Composition of Bird Communities Following Stand-Replacement Fires in Northern Rocky Mountain (U.S.A.) Conifer Forests

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Abstract: *During the two breeding seasons immediately following the numerous and widespread fires of 1988, I estimated bird community composition in each of 34 burned-forest sites in western Montana and northern Wyoming. I detected an average of 45 species per site and a total of 87 species in the sites combined. A compilation of these data with bird-count data from more than 200 additional studies conducted across 15 major vegetation cover types in the northern Rocky Mountain region showed that 15 bird species are generally more abundant in early post-fire communities than in any other major cover type occurring in the northern Rockies. One bird species (Black-backed Woodpecker,* Picoides arcticus*) seems to be nearly restricted in its habitat distribution to standing dead forests created by stand-replacement fires. Bird communities in recently burned forests are different in composition from those that characterize other Rocky Mountain cover types (including early-successional clearcuts) primarily because members of three feeding guilds are especially abundant therein: woodpeckers, flycatchers, and seedeaters. Standing, fire-killed trees provided nest sites for nearly two-thirds of 31 species that were found nesting in the burned sites. Broken-top snags and standing dead aspens were used as nest sites for cavity-nesting species significantly more often than expected on the basis of their relative abundance. Moreover, because nearly all of the broken-top snags that were used were present before the fire, forest conditions prior to a fire (especially the presence of snags) may be important in determining the suitability of a site to cavity-nesting birds after a fire. For bird species that were relatively abundant in or relatively restricted to burned forests, stand-replacement fires may be necessary for long-term maintenance of their populations. Unfortunately, the current fire policy of public land-management agencies does not encourage maintenance of stand-replacement fire regimes, which may be necessary for the creation of conditions needed by the most fire-dependent bird species. In addition, salvage cutting may reduce the suitability of burned-forest habitat for birds by removing the most important element—standing, fire-killed trees—needed for feeding, nesting, or both by the majority of bird species that used burned forests.*

Composición de las comunidades de aves luego del reemplazo de rodales a causa de incendios forestales en bosques de coníferas de las montañas Rocosas del norte

Resumen: *Durante las dos últimas temporadas de cría immediatamente después de los numerosos y extensos incendios de 1988, estimé la composición de la comunidad de aves en cada uno de los sitios de bosques incendiados, en el oeste de Montana y el norte de Wyoming. Detecté un promedio de 45 especies por sitio y un total de 87 especies en todos los sitios combinados. Una recopilación de estos datos con otros de conteo de aves a partir de más de 200 sitios adicionales, conducido a lo largo de 15 tipos principales de cobertura de vegetación en las montañas Rocosas del norte mostró que 15 especies de aves eran en general más abundantes en las comunidades tempranas posteriores al incendio, que en cualquier otro tipo principal de cobertura presente en las Rocosas del norte. Una especie de ave (el pájaro carpintero de espalda negra,* Picoides arcticus*) parece estar restringida en su distribución a los árboles muertos en pie, que quedan a causa del reemplazo de rodales a partir de los incendios. Las comunidades de aves en los bosques recientemente incendiados, son diferentes en composición de aquellos que caracterizan otros tipos de cobertura de las montañas Rocosas (in-*

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cluyendo la tala durante la sucesión temprana) principalmente porque los miembros de tres gremios alimenticios son especialmente abundantes en ellos: los pájaros carpinteros que se alimentan de las abundantes larvas de los escarabajos, los insectivoros y los comedores de semillas. Los árboles muertos en pie que quedaron después de los incendios proveen de sitios para el anidamiento de casi dos tercios de las 31 especies que se encontraron anidando en sitios incendiados. Las cavidades abiertas en los troncos a causa de la rotura de ramas y los álamos muertos que quedaron en pie, fueron usados como sitios para anidamiento por especies que anidan en cavidades más frecuentemente que lo esperado en función de su frecuencia relativa. Más aún, dado que la casi totalidad de las cavidades de los troncos que fueron utilizadas estaban presentes antes del incendio, las condiciones anteriores al incendio (especialmente la presencia de tocones) podrían ser importantes en la determinación de la adaptabilidad de un sitio después de un incendio para las aves que anidan en cavidades. Para las especies que fueron relativamente abundantes o estuvieron relativamente restrictas a los bosques incendiados, el reemplazo de rodales a partir de incendios podría ser necesario para el mantenimiento a largo plazo de sus poblaciones. Desafortunadamente, la presente estrategia sobre incendios a cargo de las agencias de manejo de las tierras públicas no promueve el mantenimiento de los regímenes de incendios para el reemplazo de rodales, los que serían necesarios para la creación de las condiciones requeridas por la mayoría de las especies que dependen de los incendios. En forma adicional, una tala de recuperación podría reducir la adaptabilidad de los hábitats de bosques incendiados para las aves al remover los elementos más importantes, árboles muertos en pie a causa de los incendios, necesarios para la alimentación y/o el anidamiento de la mayoría de las especies de aves que hacen uso de los bosques incendiados.

Introduction

"Of all biotic and abiotic influences on vegetation, fires were the most prevalent major disturbances on the [Rocky Mountain] landscape prior to European settlement" (Gruell 1983). Within all forest zones, climax forests that have escaped fire are rare in the Northern Rockies (Habeck & Mutch 1973). For mid- to high-elevation forest types within the Northern Rockies, the predominant fire regime is one of infrequent, intense, stand-replacement fires, not one of frequent, low-intensity, understory burns (Fischer & Bradley 1987). The origin of most Rocky Mountain forest stands can be traced to stand-replacement, as opposed to mild, understory fires (Arno 1980; Heinselman 1981; DeByle et al. 1987). This implies that much of the variety in forest cover types across the northern Rocky Mountains is more a product of the presence of a variety of successional stages following stand-replacement fires than the presence of a multitude of climax community types. The importance of stand-replacement fires in this forest system should give the maintenance of such fires a high priority in land-management goals but, instead, the historical effort has been to eradicate such fires from these systems. In so doing, we have created a landscape with much less early successional post-fire habitat than existed prior to the era of fire suppression, when half the forest area burned every 100 years and roughly 35% of the forested land was less than 40 years of age at any one point in time (Barrows 1951; Gruell 1980). Even in wilderness areas, where fire control has been minimal, the annual area burned by stand-replacement fires during presettlement times was 1.5 times what it is today (Brown et al. 1994). The biological consequences of allowing a reduced amount of land to burn are unclear, but there is a distinct possibility that those plant and animal species that have evolved to depend on early post-fire communities may have been negatively affected by fire-control policies over the last 50 years.

Given the unique vegetative physiognomy following a stand-replacement fire, we might expect the bird communities associated with early post-fire forests to be unique as well. A review of the literature dealing with early post-fire bird communities in the northern Rocky Mountains (Blackford 1955; Koplin 1969; Davis 1976; Taylor & Barmore 1980; Harris 1982) suggests that some bird species are relatively abundant in recently burned forests (such as Black-backed Woodpecker [*Picoides arcticus*], Hairy Woodpecker [*Picoides villosus*], American Robin [*Turdus migratorius*], Dark-eyed Junco [*Junco hyemalis*]). Most of these species occur in other cover types as well, however, so the loss of fire would not necessarily threaten the maintenance of their populations. Unfortunately, existing descriptions of post-forest-fire bird communities are largely anecdotal (without replication across a number of burns of the same age), of variable time periods after a burn (rarely soon afterward), and not designed to evaluate (through a comparison with other vegetation types) whether there exists a unique combination or association of bird species that occupy recently burned areas.

The purpose of this study, therefore, was to conduct bird counts in a number of different northern Rocky Mountain conifer forests that burned in 1988 to determine (1) which bird species are relatively abundant in early post-fire forests; (2) whether any of those bird species are relatively restricted to such conditions; and (3) whether different bird species vary significantly and similarly in abundance among burns.

Methods

Study Sites and Bird Counts

All of the 1988 forest fires in Montana had been mapped onto 7.5-minute topographic quadrangle maps by the U.S. Forest Service, Region I. I obtained burn-perimeter maps for the 50 fires that exceeded 40 ha, and either I or another observer conducted point counts in each site in one or both of the ensuing two years (Table 1). The areal extent of a given burn was obtained from calculations by the Forest Service. Some named burns were close enough to others of the same age that they were effectively larger than that indicated by the calculated area. In the absence of biological information about how far apart two fires need to be, to be considered separate, however, I used the boundaries and aerial coverages designated by the Forest Service. I also grouped burns into three broad categories for analysis: small, <400 ha; medium, 400–2000 ha; and large, greater than 2000 ha. Approximately half of the sites were visited in 1989 and half in 1990 (Table 1).

I estimated the abundance of all landbird species through the use of point counts (Hutto et al. 1986). Each point was located at least 200 m from other points, and point positions were aligned along a transect route through the center of the burn. No point was located closer than 100 m from the edge of a burn. At each point, an observer recorded the date, time of day, and number of individuals of each bird species detected by sight or sound within and beyond a 100-m radius from the point. I used a relatively large fixed radius for the point counts because of the open nature of burned forests. Birds that were detected beyond 100 m and then subsequently moved to within the 100-m radius during the count were recorded as detections within 100 m. All sites were visited during the active breeding season (between early June and mid-July), and most sites were visited during only one of the two years following the fires (Table 2). The number of observers who collected data from each site was variable. I minimized observer bias by requiring a period of field training before an observer could conduct counts and by ensuring that each conducted counts across a wide spectrum of fire sizes and

Table 1. Locations, sizes, and number of point counts conducted in each of 33 sites in the northern Rocky Mountains that burned in 1988 and one site (Sawmill Gulch) that burned in 1987.

US Forest Service Name	*Latitude (N)*	*Longitude (W)*	*Area (ha)*	*No. of Points 1989*	*No. of Points 1990*
Sawmill Gulch	46°56′	113°59′	40	9	0
Madison Gulch	46°58′	114°25′	400	10	17
Canyon Creek	47°12′	112°59′	97,370	8	42
Lolo Creek	46°50′	114°10′	900	10	14
Snowbowl	46°57′	114°02′	40	6	7
Upper Emery	48°21′	113°54′	70	5	0
Red Bench (USFS)	48°47′	114°27′	15,180	9	12
Red Bench (GNP)	48°45′	114°25′	15,180	12	77
Corral Creek	45°03′	111°33′	575	11	0
Hunter	42°42′	110°35′	2220	14	34
Huck (YNP)	44°10′	110°40′	161,880	18	0
North Fork (YNP)	44°45′	110°44′	277,880	9	0
Combination	46°26′	113°25′	3630	0	32
Cedar Creek	46°17′	115°43′	30	0	6
White Creek	46°20′	115°40′	35	0	7
Green Creek Point	45°58′	115°53′	55	0	4
Rock Creeks	46°03′	114°21′	2240	0	24
Upper Lost Horse	46°25′	114°30′	2540	0	18
Lake Alva	47°18′	113°34′	90	0	8
Glen Lake	46°27′	114°16′	50	0	7
Blodgett Canyon	46°15′	114°25′	485	0	5
Ruby Rapids	45°24′	116°11′	880	0	7
Warm Springs	46°26′	111°50′	18,980	0	23
Squaw Gulch	46°34′	112°04′	55	0	8
Girard Gulch	46°10′	112°39′	60	0	9
Camp Creek	45°39′	114°58′	3240	0	30
Homestake	45°55′	112°23′	25	0	4
Goldflint	45°57′	112°22′	145	0	9
Wolf Lake (YNP)	44°40′	110°25′	121,400	0	15
Grant Village (YNP)	44°20′	110°50′	242,800	0	22
Coal Ridge	48°42′	114°27′	60	0	7
Totem Peak	46°21′	114°16′	2915	0	1

Table 2. Statistics for 87 bird species detected among 33 burned forest sites in the northern Rocky Mountains: number of sites occupied, mean number of individuals detected per 100-m-radius point (n = 597), percentage of 100-m-radius points on which the species was detected, migratory status, feeding zone, diet, and known nest site.

Species	*No. of Sites*	*No. of Individuals*	*Detection (%)*	*Status*[a]	*Feeding Zone*[b]	*Diet*[c]	*Nest Site*[d]
Osprey, *Pandion haliaetus*	4	0.010	0.84	M	W	F	S/O
Sharp-shinned Hawk, *Accipiter striatus*	4	0.007	0.67	M	G/A	V	—
Cooper's Hawk, *Accipiter cooperii*	2	0.003	0.34	M	G/A	V	—
Red-tailed Hawk, *Buteo jamaicensis*	8	0.035	2.68	M	G	V	S/C
American Kestrel, *Falco sparverius*	5	0.015	1.34	M	G	V	S/O
Blue Grouse, *Dendragapus obscurus*	4	0.010	1.01	R	G	O	—
Ruffed Grouse, *Bonasa umbellus*	4	0.012	1.17	R	G	O	—
Sandhill Crane, *Grus canadensis*	3	0.013	0.84	M	G	V	—
Spotted Sandpiper, *Actitis macularia*	4	0.017	1.51	M	G	I	—
Common Snipe, *Gallinago gallinago*	4	0.052	3.85	M	G	I	—
Mourning Dove, *Zenaida macroura*	4	0.032	1.68	M	G	S	—
Common Nighthawk, *Chordeiles minor*	2	0.005	0.34	M	A	I	—
Vaux's Swift, *Chaetura vauxi*	3	0.025	0.84	M	A	I	—
Calliope Hummingbird, *Stellula calliope*	6	0.012	1.17	M	F	N	—
Rufous Hummingbird, *Selasphorus rufus*	4	0.049	2.51	M	F	N	—
Belted Kingfisher, *Ceryle alcyon*	1	0.002	0.17	M	W	F	—
Red-naped Sapsucker, *Sphyrapicus nuchalis*	4	0.062	4.52	M	B	I	S/C
Williamson's Sapsucker, *Sphyrapicus thyroideus*	5	0.013	1.34	M	B	I	—
Downy Woodpecker, *Picoides pubescens*	2	0.003	0.34	R	B	I	—
Hairy Woodpecker, *Picoides villosus*	30	0.213	17.42	R	B	I	S/C
Three-toed Woodpecker, *Picoides tridactylus*	14	0.099	8.04	R	B	I	S/C
Black-backed Woodpecker, *Picoides arcticus*	11	0.062	5.53	R	B	I	S/C
Northern Flicker, *Colaptes auratus*	28	0.305	26.47	M	G	I	S/C
Pileated Woodpecker, *Dryocopus pileatus*	4	0.018	1.51	R	B	I	—
Olive-sided Flycatcher, *Contopus borealis*	18	0.168	15.58	M	A	I	F/O
Western Wood-Pewee, *Contopus sordidulus*	11	0.104	8.88	M	A	I	S/O
Willow Flycatcher, *Empidonax traillii*	2	0.008	0.67	M	A	I	—
Hammond's Flycatcher, *Empidonax hammondii*	9	0.045	3.52	M	A	I	—
Dusky Flycatcher, *Empidonax oberholseri*	16	0.147	12.73	M	A	I	F/O
Tree Swallow, *Tachycineta bicolor*	6	0.310	11.39	M	A	I	S/C
Cliff Swallow, *Hirundo pyrrhonota*	1	0.020	0.50	M	A	I	—
Gray Jay, *Perisorius canadensis*	8	0.027	2.18	R	F/G	O	—
Steller's Jay, *Cyanocitta stelleri*	6	0.032	2.18	R	F/G	O	—
Clark's Nutcracker, *Nucifraga columbiana*	18	0.157	10.89	R	F/G	S	—
Black-billed Magpie, *Pica pica*	1	0.002	0.17	R	G	O	—
Common Raven, *Corvus corax*	18	0.121	10.05	R	F/G	O	F/O
Black-capped Chickadee, *Parus atricapillus*	13	0.039	3.18	R	F	I	S/C
Mountain Chickadee, *Parus gambeli*	21	0.164	13.23	R	F	I	S/C
Chestnut-backed Chickadee, *Parus rufescens*	1	0.003	0.17	R	F	I	—
Red-breasted Nuthatch, *Sitta canadensis*	24	0.317	24.12	R	B	I	S/C
Brown Creeper, *Certhis americana*	2	0.003	0.34	R	B	I	—
Rock Wren, *Salpinctes obsoletus*	2	0.005	0.50	M	G	I	—
House Wren, *Troglodytes aedon*	8	0.067	5.53	M	G	I	S/C
Winter Wren, *Troglodytes troglodytes*	4	0.010	1.01	M	G	I	—
American Dipper, *Cinclus mexicanus*	1	0.002	0.17	M	W	I	—
Golden-crowned Kinglet, *Regulus satrapa*	2	0.015	0.67	M	F	I	—
Ruby-crowned Kinglet, *Regulus calendula*	20	0.137	12.73	M	F	I	—
Western Bluebird, *Sialia mexicana*	2	0.010	0.84	M	G	I	S/C
Mountain Bluebird, *Sialia currucoides*	24	0.385	24.12	M	G	I	S/C
Townsend's Solitaire, *Myadestes townsendi*	25	0.193	16.75	M	G	I	G/O
Swainson's Thrush, *Catharus swainsoni*	22	0.238	16.75	M	F	I	—
Hermit Thrush, *Catharus guttatus*	12	0.042	4.02	M	G	I	—
American Robin, *Turdus migratorius*	32	0.734	50.59	M	G	I	S/O
Varied Thrush, *Ixoreus naevius*	7	0.045	4.02	M	G	I	—
Cedar Waxwing, *Bombycilla cedrorum*	2	0.008	0.67	M	A	I	—
European Starling, *Sturnus vulgaris*	3	0.030	2.18	R	G	I	S/C
Solitary Vireo, *Vireo solitarius*	7	0.020	2.01	M	F	I	—
Warbling Vireo, *Vireo gilvus*	11	0.121	9.88	M	F	I	S/O
Orange-crowned Warbler, *Vermivora celata*	6	0.032	2.51	M	F	I	—

Table 2. Continued

Species	No. of Sites	No. of Individuals	Detection (%)	Status[a]	Feeding Zone[b]	Diet[c]	Nest Site[d]
Nashville Warbler, *Vermivora ruficapilla*	1	0.002	0.17	M	F	I	G/O
Yellow Warbler, *Dendroica petechia*	3	0.008	0.84	M	F	I	—
Yellow-rumped Warbler, *Dendroica coronata*	29	0.409	31.66	M	F	I	F/O
Townsend's Warbler, *Dendroica townsendi*	9	0.034	3.18	M	F	I	—
American Redstart, *Setophaga ruticilla*	1	0.002	0.17	M	F	I	—
Northern Waterthrush, *Seiurus noveboracensis*	3	0.062	4.36	M	G	I	—
MacGillivray's Warbler, *Oporornis tolmiei*	18	0.141	11.22	M	F	I	—
Wilson's Warbler, *Wilsonia pusilla*	6	0.025	2.35	M	F	I	—
Western Tanager, *Piranga ludoviciana*	28	0.253	21.11	M	F	I	F/O
Black-headed Grosbeak, *Pheucticus melanocephalus*	5	0.015	1.51	M	F	I	—
Lazuli Bunting, *Passerina amoena*	13	0.221	16.08	M	G	I	F/O
Green-tailed Towhee, *Pipilo chlorurus*	1	0.022	1.84	M	G	I	—
Rufous-sided Towhee, *Pipilo erythrophthalmus*	2	0.005	0.50	M	G	I	—
Chipping Sparrow, *Spizella passerina*	27	0.591	36.68	M	G/F	I/S	—
Vesper Sparrow, *Pooecetes gramineus*	3	0.023	1.01	M	G	I/S	—
Fox Sparrow, *Passerella iliaca*	5	0.023	2.35	M	G	I	—
Song Sparrow, *Melospiza melodia*	2	0.015	1.34	M	G	I	—
Lincoln's Sparrow, *Melospiza lincolnii*	11	0.065	5.03	M	G	I	—
White-crowned Sparrow, *Zonotrichia leucophrys*	7	0.094	7.54	M	G	I/S	G/O
Dark-eyed Junco, *Junco hyemalis*	32	1.027	61.31	M	G	I/S	G/O
Red-winged Blackbird, *Agelaius phoeniceus*	2	0.055	2.85	M	G	I	—
Brewer's Blackbird, *Euphagus cyanocephalus*	1	0.005	0.34	M	G	I	—
Brown-headed Cowbird, *Molothrus ater*	19	0.085	8.21	M	G	I	—
Pine Grosbeak, *Pinicola enucleator*	2	0.008	0.67	R	F	S	—
Cassin's Finch, *Carpodacus cassinii*	21	0.228	15.75	M	F	I	F/O
Red Crossbill, *Loxia curvirostra*	23	0.261	12.90	R	F	S	—
Pine Siskin, *Carduelis pinus*	31	1.179	52.76	M	F	I/S	F/O
Evening Grosbeak, *Coccothraustes vespertinus*	3	0.039	1.84	M	F	I/S	—

[a] *M = migrant; R = resident. Classification based on Ehrlich et al. (1988).*

[b] *A = air; B = tree bole or branch; G = ground; F = foliage; W = water. Classification based on Ehrlich et al. (1988) and my own observations.*

[c] *F = fish; I = insects; N = nectar; O = omnivore; S = seeds; V = vertebrates. Classification based on Ehrlich et al. (1988) and my own observations.*

[d] *F/O = foliage, open; G/O = ground, open; S/C = snag, cavity; S/O = snag, open. Classification based on my own observations of nests.*

geographic locations. All counts were conducted between 0630 hours and 1100 hours, and each lasted 10 minutes.

Vegetation and Landscape Data

At each point from which a bird count was conducted, the observer also recorded information about the surrounding vegetation structure. All measurements were taken from within radii that were less than the 100-m radius within which birds were detected; nevertheless, I assumed that these measurements were representative of the larger area surrounding each point. Measurements included (1) overstory composition prior to the fire, as estimated by the proportionate makeup of each of eight tree-species groups (ponderosa pine [*Pinus ponderosa*]; Douglas-fir [*Pseudotsuga menziesii*]; western larch [*Larix occidentalis*]; lodgepole pine [*Pinus contorta*]; whitebark pine [*Pinus albicaulis*] or limber pine [*Pinus flexilis*]; spruce [*Picea* spp.]; subalpine fir [*Abies lasiocarpa*]; grand fir [*Abies grandis*] or western redcedar [*Thuja plicata*]; and quaking aspen [*Populus tremuloides*] or cottonwood [*Populus* spp.]) within 50 m; (2) fire severity within 50 m, classified as (a) unburned, (b) more than 60% of the trees having green needles/leaves (versus brown needles or none), (c) between 40 and 60% of the trees having green needles, (d) between 5 and 40% of the trees having green needles, (e) less than 5% of the trees having green needles but most still having visible twigs, (f) all trees having neither needles nor twigs, and (g) mostly broken stumps—very few standing trees left; (3) number of trees 10 to 30 cm diameter at breast height (dbh) within a 15-m radius; (4) number of trees more than 30 cm dbh within a 15-m radius; (5) percentage of shrub cover, as estimated by eye within 25 m; (6) percentage of grass/forb cover, as estimated by eye within 25 m; (7) percentage of the ground covered by plants with composite flowers, as estimated by eye within 25 m; (8) percentage of ground covered by plants with tubular corollas, as estimated by eye within 25 m; (9) percentage ground covered by dead and downed trees (>10 cm dbh), as estimated by eye within 25 m; (10) whether any trees within 100 m had been cut after the fire and prior to our bird counts; (11) whether a perennial stream was within 100 m; and (12) whether an unburned forest edge was nearby, beyond 100 m but within 150 m.

Habitat Distribution of Birds

To determine the broader habitat distribution of the bird species that I detected in burned forests, I used published and unpublished census data from all the independent studies I could find for each of 15 broadly defined Rocky Mountain cover types: riparian bottomland, riparian streamside, aspen, grassland, sagebrush, pinyon-juniper, ponderosa pine, mixed conifer, lodgepole pine, spruce-fir, cedar-hemlock, post-fire forests in early succession (<10 years old), post-fire forests in mid-succession (10–40 years old), clearcut forests in early succession (<10 years old), and clearcut forests in mid-succession (10–40 years old). Because of the limited number of studies in any of the latter four categories, each included data from a variety of conifer forest types. To keep the information as relevant as possible to the northern Rocky Mountains while still achieving decent sample sizes for the various cover types, I included data from studies conducted in Alberta, eastern British Columbia,. Colorado, Idaho, Montana, North Dakota, eastern Oregon, Utah, eastern Washington, and Wyoming. I recorded, for each cover type, the proportion of studies in which a given species was detected. Bird species that were present but too rare for density or abundance estimates (often noted with a "+" in the literature) were counted as present, but those recorded as "incidental" or "accidental" were not. An acceptable "study" was one that involved at least two days of census work (or 18 point counts) during a single season. Several studies included data from more than one site but, except for my own work in burned forests, I treated those data as a single sample unit. When an author provided data from more than one season, I used data from the most recent year available (see Table 3 for references). Similar methods have been used by Wiens (1975) and Raphael (1987*a*) to estimate probabilities of occurrence for bird species of mixed-conifer and spruce-fir forests, respectively.

Records of Trees and Nests Used by Woodpeckers

I examined patterns of tree species use in three sites (Grant Village, North Fork, and Canyon Creek) by walking haphazardly oriented, straight-line transects and, for each tree more than 10 cm dbh within 5 m of the transect, recording the tree species and presence of woodpecker feeding activity (small holes and/or bark flaking). I continued along a transect until I either counted 200 trees or came to the edge of the burn; I conducted two transects in each site. Using the same methodology, I collected data in the summer of 1993 on both the species and sizes (in 10-cm-dbh increments) of trees used by woodpeckers from a site burned in 1991 (Blackfoot-Clearwater Game Range; 47°02′N, 113°20′W).

All instances of nesting were obtained incidentally to the bird census work. Upon discovering a nest, I recorded the following: bird species, date, site, nest location, plant species, height of plant, height of nest, and, when possible, number of eggs or young present. In the case of snag-nesting species, I also recorded the dbh, snag condition (broken or intact top), and whether the broken-top condition was present before the fire (as evidenced by burned rather than unburned heartwood at the break point).

Bird Nomenclature and Analysis

The taxonomic arrangement and English names for all species mentioned in the text are based on the A.O.U. Checklist (American Ornithologists' Union 1983, and supplements). Both Latin and English names are given in Table 2.

Statistical analyses were conducted with SPSS/PC+ software. To investigate the relative similarity among bird communities characteristic of each of 15 Rocky Mountain cover types, I generated an average-linkage within-groups dendrogram based on the squared Euclidean distance between bird-occurrence probabilities. For a given bird species, I tested whether the proportion of points occupied and mean number of birds per point differed significantly among sites with chi-square and Kruskal-Wallace ANOVA tests, respectively. To investigate whether the pattern of relative abundance across sites varied among bird species, I used a subset of the 20 most common bird species and the 10 most heavily sampled sites and tested the significance of the species by site interaction through a two-way ANOVA. The relative importance of each local-scale vegetation characteristic in predicting the mean number of birds per point at a site was established through partial correlation analyses. I restricted these analyses to species that were detected in at least five sites and to a subset of 13 continuous independent variables (the first 13 listed above), which were not significantly intercorrelated ($p < 0.05$). I also combined the single point obtained from the Totem Peak site with points from the nearby Glen Lake site.

Results

I detected a total of 87 species in one- to two-year-old burns (mean = 45 species per site), of which 77% were migrants that winter to the south (Table 2). Bird-community composition in recently burned forests is relatively distinct from that in other Rocky Mountain habitat types, but it clusters most closely with the two clearcut forests and mid-successional, post-fire forests (Fig. 1). A number of species seem to be relatively abundant in early

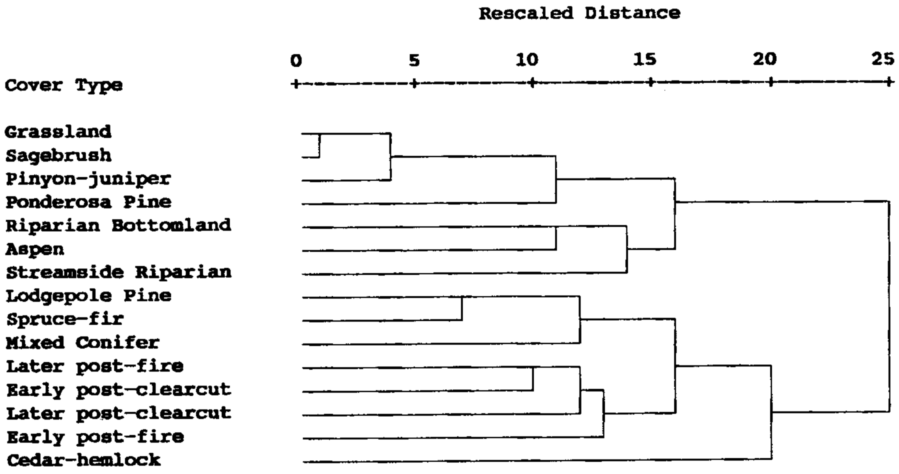

Figure 1. The pattern of similarity of bird communities among 15 major Rocky Mountain cover types. Dendrogram based on the average-linkage within-groups clustering method using squared Euclidean distances between bird occurrence probabilities given in Table 3.

post-fire forests and contribute to the distinctiveness of bird communities therein. In particular, 15 species were more frequently detected in early post-fire forests than they were in any other major cover type that occurs in the northern Rockies (Table 3). Other authors (Blackford 1955; West & Speirs 1959; Koplin 1969; Bock & Lynch 1970; Heinselman 1973; Niemi 1978; Pfister 1980; Taylor & Barmore 1980; Apfelbaum & Haney 1981, 1985; Harris 1982) have noted that many of the same species (such as Black-backed Woodpecker, Three-toed Woodpecker [*Picoides tridactylus*], Olive-sided Flycatcher [*Contopus borealis*], American Robin, Dark-eyed Junco) either appeared only after fire or dominated early post-fire bird communities. Bent (1939) also wrote about the abundance of Black-backed Woodpeckers in fire-killed forests, quoting Manly Hardy, who said he shot the heads off six within a few minutes when he was short of material for a stew!

Some species are not only more abundant in burned forests, but they are relatively restricted in their habitat distribution to early post-fire forests (Table 3). Of the 77 species for which I obtained an estimate of the breadth of habitats occupied, only two were more specialized than the Black-backed Woodpecker (Table 3). Even though Black-backed Woodpeckers were recorded on rare occasions (≤ 12% of the studies) in each of three other cover types (Table 3), the authors of several studies (Davis 1976; Taylor & Barmore 1980; Medin 1985; Skinner 1989) noted the presence of either a burned forest nearby or a prior burning treatment on their plot. Thus, my measure of habitat specialization for Black-backed Woodpeckers is probably conservative and is consistent with the suggestion that this species evolved in close association with burned forests (Bock & Bock 1974; Short 1982). I am aware of unpublished records of Black-backed Woodpeckers in unburned forests associated with severe budworm outbreaks in northern Idaho, and of unpublished nesting records in unburned and selectively harvested forests in western Montana, but based on the comprehensive literature review herein and on my own field experience, these appear to be the exception more than the rule.

Insectivorous diets characterize most (78%) species that comprise early post-fire bird communities (Table 2). The number of bark-probing insectivore species that occur on the majority of studies in recently burned forest is unmatched by that in any other vegetative type in the northern Rockies (see Table 3).

Not all tree species and sizes were equally used by woodpeckers. At least half of the ponderosa pine, Douglas-fir, and western larch that I sampled showed signs of woodpecker feeding, but significantly smaller proportions (less than 3%) of Engelmann spruce, lodgepole pine, and subalpine fir showed signs of feeding activity (Table 4). In addition, larger trees (> 10 cm dbh) of each species were significantly more likely to show evidence of feeding use than were smaller trees (Table 5), which corresponds well with the pattern of use by beetle larvae (Amman & Ryan 1991).

I found active nests for 31 (36%) of the 87 species that I detected on point counts (Table 2). Standing dead trees provided nest sites for the majority (61%) of species, including open-nesting species (Table 6). Eleven (52%) of the 21 open-cup nests that I found were positioned in burned snags, as were five of the 12 open-cup nests that were placed above ground. Broken-top snags were especially important as nest sites. Of the 48 cavity nests that I found, 35% were located in broken-top conifer or broken-top aspen snags, even though such snags comprised only 6% of the trees available (Table 6). Nearly all of these trees had their tops broken before the fire occurred, as evidenced by blackened wood across the broken top. An additional 38% of the nests were in intact-top aspen snags (Table 6). While most of the intact-top aspen were probably not dead before the fire event, most did have already-existing cavities, as evidenced by the blackened entrances of numerous nest holes. Thus, 73% of the nests were located in already ex-

Table 3. **Percentage of (*n*) studies in which a given species was detected across a fairly complete cross-section of northern Rocky Mountain dryland habitats for 77 of the 87 species detected in burned forests.**

		Cover Type[a]														
Species[b]	*B*[c]	*BOT*	*STR*	*ASP*	*GRA*	*SAG*	*P-J*	*P-P*	*M-C*	*LOD*	*S-F*	*C-H*	*EBU*	*MBU*	*ECC*	*MCC*
No. of Studies (*n*)	—	20	14	34	20	13	6	10	51	11	25	7	23	5	10	10
American Kestrel	9.61	45	7	9	20	15	33	20	8	0	8	0	17	40	20	40
Mourning Dove	7.55	75	0	6	25	46	67	70	16	0	4	0	13	40	20	10
Common Nighthawk	8.50	15	0	0	5	8	0	10	10	9	0	0	9	20	10	20
Vaux's Swift	5.12	10	0	0	0	0	0	0	4	0	0	14	13	0	20	20
Calliope Hummingbird	6.38	5	21	3	0	0	0	10	29	0	4	0	26	40	10	10
Rufous Hummingbird	6.01	5	0	3	0	0	0	0	8	0	8	14	22	20	30	40
Belted Kingfisher	1.77	30	7	0	0	0	0	0	0	0	0	0	4	0	0	0
Red-naped Sapsucker	8.05	25	36	38	0	0	0	10	31	9	8	43	17	0	30	70
Williamson's Sapsucker	6.24	0	0	3	0	0	0	10	29	27	36	0	26	20	0	10
Downy Woodpecker	4.50	55	14	35	0	0	0	0	4	9	8	0	13	0	0	10
Hairy Woodpecker	10.23	35	7	24	0	0	17	30	55	45	72	57	96	60	60	90
Three-toed Woodpecker	3.28	0	0	0	0	0	0	0	6	27	44	0	65	0	10	0
Black-backed Woodpecker	1.67	0	0	0	0	0	0	0	12	9	4	0	78	0	0	0
Northern Flicker	11.93	80	14	71	10	8	67	70	65	45	60	14	74	80	70	90
Pileated Woodpecker	4.95	10	7	0	0	0	0	10	22	0	0	71	9	40	10	20
Olive-sided Flycatcher	6.35	0	0	6	0	0	0	0	22	0	44	29	74	40	60	40
Western Wood-Pewee	6.90	75	7	79	0	0	0	70	18	0	32	14	65	20	10	10
Willow Flycatcher	5.84	10	50	3	10	0	0	0	6	0	4	29	17	0	10	30
Hammond's Flycatcher	5.68	5	21	9	0	0	0	20	55	9	28	100	30	0	0	30
Dusky Flycatcher	8.35	5	57	12	0	0	17	20	37	0	20	14	48	60	20	70
Tree Swallow	7.20	35	21	41	0	0	0	0	6	0	12	29	30	0	40	10
Cliff Swallow	4.60	10	7	0	5	8	0	0	0	0	0	0	4	0	0	0
Gray Jay	7.42	0	7	3	0	0	0	0	35	73	52	29	39	20	40	60
Steller's Jay	8.16	5	0	6	0	0	0	30	20	18	32	14	13	40	10	40
Clark's Nutcracker	5.66	0	0	0	0	0	0	20	27	45	48	0	65	60	10	0
Black-billed Magpie	4.33	40	0	3	15	0	17	30	2	0	4	0	4	0	0	0
Common Raven	8.07	0	14	9	5	8	17	0	33	9	8	43	61	40	50	10
Black-capped Chickadee	9.65	60	43	62	5	0	0	20	33	9	8	71	48	40	20	50
Mountain Chickadee	9.58	5	14	18	0	0	17	60	98	91	92	57	70	40	40	60
Chestnut-backed Chickadee	1.43	0	0	0	0	0	0	0	2	0	0	100	0	0	0	20
Red-breasted Nuthatch	9.16	5	21	24	0	0	0	20	86	55	80	86	74	60	30	50
Brown Creeper	5.77	0	0	3	0	0	0	10	41	45	68	57	13	0	10	20
Rock Wren	3.95	5	0	3	0	15	50	0	2	0	0	0	9	40	0	10
House Wren	8.18	55	21	85	0	0	17	40	14	9	8	0	26	40	20	50
Winter Wren	2.91	0	14	0	0	0	0	0	24	0	4	86	9	0	10	10
Golden-crowned Kinglet	4.31	0	7	0	0	0	0	0	65	18	80	86	9	0	0	20
Ruby-crowned Kinglet	7.57	0	14	15	0	0	0	0	86	64	100	57	52	40	20	40
Western Bluebird	1.43	0	0	0	0	0	0	40	4	0	0	0	4	0	0	0
Mountain Bluebird	6.78	5	0	47	5	0	50	10	8	0	12	0	91	60	80	70
Townsend's Solitaire	8.95	5	0	9	0	0	17	30	39	27	32	29	70	60	60	70
Swainson's Thrush	7.92	10	71	15	0	0	0	0	82	18	44	100	65	20	30	60
Hermit Thursh	7.20	5	0	47	0	0	0	20	45	64	72	0	22	40	10	20
American Robin	12.63	95	79	88	10	8	17	90	84	82	88	71	100	100	90	90
Varied Thrush	3.73	0	0	0	0	0	0	0	24	0	12	86	13	20	10	20
Cedar Waxwing	4.18	25	14	3	0	0	0	0	4	0	0	0	9	0	10	40
European Starling	4.20	35	0	9	0	8	0	0	4	0	0	0	22	20	0	0
Solitary Vireo	5.01	15	7	6	0	0	0	60	71	0	0	71	4	0	10	30
Warbling Vireo	8.83	80	71	100	0	0	0	20	63	18	24	14	39	40	20	50
Orange-crowned Warbler	7.33	10	7	18	0	0	0	10	35	0	16	29	4	40	0	30
Nashville Warbler	3.09	5	7	0	0	0	0	0	22	0	0	14	0	0	0	0
Yellow Warbler	5.75	70	71	38	10	0	0	10	12	0	0	14	22	0	0	30
Yellow-rumped Warbler	10.90	15	29	71	0	0	17	70	100	91	100	71	100	100	60	100
Townsend's Warbler	3.89	0	14	3	0	0	0	0	63	0	16	100	17	0	10	20
American Redstart	2.67	30	29	0	0	0	0	0	6	0	0	0	4	0	0	0
Northern Waterthrush	2.86	15	14	0	0	0	0	0	0	0	0	0	9	0	0	0
MacGillivray's Warbler	9.17	25	71	24	10	0	0	10	67	0	12	71	48	60	60	60
Wilson's Warbler	5.33	0	29	0	0	0	0	0	4	0	12	29	26	20	0	50
Western Tanager	8.63	15	14	18	0	0	0	50	96	9	60	71	83	20	50	60
Black-headed Grosbeak	8.91	50	50	21	10	0	0	20	24	9	4	29	30	20	0	50

Table 3. Continued

		Cover Type[a]														
Species[b]	*B*[c]	*BOT*	*STR*	*ASP*	*GRA*	*SAG*	*P-J*	*P-P*	*M-C*	*LOD*	*S-F*	*C-H*	*EBU*	*MBU*	*ECC*	*MCC*
Lazuli Bunting	7.68	45	21	9	10	15	0	20	10	0	4	0	39	0	10	30
Green-tailed Towhee	4.79	0	0	9	0	8	17	40	2	0	8	0	13	0	0	10
Rufous-sided Towhee	6.25	25	7	3	5	8	50	40	6	0	0	0	4	40	0	20
Chipping Sparrow	10.56	15	29	29	5	0	50	80	92	18	64	43	96	100	80	90
Veser Sparow	3.87	5	0	0	35	77	17	0	6	0	0	0	9	40	0	0
Fox Sparrow	6.71	5	50	3	0	0	0	0	8	0	12	29	17	40	20	40
Song Sparrow	6.05	65	79	24	10	0	0	20	10	0	0	29	17	0	0	50
Lincoln's Sparrow	5.87	5	50	9	0	0	0	0	4	18	28	0	35	0	10	20
White-crowned Sparrow	5.59	5	36	35	0	8	0	0	6	0	12	0	43	0	10	10
Dark-eyed Junco	10.29	5	21	76	0	0	0	60	100	100	96	71	100	100	90	100
Red-winged Blackbird	5.07	15	21	0	15	15	0	0	2	0	0	0	13	0	0	0
Brewer's Blackbird	4.10	5	0	0	10	15	0	0	4	0	0	0	13	0	0	0
Brown-headed Cowbird	11.44	45	50	15	55	31	33	10	51	9	8	14	61	40	20	30
Pine Grosbeak	3.01	0	0	0	0	0	0	0	8	36	56	0	9	0	10	0
Cassin's Finch	8.33	10	0	29	0	0	17	30	51	18	60	14	83	20	20	70
Red Crossbill	7.94	5	14	6	0	0	0	30	45	27	48	14	61	0	20	40
Pine Siskin	9.84	10	29	50	0	0	0	60	94	64	72	57	96	20	70	100
Evening Grosbeak	5.93	15	14	6	0	0	0	20	61	9	24	0	13	0	10	10

[a] *BOT = cottonwood bottomland (Dumas 1950 [2 sites]; Thorne 1950; Newhouse 1960; Seidensticker et al. 1968; Hurley et al. 1971; Kingery & Bottorff 1972; Johnson 1973; Andrews 1975; Kertell & Scott 1975; Jepson 1981; Mosconi & Hutto 1981 [2 sites]; Jones 1982; Berkey 1983f, 1983g; Gifford 1983; Gyug 1983b; Finch 1989; Goble 1992).*

STR = streamside riparian (Salt 1957; Manuwal 1967c, 1968; Cody 1974; Schimpf 1975; Burns et al. 1982; Figgs 1984; Hallock 1984; Lederer 1984; Blakesley & Reese 1988; Knopf et al. 1988; Finch 1989; Hutto, unpublished field notes [2 sites]).

ASP = aspen (Dumas 1950; Salt 1957; Bottorff 1972; Flack 1976 [22 sites]; Hansley 1978; Thompson 1978; DeByle 1981; Smith & MacMahon 1981; Farnes & Andrew 1982; Scott & Crouch 1987, 1988a; Finch & Reynolds 1988).

GRA = grassland (Wing 1947; Dumas 1950 [2 sites]; Owens & Myres 1973; Cody 1974; Thompson & Dahmer 1978c, 1978d; Jenni & Bicak 1980; Berkey 1983a, 1983b, 1983c, 1983d, 1983e; Johnson & Schwartz 1991, 1992a, 1992b, 1992c, 1992d, 1992e; Doremus 1993b).

SAG = sagebrush (Dumas 1950; Scott et al. 1964; Cody 1974; Scott 1975; Hoppes 1978; Thompson 1978; Thompson & Dahmer 1978a, 1978b; Castrale & Parker 1981a, 1981b; Wiens & Rotenberry 1981; Pyle 1989; Doremus 1993a).

P-J = pinyon-juniper (Hering 1957; Beidleman 1960b; Lang & Sullivan 1980; Salamacha 1984; Kelly & Kelly 1989; Graham & Nettell 1992).

P-P = Ponderosa pine (Hering 1948, 1958, 1984; Lawhead 1949; Dumas 1950; Thatcher 1952a; Beidleman 1960a; Toole & Chase 1981; Traynor 1983; Lyon, unpublished field notes).

M-C = mixed-conifer (Dumas 1950; Snyder 1950; Thatcher 1952c; Grant 1965; Manuwal 1967b, 1967c, 1968; Frissell 1973; Connor 1978; Thompson 1978; McClelland 1980 [2 sites]; Harris 1982; Aney 1984; Mannan & Meslow 1984 [2 sites]; Poll & VanDeVlasakker 1984; Garton 1985 [4 sites]; Medin 1985 [2 sites]; Hunt 1989 [14 sites]; Lederer 1989; Medin & Booth 1989 [2 sites]; Skinner 1989 [2 sites]; Hejl & Woods 1991 [2 sites]; Tobalske et al. 1991 [2 sites]; Moore 1992; Hutto, unpublished field notes; Lyon, unpublished field notes).

LOD = lodgepole pine (Snyder 1950; Thatcher 1952b; Salt 1957; Kingery 1970; Davis 1976; Austin & Perry 1979; Pfister 1980; Raphael 1987b; Scott & Crouch 1988a; Hallock 1990).

S-F = spruce-fir (Dumas 1950; Snyder 1950; Salt 1957 [2 sites]; Webster 1967; Burr 1969a, 1969b; Archie & Hudson 1973; Davis 1976; Thompson 1978; Pfister 1980; Smith 1980; Taylor & Barmore 1980 [2 sites]; Smith & MacMahon 1981 [2 sites]; Scott et al. 1982; Poll 1984; Raphael 1987a; Finch & Reynolds 1988 [2 sites]; Hallock 1989; Catt 1991; Keller & Anderson 1992; Lyon, unpublished field notes).

C-H = cedar-hemlock (Peterson 1982; Gyug 1983a; Mitchell & Bratkovich 1992; Weller 1992, 1993; Jacobson & Weller 1993; Hutto, unpublished field notes).

EBU = early successional burned forest (Davis, 1976; Pfister 1980 [2 sites]; Taylor & Barmore 1980 [2 sites]; Harris 1982 [2 sites]; Skinner 1989 [2 sites]; Hutto, this study, 14 sites).

MBU = mid-successional burned forest (Davis 1976; Taylor & Barmore 1980; Catt 1991; Hutto, unpublished field notes [2 sites]).

ECC = early successional clearcut (Davis 1976 [2 sites]; McClelland 1980; Peterson 1982; Hallock 1990; Catt 1991; Tobalske et al. 1991; Mitchell & Bratkovich 1992; Moore 1992; Hutto, unpublished field notes).

MCC = mid-successional clearcut (Austin & Perry 1979 [2 sites]; Peterson 1982 [2 sites]; Hallock 1990 [2 sites]; Mitchell & Bratkovich 1992 [2 sites]; Hutto, unpublished field notes [2 sites]).

[b] *Scientific names given in Table 2.*

[c] *$B = 1/\Sigma p_i^2$, where p = the proportionate occurrence in habitat i. B ranges from 1, if a species were completely restricted to a single habitat type, to 15, if a species were equally distributed across all 15 habitat types.*

isting broken-top snags or aspen, and these trees comprised only 8% of those available. Even primary cavity nesters used broken-top snags or aspen significantly more often than expected on the basis of tree availability (67% of 27 nests; $G = 22.5, p < 0.001$).

A given species did not occur with equal likelihood (chi-square tests) or in equal abundance (Kruskal-Wallace ANOVAs) among burns (Table 7). This was not a simple consequence of the fact that the study sites differed in aerial extent; bird abundance generally did not vary with size of the burn (Pearson rank correlations, $p > 0.05$; Table 7). Moreover, relative bird abundances among study sites varied significantly among species (ANOVA, significant species by site interaction; $F_{171,6560} = 4.75, p < 0.001$), which suggests that the within-site factors most important in predicting the presence of one

Table 4. The numbers of seven species of conifers (>10 cm diameter at breast height) encountered along a series of transects in the Grant Village, North Fork, Canyon Creek, and Blackfoot-Clearwater sites, and the percentages of those used by woodpeckers for feeding purposes.

Tree Species	*(n)*	*Woodpecker use (%)**
Ponderosa pine, *Pinus ponderosa*	297	80.5
Western larch, *Larix occidentalis*	100	64.0
Douglas-fir, *Pseudotsuga menziesii*	593	47.9
Engelmann spruce, *Picea engelmanni*	109	2.3
Lodgepole pine, *Pinus contorta*	647	0.2
Subalpine fir, *Abies lasiocarpa*	172	0.0

**Percentages differ significantly among tree species ($G = 1081$, $p = 0.000$).*

Table 6. Number (%) of cavity and open-cup nests in each of six classes of potential nest sites.

Nest Site	*Cavity Nests*	*Open-Cup Nests*	*Available (%)**
Broken-Top Conifer	15 (31)	3 (14)	6
Intact-Top Conifer	12 (25)	9 (44)	92
Broken-Top Aspen	2 (4)	0 (0)	0
Intact-Top Aspen	18 (38)	0 (0)	2
In Bank, On Ground	1 (2)	8 (38)	n/a
In Shrub	0 (0)	1 (5)	n/a

**Based on a sample of 200 trees along a single, 10-m-wide transect in the Canyon Creek site.*

species are not the same as those that best predict the presence of another. Accordingly, the single variable that shows the best partial correlation with bird abundance varies widely among species (Table 7).

Discussion

Contrary to what one might expect to find immediately after a major disturbance event, I detected a large number of species in forests that had undergone stand-replacement fires. Huff et al. (1985) also noted that the density and diversity of bird species in one- to two-year-old burned forests in the Olympic Mountains, Washington, were as great as in adjacent old-growth forests. These numbers are not an artifact of birds simply passing through on their way from one adjacent unburned area to another. Most species we detected were feeding in the burned forests, and at least a third (36%) of those detected were nesting therein as well. If the birds were merely feeding while passing through, I should have detected more species and individuals in small burns and fewer in large burns because the probability of passage should decrease with increased isolation from unburned source areas. In fact, the presence of a species was largely independent of burn size; in only two cases (Townsend's Solitaire [*Myadestes townsendi*] and Solitary Vireo [*Vireo solitarius*]) was bird abundance significantly negatively correlated with burn size, and those species may indeed have been present in the smaller burns because of the proximity of unburned forest to some of the census points.

Several bird species seem to be relatively restricted in distribution to early post-fire conditions. These include Olive-sided Flycatcher, Three-toed Woodpecker, Black-backed Woodpecker, Clark's Nutcracker [*Nucifraga columbiana*], and Mountain Bluebird [*Sialia currucoides*]. Although none of these species may be considered an early post-fire obligate in the strictest sense, few strict obligates are associated with any habitat (Niemi & Probst 1990). I believe it would be difficult to find a forest-bird species more restricted to a single vegetation cover type in the northern Rockies than the Black-backed Woodpecker is to early post-fire conditions. Although it is possible that Black-backed Woodpecker populations are maintained by source refuges of low numbers in unburned forests, it is equally likely that their populations are maintained by a patchwork of recently burned forests. The relatively low numbers in unburned forests may be sink populations that are maintained by birds that emigrate from burns when conditions become less suitable 5–6 years after a fire.

Table 5. The sizes of each of three species of trees used by woodpeckers for feeding purposes in the Blackfoot-Clearwater site.

	Tree Diameter at Breast Height (cm)					
Tree Status	*0–10*	*10–20*	*20–30*	*30–40*	*>40*	*Significance**
Douglas-fir, *Pseudotsuga menziesii*						
not fed upon	269	180	77	9	0	
fed upon	10	70	123	24	10	0.0000
Ponderosa pine, *Pinus ponderosa*						
not fed upon	261	39	17	1	1	
fed upon	72	175	48	7	9	0.0000
Western Larch, *Larix occidentalis*						
not fed upon	16	4	0	0	0	
fed upon	11	30	3	0	0	0.0001

**Based on G-test of independence between tree size and signs of feeding activity.*

Table 7. Statistical results (p values) from analyses of bird communities following fire in conifer forests.

	Variation among Sites			
Species[a]	*Abundance*[b]	*Occurrence*[c]	*Burn Size*[d]	*Best Correlate*[e]
Red-tailed Hawk	0.164	0.293	−0.015	fire intensity (−)
American Kestrel	0.865	0.958	0.334	fire intensity (−)
Calliope Hummingbird	0.037	0.830	−0.134	larch cover
Williamson's Sapsucker	0.000	0.646	0.110	fir-cedar cover
Hairy Woodpecker	0.003	0.003	−0.362	fire intensity (−)
Three-toed Woodpecker	0.000	0.000	0.193	larch cover
Black-backed Woodpecker	0.003	0.006	0.237	number of small trees
Northern Flicker	0.000	0.000	−0.053	number of small trees
Olive-sided Flycatcher	0.000	0.000	0.276	ground cover
Western Wood-Pewee	0.000	0.000	−0.210	deciduous tree cover
Hammond's Flycatcher	0.043	0.080	−0.106	shrub cover
Dusky Flycatcher	0.000	0.000	−0.122	deciduous tree cover
Tree Swallow	0.000	0.000	0.499*	number of small trees
Gray Jay	0.000	0.151	−0.105	Douglas-fir cover
Steller's Jay	0.000	0.000	−0.089	subalpine fir cover
Clark's Nutcracker	0.000	0.000	0.088	ground cover (−)
Common Raven	0.000	0.000	0.198	fir-cedar cover (−)
Black-capped Chickadee	0.017	0.175	−0.008	spruce cover (−)
Mountain Chickadee	0.000	0.000	0.196	shrub cover (−)
Red-breasted Nuthatch	0.000	0.000	−0.337	lodgepole cover (−)
House Wren	0.000	0.000	−0.219	fir-cedar cover
Ruby-crowned Kinglet	0.000	0.000	0.004	subalpine fir cover (−)
Mountain Bluebird	0.000	0.000	0.032	fire intensity
Townsend's Solitaire	0.000	0.000	−0.430*	spruce cover (−)
Swainson's Thrush	0.000	0.000	−0.140	larch cover
Hermit Thrush	0.000	0.000	−0.079	ponderosa pine (−)
American Robin	0.000	0.000	0.160	number of small trees (−)
Varied Thrush	0.000	0.000	−0.078	subalpine fir cover
Solitary Vireo	0.000	0.023	−0.552**	larch cover
Warbling Vireo	0.000	0.000	0.218	deciduous tree cover
Orange-crowned Warbler	0.001	0.029	−0.284	larch cover
Yellow-rumped Warbler	0.000	0.000	0.339	number of big trees
Townsend's Warbler	0.000	0.014	−0.038	fire intensity (−)
MacGillivray's Warbler	0.000	0.000	−0.132	larch cover
Wilson's Warbler	0.141	0.342	0.240	number of small trees
Western Tanager	0.000	0.000	−0.310	subalpine fir cover (−)
Black-headed Grosbeak	0.000	0.333	0.062	deciduous tree cover
Lazuli Bunting	0.000	0.000	−0.275	ground cover
Chipping Sparrow	0.000	0.000	−0.307	ponderosa pine
Fox Sparrow	0.001	0.045	−0.014	spruce cover
Lincoln's Sparrow	0.001	0.000	0.361	number of big trees
White-crowned Sparrow	0.000	0.000	0.507*	deciduous tree cover
Dark-eyed Junco	0.000	0.000	0.358	number of big trees
Brown-headed Cowbird	0.000	0.000	0.228	subalpine fir cover (−)
Cassin's Finch	0.000	0.000	−0.144	fire intensity
Red Crossbill	0.000	0.000	0.209	deciduous tree cover (−)
Pine Siskin	0.000	0.000	0.114	intensity[a]

[a] *Scientific names given in Table 2.*

[b] *p value associated with Kruskal-Wallis ANOVA, which was used to test for among-site differences in mean number of individuals per point.*

[c] *p value associated with G-test, which was used to test for among-site differences in the probability of occurrence.*

[d] *Pearson rank correlation between mean number of individuals per point and burn size. Asterisk indicates significance at $p < 0.05$, and double asterisk indicates significance at $p < 0.01$. Analyses included only sites with at least five sample points.*

[e] *Independent variable with highest partial correlation from multiple regression that included 13 independent variables.*

Detailed studies of movement patterns and demography, needed to resolve this issue, are presently lacking.

In addition to the relative restriction of a few species to early post-fire conditions, many more were simply relatively abundant therein. In the results I note 15 species (including the five listed above) that were more frequently detected in recently burned forest than in any other cover type available in the northern Rockies. An additional six species (Common Nighthawk [*Chordeiles minor*], Calliope Hummingbird [*Stellula calliope*], Northern Flicker [*Colaptes auratus*], Steller's Jay [*Cyanocitta stelleri*], Orange-crowned Warbler [*Vermivora celata*], and Chipping Sparrow [*Spizella passerina*]) were most abundant in the slightly older burned forests (10–40 years after fire) (Table 3). Three species (American Robin, Yellow-rumped Warbler [*Dendroica coronata*], and Dark-eyed Junco) were detected in both early- and mid-successional burned forest studies 100% of the time. Thus, burned forests may be of critical importance to a large number of Rocky Mountain bird species that are either relatively restricted to or relatively abundant in such forests.

The picture I paint of bird communities in burned forests contrasts sharply with that painted by other authors (Emlen 1970; Bendell 1974; Lyon et al. 1978; Niemi 1978; Lyon & Marzluff 1985), who have stated that bird communities change little after fire. After a careful review of those papers and the papers that those authors summarized, however, it is clear that the no-effect conclusions have emerged, in part, from studies of low-intensity fires or nonforested habitats and almost always from comparisons of one or two study sites and one or two controls—far too little replication to draw general conclusions about fire effects. Most important, however, the no-effect conclusions are based on composite statistics such as total bird density, species richness, and within-guild abundances, which hide more than they reveal in terms of biological effects of fire on specific species.

Bird species that use burned forests occupy a variety of feeding guilds and most rely heavily on the standing dead trees for food acquisition. For example, several bird species detected in recently burned forests may be taking advantage of the increased availability of conifer seeds after cones open in response to fire. Seed eaters that feed on conifer seeds (especially Clark's Nutcracker, Cassin's Finch [*Carpodacus cassinii*], Red Crossbill [*Loxia curvirostra*], and Pine Siskin [*Carduelis pinus*]) were more abundant in early post-fire habitat than in any other cover type, and they were significantly more abundant (Mann-Whitney $U = 29{,}568, p < 0.001$) in the first year than in the second year following a fire, when conifer-seed resources would have been more depleted. Another feeding group that seems to depend on food provided by the burned trees includes the bark-probing woodpeckers, which eat primarily wood-boring beetles (Beal 1911). Woodpeckers are clearly responding to the increase in availability of cerambicid and buprestid beetle larvae (Evans 1964; Komarek 1969; Bock & Bock 1974; Fellin 1980; Harris 1982; Amman & Ryan 1991), which in some cases are themselves responding to the increase in availability of unburned wood that lies beneath the bark of fire-killed trees (Amman & Ryan 1991). Adult beetles in the genus *Melanophila* are, in fact, specialized to feed on fire-killed trees and are capable of using infrared sensors to detect and colonize burned forests more than 161 km distant (Evans 1964, 1966). Finally, aerial insectivores (flycatchers, swallows) relied on standing dead trees as perch sites from which they sallied into the open air space for their prey.

Because the pattern of relative bird abundances differed among sites, the relative suitabilities of sites probably also differed among bird species. The same conclusion is suggested by results of the partial correlation analysis, in which the specific elements associated with bird abundance differ among species.

Most (77%) of the bird species I detected in burned forests were migrants. With concern about declining populations of migrants (Askins et al. 1990), perhaps conservation biologists should be devoting more attention to the loss of early successional habitats born of "natural" disturbance by investigating the extent to which such habitats are necessary for the maintenance of viable populations.

Conservation and Management Implications

The Importance of Stand-Replacement Fires

Fires are clearly beneficial to numerous bird species and are apparently necessary for some. The same case has been made for plants, in which some species germinate and flower only within 1–3 years after a fire and then bank their seeds for storage until the next fire (Heinselman 1981). Fire is such an important creator of the ecological variety in Rocky Mountain landscapes (Arno 1980; Gruell 1983) that the conservation of biological diversity is likely to be accomplished only through the conservation of fire as a process. Fire is in fact ". . .the only natural agent that is sufficiently widespread, abundant, fast, and regular to hold plant successions in seral stages on a vast scale and, therefore, to maintain the diversity of animal life that is so dependent upon such successional vegetation" (Komarek 1966). Efforts to meet legal mandates to maintain biodiversity should, therefore, be directed toward maintaining processes like fire, which create the variety of vegetative cover types upon which the great variety of wildlife species depend (Hansen et al. 1991).

Unfortunately, we are not currently managing the land to maintain the kind of early successional seral stages that follow stand-replacement fires and, hence, many fire-dependent plant and animal species. Why not? First, prescribed fires in conifer forests are most often low-intensity, understory burns that are justified by the argument that, with past fire prevention, forest composition is now "unnatural" and that we need to reintroduce a native fire regime of frequent, mild, understory burns to restore forests and to prevent catastrophic crown fires, which are "destructive" and "unnatural" (Biswell 1968; Alexander & Dube 1982). This justification holds only for a very limited number of habitat types, however (for example, low-elevation ponderosa pine forests). Most of the forested landscape in the northern Rockies evolved under a regime of high-intensity, large fires every 50–100 years (Fischer & Bradley 1987), not under a regime of low-intensity, frequent understory burns. A study of fire history in the Selway-Bitterroot Wilderness showed that less than 10% of the forested land experienced nonlethal fire; most of the forest types experienced partly to completely lethal fires every 100–200 years (Brown et al. 1994). Although some might argue that all forest types have been subjected to fire suppression for too long and that unnaturally dense understory buildups are leading to unnaturally severe fires, the stand-replacement fires that currently consume forests that evolved under that regime (for example, the 1988 Yellowstone fires) are not at all unusual in intensity or extent (Romme & Despain 1989).

Second, current human population and human settlement trends allow for the retention of very few areas large enough to allow free-ranging fire, and almost none of those areas have prescriptions allowing stand-replacement fires to occur (Agee 1991). Even when there is plenty of space to let fires burn, the general response is to expend enormous resources to eradicate fire because of the damage it does to timber resources, the danger it poses to humans and their buildings, and—despite ample evidence to the contrary—the damage it may do to tourism because of the visual impact. Brown and Arno (1991) have addressed this growing predicament of putting fire back into the landscape while still operating within the economic, social, and political constraints that society continues to impose: It will not be easy.

Third, there is a lack of public education about the benefits of stand-replacement fires. The biological naivete surrounding the 1988 fires was astounding and did more to muster opposition than support for "let it burn" wilderness policies. The lack of understanding demonstrated by the public, especially prominent politicians, generated a good bit of the conflict over policy (Cutler 1988). Simple facts—for example, there exists a strong distributional association between some bird species and burned forests—should be used to garner support from the public for liberal prescribed-fire policies.

Fourth, forests are not being managed in ways that mimic natural processes. One could argue that the loss of burned forest acreage due to fire control has been compensated for, at least in part, by timber harvesting. Many people believe that the conditions present after a clearcut are basically the same as those present after a severe fire (Kohrt 1988; Maschera 1988; Eggleston 1989; Swift 1993). But conditions created by a stand-replacement fire are biologically unique, at least in terms of the biomass of standing, dead trees that remain and, to a much greater extent, in terms of ecosystem structure and function. Clearcutting is, in general, a poor substitute for fire because such timber harvesting does not retain some of the most important elements, such as standing, dead trees, that are integral components of the post-fire ecosystem and that probably contribute to unique successional pathways (Agee 1991; Hansen et al. 1991) and wildlife communities.

Stand-replacement fires should not be viewed as unnatural disasters that can (and should) be prevented (Kipp 1931). As Heinselman (1985) has argued, plans to maintain stand-replacement fire regimes are justified in at least the more remote of our public lands, and prescribed-fire regimes should not be limited to periodic, mild, understory burning in lower-elevation ponderosa pine forests. Managers must also be careful to mimic all aspects of natural disturbance (such as timing, frequency, and intensity) and not just introduce disturbance as such (Hobbs & Huenneke 1992). Finally, because the pattern of relative bird abundances differs among burns, managers probably need to provide a diversity of burned cover types, intensities, and maybe even a variety in landscape contexts of burns to provide for the variety of species that may depend on fire.

Post-fire Timber Harvesting

On public lands, managers should leave an adequate amount of standing, dead trees after a fire because of the species that depend on that forest element. The current tendency to expedite timber "salvage" sales on burned forest lands needs to be re-examined. Already, as much as 60% of all timber sales on some forests in the Northern Region of the U.S. Forest Service come from salvaged timber (Schwennesen 1992). These sales, which are often exempt from public notice or comment, are generally supported by a well-meaning but misguided public that believes "dead and dying timber ought to be harvested and put to use" (Schwennesen 1992).

If some bird species require burned forests for the maintenance of viable populations (which is strongly suggested by this study), then post-fire salvage cutting may be conducted too frequently to be justified on the basis of sound ecosystem management. In instances where a salvage cut is deemed necessary, managers who wish to mitigate such effects by leaving some of the standing dead trees should be aware that bird species differ in the microhabitats they occupy within a burn. Therefore, methods that tend to "homogenize" the stand structure (such as selective removal of all trees of a certain size and/or species) will probably not maintain the variety of microhabitats and, therefore, bird species that would otherwise use the site. Selective tree removal also generally results in removal of the very tree species (Table 4) and sizes (Table 5) preferred by the more fire-dependent birds. It may be best, instead, to take trees from one part of the burn and leave another part of the burned area untouched. That way, some of the guesswork associated with choosing what to leave is avoided. This is clearly an area that deserves additional research attention.

Implications for Live-Tree Harvesting Methods

It is unfortunate that the effect of a timber harvesting method on birds (and other vertebrates) is nearly always evaluated in terms of how much the bird community composition changes from before to immediately after harvest (Hutto et al. 1993; Hejl et al. 1995). The method that best mitigates immediate harvest effects (that produces the least change) is generally viewed as the best alternative. Instead, maybe managers should favor methods that minimize deviation not from the bird communities typically associated with the pre-cut forest, but from those associated with the series of post-fire successional communities anticipated to have eventually occurred on that particular plot of land. In this light, many of the "new forestry" thinning practices, which appear favorable in terms of mitigating the immediate effects of cutting, may not represent the best strategy in terms of minimizing the impact of timber harvesting on natural patterns and processes. This is because many of the newer harvesting practices in mid- to high-elevation conifer forests create structurally artificial stands of thinned trees, which may bring "unnatural" combinations of bird species together, eliminate the full range of seral stages, and, perhaps worst of all, reduce the prospect of fire in the future (Gruell 1980). Recent full-page ads by the timber industry in the northern Rocky Mountains (for example, Missoulian, 24 August 1994, p. A-10), have, in fact, emphasized the fire-prevention "benefit" of forest thinning. Such a consequence may be fine at the urban-forest interface. It may be a well-intentioned but misplaced goal, however, for forested wildlands.

Most selective harvesting and thinning methods also result in the loss of large trees, many of which are otherwise destined to become the kind of snags that many primary and secondary cavity nesters depend on for nesting purposes should a stand-replacement fire occur. The predominant use of already existing snags by cavity nesters in burned forests (Table 6) implies that excavation is much easier in those than in the plentiful but otherwise less suitable (sometimes case-hardened) standing, dead trees. Because the most suitable nest trees for cavity excavation are snags that are themselves old-growth elements, one might even suggest that many of the fire-dependent, cavity-nesting birds depend not only on forests that burn, but on older forests that burn. Clearly, the relationship between pre-fire forest structure and post-fire bird communities deserves more attention.

A comparison of the bird communities in recent clearcuts and recent burns (Fig. 1) reveals a fair amount of similarity in the face of some important differences between the two cover types (Table 3), due primarily to the presence of standing dead trees in the burned sites, which are used for feeding and/or nesting purposes by a large number of bird species (see also Davis 1976). I found an even greater overall similarity between clearcuts and burns that are in mid-successional stages, suggesting that, when considered over all post-harvest successional stages, clearcutting may come closer to matching the natural patterns of bird occupancy on a patch of land than do many (or most) other cutting practices. I must reiterate, however, that the relative abundances of many species differ quite markedly between recently burned and recently cut forests. Even in mid-successional burns and clearcuts, which showed a greater relative similarity in bird-community composition than the earlier stages did, there were still significant differences in the absolute abundances of a large number of individual species (for example, compare the two abundance estimates for Calliope Hummingbird, Red-naped Sapsucker [*Sphyrapicus nuchalis*), Clark's Nutcracker, and Cedar Waxwing [*Bombycilla cedrorum*]). Therefore, even though the bird communities in clearcuts begin to look similar to those in fire-disturbed forests after a decade or two (Fig. 1), the bird communities are still quite different (in an absolute sense) from those that occur after a natural fire. Perhaps the best alternative to traditional harvesting methods in forests that evolved under standard-replacement fire regime may be to conduct some sort of partial harvest, after which the remaining forest would be burned lethally.

Fire (and its aftermath) should be seen for what it is: a natural process that creates and maintains much of the variety and biological diversity of the Northern Rockies. Most current cutting practices neither create large amounts of standing dead timber nor allow forests to cycle through stages of early succession that are physiognomically similar to those that follow stand-replacement fires. Unless managers begin to couple lethal burning with their cutting practices in those forests that evolved under stand-replacement fire regimes, traditional land-management practices will not achieve the goals of ecosystem management.

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