Population fluctuations in spruce grouse: what determines their numbers in spring?

D. A. BOAG AND M. A. SCHROEDER[1]

Department of Zoology, University of Alberta, Edmonton, Alta., Canada T6G 2E9

Received January 14, 1987

BOAG, D. A., and SCHROEDER, M. A. 1987. Population fluctuations in spruce grouse: what determines their numbers in spring? Can. J. Zool. **65**: 2430–2435.

The number of spruce grouse (*Falcipennis* (*Canachites*) *franklinii*) present in the spring population on a 247-ha block of pine-dominated habitat in southwestern Alberta was counted annually over a 21-year period. During the first 5 years of this study, the population increased steadily from 7.3 to 16.6 grouse/100 ha. Subsequently, for a period of 11 years, numbers were relatively stable at higher densities (19.0–29.1 grouse/100 ha). During the last 5-year period, the population declined to levels lower than at the onset of the study (16.6–4.9 grouse/100 ha). Year to year fluctuations in the size of this population were considered in the light of two hypotheses put forward to explain such fluctuations (spacing behaviour and breeding success). We concluded that both hypotheses were needed to explain our observations. During those years when spring population size fell below the mean number of grouse recorded over the 21-year period (17.8/100 ha), there was some evidence that breeding success in one year may have influenced population size the following spring but we found no evidence that spacing behaviour was important in limiting numbers under these conditions. On the other hand, when the size of the spring population was greater than the mean there was no evidence that breeding success influenced changes in population size the following spring, but there was evidence that spacing behaviour was limiting recruitment. The long-term change in population size appeared to be tied to the status of the fire sere inhabited: maturation of the forest (principally an increase in the height) was accompanied by a decline in population size.

BOAG, D. A., et SCHROEDER, M. A. 1987. Population fluctuations in spruce grouse: what determines their numbers in spring? Can. J. Zool. **65** : 2430–2435.

Le nombre de Tétras du Canada (*Falcipennis* (*Canachites*) *franklinii*) présents au sein de la population de printemps a été déterminé chaque année durant 21 ans dans un bloc de 247 ha d'une forêt de pins du sud-ouest de l'Alberta. Au cours des 5 premières années de l'étude, la population a augmenté progressivement de 7,3 à 16,6 tétras/100 ha. Ensuite, durant une période de 11 ans, les nombres sont restés relativement élevés et stables (19,0–29,1 tétras/100 ha). Durant les 5 dernières années, la population a accusé un déclin jusqu'à atteindre une densité plus faible que celle qui prévalait au début de l'étude (16,6–4,9 tétras/100 ha). Les fluctuations annuelles de densité de cette population ont été examinées à la lumière de deux hypothèses (comportement d'espacement et succès de la reproduction). Il faut conclure que les deux hypothèses sont nécessaires pour expliquer les fluctuations. Au cours des années où la densité de la population de printemps a baissé sous la valeur moyenne des 21 ans (17,8/100 ha), il semble que le succès de la reproduction une année ait influencé la densité de la population du printemps suivant, mais le comportement d'espacement ne semble pas avoir limité le nombre dans ces conditions. D'autre part, lorsque la densité de la population dépassait la densité moyenne des 21 ans, le succès de la reproduction ne semblait pas influencer la taille de la population du printemps suivant, mais le comportement d'espacement contribuait probablement à limiter le recrutement. Le changement à long terme au sein de cette population était probablement relié au stade de succession atteint par l'habitat depuis le feu; la maturation de la forêt (particulièrement l'augmentation en hauteur) a coincidé avec le déclin de la population.

[Traduit par la revue]

Introduction

In a recent publication Bergerud et al. (1985) discussed two hypotheses postulated to explain annual changes in the density of spring populations of ptarmigan (*Lagopus* spp.). One, the spacing behaviour hypothesis (Watson 1967; Watson and Moss 1980; Hannon 1983), states that the density of breeding ptarmigan is a function of territory size which, in turn, is influenced by the nature of the habitat and the spacing behaviour of the birds themselves, the latter being subject to change through nutrition (Miller et al. 1970) or genetics (Bergerud 1970). According to this hypothesis, the number of young fledged annually is of little consequence since it is usually more than adequate to maintain numbers; those potential recruits unable to acquire territories are expelled and usually doomed. The second, the breeding success hypothesis (Bergerud 1970; Myrberget 1972), states that density of ptarmigan in the spring breeding population directly reflects the numbers surviving the preceding winter which, in turn, is a function of the number of young fledged the previous season. Accordingly, habitat occupied and size of territory are a consequence, and not a cause, of the number of surviving young being recruited.

In their review, Bergerud et al. (1985: p. 2240) considered data from studies of *Lagopus* spp. that spanned 4 to 19 years in 11 populations. They concluded that "changes in the breeding success are sufficient to explain the dynamics in [spring] population size" the following year. Thus, they rejected the spacing behaviour hypothesis and suggested that territorial behaviour was only "a breeding tactic to space birds relative to environmental requisites."

In this paper we consider the fluctuation in numbers of Franklin's spruce grouse (*Falcipennis* (*Canachites*) *franklinii*) (classification follows Potapov 1985), in light of the two hypotheses described above, using data collected over a 21-year period in southwestern Alberta. We also provide evidence that the density of this species, like that of other tetraonids such as blue grouse (*Dendragapus obscurus*; Bendell and Elliott 1966; Zwickel and Bendell 1985), ruffed grouse (*Bonasa umbellus*; Gullion 1970), and sharp-tailed grouse (*Tympanuchus phasianellus*; Moyles 1981), is influenced by successional events in the habitat.

Study area and methods

Spruce grouse were counted annually from 1965 to 1985 on a block (247 ha) of coniferous forest dominated by lodgepole pine (*Pinus contorta*) and surrounded contiguously by forest of the same type in the foothills of southwestern Alberta (50°89′ N, 114°59′ W). Details of the

[1]Present address: Department of Fishery and Wildlife Biology, Colorado State University, Fort Collins, CO, U.S.A. 80523.

vegetation are given in Boag et al. (1979) and of the exact areas counted in Smyth and Boag (1984).

Grouse were counted using the procedures outlined in Boag and McKinnon (1982) and marked individually after capture (Boag et al. 1979). To eliminate potential effects of migration (Schroeder 1985) on counts, only birds found on the area between 16 May and 15 August were considered resident during the reproductive season. Each year, the number of chicks surviving to at least 5 weeks of age (Smyth and Boag 1984) was estimated by multiplying the number of females that survived through the breeding season (corrected for unnatural mortality such as snaring deaths) by the average number of chicks per hen, using only brood counts (including zero) from hens sighted after their chicks were (or would have been had they survived) 5 weeks of age.

In 1984 and 1985, grouse were also counted on 31 blocks of habitat dominated by lodgepole pine. The blocks were chosen to provide within-stand homogeneity but between-stand heterogeneity, in terms of age of pine overstory. All blocks were within a radius of 10 km of the study area, ranged in size from 26 to 61 ha ($\bar{x}$ = 31.8 ha), and were surrounded in most cases by contiguous forest of mainly lodgepole pine. We used a playback of the female cantus (Nugent and Boag 1982) to count grouse on these blocks of habitat. This method is effective for enumerating only the territorial males present, all of which respond if the call is played at 150-m intervals throughout the block of habitat (M.A. Schroeder and D.A. Boag, manuscript in preparation). Males responded by either displaying *in situ* with wing claps (MacDonald 1968), or moving directly towards the source of the playback, either walking or flying (Boag and McKinnon 1982).

We measured the impact of succession between 1967 and 1984 on the attributes of the habitat on the study area by considering the following variables: canopy height (m), canopy coverage (%), stem density of pine (*Pinus contorta*), spruce (*Picea glauca*), poplar (*Populus* spp.), and willow (*Salix* spp.). A series of randomly selected 50-m^2 plots (225 in 1967 and 132 in 1984) were used in this exercise.

These habitat variables were also measured at all listening stations (n = 12–25) where males were counted on the 31 blocks of habitat in 1984 and 1985. Additional variables recorded were the percentage coverage of trees, shrubs, ground vegetation, and fallen tree debris, the slope of the ground, and the stem density of the shrub layer (lower than breast height) on the 50-m^2 plots. These data were used to run correlation analyses against the density of resident male spruce grouse.

Results

The number of spruce grouse resident on the study area in the spring averaged 43.9 individuals (17.8/100 ha), ranging from a high of 72 birds (29.1/100 ha) in 1979 to a low of 12 birds (4.9/100 ha) in 1985 (Fig. 1). By 1970 the population had exceeded this mean number, having grown steadily from 1965 (Fig. 1). During this initial period of growth the sex ratio was biased slightly in favour of females ($\bar{x}$ (males:females) = 0.94:1; paired t = 1.82; $P > 0.05$) and the age structure showed a large proportion of yearlings (males: 0.45; females: 0.45). From 1970 to 1981 (with the exception of 1976) numbers resident in spring exceeded the mean. During these years the sex ratio was reversed with a slight bias in favour of males ($\bar{x}$ = 1:0.96; paired t = 2.23; $P < 0.05$) and the proportion of yearlings in the annual count declined somewhat (males: 0.32; females: 0.36). Both these trends were exaggerated during periods of decline in numbers (1976 and 1982 to 1985) when the bias in the sex ratio favoured males even more (1:0.49; paired t = 14.06; $P < 0.001$) and the proportion of yearlings in the spring population declined considerably (males: 0.23; females: 0.20).

To what extent can these changes in spring numbers, and accompanying attributes of this population of spruce grouse, be attributed to one or other of the hypotheses discussed above? Table 1 presents a series of predictions derived from these two hypotheses. Here we examine the extent to which these

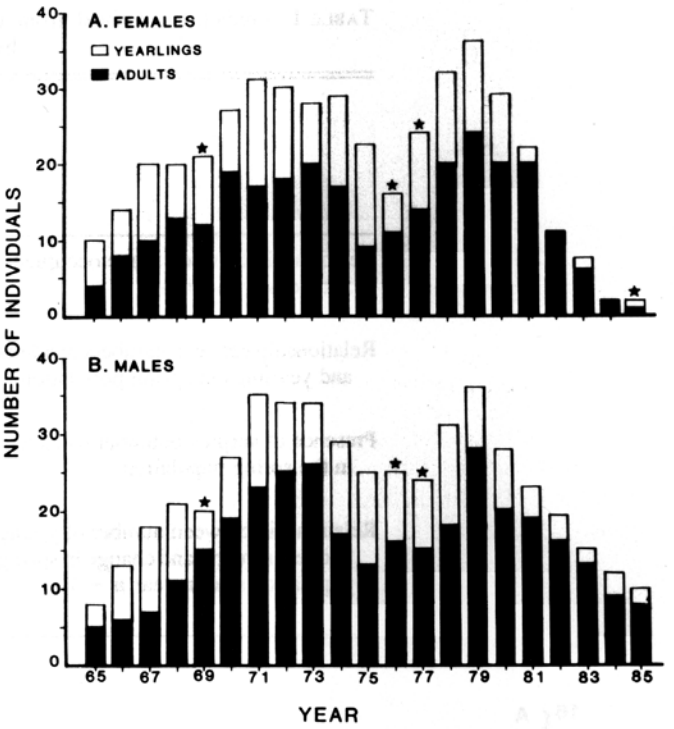

FIG. 1. The number of adult and yearling spruce grouse recorded from May 16 to August 15 on a 247-ha study area dominated by lodgepole pine in southwestern Alberta, 1965 to 1985. Stars above a given year indicate that the numbers recorded in that year were minimal because they were based on marked birds known to have been alive in the previous year and surviving into the subsequent one; some birds probably survived into the year not counted (either completely as in 1969 or in part as in 1975–1977) but died before being counted the following year. Female count in 1985 is minimal.

predictions are supported by the data from the population of spruce grouse under consideration.

The areas occupied by adult female spruce grouse in spring (n = 23), based on radiotelemetry locations recorded in 1974, 1975, 1977, and 1983, were plotted against density of females in these years; the relationship was inverse ($P < 0.01$) (M. A. Schroeder and D.A. Boag, manuscript in preparation) suggesting support for the spacing behaviour hypothesis. Nevertheless, the decline in density from 1974 to 1983 (72%) was not reflected by a commensurate increase in space occupied. In 1983 the area occupied by females was only 69% of that occupied in 1974 (M.A. Schroeder and D.A. Boag, manuscript in preparation), suggesting that spacing behaviour was not the only factor influencing numbers, at least in 1983. Using the median size of areas occupied by females (adults: 5.3 ha; yearlings: 14.5 ha; M.A. Schroeder and D.A. Boag, manuscript in preparation) for these 4 years, when the average number of females (20.8) was close to that for the whole 21 years (20.0) (Fig. 1), and applying it to the situation in 1979, when maximum numbers were recorded, gave a total area occupied by females of 301 ha (127 ha by adults and 174 ha by yearlings). This total exceeded that of the study area (247 ha) by 22%, suggesting that either areas occupied were smaller in 1979 than those recorded when populations were lower, or that the overlap among them was much greater.

The relationship between numbers of adults and yearlings in the spring population was positive for both sexes when data for all 21 years were considered (Figs. 2A and 2B: females: r_s = 0.489, P = 0.02; males: r_s = 0.296, P = 0.19) which is opposite

TABLE 1. Predictions derived from the spacing behaviour and breeding success hypotheses

	Predictions from the hypotheses	
	Spacing behaviour	Breeding success
Relationship between space occupied and density in spring	Strongly negative	No necessary relationship
Relationship between numbers of adults and yearlings in spring population	Strongly negative	No necessary relationship
Presence of surplus potential recruits in the spring population	Present in most years	Never present
Relationship between number of young fledged in year n and change in spring population size in year $n + 1$	No necessary relationship	Strongly positive

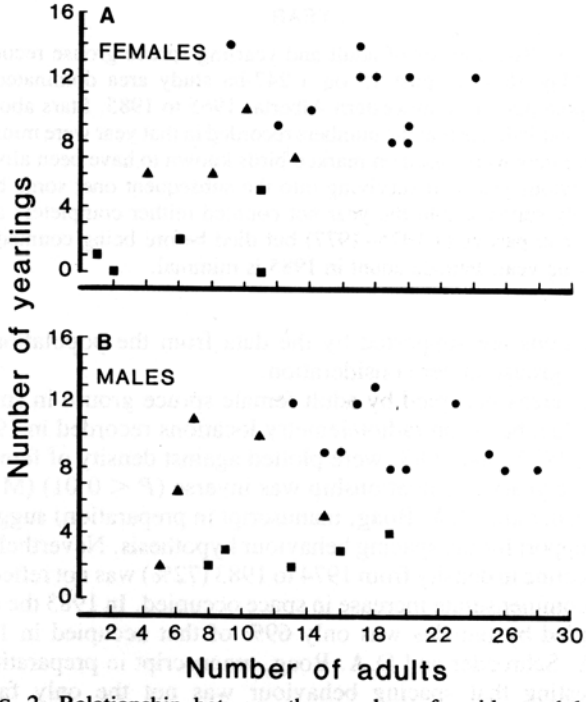

FIG. 2. Relationship between the number of resident adult and yearling spruce grouse in the spring population over a 21-year period in southwestern Alberta, expressed as years when numbers were below the mean and population was rising (triangles) and declining (squares), and as years when numbers were above the mean (circles).

to that predicted under the spacing behaviour hypothesis. If, however, the years when numbers in the spring fell above and below the mean for each sex were considered separately, this relationship changed (Figs. 2A and 2B). During the years when numbers of each sex were above the mean, the relationship was negative (females: $r_s = -0.374$, $P = 0.23$; males: $r_s = -0.528$, $P = 0.10$), but when this number fell below the mean, there was no relationship (females: $r_s = 0.142$, $P = 0.28$; males: $r_s = -0.123$, $P = 0.73$), suggesting some support for the spacing behaviour hypothesis only during the years of high numbers.

The existence of a nonterritorial adult cohort in this population remains unknown because the appropriate manipulations have not been undertaken. The situation in spruce grouse is complicated by the existence of a normally nonterritorial cohort of yearling males (McKinnon 1983) which is present in the spring population. Circumstantial evidence of a surplus among females was recorded in the mid and late 1970s when both Herzog and Boag (1977, 1978) and Nugent (1979) showed that females were territorial and drove off trespassers. The latter were never seen subsequently on the study area, suggesting the existence of a number of potential recruits that were excluded by spacing behaviour during the years of high numbers. McKinnon (1983) performed removals of resident males and females but got only partial replacement, probably because the population by that time was in the period of major decline at the onset of the 1980s.

The relationship between the number of young fledged on the study area and the change in size of the population the following spring was determined for the entire period of this study (Fig. 3A). We chose to use the total number of young fledged on the study area rather than an estimate of the number of young fledged per female in the population because the latter value can be the same despite very different numbers of young produced when the size of the female cohort varies among years. For example, 10 females raising 4.0 young/female produce 40 young in total whereas 20 females raising 3.0 young/female produce 60 young in total, a decline in rate but an increase in the number of young available to be recruited. The plotted values showed no relationship between these variables ($r_s = -0.131$, $P = 0.58$), suggesting that the breeding success hypothesis was not supported for this entire period.

To include the entire 21-year period in a single analysis assumed that conditions in the habitat remained relatively constant throughout the period. The validity of this assumption is open to question, particularly as the forest habitat in question was a fire sere. Furthermore, the size of the spring population varied considerably around the mean number (43.9), from 12 to 72 birds over the 21 years. If changes in spacing behaviour were the major cause of year to year changes in spring population size, one would predict this mechanism to be more effective

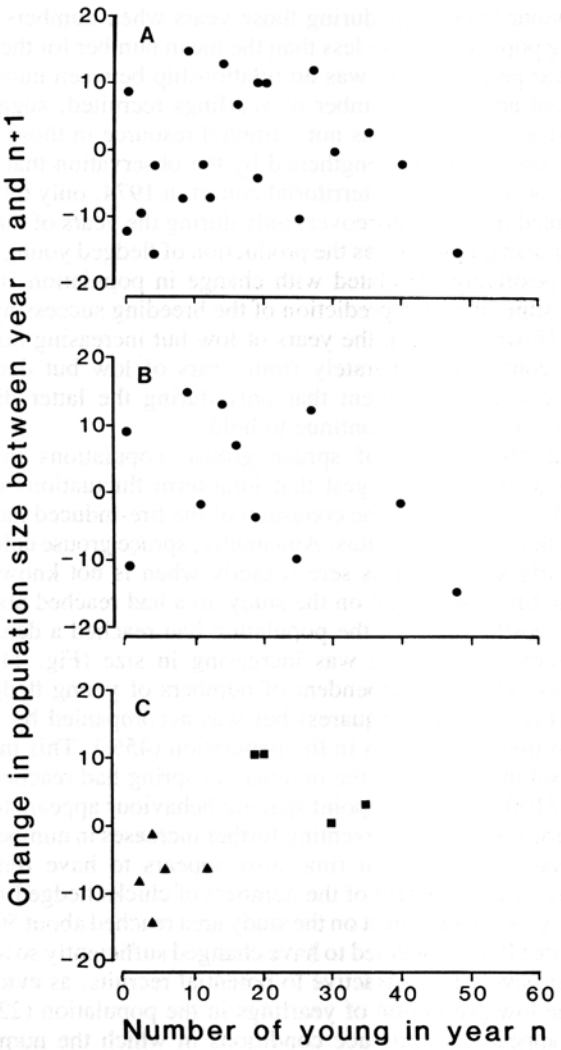

FIG. 3. Relationship between the number of young spruce grouse produced (number/female × number of females) in a given year on the study area and the change in the size of the population the following breeding season. (A) All years (1965–1984). (B) When the spring population numbered more than the mean value for all 21 years (43.9 grouse). (C) When the spring population was less than the mean value (solid squares are years of increase: 1965–1966 to 1968–1969; and solid triangles are years of decline: 1975–1976 and 1981–1982 to 1984–1985).

when numbers exceeded the mean level. Thus, we subdivided the period in question into two groups of years, those in which the spring population was "high" (above the mean number of 43.9 birds) and "low" (below the mean value), and plotted the number of young fledged against change in numbers the next spring. It is apparent that when the population was high there was no relationship between these variables (Fig. 3B) ($r_s = -0.320$, $P = 0.34$). However, when population size was low (increasing in the 1960s and declining in the 1980s) the relationship was positive (Fig. 3C) ($r_s = 0.798$, $P = 0.02$). This suggests that the number of young fledged ought to have been greater during the increase phase than during the decline, a fact borne out in terms of both total number of young fledged (increase: $\bar{x} = 23.6$; decrease: $\bar{x} = 6.8$; rank test, $P = < 0.05$), and number of young per female in the population (Fig. 4; $r_s = -0.68$, $P < 0.01$). In separating the years of population increase from those of decline in Fig. 3C, it becomes apparent that the change in spring population size in year $x + 1$ was

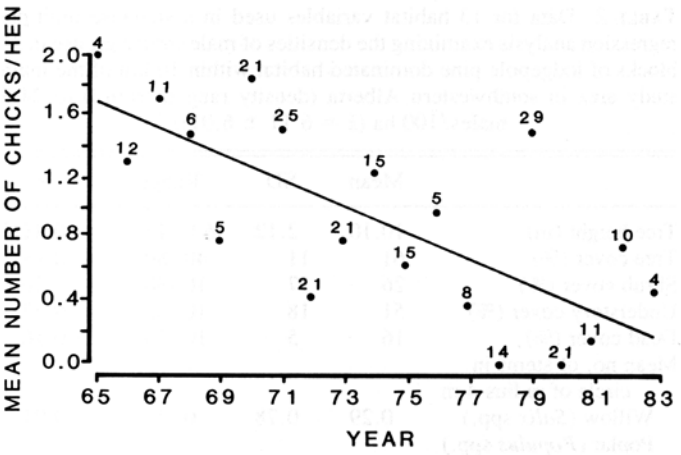

FIG. 4. Mean number of young spruce grouse produced to independence (5+ weeks of age) per female on the study area in each year of the study; only females for which the fate of their reproductive attempt was known were included in the analysis (sample size indicated above each point) ($r = -0.679$; $P = 0.001$). Line fitted by regression equation.

potentially influenced more by breeding success in year x during the latter period ($r_s = 0.368$; $P = 0.54$) than the former ($r_s = -0.8$; $P = 0.20$).

The pattern of change in numbers of spruce grouse in the spring population (Fig. 1) has been accompanied by a slow decline in average annual number of chicks fledged per female (Fig. 4). Since productivity was unrelated to population density on this study area (Smyth and Boag 1984), another explanation must be sought to explain this decline. One such explanation may lie in changes in the habitat as this fire sere matured. Between 1967, when McCourt (1969) randomly sampled 225 sites, and 1984, when Schroeder (unpublished data) sampled 132 randomly selected sites in the same area, the mean height of the lodgepole pine trees dominating the study area increased from 7.3 to 10.6 m and their coverage rose from a mean of 34 to 64%. Additionally, this fire sere has undergone some self thinning with mean stem density of pine falling slightly ($\bar{x} = 19.2$ to 17.6 stems/50 m^2) but the number of spruce has increased ($\bar{x} = 1.5$ to 6.5 stems/50 m^2). The spring density in 1967 was 7.9 males/100 ha and rising; by 1984 it was 4.5 males/100 ha and falling. If the successional state of the forest habitat were influencing spring population size, one would predict variation in population size on the blocks of habitat that were in various successional states.

We censused 31 such blocks of pine-dominated forest in the same valley as the study area, recording not only the number of territorial males present but also the characteristics of the forest habitat. Of the attributes recorded, only canopy height was significantly correlated with numbers of male grouse recorded (Table 2).

This factor, plus hardwood sapling density and slope, explained 47% of the variance in the numbers of males among blocks of habitat (Table 2). These results suggest that the physiognomy of the forest (reflecting a combination of age, aspect, and altitude) influenced the density of spruce grouse present; in this case the more mature the forest the fewer the grouse, consistent with the suggestion from the changes recorded on the study area.

Discussion

The observations reported herein suggest that year to year fluctuations in the size of spruce grouse populations cannot be

TABLE 2. Data for 13 habitat variables used in a stepwise multiple regression analysis examining the densities of male spruce grouse in 31 blocks of lodgepole pine dominated habitat within 10 km of the main study area in southwestern Alberta (density ranged from 0 to 24.8 males/100 ha ($\bar{x}$ = 6.11 ± 6.01))

	Mean	SD	Range	r
Tree height (m)	10.10	2.12	6.0–15.0	−0.41[ab]
Tree cover (%)	61	11	40–80	0.11
Shrub cover (%)	26	17	10–80	−0.26
Understory cover (%)	51	18	10–80	−0.33
Dead cover (%)	16	5	10–20	−0.16
Mean no. of stems in circle of radius 4 m				
Willow (*Salix* spp.)	0.29	0.78	0–3	0.01
Poplar (*Populus* spp.)				
Shrub[c]	0.29	0.64	0–3	−0.32[b]
Tree[d]	1.10	2.95	0–15	−0.29
Pine (*Pinus contorta*)				
Shrub	3.23	4.17	0–16	0.34
Tree	15.58	11.43	0–55	0.26
Spruce (*Picea glauca*)				
Shrub	2.58	2.13	0–8	0.10
Tree	3.77	4.98	0–26	0.21
Slope	6.39	4.14	0–16	−0.16[b]

[a] $P = 0.024$.
[b] Variables entering the multiple regression equation: $Y = -1.54$ (canopy height) − 4.46 (poplar shrub) − 0.83 (slope) + 28.31. $F = 7.88$; $P < 0.01$ ($r = 0.683$).
[c] Shorter than breast height.
[d] Taller than breast height.

explained by invoking only one of the two hypotheses postulated to explain spring population densities of grouse, a conclusion similarly reached by Errington (1956). Both hypotheses (spacing behaviour and breeding success) appear to be needed to explain our data set which spanned a period of 21 years. Support for the predictions of the spacing behaviour hypothesis was strongest for the years 1970 to 1980 (except for 1976) when numbers in the spring population were above the mean number for the 21-year period. Only during those years was there a negative relationship between the number of adults resident in the population and the number of newly established yearlings, suggesting that the spacing behaviour of the adults was influencing rates of recruitment of new birds; the more resident adults the less space available for yearlings to occupy. Herzog and Boag (1977, 1978) and Nugent (1979), working with this population when numbers were higher than the mean, recorded the loss of marked yearling females during the spring season when females were territorial. Some of the females not seen again on the study area were known to have retreated in response to a playback of the calls of an established female, lending credence to the proposition that the spacing behaviour (including vocalizations) of the established birds was limiting the number of newly recruited birds. Furthermore, it was only during these same years that there was no relationship between the numbers of young fledged in one year and the density of grouse in the population the next. Indeed, the relationship tended to be negative, the opposite of what is predicted by the breeding success hypothesis, suggesting that production of fledged young was not having any major influence on the number of birds recruited on the same ground the following spring.

By contrast, there was no apparent support for the spacing behaviour hypothesis during those years when numbers in the spring population were less than the mean number for the entire 21-year period. There was no relationship between number of resident adults and number of yearlings recruited, suggesting that space available was not a limited resource in those years. This conclusion is strengthened by the observation that of the space occupied by the territorial cohort in 1974, only 69% was occupied in 1983. Moreover, only during the years of numbers lower than the mean was the production of fledged young in one year positively correlated with change in population size the next, supporting the prediction of the breeding success hypothesis. However, when the years of low but increasing numbers were considered separately from years of low but declining numbers, it was evident that only during the latter did this positive relationship continue to hold.

Our observations of spruce grouse populations in pine-dominated habitat suggest that long-term fluctuations in size are ultimately tied to the condition of the fire-induced habitat,a reflection of its seral status. Apparently, spruce grouse colonized the early stages of this sere (exactly when is not known) but by the time the habitat on the study area had reached about 35 years postfire (1965), the population had reached a density of 7.5 birds/100 ha and was increasing in size (Fig. 1). This increase seemed independent of numbers of young fledged *in situ* (Fig. 3C, solid squares) but was accompanied by a high proportion of yearlings in the population (45%). This increase stopped in 1971 when the numbers in spring had reached 26.7 birds/100 ha at which point spacing behaviour appears to have become effective in preventing further increases in numbers; the population size at that time also appears to have remained relatively independent of the numbers of chicks fledged *in situ*. Finally, when the forest on the study area reached about 50 years postfire (1980) it seemed to have changed sufficiently so as to be progressively less attractive to potential recruits, as evidenced by the low proportion of yearlings in the population (22%). It also appeared to produce conditions in which the number of young fledged was also reduced (Fig. 4). Szuba and Bendell (1983) have also shown a significant inverse correlation between canopy height of jack pine (*Pinus banksiana*) forests and spruce grouse density (based on the number of grouse counted per unit time of walked transect) in north central Ontario. This relationship was also associated with forest age: younger pine plantations (11–12 years) supported higher numbers than older plantations (28–62 years), apparently a function of development of a coniferous understory and its relative attractiveness to the birds.

From our observations it is apparent that both space (size of the study area chosen) and time (length of the study in years) could influence the conclusions reached. For example, had the study area been a great deal larger it is probable that it would have included some of the habitat that, even in 1985, was still supporting high densities of grouse (Table 2). Earlier, these areas may have held few grouse such that this heterogeneity could have masked the sort of density changes recorded on the smaller, more homogeneous study area. Likewise, by studying the same population over an extended period of time we have been forced to change our opinion about the relative importance of spacing behaviour and breeding success in determining population size: after 12 years of study we believed that the former was more important than the latter (Boag et al. 1979), after 17 years McKinnon (1983) questioned this conclusion, and finally after 21 years we believe that both mechanisms are necessary to explain our observations.

Acknowledgements

The data used in this paper were gathered by the following graduate students: K.H. McCourt, R.A. McLauchlin, D.M. Keppie, P.W. Herzog, D.P. Nugent, K.E. Smyth, and D.T. McKinnon and their field assistants. We thank them and B.D. Mott who conducted the counts in 1985. We acknowledge with thanks the constructive comments of A.V. Andryev, J.F. Bendell, L.H. Ellison, D.T. McKinnon, P. Wegge, and A. Watson on earlier drafts of this manuscript. The studies on which this paper is based have been supported throughout by the Natural Sciences and Engineering Research Council of Canada through operating grants to D.A.B. Additional support has come from the Boreal Institute for Northern Studies and the University of Alberta. To all agencies we express our gratitude.

BENDELL, J. F., and ELLIOTT, P. W. 1966. Habitat selection in blue grouse. Condor, **68**: 431–446.

BERGERUD, A. T. 1970. Population dynamics of the willow ptarmigan *Lagopus lagopus alleni* L. in Newfoundland 1955 to 1965. Oikos, **21**: 299–325.

BERGERUD, A. T., MOSSOP, D. H., and MYRBERGET, S. 1985. A critique of the mechanics of annual changes in ptarmigan numbers. Can. J. Zool. **63**: 2240–2248.

BOAG, D. A., and MCKINNON, D. T. 1982. Spruce grouse. *In* Handbook of census methods for terrestrial vertebrates. *Edited by* D. E. Davies. CRC Press, Inc., Boca Raton, FL. pp. 61–62.

BOAG, D. A., MCCOURT, K. H., HERZOG, P. W., and ALWAY, J. H. 1979. Population regulation in spruce grouse: a working hypothesis. Can. J. Zool. **57**: 2275–2284.

ERRINGTON, D. L. 1956. Factors limiting higher vertebrates populations. Science (Washington, D.C.), **124**: 304–307.

GULLION, G. W. 1970. Factors influencing ruffed grouse populations. Trans. North Am. Wildl. Nat. Resour. Conf. **35**: 93–105.

HANNON, S. J. 1983. Spacing and breeding density of willow ptarmigan in response to an experimental alteration in sex ratio. J. Anim. Ecol. **52**: 807–820.

HERZOG, P. W., and BOAG, D. A. 1977. Seasonal changes in aggressive behavior of female spruce grouse. Can. J. Zool. **55**: 1734–1739.

——— 1978. Dispersion and mobility in a local population of spruce grouse. J. Wildl. Manage. **42**: 853–865.

MACDONALD, S. D. 1968. The courtship and territorial behavior of Franklin's race of the spruce grouse. Living Bird, **7**: 5–25.

MCCOURT, K. H. 1969. Dispersion and dispersal of female and juvenile Franklin's grouse in lodgepole pine forest in southwestern Alberta. M.Sc. thesis, University of Alberta, Edmonton.

MCKINNON, D. T. 1983. Recruitment into a local population of spruce grouse. M.Sc. thesis, University of Alberta, Edmonton.

MILLER, G. R., WATSON, A., and JENKINS, D. 1970. Responses of red grouse populations to experimental improvement of their food supply. Br. Ecol. Soc. Symp. **10**: 323–334.

MOYLES, D. L. J. 1981. Seasonal and daily use of plant communities by sharp-tailed grouse (*Pedioecetes phasianellus*) in the parklands of Alberta. Can. Field-Nat. **95**: 287–291.

MYRBERGET, S. 1972. Fluctuations in a north Norwegian population of willow grouse. Proc. Int. Ornithol. Congr. **15**: 107–120.

NUGENT, D. P. 1979. A behavioral analysis of communication among Franklin's grouse during the breeding season. M.Sc. thesis, University of Alberta, Edmonton.

NUGENT, D. P., and BOAG, D. A. 1982. Communication among territorial female spruce grouse. Can. J. Zool. **60**: 2624–2632.

POTAPOV, R. L. 1985. Fauna of the USSR: birds. Vol. III. Order Galliformes, family Tetraonidae. Science Institute, Leningrad. (In Russian.)

SCHROEDER, M. A. 1985. Behavioral differences of female spruce grouse undertaking short and long migrations. Condor, **87**: 281–286.

SMYTH, K. E., and BOAG, D. A. 1984. Production in spruce grouse and its relationship to environmental factors and population parameters. Can. J. Zool. **62**: 2250–2257.

SZUBA, K. J., and BENDELL, J. F. 1983. Population densities and habitats of spruce grouse in Ontario. *In* Resources and dynamics of the boreal zone, proceedings of a conference, Thunder Bay, Ont., August 1982. *Edited by* R. W. Wein, R. R. Riewe, and I. R. Methren. Association of Canadian Universities for Northern Studies, Ottawa.

WATSON, A. 1967. Population control by territorial behavior in red grouse. Nature (London), **125**: 1274–1275.

WATSON, A., and MOSS, R. 1980. Advances in our understanding of the population dynamics of red grouse from a recent fluctuation in numbers. Ardea, **68**: 103–111.

ZWICKEL, F. C., and BENDELL, J. F. 1985. Blue grouse—effects on, and influences of, a changing forest. For. Chron. **61**: 185–188.