THE OCCUPATION OF SMALL ISLANDS BY PASSERINE BIRDS

DOUGLASS H. MORSE

Comparisons of island and mainland faunas have provided great insight into how communities are structured (see MacArthur 1972). In particular, islands permit natural comparisons of how animals under varying degrees of faunal impoverishment exploit their resources. To date, most islands studied from this point of view are sufficiently large to support sizeable populations of many or all of the species that occupy them. Further, island populations typically studied are either of unknown genetic relationship to their mainland counterparts, or they are easily distinguished from them, often being considered separate subspecies or even species.

In this paper I report upon the patterns by which passerine birds occupy extremely small forested islands and adjacent large mainland habitats in and around Muscongus Bay, Maine, thus expanding upon earlier observations (Morse 1971a). I attempt to answer the following questions: From which mainland habitats do the inhabitants of these islands come? Which characteristics of the islands best predict the number of species that will occupy them? What factors best account for the presence or absence of any given species on the islands? How stable are the island assemblages in time? How does the total density of birds and the densities of individual species compare with the densities on the mainland? Then, where appropriate, I relate my findings to island biogeographic theory (MacArthur and Wilson 1963, 1967, Diamond 1975).

Small islands of this sort are excellent systems for answering such questions. By virtue of their small size (0.1–4.0 ha), it is often possible to determine the minimal conditions (space, etc.) required for a species to establish itself. Potentially key variables (physical characteristics of the forest, food supply, etc.) can be monitored readily. A variety of species compositions provides the opportunity to evaluate the effects of certain species upon others. Lastly, the birds of any given species inhabiting these islands almost certainly belong to the same gene pool as those on the adjacent mainland (Morse 1971a), so one can eliminate evolutionary change as the basis for such differences.

STUDY AREA AND METHODS

Most of the 12 islands censused are partially or totally forested by white spruces (*Picea glauca*), with small but varying amounts of balsam fir (*Abies balsamea*), red oak (*Quercus rubra*), and white birch (*Betula papyrifera*). Two of the islands, however, contain substantial amounts of mountain maple (*Acer spicatum*), striped maple (*A. pensylvanicum*), and yellow birch (*Betula lutea*). In addition, some have sizeable open areas sparsely covered by various grasses, raspberry (*Rubus* sp.), bayberry (*Myrica pennsylvanica*), or goldenrod (*Solidago* spp.). Since my primary concern lay with the forest-dwelling birds, I have included typically open-country species only when they used the forested areas of these islands. These islands are described in detail elsewhere (Morse 1971a, 1973a). No visible successional change occurred during the period of the study.

Records of breeding and visiting species were made during intensive studies upon the warblers (Parulidae) of the islands (Morse 1971a, 1973a). These studies provided information on the fledging success of the warblers during the 1967–1970 seasons. During that period, several of these birds were either individually marked or identified by their songs. Observations of other species were designed to give an accurate measure of presence or absence, even though abundances are in some cases estimates where many pairs were present (e.g., Song Sparrow, *Melospiza melodia*). After 1970, I made at least six censuses each year between 10 June (after the last spring migrants) and 15 July (after the latest establishment of breeding individuals) (Morse 1971a, 1973a). These censuses ranged from 15–20 min per visit on the smallest islands (under 0.2 ha) to an hour or more on the largest islands. Minimum criteria for colonization were satisfied if a species was seen on half or more of the censuses and if both a male and a female were detected (i.e., settlement of a minimum breeding unit). Year-by-year lists of breeding species are available on request.

Several aquatic species (herons, ducks, gulls) nested on these islands but foraged elsewhere. Since I have no evidence that any of these birds competed for nest sites or food resources with fully resident species or that they preyed upon these residents regularly, I will not consider them further.

To determine food supplies available to the foliage-inhabiting species, I measured the biomass of foliage-inhabiting insects on these islands during the 1968–1970 seasons, using the same technique as in my other studies (Morse 1973a, 1976). Weekly or biweekly I collected 20 live branches at random (approximately 0.2 m² and 6.0 m³) with their associated arthropods on the islands and mainland, attempting to lose as few arthropods as possible. The branches were placed in plastic bags, fumigated, and then beaten over a screen of hardware cloth. Data on arthropods so obtained were pooled for each two-week period, permitting a direct comparison of island and mainland insect stocks. Although this technique extracts over 99% of the arthropods on the branches at the time that they are placed in the bags (Morse 1973a), it underestimates the abundance of strongly-

flying insects. However, since most of the foliage-foraging birds were primarily gleaners, this potential problem should not bias the results seriously.

RESULTS

THE SPECIES POOL

One can construct a mainland species pool (Appendix I) with considerable accuracy from several sources of information. Mainland is here defined as that land physically connected to the continental shoreline, plus islands of over 25 ha in size. These large islands are partly or totally covered with spruces. Earlier (Morse 1966) I compiled lists of species nesting in spruce forests, deciduous forests, hurricane-damaged areas, and edge situations on Hog Island, a large island (132 ha) separated at points from the mainland by not over 200 m. This compilation was based upon personal field work and the breeding-bird censuses of Cadbury and Cruickshank from 1937 to 1958. Subsequent intensive field work has added but two more species to these lists. Thus, the updated lists presented as Appendix I appear to be largely complete.

Another group of species breeds on the mainland within 2 km of the shoreline, but does not occur on the Hog Island lists (Appendix I). I compiled this list from personal observations made since 1957 and from Cruickshank (no date). Over half of these species occur in open-country or brushy areas, and most of the remaining species typically occur in deciduous forests.

CONTRIBUTIONS OF THE DIFFERENT COMPONENTS

Seventeen species of small passerine birds bred on forested parts of the small islands during the 1967–1975 period. They came entirely from the first two components of the mainland species pool: (1) the spruce forest and (2) the adjacent deciduous, disturbed, and edge areas (henceforth referred to as deciduous-edge areas). These two components made similar contributions to the island species pool (nine from the spruce forest group, eight from the deciduous-edge group).

The two components also contributed rather similar numbers of species-years (defined as the occupation of an island by a species during one breeding season) on the islands (Table 1). However, the relative abundance of the deciduous-edge species was much greater than that of the coniferous species (Table 1), because several members of the deciduous-edge group established considerably more dense populations than did those of the spruce

TABLE 1. Contributions of spruce and deciduous-edge components to island populations of birds during 1967–1975 period.

| Island | Species-years[a] | | Total pairs of individuals | |
	Spruce	Deciduous-edge	Spruce	Deciduous-edge
Strawberry	0	8	0	8
Byer's	0	11	0	11
Crotch	7	8	7	16
Crow	15	11	15	38
Jim's	25	12	25	42
Ram	18	12	18	26
Crane	20	31	20	93
Indian	28	12	28	27
Thief	41	20	45	92
Franklin	0	31	0	174
Haddock	15	26	15	116
Wreck	22	29	28	163
TOTALS	191	223	201	806
PERCENTAGE	46.1	53.9	20.0	80.0

[a] One species-year represents the occupation of an island for one year by one or more breeding pairs of a species.

forest group. This characteristic was especially striking in the case of the Song Sparrow, which made up 44.8% of the total number of birds. Not suprisingly, the Song Sparrow is an extremely successful colonizer in other areas as well (Beer et al. 1956, Yeaton and Cody 1974). The spruce-forest component was much more evenly distributed than that of the deciduous-edge component, because the former was comprised of species that seldom attained a density greater than one pair per island (Fig. 1).

FOOD SUPPLY

The foliage sampling for arthropods indicated a rather constant average biomass of insects through the season (Fig. 2). During the first part of the season, the average biomass was similar to that of a white spruce forest on the mainland, while later it exceeded that of the mainland. Therefore, the abundance of food on the foliage does not appear to account for the absence of many species from these islands. Other possible food sources (from ground, litter, etc.) were not systematically measured.

NUMBER OF SPECIES PRESENT

Using stepwise multiple regression, I tested six potentially important factors (the independent variables of Table 2) for their relationship to the number of species that occupied an island. I used three different measures of species numbers—cumulative list of species over 1967–1975 period, maximum

TABLE 2. Dependent and independent variables for multiple regression analysis.

	Dependent variables			Independent variables					
Island	Total species	Spruce-forest species	Deciduous-edge species	Forest area (ha)	Overall area vegetated	Distance to main-land (m)	Spruce forest area (ha)	Forest height (m)	Ground cover in forest (ha)
Crane	9, 9, 5.7[a]	5, 5, 2.5[a]	4, 4, 3.2[a]	0.53	2.81	230	0.52	14	0.12
Jim's	10, 6, 4.6	6, 5, 3.1	4, 4, 1.5	0.49	0.49	500	0.44	14	0.03
Indian	9, 6, 5.0	6, 5, 3.5	3, 3, 1.5	0.69	0.69	230	0.59	16	0.07
Thief	13, 9, 7.6	8, 7, 5.1	5, 4, 2.5	1.50	1.64	1,070	1.49	15	0.02
Crow	6, 4, 3.3	3, 3, 1.9	3, 2, 1.4	0.35	0.60	360	0.21	13	0.11
Ram	5, 5, 4.3	3, 3, 2.6	2, 2, 1.7	0.39	0.39	640	0.35	14	0.08
Crotch	3, 3, 1.9	2, 2, 0.9	1, 1, 1.0	0.16	0.16	720	0.16	12	0.02
Wreck	13, 10, 7.3	6, 5, 3.1	7, 5, 4.2	3.86	3.86	1,200	2.12	14	1.05
Haddock	9, 8, 5.1	5, 5, 1.9	4, 4, 3.2	1.86	2.57	2,160	1.13	14	0.37
Franklin	5, 5, 4.4	0, 0, 0.0	5, 5, 4.4	1.77	3.49	1,160	1.77	14	1.75
Byer's	2, 2, 1.4	0, 0, 0.0	2, 2, 1.4	0.11	0.11	280	0.11	12	0.02
Strawberry	1, 1, 1.0	0, 0 ,0.0	1, 1, 1.0	0.10	0.10	360	0.10	14	0.00

[a] The three figures in order are cumulative list of species over 1967–75 period, maximum number of species in a year during this period, and mean number of species per year.

number of species in any year, and mean number of species per year (Table 2). None of the statements in this section should be taken to imply a cause-and-effect relationship between the variables and the birds present.

Only four variables (forest size, ground cover, forest height, and area vegetated) contributed significantly to this variance in any of the measures (Table 3). These variables had different effects on the three measures of species numbers. Cumulative and mean numbers of species showed considerably more similarity to each other in this regard than either did to the maximum count per year. Forest size contributed significantly to the variance in the cumulative and mean numbers, but not to maximum numbers. Height of forest made the next largest contribution to the variance in cumulative and mean numbers, though attaining statistical significance only in the case of the mean species number. The amount of ground cover and area vege-

tated were the most important variables for the maximum numbers.

I then divided the species pools into spruce and deciduous-edge components (Table 4). The pattern seen in the spruce component closely resembled that of the total species pool. Forest size and forest height made significant contributions to the variance of both the cumulative and mean numbers of species, and area vegetated contributed most to the variance of the maximum yearly count.

The pattern of the deciduous-edge component differed somewhat from that of the total pool and the coniferous component. Again, forest size made a significant contribution to both the cumulative and mean numbers of species, but the effect was much larger for the cumulative list of species than for the mean number of species. However, the area
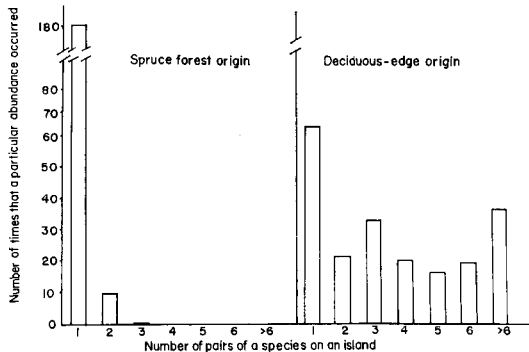

FIGURE 1. Number of times that species nested at various densities (pairs per island) during 1967–1975 period.
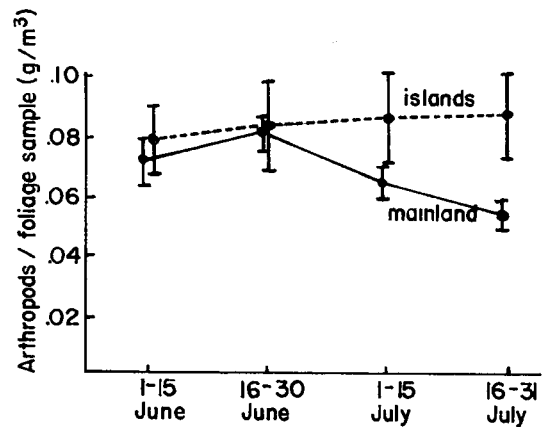

FIGURE 2. Biomass of arthropods throughout the season (±1 SE). Data are pooled from 1968–1970 seasons, each point representing a minimum of five samples. Mainland date from Morse (1976).

TABLE 3. Relative contributions of independent variables to the multiple correlation coefficient, R^2, for the total number of bird species.

Independent variable	Cumulative		Maximum/year		Mean	
	R^2	F	R^2	F	R^2	F
Forest area	.4351	7.70*	.0316	1.91	.5007	10.03**
Overall area vegetated	.0499	1.63	.5433	11.90**	.0836	3.15
Distance to mainland	.0039	0.11	.0000	0.00	.0009	0.02
Area of spruce forest	.0002	0.01	.0002	0.01	.0042	0.14
Forest height	.1243	3.77	.0512	2.78	.1950	5.77*
Area in forest with ground cover	.1771	4.12	.2585	11.73**	.0357	1.06
TOTAL R^2	.7907	—	.8847	—	.8200	—

* = significance at 0.05 level.
** = significance at 0.01 level.

vegetated made the greatest contribution to the variance of the mean number of species, but little to the cumulative number of species. Also, area vegetated made the only significant contribution to the variance in the maximum number of species recorded in any one year.

RELATION OF NUMBER OF SPECIES TO AREA

The three smallest islands (under 0.2 ha) diverged markedly from a straight line in a log-log plot of area and number of species. The corresponding slope of the regression, z (MacArthur and Wilson 1967), was relatively high, falling in the range of 0.5 (0.48 for mean number of species per year, 0.51 for maximum number of species in any one year, 0.55 for the cumulative number of species over the years of the study). However, when the three smallest islands were removed from the analysis and the z values recalculated, they approached 0.2 (0.21 for mean number of spe-

cies, 0.23 for maximum number of species, 0.20 for cumulative number of species). The area of these three islands falls below the territory size of most of the island inhabitants (see below).

BASIS FOR THE PRESENCE OR ABSENCE OF CERTAIN SPECIES ON THE ISLANDS

In several cases I can explain why certain species occupied the islands and others did not. One potentially important consideration is whether the size of the island forests equalled or exceeded the size of species' territories on the mainland. Measures of average territory size on the adjacent mainland existed for 9 of the 17 species found on the small islands, and 8 other potentially colonizing species from the spruce-forest and deciduous-edge categories that were not recorded on the small islands (Table 5). I could compare these territory sizes with the area of the island forest where only one pair

TABLE 4. Relative contributions of independent variables to the multiple correlation coefficient, R^2, for the number of bird species in the coniferous and deciduous-edge components.

Independent variable	Spruce-forest species						Deciduous-edge species					
	Cumulative		Maximum/yr		Mean		Cumulative		Maximum/yr		Mean	
	R^2	F	R^2	F	R^2	F	R^2	F	R^2	F	R^2	F
Forest area	.1952	5.29	.0290	0.83	.2140	5.93*	.7628	32.16**	.0017	0.07	.0134	7.04*
Overall area vegetated	.0356	0.98	.2215	6.51*	.0056	0.14	.0503	2.43	.7392	38.35**	.9694	316.90**
Distance to mainland	.0001	0.00	.0021	0.06	.0063	0.14	.0227	1.11	.0000	0.00	.0000	0.02
Area of spruce forest	.0925	1.54	.1036	1.63	.0016	0.03	.0000	0.00	.0038	0.13	.0036	2.15
Forest height	.3660	5.77*	.3243	4.80	.4070	6.86*	.0153	0.72	.0057	2.44	.0002	0.09
Area in forest with ground cover	.0952	1.71	.1124	1.95	.0904	1.62	.0048	0.20	.0000	0.00	.0000	0.00

* = significance at 0.05 level.
** = significance at 0.001 level.

TABLE 5. Sizes of territories in and about mainland spruce forests.[a]

Species	Area (ha ± 1 SE)	Range	Sample size	Habitat
SPECIES OCCURRING ON SMALL ISLANDS				
Winter Wren	3.64	–	2	red spruce
Golden-crowned Kinglet	0.72	–	6	white spruce
Northern Parula	1.33	–	2	white spruce
Northern Parula	0.40 ± 0.04	0.30–0.51	5	spruce edge
Magnolia Warbler	0.72 ± 0.06	0.51–1.05	9	white spruce
Yellow-rumped Warbler	0.81 ± 0.03	0.60–1.03	17	white spruce
Black-throated Green Warbler	0.43 ± 0.01	0.35–0.55	28	white spruce
Yellowthroat	0.29	–	11	damaged spruce
White-throated Sparrow	1.67	–	3	white spruce
White-throated Sparrow	0.35	–	9	damaged spruce
White-throated Sparrow	0.49	–	6	spruce edge
Song Sparrow	0.18	–	18	damaged spruce
Song Sparrow	0.49	–	6	spruce edge
SPECIES NOT OCCURRING ON SMALL ISLANDS				
Blue Jay	4.00	–	2	red spruce
Red-breasted Nuthatch	1.34	–	3	white spruce
Brown Creeper	2.22	–	2	red spruce
American Robin	4.00	–	2	white spruce
Hermit Thrush	2.00	–	2	white spruce
Nashville Warbler	2.22	–	2	red spruce
Blackburnian Warbler	0.46 ± 0.01	0.36–0.56	22	white spruce
Dark-eyed Junco	1.67	–	6	white spruce

[a] Territories with standard errors and ranges were determined from observations made in 1969–1972 and in 1974 (from Morse 1976). Other data are from unpublished observations in which the census area has been divided by the number of pairs present, so that no means or extremes are available.

of any given species was present (as in the spruce-forest warblers), or with the area divided by the number of pairs present in other cases. While the latter measure does not account for the possibility of territorial overlap, I assume it to be small, relative to the overall space occupied. Territorial overlap between conspecifics was low or nonexistent where observed in the mainland situations (Morse 1976) that were used for comparison.

Mainland territory size (Table 5) accurately predicted the presence or absence of many, though not all, species. Six of the nine colonizing species occurred only in island forests larger than their mean territory size on the mainland (Winter Wren, Golden-crowned Kinglet, Magnolia Warbler, Black-throated Green Warbler, Yellowthroat, and White-throated Sparrow), while the other three species occupied island forests smaller than their mean territory size on the mainland (Northern Parula, Yellow-rumped Warbler, and Song Sparrow). The smallest islands occupied by Northern Parulas and Yellow-rumped Warblers were also smaller than their minimum territory sizes on the mainland. Of the eight non-colonizing species, all but the Blackburnian Warbler had territory sizes larger than most or all of the island forests censused.

Considering the foliage-gleaning guild in detail, Northern Parulas and Yellow-rumped

Warblers occupied more islands than would be predicted on the basis of mainland territory size. Body size (Appendix II), another measure of energetic demand, accurately predicted the presence of Northern Parulas on more islands than any other warbler, but the relatively large Yellow-rumped Warbler appeared far more often than it should have according to this measure. However, the social dominance ranking of these warblers (Morse 1971a, 1974, 1977) inversely matched the frequency with which they occupied the islands relative to each other: Northern Parulas > Yellow-rumped > Black-throated Green > Magnolia. Only in 1974 and 1975, when Yellow-rumped Warblers nested upon Crow Island in the absence of Northern Parulas, did an exception to this relationship occur.

The ground-foraging guild may be organized similarly to the spruce-forest warblers of the foliage-gleaning guild. This was suggested by the presence on several islands of the Swainson's Thrush, a species that apparently is socially subordinate to the Hermit Thrush (Morse 1972). Swainson's Thrushes occupied a wider range of habitats in the absence of Hermit Thrushes than where sympatric with them (Morse 1971b, 1972). The distribution of White-throated and Song sparrows on these islands might have a like explanation, since Song Sparrows expanded

their activities into the midst of these island spruce forests where White-throated Sparrows were absent or infrequent (unpubl. data).

Species whose presence would not be predicted on the basis of mainland territorial size often were low in the social hierarchy; they underwent ecological release on the small islands in the absence of their dominants. This release took place in at least three ways: more intensive use of a given territory (associated with decreased territory size), changes in foliage-usage patterns, and changes in habitats occupied. Size of mainland territory was a good predictor of presence or absence of species high in the hierarchy, but a poor predictor for species low in the hierarchy.

ADDITIONAL COMMENTS ON THE DISTRIBUTION OF CERTAIN SPECIES

Magnolia Warblers first bred on the small islands in 1975, when a pair raised young successfully on Thief Island. Judging from their large territory size on the mainland (Table 5) and their high dominance ranking, they would be predicted only on Thief Island. Nevertheless, their frequency there was unexpectedly low, since that forest is twice as large as their average mainland territory. However, four of the five vagrant Magnolia Warblers seen between 1967 and 1975 were on Thief Island. These sightings suggest that this island had characteristics making it more attractive to this species, than the other islands. When compared with the number expected by chance alone, this small sample approaches significance ($P = 0.062$ in a one-tailed Fisher test).

Blackburnian Warblers occupied territories on the mainland that were considerably smaller than several of the forests on the small islands (Table 5); however, they did not nest on any of these islands. They were the only species that concentrated their activities on the mainland in parts of the forest that were generally not represented on the island (the tops of trees taller than those usually found on the tiny islands; Morse 1968, 1971a). However, four of the six vagrant Blackburnian Warblers found on these islands between 1967 and 1975 occurred on Indian Island, the only small island containing spruce trees approaching the height that these birds frequent in the mainland forests. This small sample also approaches significance ($P = 0.072$ in a one-tailed Fisher test) when compared with the expected.

TABLE 6. Cumulative pairs per year on islands.

Species	1967–1971	1972–1975
SPRUCE-FOREST SPECIES		
Swainson's Thrush	4.2	1.3
Northern Parula	8.8	7.7
Yellow-rumped Warbler	6.8	4.0
Black-throated Green Warbler	2.6	0.7
Purple Finch	4.0	3.0
White-throated Sparrow	3.0	0.3
DECIDUOUS-EDGE SPECIES[a]		
Yellow Warbler[b]	1.2	4.0
American Redstart[b]	0.6	1.7
Catbird	0.6	0.7
Yellowthroat	1.6	2.7

[a] Does not include Song Sparrows.
[b] Does not include sizeable populations of these species on Crane, Franklin, Haddock, and Wreck islands. These populations (and Song Sparrows) were not included because, during some or all years, counts were estimates. However, they showed no signs of decrease during 1972–1975 period.

CHANGES DURING THE PERIOD OF STUDY

Results reported thus far suggest a highly predictable pattern of colonization on the islands. However, in light of two extremely poor breeding seasons associated with inclement weather (1972 and 1973; Morse 1976), I compared the frequency with which species occupied these islands from 1967 to 1971 with their frequency from 1972 to 1975. Species closely associated with spruce showed an overall marked drop in density, while species of the deciduous-edge component increased simultaneously (Table 6). The decrease in numbers of spruce-forest birds was significant when considered at the level of the species ($P = 0.05$ in a two-tailed Wilcoxon test), and the increase among deciduous-edge species at this level showed a consistent trend, though the number of species available for analysis (n = 4) was too small for statistical treatment.

The results suggest that: (1) the inclement conditions substantially decreased populations of spruce-forest species, but not the deciduous-edge species; and (2) deciduous-edge species occupied the space left by the spruce-forest species. This pattern closely parallels one seen in large adjacent forests (Morse 1976). In that case, numbers of Black-throated Green Warblers decreased abruptly in white spruce forests, though not in red spruce forests. Simultaneously, a marked increase of the American Redstart, a predominantly deciduous-forest species, occurred in the only forest censused that contained both species.

TURNOVER OF SPECIES AND INDIVIDUALS

Rates of extinction and rates of new colonization of species differed widely but were gen-

TABLE 7. Colonization and extinction rates of bird faunas.

Island	Percentage of species disappearing from one year to the next[a]	Percentage of species appearing that were not present in preceding year[a]
Crane	15.7[b] (8)	15.7[c] (8)
Jim's	26.3 (10)	26.3 (10)
Indian	20.0 (8)	15.0 (6)
Thief	18.6 (11)	18.6 (11)
Crow	16.7 (6)	16.7 (5)
Ram	10.0 (3)	6.7 (2)
Crotch	13.3 (2)	20.0 (3)
Wreck	15.7 (8)	17.6 (9)
Haddock	17.1 (7)	19.5 (8)
Franklin	3.8 (1)	3.8 (1)
Byer's	18.2 (2)	27.3 (3)
Strawberry	0.0 (0)	0.0 (0)
Cumulative	16.7 (66)	16.7 (66)

[a] Numbers of extinctions or colonizations in parentheses.
[b] Calculated from the equation $e = xE/t(\sum s)$, where $e =$ extinction rate, $x =$ number of years censused, $E =$ the number of species that became extinct, $t =$ number of years intervening, and $s =$ number of species recorded in a yearly census.
[c] Calculated from the equation $c = xC/t(\sum s)$; where $c =$ colonization rate; $C =$ number of species that colonized; and x, t, and s are as above.

erally high (Table 7). Taken as a whole, extinctions balanced colonizations, so I conclude that these islands were in equilibrium (Table 7). I assume that the pattern observed on individual islands can be attributed largely to random processes.

The actual turnover of individuals probably was even considerably higher than the foregoing data suggest. I can document this in one case. When several known individual spruce-forest warblers on these islands were followed from 1967 through 1969, considerable turnover occurred in these birds, even when islands were constantly occupied by the species in question (Morse 1971a). The mean length of occupation by an individual was 1.3 breeding seasons, though in extreme cases birds occupied an island for as many as three years. Since the mean period of occupation for the warbler species on these islands was 4.2 years, the turnover rate of individuals was 3.2 times that of the species.

INVASION RATES

I noted vagrant warblers wherever I saw them. These nonresident individuals occurred frequently enough to saturate the islands upon occasion, or at least to breed upon them more often than they were observed to do (Table 8). At least some wandering birds were potentially reproductive, as they established themselves and successfully raised young in certain cases (Morse 1971a). I must emphasize, however, that these data dealt with male birds only, which were conspicuous because of their almost continual singing. I seldom saw vagrant females, though I assume that they were frequently present, since late-arriving males found females.

OVERALL DENSITY AND BIOMASS

With a few conspicuous exceptions, the overall density of birds changed inversely with forest size (Fig. 3A). However, the smallest islands (0.10 and 0.11 ha) did not have densities as high as would be predicted from the general trend. This difference probably resulted from their peculiar size, where two pairs of birds could seldom, if ever, be supported, even though more space was available than required by a single pair of birds. Densities from two other islands were considerably higher than those of other comparably sized forests (circled data points in Fig. 3A). This difference may be associated with the sizeable amount of adjacent non-forested area on these islands, which was used to varying degrees by some of the forest-nesting birds in question. This explanation is consistent with the fore-

TABLE 8. Frequency of vagrant birds and occupation patterns of small islands during the 1967–1969 seasons (10 June–15 July).

Species	No. observations of vagrants[a]	Corrected no. observations of vagrants[b]	No. island-years occupied	No. island-years vacant	No. island-years vacant on islands occupied by species at least once[c]
Northern Parula	6 (2)	18	22	5	3
Yellow Warbler	2 (1)	6	12	15	12
Magnolia Warbler	4 (0)	12	0	27	3
Yellow-rumped Warbler	5 (3)	15	17	10	3
Black-throated Green Warbler	6 (6)	18	8	19	4
Blackburnian Warbler	5 (0)	15	0	27	0
Chestnut-sided Warbler	2 (0)	6	0	27	0
American Redstart	6 (1)	18	10	17	12

[a] Data either previously unpublished or from Morse (1971a). Figures in parentheses refer to individuals observed on islands already occupied by other individuals of the same species.
[b] I visited the islands once every three days on the average, so that multiplying by 3 produces a daily total.
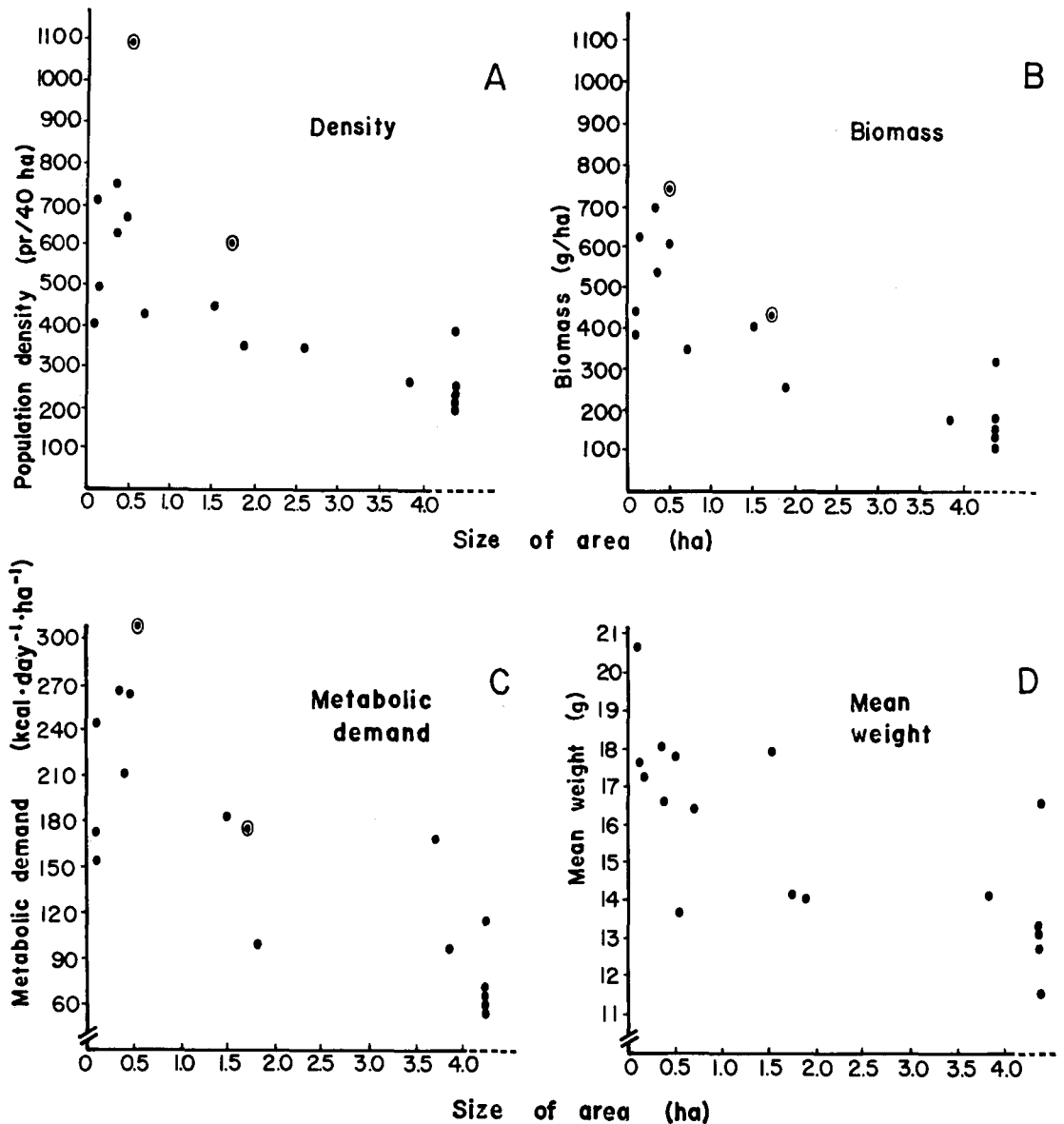[c] During the years of 1967 through 1975.

FIGURE 3. (A) Mean density, (B) biomass, (C) estimated metabolic demand, and (D) mean weights of birds on islands of varied size. Circled symbols represent forests with considerable unforested area about them. Symbols to right of 4.0 ha line represent maximum and minimum values from plots in large mainland forests. Metabolic demand (M) calculated using the equation $M = KW^b$, where $K = 129$, W = weight in grams, and $b = 0.724$ (Lasiewski and Dawson 1967).

going observation that size of vegetated area (forested and unforested) was the best indicator of the numbers of deciduous-edge species present.

The biomass (g/ha) and estimated metabolic demand (Kcal · day⁻¹ · ha⁻¹) of nesting birds also changed inversely with forest size (Fig. 3B and C). The biomass, but not the metabolic demand, of the two high-density populations fell nearer to that of other plots than in the preceding comparison. The mean size of the birds on the smallest island was

larger than that on the larger islands (Fig. 3D); this results primarily from the predominance of Song Sparrows on the former.

Population density, biomass, metabolic demand, and average weight of birds (Table 9, Fig. 3) on the smallest islands were all greater than those of mainland populations ($P < 0.01$ in one-tailed Mann-Whitney U tests). The second largest island of the group, Haddock Island (1.86 ha), had a population density, biomass, and metabolic demand that approached those of the highest-density large

TABLE 9. Density and biomass of tree foragers[a] and ground-understory foragers.[b]

| Areas | Density ± SE (pr/40 ha) | | Biomass ± SE (g/ha) | | Metabolic demand ± SE (Kcal·day^{-1}·ha^{-1}) | |
	Ground-understory	Tree	Ground-understory	Tree	Ground-understory	Tree
Tiny islands	354 ± 41.9	223 ± 34.8	357 ± 39.2	118 ± 19.5	138 ± 13.3	57 ± 11.1
Large forests	63 ± 14.5	201 ± 15.1	94 ± 26.6	89 ± 7.5	31 ± 8.0	41.3 ± 3.1

[a] Red-breasted Nuthatch, Brown Creeper, Golden-crowned Kinglet, Ruby-crowned Kinglet, Red-eyed Vireo, Black-and-white Warbler, Northern Parula, Yellow Warbler, Magnolia Warbler, Yellow-rumped Warbler, Black-throated Green Warbler, Blackburnian Warbler, Canada Warbler, American Redstart, Purple Finch.
[b] Winter Wren, Catbird, American Robin, Hermit Thrush, Swainson's Thrush, Yellowthroat, Dark-eyed Junco, White-throated Sparrow, Song Sparrow.

spruce forest censused, while on the largest island, Wreck Island, (3.86 ha), these variables approached those of most large spruce forests. However, the forest of these islands did not closely resemble the undisturbed large spruce forests because the islands had much deciduous, as well as coniferous, growth (Morse 1973a).

The difference between the small islands and the large forests resulted mostly from an increase in density, biomass, and metabolic demands of ground and understory foragers on the small islands (Table 9). All three measures of the ground and understory component were significantly greater on these islands than in the large forests ($P < 0.001$ in one-tailed Mann-Whitney U tests). While the density, biomass, and metabolic demand of tree-foraging species were slightly higher on the islands than in the large forests, these differences did not approach significance ($P > 0.05$).

DENSITY OF INDIVIDUAL SPECIES

When a single pair of a species occurred on an island they usually ranged widely over it, probably using all parts as frequently as they would parts of intensely defended territories on the adjacent mainland. Some species used much smaller areas on the islands than they did on the mainland, while other species did not markedly change the size of their territories on the islands, only occupying islands of a size consistent with their mainland territories. By comparing the data on mainland territory size in Table 5 with the smallest-sized island occupied, one may roughly estimate the amount of intraspecific crowding that will be tolerated by the different species (Table 10). Five of the eight species for which the necessary data were available did not decrease their areas of occupancy (Winter Wren, Golden-crowned Kinglet, Magnolia Warbler, Black-throated Green Warbler, and White-throated Sparrow), while three species did (Northern Parula, Yellow-rumped

Warbler, and Song Sparrow). The data available clearly did not completely document the extent of the ability of the Song Sparrow to reduce its area, as two pairs nested on an island of 0.16 ha each year, suggesting that the figure of 0.10 ha can be reduced to 0.08 ha, at least. Further, this species nested each year on an island of 0.10 ha, as well as on an island of 0.11 ha, suggesting that this level of crowding was readily tolerated.

The differences in density of species present both on the small islands and in the large forests appeared to result from the disappearance of potential competitors encountered in the large forests. In the case of the three species for which relatively accurate measures of substantial ecological release exist, changes in density probably occurred for the following reasons: (1) (Northern Parula, Yellow-rumped Warbler, and Song Sparrow) Northern Parulas on the tiny islands existed in the absence of several potential competitors. Golden-crowned Kinglets, which appeared to be a major factor responsible for the low density of Northern Parulas in dense spruce forests (Morse 1967), bred but rarely on the tiny islands. This species nested only on Thief Island, the only primarily spruce-covered island larger than the average Northern Parula

TABLE 10. Comparison of the sizes of areas (ha) occupied on small islands and in large populations.

Species	Territory size ($\bar{x}$) in large populations	Size of smallest island occupied	Size of next smallest island	Minimum contraction
Winter Wren	3.64	3.86	1.86	None
Golden-crowned Kinglet	0.72	1.50	0.69	None
Northern Parula	0.40	0.16	0.11	2.5
Magnolia Warbler	0.72	1.50	0.69	None
Yellow-rumped Warbler	0.81	0.35	0.16	2.3
Black-throated Green Warbler	0.43	0.49	0.39	None
White-throated Sparrow	0.49	0.49	0.39	None
Song Sparrow	0.49	0.10	—	4.9+

territory in dense mainland spruce forests (Table 5). In edge situations on islands smaller than the Northern Parula's customary mainland territory size (which were seldom frequented by Golden-crowned Kinglets), only one other warbler (Yellow-rumped) was present, in contrast to four species of warblers (Yellow-rumped, Black-throated Green, Magnolia, Blackburnian) and the kinglet in the large forests. Further, on the smallest island occupied by Northern Parulas, where their territories were only 40% of their average size in edge situations on the mainland, the birds occurred in the absence of other foliage-gleaning species. (2) A similar pattern held for the Yellow-rumped Warbler, which also was present with a reduced number of other warblers on the small islands, a number which decreased with forest size. (3) The Song Sparrow coexisted in large forests and deciduous-edge situations with two other common ground-dwelling sparrows, the Dark-eyed Junco and White-throated Sparrow. Juncos did not nest on these islands during the study, and White-throated Sparrows only nested sporadically. Islands containing the highest density of Song Sparrows did not have White-throated Sparrows on them. Song Sparrows foraged regularly into the midst of the spruce forests. Also, they foraged in the low, live foliage of the spruces on the tiny islands, a mode of foraging not observed elsewhere in this area except occasionally in juveniles (unpubl. data). Yeaton and Cody (1974) noted similar patterns of release in this species.

DISCUSSION

Many of my results invite comparison with the predictions of MacArthur and Wilson (1967) and those of other more recent papers on island biogeography. In contrast to many of those studies, the islands that I have studied are distinctive in at least five ways: no distance effect exists; dispersal is probably adequate to insure saturation in most instances; the size of these islands is smaller than that apparently required by many species to establish themselves; these island populations are not genetically isolated; and the species are migratory.

NUMBER OF SPECIES

The low z values obtained after the three smallest islands (<0.2 ha) were eliminated from the calculations approximate the values usually obtained from mainland censuses of different-sized areas (MacArthur and Wilson

1967). This result suggests that the islands are almost as available to would-be colonists as is the mainland. The three smallest islands were no farther from the mainland on the average than were the somewhat larger islands (Table 4), so that their small number of species cannot be attributed to isolation. Since these islands are considerably smaller than the average territory sizes of many likely colonizers, this itself probably accounts for the result obtained. Diamond and Mayr (1976) noted a similar trend on the smallest islands surveyed in their study of the Solomon Archipelago, though no islands censused were as small as those considered here.

Increases in numbers of species with area are often believed to result, in part, from large areas having greater habitat ranges than small ones (Hamilton et al. 1964). However, because of the uniformity of the islands in this study, the actual size of an island probably is more important in accounting for the number of species present on it than are more specific measures of the environment. Simberloff's (1976a) experimental results upon the fauna of mangrove islets suggest a similar explanation.

The absence of a species, even for a single year, may provide the opportunity for another species to occupy the area. The cumulative count over the 1967–1975 period thus is the best measurement of the number of species that find the attributes of the islands satisfactory for inhabitation; its magnitude is probably not primarily a function of interactions between species. If the mean number of species per year and the minimum yearly counts differ markedly, as occasionally occurred in this study, non-interactive conditions may have been experienced as well. In particular, certain results obtained from 1973 to 1975 (Table 6) favor this interpretation. However, the largest number of species to occupy an area in a year should produce a situation in which interspecific interactions reach a maximum.

Numbers of species on the islands remained rather constant during the study period. The decrease of the spruce-forest component and corresponding increase of the deciduous-edge component following two poor breeding seasons provided a strong test of the hypothesis that these islands are basically in equilibrium. I cannot explain, however, why the spruce-forest group apparently dropped below its carrying capacity, while the deciduous-edge group did not. The spruce-forest species now appear to be re-establishing themselves, and

it will be instructive to determine to what degree they will reattain their pre-1972 concentrations.

TURNOVER

While the turnover of species on these islands is not identical to that occurring on islands with low invasion rates and isolated breeding populations (see Lynch and Johnson 1974, Smith 1975, Simberloff 1976b), comparison is profitable. The rates of new colonization and extinction on these islands (16.7%/yr) are well over an order of magnitude higher than those reported from the California Channel Islands (0.3–1.2%/yr); Karkar, East Indies (0.32%/yr; Diamond 1969, 1971); and Mona Island, West Indies (0.29%/yr; Terborgh and Faaborg 1973). However, these authors' turnover rates are minimal, as their study areas were only censused twice at approximately 50-yr intervals, with the result that many colonizations and subsequent extinctions may have gone unnoticed between the censuses. When I use only my 1967 and 1975 data (first and last years), the mean turnover rate calculated for my islands drops to 3.6%/yr, still much higher than the results of others, but considerably nearer to them. Most of the colonizations and extinctions on my islands took place between 1967 and 1975 and hence were not accounted for in this abbreviated calculation. These results support the notion that actual turnover rates for the other studies were considerably higher than the minimum ones that were calculated with their data base.

Lynch and Johnson (1974) have challenged many of Diamond's interpretations of individual colonizations and extinctions, and concluded that his turnover rates were probably far too high. While several of Lynch and Johnson's arguments could be resolved only with new data, my results are based upon year-to-year intensive censusing of demonstrably breeding individuals and, thus, are not subject to alternative explanation.

Though my results seem high in the context that I have presented them, even higher turnover rates than these have been recorded in near-shore situations for a nearly complete insect fauna (Simberloff and Wilson 1970, Simberloff 1974) and for ants (Goldstein 1975). Simberloff and Wilson found turnover rates of 2%/day on mangrove islets in the Florida Keys (subsequently considered an overestimate of true turnover by Simberloff [1976b]), and Goldstein reported turnover rates of 33%/yr on small islands off the Connecticut coast.

PATTERNS OF RESOURCE EXPLOITATION

This study and my earlier one (Morse 1971a) demonstrate that some species modify their patterns of resource exploitation on these islands, while others show little, if any, such tendency. The most flexible species were the most frequent occupants of these small islands, and in at least some cases, were also the most successful reproductively (Morse 1971a). Subtle changes in niche overlap and niche width occurred among some of these species (Morse 1971a), but the present study indicates that the greatest changes in resource exploitation in the presence of other species lay in changes in the intensity with which any given part of a territory was used. In the absence of certain other species, some species successfully occupied territories less than one-fifth the size of those used when the others were present. Similar patterns have been noted by other workers (e.g., Beer et al. 1956, Yeaton and Cody 1974).

The tendency of deciduous-edge species to make regular use of non-arborescent vegetation next to the forests probably accounted for the disproportionately high success of the deciduous-edge species in colonizing these islands. While the deciduous-edge species occupied these islands with a frequency similar to that of spruce-forest species, deciduous-edge species occupied areas for which the spruce-forest species, but not the deciduous-edge species, were presumably specially adapted. If new areas of unspecified nature became available, the latter group would probably make the heavier contribution to colonization. This result is not surprising, because others (e.g., Wilson 1961, MacArthur et al. 1972, Diamond 1974) have reported that species from marginal or disturbed mainland habitats are the most frequent of island inhabitants.

DENSITY, BIOMASS, AND METABOLIC DEMAND

Population densities of individual species were often much greater than those of the adjacent mainland; further, the cumulative density, biomass, and metabolic demand of birds on these islands often considerably exceeded those of the mainland. Other studies of population density on islands (reviewed by Simberloff 1974) do not as a whole reveal any simple pattern, and presumably data on biomass and metabolic demand would yield a

comparable picture. It appears necessary, as Diamond (1970) suggested, to examine each situation individually. The result obtained could be caused by differences in (1) numbers of competitors from taxonomic groups not considered here, (2) simple concentrations of available resources (a non-interactive situation), (3) numbers of predators, or (4) a combination of some or all of these factors.

Numbers of species from potentially competing taxonomic groups also decrease markedly on these small islands (e.g., mammals, Crowell 1973, Morse 1973b). However, since the possibility of competition with these animals has not been explored, little more can be said about this matter. The food supply should be correlated with the numbers of competitors present, but the ease with which food may be procured could be a factor determining the density and biomass of individuals present in a non-interactive situation. Since the amount of insects does not differ markedly in large forests and on tiny islands (Fig. 2) during the periods most critical to the success of nesting individuals (Morse 1968), this factor appears unlikely to account for the differences in density observed. The volume of foliage per unit area in large forests and on tiny islands does not differ, though trees in the large forests are taller than those on the tiny islands (Morse 1971a, 1976). Energy flow could be higher on the islands than on the mainland, but there is no clear reason why this should be the case.

Known predatory losses on the mainland result primarily from nest-robbing and capture of fledglings by Blue Jays and red squirrels (*Tamiasciurus canadensis*; Morse 1976). With one exception, I have never seen a red squirrel on these tiny islands, and Blue Jays occurred but infrequently. Therefore, predation almost certainly is less intense on the islands than on the mainland. It seems questionable, however, whether predatory pressure would significantly depress the numbers of breeding adults on the mainland, especially when extra nonbreeding individuals were present, as was often the case during some years of the study. The only large forest without red squirrels (Harbor Island) that I have studied had a substantially higher overall density of birds than did the four other mainland-type spruce forests censused (highest score plotted for large forests in Fig. 3).

No one of these factors can unequivocally account for these differences in density, but the predation hypothesis is supported by some concrete information, the competition hypothesis is consistent with the data, and the resource-availability hypothesis has little to recommend it.

SUMMARY

Breeding landbirds on 12 small (0.1–4.0 ha), forested islands in Muscongus Bay, Maine, were censused from 1967 through 1975. All 17 species that bred also occupied spruce forests or adjacent disturbed habitats on the nearby mainland. Similar numbers of species came from both areas, but since most islands were spruce-covered, the contribution from the disturbed areas exceeded that predicted by chance. Size of forest accounted for the greatest amount of variation in numbers of species present, while the total area vegetated, amount of ground cover, and forest height made lesser contributions. Total vegetated area accounted for the greatest amount of variation in numbers of species present from the disturbed areas, however, even though this study only treated the species that occupied the forested parts of the islands. When the smallest islands (<0.2 ha) were removed from the calculation, z (slope of the log-log regression of species against area) fell near 0.20, which approaches a typical mainland figure. Including the smallest islands in the calculation, z was about 0.50, probably because these islands were too small to support most species. Some species occurred only on islands at least as large as their territory sizes on the mainland, while others decreased their territory size considerably. Those bird species not predicted on the basis of the size of their mainland territories often were low in the social hierarchy and demonstrated ecological release on the islands. Following two poor breeding seasons, spruce-forest species declined markedly, while those of disturbed areas increased; consequently, the islands remained in equilibrium when taken as a group. Turnover rates of species averaged 16.7%/yr. Numbers of vagrants actually observed were adequate to saturate the islands, at least in some years. Overall density, biomass, and metabolic demand generally changed inversely with forest size and exceeded those on the adjacent mainland.

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APPENDIX I. Species pool of breeding landbirds from mainland and large inshore islands.[a]

SPRUCE FOREST COMPONENT[b]—Yellow-bellied Flycatcher (*Empidonax flaviventris*), Blue Jay (*Cyanocitta cristata*), Black-capped Chickadee (*Parus atricapillus*), Red-breasted Nuthatch (*Sitta canadensis*), Brown Creeper (*Certhia familiaris*), Winter Wren (*Troglodytes troglodytes*)[d], Hermit Thrush (*Catharus guttatus*), Swainson's Thrush (*C. ustulatus*), Golden-crowned Kinglet (*Regulus satrapa*), Solitary Vireo (*Vireo solitarius*), Northern Parula (*Parula americana*)[d], Magnolia Warbler (*Dendroica magnolia*), Cape May Warbler (*D. tigrina*), Yellow-rumped Warbler (*D. coronata*), Black-throated Green Warbler (*D. virens*), Blackburnian Warbler (*D. fusca*), Bay-breasted Warbler (*D. castanea*), Brown-headed Cowbird (*Molothrus ater*), Purple Finch (*Carpodacus purpureus*), Pine Siskin (*Carduelis pinus*), Red Crossbill (*Loxia curvirostra*), White-winged Crossbill (*L. leucoptera*), Dark-eyed Junco (*Junco hyemalis*), White-throated Sparrow (*Zonotrichia albicollis*).

DECIDUOUS-EDGE COMPONENT[c]—Mourning Dove (*Zenaida macroura*), Ruby-throated Hummingbird (*Archilochus colubris*), Common Flicker (*Colaptes auratus*), Hairy Woodpecker (*Picoides villosus*), Downy Woodpecker (*P. pubescens*), Eastern Wood Pewee (*Contopus virens*), Olive-sided Flycatcher (*Nuttallornis borealis*), Catbird (*Dumetella carolinensis*), American Robin (*Turdus migratorius*), Cedar Waxwing (*Bombycilla cedrorum*), Red-eyed Vireo (*Vireo olivaceus*), Black-and-white Warbler (*Mniotilta varia*), Nashville Warbler (*Vermivora ruficapilla*), Yellow Warbler (*Dendroica petechia*), Chestnut-sided Warbler (*D. pensylvanica*), Ovenbird (*Seiurus aurocapillus*), Yellowthroat (*Geothlypis trichas*), Canada Warbler (*Wilsonia canadensis*), American Redstart (*Setophaga ruticilla*), American Goldfinch (*Carduelis tristis*), Rufous-sided Towhee (*Pipilo erythrophthalmus*), Chipping Sparrow (*Spizella passerina*), Song Sparrow (*Melospiza melodia*).

OTHER SPECIES COMPONENT[e]—Black-billed Cuckoo (*Coccyzus erythropthalmus*), Whip-poor-will (*Caprimulgus vociferus*), Eastern Kingbird (*Tyrannus tyrannus*), Great Crested Flycatcher (*Myiarchus crinitus*), Alder Flycatcher (*Empidonax alnorum*), Least Flycatcher (*E. minimus*), White-breasted Nuthatch (*Sitta carolinensis*), Brown Thrasher (*Toxostoma rufum*), Wood Thrush (*Hylocichla mustelina*), Veery (*Catharus fuscescens*), Eastern Bluebird (*Sialia sialis*), Tennessee Warbler (*Vermivora peregrina*), Black-throated Blue Warbler (*Dendroica caerulescens*), Northern Waterthrush (*Seiurus noveboracensis*), Bobolink (*Dolichonyx oryzivorus*), Eastern Meadowlark (*Sturnella magna*), Redwinged Blackbird (*Agelaius phoeniceus*), Common Grackle (*Quiscalus quiscula*), Northern Oriole (*Icterus galbula*), Scarlet Tanager (*Piranga olivacea*), Rose-breasted Grosbeak (*Pheucticus ludovicianus*), Indigo Bunting (*Passerina cyanea*), Savannah Sparrow (*Passerculus sandwichensis*), Field Sparrow (*Spizella pusilla*), Swamp Sparrow (*Melospiza georgiana*).

[e] Nesting on mainland within 2 km of shore.

APPENDIX II. Weights (g) of species used in calculations.[a]

Red-breasted Nuthatch, 10.3; Brown Creeper, 8.4; Winter Wren, 9.0; Catbird 34.5; American Robin, 76.2; Hermit Thrush, 29.7; Swainson's Thrush, 29.6; Golden-crowned Kinglet, 6.0; Ruby-crowned Kinglet (*Regulus calendula*), 6.5; Red-eyed Vireo, 16.9; Black-and-white Warbler, 10.2; Northern Parula, 7.0; Yellow Warbler, 9.6; Magnolia Warbler, 9.8; Yellow-rumped Warbler, 11.5; Black-throated Green Warbler, 9.2; Blackburnian Warbler, 10.3; Yellowthroat, 9.5; Canada Warbler, 9.0; American Redstart, 8.0; Purple Finch, 24.5; Dark-eyed Junco, 20.5; White-throated Sparrow, 26.5; Song Sparrow, 20.7.

[a] Data represent mean weights of males and females combined from birds captured in study areas, supplemented by Stewart (1937), Baldwin and Kendeigh (1938), and Poole (1938). With rare exceptions sample sizes or data from other sources are inadequate to calculate confidence intervals.

[a] From Cruickshank (no date); Morse (1966, unpubl. data). Does not include several species directly dependent upon human habitation for nest sites.
[b] Many of these species also nested in the deciduous-edge habitats.
[c] Deciduous growth, mixed deciduous growth, areas of blown-over trees, and edge of forest. Many of these species also nested in habitats supporting species in last category.
[d] Placed in deciduous-edge component by Morse (1966). Subsequent observations justify inclusion in spruce forest component.

Department of Zoology, University of Maryland, College Park, Maryland 20742. Accepted for publication 9 December 1976.