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# Spruce Grouse populations in successional lodgepole pine

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Spruce Grouse *Dendragapus canadensis* were studied on a 247 ha main study area from 1965 to 1985 and on 31 additional areas (25.9–61.3 ha) in 1984 in southwestern Alberta. Numbers of cocks and/or hens were estimated annually with the use of transects, dogs, and/or playbacks of a hen's aggressive call. In addition, radio transmitters were placed on 28 cock and 65 hen Spruce Grouse on the main study area during 1982–84. Results showed that production (chicks per hen) and recruitment (yearling proportion) both declined between 1965 and 1985 ($P < 0.05$) on the main area when mean tree height increased from 7.3 m to 10.6 m. Radio-marked cock and hen Spruce Grouse selected habitats with relatively short trees, high tree cover, sparse shrub cover, and low densities of *Populus* spp., *Pinus contorta* and *Picea glauca*. Densities of territorial cock Spruce Grouse on 31 additional areas were negatively correlated with canopy height ($P = 0.015$). Overall, results indicated that densities of Spruce Grouse may be related to the successional stage of lodgepole pine forest.

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## Introduction

Succession can refer to a gradual progression between transition stages of habitat which ultimately results in a stable climax community. Lodgepole pine *Pinus contorta* forest in North America is often considered to be a successional habitat (Boag and Schroeder 1987). Without disturbance, lodgepole pine generally changes toward a mature western spruce-fir forest (*Picea-Abies*) (Kuchler 1964). However, perturbations in the form of fire often maintain the habitat in its fire-adapted lodgepole pine stage.

The Spruce Grouse *Dendragapus canadensis* is considered a typical species of boreal forests in North America. Both intrinsic and extrinsic factors, including habitat, may influence the population fluctuations of Spruce Grouse (Boag and Schroeder 1987). However, a direct relationship between changes in both habitat and populations of Spruce Grouse has been difficult to document.

Our objective was to examine the relationship between Spruce Grouse populations and lodgepole pine forests in southwestern Alberta. To strengthen the results, three relatively independent analyses were conducted: (1) the possible relationship between production/recruitment and habitat was examined for a study area undergoing successional changes between 1965 and 1985, (2) the habitat used by radio-marked Spruce Grouse between 1982 and 1984 was compared with habitat at random locations, and (3) numbers of territorial cocks were examined on 31 areas characterized by different habitat types.

## Methods

Spruce Grouse were counted (Boag and McKinnon 1982, Boag and Schroeder 1987), captured (Zwickel and Bendell 1967, Schroeder 1986), and banded (Boag et al. 1979) annually between 1965 and 1985 on the "main" 247 ha study area in southwestern Alberta

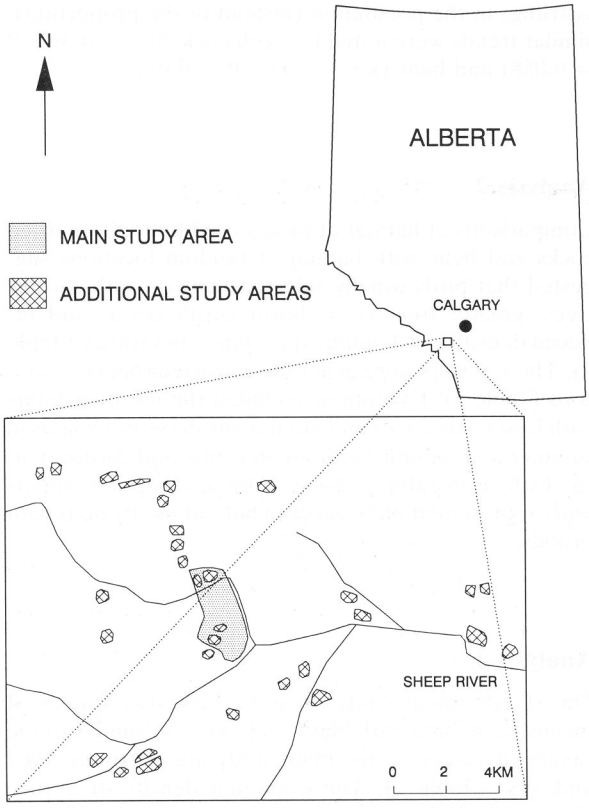


Fig. 1. Distribution of main study area and 31 additional study areas for research on Spruce Grouse in southwestern Alberta.

(50°89′N, 114°59′W) (Fig. 1). Although the forest was dominated by lodgepole pine, other species such as white spruce *Picea glauca*, poplar *Populus* spp., and willow *Salix* spp. were common.

Relationships between habitat and Spruce Grouse were examined in different ways. First, changes in forest structure between 1967 and 1984 on the main study area were examined by measuring canopy height (m), canopy coverage (%), and stem density of pine, spruce, poplar, and willow on 225 randomly selected 50 $m^2$ plots in 1967 (McCourt 1969) and 132 plots in 1984 (Boag and Schroeder 1987). The number of chicks surviving to at least 5 weeks of age (Smyth and Boag 1984) and the proportion of yearlings in the population were examined for the 1965–85 period when successional changes in habitat were observed.

Table 1. Habitat on main study area for Spruce Grouse in southwestern Alberta for 225 locations in 1967 (McCourt 1969) and 132 locations in 1984 (Boag and Schroeder 1987).

| Variable | 1967 ($\bar{x}$)[a] | 1984 | |
|---|---|---|---|
| | | ($\bar{x}$) | (SD) |
| Tree height (m) | 7.5 | 10.6 | 2.6 |
| Tree cover (%) | 47 | 64 | 18 |
| Density (stems 50 $m^{-2}$) | | | |
| Willow | 1.8 | 0.6 | 1.9 |
| Poplar | 0.1 | 1.3 | 5.4 |
| Pine | 24.1 | 17.6 | 10.7 |
| Spruce | 1.5 | 6.5 | 7.2 |
| Slope (°) | 8.9 | 8.7 | 3.2 |

[a]Standard deviations were not available for data collected in 1967.

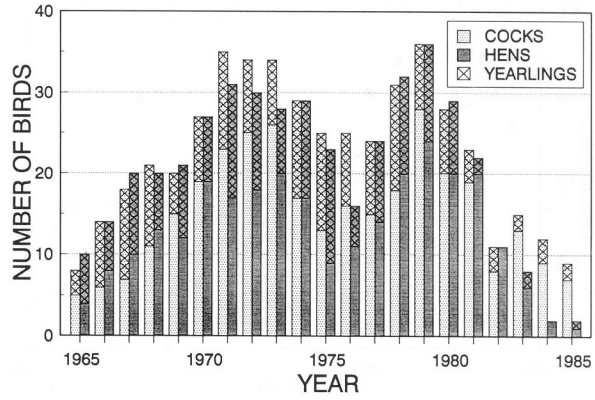


Fig. 2. Numbers of adult and yearling Spruce Grouse seen between 16 May and 15 August on the main study area in southwestern Alberta, 1965–85.

Second, habitat use was analyzed for Spruce Grouse harnessed with radio transmitters and tracked with a hand-held Yagi antenna. Twenty-eight cock and 65 hen Spruce Grouse were tracked between 1982 and 1984 in all seasons including winter (16 October–31 March), spring (1 April–15 May), summer (16 May–15 August), and autumn (16 August–15 October). These seasons were separated as a result of analyses of behavior, such as movement and dispersion within a season (Herzog and Boag 1978), and timing of migration and dispersal (Herzog and Keppie 1980, Schroeder 1985). Habitat data at random ($n$ = 132) and observed (453 cock and 929 hen) locations were compared to provide an indication of preferences.

Third, because previous examinations of habitat were basically a posteriori, we obtained habitat data from 31 "additional" sites ranging in size from 26 to 61 ha in 1984 (Fig. 1) and compared these with estimates of numbers of cock Spruce Grouse. The areas chosen were homogeneous within stands, but different between stands. The forests were dominated by lodgepole pine or white spruce of differing height, age, slope, aspect, elevation, and/or fire history. We counted grouse on each block of habitat by using a playback of the hen's aggressive call which prompted a response from both hens and cocks (Nugent and Boag 1982). All observed Spruce Grouse were captured and banded or identified. Playbacks were conducted at a minimum of 12 locations separated by 150 m on each area. The method was particularly effective for enumerating territorial cocks

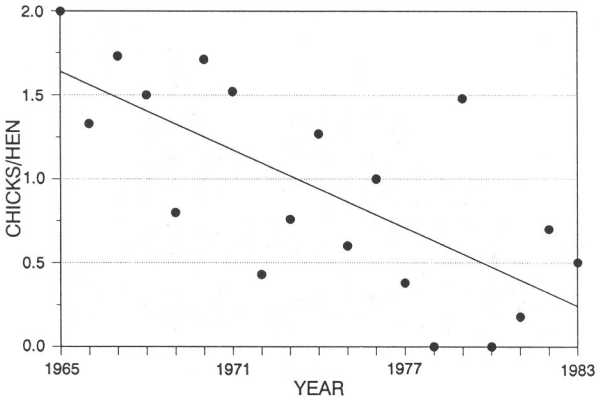


Fig. 3. Mean numbers of young Spruce Grouse at 5+ weeks of age per hen on the main study area in southwestern Alberta, 1965–83. Only hens with known reproductive fates were included in the analysis ($r = -0.686$, $P = 0.001$).

(MacDonald 1968, Boag and McKinnon 1982, Boag and Schroeder 1987, Schroeder and Boag 1989).

Average measurements for attributes of the habitat on each of the 31 additional study areas were compared with estimated numbers of territorial cocks on the same areas with linear regressions. In addition, habitat at each playback location was examined in relation to the presence or absence of cocks (as determined by playbacks) with logistic regressions. All analyses were conducted with SAS (SAS Institute Inc. 1985).

# Results

## Analysis 1

Measurements of habitat on the main study area at randomly selected sites in 1967 and 1984 suggested that changes occurred in several habitat variables (Table 1). In general, tree height, tree cover, and spruce density increased and pine density decreased. All these changes were consistent with expected successional changes.

Although spring numbers of Spruce Grouse fluctuated dramatically between 1965 and 1985 on the main study area, trends in population changes were not consistent (Fig. 2). However, because grouse numbers may fluctuate for several reasons besides changes in habitat (Boag and Schroeder 1987), other characteristics of the population were also examined. Productivity (average number of chicks fledged per hen) declined between 1965 and 1983 (Fig. 3) and recruitment (proportion of yearlings in population) declined between 1965 and 1985 (Fig. 4). Results for 1984 and 1985 were not included in analyses of productivity because they were based on extremely low sample sizes (Fig. 2). When recruitment was examined as the absolute number of yearlings in the population (instead of the proportion), similar trends were noted for both cocks ($r = -0.365$, $P = 0.058$) and hens ($r = -0.427$, $P = 0.031$).

## Analysis 2

Comparisons of habitat at places used by radio-marked cocks and hens with habitat at random locations suggested that birds usually selected habitats with shorter trees, greater tree cover, lesser shrub cover, and reduced densities of *Populus* spp., pine, and spruce (Table 2). These results were generally consistent between seasons (Table 3). Exceptions included the use of habitats with lesser tree cover and greater shrub cover by hens in summer and habitats with greater pine and spruce density by hens in autumn. Some of these exceptions apparently represented differences in habitat use by hens with broods.

## Analysis 3

On 31 additional study areas in 1984, the ranges of means for habitat variables (Table 4) were similar to the ranges of values on the main study area between 1967 and 1984 (Table 1). The estimated density of Spruce Grouse on these blocks ranged from 0 to 28 cocks per 100 ha. Higher numbers of cocks were positively correlated with lower canopy heights (Fig. 5).

When the specific habitat at each of 422 places where grouse were searched for was examined with a logistic regression (regardless of study area designations), similar habitat relationships were detected. Habitat at locations where cocks were located had shorter canopies, lower densities of *Populus* spp., and higher densities of spruce than locations where grouse were not detected (Table 4).

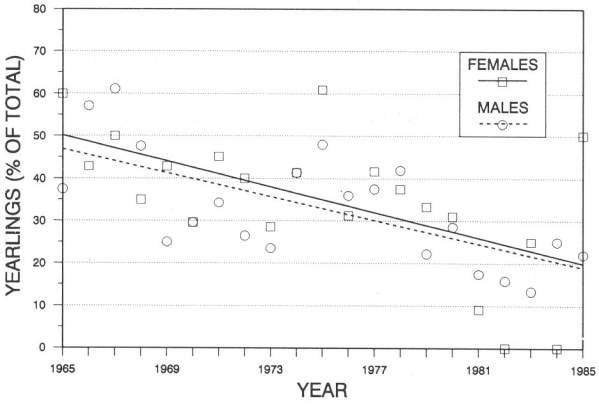


Fig. 4. Proportion of yearling cock ($r = -0.637$, $P = 0.001$) and hen ($r = -0.539$, $P = 0.007$) Spruce Grouse on the main study area in southwestern Alberta, 1965–85.

Table 2. Comparisons of habitat variables at observed locations of cock ($n$ = 453) and hen ($n$ = 929) Spruce Grouse with habitat variables at random locations ($n$ = 132) in southwestern Alberta during 1982–84. *P < 0.05; **P < 0.01; ***P < 0.001.

| Variable | Random | | Males | | Females | |
|---|---|---|---|---|---|---|
| | x̄ | SD | x̄ | SD | x̄ | SD |
| Tree height (m) | 10.6 | 2.6 | 9.6*** | 1.2 | 9.5*** | 1.5 |
| Tree cover (%) | | | | | | |
| Tree | 64 | 18 | 69 *** | 12 | 68 *** | 13 |
| Shrub | 33 | 26 | 27 ** | 19 | 27 *** | 17 |
| Density (stems 50 $m^{-2}$) | | | | | | |
| Willow | 0.6 | 1.9 | 0.3 | 1.3 | 1.4** | 3.1 |
| Poplar | 1.3 | 5.4 | 0.2*** | 1.1 | 0.4*** | 2.0 |
| Pine | 17.5 | 9.8 | 14.0*** | 6.1 | 16.9* | 6.5 |
| Spruce | 6.5 | 4.9 | 5.3** | 3.7 | 6.1 | 4.1 |

## Discussion

On the main study area, productivity and recruitment of Spruce Grouse declined between 1965 and 1985, but numbers of breeding adults showed no consistent trend. It was apparent from both banding and population information that most recruits (particularly females) were produced in habitats off the main study area. Consequently, the inconsistent trends in population size may have been due to changes in productivity on adjacent sites in addition to changes on the main study area.

Comparison of productivity with population changes in the following year showed a positive relationship during years with relatively low populations and no relationship during years with high populations (Boag and Schroeder 1987). The lack of a relationship would suggest that intrinsic regulatory mechanisms such as territoriality are important considerations for determining population abundance while a positive relationship would suggest that extrinsic regulatory mechanisms such as predation, production, and recruitment are more important (McKinnon 1983).

Support for a relationship between habitat and populations of Spruce Grouse was obtained from the results of the three different analyses in this study. First, both production and recruitment declined between 1965 and 1985 on the main study area, at the same time as the habitat was undergoing dramatic successional changes such as an increase in tree height. Second, radiomarked Spruce Grouse on the main study area apparently selected habitats with relatively short and/or sparse canopies throughout the year. Third, on the 31 additional study areas Spruce Grouse were more common in relatively short forests of lodgepole pine. Although this evidence is based on correlations, all three analyses provide relatively independent indications of the greater use by Spruce Grouse of young and/or short forests.

Some characteristics of each forest could be attributed to the date of previous fires, topography, elevation, and aspect. Together, these factors added to the habitat heterogeneity of forests in this region, and consequently the diversity of Spruce Grouse populations. These results do not imply that Spruce Grouse selected forests with a particular height; many other variables may be related to canopy height including the quantity and composition of grasses, forbs, and shrubs. However, they do suggest that Spruce Grouse may be adapted to the successional stage of habitat.

The probability that Spruce Grouse are most numerous in short and/or young forests suggests that lodgepole pine forests could be burned and/or harvested in

Table 3. Examination of seasonal habitat use by Spruce Grouse and random habitat in southwestern Alberta during 1982–84.

| Variable | Random | Winter | | Spring | | Summer | | Autumn | |
|---|---|---|---|---|---|---|---|---|---|
| | | Cocks | Hens | Cocks | Hens | Cocks | Hens | Cocks | Hens |
| Sample size | 132 | 90 | 494 | 136 | 187 | 193 | 110 | 34 | 138 |
| Tree height (m) | 10.6 | 9.9 | 9.6 | 10.0 | 9.9 | 9.2 | 9.4 | 9.4 | 8.6 |
| Tree cover (%) | | | | | | | | | |
| Tree | 64 | 68 | 69 | 67 | 67 | 73 | 60 | 65 | 69 |
| Shrub | 33 | 29 | 25 | 25 | 25 | 28 | 33 | 29 | 29 |
| Density (stems 50 $m^{-2}$) | | | | | | | | | |
| Willow | 0.6 | 0.7 | 1.6 | 0.3 | 1.0 | 0.2 | 0.5 | 0.3 | 1.6 |
| Poplar | 1.3 | 0.2 | 0.4 | 0.2 | 0.4 | 0.3 | 0.7 | 0.2 | 0.6 |
| Pine | 17.5 | 15.1 | 17.3 | 13.3 | 12.9 | 13.7 | 8.9 | 15.2 | 26.8 |
| Spruce | 6.5 | 2.1 | 5.4 | 4.5 | 4.0 | 7.4 | 4.8 | 4.4 | 12.4 |

Table 4. Habitat in relation to estimated densities of territorial cock Spruce Grouse at 422 locations on 31 additional Spruce Grouse study areas in southwestern Alberta during 1984 (Boag and Schroeder 1987).

| Variable | Means for 31 areas | | | Linear[a] | | Logistic[b] | |
|---|---|---|---|---|---|---|---|
| | $\bar{x}$ | SD | Range | r | P | $\chi^2$ | P |
| Tree height (m) | 10.1 | 2.1 | 6.0–15.0 | –0.43 | 0.015 | 6.09 | 0.014 |
| Tree cover (%) | | | | | | | |
| Tree | 61 | 11 | 40–80 | 0.11 | 0.544 | 0.38 | 0.539 |
| Shrub | 26 | 17 | 10–80 | –0.26 | 0.102 | 1.07 | 0.301 |
| Density (stems 50 $m^{-2}$) | | | | | | | |
| Willow | 0.3 | 0.8 | 0–3 | 0.01 | 0.998 | 0.24 | 0.624 |
| Poplar | 1.1 | 3.0 | 0–15 | –0.29 | 0.088 | 4.22 | 0.040 |
| Pine | 15.5 | 11.4 | 0–55 | 0.26 | 0.102 | 2.64 | 0.104 |
| Spruce | 3.7 | 5.0 | 0–26 | 0.21 | 0.223 | 11.78 | 0.001 |
| Slope (°) | 6.4 | 4.1 | 0–16 | –0.16 | 0.386 | 1.83 | 0.176 |

[a]Linear regression based on means for each of 31 study areas.
[b]Logistic regression based on presence/absence data for 422 locations througout 31 study areas.

order to improve the habitat for Spruce Grouse. However, we do not yet understand the relationship between Spruce Grouse and young forests. For example, while canopy height may be an important indicator of forest quality, what factors are important in influencing the reproductive success and/or recruitment pressure of Spruce Grouse?

One possibility is that as forest canopy increases in both coverage and height, grass and forb cover may be adversely affected by increased shading. As a consequence of reduced grass and forb cover (and a decrease in associated insects), productivity of Spruce Grouse may be adversely affected (Keppie and Herzog 1978, Redmond et al. 1982). In addition, both cock and hen yearlings may be less likely to settle in areas with inadequate nesting cover.

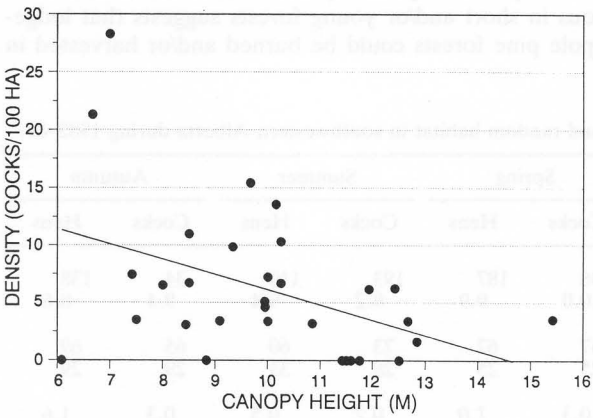


Fig. 5. Canopy height and estimated density of territorial cock Spruce Grouse on 31 additional study areas in southwestern Alberta in 1984 (r = –0.43, P = 0.015).

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