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**Species-area relationship of birds on small islands at Isle Royale, Michigan.**—Most studies of avian biogeography have described species distribution patterns across huge archipelagoes (Simberloff, pp. 411–455 in *Perspectives in Ornithology*, A. H. Brush and G. A. Clark, Jr., eds., Cambridge Univ. Press, Cambridge, England, 1983). In comparison, bird populations on groups of small islands close to one another and to the species source pool have received little attention (but see Galli et al., *Auk* 93:356–364, 1976; Morse, *Condor* 79:399–412, 1977; Rusterholz and Howe, *Evolution* 33:468–477, 1979). The factors that influence species composition on such islands are likely to be quite different from those considered in the classic theoretical models of island biogeography (MacArthur and Wilson, *Island Biogeography*, Princeton Univ. Press, Princeton, New Jersey, 1967). Very small islands are mostly inhabited by migrant birds that “go extinct” and “recolonize” each year, and the proximity of islands enables birds to defend territories that include more than one island.

This paper presents data on the number of bird species on 36 small islands at the northeast end of Isle Royale Wilderness National Park, Michigan. The results show that the use of multiple islands by breeding birds complicates the interpretation of species-area data from very small islands.

*Methods.*—The 36 islands, ranging from 3 m<sup>2</sup> to 20.6 ha, are all within 1.5 km of Isle Royale, which is as close as 18 km from the north shore of Lake Superior. Isle Royale contains essentially all breeding birds present on the adjacent Canadian mainland (Jordon and Shelton, *Wildlife of Isle Royale*, Isle Royale Nat. Hist. Assoc., Houghton, Michigan, 1982), and the water between islands does not present a barrier to regular avian colonization. Dominant trees on these islands include white spruce (*Picea glauca*), balsam fir (*Abies balsamea*), and paper birch (*Betula papyrifera*). Two censuses of the breeding bird populations on each island were made between 11 June and 12 July 1983. Because all islands are narrowly elongated along a NE–SW axis, bird populations could be counted accurately by walking the length of the island, and census duration was roughly proportional to island area. A species was considered present if it was recorded on at least one census; the number of males was estimated by averaging the results of the two censuses. By sampling each island on only two occasions, I may have generated an incomplete record of species occurrences by overlooking inconspicuous species, and I may have overestimated birds that traveled between islands.

Species-area data were fitted by the power function,  $S = cA^z$ , where  $S$  is number of species + 1 (several islands had zero species),  $A$  is island area (ha; excluding the exposed, rocky shores of the outermost islands), and the parameters  $c$  and  $z$  are estimated by the intercept and slope of the regression of log-species on log-area. The correlation coefficient, used to assess the fit of the model, was calculated by a second regression of species number on area raised to the power  $z$  obtained from the original log-log regression (Martin, *Am. Nat.* 118:823–837, 1981).

*Results and discussion.*—The number of breeding species increases as a function of island area throughout the range of island sizes present in the study (Table 1). The log-log regression equation of species richness on area explains most of the variance among islands in species richness ( $r = 0.953$ ,  $P < 0.0001$ ;  $z = 0.281 \pm 0.063$  [95% CI],  $c = 4.33 \pm 1.17$ ). After excluding the two smallest islands (3 m<sup>2</sup> and 10 m<sup>2</sup>), which are well below the minimum size necessary to support breeding birds, the slope and intercept increase to  $z = 0.341 \pm 0.063$  and  $c = 4.46 \pm 1.16$ , but the fit of the power function remains unaltered ( $r = 0.957$ ,  $P < 0.0001$ ).

TABLE 1  
ESTIMATED NUMBER OF MALES OF THE 10 MOST COMMON SPECIES ON 36 ISLANDS

Island	Size (ha)	No. of males present									
		SS <sup>a</sup>	YR	NA	MA	WW	WT	AR	ST	BL	RN
Hidden Rock	0.0003	0	0	0	0	0	0	0	0	0	0
Split Rock	0.001	0	0	0	0	0	0	0	0	0	0
Storm	0.02	0.5	0	0	0	0	0	0	0	0	0
Short	0.03	0	0	0	0	0	0	0	0	0	0
Kemmer	0.03	0.5	0.5	0	0	0	0	0	0	0	0
East Split	0.05	1.0	0	0	0	0	0	0	0	0	0
First	0.05	0.5	0.5	0	0	0	0	0	0	0	0
West Split	0.08	1.0	0	0	0	0	0	0	0	0	0
Emerson	0.09	0.5	0.5	0	0	0	0	0	0	0	0
Musselman	0.10	1.0	0	0	0	0	0	0	0	0	0
Middle Tobin	0.11	0.5	0.5	0	0	0	0	0	0	0	0
Green	0.15	1.0	0.5	0	0	0	0	0	0	0	0
West Tobin	0.17	1.0	1.0	0	0	0	0	0	0	0	0
Hidden	0.18	1.0	0.5	0	0	0	0	0	0	0	0
Gem	0.19	1.0	0.5	0	0	0	0	0	0	0	0
Howe	0.22	0.5	0	0	0	0	0	0	0	0	0
Lion	0.34	2.0	0	0	0	0	0	0	0	0	0
Porter Islet	0.35	1.0	0.5	0	0	0	0	0	0	0	0
Baily	0.36	1.0	0	0	0	0	0	0	0	0	0
East Tobin	0.37	1.0	1.0	0.5	0	0	0	0	0	0	0
Third	0.40	1.0	1.0	0	0	0	0	0	0	0	0
Flag	0.49	2.5	1.0	0	0	0	0	0	0	0	0
Savage	0.71	0	1.0	0	0.5	1.0	0	0	0	0	0
Smith	0.88	1.0	1.0	0	0	0	0	0	0	0	0
Merritt I	0.93	0.5	1.0	0.5	0.5	0	0.5	0	0	0	0
Gale	1.01	1.0	1.5	0.5	1.0	0	1.0	0.5	0	0	0
Second	1.20	2.0	1.0	0	1.0	0	0	0.5	0	0	0
Merritt II	1.43	2.0	1.0	0	0.5	0	0.5	1.5	0	0	0
Newman	1.69	1.0	2.0	1.0	0.5	0	0	0	0.5	0	0
North Gov't.	1.84	3.0	1.0	1.0	0	0	0	1.0	0.5	0	0
Boys	2.87	1.0	2.0	1.0	1.0	1.0	2.0	1.0	0	0	0
South Gov't.	3.73	4.0	4.5	0.5	0	1.0	0	1.0	0.5	0	0
Long	3.97	2.5	2.0	0.5	0	1.0	0.5	0	0	0.5	0
Minong	7.81	1.0	2.0	2.0	1.5	0.5	1.5	1.0	1.0	0	0
Edwards	10.47	3.0	6.0	5.0	2.0	2.0	0	2.0	1.0	1.0	2.0
Porter	20.58	4.0	12.0	9.0	8.5	3.0	7.0	1.0	3.0	0.5	1.0

<sup>a</sup> Abbreviations of species are as follows: SS = Song Sparrow (*Melospiza melodia*), YR = Yellow-rumped Warbler (*Dendroica coronata*), NA = Nashville Warbler (*Vermivora ruficapilla*), MA = Magnolia Warbler (*D. magnolia*), WW = Winter Wren (*Troglodytes troglodytes*), WT = White-throated Sparrow (*Zonotrichia albicollis*), AR = American Redstart (*Setophaga ruticilla*), ST = Swainson's Thrush (*Catharus ustulatus*), BL = Blackburnian Warbler (*D. fusca*), and RN = Red-breasted Nuthatch (*Sitta canadensis*).

TABLE 2  
COMPARISON OF SIZE (HA) OF THE SMALLEST ISLAND OCCUPIED AT ISLE ROYALE AND  
AVERAGE TERRITORY SIZE IN A LARGE POPULATION IN MAINE

Species	Smallest island occupied at Isle Royale	Mean (N) territory size in Maine <sup>a</sup>	Smallest island expressed as % of mean territory size in Maine
Song Sparrow	0.02	0.26 (24)	7.7
Yellow-rumped Warbler	0.03	0.81 (17)	3.7
Winter Wren	0.71	3.64 (2)	19.5
Magnolia Warbler	0.71	0.72 (9)	98.6
White-throated Sparrow	0.93	0.62 (18)	150.0

<sup>a</sup> Data for mainland population in Maine from Morse (1977: Table 5).

The biological significance of the parameters  $c$  and  $z$  of the species-area curve has been considered for some time (MacArthur and Wilson 1967; Connor and McCoy, *Am. Nat.* 113:791–833, 1979; Gould, *Am. Nat.* 144:335–343, 1979; Martin 1981). The coefficient  $c$  is the projected number of species on an island of unit area (one ha, in this study), and is useful for comparisons of species diversity among sets of archipelagoes with equal  $z$ 's (Gould 1979). According to my analysis, an average of 4.3–4.5 breeding species should occur on a one-ha island at Isle Royale. Maximum increases in species diversity with incremental increases in area (maximum  $z$  values) seem to occur in groups of small islands. The  $z$  calculated for the islands in this study is lower than the values for six groups of islands of similar size reviewed by Martin (1981,  $z = 0.388$ – $0.542$ ), probably because my smallest islands were only barely large enough to support breeding birds, so that males on these islands had multiple islands in their territories. Including only islands at least 0.1 ha in the regression gives an estimate within the range of slopes summarized by Martin ( $z = 0.392 \pm 0.108$ ,  $N = 26$ ,  $r = 0.963$ ,  $P < 0.0001$ ).

My results permit estimation of the minimum area requirements for several common species of birds at Isle Royale. Song Sparrows appear on a 0.02 ha island, but do not regularly occur below roughly 0.05 ha. Yellow-rumped Warblers breed on the majority of islands greater than 0.10 ha. Nashville and Magnolia warblers do not breed on islands smaller than 0.4–0.7 ha, and Winter Wrens and White-throated Sparrows require approximately 0.7–0.9 ha. These smallest-island records should be accepted with caution, however, as these birds may use more than one island. For example, it is probably not reasonable to suppose that a pair of Song Sparrows confined their breeding activities to an island only 0.02 ha in size (Storm Island, Table 1). In fact, I made a number of observations of Song Sparrows and Yellow-rumped Warblers traveling between adjacent islands.

These results support the observation that some birds occupy smaller areas on islands than in mainland habitats (Yeaton and Cody, *Theor. Popul. Biol.* 5:42–58, 1974; Morse 1977). Morse (1977) compared mainland and island territory sizes of eight passerines on the coast of Maine and concluded that Song Sparrows, Yellow-rumped Warblers, and Northern Parulas (*Parula americana*) defended smaller territories on islands because of the absence of competitors. Five of Morse's (1977) species also occur in my study area (Table 2). At Isle Royale, the smallest islands occupied by Song Sparrows, Yellow-rumped Warblers, and Winter Wrens are 5–27 times smaller than the average territory sizes of these species in Morse's (1977) mainland populations. Magnolia Warblers and White-throated Sparrows

occupy areas of similar size on islands at Isle Royale and on the mainland in Maine (Table 2). Although these data are consistent with the hypothesis that certain species experience competitive release on islands at Isle Royale, they may also reflect the use of multiple islands by breeding males. Concurrent use of several islands would cause underestimation of area requirements, and might create the appearance of competitive release. Thus, studies of competitive release on archipelagoes of very small islands should include detailed observations of marked birds to determine individual patterns of island use.

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**Avoidance of acoustic interference by Ovenbirds.**—Two birds singing at the same time may mask each others' signals. In order to have their signals heard, birds should actively avoid both intraspecific and interspecific interference through temporal changes in the delivery of advertisement songs (Ficken et al., *Science* 183:762–763, 1974; Wasserman, *Anim. Behav.* 25:949–952, 1977), although experimental evidence is scarce (Schroeder and Wiley, *Auk* 100:414–423, 1983). Here, we report on the use of playbacks to investigate whether Ovenbirds (*Seiurus aurocapillus*) actively avoid intraspecific acoustic overlap. Lein (*Wilson Bull.* 93:21–41, 1981) has previously suggested that intraspecific avoidance occurs in this species.

The study site, at the University of Wisconsin–Milwaukee Field Station, Saukville, Ozaukee County, Wisconsin, was in an original growth, upland beech-maple forest. The playback tape consisted of 50 Ovenbird songs played at randomly determined intervals (6–48 sec) over a 12-min period. The response of the Ovenbirds was recorded with a Sennheiser MKH 104 omnidirectional condenser microphone connected to a Nagra III tape recorder placed 3 m from the speaker and 1.5 m off the ground. Recordings were made on five days (one experiment per day, with a different Ovenbird each day) between 15 June and 2 July 1968. All five Ovenbirds were color-banded. The Ovenbirds were in the nestling period of the nesting cycle during the study.

To determine the relative timing of songs, the tapes were analyzed using a Bruel and Kjaer 2305 graphic level recorder with a 2000 Hz high pass filter. The length of each song and the interval between songs were then measured. The predicted number of Ovenbird songs begun during a stimulus song is:

$$F = p(s)f$$

where  $f$  is the total number of nonstimulus songs and  $p(s)$  is the portion of recording time during which the stimulus tape was playing (Ficken et al. 1974). For this study  $p(s)$  equals 0.135.

A replicated goodness of fit test ( $G$ -statistic) was used for the statistical analysis (Sokal and Rohlf, *Biometry*, W. H. Freeman, San Francisco, California, 1981). This test permitted comparison of observed and expected values for each individual replicate as well as for the pooled results. In addition, a test of the heterogeneity of the ratios of the replicates was performed.