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DIFFERENTIAL PASSERINE DENSITY AND DIVERSITY BETWEEN NEWFOUNDLAND AND OFFSHORE GULL ISLAND

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Characteristically, islands have impoverished biotas (MacArthur and Wilson 1963, 1967; Diamond 1975; many others). Several reasons have been proposed to account for this depauperate condition. Remoteness of the island (MacArthur and Wilson 1963, 1967; Simberloff and Wilson 1969) and island size (Diamond 1975, MacArthur and Wilson 1967, Power 1976) can both affect the equilibrium number of species, either directly or indirectly, with small, remote islands having the fewest species. The potential reduction of habitat diversity on small islands may also indirectly lead to increased interspecific competition, and consistent with the competitive exclusion principle, a reduction in number of species may result through loss of close competitors (Grant 1966a, MacArthur and Wilson 1967, Morse 1971). Other indirect effects of island size, isolation or topography have been proposed as factors determining equilibrium numbers of species on islands (MacArthur et al. 1973, Morse 1971). Few of the above notions have escaped some criticism (e.g., Grant 1966a, Lynch and Johnson 1974).

Differences in numbers of species often occur concomitantly with changes in the density of island avifaunas. Increases in density commonly occur and are usually attributable to an increase in the density of a few species, relative to their mainland densities (Crowell 1961, Grant 1966b, MacArthur et al. 1972). However, lower net densities of island avifaunas have also been reported. These have been attributed to species expanding into suboptimal habitat where they occur in lower densities (Diamond 1970), to deterioration of the local gene pool (Diamond 1970), or to simply a decrease in species richness without a concomitant increase in densities of remaining species (MacArthur et al. 1972, Yeaton and Cody 1974).

Species also differ in their abilities to colonize small islands, making it possible in some instances to predict systematically the order of colonization of island chains, knowing the likely source population (Morse 1971, Diamond 1975, Terborgh et al. 1978). A consequence of this differential colonization ability of bird species is that an island adjacent to another island will have a different reservoir of potential colonizers than an island directly offshore from a continental land mass. The island source community ought to be one already selected for colonization ability, as has been found by Terborgh and Faaborg (1973) and Terborgh et al. (1978).

Another well-known biogeographical phenomenon is the decline of species diversity and richness with increasing latitude and/or harshness of climate (Klopfer and MacArthur 1960, 1961; Rotenberry 1978). The proportion of the community made up of nonpasserines also declines with increasing latitude (Klopfer and MacArthur 1960). Most studies of island biogeography have been conducted in tropical or warm temperate latitudes. The few studies farther north have considered only a few taxa (Morse 1971, but see Morse 1977, Cody and Cody 1972).

Newfoundland is a large island off the coast of eastern Canada. It shows a markedly depauperate avifauna, relative to adjacent Nova Scotia and Gaspé, Quebec (Peters and Burleigh 1951, Godfrey 1966). For example, Godfrey (1966) shows that over a quarter of the species breeding in Nova Scotia do not breed in Newfoundland, although recent records may alter that figure slightly. Gull Island (47°15′N, 52°46′W) is a small island off the east coast of Newfoundland, in the Witless Bay Seabird Sanctuary. This study examined the species diversity, richness and density of the land birds on Gull Island, to see if the low species richness of Newfoundland itself influenced the degree or pattern of species change between Gull Island and the adjacent coast of Newfoundland.

METHODS

Study area.—Gull Island, in the Witless Bay Seabird Sanctuary, comprises 0.95 km^2 and is 1.6 km from the nearest point of land (Fig. 1). Open grassy areas occur along the shore in which there are large numbers of nesting burrows of Common Puffins (*Fratercula arctica*). Inland mature boreal forest with balsam fir (*Abies balsamea*), white spruce (*Picea glauca*) and white birch (*Betula papyrifera*) predominate. Dead trees are common and there are bogs.

South Head, Witless Bay (47°17′N, 52°47′W) was the adjacent mainland area studied. Grassy fields and bogs were more abundant here than on Gull Island. Forested areas were comparable in species composition, but younger due to cutting. The 2 areas lie within the boreal forest region of Rowe (1972).

The vegetation of the 2 areas was compared quantitatively and reported with a detailed comparison of the ecological differences between sites for selected avian species (Vassallo and Rice, in press). Briefly, the South Head forest had fewer large dead trees and the most densely vegetated areas were denser than any on Gull Island. The trees in these exceptionally dense areas were mostly black spruce (*P. mariana*), which were more abundant on South Head than on Gull Island. White birch was more common on Gull Island. However, all habitat types were present at both sites and differences were of quantitatively extreme densities, not qualitative attributes.

Census methods.—Line transects were established at both localities along preexisting pathways (Fig. 2). Transects on the island and mainland measured 1.44 and 1.62 km, respectively. Both transects traversed open and forested areas, and although open areas were more abundant at South Head than Gull Island, lines at South Head were oriented so that comparable amounts of each habitat were censused. Censuses began within 1 h of sunrise and data from

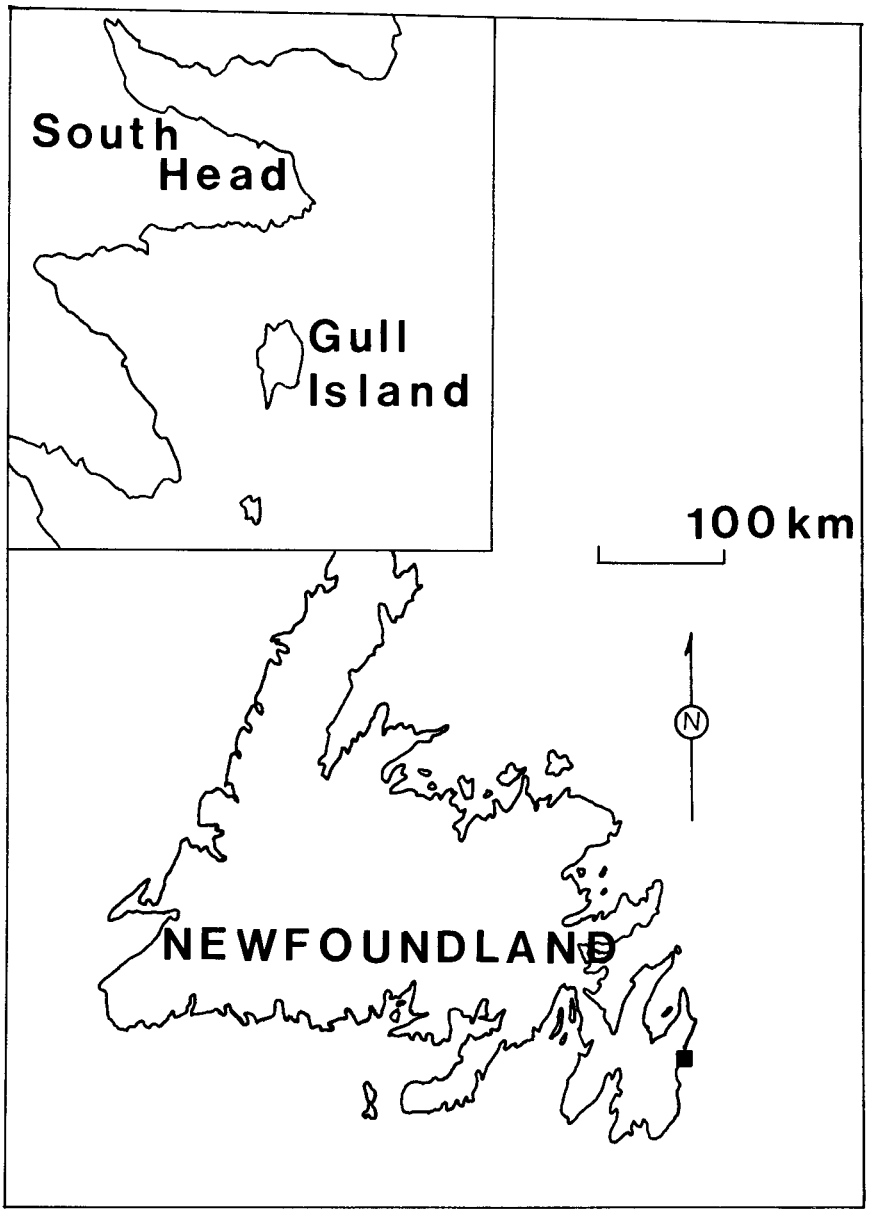

FIG. 1. Map of the island of Newfoundland, showing the location of the study area on the Avalon Peninsula. The inset shows Gull Island and South Head, Witless Bay.

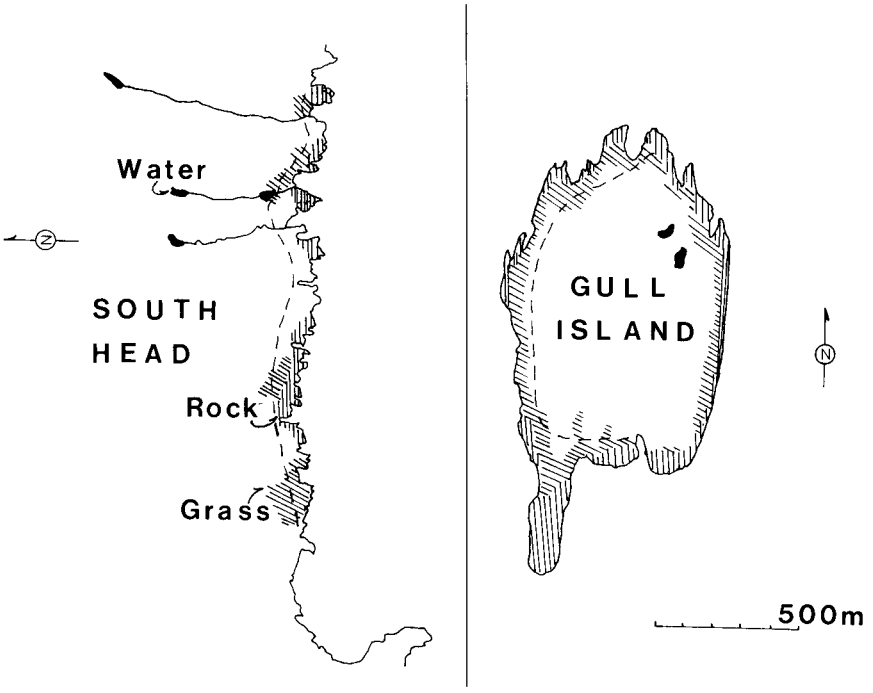

FIG. 2. Map of the 2 areas, showing major topographic features. The broken lines indicate the transect lines, vertical barring areas of exposed rock, slanted barring areas of grassy meadow, black areas open fresh water and all unshaded land areas are boreal forest.

censuses interrupted by inclement weather were discarded. Thirty censuses were done at South Head between 18 May and 19 July 1977, and 11 on Gull Island between 16 June and 26 July. Additional species seen at other times of day are considered in the comparisons of species richness, but not in the calculations of density or diversity measures.

Analyses.—Diversity indices were calculated for all censuses, using Shannon's Index (Pielou 1966a, b). Because the underlying distribution is unknown, a Kruskal Wallis test (Sokal and Rohlf 1969) was used to compare diversity indices between sites.

Bird densities were calculated for each census day as birds per km of line transect. No attempt was made to weight density by proximity to the line transects, because of greatly different patterns of species detectability between habitat types. To compare monthly and seasonal densities between areas we used t-tests of $\log_{10}$ of the abundance measures, after testing for homogeneity of variances. For species common at both sites, individual species densities were compared in the same way. However, densities were first compared within each site between June and July, and data for the 2 months were not combined if abundances changed significantly between months.

RESULTS

Thirteen species of passerines were observed on Gull Island, whereas 25 species were seen on South Head (Table 1). Eleven species were com-

TABLE 1
PASSERINE BIRDS OBSERVED ON SOUTH HEAD OR GULL ISLAND DURING MORNING CENSUSES (X) OR OTHER TIMES (T)

Species	South Head	Gull Island
Eastern Kingbird (*Tyrannus tyrannus*)	X[a]	
Yellow-bellied Flycatcher (*Empidonax flaviventris*)	X	X
Common Crow (*Corvus brachyrhynchos*)	X	
Common Raven (*Corvus corax*)	T[a]	X
Black-capped Chickadee (*Parus atricapillus*)	X	
Boreal Chickadee (*P. hudsonicus*)	X	X
Red-breasted Nuthatch (*Sitta canadensis*)	X[a]	
Brown Creeper (*Certhia familiaris*)		X[a]
Winter Wren (*Troglodytes troglodytes*)		X
American Robin (*Turdus migratorius*)	X	X
Gray-cheeked Thrush (*Catharus minimus*)	X	X
Golden-crowned Kinglet (*Regulus satrapa*)	X[a]	
Starling (*Sturnus vulgaris*)	X[a]	
Northern Parula (*Parula americana*)	T[a]	
Blackpoll Warbler (*Dendroica striata*)	X	X
Northern Waterhrush (*Seiurus noveboracensis*)	X	X
Wilson Warbler (*Wilsonia pusilla*)	X	
Rusty Blackbird (*Euphagus carolinus*)	T[a]	
Pine Grosbeak (*Pinicola enucleator*)	X	X
Pine Siskin (*Carduelis pinus*)	X	X
Red Crossbill (*Loxia curvirostra*)	X	
White-winged Crossbill (*Loxia leucoptera*)	X	X
Savannah Sparrow (*Passerculus sandwichensis*)	X	
Dark-eyed Junco (*Junco hyemalis*)	X	
White-throated Sparrow (*Zonotrichia albicollis*)	X	
Fox Sparrow (*Passerella iliaca*)	X	X
Swamp Sparrow (*Melospiza georgiana*)	X	

[a] Not seen more than twice during summer.

mon to both sites, 2 others were recorded only on the island and 14 were recorded only on South Head. With the exception of the Brown Creeper (*Certhia familiaris*), all rarely encountered species were recorded at South Head rather than Gull Island. Not all species restricted to South Head were rare ones, however, as 8 species frequently seen there were never seen on Gull Island.

One striking difference between the avifaunas of South Head and Gull Island was the number of congeners present. At South Head 2 species of *Parus*, 2 of *Loxia* and 2 of *Corvus* were recorded, whereas on Gull Island only 1 species of each genus was present. Furthermore, at South Head 5 species of sparrows and juncos and 4 species of warblers were noted, but

TABLE 2

MONTHLY MEAN BIRD SPECIES DIVERSITIES AND DENSITIES FOR SOUTH HEAD AND GULL ISLAND FOR SUMMER 1977

	Diversity		Density (birds/km)		
	$\bar{x} \pm$ SD	Range	$\bar{x} \pm$ SD	Range	N
South Head					
June	3.323 ± 0.836	2.983–3.749	37.2 ± 1.22	28.5–51.8	15
July	3.617 ± 0.843	3.345–4.278	41.1 ± 1.19	35.2–47.5	7
Gull Island					
June	2.819 ± 0.171	2.677–2.895	31.5 ± 1.36	19.4–43.7	5
July	2.446 ± 0.236	2.330–2.615	27.6 ± 1.20	22.2–36.8	6

on Gull Island only 1 sparrow and 2 warblers were recorded. The decreased number of species on Gull Island results from a loss of taxonomically related species, rather than the complete loss of certain higher taxa or ecological guilds. As with richness, South Head species diversity was significantly higher than species diversity on Gull Island ($P < 0.005$, Table 2).

Total densities of birds did not differ between June and July at either Gull Island ($t = 0.889$, df = 9, NS) or South Head ($t = 1.125$, df = 20, NS; Table 2). There was a significantly higher density of birds per km at South Head than on Gull Island ($t = 3.458$, df = 31, $P < 0.01$). When densities of individual species are compared between sites a number of differences appear. American Robins (*Turdus migratorius*) and Blackpoll Warblers (*Dendroica striata*) have significantly higher densities at South Head, whereas Northern Waterthrushes (*Seiurus noveboracensis*), Boreal Chickadees (*Parus hudsonicus*) and Gray-cheeked Thrushes (*Catharus minimus*) have higher densities on Gull Island. In fact, for June, the density of Boreal Chickadees on Gull Island was significantly greater than the combined density of both chickadee species at South Head ($t = 2.220$, df = 18, $P < 0.05$), although the difference was not present in July ($t = 0.366$, df = 11, NS).

DISCUSSION

Consistent with contemporary theory, Gull Island had a lower number of species and a lower species diversity than did the adjacent mainland area. The species that were missing were a nonrandom subset of the South Head avifauna. On South Head 19 of 25 species recorded had a congeneric or close confamilial species present. On Gull Island only 5 species had

TABLE 3
MEAN DENSITIES AND SD OF INDIVIDUAL SPECIES AT EACH LOCALITY[a]

Species	South Head		Gull Island		"t" between sites (DF)
	June $\bar{x} \pm$ SD	July $\bar{x} \pm$ SD	June $\bar{x} \pm$ SD	July $\bar{x} \pm$ SD	
Fox Sparrow	5.79 ± 1.25	6.75 ± 1.23	5.81 ± 1.58	7.78 ± 1.85	1.38 (31)
Pine Siskin	4.50 ± 1.90	3.80 ± 2.16	4.43 ± 1.73	2.33 ± 1.72	1.58 (31)
American Robin	2.99 ± 1.29	2.56 ± 2.78	0.92 ± 1.34	0.99 ± 1.24	7.12 (31)***
Gray-cheeked Thrush	1.35 ± 1.56	1.86 ± 1.36	2.74 ± 1.20	3.32 ± 1.38	6.10 (31)***
Northern Waterthrush	4.27 ± 1.30	3.29 ± 1.24 2.30 (20)*	5.39 ± 1.45	7.39 ± 1.68	1.55 (18) June 3.76 (11) July**
Blackpoll Warbler	6.18 ± 1.39	5.61 ± 1.41	2.48 ± 1.39	0.99 ± 1.71 3.66 (9)**	5.89 (18) June** 7.06 (11) July**
Boreal Chickadee	2.28 ± 1.93	1.74 ± 1.80	6.45 ± 1.69	2.57 ± 2.00 2.42 (9)*	3.19 (18) June** 1.09 (11) July
Black-capped Chickadee	1.46 ± 1.51	1.45 ± 1.68			
Boreal and Black-capped chickadees	3.74	3.19	vs Boreal Chickadee		2.22 (18) June* 0.37 (11) July

[a] If monthly mean densities differed significantly within a site, "t-values and degrees of freedom are entered below the densities. Mean densities and standard deviations (SD) are birds/km of transect.
* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

close relatives present among the 11 shared species. The probability of randomly selecting 11 species from the South Head avifauna and having only 5 close taxonomic relatives is 0.014 (binomial test; the Emberizidae were separated by subfamily and all other divisions were at family level). Furthermore, the 2 species added to the Gull Island avifauna are both of families not recorded at South Head nor with other species present on Gull Island. Taxonomic closeness is commonly taken to imply some degree of ecological similarity and potential for competition (e.g., Emlen 1973:316). Therefore, these data support the notion that competitive ecological interactions play an important role in the dynamics of island biogeography, at least for small, nearshore islands (Morse 1971, 1977). The proximity of Gull Island to South Head and its relatively large size render isolation or inadequate island size unlikely explanations for the nonrandom change in species richness.

As with most other studies, it would be difficult to fully assess all effects

of habitat differences between Gull Island and South Head on bird species richness, density and diversity. The absence of pasture and small extent of bogs on Gull Island could account for the absence of Starlings (*Sturnus vulgaris*) and Swamp Sparrows (*Melospiza georgiana*), respectively, and the larger extent of windfallen trees and associated litter and undergrowth on Gull Island could account for the presence of the Winter Wren (*Troglodytes troglodytes*). Otherwise, the vegetational differences between the island and South Head are consistently differences in extremes of density reached by various plant taxa, rather than differences in overall habitat diversity or species composition (Vassallo and Rice, in press). Therefore, using habitat differences to account for the bird species distributions found here is only possible on a piecemeal, nonpredictive basis.

Although the total density of passerines on Gull Island was lower than at South Head, this difference does not appear to be simply a reflection of a lower habitat diversity on Gull Island. This density reduction did not reflect either an overall decline in numbers of each species, nor merely the effects of an uncompensated loss of some taxa. Some density differences, such as the increased density of Boreal Chickadees on Gull Island in the absence of the Black-capped Chickadee (*P. atricapillus*), are consistent with the notion of competitive release (MacArthur et al. 1972, MacArthur et al. 1973, Yeaton and Cody 1974). However, other species, e.g., the Gray-cheeked Thrush, also showed a significant increase in density, although 2 thrushes were present at both sites. Furthermore, the Blackpoll Warbler was exposed to fewer potentially competing canopy foragers and at least as much suitable habitat on the island but nonetheless had a lower density there.

Apparently, as with the effects of changing habitat diversity on bird species diversity and richness, the density effects of changes in the avian community do not follow a few rigorously predictable rules. The community dynamics are complex, and conditions in which density compensation and competitive release will occur are not universally specifiable.

In this study, we found a lower species diversity, a loss of close ecological and taxonomic relatives and a decrease in overall avian density on Gull Island. These effects were all observed, although the mainland area is itself an island showing substantial decreases in bird species richness and diversity relative to continental North America. The factors producing the difference in island fauna apparently do not merely filter once to produce an island fauna of good colonists ("supertramps" of Diamond 1975), but similar effects are produced through the community dynamics of colonization when the island itself becomes a source for another island (Terborgh and Faaborg 1973, Terborgh et al. 1978).

SUMMARY

Although the island of Newfoundland shows a characteristically depauperate avifauna relative to continental Maritime Canada, Gull Island, a small offshore island, has lower passerine species richness than does a nearby area of comparable habitat on the Newfoundland coast. The decrease from 25 to 13 species was due neither to the loss of all members of some higher taxa nor to completely stochastic species losses. Rather it reflected the reduction of groups of congeneric or confamilial species in the coastal area to single species represented on the island. Overall density compensation did not occur, and patterns of density difference of individual species showed some insular increases, some decreases, and some cases of no difference. Habitat differences between the sites account for much but not all of these avian community differences.

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The following opinion has been published by the ICZN in the Bulletin of Zoological Nomenclature, Vol. 38, Pt. 2, 30 Apr. 1981: Opinion No. 1180 (p. 12) "*Thamnophilus amazonicus* Sclater, 1858 (Aves): conserved." The ICZN cannot supply separates of Opinions.