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Spruce Grouse in Habitat Patches in the Adirondack Mountains: Dispersal vs. Rarity

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The contribution of habitat isolation and species dispersal to species occupancy of habitat patches is an important, unresolved issue in the debate over the sizes and configurations of wildlife reserves. Random sampling of rare species could also account for absences of species from habitat patches, but few quantitative data are available to test between these alternatives.

Haila and Järvinen (1983) and Järvinen and Haila (1984) have applied a stochastic sampling model to census data of northern European birds on an island. Their results support the hypothesis that, for most species, observed occupation of an island is similar to occupation of similar-sized patches from a mainland habitat. Here, I apply this model to data from Fritz (1979, 1981). The alternative hypothesis tested was: Can the absence of Spruce Grouse (*Dendragapus canadensis*) from small habitat patches be attributed to rarity? In other words, would Spruce Grouse be expected to be absent from similar-sized areas in large, contiguous forest blocks?

I reported (Fritz 1979, 1981) that 7 patches that previously had supported Spruce Grouse populations or were of sufficient size to support them were unoccupied in 1977. I concluded that dispersal was insufficient to lead to recolonization of the unoccupied patches. Further censuses of these patches conducted from 1978 to 1980 showed that none were recolonized and that 7 more populations had become extinct. Data from 4 yr will provide a test of the hypothesis that rarity and not dispersal may be responsible for the absence of Spruce Grouse from these patches.

I used the Poisson model of Haila and Järvinen (1983), employing a mean density representative of a contiguous habitat. Of the 7 populations for which Spruce Grouse density was known (Fritz 1981), 4 eventually became extinct, while 2 other patches were too small to be considered equivalent to a large, contiguous habitat. Only 1 site, Grasse River, is large enough to be considered representative of a contiguous habitat as required by the model. The mean density of Spruce Grouse at that site for 3 yr was 4.3 pairs/km^2.

During 1977 and 1978, none of the patch sizes differed in observed occupancy more than expected by the Poisson model (Table 1). In 1978, 3 previously occupied patches became extinct. Three more populations went extinct in 1979, and 1 in 1980. Analysis of the last 2 yr shows that for the 50-ha patch size, observed occupancy was significantly less than expected from the model ($P < 0.025$). Dispersal had not led to recolonization of any of the unoccupied patches. Expected values (Table 1) were derived by assuming that only a single year's census data were available. However, when a series of censuses are used, the expected fraction of patches occupied must be adjusted as described in Haila and Järvinen (1983). When this was done, the agreement between observed and expected occupancy based on the model is even poorer ($\chi^2 = 6.486$, $P < 0.01$) for 50-ha patches.

Observed and expected occupancy for patches of

TABLE 1. Observed and expected occupancy of Spruce Grouse in different-sized habitat patches in the Adirondack Mountains. Expected occupancy is based on the assumptions that pairs in patches are distributed in a Poisson distribution and that occupancy is known for only one year. Agreement between observed and expected occupancy was determined with Chi-square tests.

	Patch size		
Year	50 ha	150 ha	300 ha
1977			
Observed	0.60 (9/15)	0.89 (8/9)	1.00 (8/8)
Expected	0.884	0.998	1.00
P	<0.25	<0.75	=1.0
1978			
Observed	0.47 (7/15)	0.78 (7/9)	1.00 (8/8)
Expected	0.884	0.998	1.00
P	<0.10	<0.60	=1.0
1979			
Observed	0.33 (5/15)	0.67 (6/9)	1.00 (8/8)
Expected	0.884	0.998	1.00
P	<0.025	<0.40	=1.0
1980			
Observed	0.33 (5/15)	0.56 (5/9)	1.00 (8/8)
Expected	0.884	0.998	1.00
P	<0.025	<0.20	=1.0

150 and 300 ha did not differ significantly in any year (Table 1). This may be because small numbers of patches severely restrict the usefulness of the Chi-square test in interpreting occupancy data. Therefore, a significant difference would require that only 3 of 9 sites be occupied.

If rarity and not dispersal accounted for the occupancy of isolated patches by Spruce Grouse, then over the period of these censuses some recolonization should have been detected. Instead, no recolonization occurred. Although species rarity certainly can be an explanation for species occupancy of patches, it does not appear to be primarily responsible for patch occupancy by Spruce Grouse in the Adirondack Mountains. On the contrary, the inverse correlation of patch occupancy with interpatch distance (Fritz 1979) supports the implication of the importance of dispersal, but this is confounded by the small size of isolated patches. More direct evidence for the inadequacy of dispersal is wanting. However, Haila and Järvinen (1983) argue that the absence of a grouse (*Bonasa bonasia*) from the island in their study was due to its poor dispersal ability.

In conclusion, analysis of an expanded data set using the model of Haila and Järvinen (1983) does not support the hypothesis that species rarity alone can account for the absence of Spruce Grouse from suitable habitat patches. Dispersal could be responsible for the observed pattern of patch occupancy. Dispersal was not sufficient to lead to recolonization of any of the unoccupied patches during the 4 yr studied, and the additional observed extinctions of 4 of the 9 smallest patches were consistent with expectations from the extinction time model (Fritz 1979).

That Spruce Grouse population dynamics in this mosaic of habitat patches apparently is not an equilibrium process raises additional concern over the effect of habitat fragmentation in the design of wildlife reserves. The issue of dispersal vs. rarity in species occupancy of habitat patches or islands demands further investigation in light of the conflicting results of Haila and Järvinen (1983) and this study. The utility of *post hoc* statistical tests in answering this important question is limited, however. Larger samples of islands or habitat patches would offer more convincing data, but experimental tests are likely to provide the strongest evidence of the influence of dispersal and rarity in patch occupancy.

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