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Species-area relationships of winter residents in isolated woodlots.—The number of bird species breeding within woodlots or using woodlots temporarily during migration is strongly correlated with woodlot area (e.g., Martin 1980, Ambuel and Temple 1983, Blake 1986).

Species-area relationships of winter bird communities, however, have received little attention (Haila 1981), despite potentially strong effects of forest area on both weather severity and food availability (Forman and Godron 1981).

Woodlots in east-central Illinois are isolated from each other by cropland, and the transition from bare ground to woodlot vegetation is generally sharp, thus forming distinct patches of habitat. Here I examine relationships between area of isolated woodlots in east-central Illinois and number of species of birds found in these woodlots during winter. Species-area relationships are compared among trophic groups to examine potential effects of variation in availability of food resources among communities.

Methods.—I censused 5 woodlots during the winter of 1979–80 to gain a preliminary assessment of the species-area effect. Eleven woodlots, ranging in size from 1.8 to 600 ha, were censused during the winter of 1980–81 to include a greater variety of sizes. Number and choice of woodlots were dictated by the landscape of east-central Illinois. Only woodlots that possessed a relatively mature canopy and well-developed understory, showed no evidence of recent, heavy disturbance, and were surrounded by nonforest habitat were included.

I surveyed birds using the point-count technique (Ferry and Frochot 1970). I visited each observation point for 10 min during a census and recorded all birds seen or heard within or below the canopy. Survey points were at least 150 m apart. Each woodlot was censused 3 or 4 times during December–February of each year.

Number of observation points increased with area in order to obtain a reasonably complete count of species present in larger woodlots. Total number of species recorded generally increases with sample effort, but at some point additional observations do not increase the species total. Species accumulation curves (cumulative number of species plotted against number of observation points) reached or approached an asymptote for all woodlots, indicating that species richness of woodlots was determined adequately (Blake and Karr 1982).

I conducted censuses from sunrise until 2.5 h after sunrise on days with little or no wind and no precipitation in order to minimize potential confounding effects of weather. In addition, I censused woodlots in an order unrelated to woodlot area, thereby reducing potential effects of weather on the species-area relationship.

I analyzed species composition on the basis of both migratory status and primary foraging habit. I used Kendeigh (1982) as the primary guide for assigning species to categories (permanent residents, winter residents, transients) based on their status in east-central Illinois. Some species fell into two categories. For example, low permanent resident populations of some species (e.g., Brown Creeper [*Certhia americana*]) are augmented during winter by individuals that breed farther north. Transients overlap temporally with permanent and winter residents but do not normally remain in east-central Illinois throughout winter.

I divided species according to primary food type and foraging location (Martin et al. 1951, Williams and Batzli 1979). Species that used two types of food or locations in approximately equal proportions were assigned ½ to each group. Categories included granivores, insectivores that obtain insects from the bark of trunks and large limbs (by drilling or gleaning), insectivores that glean insects from small twigs and brush piles, frugivores, and sapsuckers.

I evaluated species-area relationships according to the exponential function rather than the power function, because the former model accounted for a greater amount of variation in species number (Blake and Karr 1982) and because the exponential function resulted in a better fit. No data set departed from normality.

Summary data on temperature and snowfall for the winters of 1979–80 and 1980–81 were obtained from the State Water Survey Division, Illinois Department of Energy and Natural Resources (Table 1).

Bird community composition.—Thirty-one species of birds were recorded during winter in one or more of the 11 woodlots in east-central Illinois, 19 in 1979, and 30 in 1980 (Appendix 1). Species present on small islands were, in almost all cases, also present on

TABLE 1

MONTHLY TEMPERATURE AND PRECIPITATION DATA FOR THE MONTHS OF NOVEMBER–FEBRUARY 1979–80 AND 1980–81 IN EAST-CENTRAL ILLINOIS

	1979–80				1980–81			
	Nov.	Dec.	Jan.	Feb.	Nov.	Dec.	Jan.	Feb.
Mean maximum temperature (°C)	9.1	7.1	0.7	−1.1	10.1	5.9	−0.1	4.3
Mean minimum temperature (°C)	0.5	−2.9	−6.8	−8.4	0.5	−4.2	−8.4	−5.8
Precipitation (mm)	68.8	29.0	19.6	43.2	41.4	34.8	16.3	56.1

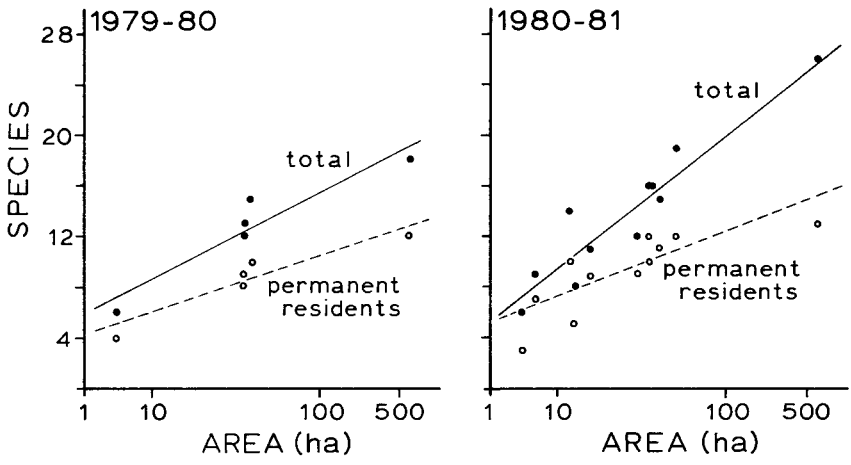

FIG. 1. Total number of species and number of permanent resident species recorded during winters of 1979–80 and 1980–81 plotted against area (log scale) of woodlots. Solid circles and lines refer to total species number, and open circles and dashed lines refer to permanent residents. Lines were fitted by linear regression (exponential model) (see Table 3).

larger islands. Greater species numbers in 1980 were partially due to the larger number of woodlots surveyed, and, apparently, also to a higher number of transients in 1980; numbers of resident species were more similar between years (Appendix 1) (Fig. 1).

Granivores feeding on small seeds were the dominant trophic group, in terms of number of species, in all woodlots (Table 2). Seed eaters showed the greatest change between years, both at individual woodlots and overall, but, in general, more species were present in larger woodlots. Three species relying on acorns as a primary food were uncommon or absent in the smallest woodlots, but all were present in all woodlots greater than 5 ha. Number of species taking insects from bark, either by drilling into or gleaning from the surface, also was greater in larger woodlots (Table 2). This was particularly true for species gleaning insects from trunks and those gleaning insects from small twigs.

Species-area relationships.—Total number of species correlated strongly with area in both winters (Fig. 1) (Table 3). The rate of increase (slope) in species number with area was higher in 1980, but not significantly so (t-test, $P > 0.05$). The higher slope in 1980 was a result of greater species totals in larger rather than small woodlots, and intercepts did not differ ($P > 0.05$) between years. Results did not differ between years when I recalculated the species-area relationship for 1980 using only those woodlots censused in both 1980 and 1979. Number of permanent residents correlated significantly with area in both years (Fig. 1) (Table 3), and the results did not differ significantly between years.

I combined all granivores and all bark insectivores into two groups to examine correlations with area. Bark insectivores correlated significantly with area in 1979 and 1980, but granivores showed a significant correlation only in 1980 (Table 3). The species-area intercept was higher for granivores than for bark insectivores in both years (1979: $t = 2.13$, df = 8, $0.10 > P > 0.05$; 1980: $t = 2.83$, df = 20, $P < 0.02$), reflecting the greater number of granivore species in all woodlots.

Discussion.—Woodlots in east-central Illinois provide valuable habitat for birds during

TABLE 2
SPECIES NUMBERS IN DIFFERENT TROPHIC GROUPS

Trophic group	Woodlot size (ha)										
	1.8	2.3	4.7	5.1	6.5	16.2	24	24	28	40	600
1979											
Granivores											
Small seeds	3						3.5	5	4		5
Acorns	1						3	3	3		3
Insectivores											
Bark drill	1						2.5	2.5	2.5		2.5
Trunk glean	1						1.5	1	2.5		3
Twig glean									1.5		2.5
Frugivores							1.5	1.5	1.5		1.5
Sapsucker											0.5
1980											
Granivores											
Small seeds	4	4	5	3	4	4	6.5	6.5	6	6	10
Acorns		2	3	2	3	3	3	3	3	3	3
Insectivores											
Bark drill	1	1	1.5	1.5	1	1.5	2.5	2	1.5	2.5	2.5
Trunk glean	1	1	1.5	1	1	1	1.5	1.5	1.5	2.5	2
Twig glean		1	1.5	0.5	2	1.5	1.5	1	1.5	1.5	3
Frugivores			1.5	0.5	2	1.5	1.5	1	1.5	1.5	3.0
Sapsucker											0.5

breeding and migration seasons, and area of the woodlots influences the number of species that use them at these times (Blake and Karr 1984, Blake 1986). Woodlot size also influences winter bird populations. Permanent residents varied with area in the same way between seasons; no difference in the species-area relationship was apparent beween summer and winter for this group (Blake 1983 for summer data).

Although habitat structure influences composition of many bird communities (Cody 1985), differences in habitat among forest patches appear to exert little influence on bird species richness of woodlots—relative to the influence of area—at least in cases where habitat heterogeneity does not increase markedly with area (Blake and Karr 1982, Ambuel and Temple 1983, Blake 1983). Woodlots censused during this study were selected initially partially on the basis of general similarity in vegetation. Differences in habitat occurred among woodlots, but such differences were not correlated with area of woodlots (Blake and Karr 1982). Also, various aspects of habitat structure did account for some additional variation in number of bird species during the winter of 1980–81 (Blake and Karr 1982) but much less than that accounted for by area.

A lack of correlation between species numbers and habitat variables does not necessarily indicate that habitat structure does not influence bird communities of isolated woodlots. Environmental variation certainly is expected to increase as area increases and may account for much of the species-area effect (Williamson 1981). However, such variation may be apparent on a different scale or may involve factors (e.g., soil types) that typically are not

TABLE 3
RESULTS OF SPECIES-AREA REGRESSIONS (SEMI-LOG)

Species group	1979–80				1980–81			
	Intercept	Slope	r^2	P	Intercept	Slope	r^2	P
Total species	6.0	2.04	0.900	<0.012	5.2	3.18	0.902	<0.0001
Permanent residents	4.1	1.36	0.891	<0.014	5.2	1.53	0.648	<0.001
Granivores	4.5	0.66	0.687	<0.08	4.2	1.42	0.853	<0.0001
Bark insectivores	1.3	1.05	0.803	<0.037	2.1	0.89	0.829	<0.0001

measured. An increase in environmental heterogeneity may, by providing a greater variety of resources, allow a greater number of species to coexist. Similarly, differences in area among woodlots may influence the amount of some critical habitat present, resulting in stochastic loss of some species from smaller woodlots (Williamson 1981). Loss of critical microhabitats or refugia, required during periods of stress, is a probable cause of species loss from some islands (Karr 1982).

Habitat structure may influence species distribution patterns during winter through effects on weather and food resources. Unusually severe weather may cause major reductions in winter bird populations, as occurred during the winter of 1976–77 in southern Illinois (Graber and Graber 1979). Vegetation moderates the influence of weather, particularly wind, and the microenvironment within the center of a large forest is less severe and less variable than at the center of a small woodlot (Forman and Godron 1981). In a large forest, birds may concentrate their activities in areas that provide protection from weather (Carpenter 1935), an option that is not as readily available in small woodlots. Low temperatures and high winds cause some species to shift foraging locations from exposed to more protected sites as weather becomes more severe (Grubb 1975). Small forests may not provide sufficient cover to allow such behavioral flexibility.

The greater number of species in larger forests also occurs because large forests may support bird species that are dependent on spatially variable food supplies (e.g., Red-headed Woodpecker [Graber et al. 1977]). The irregular occurrence of frugivores (e.g., Cedar Waxwing) in large woodlots and their absence from small woodlots probably reflects this effect.

Haila (1981) reported berry and seed eaters on very small islands during winter; such species were considered habitat generalists, moving among islands and habitats in search of available and patchily distributed food resources. In the present study, however, woodlots generally were well-separated, and species richness was not correlated with measures of forest isolation (Blake and Karr 1982). Insectivorous birds, which are more dependent on specific habitat requirements and predictable food supplies (Haila 1981), are more dependent on large woodlots, which provide greater availability of these foods. Few insectivores occurred in small woodlots during winter in east-central Illinois, but numbers increased strongly with woodlot area. Higher species totals for granivores, as compared to bark insectivores, in small woodlots probably reflects the fact that granivores may forage in nonwooded habitat near woodlot borders, if such habitat exists. At the same time, the correlation between granivores and area reflects the greater foraging area and the better microenvironmental conditions for granivores both around and within large woodlots.

For species that winter in Illinois and other heavily disturbed regions, habitat that provides sufficient shelter and food may be in short supply, and isolated woodlots may be an important refuge during winter. The importance of habitat islands to bird populations extends beyond the breeding season, and additional, more detailed studies during nonbreeding seasons are needed.

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