# Effects of Fire on a Ruffed Grouse Population[1]

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FIRE is often a recurrent natural phenomenon which significantly influences animal populations and their environment. While much has been published on effects of fire upon soils and plant communities, there is a dearth of quantitative information about short-term impacts of fire on birds and mammals (Howard *et al.* 1959, Spencer and Hakala, 1964).

This paper evaluates the effect of a wildfire upon the ruffed grouse (*Bonasa umbellus*) population on a 4-square-mile study area in central Alberta. Two years of demographic information prior to the fire were available, and we were thus able to compare various population parameters before and after the fire, and also on burned versus unburned areas.

## METHODS

### Study Areas

This study was conducted near Rochester, Alberta, 60 miles north of Edmonton. Prior to the fire of 25 May 1968, the "Main"

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[1] A contribution of the Department of Wildlife Ecology, University of Wisconsin, and the Research Council of Alberta.

study area of 4 square miles was about 27 percent aspen-dominated upland, 20 percent old burn, 32 percent open bog, 11 percent spruce woods and 9 percent cultivated farmland. These major cover types have been analyzed in detail by Rusch *et al.* (*in press*), and are described only briefly below.

Tree cover on the upland was mainly aspen (*Populus tremuloides*) and balsam poplar (*P. balsamifera*) with some jack pine (*Pinus banksiana*). Scattered white birch (*Betula papyrifera*) and white spruce (*Picea glauca*) were also present. Dominant upland shrubs were alder (*Alnus crispa* and *A. rugosa*), rose (*Rosa* spp.) willow (*Salix* spp.), beaked hazel (*Corylus cornuta*) and low-bush cranberry (*Viburnum edule*). Ground cover included blueberries (*Vaccinium* spp.) bearberry (*Arctostaphylos uva-ursi*), and smooth wild strawberries (*Fragaria glauca*).

Areas of old burn were characterized by scattered large jack pines, small stands of surviving aspen, and extensive regeneration of aspen and willow. The spruce woods had dense stands of black spruce (*Picea balsamea*) with sphagnum moss and Labrador-tea (*Ledum groenlandicum*) as principal ground-cover species. Open bogs consisted of stunted tamarack (*Larix laricina*) and scrub birch (*Betula glandulosa*) on a predominately sedge (*Carex* spp.) mat.

Three other study areas were used to obtain comparative data for ruffed grouse populations on unburned sites. "Richardson's" area (102 acres) was all upland with aspen and balsam poplar providing most tree cover; beaked hazel, rose and alder were dominant shrubs. The "Jack Pine" area (118 acres) had both aspen and jack pine stands in about equal proportions. Richardson's and the Jack Pine area included study areas described by Meslow and Keith (1968) and Rusch and Keith (*in press*) as the "Landing trail" and "Moores-Pinewoods" study areas. "Halls" area (63 acres) was a mixture of typical black spruce and upland aspen communities with frequent intervening willow swales.

The 4-square-mile Main area was surveyed with 17 north-south lines, each having 33 stations, providing a rectangular grid of 660 x 330 feet for orientation. The three smaller study areas were each surveyed with four lines, providing a grid of 330 x 330 feet.

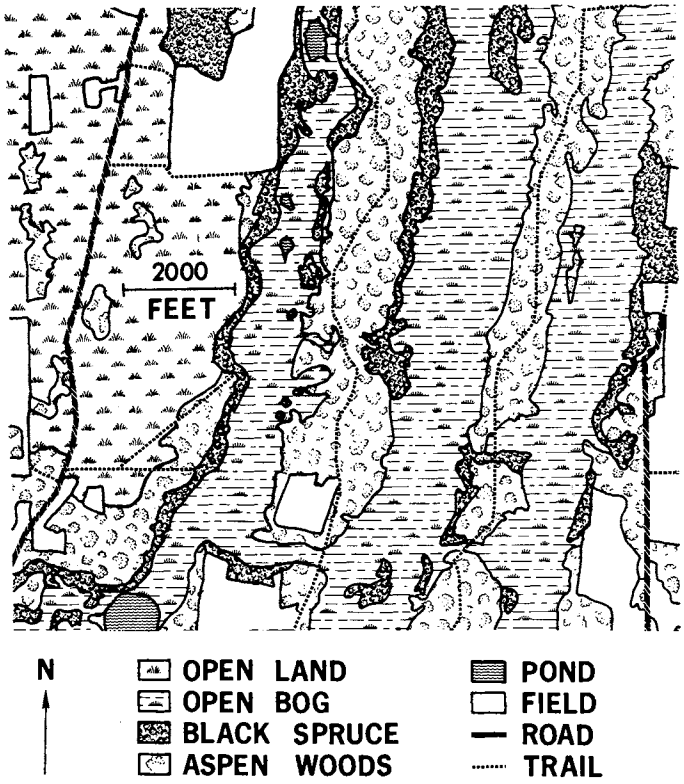


FIG. 1. Cover map of 4-square-mile Main study area before May 1968 fire.

## VEGETATION ANALYSIS

A cover map of the Main area (Fig. 1) had been made before the fire from aerial photographs taken in 1964 and from a vegetation survey in 1967 (Rusch *et al. in press*). The latter consisted of quarter-method (Cottam and Curtis, 1956) and line-intercept (Bauer 1943) samples of the woody vegetation at 460 stations. Point-centers were situated 50 feet south and 50 feet east of each grid station on the non-agricultural land. Distance to the nearest tree and sampling was measured in each quarter, as was the basal area in square inches for each stem. We also recorded the distance

to the nearest shrub and its height. Shrub and seedling cover and average height for each species was recorded along the 100 feet of line between each grid station and the quarter-method sampling point.

For vegetation analyses at drumming logs, we centered the point quarter at the drumming "stage" and also sampled 25 feet of line intercept along each cardinal compass direction. In addition we recorded all woody stems within a 10-foot radius of the drumming stage.

Post-fire analysis of living vegetation was conducted at 30 drumming-log sites and at 20 severely and moderately burned upland grid stations 16 months after the fire. Post-fire vegetation was compared to pre-fire vegetation at these same drumming logs and grid stations.

### Mapping the Fire

We walked the 17 grid lines on the Main study area immediately after the fire, and at each of the stations we recorded the intensity and distribution of the burn (Fig. 2). Burn intensity was arbitrarily recorded as "severe" burn if the ground cover was completely blackened and all shrubs and most trees were killed. The burn was classed as "moderate" if more than 50 percent of the ground cover was burned, but few trees and shrubs were killed. A "light" burn was where the ground cover was less than 50 percent burned and no trees and few shrubs were killed.

### Trapping and Marking Grouse

Drumming males were captured in the spring (mid-April to mid-May) with mirror traps (Tanner and Bowers, 1948). From early August to late October or early November, lily-pad traps (Low, 1935) with extension wings were used to trap all sex and age groups of grouse. Occasionally, grouse were caught in National live-traps set for snowshoe hares (*Lepus americanus*) and red squirrels (*Tamiasciurus hudsonicus*). Grouse were banded with one aluminum band giving our address and a reward notice, and three colored aluminum bands which facilitated field recognition of individuals. Grouse were also selectively marked by sex and age

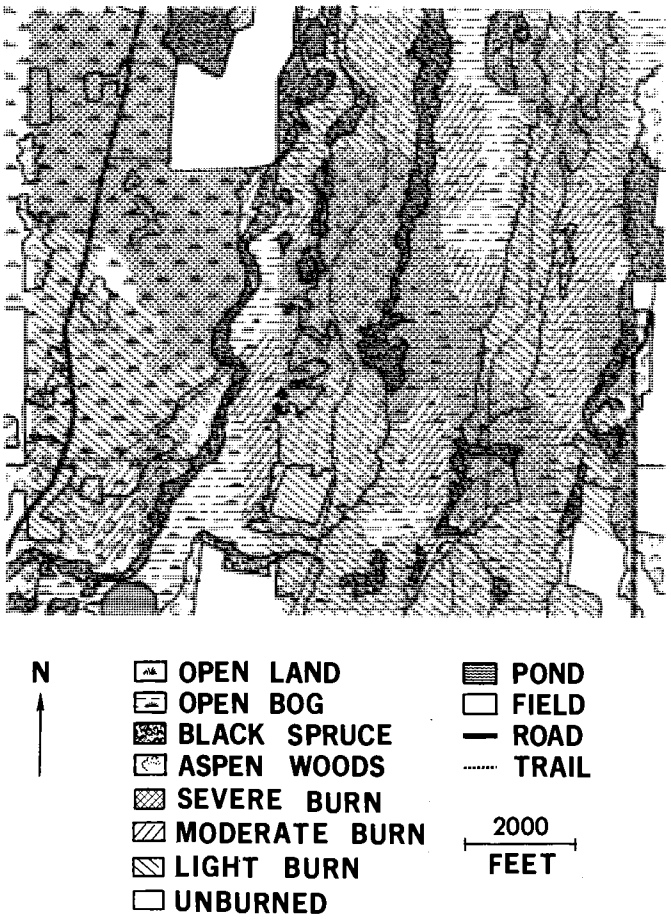


FIG. 2. Cover map of Main study area showing distribution and intensity of the fire. Severe burn—ground completely blackened, most trees, all shrubs killed. Moderate burn—ground more than 50 percent burned, few trees, most shrubs killed. Light burn—ground less than 50 percent burned, no trees and few shrubs killed.

with red (rhodamine-B), blue (methyl blue), yellow (picric acid), green (malachite green) and violet (methyl violet) dyes. The sex and age classes distinguished and marked were adult male, adult female, juvenile male, juvenile female, and juvenile of undetermined sex.

### Aging and Sexing Grouse

We aged grouse trapped in late summer by wing molt patterns (Bump *et al.* 1947). At other seasons, ages were determined by feather sheathing and ninth primary diameter (Dorney and Holzer, 1957). The bursa of Fabricius was used as an additional aging criterion with dead birds (Hale *et al.* 1954).

The length of central rectrices and tail band continuity were used to determine the sex of adult birds (Hale *et al.*, 1954).

### Estimating Grouse Populations

We used three methods to estimate numbers of grouse; (1) a complete inventory of drumming males in spring, (2) a "King" or strip-census usually conducted monthly by walking the grid lines, and (3) a Lincoln-index estimate in spring based on marked/unmarked ratios of grouse observed after the drumming males had been trapped and marked.

Drumming male counts were the most reliable indices because they provided a complete count of one cohort of the population. Marked/unmarked ratios were obtained by a crew of five men who systematically traversed the study areas.

Grid lines on the Main area were walked monthly (36 miles) and those on the small areas were walked twice monthly (2 miles each) to obtain grouse flushes for strip census estimates.

### Measurement of Reproductive Success

Random observations of brood size and number of hens with broods were important reproductive indices. Only broods judged to be completely counted by an intensive search were included in brood-size calculations. In summer, the flushing ratio of single adults to broods was used to compare productivity on burned versus unburned areas. Such ratios were obtained by systematic searches of selected blocks of aspen upland. The data from the unburned study areas were pooled and then compared with information from the burn. Age ratios of grouse captured during the fall in lily-pad traps provided further indices to productivity between areas and between years.

### Estimates of Grouse Mortality and Survival

Changes in average monthly brood sizes during the summer were used to determine brood mortality. When a "broody" hen or chicks were observed, we searched the immediate area to flush and count all grouse.

Declines in monthly strip-census estimates provided an index of mortality among adult-size grouse from September to May.

Over-winter mortality on the Main area was measured directly in the spring by an intensive search for grouse remains on 80 percent of the aspen upland and small portions of other cover types. In this search, (or "beatout") a crew of five men systematically traversed the area, 10-15 feet apart, marking their passage with tissue paper to minimize overlap and omission of any area. All observations of grouse were recorded; remains of grouse ("kills") were collected and their location marked with vinyl flagging tape. We tested the efficiency of the "beatout" by placing 157 intact grouse carcasses at randomly selected locations on the aspen upland. Thirty-seven "kills" were so placed in winter 1968-69 and 120 in 1969-70. The latter 120 carcasses were set out approximately 30 at a time at one-month intervals beginning 1 November. The beatout crew found 75 percent of the placed "kills" for which any remains were present in May of the 2 years.

Seasonal and/or annual replacement of marked males on drumming logs, and male recapture rates from spring to spring, were also used to measure survival.

## RESULTS AND DISCUSSION

### Description of Fire

Several fires occurred in previous years on the western one-third of the Main study area. The most recent of these fires, in 1964 and 1967, resulted in destruction of nearly all upland forest stands. The remainder of the Main area had not been burned for at least 30 years.

The pertinent meteorological factors leading up to the fire were a drier and warmer than usual late winter and spring in 1968.

April-May precipitation was 56 percent of normal; mean temperatures in February and March were 10°F above normal, resulting in a virtual absence of snow cover after late February.

The fire of May 1968 originated in burning brush piles on recently cleared land 1 mile east of the study area.

On the morning of 24 May, sparks fanned by strong southeast winds spread from the smouldering brush piles into the nearby bush. By noon the fire had reached a point 0.5 mile east of the Main area on a 0.75-mile front. During the night the blaze was arrested along a fireguard on the eastern border of the study area. Next morning 25 May, it jumped the guard and swept across most of the study area during the day.

## Effects of Fire on the Vegetation

Only a small portion of the upland (7 percent) on the Main area was untouched by fire (Fig. 2). Nearly 85 percent of the aspen dominated upland suffered moderate and severe burn. On the entire study area 16 percent was unburned, about 14 percent was light burn, and about 70 percent was moderate and severe burn (Fig. 2).

Pre-and post-fire samples at 20 stations in the upland aspen community indicated explosive postfire regeneration of aspen and balsam poplar (Table 1). The pre-fire coverage of these species was less than 1 percent while post-fire coverage rose to nearly 13 percent. Alder coverage was 36 percent before the fire, and only 4 percent one year after.

The density of living stems at stations also reflected the effect of the fire. Shrub stems per acre decreased from 3111 to 62, while trees decreased from 254 to 23 per acre. Conversely, sapling stems per acre increased from 166 to 1054, illustrating regeneration of aspen and balsam poplar.

The height of dominant shrubs (woody non-tree species) indicated that most present in 1969 samples were due to fire induced root-sprouting. Alder and willow averaged 8 and 6 feet tall, respectively, before the fire and 3 and 3.5 feet tall 1 year after the fire. Post-fire recovery of vegetation was also visibly evident (Figs. 3 and 4). Vegetation responses of the type noted here have

TABLE 1. WOODY VEGETATION IN UPLAND ASPEN COMMUNITY ONE SUMMER (1967) BEFORE THE FIRE AND ONE SUMMER (1969) AFTER THE FIRE. SAMPLING LOCATIONS WERE THE SAME EACH SUMMER. EXCLUDES SHRUB AND "SEEDLING" SPECIES CONTRIBUTING LESS THAN 1 PERCENT COVERAGE IN BOTH YEARS.

| Species | Shrubs and Seedlings[1] Line-intercept (percent coverage along 2,000 feet of line) | |
|---|---|---|
| | July 1967 | August 1969 |
| *Alnus crispa* and *A. rugosa* | 35.8 | 3.8 |
| *Viburnum edule* | 25.2 | 9.0 |
| *Rosa* spp. | 17.2 | 10.6 |
| *Rubus* spp. | 17.1 | 12.0 |
| *Salix* spp. | 3.8 | 2.8 |
| *Populus tremuloides* | 0.2 | 9.9 |
| *Populus balsamifera* | 0.1 | 2.4 |
| Totals | 99.4 | 50.5 |
| Living stems per acre | | |
| Trees | 254 | 23 |
| Saplings[2] | 166 | 1,054 |
| Shrubs | 3,111 | 62 |

[1] Shrubs—woody non-tree species.
"Seedlings"—tree species < 3 feet tall; mainly rootsprouts
[2] Saplings—tree species < 4 inches diameter, and ≥ 3 feet tall; 60 percent aspen, 40 percent balsam poplar in 1967; 50 percent aspen, 50 percent balsam poplar in 1969.

been previously documented (Lutz, 1956; Ahlgren and Ahlgren, 1960; and Spencer and Hakala, 1964).

Vegetation analyses were also conducted at 30 drumming-log sites in moderate and severe burn, and compared with pre-fire samples at these same drumming logs (Table 2). Line-intercept data showed pre- and post-fire differences similar to those which occurred at grid stations. Aspen coverage at logs increased from less than 1 percent to about 10 percent, while alder coverage decreased from 29 to 3 percent. Shrub stems per acre decreased from 2436 to 180 and tree stems decreased from 163 to 29 per acre. The height of shrubs at log sites, as at stations, indicated that regeneration had taken place. Alder and willow averaged 8 and 9 feet tall, respectively, before the fire and 3.5 and 3 feet 1 year after. Density of aspen and balsam poplar saplings increased from 207 to 338 per acre, considerably below the sixfold increase recorded at grid stations (Tables 1 and 2).

TABLE 2. WOODY VEGETATION AT 30 DRUMMING LOG SITES ONE SUMMER (1967) BEFORE THE FIRE AND ONE SUMMER (1969) AFTER THE FIRE. SAMPLED LOGS WERE THE SAME EACH SUMMER. EXCLUDES SHRUB AND "SEEDLING" SPECIES CONTRIBUTING LESS THAN 1 PERCENT COVERAGE IN BOTH YEARS

| Species | Shrubs and seedlings[1] Line-intercept (percent coverage along 3,000 feet of line) | |
|---|---|---|
| | July 1967 | August 1969 |
| *Alnus crispa* and *A. rugosa* | 28.7 | 2.9 |
| *Viburnum edule* | 10.3 | 5.0 |
| *Rosa* spp. | 9.8 | 9.3 |
| *Salix* spp. | 4.9 | 3.4 |
| *Rubus strigosus* | 4.4 | 8.4 |
| *Populus tremuloides* | 0.1 | 9.2 |
| Totals | 58.2 | 38.2 |
| Living stems per acre | | |
| Trees | 163 | 29 |
| Saplings[2] | 207 | 338 |
| Shrubs | 2,436 | 180 |

[1] Shrubs—woody non-tree species.
"Seedlings"—tree species < 3 feet tall; mainly root sprouts
[2] Saplings—tree species < 4 inches diameter and ≥ 3 feet tall; 85 percent aspen, 5 percent balsam poplar in 1967; 80 percent aspen, 10 percent balsam poplar in 1969.

## GROUSE DISTRIBUTION

Gullion and Marshall (1968) and others note that adult male ruffed grouse exhibit a strong year-round attachment to drumming-log sites. Rusch (unpubl.) observed a progressive decrease in the number of occupied logs from a peak in April-May (breeding season) to a low in August, followed by a lesser activity peak in mid-October. Increased use of logs in mid-October was apparently caused by young males establishing drumming sites after brood break-up in early September, and by a resurgence of territoriality among previously established adult males. We checked all known drumming logs on the Main area and on the three unburned study areas at regular intervals after the 1968 fire (Table 3A). Seasonal (June through October) *trends* in use of logs were similar on burned and unburned sites, with no suggestion of a fire effect on this aspect of grouse behavior. Numerical differences between areas and between years are considered later.

FIG. 3. An area of severe burn on aspen upland of Main study area immediately after the fire.

FIG. 4. An area of severe burn on aspen upland of Main study area 15 months after the fire.

TABLE 3. SEASONAL USE OF DRUMMING LOGS, AND DENSITIES OF RUFFED GROUSE ON ROCHESTER STUDY AREAS

| | | | Burned Main Area (730 Acres) | | | | Unburned Small Areas (283 Acres) | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | | | 1967 | 1968 | 1969 | 1970 | 1967 | 1968 | 1969 | 1970 |
| A. | Number of males on drumming logs per 100 acres of upland | April-May | 5.2 | 8.6 | 5.6 | 3.4 | 5.7 | 7.7 | 6.9 | 9.2 |
| B. | Occupied drumming logs per 100 acres | June-July | — | 5.9 | 2.6 | — | — | 5.8 | 1.9 | — |
| | | August | — | 3.4 | 1.2 | — | — | 1.5 | 1.5 | — |
| | | October | — | 6.1 | 4.8 | — | — | 6.1 | 6.9 | — |
| C. | Total number of grouse per 100 acres | October 7 | — | 12 | 18 | — | — | — | 33 | — |
| | | January 7 | — | — | 17 | 12 | — | — | — | 23 |
| | | April | — | — | 12 | 11 | — | — | — | 18 |

Locations of both pre- and post-fire drumming logs were mapped and numbers of logs within each category of burn intensity recorded (Table 4). There were no significant differences between pre- or post-fire distribution of occupied drumming logs ($X^2 = 2.85$, $P = 0.43$). Thus it appears that occupied drumming logs were similarly distributed within the upland forest stands before and after the fire, and that the intensity of the burn had no immediate effect upon the subsequent distribution of occupied logs.

We also examined the distribution of all ruffed grouse flushes during the strip-censuses and the systematic searches in spring on the Main area. No significant differences ($X^2 = 6.96$, $P = 0.08$) were noted between the proportion of pre-fire and post-fire flushes on each class of burn intensity (Table 4). Apparently, ruffed grouse were similarly distributed in the upland forest stands before and after the fire, both annually and seasonally.

### Grouse Numbers

Immediately after the fire, population estimates on the Main area showed a decline of 50 percent from 180 to 90 birds (Fig. 5). We believe this loss was mainly due to egress; during the fire we saw grouse successfully avoiding the flames, and observed no fire-killed grouse although our subsequent mapping of the burn and other field activities kept us on the area daily.

The population curve for May 1968 through April 1969 (Fig. 5) differs from other years in the absence of a July peak reflecting the annual increment of young to the population.

The small but statistically significant increase (Fig. 5) in the estimated numbers of grouse on the Main area in December and January 1968-69 over October 1968 estimates can only be attributed to ingress. Grouse populations were estimated to be 100 birds in spring 1969 on the Main area, about the same number as immediately after the fire. In 1969, estimates of 260 (77 adults) and 180 (79 adults) birds in July and August, respectively, indicated that reproduction was much improved over 1968 when during the same months there were 75 and 72 birds present, all adults. There were about 80 juveniles in the total estimated population of 156 in September 1969.

TABLE 4. DISTRIBUTION OF OCCUPIED DRUMMING LOGS AND TOTAL RUFFED GROUSE FLUSHES ON MAIN STUDY AREA IN PRE- AND POST-FIRE YEARS

| Intensity of Burn[2] | Percent of drumming logs in area[1] Pre-fire April 1966-May 1968 | Post-fire June 1968-May 1970 | |
|---|---|---|---|
| Unburned (7)[3] | 8 | 6 | |
| Light (7) | 5 | 1 | |
| Moderate (49) | 53 | 66 | |
| Severe (36) | 34 | 25 | |
| Sample size | 147 | 64 | $X^2 = 2.85$ ($P = 0.43$) |
| | Percent of total flushes in area[4] | | |
| Unburned | 9 | 6 | |
| Light | 10 | 16 | |
| Moderate | 44 | 49 | |
| Severe | 37 | 28 | |
| Sample size | 350 | 128 | $X^2 = 6.96$ ($P = 0.08$) |

[1] Includes only logs occupied April-May.
[2] Light burn.—50 percent of ground burned, no trees and few shrubs killed. Moderate burn.—50 percent of ground burned, few trees, but most shrubs killed.
Severe burn.—100 percent of ground burned, most trees, all shrubs killed.
[3] Percent aspen upland in each area.
[4] Flushes obtained from King census and systematic searches.

The general pattern of decline in numbers of grouse on the Main area from July to mid-November 1969 was similar to that of 1966 and 1967 (Fig. 5). On the other hand, during the fire year 1968 numbers on the Main area did not decline, but remained fairly stationary until after mid-winter.

While the shape of the annual population curve on the Main area apparently returned to normal 1 year after the fire, estimated number of grouse in both the springs of 1969 and 1970 were only 50 percent of the 1968 pre-fire population.

While we have no total population estimates for the small study areas before the fire which are comparable to those for the Main area, one available pre-fire index is the density of drumming males in spring (Table 3B). Before the fire, densities were similar on the Main and small study areas. However, post-fire densities of drumming males exhibited marked differences, particularly by spring 1970 when small-area densities were almost three times those on the Main area. Post-fire estimates of total grouse numbers also show higher

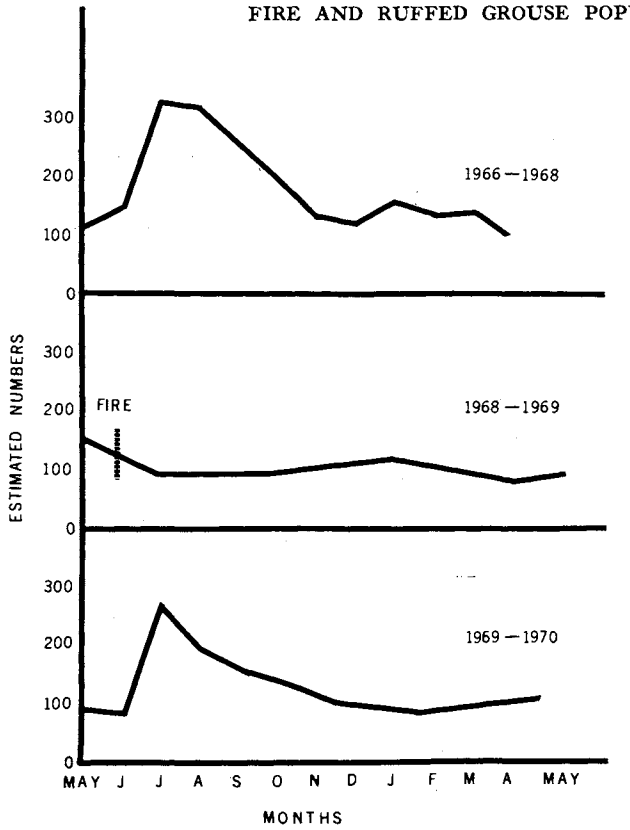


FIG. 5. Population curves for ruffed grouse on Main study area for 2 years before (average of 1966-67 and 1967-68) and 2 years after the May 1968 fire. Estimates based on King strip-censuses and marked/unmarked ratios in May. Pre-fire information from Rusch and Keith (*in press*).

densities on the small unburned areas than on the burned Main area (Table 3C).

## REPRODUCTION

There was about a two-fold increase in fall over spring populations during pre-fire years. In the year of the fire, however, numbers in spring and fall were similar (Fig. 5). The May 1968 fire occurred while hens were incubating, and undoubtedly destroyed many nests; 8 of 10 known to us were so lost. Evidence of renesting was limited

to observation of a 4-week-old brood in August, and to finding a 1-week-old chick at a sharp-shinned hawk (*Accipiter striatus*) nest in late July. Renesting is, of course, generally infrequent among ruffed grouse (Bump *et al.* 1947:364).

One index to productivity was the ratio of brood to single flushes during June-August (Table 5C). A fire effect is seen in the markedly smaller proportion of brood flushes on the Main area in 1968 than in pre-fire years; the 1969 data indicate complete recovery of production. Flushing ratios from unburned study areas during 1968 and 1969 corroborated these conclusions.

Poor reproduction during the year of the fire was also reflected in: (1) fall age ratios among grouse captured in lily pad traps, (2) yearling/adult ratios among drumming males the following spring (Table 5A), and (3) in overall fall trapping success.

Adults made up 14 percent of captures in lily-pad traps on the Main area during the two falls preceding the fire; 46 percent during the fire year, and 16 percent 1 year later (Table 5B). On the Landing Trail, a small unburned study area, adults comprised 27 percent of captures during the fire year, and 8 percent 1 year later.

Adults constituted 35, 38, and 27 percent of males captured at drumming logs during the three springs preceding the fire (Table 5A), but 74 in spring 1969. The proportion of adults among drummers trapped on the small study areas was 34 percent in 1969.

Trapping success was higher on the unburned Landing Trail area in 1968 (14 captures per 100 trap days) than on the Main area (7 captures per 100 trap days). Captures had averaged 20 per 100 trap days during the two preceding falls on the Main area. Increased trap success on the Main area in 1969 (11 captures per 100 trap days) was associated with an increased proportion of juveniles (Table 5B), further indicating that recruitment was improved over the previous year.

### Mortality and Survival

Overwinter mortality was estimated from (1) the number of kills found in May and (2) shrinkage of population estimates. The estimated total number of kills on the Main area accounted for approximately 38 and 55 percent of estimated prefire populations of October

TABLE 5. COMPOSITION OF RUFFED GROUSE POPULATIONS ON MAIN AND SMALL STUDY AREAS

| | | Main area (burned) | | | | Small areas (unburned) | | | |
|---|---|---|---|---|---|---|---|---|---|
| | | 1967 | 1968 | 1969 | 1970 | 1967 | 1968 | 1969 | 1970 |
| A. | Percent adults among males trapped on drumming logs (April-May) | 38(38) | 27(63)[1] | 74(41) | 60(25) | 38(14) | 27(20) | 42(18) | 30(24) |
| B. | Percent adults among grouse trapped in lily-pad traps (Aug.-Nov.) | 14(262) | 46[2](39) | 16(84) | — | — | 23(30) | 8(29) | — |
| C. | Percent of total flushes as broods (July-August) | 84(25) | 4[3](23) | 68(47) | — | — | 33(15) | 62(16) | — |

[1] Sample size.

[2] Significantly higher proportion of adults than during any other year on Main area, $X^2$ (1967 versus 1968) = 25.3 ($P < .001$), $X^2$ (1968 versus 1969) = 9.05 ($P < .001$), $X^2$ (1967 versus 1969) = 2.69 ($P = 0.10$).

[3] Significantly lower proportion of brood flushes than during all other years on Main area, $X^2$ rates (1967 versus 1968) = 30.4 ($P < .001$), $X^2$ rates (1968 versus 1969) = 25.0 ($P < .001$), $X^2$ rates (1967 versus 1969) = 2.01 ($P = 0.16$).

15 in 1966-67 and 1967-68; and 63 and 30 percent in 1968-69 and 1969-70. On the basis of shrinkage of population estimates, mortality between October 15 and the following May was 55 and 30 percent in 1966-67 and 1967-68; and 0 and 27 percent in 1968-69 and 1969-70. The results of these two methods are partially contradictory, but neither alone is satisfactory because of possible ingress, and high variances associated with population estimates. Obviously contradictory are the 1968-69 data when kills found in May amounted to 63 percent of October 15 populations but where no apparent population shrinkage occurred.

Population estimates (Fig. 5) suggest that ingress occurred during the winter of 1968-69 on the Main area, and some of the 54 kills estimated to be present in May 1969 could represent ingressing birds. Indeed, ingress must have occurred here since there were 54 kills even though no measurable population shrinkage occurred. Considering both sets of data, it seems unlikely that overwinter mortality was significantly different between the pre- and post-fire years.

Survival of the drumming-male cohort was determined directly through recapture rates of marked birds from spring to spring. On the Main area survival was 52 percent during 1968-69 and 40 percent during 1969-70, not significantly different from the 42 and 41 percent of the previous 2 years (Rusch and Keith, *in press*). Survival among drumming males on the unburned study areas was 49 percent for 1968–69 and 51 percent for 1969–70.

The high proportion of adults among drumming males on the Main area in spring 1969 may have been partially due to insufficient recruitment in 1968 to replace adults lost through normal mortality. During the "fall shuffle" (Bump *et al.* 1947 and Rusch and Keith *in press*) transient juveniles from unburned areas could have replaced lost adults, but they apparently did not. Note too that even by spring 1970 60 percent of the drumming males on the Main area were adults, while only 38 percent were adults on the small study areas. Of 71 males which disappeared from drumming logs on the Main area after spring 1968, only 13 (18 percent) were replaced. This compares with a pre-fire replacement of 21 of 56 birds (37 percent) on the Main area, over a similar period of time.

The most likely explanation for low post-fire replacement rate

rests with vegetation changes caused by the fire. Drumming sites on the area were apparently unattractive to juvenile males.

### Movement

Spring sex ratios among ruffed grouse were 50:50 in 1966-68 (Rusch and Keith, *in press*). As noted earlier, the 50 percent reduction of population on the Main area immediately following the fire in late May 1968 was evidently caused by egress. Pre-fire data indicated that the 63 drumming males comprised about one-third (35 percent) of the estimated total population of 180 birds, while a post-fire check (June 30) of drumming logs showed that at least 43 males remained and thereby comprised about one-half (48 percent) of the estimated total population of 90 birds. If we assume that the missing 20 males left the study area, and that both non-drumming males and females egressed at similar rates, then the sex ratio of emigrants would have been 36 males to 54 females. This sex specific egress would have left a resident population sex ratio of 54 males to 36 females (i.e., a 60 : 40 ratio). The 20 abandoned drumming logs were on severely burned sites, and in some cases there was total destruction of the log. Six of the 20 males which had used these drumming logs reappeared on nearby logs the following spring (1969). Male ruffed grouse typically exhibit strong attachment to the drumming sites year-round (Gullion and Marshall, 1968), while females are much more mobile (Rusch and Keith, *in press*). We have one record of a male grouse, trapped at a drumming log in spring 1968 before the fire that was shot 2.5 miles away in fall 1969. This bird likely moved after the fire and established a new drumming log close to where he was shot. Female ruffed grouse who lost nests in the fire probably had little subsequent attachment to the area. The unbalanced adult sex ratio which followed the fire persisted through spring 1969, when 41 drummers made up 45 percent of the estimated May population of 95 birds. Additional evidence for a high proportion of males is seen in fall-trapped samples during 1968 and 1969. In 1968, 75 percent of 18 adults were males, and in 1969, 78 percent of 14 adults were males, compared with an average of 57 percent males among adults in the previous 2 years. By spring 1970 the number of drumming males on the Main area had declined to 25 in an estimated population

of 100 birds, somewhat below the pre-fire figure of 35 percent. On the unburned study areas, drumming males comprised 30 and 34 percent, respectively, of the estimated spring 1969 and 1970 populations.

Ingress of ruffed grouse in winter 1968-69 was discussed in the preceding section.

We also examined the post-fire locations of marked drummers to determine if these birds moved to new logs with greater frequency than drumming males had before the fire. During the two springs prior to the fire, 17 of 40 (43 percent) surviving males recaptured at drumming logs had moved to new logs. During the two springs after the fire, 16 of 26 (61 percent) surviving males had moved to new logs. This is a highly significant ($X^2 = 13.4$, $P < .001$) difference which suggests further fire induced movement. There was no discernable pattern to the above movement of drumming males and as noted earlier, these movements did not significantly alter the post-fire distribution of occupied drumming logs. Grouse did not always move to logs in less intensively burned areas, as might be expected; indeed, four birds actually moved to more intensively burned sites. In the pre-fire sample the mean distance moved by 17 drumming males was 27 yards, while 16 moved a mean distance of 60 yards after the fire ($t = 4.76$, $P < .001$).

## SUMMARY AND CONCLUSIONS

The fire of May 1968 effected major changes in vegetation on the Main study area. Among these changes were reduced coverage of woody shrubs, and a spectacular increase in aspen 3 feet in height through root sprouting. Tree and shrub stem densities decreased, while poplar (aspen and balsam) <3 feet in height increased.

The salient responses by grouse populations to the fire and associated vegetational changes were as follows:

1. The distribution of ruffed grouse flushes and of occupied drumming logs on the Main study area was similar before and after the fire, evidently being little affected by areas of severe and moderate burn on the aspen upland.

2. A 50 percent reduction in numbers within 48 hours after the May 1968 fire was caused by egress. Females apparently outnum-

bered males by about three-to-two in the emigrating cohort. The immediate post-fire population level persisted with little change for approximately 1 year. The normal June-July increase in numbers did not occur on the burned study area in 1968 due to reproductive failure. Spring populations in 1969 and 1970 were similar on the burn, and at about 50 percent of the pre-fire 1968 level.

3. The nearly complete reproductive failure in 1968 was due to nest destruction by fire. It was reflected in the paucity of juveniles among (a) grouse trapped during August-November, and (b) males captured at drumming logs in spring 1969; it was also reflected in the greater ratio of brood to single flushes on unburned areas versus the burned Main area in summer 1968. Reproductive success returned to normal in 1969.

4. Overall mortality after the fire was similar to pre-fire mortality on the Main area.

5. The proportion of drumming males in the population rose from 35 percent pre-fire to at least 48 percent post-fire. This was caused by the differential egress of females noted above. The abnormally high percentage of drumming males persisted until spring 1970 when the proportion of drummers dropped to 25 percent of the total population.

6. A progressive decrease occurred in the number of drumming males on the burned area from spring 1968 to 1970. This resulted from non-replacement of males lost through normal mortality. By spring 1970, the density of drumming males on unburned study areas was almost three times that on the burn, whereas pre-fire densities had been similar.

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