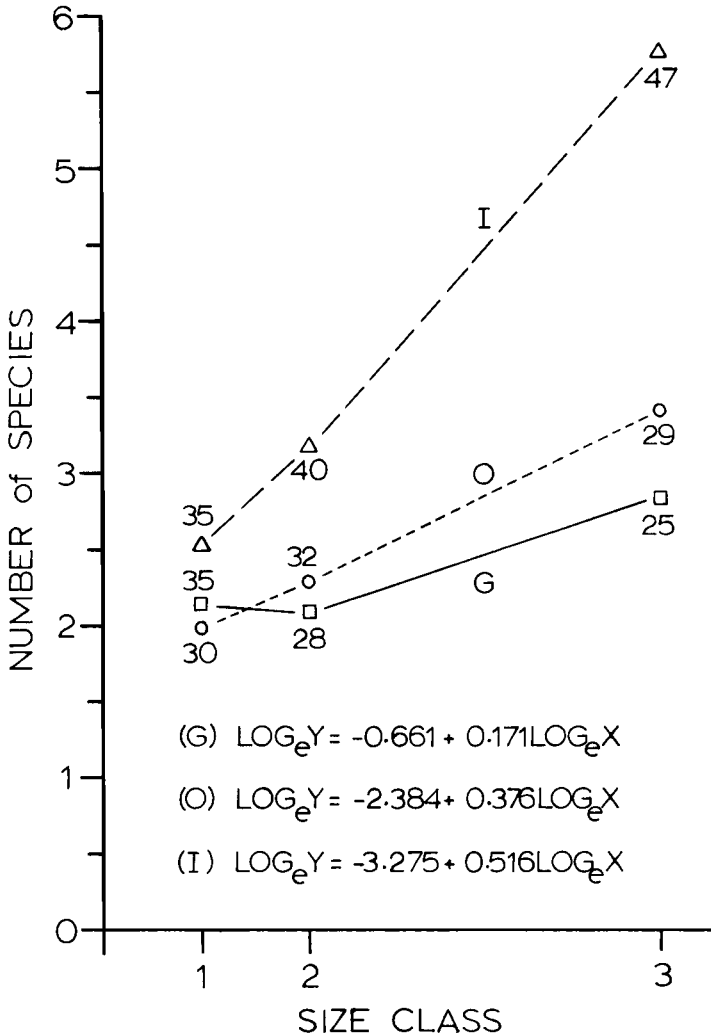
Fig. 2. Mean number of species of granivores (G), omnivores (O), and insectivores (I) censused during 1976 and 1977 in each of three increasing size classes of shelterbelts. The numbers indicate mean percentage representation of each food habits group for each size class. The regression equations are based on all 69 shelterbelts and all are highly significant ($P < 0.001$).

guild increased [$F(2, 22) = 57.31$, $P < 0.001$] with area (Fig. 2), but species number differed among groups ($F = 36.06$, $P < 0.001$), as did the rate of increase in the number of species with area ($F = 13.67$, $P < 0.001$). Regression slopes were significantly different in the order insectivores > omnivores > granivores (by t-tests, $P < 0.01$). These differences resulted in insectivores representing an increasing proportion of species, granivores a decreasing proportion, and omnivores changing only slightly as plot size increased (Fig. 2).

The number of individuals in each food habits group also increased ($F = 14.97$, $P < 0.001$) with area (Fig. 3) and differed among groups ($F = 30.71$, $P < 0.001$). Granivores comprised the greatest proportion of individuals in the communities,
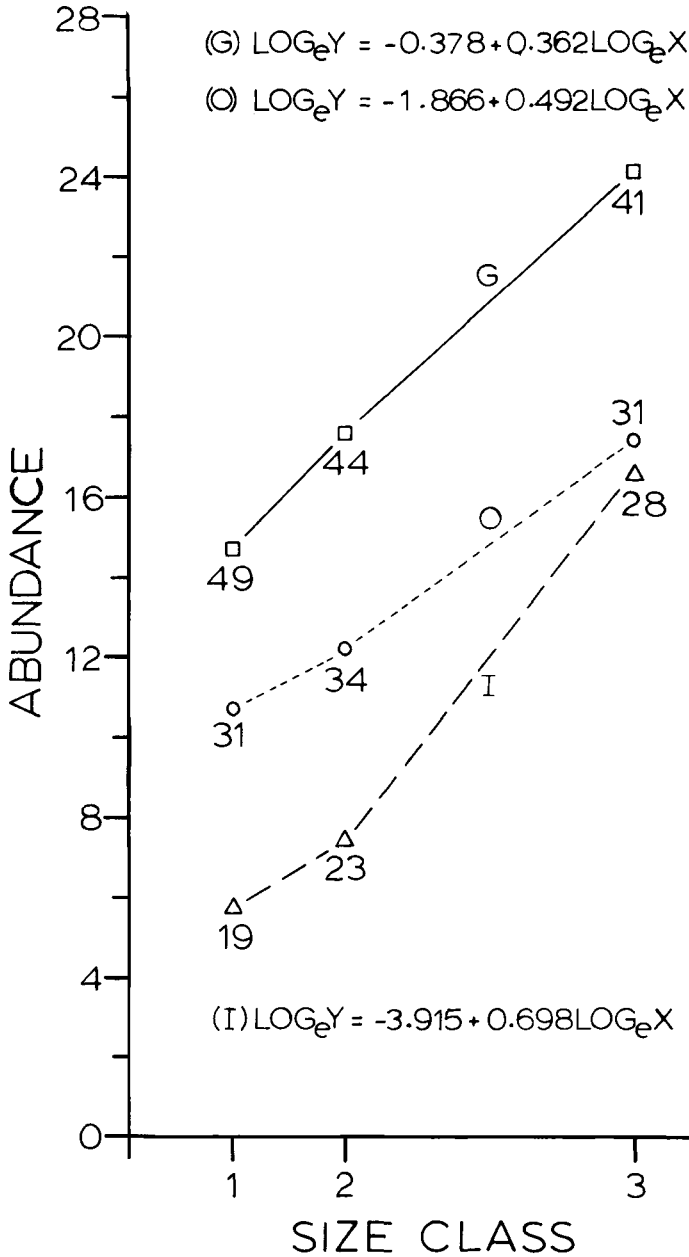
Fig. 3. Mean abundance of granivores (G), omnivores (O), and insectivores (I) censused during 1976 and 1977 in each of three increasing size classes of shelterbelts. The numbers indicate the mean percentage representation of each food habits group for each size class. The regression equations are based on all 69 shelterbelts and all are highly significant ($P < 0.001$).

however, even though the porportional representation of granivores decreased and insectivores increased with increasing area (Fig. 3).

Total abundance.—The total number of individuals in a shelterbelt increased linearly with area (Fig. 4), the linear correlation ($r = 0.789$) being higher ($P < 0.02$)
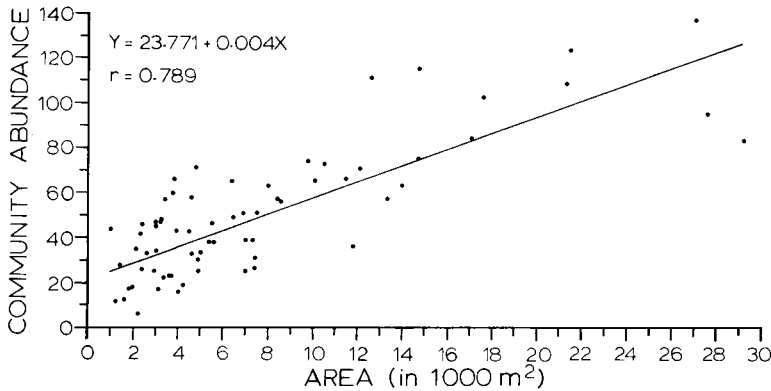
Fig. 4. Community abundance plotted against area for all shelterbelts. Community abundance represents the total number of individuals censused in each shelterbelt averaged over 1976 and 1977 breeding seasons. The correlation exhibited is highly significant ($P < 0.001$).

than for the power function ($r = 0.658$). May (1975) and Diamond and Mayr (1976) suggested that abundance should increase proportionally with area, although I know of no published study that illustrates this relationship. Abundance of shelterbelt birds did not increase proportionally with area. The exponent of the power function should equal 1.0 (e.g. $D = cA^1$, where D is abundance, A is area, and c is the intercept), and the intercept of the arithmetic relationship should pass through the origin for proportional relationships. The exponent ($z = 0.643$) was greater than 0.5 ($P < 0.05$, $t = 1.959$) but less than 1.0 ($P < 0.001$, $t = 6.102$) for shelterbelt birds. Abundance increased more slowly than area; a 167% increase in area yielded a 100% increase in abundance. Thus, there were more individuals per unit area (greater density) in smaller shelterbelts (Fig. 5).

The greater densities in smaller shelterbelts were due mostly to species that rely on food sources outside of shelterbelts. The number of individuals of the most common vagrant species [i.e. Common Grackle (*Quiscalus quiscula*), House Sparrow (*Passer domesticus*), American Robin (*Turdus migratorius*)], which do not respond to area (Table 2), were subtracted from the total number of individuals in the community to provide a rough index of the number of individuals that forage primarily within shelterbelts. There are additional species that obtain part of their food requirements outside of shelterbelts, but they should be partially compensated for, because the three most common vagrants obtain some of their food within shelterbelts. An ideal index would allow subtraction of a certain fraction of each species' abundance based on the fraction of time it spent outside of shelterbelts, but such information was not obtained. This analysis, however, does support the hypothesis that the number of individuals that concentrate their feeding within shelterbelts increased proportionally with area and density remained constant for increasing area. The adjusted abundances increased with area with a power function slope ($z = 0.864$) that did not differ ($P > 0.05$, $t = 1.505$) from 1.0 and an arithmetic intercept (4.337) that did not differ ($P > 0.05$, $t = 0.942$) from 0 (Fig. 6).

Area was more important than edge in determining the number of individuals in a shelterbelt. Abundance was more highly ($P < 0.02$) correlated with area ($r = 0.889$) than with edge ($r = 0.780$). Further, edge explained an insignificant ($P = 0.194$) amount of additional variation (0.6%) when added after area, but area ex-
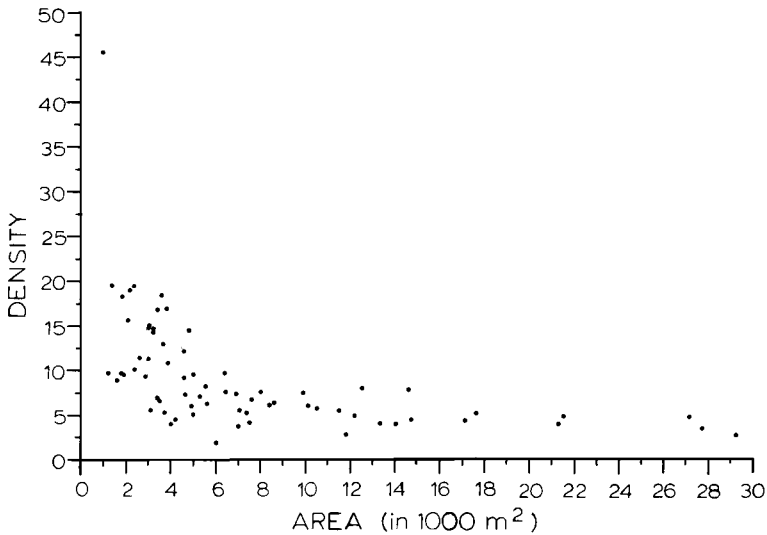
Fig. 5.   Standardized community density plotted against area for 69 shelterbelts. Standardized density represents the number of birds per 984 m² (the smallest shelterbelt).

plained a significant ($P < 0.001$) amount of additional variation (15.0%) when added after edge.

Species relations.—The strong relationship with area exhibited by many species (Table 2) can be attributed to territoriality. Some species require a minimum area before they occupy a belt. Minimum size requirements may be complicated because of the edge effect. As a result, abundances of species were separately analyzed with respect to length, width, and total perimeter (edge) of shelterbelts. The increase in abundance of each species was more highly correlated with area than with width or edge. Several species exhibited correlations with length that were as high as for area, although none illustrated a higher correlation ($P > 0.10$) to length than area (Table 2). Thus, area was the most appropriate parameter for determining minimum size restrictions.

Only 6–7 species, on the average, coexisted in shelterbelts 3,100 m² in area (Fig. 1), although 3,100 m² was sufficient to meet the minimum area requirements of 20 common species plus other uncommon species. New Jersey woodlots similarly had only 6–7 species on plots 7,000 m² in area, where 20 common or relatively common species could coexist based on minimum size requirements (Galli 1975). When analyzed over similar area ranges, the species-area coefficient of shelterbelts (-0.971) illustrates that there are 1.9 times as many species as found in New Jersey woodlots ($S = -1.878A^{0.389}$) for any given area (cf. Gould 1979). The greater richness of shelterbelts may be due to the greater amount of edge and associated resources in shelterbelts as compared to New Jersey woodlots. Regardless of whether the minimum area threshold for a source pool size of 20 common species is 3,100 or 7,000 m², when that size is reached, the actual number of coexisting species is similar between forest islands in South Dakota and New Jersey. The number that coexist, however, is less than one-third the number of species available to colonize at that area.

TABLE 2. Area of the smallest shelterbelt (Minimum area) inhabited by each of the 20 most common species and the number of shelterbelts smaller (Number smaller) than this minimum area, plus correlations of these species with area, length, and the number of species (NSPP) of each shelterbelt.

Species[a]	Minimum area (m²)	Number smaller	Correlations[b] Area	Length	NSPP
Common Grackle	984	0	0.149	0.090	0.312**
Mourning Dove	984	0	0.487***	0.418***	0.624***
American Robin	984	0	0.227	0.259	0.306*
House Sparrow	984	0	0.004	0.001	0.033
Orchard Oriole	2,094	6	0.533***	0.511***	0.724***
Brown Thrasher	3,004	14	0.653***	0.525***	0.587***
Western Kingbird	1,454	2	0.218	0.227	0.329**
Eastern Kingbird	1,454	2	0.533***	0.630***	0.650***
American Goldfinch	1,672	3	0.645***	0.555***	0.680***
Yellowthroat	3,004	14	0.365**	0.380**	0.521***
Red-winged Blackbird	1,672	3	0.189	0.181	0.315**
House Wren	2,264	7	0.455***	0.415***	0.506***
Brown-headed Cowbird	3,009	15	0.403***	0.485***	0.430***
Black-billed Cuckoo	4,555	28	0.680***	0.566***	0.640***
Song Sparrow	2,264	7	0.629***	0.586***	0.685***
Eastern Wood Pewee	3,004	14	0.288*	0.181	0.470*
Common Flicker	2,264	7	0.535***	0.404***	0.530***
Blue Jay	3,009	15	0.732***	0.671***	0.522***
Northern Oriole	3,000	13	0.299*	0.295*	0.356**
Warbling Vireo	2,411	10	0.392**	0.388**	0.576***

[a] Scientific names are presented in the Appendix.
[b] * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

Galli et al. (1976) and Rusterholz and Howe (1979) suggest that once minimum area requirements are met, habitat restricts the presence of species. Habitat suitability may preclude some species from colonizing, but it seems unlikely that the habitat of these islands is consistently unsuitable for two-thirds of the available species. Habitat restrictions were investigated in greater detail.

Subsets of measured habitat features that best predicted presence and abundance of each of the 14 most common species were delineated through stepwise multiple regression (see Methods). Minimum and maximum values of these habitat features were obtained for each species based on shelterbelts that they actually occupied. All shelterbelts that exceeded minimum size and included habitat features that were between minimum and maximum values obtained from shelterbelts actually occupied were considered to provide suitable habitat conditions. Finally, the predictive equations generated by multiple regression were applied to those belts considered to include suitable habitat conditions. The belt was then considered suitable when two or more individuals were predicted. This analysis assumes, along with all other studies of bird habitat preferences, that the habitat features considered to be important were the same, or related to the same, as those that birds select as important.

The results (Table 3) show that all species occupied fewer shelterbelts than were considered suitable based on the range of habitat conditions that these species actually occupied during the study. Only a few shelterbelts that were actually occupied were predicted as unsuitable. This lends credibility to the accuracy of the predictions and suggests that estimates may be somewhat conservative. These results suggest that habitat suitability is not always the factor explaining presence or absence of species in a given community.

Limitation of total species numbers.—Species may be absent from communities with suitable habitat conditions by chance (see below) or when the total number of
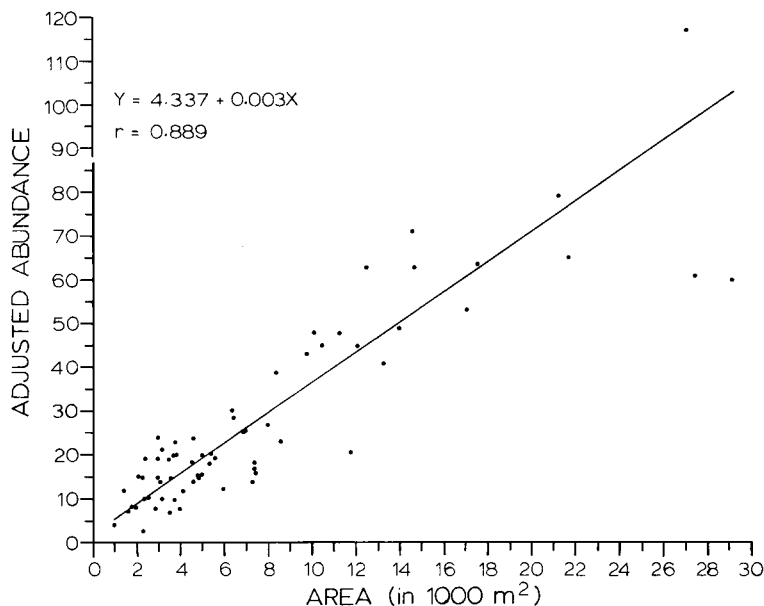
Fig. 6. Community abundance adjusted by subtraction of the abundances of Common Grackles, House Sparrows, and American Robins from each of the 69 shelterbelts plotted against area. All abundances are based on the average of 1976 and 1977 censuses. The correlation exhibited is highly significant ($P < 0.001$).

species that can coexist in communities is limited below the number available from the source pool. If the total number of species that can coexist within an island community (S) is limited and the species assemblage represents a random sample of the source pool, then the probability of any particular species occurring within that community (or the proportion of communities with the same S that are occupied) is equal to the number of coexisting species (S) divided by the source pool size (P). The proportion of communities occupied by any particular species increases with increasing S, because there is an increasing probability (S/P increases) of randomly drawing it as one of the S species for large S. As a result, the proportion of communities occupied by any given species should increase as an isometric (proportional) function of species number (i.e. $P_c = cS^1$, where S is total number of species in a community, P_c is the proportion of communities of a given S that are occupied, and c is a fitted constant), when the total number of species that can coexist is limited and presence of that particular species is based solely on chance. Thus, species should be absent from some communities with suitable habitat conditions when the total number of species that can coexist is limited and the number of suitable communities exceeds the number of communities expected to be occupied based on random sampling. Further, a species should be absent from fewer communities with suitable habitat conditions for high S than low S, because it is expected to occupy a higher proportion of communities of high S (i.e. higher S/P). Shelterbelt birds were absent from some communities with suitable habitat conditions (Table 3), and they were absent from fewer communities with suitable habitat conditions for high S (Table 4). These results suggest that the total number of species in a community is limited.

TABLE 3. Numbers of shelterbelts actually occupied and the number predicted as suitable based on habitat conditions. The differences show the greater number predicted as suitable than actually occupied. Shelterbelts that were occupied but that were not predicted as suitable are displayed as wrong predictions.

Species[a]	Actual	Suitable	Difference	Wrong
Mourning Dove	67	69	2	0
Common Grackle	68	69	1	0
American Robin	61	65	4	0
House Sparrow	54	65	11	0
Orchard Oriole	51	55	4	0
Brown Thrasher	43	51	8	0
Western Kingbird	35	44	9	1
Eastern Kingbird	35	40	5	0
Red-winged Blackbird	30	39	9	1
Yellowthroat	24	34	10	0
House Wren	21	32	11	0
Eastern Wood Pewee	15	29	14	0
Song Sparrow	19	31	12	1
Common Flicker	16	32	16	1

[a] Scientific names are presented in the Appendix.

Chance vs. interactions.—The proportion of communities occupied by shelterbelt bird species increased with increasing numbers of total species, but few increases were isometric (Fig. 7). Isometry of the relationship can be examined by calculating the power function slope; the relationship is isometric when the slope equals 1.0 (see above). An isometric relationship is expected only when occurrence is determined solely by chance (i.e. when all species combinations are compatible and all habitat conditions are suitable). In reality, chance occupations should be modified by habitat conditions and abundance of ecologically similar species. The effect of ecologically similar species was examined by assigning species to guild classifications following Root (1967), Karr (1971), and Willson (1974).

Only three species illustrated isometric relationships (z is not different from 1.0, $P > 0.10$). Two of these species (Fig. 7), Brown Thrasher (*Toxostoma rufum*) and Eastern Kingbird (*Tyrannus tyrannus*), belong to guilds with no other members. The third species, Orchard Oriole (*Icterus spurius*), shares its guild with one other

TABLE 4. Numbers of shelterbelts predicted as suitable but that were not occupied distributed among richness classes (see Fig. 7).

Species[a]	Richness classes								
	1	2	3	4	5	6	7	8	9
Mourning Dove		1			1				
Common Grackle				1					
American Robin			2	2	1				
House Sparrow			4	2	2	1		1	1
Orchard Oriole			1	2		1			
Brown Thrasher			1	3	2	1	1		
Western Kingbird			1	2	1	3	2		
Eastern Kingbird			1	3	1				
Red-winged Blackbird			2	1	1	3	2		
Yellowthroat			2	4	2	1	1		
House Wren			3	5	1	2			
Eastern Wood Pewee			4	5	1	2	1	1	
Song Sparrow			3	5	2		2		
Common Flicker			4	6	2	1	2	1	

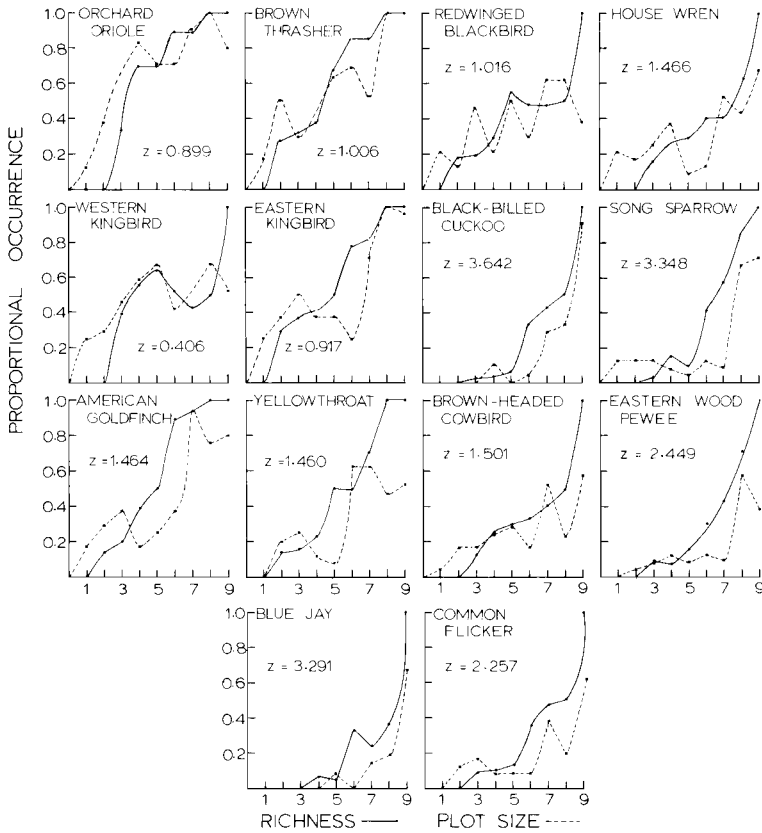[a] Scientific names are presented in the Appendix.

Fig. 7.   The proportion of shelterbelt bird communities that are divided into nine richness and size classes in which 14 common bird species occur. Richness classes represent shelterbelts of a set number of coexisting species. Each richness class represents an increase by two species, i.e. class 1 represents all shelterbelts with 1–2 total bird species and class 9 represents all shelterbelts with 17–18 bird species. Each class of plot sizes represents 8 shelterbelts of increasing size in the first 6 classes and 7 shelterbelts for the last 3 classes. z represents the log-log slope for the species richness-proportional occurrence relationship.

species, Warbling Vireo (*Vireo gilvus*), but the vireo is uncommon. All other species belong to guilds with two or more species, and all, except the Western Kingbird (*Tyrannus verticalis*) and Red-winged Blackbird (*Agelaius phoeniceus*), exhibit slopes that are significantly ($P < 0.05$) greater than 1.0. Species such as the Black-billed Cuckoo (*Coccyzus erythrophthalmus*) and Song Sparrow (*Melospiza melodia*), which belong to guilds with several member species, show high slopes ($z \gg 1$) and occur in much lower proportions of the communities than species that are the sole member of their guilds or that belong to guilds with only one or two members.

The low slopes of the Red-winged Blackbird and Western Kingbird may result from more direct interactions. The Song Sparrow and redwing share the same guild, but the redwing occurs in a greater proportion of communities than the Song Sparrow; redwings are less restricted to shelterbelts to forage. The redwing, however, illustrates a slight decrease in its proportional occurrence at the same richness class that the Song Sparrow begins to increase rapidly (Fig. 7). The Western Kingbird shares its guild with one other species [(Eastern Wood Pewee (*Contopus virens*)].

TABLE 5. Ratios of the number of species per guild (*S/G*) for the 10 largest shelterbelt communities (actual) and for communities with the same number of species generated by random procedures. Each random *S/G* ratio represents a mean based on 100 random communities. All actual *S/G* ratios are less (*P* < 0.001) than random *S/G* ratios.

Number of species	Actual *S/G*	Random *S/G*	SE
18	1.282	1.743	0.020
16	1.231	1.681	0.023
16	1.231	1.681	0.023
15	1.071	1.655	0.026
15	1.250	1.655	0.026
14	1.273	1.627	0.027
14	1.167	1.627	0.027
13	1.183	1.553	0.023
12	1.091	1.518	0.022
11	1.100	1.479	0.021

The Eastern Wood Pewee is a forest interior species and does not increase significantly until large plot sizes and species numbers are reached (Fig. 7). The Western Kingbird decreases in its proportional occurrence when the Eastern Wood Pewee begins to increase significantly.

These results suggest that the total number of species in a community is limited and the presence of any particular species is a function of both chance and competition. Species are absent from a proportion of communities expected by chance ($z = 1$) when they are the sole member of their guild. Species are absent from a greater proportion of communities than predicted by chance ($z > 1$) when they share their guild with other members, and, in general, species in increasingly larger guilds are absent from increasingly more communities than predicted by chance ($z \gg 1$).

Community structure.—The decreased proportion of communities occupied by species that belong to large guilds suggests that birds may avoid coexistence with ecologically similar species. If resource overlaps are minimized in shelterbelt bird communities due to reduced coexistence of guild members, then the number of species per guild should approach 1.0 for each community. The 69 shelterbelts averaged 1.06 species per guild. This low ratio indicates that species composition reflects minimum resource overlap among coexisting species. Random distribution of the few species in a community, however, might provide similar results (Simberloff 1970, Cox and Ricklefs 1977).

I used the random generation model of Simberloff (1970) to test whether these ratios could occur by chance. This model is based on randomly selecting species from a source pool to allow comparisons of ratios for the number of species per guild in random communities relative to actual communities. I generated 100 random communities for each real community. I applied the model only to the 10 largest shelterbelts because minimum size restrictions imposed by smaller shelterbelts complicated the determination of source pool size. I used all bird species found in the 69 study belts as the source pool. Other woodland bird species that should be able to use shelterbelts for nesting have been recorded in South Dakota. Their rarity in shelterbelt bird communities (as evidenced by their absence from all 69 belts during both years of study), however, signifies that they are of minor importance. Based on this source pool, all 10 belts had fewer (*P* < 0.001) species per guild than predicted by chance (Table 5). Thus, ordering of the communities to reduce resource overlaps is indicated.

Application of a model for interacting species.—Schoener (1976) presented models

for species that interacted and for species that did not interact to divide resource quantities. The interactive model fit more land-bird data sets than did the noninteractive model. Additional support for the interactive model is provided by Martin (in press). In his interactive model, the slope (z) of the species-area relationship is predicted by the equation: $z = 1 - [1/(2 - S/P)]$, where S is species numbers and P is the source pool size. From this equation, z should approach 0.5 when S is small relative to P.

The number of species of birds that coexist in shelterbelts is much lower than the number available. The species-area slope (0.39, Fig. 1), however, was below 0.5. This may be due to the incorporation of species that do not rely on food within the belt. If species are not limited by food within the belt, then nearly equal numbers of species could exist in small and large belts and the slope would approach 0. Granivores and omnivores exhibit low and intermediate restrictions to feeding within shelterbelts and show low and intermediate slopes (Fig. 2). Insectivores are most restricted to feeding within shelterbelts and show a slope that does not differ ($P > 0.05$) from 0.5. On true islands, all birds are mostly confined to feeding only on the island, so the slope for all species on small islands should be closer to 0.5. The species-area slope for small islands in a Minnesota lake (0.46) was very close to 0.5 (Rusterholz and Howe 1979).

Calculation of the species-area slopes through regression provides an estimate of the average increase in species number throughout the range of island areas. If the average number of species in each food habits group found in all belts is used as an estimate of S and the total number of species of each food habits group found during this study as an estimate of P, the equation derived by Schoener (1976) can be used to predict z. The slope ($z = 0.46$) predicted for insectivores was slightly below 0.5 but not significantly different ($P > 0.10$) from the observed slope ($z = 0.516$, Fig. 2). The slope ($z = 0.33$) predicted for granivores was higher $P < 0.001$) than the observed slope ($z = 0.171$, Fig. 2), and the slope ($z = 0.46$) predicted for omnivores was marginally higher ($P < 0.10$) than the observed slope ($z = 0.376$, Fig. 2). Thus, granivores and omnivores, which exhibit low and intermediate restrictions to feeding within shelterbelts, show poor and intermediate fits to the model for interacting species. Insectivores, which are the most restricted to obtaining food within shelterbelts, show a close fit to the interactive model.

Isolation.—The degree of isolation is another factor affecting insular equilibrium levels (Johnson 1975; Power 1975, 1976; Diamond et al. 1976; Gilpin and Diamond 1976). Isolation of shelterbelts was measured in two ways: distance to nearest other woody cover, and whether or not the shelterbelt bordered a tree claim (a rectangular, 4-ha or larger, block of trees). Other woody cover included any other woody habitat, such as other shelterbelts, tree claims, and riparian areas. Multiple regression analysis showed the presence of tree claims was associated with a reduction ($P < 0.01$) in species number. Distance to nearest other woody cover exhibited a marginal ($P < 0.10$) positive association with species numbers, but this association appeared to be due to the effect of tree claims. Both relationships are probably a sampling effect.

Shelterbelts that border tree claims are not really separate islands, and birds use the tree claims in conjunction with the shelterbelts (pers. obs.). As a result, species with territories that include both shelterbelt and tree claim may be missed in the censuses if they stay in that portion of their territory that lies in the tree claim during

the periods of censuses. If the seven shelterbelts that bordered tree claims are dropped from the analyses, the species-area correlation ($r = 0.854$) is similar to the correlation ($r = 0.844$) for all 69 belts, and the influence of distance to nearest other woody cover becomes insignificant ($P > 0.10$).

Habitat diversity.—Many studies have identified habitat diversity, related to area, as the main factor accounting for increasing numbers of bird species on islands (Power 1972, 1975, 1976; Harris 1973; Lack 1973; Amerson 1975). In natural island situations, an increase in area increases the probability of plant propagule immigration and increases the diversity of sites for establishment. As a result, plant diversity increases with area (Kilburn 1966, Power 1972, Johnson 1975, Harner and Harper 1976) and elevation (Power 1975, 1976; Amerson 1975). In shelterbelts, overstory composition is determined by the planting strategy, and understory is modified by the care of the belt. Multiple regression analysis demonstrated that the diversity of shrub and tree species was not a significant factor ($P > 0.10$) explaining variation in number of bird species in shelterbelts (Martin 1978). Cultivation of belts in their first 5 yr to reduce competition for water between planted trees and natural weeds and subsequent mowing or severe grazing allows little natural diversity in the understory. A shrub understory develops in some cases, but the lack of woody species' propagules and/or suitable microenvironment for their establishment often results in a tall grass understory. In general, shelterbelts are constant in their structural characteristics, consisting of a tree layer, shrub rows along the outside edges, and an interior grass layer. The nonsignificant ($P > 0.10$) 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 ($r = 0.090$) demonstrate the minor relationship between area and habitat diversity. Thus, the importance of area in affecting bird species numbers and abundances is largely separated from the influence of habitat factors.

CONCLUSIONS

LIMITATION OF SHELTERBELT BIRDS

Limits on abundance.—The total number of individuals increased linearly with area, but density decreased with increasing area. This could suggest that more resources were available per unit area in small shelterbelts or individuals were not distributed relative to resources. Some species, however, relied on food resources found outside of shelterbelts. When the abundances of the three most common vagrants are subtracted from total abundance, the resulting adjusted abundance increased proportionally with area; there was a constant density over all areas. If it is assumed that density of resources remains more or less constant over the range of areas, then the constant density of birds that forage mostly within shelterbelts suggests that the number of individuals are distributed among belts relative to resources.

Application of a model for species that interact to divide resources (Schoener 1976) to different ecological (primary food habits) groups also indicated that individuals that foraged within shelterbelts were interacting to disperse themselves relative to resources. Groups that were increasingly constrained to obtaining their food within shelterbelts exhibited increasingly better fits to the model for interacting species.

Limits of species numbers.—The total number of species that coexist within a

shelterbelt is limited below the number available to coexist. The number of species that coexisted in a moderately small shelterbelt (3,100 m²) represented approximately one-third of the number of common species for which minimum size requirements were exceeded. The absence of the extra 67% could not be explained by a lack of suitable habitat in all cases.

The occupation of shelterbelts may have been precluded in some instances by isolation or dispersal barriers, but I feel this constraint was miminized for several reasons. First, analyses were based on species found in many shelterbelts. Their commonness suggests that isolation or dispersal was a minimal factor. Second, while shelterbelts do not represent a large proportion of the land area of eastern South Dakota, they are commonly distributed with slightly more than two shelterbelts, on average, per 259 ha. Because the majority of birds are migratory, the small distances between shelterbelts should have a minimal effect. Further, eastern South Dakota offers little topographic relief to inhibit or modify dispersal. Finally, isolation of shelterbelts did not exhibit any negative effect on species numbers.

Absence of species from shelterbelts with suitable habitat could be explained if the total number of species that coexist within a shelterbelt were limited. When the number of species that can coexist is limited, then any particular species should only be present in a fraction (S/P) of the communities based on chance and in fewer communities when species interactions and habitat conditions place additional constraints. Thus, species should be absent from some communities with suitable habitat conditions when species numbers are limited and the number of communities with suitable habitat exceeds the number of communities expected to be occupied when chance and interactions are taken into account.

DISTRIBUTION OF SPECIES: INTERACTION OR CHANCE?

The above results demonstrate that the total numbers of species and individuals in shelterbelts are limited, but they do not indicate whether distributions of species among and within shelterbelts are due to competitive interactions or random occurrences. Using guilds as a measure of ecological similarity, I found that the composition of species within communities did not represent a random subset of the source pool; the number of species per guild was lower than expected by chance in the 10 largest communities.

The failure of previous studies to find a lower number of ecologically similar species than expected by chance may have been complicated by several factors. First, previous analyses assumed congeners were the most similar ecologically. Coexisting congeners on islands are not necessarily similar ecologically and, hence, competitors (see Lack 1976). Further, even species in different taxonomic families can exert strong competitive effects on each other (Sherry 1979). Second, it might be predicted that taxonomically close species (congeners) may be more similar in their dispersal and colonization capabilities than less related species. As a result, increased sympatry might be expected on islands. Because sympatry is generally increased only slightly or not at all, competitive exclusion may be limiting the buildup of sympatry (Terborgh 1973). Third, earlier studies used large source pools, which reduces the chance that congeners will be randomly drawn. The abundance of some continental species is so low that the probability of immigration approaches zero. Other species are weak flyers or inhibited by overwater flights. Finally, environmental conditions on islands are unsuitable for some species. The failure of suboscines as

island colonists (Terborgh 1973) and the success of second-growth species (MacArthur et al. 1972) demonstrate the enormous differences in dispersal and colonizing abilities of different taxonomical and ecological groups of the source pool. Thus, more realistic estimates of source-pool sizes and more direct considerations of resource utilization strategies may have led to different results.

Other evidence suggesting that the distribution of birds among and within shelterbelts was influenced by interactions among species was derived from the influence of the number of guild members on proportional occurrence relationships. If a species has a greater probability of being driven to extinction when it colonizes an island that already supports another member of the same guild, then species that are in a guild with many members should be absent from more communities than species that belong to smaller guilds. The results showed that species that were the sole member of their guild occurred in a proportion of the communities predicted by chance. Species that shared their guild with other members were present in fewer communities than predicted by chance and, in general, the proportion of communities occupied was increasingly less than the proportion expected to be occupied by chance as the number of guild members increased.

The proportional occurrence relationships could not be explained solely as a function of interaction; additional factors caused absences. Habitat conditions partly account for presence and absence of species. Habitat conditions probably were not the major cause of observed species distributions, however, because species were often absent from communities with habitat conditions similar to the ones they occupied (Table 3). Finally, it is clear that species were absent from some communities simply owing to chance events, such as accidentally missing communities or arriving after ecologically similar species had already colonized, because species were absent from at least a proportion of communities expected by chance $(1 - S/P)$. In short, species numbers and community structure were dictated by competitive interactions, while distribution patterns (presence and absence) of individual species among communities were a function of the combined effects of habitat, chance, and competitive interactions.

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APPENDIX. Common and scientific names and guild classifications of breeding birds of 69 shelterbelts.

Common name	Scientific name	G^a
Mourning Dove	*Zenaida macroura*	123
Common Grackle	*Quiscalus quiscula*	134
American Robin	*Turdus migratorius*	323
House Sparrow	*Passer domesticus*	354
Orchard Oriole	*Icterus spurius*	254
Brown Thrasher	*Toxostoma rufum*	223
Western Kingbird	*Tyrannus verticalis*	245
Eastern Kingbird	*Tyrannus tyrannus*	255
American Goldfinch	*Carduelis tristis*	144
Red-winged Blackbird	*Agelaius phoeniceus*	334
Yellowthroat	*Geothlypis trichas*	234
House Wren	*Troglodytes aedon*	234
Brown-headed Cowbird	*Molothrus ater*	144
Song Sparrow	*Melospiza melodia*	334
Common Flicker	*Colaptes auratus*	211
Eastern Wood Pewee	*Contopus virens*	245
Black-billed Cuckoo	*Coccyzus erythropthalmus*	244
Northern Oriole	*Icterus galbula*	244
Blue Jay	*Cyanocitta cristata*	344
Warbling Vireo	*Vireo gilvus*	254
Red-headed Woodpecker	*Melanerpes erythrocephalus*	211
Starling	*Sturnus vulgaris*	244
Yellow Warbler	*Dendroica petechia*	244
Vesper Sparrow	*Pooecetes gramineus*	334
Black-capped Chickadee	*Parus atricapillus*	242
Clay-colored Sparrow	*Spizella pallida*	134
Chipping Sparrow	*Spizella passerina*	344
Downy Woodpecker	*Picoides pubescens*	211
Swainson's Thrush	*Catharus ustulatus*	223
Ring-necked Pheasant	*Phasianus colchicus*	122
Gray Catbird	*Dumetella carolinensis*	234
Great-horned Owl	*Bubo virginianus*	
Black-headed Grosbeak	*Pheucticus melanocephalus*	344
Rose-breasted Grosbeak	*Pheucticus ludovicianus*	334
Black-billed Magpie	*Pica pica*	
Dickcissel	*Spiza americana*	334
Blue Grosbeak	*Guiraca caerulea*	334
Lark Sparrow	*Chondestes grammacus*	323
Solitary Vireo	*Vireo solitarius*	244
Harris' Sparrow	*Zonotrichia querula*	334
Common Nighthawk	*Chordeiles minor*	

[a] First number = primary food habits: 1 = granivore, 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.