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BIRD POPULATIONS BEFORE AND AFTER WILDFIRE IN A GREAT LAKES PINE FOREST

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ABSTRACT.—Birds in a 6.25-ha quadrat in a 73-year-old jack pine-black spruce forest (*Pinus banksiana-Picea mariana*) in Cook Co., Minnesota were intensively studied in June 1976. A wildfire burned through the area in August. The following spring we resurveyed the same quadrat to determine the first-year changes in bird populations. Species and guilds were compared by density, territorial space, existence energy, and importance values. Twelve species had territories in the study grid before the fire; six were not there the following spring, but eight additional species had established territories. Tree-foliage searchers had the greatest importance value before the fire and ground-brush foragers the greatest value afterwards. Density, total biomass, and combined existence energy of birds decreased after the fire by 50, 23, and 41%, respectively, but species using the area after the fire were 63% heavier on the average. Average energy consumption per unit of body weight was calculated to be 23% less after the fire. Fire apparently reduced the total food available for birds, but increased the kinds of food, especially at or near the ground.

Studies of forest systems immediately before and after wildfire are few. Lyon et al. (1978) noted the need for information on short-term responses after fire. We were presented with an opportunity to examine first-year responses of bird populations when a 6.25-ha study grid, intensively studied in June 1976, was accidentally burned on 21–28 August 1976. In May following the fire, we again censused all birds and vegetation in the same grid as before.

The study area is in northern Cook Co., Minnesota (UTM: 53397/6545) on the east shore of Devil's Walk Bay, Saganaga Lake, in the Boundary Waters Canoe Area Wilderness of Superior National Forest. The history and ecology of the vegetation of this area were described by Grigal and Ohmann (1975) and Heinselman (1973). The unburned community corresponded well to the jack pine-black spruce (see Table 1 for scientific names) forest type described by Ohmann and Ream (1972).

The area was severely burned in 1903 (M. L. Heinselman, pers. comm.). In spring 1976, the site supported an even-aged jack pine forest with aspen and black spruce in draws and depressions. Upland ground cover, other than mosses, was sparse. Balsam fir and black spruce, most less than 20 years of age, were present as a widely scattered understory.

Bailey (1978) classified this ecoregion as the spruce-fir section of the Laurentian Mixed Forest Province. Wildfires, generally occurring during dry periods under the influence of strong winds (Heinselman 1971, 1973), are common in this area. Patches of vegetation commonly escape fire, especially if partially protected by moist draws, bogs, or lakes. Larger overstory trees also frequently survive fire, even when most other vegetation above ground is destroyed. Dense stands of jack pine develop after fire, with many associated herb and shrub species that do not persist beyond a few years under the developing jack pine canopy.

MacArthur and MacArthur (1961), Karr (1968), Karr and Roth (1971), Willson (1974), Roth (1976) and others have demonstrated that bird diversity is closely related to vegetational structure. Heinselman (1971) and Loucks (1970) reported that plant species richness and structural complexity of communities are frequently increased by fire. Because fires do not burn evenly, and because species are differentially affected by fires, both the number of species and community diversity usually increase. Moreover, fire generally leads to a mosaic of different-aged communities within a larger forest, each with different composition (Heinselman 1970). Fire accents and further differentiates communities that are dissimilar because of edaphic or topographic

TABLE 1. Trees and shrubs 2.54 cm dbh and greater. Basal area was determined by quadrat (2 × 50 m) sampling in 1976 (pre-burn) and prism sampling in 1977 (post-burn). Frequency and density data are from 1976 quadrats. Density data are provided for two size-classes. Data are provided solely for descriptive purposes and, therefore, statistical analyses have been omitted. Species present but not sampled are designated "P."

	1976 (1977)				
	Basal area (m^2/ha)		Density (no./ha)		Frequency
Species	Alive	Dead	Less than 10.2 cm dbh	More than 10.2 cm dbh	(all sizes)
Alder (*Alnus rugosa*)	.04 (.04)	0 (0)	29	0	6.25
Balsam fir (*Abies balsamea*)	.9 (0)	0 (3.0)	378	0	6.25
Black ash (*Fraxinus nigra*)	P (P)				
Black spruce (*Picea mariana*)	23.3 (10.9)	1.6 (7.2)	1,629	815	100
Dogwood (*Cornus rugosa*)	P (P)				
Jack pine (*Pinus banksiana*)	43.4 (36.1)	2.9 (10.2)	291	1,484	62.5
Mountain ash (*Sorbus americana*)	P	(P)			
Mountain maple (*Acer spicatum*)	P (P)				
Paper birch (*Betula papyrifera*)	.04 (0)	0 (.7)	58	0	12.5
Pin cherry (*Prunus pensylvanica*)	P (P)				
Quaking aspen (*Populus tremuloides*)	4.2 (3.8)	0 (3.4)	0	58	6.25

variations. In this study, we examine the first-year effects of fire on bird populations within a relatively homogeneous, small area (6.25 ha) of a jack pine forest.

METHODS

In spring 1976, a 250 × 250-m (6.25 ha) quadrat was established in an upland, relatively homogeneous portion of a 73-year-old forest. The quadrat was subdivided into 50 × 50-m plots and each plot corner was flagged for reference. We sampled this grid over four days in early June, 1976 and five days in late May, 1977. Censuses were done on calm, clear days and were repeated until no additional species could be found. Bird censuses, taken in morning and evening, averaged three hours each and spanned the twilight period.

We censused birds by means of both spot-map (Williams 1936) and flush-plot (Kendeigh 1944) methods. Each line of the grid was walked slowly and locations and movements of birds were plotted on prepared forms. After all field work was completed, we compiled locations and movements for all censuses of each species on summary sheets from which territories were then estimated and sketched. Repeated plots of the same species in the same general location, singing, and movements when flushed only within a restricted area were taken as indication of territorial behavior. Other birds that were plotted that failed to meet these criteria were regarded as visitors or transients and were not included in the guild summaries. In all cases, these were species different from those with territorities in the study area. Density, territory size, and frequency (percent of 50 × 50-m plots covered, at least in part, by a territory) were determined for each species.

Curtis (1959) developed and refined the use of importance values for comparing the relative importance of plant species in a community. These values simultaneously considered numbers (density), distribution (frequency) and size (cover) of the combined individuals of a species relative to density, frequency and cover of all individuals of all species combined. This method of community analysis gained wide acceptance among forest and plant ecologists, and we believe it has application for animals, especially birds. By considering several criteria simultaneously, each measuring somewhat different characteristics of a species population, Curtis's method gives a more sensitive indication of resource usage. We calculated importance values on the basis of frequency, cover (sum of all territories of a species in the 6.25-ha study grid) and existence energy. Existence energy was calculated from the formulas developed by Kendeigh (1970). For this, mean monthly temperatures were taken from the National Weather Services weekly summary. Bird weights were averaged from published reports of adult weights (Stewart 1937, Poole 1938, Stegeman 1955, Tordoff and Mengel 1956, Johnston and Haines 1957, Graber and Graber 1962, and Murray and Jehl 1964).

Each of the three components of importance value of a species was calculated relative to the sum of the values for that component for all species that were defending territories in the community. Thus, the importance value of each species was the sum of three related, relative values based on all territorial birds. Importance values, as we use them, reflect numbers, distribution and territorial size, and energy required to maintain a species. They provide an abstract number, ranging from 0 to 300, that indicates one species' use of resources relative to other nesting birds.

Guild designations follow those of Bock and Lynch (1970). Diversity was calculated using H′ (base 10) index (Pielou 1975), to provide additional information on the changes in species richness and evenness combined (Hurlbert 1971, Rabenold 1978).

Small trees, shrubs and herbs were sampled in 125 stratified, random .1 m^2 quadrats, five in each of the 50 × 50-m subplots. Woody plants greater than 2.54 cm diameter breast height (dbh) were sampled in 25 strip quadrats, 2 × 25 m, one in each of the subplots, and by 25 random prism plot points (Husch 1963).

RESULTS

VEGETATIONAL CHANGES

Combined cover of trees before the fire was 98%; following the fire the total tree cover was 48%. On the ground, herbs and small woody plants, in contrast, had a combined cover of 28% before the fire and 51% the spring following the fire. Bryophytes, however, covered 83% of the ground before the fire and only 14% afterwards.

TABLE 2. Breeding bird importance values based on relative frequency, relative territory area, and relative existence energy. Visitors (V) and peripheral (P) species are cited but not included in calculations.

Guild	Species		Pre-burn	Post-burn
Flycatchers		TOTAL	0	10.4
	Olive-sided Flycatcher (*Nuttallornis borealis*)			10.4
	Tree Swallow (*Iridoprocne bicolor*)			V
Tree-foliage searchers		TOTAL	197.7	80.0
	Bay-breasted Warbler (*Dendroica castanea*)		35.0	8.9
	Blackburnian Warbler (*Dendroica fusca*)		73.4	37.9
	Boreal Chickadee (*Parus hudsonicus*)		24.0	9.2
	Pine Grosbeak (*Pinicola enucleator*)		V	
	Red-eyed Vireo (*Vireo olivaceus*)		30.6	P
	Rose-breasted Grosbeak (*Pheucticus ludovicianus*)			P
	Ruby-crowned Kinglet (*Regulus calendula*)		12.6	3.6
	Solitary Vireo (*Vireo solitarius*)		9.2	
	Yellow-rumped Warbler (*Dendroica coronata*)		12.9	20.4
Timber gleaners		TOTAL	31.5	24.2
	Brown Creeper (*Certhia familiaris*)		18.8	24.2
	Red-breasted Nuthatch (*Sitta canadensis*)		12.7	
Timber drillers		TOTAL	0	40.4
	Black-backed Three-toed Woodpecker (*Picoides arcticus*)			40.4
Ground-brush foragers		TOTAL	70.6	144.7
	Blue Jay (*Cyanocitta cristata*)			V
	Chestnut-sided Warbler (*Dendroica pensylvanica*)			P
	Common Grackle (*Quiscalus quiscula*)			V
	Gray-cheeked Thrush (*Catharus minimus*)			17.3
	Gray Jay (*Perisoreus canadensis*)		V	
	Hermit Thrush (*Catharus guttatus*)		7.7	
	Ovenbird (*Seiurus aurocapillus*)		56.2	
	Purple Finch (*Carpodacus purpureus*)			6.8
	Common Raven (*Corvus corax*)			V
	American Robin (*Turdus migratorius*)			17.7
	Dark-eyed Junco (*Junco hyemalis*)			45.9
	Spruce Grouse (*Canachites canadensis*)		V	
	Starling (*Sturnus vulgaris*)			V
	Swainson's Thrush (*Catharus ustulatus*)			10.9
	White-throated Sparrow (*Zonotrichia albicollis*)			46.1
	Winter Wren (*Troglodytes troglodytes*)		6.7	
	Common Flicker (*Colaptes auratus*)			V
		TOTAL	299.8	299.7
		Mean ($\bar{x}$)	24.4	21.4
		Variance	401.8	210.7

At least some members of all tree species survived the fire. Balsam fir, however, was eliminated except for a few stems in boggy sites, and paper birch was reduced to sprout regrowth from surviving roots (Table 1). Total species richness of all plants increased from 77 to 86.

Big-leaved aster (*Aster macrophyllus*) was the most important herb before the fire with a ground cover of 7%; afterward, this plant still covered 6% of the ground. Fireweed (*Epilobium angustifolium*), wild geranium (*Geranium bicknellii*) and fringed bindweed (*Polygonum cilinode*), not present before the fire, afterward covered 12, 16, and 36% of the ground, respectively.

BIRD RESPONSES

Territories of 12 species in three guilds were established in the study area before the fire; 14 species in five guilds had territories the following spring (Table 2). Eight of the species with territories in the burned forest were not present before the fire; the most important, based on importance values (see Table 2), were the White-throated Sparrow, Dark-eyed Junco and Black-backed Three-toe Woodpecker. Five species that had territories in the area before the fire were absent the following year. Six additional visiting species used the area after the fire whereas only three species visited

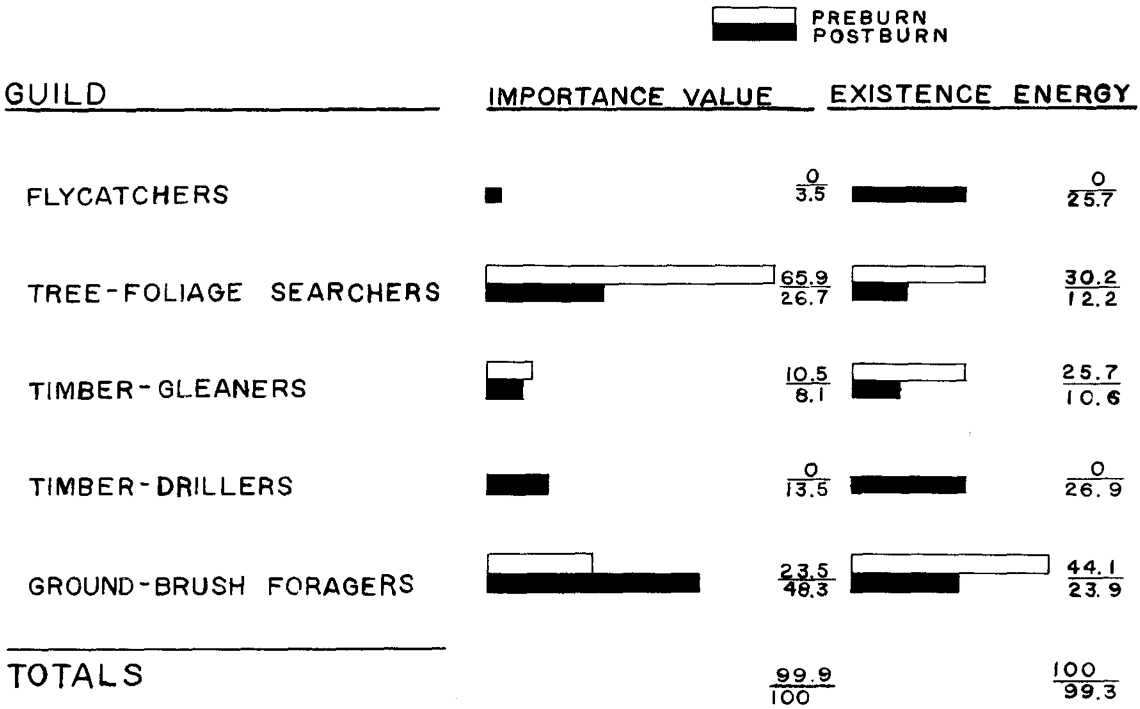

FIGURE 1. Comparison of guilds. A. Importance values, expressed as a percent of total importance for all guilds combined. B. Mean existence energy, expressed as mean existence energy per bird in a guild as a percent of total mean value for all guilds.

the area beforehand. None of the species was present both years. Three peripheral (seen or heard adjacent to the study area) species were tallied after the fire; of these, two had not been found in the unburned forest, whereas the third, the Red-eyed Vireo, was an important tree-foliage searcher in the unburned forest.

Tree-foliage searchers had the highest importance value of all guilds before the fire; the three species with the highest importance values were the Blackburnian Warbler, Bay-breasted Warbler, and Red-eyed Vireo. This guild proportionately suffered the greatest decline following the fire (Fig. 1). Among tree-foliage searchers, the Yellow-rumped Warbler was the only species that appeared to profit from the fire (Table 2).

The importance value of the ground-brush forager guild increased proportionately after the fire (Fig. 1). The Ovenbird represented nearly 80% of the total importance of this guild before the fire, but was absent after it. In its stead were six ground-brush foragers not present before the fire; most important were the White-throated Sparrow, Dark-eyed Junco, American Robin, and Gray-cheeked Thrush. The Hermit Thrush occurred only in the unburned forest. Five of the visiting species and one of the peripheral species seen after the fire were also members of this guild.

Density of territorial birds (pairs per 6.25 ha) decreased by over half, from 82 pairs before the fire to 39 pairs after (Table 3). Only flycatchers and woodpeckers increased in numbers; no representative species of these guilds was found in this unburned forest. The guild with greatest decrease after the fire was that of tree-foliage searchers, which dropped from 55 pairs to 17 pairs. A parallel decrease was found in timber gleaners, from 11 to 4 pairs; this decrease resulted from the absence of Red-breasted Nuthatches in the burned forest. Brown Creepers, the other species in this guild, increased from 1 to 4 pairs following the fire.

The density of ground-brush foragers scarcely changed following the fire, but species composition of this guild altered completely. Percent of ground-brush foragers, relative to all guilds, increased from 20 to 38% because of the overall decrease in bird density after the fire (Table 3).

H′ diversity was higher after the fire, 1.03 compared to .93. Evenness ($J' = H'/H'max$, where $H'max = Log_{10}S$, where S = species richness) increased slightly from .88 to .90. Perhaps more evident was the wider distribution of existence energy among guilds

TABLE 3. Summary of breeding bird data.

Guild	Species richness (no.)	Breeding density (pairs/ 6.25 ha)	Population biomass per 6.25 ha* (g)	Mean wt. per individual* (g)	H' diversity (base 10)	Total existence energy* (kcal/day)	Existence energy per bird-day* (kcal)	Visitors/ transients (species no.)
Flycatchers								
Pre-burn	0	0	0	—	0	0	—	0
Post-burn	1	1	221	31.6	0	23	21.3	1
Tree-foliage searchers								
Pre-burn	7	55	4,015	11.2	.722	616	11.2	1
Post-burn	5	17	1,218	10.8	.569	175	10.1	0
Timber gleaners								
Pre-burn	2	11	616	8.0	.292	103	9.5	0
Post-burn	1	4	209	7.7	0	36	8.7	0
Timber drillers								
Pre-burn	0	0	0	—	0	0	—	0
Post-burn	1	2	755	58.1	0	45	22.3	0
Ground-brush foragers								
Pre-burn	3	16	2,132	20.3	.333	265	16.3	2
Post-burn	6	15	2,823	28.2	.675	305	19.8	5
Total all guilds								
Pre-burn	12	82	6,763	12.7	.951	984	12.0	3
Post-burn	14	39	5,226	20.1	1.034	584	14.6	6

* Values calculated from our data and published data (see Methods).

(Fig. 1) and decreased variance of importance values of species after the fire (Table 2).

Total bird biomass, exclusive of eggs and young, calculated from our density observations and published weights (see Methods), decreased by 23% after the fire while mean bird weight increased from 12.7 to 20.1 g (Table 3). Most of the increase in bird size could be attributed to the decrease in the lighter tree-foliage searchers and an increase in the heavier ground-brush foragers, along with the addition of the more massive Black-backed Three-toed Woodpecker. Within the ground-brush forager guild, however, average bird weight also increased from 20.3 to 28.2 g after the fire.

Combined existence energy calculated for birds in the study area decreased by 41% after the fire, from 984 to 584 kcal per bird day. This decrease in energy consumption is, proportionately, far greater than the decrease noted above in biomass. Analysis by guild reveals that the tree-foliage searchers and timber gleaners consumed much less energy after the fire whereas total existence energy of all other guilds increased (Table 3).

A comparison of existence energy to population biomass gives insight into the efficiency of energy use by the birds. Overall, this ratio dropped, indicating that birds in the study area after the fire used energy more efficiently. Timber gleaners were least efficient; timber drillers were most efficient (Table 3). Where guilds were represented both before and after the fire, the comparison of the existence energy/biomass ratio is close, except for a small decrease in ground-brush foragers. The presence of fewer of the smaller, less efficient tree-foliage searchers and more of the larger, more efficient woodpeckers and ground-brush foragers accounts for the greater efficiency increase in energy use by birds in the burned forest.

DISCUSSION

Spatial and structural diversity of the vegetation in the study area increased markedly in the spring following wildfire. Upland and slope vegetation was most completely altered. Moss ground cover was replaced with a lush understory of herbs and jack pine seedlings. Some large trees survived and even most of those killed remained standing. In draws, many mature aspen and jack pine survived and aspen damaged by fire sprouted profusely. Aspen sprouts, together with jack pine seedlings and herbaceous regrowth created a dense understory that approached that of uplands and slopes. Other researchers also have reported rapid regrowth in coniferous forests after fire (Ahlgren and Ahlgren 1960, Sykes 1971). Trees were wind-thrown, especially in and around bogs. Brushy tangles were created. Otherwise, many of the bog communities were scarcely altered by fire.

Based on criteria developed by Ahlgren (1960), about 80% of the jack pine/feather moss communities were severely burned. Some draws, and most remaining jack pine communities, received a hard burn which consumed litter and duff and scorched tree crowns. Most draws, however, received only a light burn.

This study supports the general conclusions of Loucks (1970) and Heinselman (1971, 1973) that wildfire can increase plant diversity. Loucks, however, based his conclusions on changes after a greater elapsed interval. Similarly, Heinselman's conclusions on wildfire applied, primarily, to large areas. We found rapid increases in richness and structural diversity even within our small area.

Richness and evenness of birds increased in the breeding season after fire within the study area. Caswell (1976) and Huston (1979) noted that disturbance should disrupt dominant species and open opportunities for establishment of additional species or increases in others already present. This certainly happened and is seen in the bird data as increased evenness in species using the burned forest (Fig. 1) and decreased variance in the importance values for post-fire species (Table 2). Hagar (1960), Lawrence (1966), Bock and Lynch (1970), and others have reported similar increases in bird species following fire. Niemi (1978), however, reported an increase only in the woodpecker guild in another study in northern Minnesota where a burned community three years after a fire was compared to an unburned control. Blackford (1955) and Koplin (1969) also found more woodpeckers after fire. Miller and Keen (1960) noted that bark beetles in western conifers concentrated on fire-injured trees. In our area, the Black-backed Three-toed Woodpecker fed almost exclusively on severely burned jack pine, most of which appeared to be dead. Wood borers were abundant.

The increased richness in the ground-brush foraging guild resulted from a different set of species than those representing this guild before the fire. Total number of birds decreased slightly while species doubled, from three to six, and biomass and existence energy increased substantially. We interpret these data to suggest an increase in opportunity for ground-brush foragers after the fire. The observed increase in relative abundance of bird species with establishment of opportunistic species supports Tramer's (1969) conclusions. Buffington (1967) reported that soil fauna were more scarce one year after a fire in New Jersey, except for two species of ants. Numerous other studies have revealed similar findings (Lyon et al. 1978). Seeds were evidently abundant in the soil, judging from the growth of annual herbs; the lush regrowth of vegetation surely supported insects. Increased cover above the moss carpet may have provided attractive nest sites for some species but loss of moss cover and leaf litter probably is related to the disappearance of the Ovenbird.

In our study area, at least, flycatchers were not present in the unburned forest, but one pair established itself the year after the fire. Brown Creepers also favored the burned forest, perhaps because there were more nesting sites (Apfelbaum and Haney 1977). Nuthatches, on the other hand, may have disappeared because the fire eliminated older snags used for their nests.

Wiens (1975) reported 329–1,456 breeding birds per km^2 in various North American coniferous forests. Over the same areas, standing crop biomass averaged 65–283 g/ha. Bird densities in our study were extrapolated to be 1,314 individuals per km^2 before the fire and 642/km^2 afterward. Our calculations of standing crop biomass were 167 g/ha before the fire and 129 g/ha afterwards.

In North America, bird populations in spruce-hardwood and closed boreal forests, based on species richness and H′ diversity, are very stable compared to populations in other types of forests (Peterson 1975). Results of our study are based on relatively homogeneous vegetation, unlike the Peterson study. We have no data, however, on flux in bird populations in the absence of fire, and we know of no reported studies in which this has been examined in a local area in similar communities.

In his studies of birds in North American coniferous forests, Wiens (1975) reported that 17–27% and 30–46% of all individuals present belonged to the most abundant and second most abundant species combined with the first, respectively. We estimated dominance by relative importance value. Our most dominant species in the unburned forest, the Blackburnian Warbler, accounted for 24% of total relative importance. Combined with importance of the Ovenbird, the second most dominant species, the value was 43% of total dominance. In theory, importance value should be a more complete assessment of dominance and resource use because it is based on numbers as well as energy and spatial relationships. Importance, however, is more time-consuming to determine.

After the fire, species dominance relationships were altered from those described above. Dominance was shared by more species, as Caswell (1976) predicted. The two most important species, for example, were equally dominant based on relative importance. These were the White-throated Sparrow and the Dark-eyed Junco, each with 15% of total relative importance. Thus, our pre-burn dominance values for the two most important species were on the upper edge of the range reported by Wiens (1975) while the post-burn values were on the lower edge of his range, just as our pre-burn and post-burn density and biomass data were in the upper and lower limits of the ranges given by Wiens.

CONCLUSIONS

Data from bird populations in a small (6.25-ha) area studied intensively the year before and the year after wildfire burned through it, support the generalizations concerning effects of fire on plant diversity and responses in bird populations, most of which were based on larger areas over longer periods. Although density and biomass of the avifauna decreased after fire, species richness increased, not only in birds visiting the site, but also in those establishing territories. Using density, territorial cover and frequency data, we calculated importance values for each territorial species. With importance value as a measure of dominance, our data agreed well with published reports for bird populations in other coniferous forests and further supported our observation that wildfire increased evenness.

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Native Names of Mexican Birds.—Lillian R. Birkenstein and Roy E. Tomlinson. 1981. Resource Publication 139, U.S. Dept. of the Interior, Fish and Wildlife Service, Washington, DC. 159 p. Paper cover. This book provides a list of over 3,000 native Mexican bird names in taxonomic sequence representing nearly 1,000 species. An accepted English common name and all presently known Mexican names, in Spanish or Indian dialects, are listed for each species. Tribal origins of Indian names and the areas where particular names predominate are given. The list appears to be authoritative, comprehensive, and carefully worked out. Indexes to Mexican and English names.