Christopher J. Norment, Department of Zoology and Charles R. Conner Museum, Washington State University, Pullman, Washington 99164-4236[1]

Bird Use of Forest Patches in the Subalpine Forest-Alpine Tundra Ecotone of the Beartooth Mountains, Wyoming

Abstract

Relationships of bird species richness and abundance during the breeding season with forest area and edge were studied for ten forest patches in the subalpine forest-alpine tundra ecotone of the Beartooth Mountains, Wyoming. Species richness correlated equally well with area and edge, whereas mean number of individuals (abundance) correlated best with area. Among species that differed in their foraging habitats, species richness and abundance of those most restricted to foraging within forest habitat showed the best correlation with area. Species that foraged mostly in surrounding meadows and those that used both forest and meadow habitats correlated better with edge than with area.

Forest patches of intermediate size surrounded by meadow habitat had greater number of individuals per census than either smaller patches or a larger plot within a continuous forest stand. Number of species in intermediate-sized patches was greater in smaller patches, and approximately equal to that in the continuous forest stand. These results are attributed to the combined presence of edge habitat from which birds may forage into surrounding meadow and sufficient forest habitat for those species restricted to foraging within forest. Patterns of species distribution, importance of edge, and changes in avian community composition across the range of forest patches studied tentatively suggest that some predictions developed from the study of bird communities in forest fragments created by human disturbance may not be applicable to communities in naturally occurring forest patches in western montane coniferous forests.

Introduction

Many studies have shown that number of bird species and individuals using small patches of woodland increase with area, both where forest fragmentation has resulted from human activity (Galli *et al.* 1976, Whitcomb *et al.* 1981, Howe 1984, Hayden *et al.* 1985, Temple 1986, Blake and Karr 1987), and where woodlots have been planted in a surrounding matrix of croplands (Martin 1981a). These results have generated concern that continued loss and fragmentation of forest habitat will cause long-term declines in some forest bird populations (Robbins 1979, Butcher *et al.* 1981, Whitcomb *et al.* 1981, Ambuel and Temple 1983, Blake and Karr 1987).

Given current interest in the effects of habitat destruction on the decline of temperate forest breeding birds, examination of bird communities in naturally-occurring forest patches is important because these communities presumably are no longer adjusting to processes of habitat fragmentation (see Rosenberg and Raphael 1986). I analyzed the relationship between bird species richness and number of individuals (hereafter referred to as abundance) and area of small forest patches in a forest-tundra ecotone, and tested the prediction that species most dependent upon forest vegetation will show the greatest response to differences in forest area. To my knowledge, a study of this nature has not been previously undertaken in a habitat unaffected by human activity.

Methods

I studied bird use of forest patches in the subalpine forest-alpine tundra ecotone of the Beartooth Mountains, Wyoming. The ecotone is a mosaic of plant communities resembling those of the continuous subalpine forest or alpine tundra in physiognomy and taxonomic composition. Discrete forest stands within the ecotone occur on rocky, well-drained sites and are surrounded by meadow vegetation. There is a sharp transition between the two plant communities. Many stands occur on outcrops of rocky, well-drained soil, and are roughly circular in shape; others are narrow (ca. 20 to 50 m) strips of "ribbon forest" between broad bands of subalpine meadow, and probably have resulted from a combination of strong winter winds, snowdrift accumulation patterns, and cool summers (Billings 1969).

Ten study sites were selected to minimize differences in habitat variables other than area and edge. All sites were between 2900 and 2960 m[2] elevation and 25 to 100 m from adjacent stands of trees. All forest patches contained Englemann spruce (*Picea englemannii*), subalpine fir (*Abies lasiocarpa*), and whitebark pine (*Pinus albicaulis*).

[1]Present address: Museum of Natural History and Department of Systematics and Ecology, University of Kansas, Lawrence, Kansas 66045

TABLE 1. Characteristics of the ten forest patches, 1980 and 1981.

Site #		Area (m^2)	Edge (m)	Number of censuses (n)	Species richness	Mean species/ census ($\bar{x} \pm$ SD)	Mean individuals/ census ($\bar{x} \pm$ SD)
1980	1	600	90	5	3	0.6 ± 0.5f	0.4 ± 0.5
	2	1.200	140	5	6	3.2 ± 1.6	3.0 ± 2.4
	3	2.000	170	5	6	1.6 ± 1.1	2.8 ± 2.6
	4	5.900	330	5	5	2.2 ± 1.3	3.4 ± 3.1
	5	6.200	450	5	10	3.3 ± 0.5	5.4 ± 1.3
	6	9.000	400	5	11	5.2 ± 0.8	10.2 ± 4.0
	7	19.000	750	5	12	6.1 ± 1.1	13.0 ± 9.3
	8	22,000	580	5	13	7.4 ± 2.3	12.8 ± 6.0
	9	23.000	600	5	9	5.6 ± 1.7	14.6 ± 6.0
	10	40.000	0	5	10	5.8 ± 0.5	11.6 ± 3.6
1981	5	6.200	450	11	10	4.0 ± 1.0	7.1 ± 3.5
	7	19.000	750	11	15	7.6 ± 2.1	17.0 ± 5.8
	8	22.000	580	8	15	7.6 ± 1.6	13.6 ± 4.3
	10	40.000	0	11	15	7.0 ± 1.4	14.7 ± 4.9

Average canopy height was about 8 m. Understory vegetation was sparse, consisting primarily of whortleberry (*Vaccinium scoparium*).

Nine patches surrounded by meadow habitat varied in area from 600 to 23,000 m^2 (Table 1). To compare bird abundance in patches relative to a larger, non-isolated stand, an additional plot of 40,000 m^2 was established in a continuous forest stand of ca. 6 ha. Because I wished to analyze how reduced edge affects richness and abundance of forest interior species, boundaries were placed as far from the nearest forest/meadow habitat discontinuity as possible. Boundaries were ca. 50 m from the nearest meadow on three sides of the plot, and 25 m from meadow on the other, although some edge impacts may extend further into deciduous forest fragments (Temple 1986). Size of the plot, and distance of boundaries from the nearest meadow habitat, were limited by the discontinuous tree distribution in the ecotone.

Forest patches were mapped in the field with a 50-m tape and hand-held compass. Area of each patch was calculated by cutting out each forest patch from a map of the study area, weighing it to the nearest 0.001 g on an analytical balance, and dividing the weight by weight per unit area. Perimeter of each forest patch, hereafter referred to as "edge," was determined directly from field measurements using a 50-m tape.

Each site was censused five times during the breeding season in 1980. For comparative purposes, four plots were censused at least eight times in 1981. During each visit, I walked slowly through the site and recorded all individuals seen or heard. A minimum of 15 min/census was allocated to the smallest patches, and no census lasted more than 1.5 h. A 25 m × 25 m grid was established in the largest plot to facilitate census work. Most censuses were conducted between 0600 and 1030; each stand was also censused at least once between 1900 and 2100 to hear evening thrush choruses.

During census work in forest plots and surrounding meadows, I quantified avian habitat choice (either meadow or forest) for actively foraging birds. Data were recorded at 15-s intervals signaled with a tone pulse emitted by an electronic metronome (Wiens *et al.* 1970). No more than five observations were recorded on a single bird to reduce sampling bias. Although sequential observations of individual birds are not independent (Morrison 1984), I wished to follow each bird through a series of foraging activities and not bias my data towards conspicuous birds by recording a single observation of each bird encountered (see Wagner 1981). Species represented by fewer than 30 observations were classified according to accounts in the literature. Three foraging habitat groups (FHGs) were recognized (Table 2): 1) species for which ≥ 90 percent of all foraging observations were in meadow habitat; 2) species for which ≥ 90 percent of all foraging observations

TABLE 2. Mean abundance (number of individuals/census/plot) and foraging habits of bird species in small forest patches (600-6,200 m²), medium forest patches (9,000-23,000 m²), and a large continuous forest tract (40,000 m²). Values are averaged for all censuses, 1980 and 1981. Number of plots in each size class are given in ( ).

Species	Abundance (individuals/census/plot)			Foraging habitat				
	Small patches (n=5)	Medium patches (n=4)	Continuous tract (n=1)	FHG[1]	n	% Meadow	% Forest	Ref.[2]
Hairy Woodpecker (*Picoides villosus*)	0	0.03	0	F	4	0.0	100.0	1,9
Northern Flicker (*Colaptes auratus*)*	0.04	0.04	0	G	6	100.0	0.0	1,7
Gray Jay (*Perisoreus canadensis*)*	0.05	0.13	0.94	F	7	0.0	100.0	2
Clark's Nutcracker (*Nucifraga columbiana*)#	0.22	1.39	1.06	G	14	57.1	42.9	2,10
Mountain Chickadee (*Parus gambeli*)*	0.16	1.00	1.50	F	96	0.0	100.0	
Red-breasted Nuthatch (*Sitta canadensis*)#	0	0.03	0.19	F	9	0.0	100.0	3,9
White-breasted Nuthatch (*Sitta carolinensis*)*	0	0.10	0.06	F	0			3,9
Ruby-crowned Kinglet (*Regulus calendula*)*	0	0.81	1.19	F	37	0.0	100.0	
Mountain Bluebird (*Sialia currucoides*)*	0.31	0.74	0.06	M	161	93.2	6.8	
Hermit Thrush (*Catharus guttatus*)#	0	0.02	0.13	F	0			4
American Robin (*Turdus migratorius*)*	0.84	2.60	1.44	M	82	93.9	6.1	
Water Pipit (*Anthus spinoletta*)	0.72	0.29	0	M	178	100.0	0.0	
Yellow-rumped Warbler (*Dendroica coronata*)*	0.21	0.77	1.13	F	54	0.0	100.0	
Chipping Sparrow (*Spizella passerina*)*	0	0.21	0.06	G	30	60.0	40.0	
Vesper Sparrow (*Pooecetes gramineus*)	0.04	0	0	M	4	100.0	0.0	5
White-crowned Sparrow (*Zonotrichia leucophrys*)*	1.12	1.48	0	G	147	68.1	31.9	
Dark-eyed Junco (*Junco hyemalis*)*	0.68	2.44	3.44	G	116	37.9	62.1	
Rosy Finch (*Leucosticte arctoa*)	0	0.02	0	M	51	100.0	0.0	
Cassin's Finch (*Carpodacus cassinii*)*	0.29	1.48	0.09	G	78	57.8	42.2	
Pine Grosbeak (*Pinicola enucleator*)*	0.08	0.28	0.94	G	24	20.8	79.2	5,6,8
White-winged Crossbill (*Loxia leucoptera*)	0	0	0.13	F	2	0.0	100.0	5
Pine Siskin (*Carduelis pinus*)#	0	0.11	0.75	G	15	33.3	66.7	5,8

[1]FHG = Foraging habitat group; M = meadow-foraging species, G = generalists, F = forest-foraging species.

n = number of foraging observations.

[2]Ref = references on foraging: 1 = Bent 1939; 2 = Bent 1946; 3 = Bent 1948; 4 = Bent 1949; 5 = Bent 1968; 6 = French 1954; 7 = Gabrielson and Jewett 1940; 8 = Newton 1972; 9 = Stallcup 1968; 10 = Tomback 1977.

*Species known to breed within forest stands in the ecotone.

#Species that probably breeds within forest stands in the ecotone.

were in forest habitat; and 3) generalists that foraged in both forest and meadow habitats.

I examined species-area, abundance-area, species-edge, and abundance-edge relationships using log-log (power), semi-log (exponential), and untransformed (linear) regression functions (Martin 1981a). Best-fit functions were determined by comparisons of correlation coefficients; I determined significance of the coefficients with tables in Rohlf and Sokal (1981). Relationships of FHGs to area and edge were also examined with regression functions. Additionally, proportion of the total avian community comprised by each FHG was compared among three plot size classes: small tracts from 600 to 6,200 m^2 ($n=5$); medium tracts from 9,000 to 23,000 m^2 ($n=4$); and the largest tract (40,000 m^2). Proportion of species and total individuals in the three FHGs were calculated for each patch, based on cumulative data from all censuses. Proportions were then averaged over all plots in each size class. Size classes were separated between 6200 and 9,000 m^2 to include approximately equal numbers of patches in the small and medium classes.

Results

Species Richness and Abundance

Species richness for the nine smaller forest patches increased with both area ($Log_eY = 0.474 + 0.323Log_eX$; $r = 0.860$, $P < 0.01$) and edge ($Log_eY = 0.305 + 0.561Log_eX$; $r = 0.863$, $P < 0.01$) in 1980, with power functions providing the best fit (Fig. 1). Mean number of species per census did not differ for plots censused in both years (t-tests, $P > 0.10$). Mean abundance (individuals per census) also increased with both area ($r = 0.914$, $P < 0.01$) and edge ($r = 0.863$, $P < 0.01$) in 1980, with the linear function providing the best fit (Fig. 1). There were no between-year differences in mean abundance for patches censused in both 1980 and 1981 (t-tests, $P > 0.10$).

Several results indicate that species richness and abundance were lower in the largest forest plot, which lacked adjacent meadow habitat, than in intermediate-sized forest patches surrounded by meadow. First, at least as many individuals and species were observed per census in intermediate patches as in the largest plot, despite an approximately 200 percent difference in area (Table 1). The species richness curve also appeared to level off at an asymptote above 22,000 m^2 (Fig. 1). Second, bird abundance in the largest plot fell below values predicted by the regression equation calculated from data for the nine smaller patches (Fig. 1).

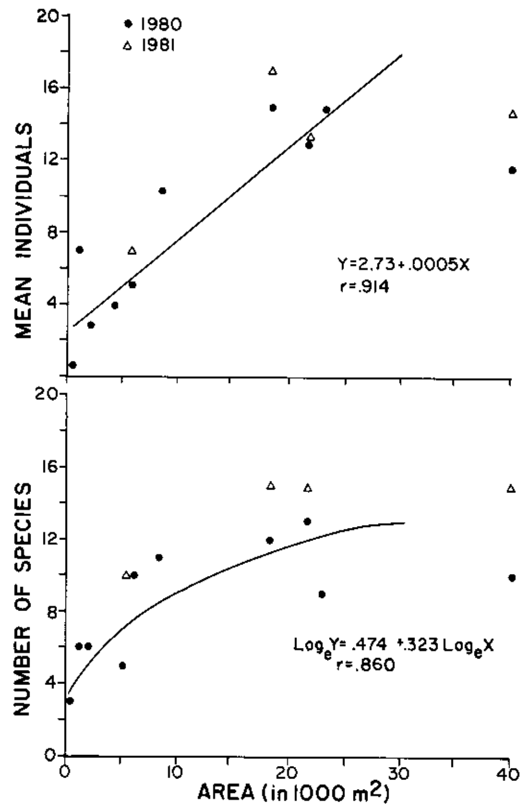

Figure 1. Mean number of individuals per census (top) and total number of bird species (bottom) plotted against area for the nine smaller forest patches. Regression lines are based upon 1980 data only (closed circles); data for 1981 (open triangles) and largest patch (plot without edge) are shown for comparison.

Foraging Habitat Groups

Of the 22 species observed, eight were placed in the generalist FHG, five in the meadow FHG, and nine in the forest FHG (Table 2). The meadow FHG included species that used forest patches for nesting [American Robin and Mountain Bluebird (all scientific names are given in Table 2)] and perch sites only (Water Pipit, Rosy Finch, and Vesper Sparrow). Except for the Dark-eyed Junco, generalists usually nested in forest habitat, although White-crowned Sparrows also nested under willow (*Salix*) clumps in meadows. Based on foraging observations and literature references (see Table 2), I placed several species that feed primarily on seeds, buds, or foliage during much of the year in the generalist FHG (Clark's Nutcracker, Pine Grosbeak, and Pine Siskin).

FHG Distribution Patterns

As predicted, meadow species were not correlated with forest patch area ($r = 0.566$, $P > 0.05$), while number of generalist species ($r = 0.893$, $P < 0.01$) and forest species ($r = 0.773$, $P < 0.05$) increased with forest patch area. When data from the largest plot were added to the regressions, the fit was decreased for meadow species and generalists, and increased ($r = 0.843$) for forest species. Edge was a better predictor of species number for the meadow FHG in forest patches ($r = 0.678$, $P < 0.05$), even though robins and Mountain Bluebirds nested within the forest patches and up to 50m from the forest edge. Edge was also a better predictor of species richness for generalists ($r = 0.911$, $P< 0.01$).

Regression of mean abundance per census against area, based on data for the nine smallest plots, were significant for the generalist ($r = 0.945$, $P < 0.01$) and forest ($r = 0.839$, $P < 0.01$) FHGs. When data from the largest plot were added, a better fit was provided only for the forest FHG ($r = 0.912$). Removal of generalist FHG species that presumably relied more heavily on resources within forest patches than in surrounding meadows (Pine Grosbeak, Clark's Nutcracker, and Pine Siskin) from the abundance-area regression reduced the fit to $r = 0.680$ for the generalist FHG. As with species number, edge provided the best estimate of abundance ($r = 0.678$, $p < 0.05$) for the meadow FHG.

As plot size increased, forest species and individuals represented an increasing proportion of the total community (Fig. 2). Proportions of generalist species and individuals were similar in all plot sizes. Meadow FHG species and individuals represented a larger proportion of the community in small patches than in intermediate patches or the largest plot.

The meadow-foraging American Robin and the generalist Dark-eyed Junco, which foraged primarily on the forest floor and in small clearings (Norment, unpublished data), were the only species abundant on all plots (Table 2). Only meadow and generalist species were observed at rates ≥ 0.5 individuals per census in small patches. Included in this group were Dark-eyed Juncos, Water Pipits,

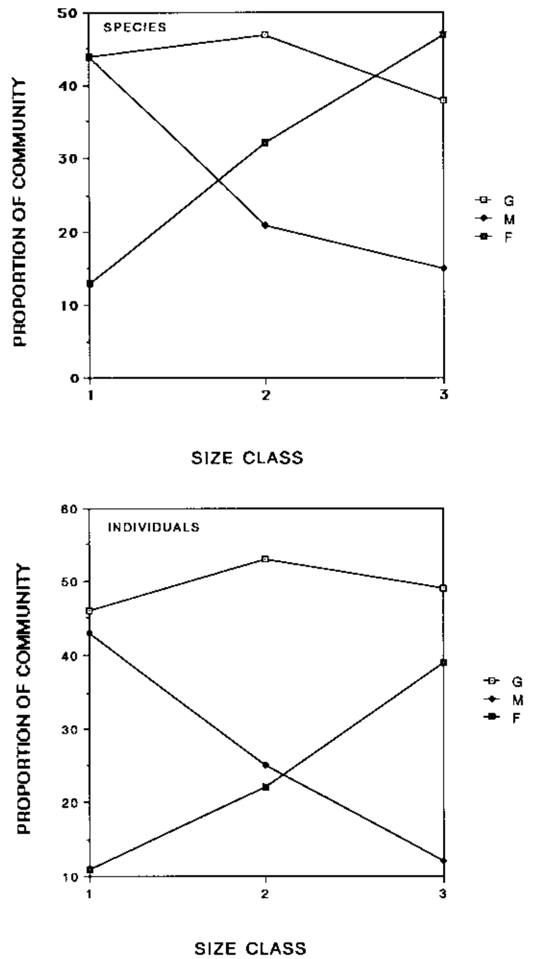

Figure 2. Average percent of total observations (number/census/plot) of species (top) and individuals (bottom) contributed by the forest FHG (F), generalist FHG (G), and meadow FHG (M) in the three plot size classes (1 = 600-6,200 m^2; 2 = 9,000-23,000 m^2; 3 = 40,000 m^2).

White-crowned Sparrows, and American Robins; the two latter species nested in very small forest patches (≤ 100 m^2) in other parts of the ecotone. Many generalist and meadow species were restricted to forest habitat near the periphery of patches, and were rarely, if ever, observed in the largest plot, which had boundaries ≥ 25 m of the nearest meadow habitat. Included in this group were the Northern Flicker, Mountain Bluebird, Water Pipit, Cassin's Finch, Chipping Sparrow, and White-crowned Sparrow (Table 2).

Members of the forest FHG were abundant only in forest patches ≥ 9,000 m^2 (Table 2). The only common members of the foliage-gleaning guild—Mountain Chickadee, Ruby-crowned Kinglet, and Yellow-rumped Warbler—were most frequently encountered in the largest plot. Bark probers and gleaners (e.g., Hairy Woodpecker and Red- and White-breasted Nuthatches) were rarely observed in the subalpine forest-alpine tundra ecotone.

Discussion

The current study is similar to previous studies of bird communities in forest fragments in that increased area accounted for increased species richness and abundance (Galli *et al.* 1976, Ambuel and Temple 1983, Freemark and Merriam 1986, Temple 1986, Blake and Karr 1987, and others). However, the strong response of the meadow and generalist FHGs to edge suggest that it is also important in determining bird species richness and abundance in forest patches in the Beartooth Mountains. Forest patch area appeared to be more important than edge for species that rely on forest habitat for both nesting and foraging.

Relatively few studies have directly analyzed edge as a variable influencing bird communities in woodland fragments. Bird species richness and abundance in South Dakota shelterbelts were positively, but less strongly, correlated with edge than with area (Martin 1981a), although the converse was found for bird communities in Minnesota shelterbelts (Yahner 1983). Bird species richness also was positively correlated with plot edge in Douglas-fir (*Pseudotsuga menziesii*) forests in California (Rosenberg and Raphael 1986). Bird species richness in Illinois forest fragments correlated most strongly with area, although some species were also influenced by amount of woodlot edge (Blake and Karr 1987).

Ecological generalists that feed in both forests and surrounding habitats are important components of bird communities in many forest fragments (Galli *et al.* 1976, Martin 1981a, Whitcomb *et al.* 1981, Blake 1983, Hansson 1983, Howe 1984, Hayden *et al.* 1985, Haila 1988). In the Beartooth Mountains, intermediate-sized patches may support more birds than either small patches or the interior areas of continuous forest because they contain sufficient habitat for forest species and are surrounded by meadows that provide abundant food for species nesting in forest stands. Use of surrounding habitat for foraging may account for increased nesting densities in riparian communities and shelterbelts surrounded by agricultural fields that provide abundant resources but lack suitable nest sites (Carothers *et al.* 1974, Martin 1981a).

Absence of species that require edge or nearby meadow habitat may partially explain lower abundance and lack of increase in species richness in the continuous forest plot. However, three additional factors may also be important. First, the largest plot may have been too small to attract forest interior species that require extensive blocks of habitat. The number of species present on the largest plot, and which probably bred in forest stands in the ecotone (15), was less than the number of breeding season non-raptors in larger areas in two other northern Rocky Mountain spruce-fir forests (Salt 1957, Thompson 1978). This could explain the absence from the ecotone of six species reported in each of the above studies, and two guilds generally present in Rocky Mountain spruce-fir forests: timber-drill, and air-perch-soar (see Smith 1980). A similar explanation may account for the absence of woodpeckers from small, forested lake islands (Howe 1979). However, potential area effects are the result of limitations on the avian community caused by patchy tree distribution and limited stand size in the ecotone, rather than arbitrary use of small plots. Whether larger plots would have yielded greater numbers of species and individuals is, in some ways, a moot point since larger, continuous stands were not found.

Second, relatively few neotropical migrants, such as wood warblers (*Dendroica* spp.) nest in spruce-fir forests (Smith 1980). Neotropical migrants are strongly affected by forest fragmentation and their species richness and abundance show strong area-dependent responses (Lynch and Whitcomb 1978, Keast and Morton 1980, Whitcomb *et al.* 1981).

Third, Englemann spruce comprised 70 percent of the trees in forest patches in the ecotone (Norment, unpublished data). Englemann spruce forests support poor avifaunas, particularly of foliage-gleaning species (Smith 1980), and bird species richness and densities decrease as Englemann spruce increases in abundance (Austin and Perry 1979, Smith and MacMahon 1981). Low densities may be due in part to low abundances of ground and foliage arthropods (Fichter 1939, Hayward 1945, Norment, unpublished data).

Conversely, forest birds capable of foraging in meadows in the Beartooth Mountains can exploit abundant arthropod populations during much of their breeding cycle (Norment 1987). Whatever the ultimate cause, a small source pool, or high ratio between number of species present in a series of habitat patches or islands and source pool size, should decrease the strength of the area response in island (or patch) situations (Schoener 1976, Martin 1981b). Thus the combined effects of a small source pool of spruce-fir forest interior species, small forest patch size, low resource levels, and lack of edge habitat may explain the relatively low bird abundance and lack of increase in species richness in the continuous plot.

Because the study did not include replicates in the largest size class, differences between the continuous forest plot and smaller forest patches could be due to specific site characteristics and not to more general effects related to area. However, census data from forest interiors ($\geq$ 25 m from the nearest edge) throughout the ecotone collected during 1980, 1981, 1984, and 1987 (Norment, unpublished data) suggest that this habitat is generally depauperate in bird species and individuals. Only 15 species were observed to nest in forest interior habitat, and all of these except the Hairy Woodpecker were observed in the large plot (Table 2). Additionally, cumulative detection rates (number of individuals observed/hour) in the interior of six forest patches $\geq$ 2.0 ha were very low or 0 for species rarely seen in the large plot. For example, cumulative detection rates for the Northern Flicker, Mountain Bluebird, Cassin's Finch, and White-crowned Sparrow were 0.07, 0.05, 0.16, and 0.05 individuals/hr (Norment, unpublished data).

Responses of bird communities to differences in area of forest fragments are influenced by patterns of resource distribution, habitat heterogeneity, the surrounding habitat matrix, isolation of forest patches, composition of the species source pool, and time since fragmentation (Butcher *et al.* 1981, Martin 1981a, Whitcomb *et al.* 1981, Blake 1983, Howe 1984, Freemark and Merriam 1986, Rosenberg and Raphael 1986, Blake and Karr 1987). Because physical and biotic characteristics of western montane coniferous forests and eastern deciduous forests differ, responses to habitat fragmentation by bird communities in these forest types also may be expected to differ (Reese and Ratti 1988). At higher elevations in the Beartooth Mountains, forest bird communities may respond less strongly to area than forest bird communities in eastern and midwestern forest fragments, although this conclusion would be strengthened by further comparative work in forest patches and continuous forest. Presumably, a long-lasting equilibrium exists between meadow and forest vegetation in the Beartooth Mountains (Billings 1969), and forest bird communities are not presently adjusting to habitat changes. Instead, abundant resources in surrounding meadows, the presence of relatively few species strongly affected by habitat fragmentation, and the highly fragmented nature of the forest-tundra ecotone may produce a system in which intermediate-sized forest patches contain more individuals than larger patches, and edge is a better predictor of species richness than area.

Acknowledgments

J. G. Blake, S. G. Johnson, and several anonymous reviewers commented on an earlier version of this manuscript. R. E. Johnson and J. N. Thompson offered guidance throughout the project; E. Franz and R. Alldredge also provided useful suggestions. D. Anderson, C. James, and M. Norment helped tremendously with the fieldwork. D. Musso and W. Newall of the US Forest Service provided much-appreciated technical support. Financial assistance was received from the Frank M. Chapman Fund of the American Museum of Natural History, Sigma Xi, and the graduate school of Washington State University.

Literature Cited

Ambuel, B., and S. A. Temple. 1983. Area-dependent changes in the bird communities and vegetation of southern Wisconsin forests. Ecology 64:1057-1068.

Austin, D. D., and M. L. Perry. 1979. Birds in six communities within a lodgepole pine forest. J. For. 77:584-586.

Bent, A. C. 1939. Life histories of North American woodpeckers. U.S. Natl. Mus. Bull. 174:13-44, 259-298.

__________. 1946. Life histories of North American jays, crows, and titmice. U.S. Natl. Mus. Bull. 191:1-32, 310-322.

__________. 1948. Life histories of North American nuthatches, thrashers, and their allies. U.S. Natl. Mus. Bull. 195:1-21, 22-25.

__________. 1949. Life histories of North American thrushes, kinglets, and their allies. U.S. Natl. Mus. Bull. 196:123-162.

__________. 1968. Life histories of North American cardinals, grosbeaks, buntings, towhees, finches, sparrows, and their allies. U.S. Natl. Mus. Bull. 237:326-346, 424-446, 527-543.

Billings, W. D. 1969. Vegetational pattern near alpine timberline as affected by fire-snowdrift interaction. Vegetatio 19:192-207.

Blake, J. G. 1983. Trophic structure of bird communities in forest patches in east-central Illinois. Wilson Bull. 98:291-296.

Blake, J. G., and J. R. Karr. 1987. Breeding birds of isolated woodlots: area and habitat relationships. Ecology 68:1724-1734.

Butcher, G. S., W. A. Niering, W. J. Barry, and R. H. Goodwin. 1981. Equilibrium biogeography and the size of nature preserves: An avian case study. Oecologia 49:29-37.

Carothers, S. W., R. R. Johnson, and S. W. Aitchison. 1974. Population structure and social organization of Southwestern riparian birds. Amer. Zool. 14:97-108.

Fichter, E. 1939. An ecological study of Wyoming spruce-fir forest arthropods with special reference to stratification. Ecol. Monogr. 9:183-215.

Freemark, K. E., and H. G. Merriam. 1986. Importance of area and habitat heterogeneity to bird assemblages in temperate forest fragments. Biol. Cons. 36:115-141.

French, N. R. 1954. Notes on breeding activities and gular sacs in the Pine Grosbeak. Condor 56:83-85.

Gabrielson, I. N., and S. G. Jewett. 1940. The birds of Oregon. Oregon State Coll., Corvallis, OR.

Galli, A. E., C. F. Leck, and R. T. T. Forman. 1976. Avian distribution patterns in forest islands of different size in central New Jersey. Auk 93:356-365.

Haila, Y. 1988. Calculating and miscalculating density: the role of habitat geometry. Ornis Scand. 19:88-92.

Hansson, L. 1983. Bird numbers across edges between mature conifer forest and clearcuts in central Sweden. Ornis Scand. 14:97-103.

Hayden, T J., J. Faaborg, and R. L. Clawson. 1985. Estimates of minimum area requirements for Missouri forest birds. Trans. Missouri Acad. Sci. 19:11-22.

Hayward, C. L. 1945. Biotic communities of the southern Wasatch and Uinta mountains, Utah. Great Basin Nat. 6:1-124.

Howe, R. W. 1979. Behavior and distribution of birds on small islands in northern Minnesota. J. Biogeog. 6:379-390.

__________. 1984. Local dynamics of bird assemblages in small forest habitat islands in Australia and North America. Ecology 65:1585-1601.

Keast, A., and E. S. Morton (eds.). 1980. Migrant birds in the Neotropics: Ecology, Behavior, Distribution, and Conservation. Smithsonian Institution, Washington, D.C.

Lynch, J. F., and R. F. Whitcomb. 1978. Effects of the insularization of the eastern deciduous forest on avifaunal diversity and turnover. *In* A. Marmelstein (ed.) Classification, inventory, and analysis of fish and wildlife habitat. FWS/OBS-78/76. U.S. Dept. Interior, Fish and Wildlife Service, Office of Biological Services, Washington, D.C. Pp. 461-489.

Martin, T. E. 1981a. Limitation in small habitat islands: chance or competition? Auk 98:715-734.

__________. 1981b. Species-area slopes and coefficients: a caution on their interpretation. Amer. Nat. 823-837.

Morrison, M. L. 1984. Influence of sample size and sampling design on analysis of avian foraging behavior. Condor 86:146-150.

Newton, I. 1972. Finches. Collins, London.

Norment, C. J. 1987. A comparison of three methods for measuring arthropod abundance in tundra habitats and its implications in avian ecology. Northwest Sci. 61:191-198.

Reese, K. P., and J. T. Ratti. 1988. Edge effect: a concept under scrutiny. N. A. Wildl. Nat. Res. Conf. 53: 127-136.

Robbins, C. S. 1979. Effects of forest fragmentation on bird populations. *In* Management of north-central and northeastern forests for nongame birds. USDA For. Ser. Gen. Tech. Rep. NC-51. Pp. 198-212.

Rohlf, F. J., and R. R. Sokal. 1981. Statistical tables. Second ed. W. H. Freeman, San Francisco, CA.

Rosenberg, K. V., and M. G. Raphael. 1986. Effects of forest fragmentation on vertebrates in Douglas-fir forests. *In* J. Verner, M. L. Morrison and C. J. Ralph (eds.) Wildlife 2000: Modeling habitat relationships of terrestrial vertebrates. Univ. Wisconsin Press, Madison, WI. Pp. 263-272.

Salt, G. W. 1957. An analysis of avifaunas in the Teton Mountains and Jackson Hole, Wyoming. Condor 59:373-393.

Schoener, T. W. 1976. The species-area relationship within archipelagos: models and evidence from island birds: *In* Proc. XVI Int. Ornithol. Congr. (1974). Pp. 639-642.

Smith, K. G. 1980. Nongame birds of Rocky Mountain spruce-fir forests and their management. *In* Management of western forests and grasslands for nongame birds. USDA For. Ser. Gen. Tech. Rep. INT-86. Pp. 258-279.

Smith, K. G., and J. A. MacMahon. 1981. Bird communities along a montane sere: community structure and organization. Auk 98:8-28.

Stallcup, P. L. 1968. Spatio-temporal relationships of nuthatches and woodpeckers in ponderosa pine forests of Colorado. Ecology 49:833-843.

Temple, S. A. 1986. Predicting impacts of habitat fragmentation on forest birds: a comparison of two models. *In* J. Verner, M. L. Morison and C. J. Ralph (eds.) Wildlife 2000: Modeling habitat relationships of terrestrial vertebrates. Univ. Wisconsin Press, Madison, WI. Pp. 301-304.

Thompson, L. S. 1978. Species abundance and habitat relationships of an insular montane avifauna. Condor 80:1-14.

Tomback, D. F. 1977. Foraging strategies of Clark's Nutcracker. Living Bird 16:123-161.

Wagner, J. L. 1981. Visibility and bias in avian foraging data. Condor 83:263-264.

Received 28 June 1988
Accepted for publication 13 July 1990

Whitcomb, R. F., C. S. Robbins, J. F. Lynch, B. L. Whitcomb, M. K. Klimkiewicz, and D. Bystrack. 1981. Effects of forest fragmentation on avifauna of the eastern deciduous forest. *In* R. L. Burgess and D. M. Sharpe (eds.) Forest island dynamics in man-dominated landscapes. Springer-Verlag, New York, NY. Pp. 123-205.

Wiens, J. A., S. G. Martin, W. R. Holthaus, and F. A. Iwen. 1970. Metronome timing in behavioral ecology studies. Ecology 51:350-352.

Yahner, R. H. 1983. Seasonal dynamics, habitat relationships, and management of avifauna in farmstead shelterbelts. J. Wildl. Manage. 47:85-104.