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DISPERSAL, OVERWINTER MORTALITY, AND POPULATION SIZE OF SPRUCE GROUSE (*CANACHITES CANADENSIS FRANKLINII*)

BY

DANIEL MACKENZIE KEPPIE

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The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research, for acceptance, a thesis entitled Dispersal, Overwinter Mortality, and Population Size of Spruce Grouse (*Canachites canadensis franklinii*) submitted by Daniel MacKenzie Keppie in partial fulfilment of the requirements for the degree of Doctor of Philosophy

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ABSTRACT

This study was conducted on Franklin's spruce grouse (*Canachites canadensis franklinii*) in southwest Alberta continuously from May 1970 through September 1973. I evaluated the hypothesis that a substantial loss of individuals, mostly juveniles, results from dispersal and mortality during autumn and winter, and this loss determines the size of the subsequent breeding population.

Essentially all grouse on a 519 hectare study area were marked. Densities of the breeding population varied from 8 to 11 males/km^2 and 7 to 10 females/km^2. Survival of adults and yearlings was similar within each year. Almost all new birds in the population were yearlings. Hence, recruitment of yearlings was the primary cause for change in total size of the breeding population. Dispersal in autumn changed only slightly the number of juveniles; numbers in winter were almost identical to numbers in late summer. Survival of all age-sex classes was high over autumn and winter. Proportions of birds emigrating in spring were variable between years, in contrast to autumn. Yearlings that immigrated in spring replaced many of the overwintering juveniles that emigrated. Emigration of juveniles in autumn and the distances they moved were independent of population size. Results of analyses between density and emigration in spring were less consistent and not as easy to interpret. Some data indicated a good correlation between emigration of juveniles in spring and adult and yearling numbers in late winter. But rates of emigration and distances dispersers moved were not changed significantly by removing all adults and yearlings from a part of the study area in late winter of one year. However, if population size affected dispersal it did so in spring rather than autumn.

Results do not support the hypothesis that losses in autumn and winter determined the size of the breeding population. Emigration and immigration in spring were the most proximal factors to determine recruitment of yearlings. Mortality did not seem to be the immediate fate of dispersing birds. Emigration was only a means of prohibiting birds from recruiting into this local population. Causal factors to the dispersal are yet unknown.

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INTRODUCTION

HYPOTHESIS

Populations of most animals exhibit high natality yet comparatively low densities of breeding individuals. Breeding populations usually show only moderate fluctuations, and Tanner (1966;742), generalizing for vertebrates, stated that, "... processes known to regulate vertebrate populations affect either reproduction or the survival of juveniles." Bendell (1972a) surveyed the literature on many species and concluded that losses of young were commonly thought to be the main cause for changes in numbers of breeding individuals. Typical conclusions in this regard come from Tompa (1964) for song sparrows (*Melospiza melodia*) and Sadleir (1965) for deermice (*Peromyscus maniculatus*). Von Haartman's (in: Proc. Int. Ornithol. Cong. 1972:180) statement that, "Winter loss is so to say a bottleneck in determining final population [size]" reflects much contemporary thought for birds.

High losses of young from autumn to spring often have been reported for tetraonids. In some cases the losses were presumed to regulate the breeding population (Boag 1966, Bendell and Elliott 1967, Zwickel and Bendell 1967a, and Weeden and Theberge 1972). However, there has been little direct study on the characteristics of the loss. Except for the continuing work on red grouse (*Lagopus l. scoticus*) (Jenkins et al. 1967, Watson and Moss 1972, among others), and work on rock ptarmigan (*Lagopus mutus*) (Watson

1965) and ruffed grouse (*Bonasa umbellus*) (Rusch and Keith 1971), tetraonids have been studied mostly in spring and summer or not intensively enough in autumn and winter to produce the needed information. Bendell (1972b) concluded that there is an obvious need to work with tetraonids from autumn to spring to assess the roles of behavior, and mortality and dispersal of young in determining the number of individuals in the breeding population. This was the stimulus for the present work. This study was designed to evaluate the hypothesis that:

> A substantial loss of individuals, mostly juveniles, results from dispersal and mortality during autumn and winter; this loss determines the size of the subsequent breeding population.

Year-round field work was required to associate population parameters from autumn to spring with those of the breeding population. A large proportion of the population needed to be marked in order to follow changes in individuals composing the group and their activities. Franklin's spruce grouse (*Canachites canadensis franklinii*) were selected for study because they are easily captured, marked, and subsequently observed, making it possible to monitor most birds. Spruce grouse were also believed to be non-migratory, which permitted year-round observations on a single study area.

MORTALITY AND DISPERSAL

Loss of individuals from a given site occurs through mortality or emigration. Morris (1957) advocated that mortality include reduced production as well as death. In many studies with animals the term *mortality* is used but it actually refers to the total loss from death and emigration. However, I use mortality as only death; loss equals total disappearance.

Emigration in this study involved mostly immature individuals, dispersing from the study area. Dispersal has been used to describe many types of movement: from simple radiating movements from a banding station to colonization in a zoogeographic context. Dispersal has been considered to be genetically controlled, to provide maximum colonization of all habitat, to increase mixing of the gene pool, and to contribute to survival of the population (Blair 1953, Olsson 1958, Howard 1960, Johnston 1961, Lidicker 1962, Murray 1967, den Boer 1968, Christian 1970, and Van Valen 1971). Wolfenbarger's (1946) extensive review demonstrates the economic importance of dispersive information for many organisms. In this study the influence of dispersal on numbers in a local population is the major concern.

Krebs et al. (1969:605) stated that the first problem in investigating dispersal is to "... devise a rigorous operational definition of a dispersing animal"; this has seldom been considered. Dispersal is a movement. The critical problem is to determine at what point this movement may affect survival and reproductive success of the individual and thus population size. Dispersal has been measured most frequently in the following two ways. 1) Movement of a juvenile from birth site to first breeding site (Howard 1949 and 1960, Olsson 1958, Johnston 1961, Tompa 1964, Berndt and Sternberg 1968, Dhondt and Hublé 1968, and Haukioja 1971). It is often difficult to locate subsequent breeding sites and frequently just a removal from the specific birth site is used. 2) Movement off a study area. This latter definition has been commonly used in population studies of tetraonids, for example, Chambers and Sharp (1958), Choate (1963), Boag (1966), Bendell and Elliott (1967), Zwickel and Bendell (1967a) and Rusch and Keith (1971). Regardless of the working definition used most population studies have given only superficial attention to dispersal. Only Krebs et al. (1969) and Myers and Krebs (1971) give objective analyses of the function of dispersal and characteristics of the individuals involved. Haukioja (1971) gave a detailed procedure for analyzing dispersal distances. Dice and Howard (1951), Andrewartha and Birch (1954), French et al. (1968), and Gates and Hale (1974) describe some of the many other methods used to analyze movement data.

The ultimate objective of my study was to account for increment and loss at the population level. Dispersal as a movement out of a study area should provide a direct measure of one type of loss. Similarly, all immigrants, dispersing from elsewhere, become a component of increment. The critical question though is whether the boundaries of the study area can be equated with the limits of the population unit. Kuenen (1960) and Bakker (1964) discussed some history of the development of the population concept; Bakker implied that its meaning varied, often relative only to the questions being studied. Den Boer (1968) was even more emphatic; he defined the population merely as a working-unit, perhaps arbitrarily set by the investigator and not necessarily a biological entity. In fact, most workers have used *population* loosely, simply meaning a group of animals they studied. But it is necessary to at least be cognizant of the problems of recognizing spatial limits that are biologically relevant to a breeding population.

Records of distances over which animals disperse will help show the area within which an individual may contact others of the same species. Relocations in my study suggest that emigrants from the study area had little subsequent contact during the breeding period with those individuals that remained within. Hence, I use population here to refer to grouse within the study area.

Distances between birth site and breeding site have been less commonly used as a measure of dispersal in population work. These measurements suffer in two ways: 1) records of brood range are often incomplete, making it difficult to determine original location; and 2) frequency distributions for distances moved are still truncated in that they only encompass the area of habitat searched. Hence, long-distance movements are seldom recorded. Haukioja (1971) discusses the problems of unequal spatial effort.

Nearly all juvenile grouse moved from their brood range in autumn or from winter range in spring but I will use *dispersal* to mean only those movements across study area boundaries (except pages 70-80). This criterion can be biologically meaningful if it reflects a genuine impact on the population. Data should be viewed with this constraint in mind.

BACKGROUND ON SPRUCE GROUSE

A brief account of the annual cycle of *C. c. franklinii* is presented here as a preface. Dates given apply to the area of this study and perhaps not elsewhere.

Spruce grouse are distributed across a broad area of coniferous forests in northern North America. The Franklin's race is one of five recognized subspecies (A.O.U. 1957); it is found principally in foothill and mountainous habitat associated with the northern and central Rocky Mountains, Cascades, and Coast Range (Aldrich 1963). These grouse appear to have a balanced sex ratio and promiscuous mating habits. Courtship is most frequent from mid-May to early June, when adults are generally more localized than yearlings. There is some spatial overlap in habitat used by individuals and there is little knowledge of how or if breeding sites are defended. Peak of hatching occurs about the end of June and broods remain intact until dispersal begins, usually in early September. Dispersal of juveniles and migration of some older birds continue until permanent snow cover. Birds tend to flock in autumn and winter, when movements become rather limited. Grouse feed almost exclusively in trees (lodgepole pine, *Pinus contorta*, this study) from late autumn to spring, although in winter they spend considerable time on the snow. Flocks decrease in size in late winter, and by May individuals appear mostly alone. Associated with the change in gregariousness, some young birds move from their wintering site and migrant adults begin to return to their breeding area.

Earlier reports that emphasized dynamics of spruce grouse populations are as follows. Densities, production, and mortality estimates were provided by Stoneberg (1967), McCourt (1969), McLachlin (1970), and Ellison (1974). Lumsden and Weeden (1963) and Zwickel and Brigham (1970) document age and sex ratios. MacDonald (1968) and Ellison (1971) reported on territorialism and Ellison (1973) described seasonal patterns of social behavior.

STUDY AREA

This research was conducted near the R.B. Miller Biological Station, 27 km west of Turner Valley, Alberta. The study area, 519 hectares, is adjacent to Gorge Creek

(50° 39'N, 114° 39'W). This area is within the high foothills of the eastern slopes of the Rocky Mountains at an elevation of 1,500-2,000 meters. Lodgepole pine, 25-35 years old and mostly 7-13 meters high, occupies nearly 70 percent of the area. Small and scattered patches of white spruce (*Picea glauca*), quaking aspen (*Populus tremuloides*), and balsam poplar (*Populus balsamifera*) are present. White spruce is the primary subdominant tree species; alder (*Alnus crispa*) and willow (*Salix spp.*) are common shrubs. Several meadows along creek bottoms and in the uplands are lightly stocked with spruce. Although the pine forest is dense overall it is a mosaic of varying densities and small openings. McCourt (1969) and McLachlin (1970) present detailed analyses of the vegetation of the region.

The Gorge Creek study area is not an isolated habitat for spruce grouse. The study area is joined on two sides by contiguous habitat occupied by grouse and suitable habitat occurs within 1 km of the remainder of the perimeter.

METHODS AND TERMINOLOGY

Approximately 1,250 man-days were spent in field work during a continuous 40 month period between mid-May 1970 and September 1973. Ninety percent of the field effort was on the Gorge Creek study area. Grouse were censused by repeatedly searching subsections of the area on a rotational basis. Pointing dogs were used to locate birds and they helped make the project feasible; 83 percent of all birds seen were located by dogs.

Most grouse were captured with an extendable snare pole (Zwickel and Bendell 1967b). Juveniles less than about 10 days old were usually caught by hand. Juveniles were too small to leg band until almost 40 days of age and until then they were marked with a numbered, fingerling fish tag (size no. 1, National Band and Tag, Newport, Kentucky) inserted in the prepatagium. Mortality of birds noosed with the snare pole was 3 percent; as experience with the method increased the mortality decreased.

The plumage of spruce grouse is distinctly sexually dimorphic after post juvenal feathers appear at 35-40 days of age. Sex was determined by plumage criteria (Zwickel and Martinsen 1967, Ellison 1968). The following age classes were used: juvenile, from hatch until 1 April; yearling, from 1 April after hatch until the second 1 April; and adult, after the second 1 April following hatch. April 1 was chosen as the initial date because it approximated the break-up of winter flocks and beginning of dispersal. Generally, age was easily determined from tail feather patterns (Zwickel and Martinsen 1967), rectrix and remige measurements (McCourt 1969, McLachlin 1970, this study), and shape and wear of outer primaries (Petrides 1942, Ellison 1968). New birds in adult plumage after about 1 September were either adult or yearling, and these birds were termed "age unknown" until 1 April.

I define the breeding population as all adult and yearling grouse seen on the study area from 15 May to 15 August. I chose 15 May as a best compromise because all birds that only wintered on the area (three exceptions) had emigrated by this date, yet probably few copulations (backdated from hatch dates) preceded this date. A final date of 15 August again excluded migrants, which had not been seen on the study area since at least the previous May. All individuals in the breeding population may not have actually mated, though presumably they were physiologically capable of doing so. Winter is defined as the period of permanent snow cover, beginning 10 November 1970, 17 December 1971, and 1 December 1972. Winter lasted through 31 March, which approximated the beginning of loss of complete snow cover. Autumn and spring are used loosely here but generally refer to intervals of 1 September to the start of winter and 1 April to 15 May, respectively.

In many instances I assume that counts of birds reflect essentially the entire universe within the study area rather than a sample of total individuals. Although statistical treatment of data in such cases is not necessary I employ significance levels as a measure of the *magnitude* of difference between numbers of birds. Statistical tests, unless noted otherwise, employed χ^2 tests for independence or a 2x2 contingency table (Yates' correction for continuity added). All significant differences reported are at least at the 0.05 level, at which the critical $\chi^2_{1\ df} = \geq 3.84$. Most results are given as percentages but were tested according to numerical data. In all tables (excluding appendices) I use a pair of like superscript letters to show significant differences among the data tested.

RESULTS

Much of my interpretation of results depends on accepting the premise that essentially all individuals were marked. Spruce grouse were encountered over 7,000 times (brood chicks excluded) on and off the study area, and in 98 percent of the contacts the bird was identified as banded or unbanded and, if banded, the entire combination could be read. In only 2 percent of the contacts did birds flush too soon for identification. Evidence that almost all grouse on the study area were marked is given in Appendices 1-4. Encounters of marked birds as a proportion of the total encounters, by age and sex, are as follows: adult and yearling males, 99 percent (2675/2705); adult and yearling females, 95 percent (1939/2038); juvenile males in September through March, 92 percent (631/684); juvenile females in September through March, 87 percent (535/618). Birds undoubtedly passed through the study area undetected, particularly in autumn and spring but least in winter. However, the only birds sighted on the study area beginning September 1970 (explained below) were those already marked when found, unmarked birds that were captured and marked when first seen, and a very few that remained unmarked from one month to the next. Such unmarked grouse were often identifiable by plumage and behavior. The only possible difference between the count of identified birds known to be present beginning September 1970 and a total count of all birds actually present was of individuals never seen. It is a circular argument whether unknown residents existed and one that is impossible to prove or disprove.

During the first summer, 1970, searching was not as efficient as in later years. Several adults were not seen until late August of 1970 but they were resident in the breeding season of 1971 and I assume they were present throughout the summer of 1970. I assume that all residents had been marked by September 1970. Unmarked adults and yearlings seen later that year for the first time were migrants and left the study area before the summer of 1971.

Most sightings of unmarked birds occurred in autumn and spring. This periodicity suggested they were immigrants. For example, 78 adults and yearlings were marked after 1 September 1970, and 82 percent were banded or first sighted in September through November and April through June (Appendices 1 and 2). Among 102 juveniles marked during September through March, 84 percent were marked or first sighted in September through November (Appendices 3 and 4). Within each sex-age category the temporal aggregation of new birds was significantly different from the expected, uniform distribution. Immigration of juveniles continued longer in autumn of 1971; eight new juveniles were recorded in December, perhaps because permanent snow cover was not established until 17 December.

Sightings of juveniles are given only after 1 September in Appendices 3 and 4. Juveniles were first detected to have departed from broods on 14, 5, and 9 September, 1970-72 respectively. All chicks known to be raised on the study area were marked by these dates, facilitating analyses of dispersal. All unmarked juveniles seen subsequently were recorded as recent immigrants. Similarly, analyses of spring dispersal were simplified because all known birds overwintering on the study area were marked; thus unmarked birds seen in spring were new to the area.

The size of a breeding population and its age and sex composition are basic parameters in population studies. These parameters must be measured on a year to year basis in order to evaluate how they are affected by overwinter mortality and dispersal. Production, survival, and dispersal are the three primary variables affecting the size of the population. The following sections will deal with these statistics. Production, as used here, is the number of juveniles raised almost to independence, that is, juveniles still alive in the late brood period at the end of summer. Knowledge of the number of juveniles produced is an essential base from which to determine the impact of dispersal. Production, the subsequent survival of juveniles, and their dispersal will determine the potential numbers of recruits into the breeding population. The actual extent of recruitment may be affected by the number of deaths in the population. Hence, annual survival of adults and yearlings must be recorded in order to help clarify the flux of population size.

BREEDING POPULATION

Numbers of grouse in the breeding population increased from 1970 through 1972, and then decreased in 1973 (Table 1). The most dramatic changes were increases in proportions of yearlings from 1970 to 1971. An increase in the number of yearlings, not a decrease in adults, caused most of the increased proportions of yearlings in 1971. Increased numbers of yearlings accounted for 79 percent of the increase in total males and the entire increase in total females between 1970 and 1971. Less of the change in total numbers during the decrease from 1972 to 1973 was caused by yearlings; the decrease in yearlings was, males and females respectively, 60 percent and 55 percent of the total reduction. In each year there was no significant difference between sexes in the percentages of yearlings. Slight differences in total numbers recorded for males versus females may not have been biologically meaningful because of the unknown proportion, particularly males, that did not mate.

Grouse observed during the breeding period were: yearlings, either raised on the study area or immigrants; adults recorded the previous year; or adults not sighted on the study area the previous year (Table 2). Yearlings and the adults not seen in the previous summer were the new

Table 1. The breeding population of spruce grouse at Gorge Creek, 1970-73.

	Year			
	1970	1971	1972	1973
Males				
Adults	30	34	40	38
Yearlings	10	21	17	14
Age unknown	1	0	0	0
Total	41	55	57	52
Males/km^2	8	11	11	10
% yearlings	25	38	30	27
Females				
Adults	28	25	31	26
Yearlings	7	21	19	13
Age unknown	1	0	0	0
Total	36	46	50	39
Females/km^2	7	9	10	8
% yearlings	20[A]	46[A]	38	33
Total	77	101	107	91
Birds/km^2	15	19	21	18

Table 2. New birds in the breeding population at Gorge Creek, 1971-73.

	Year and sex					
	1971		1972		1973	
	Males	Females	Males	Females	Males	Females
Birds in breeding population						
Yearlings	21	21	17	19	14	13
Adults						
Present the previous year	32	21	40	29	38	24
Not present, previous year	2	4	0	2	0	2
Total	55	46	57	50	52	39
New adults, as % of total adults	6	16	0	7	0	8
Yearlings, as % of total new birds	91	84	100	91	100	87

individuals in the population, and over the 3 years the yearlings constituted 91 percent (105/115) of such recruitment. Only 10 adults (5 percent, 10/194; 1971-73) were not recorded the previous summer on the study area. All but one of these 10 adults were located peripherally or used the study area in autumn or winter before being seen in summer. There was no evidence that marked birds made significant moves in breeding site once they attained adult age. Hence, the yearlings probably constituted more than the 91 percent of recruitment computed above.

PRODUCTION

Production of broods was low through the study (Table 3): over 4 years only 38 percent of all females were known to produce a brood and 29 percent successfully raised one to late summer. However, based on the presence of a brood, a nest, or a brood patch (Zwickel and Bendell 1967a) at least 60 percent of all females nested each year. Proportions of females nesting are undoubtedly minimal; some clutches were probably destroyed before the female developed a brood patch, and other females (unchecked for brood patch) may have incubated a clutch but lost the brood very early.

Summing all years, similar proportions of adults and yearlings were recorded as nesting (69 percent and 63 percent, respectively). Yet adults were more successful in producing young than were yearlings (Tables 3-5). Combining data of all

Table 3. Summary of breeding among female spruce grouse at Gorge Creek, 1970-73.

	Year							
	1970		1971		1972		1973	
	No.	%	No.	%	No.	%	No.	%
Females known to have nested[1]								
Adults	17	63	15	60	25	81^{A}	18	69
Yearlings	4	57	16	80	9	47^{A}	8	62
Total	21	60	31	69	34	68	26	67
Females known to have had broods								
Adults	14	54	10	40	15	48^{B}	9	35
Yearlings	2	29	7	35	1	5^{B,C}	6	46^{C}
Total	16	47	17	38	16	32	15	39
Broods in late summer.								
Adults	11	42	9	36	12	39^{D}	7	27
Yearlings	2	29	4	20	1	5^{D}	4	31
Total	13	38	13	29	13	26	11	28

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[1] Seen with broods, nest, or brood patch.

Table 4. Summary of production of juvenile spruce grouse at Gorge Creek, 1970-73.

	Year			
	1970	1971	1972	1973
Maximum number of juveniles recorded	66	75	67	60
Production into late summer				
Adult females				
no. broods	11	9	12	7
total juveniles	43	31	31	24
mean brood size (± 1 SE)	3.9(0.6)	3.4(0.6)	2.6(0.3)	3.4(0.5)
Yearling females				
no. broods	2	4	1	4
total juveniles	6	13	2	10
mean brood size (± 1 SE)	3.0(1.0)	3.3(0.9)	2.0(-)	2.5(0.6)
Total females				
no. broods	13	13	13	11
total juveniles	49	44	33	34
mean brood size (± 1 SE)	3.8(0.5)	3.4(0.5)	2.5(0.3)	3.1(0.4)
Total juveniles/ total females	1.25	0.96	0.66	0.85

Table 5. Nesting success and juvenile mortality in summer for spruce grouse at Gorge Creek, 1970-73

	1970		1971		1972		1973	
	No.	%	No.	%	No.	%	No.	%
Nesting success[1]								
Adults	0		3	67	9	11	6	33
Yearlings	0		6	67	4	0	1	100
Total	0		9	67[A]	14[2]	7[A]	7	43
Summer mortality of juveniles[3]								
Among broods of								
Adults	4	9	13	29[B]	33	52[B]	13	36
Yearlings	0		12	50	1	33	7	41
Total	4	8	25	36	34	51	20	38

Year

[1] Nests found - % hatch.

[2] The female was unknown for one nest.

[3] Number juvenile deaths - % of total juveniles.

years, 44 percent of the adults and 27 percent of the yearlings were known to have had broods ($P < 0.05$); 36 percent of the adults and 19 percent of the yearlings raised broods into late summer ($P < 0.05$). Several factors may account for the difference in success: more birds attempted to nest than were recorded, proportionally moreso among adults; nesting success was better for adults than yearlings; adults may have renested more than yearlings. The first two possibilities are not supported by the evidence obtained. Only one female was known to renest and two others may have done so; all were adults. Renests may have been more common for yearlings as well, but renests were probably difficult to identify (Keppie 1975).

Counts of juveniles alive at the end of the brood period (Table 4) were considered complete. Mean brood size of adults and yearlings in late summer were not significantly different (t test), but brood size among adults was always slightly larger. Numbers of juveniles produced by adults always exceeded those produced by yearlings, principally because numbers of adult females exceeded yearling females.

Two factors that contributed to loss of production are discussed here, namely nest destruction and juvenile mortality (Table 5). Thirty nests were located during laying or incubation stages but only 33 percent hatched. The cause of destruction was difficult to assess. There was no known desertion and all unsuccessful nests showed evidence of predation or at least scavenging. It was difficult to determine the extent that destruction might have been influenced by activities of field workers and dogs. Subjectively, I believe our procedures for finding nests and the time spent at them were similar in 1971-73. However, most nests were found in 1972 and 13 of the 20 unsuccessful nests occurred then. Either our activities at nests influenced predation more in 1972 than other years, contrary to our impressions, or a greater proportion of nests were located in vulnerable sites and we located many of them.

A minimum natural mortality of 42 percent (handling losses excluded) was calculated for juveniles in summer, from all broods and years combined. This mortality was the difference between the maximum number of juveniles seen in each brood and those remaining at the end of the brood period. Additional mortality undoubtedly occurred before the first counts of broods. Recorded mortality in broods of adults and yearlings was similar for all years combined, 41 percent and 46 percent respectively. Four adults and four yearlings (13 percent of all broods) were known to have lost all chicks. Juveniles in these broods were not known to have died from handling and losses of entire broods may be normal. The loss of all chicks did not seem to be dependent on brood size; brood size (earliest counts) ranged from three to four for adults and three to five for yearlings.

I believe the juvenile mortality reported here largely reflects natural losses despite an intensive effort to capture and mark young chicks. There were 222 juveniles wing-tagged within or immediately adjoining the study area prior to 36 days of age. All juveniles in this sample were in broods that could be followed through the summer. Loss until 40 days of age was 36 percent. The loss was equated to death since juveniles were censused and all considered marked before dispersal. Information is scarce on mortality of juvenile spruce grouse. McCourt (1969) reported 26 percent mortality occurred before 10-11 weeks of age but, again, birds were frequently handled. Ellison (1974) reported 19 percent mortality for juvenile spruce grouse in Alaska, as the difference between the juveniles hatched and total brood counts in August. Ellison's method may underestimate mortality because of the time period over which hatching occurs. Clutch size and mortality differed between Alaska and Alberta grouse (Ellison 1974, this study) and, hence, my data of tagged chicks should be compared to a control area with similar productivity and mortality levels. Sixty percent of the juveniles were wing-tagged before they were 10 days old, a period that is probably concurrent with much natural mortality, as was reported for juvenile blue grouse (*Dendragapus obscurus*) (Zwickel and Bendell 1967a). Hence, it is difficult to separate mortality induced by handling and tagging from that which occurs naturally. Presently there is no substantial evidence that the intensive tagging compounded natural mortality.

Several aspects of the reproductive cycle were poorest for yearlings in 1972: a lower nesting attempt, poorer nesting success, fewer broods, and a smaller mean brood size. Unless there were changes in early nest destruction between years I consider the decreased nesting attempt to have been real. Adults also showed a decrease in nesting success and mean brood size in 1972. Data on clutch size were too few for a comparison between years but I believe smaller broods in 1972 resulted from increased mortality, not smaller clutches.

The greatest change in production between years was a 25 percent reduction (44 to 33 juveniles) from 1971 to 1972 (Table 4). The lower production resulted from changes among yearling females; a smaller number of broods was more important than the change in brood size. Poorer nesting success and/or fewer attempts to nest caused decreases in yearlings with broods. An index to production was calculated from the juveniles alive at the end of summer and total females in the breeding population (Table 4). The lowest production ratio, 0.66 juveniles per female, occurred in 1972 when total population size was highest. Production ratios over the four summers were inversely associated with density, decreasing as breeding females increased ($r = -0.79$; $P > 0.05$). The most obvious point in all data collected was the low reproductive success in 1972.

SURVIVAL OF BREEDING POPULATION

Survival rates for the breeding population were calculated over both the annual and autumn-winter periods. An annual rate (%) of minimum survival (S) was obtained from individuals seen between 15 May and 15 August at Gorge Creek in year *X* that were also seen on the study area in *X* + 1. The complement of survival (100 - *S*) equals loss (death and emigration) between 15 May of *X* and *X* + 1. Survival over autumn and winter was analyzed separately because most loss was presumed to occur then. Survival over the autumn-winter period was computed from only those birds known to be alive on 31 August and the number of them that survived through the following 31 March.

Minimum annual survival rates are given in Table 6. For all years combined, annual survival rates for males and females, respectively, were 76 percent and 63 percent ($P < 0.05$). For both sexes, survival was usually slightly greater for adults than yearlings. The differences in survival rates between age classes may not be very meaningful because ~~of the rather~~ low densities of birds. For example, when the rates for both yearlings and adults are applied to the number of adults for a given year the results differ by only one or two birds (except females, 1972-73). Also within years, survival of males exceeded that of females among both adults and yearlings. No comparisons of data within and between years were significant. Some grouse were seen off the study area after they emigrated during or following the breeding period in year *X*. By including these emigrants as survivors the minimum annual survival increased to 80 percent for males and 66 percent for females.

The increased loss of yearling females in 1972-73 is described here. Nine of the 13 yearlings present in 1972 were

Table 6. Annual survival of adult and yearling spruce grouse of the breeding population[1] at Gorge Creek, 1970-73. Percentages are birds counted in year *x* that survive to 15 May of *x* + 1, and are counted on the study area in *x* + 1.

	Year					
	1970-71		1971-72		1972-73	
	No. birds in 1970	% *S* to 1971	No. birds in 1971	% *S* to 1972	No. birds in 1972	% *S* to 1973
Males						
Adult	28	82	34	74	36	78
Yearling	10	80	21	71	14	71
Total	39[2]	82	55	73	50	76
Females						
Adult	24	71	25	64	30	67
Yearling	7	57	20	65	13	31
Total	32[2]	69	45	64	43	56

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[1] Excluding birds killed during capture and removed by experiment.

[2] One bird of unknown age included.

were absent in 1973. Of these nine, four were lost in May 1972 (one known death, three assumed emigration), three were lost in winter (two deaths likely), and two (known) emigrated after 1 April 1973. Hence, the greater than normal loss in 1972-73, which reduced *s*, included much emigration.

Among years, survival through autumn and winter for males ranged from 84 to 95 percent; for total females survival ranged from 85 to 92 percent (Table 7). Over all years, survival through autumn and winter was 87 percent for males and 89 percent for females. There were no significant differences in any comparisons of survival data. These rates include some birds that survived after emigrating but they may still be minimal because the fate of others was unknown. Maximum survival of all birds was 93 percent because 7 percent of the birds alive on 31 August were either found dead or were assumed to have died before 31 March.

[illegible]ne adult and yearling grouse were found dead dur[illegible]udy; individuals were identified from band comb[illegible]s in 23 cases, and age and sex were determined for 31 an[illegible]birds respectively. To evaluate the distribution of morta[illegible] throughout the year I used only those deaths that occurr[illegible] during three full-year periods, May 1970 through April [illegible]73 (Figure 1). I used 17 birds found dead and an additi[illegible]al 26 grouse that had been localized residents. The absence of further sightings of these 26 birds was assumed to indicate their death. For these residents I assume that death occurred shortly after the last sighting. Thirty-seven of

Table 7. Survival of adult and yearling spruce grouse of the breeding population[1] at Gorge Creek over autumn and winter, 1 September - 31 March, 1970-73.

	Year					
	1970-71		1971-72		1972-73	
	Birds alive 31 Aug.	% *s* to 31 Mar.	Birds alive 31 Aug.	% *s* to 31 Mar.	Birds alive 31 Aug.	% *s* to 31 Mar.
Males						
Adult	27	96	31	81	33	85
Yearling	10	90	19	90	13	85
Total	38[2]	95	50	84	46	85
Females						
Adult	21	86	19	95	24	92
Yearling	6	100	17	88	9	67
Total	28[2]	89	36	92	33	85

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[1] Excluding those removed by experiment. Of the 231 birds, 224 were known to be alive on 31 August and 7 were seen last from 18-31 August.

[2] One bird of unknown age included.

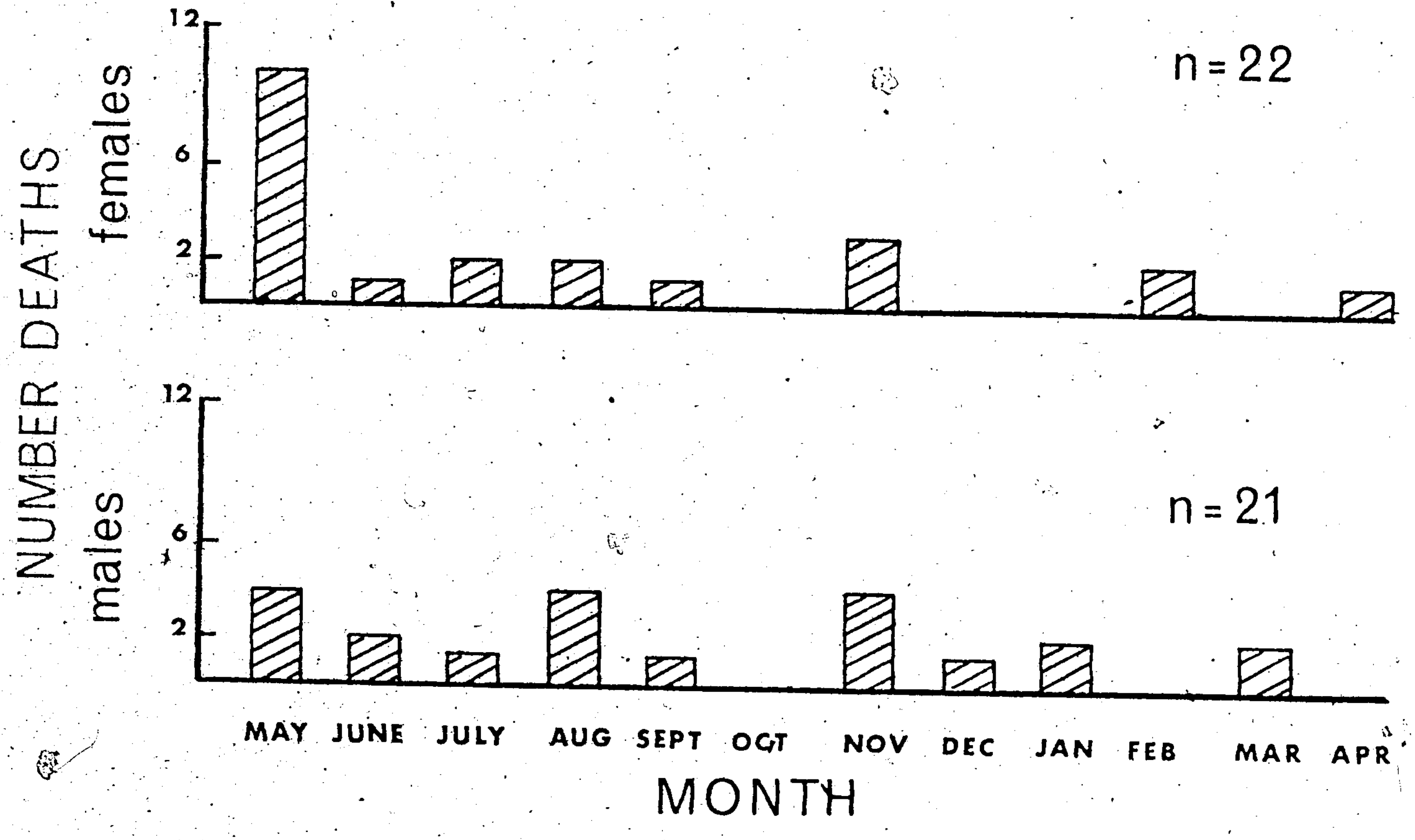

Figure 1. Time of death of 43 adult and yearling spruce grouse at Gorge Creek, May 1970 through April 1973. A mid-point date is used for 17 birds between date last seen and found dead. The month of last sighting is given for 26 other residents assumed to have died.

of these 43 birds had been part of the breeding population; the other six were present only in winter.

Fifty-two percent (11/21) of the males and 68 percent (15/22) of the females died in the period of May through August; this difference was not significant ($\chi^2 = 1.88$). The distribution of mortality for females was significantly ($\chi^2 = 11.83$) concentrated, compared with a uniform mortality through the year. The recorded mortality of males was also greatest in May through August; the difference between observed and expected values approached significance ($\chi^2 = 3.20$).

A total of 34 males and 45 females were lost from the breeding population over the 3 years (Table 8). Fifty-nine percent (20/34) of the males and 24 percent (11/45) of the females were lost during the 7-month autumn-winter period. Differences between sexes were significant ($\chi^2 = 8.21$). The observed loss of females was significantly lower ($\chi^2 = 21.04$) than expected, assuming uniform loss throughout the year; the observed - expected difference for males was not significant ($\chi^2 = 0.03$). The known and suspected mortality that occurred in autumn and winter (including hunting) was only 41 percent of the total annual loss among males and 24 percent among females.

I estimated that 51 grouse were lost from the breeding population because of death (Table 8). Grouse could be legally shot each year but hunting in the pine forest was negligible. Only three deaths were attributed to hunting.

Table 8. Loss of spruce grouse from the breeding population at Gorge Creek, 1970-72.

	Sex	
	Males	Females
Total loss, all 3 years	34	45
Mortality	23	28
May-August	7	15
September-March[1]	13	9
Time unknown	2	2
Hunter kill	1	2
Emigration	7	13
Known	5	3
May-August	1	3
September-March	3	0
Time unknown	1	0
Probable[2]	2	10
Cause unknown	4	4
September-March	3	0

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[1] Totals include 11 males and four females for which month of death was documented (Figure 1). Two other males and five other females that disappeared are also included; they presumably died although accurate dates were not obtained.

[2] Primarily composed (9/12) of yearlings last seen in May and June and assumed to be still dispersing.

Since reliable dates of death were obtained for 37 birds (77 percent, 37/48, excluding hunting) the timing of natural mortality recorded in Figure 1 was probably representative for all birds.

The size and age composition of a breeding population is affected by the survival of adults from the previous year, survival and fidelity of yearlings from the previous year, and recruitment of yearlings. Percent losses of adults (mostly mortality) were generally similar between years and had no great impact on changes in numbers. But the increased loss of yearling females during 1972-73 did help change the number of total females in 1973, as follows. Numbers of adult females decreased from 1972 to 1973 but the survival rate of adults remained constant. The decrease in adults resulted from fewer of the yearlings in 1972 progressing into the adult category of 1973. The reduction in total females in 1973 resulted from the reduced increment into the adult category and a lower recruitment of yearlings in 1973.

SURVIVAL OF JUVENILES IN WINTER

Survival over winter was calculated for those juveniles present at the start of winter (Table 9).

Winter survival rates ranged from 78 percent to 100 percent for males and 79 percent to 90 percent for females. Over the 3 years, 87 percent (123/141) of all juveniles alive at the start of winter were still alive, though perhaps off the study area, on 1 April. Survival was the same for both

Table 9. Survival of juvenile spruce grouse over winter at Gorge Creek, 1970-73. Winter began with first permanent snow cover (10 November, 17 and 1 December 1970-72, respectively) and ended 31 March.

	Winter and sex					
	1970-71		1971-72		1972-73	
	Males	Females	Males	Females	Males	Females
No. birds alive start of winter						
Raised on area	5	4	20	10	8	3
Immigrants	18	15	14	18	10	16
Total	23	19	34	28	18	19
Known winter loss: death - emigration						
Raised on area	0-0	0-0	1-0	0-0	1-0	0-0
Immigrants	0-0	2-0	0-0	0-0	1-2	0-0
Total	0-0	2-0	1-0	0-0	2-2	0-0
Assumed winter loss: death or emigration						
Raised on area	0	1	2	2	0	0
Immigrants	0	1	2	0	1	2
Total	0	2	4	2	1	2
% *known* survival ≥ 1 April[1]						
Raised on area	100	75	90*	70*	88	100
Immigrants	100	80	79*	100	70*	88
Total	100	79	85	89	78	89

[1] Reciprocal of *known* survival for total birds equals winter loss except females in 1971-72 (loss = 7%) and males in 1972-73 (loss = 28%). In four individual cases (*), winter loss cannot be obtained from the data in the above columns; in two cases birds left the study area in mid-winter but were found alive >1 April, and two other birds were seen emigrating during the very early period of dispersal (loss attributed to dispersal) but their survival to 1 April was unknown.

sexes, and there was no consistent trend in survival related to whether birds were raised on the study area or had immigrated. Survival rates listed in Table 9 may be minimal because the fate of some birds was unknown. For all years combined, 18 juveniles were lost over winter. Known mortality of five was only 4 percent of the cumulative juvenile cohort at the start of winter (5/141). Two other birds moved off the study area in winter but were seen alive after 1 April, and the fate of 11 others was not known. Clearly, overwinter mortality of juveniles was negligible.

There were differences between years in proportions of juveniles lost in winter (Table 9) but they were not significant. These differences were not known to be caused by mortality but resulted largely from birds of unknown fate. Several of these grouse were sighted near boundaries and may have moved a short distance away into habitat not regularly searched.

DISPERSAL

Dispersal involved emigration and immigration; dispersal from the study area is presented as percentage rates of emigration. Note that many birds moved during the dispersal period but did not leave the study area. Dispersal was a two-phase process. Some birds moved only in autumn, others only in spring, and others at both times. Dispersal involved only immature birds, juveniles in autumn and the same year class, now yearlings, in spring. Juveniles that remained on the study area in late winter and which were available to take part in subsequent dispersal are termed *overwintering juveniles*. Birds of other age classes migrated in autumn and spring but are not included in the dispersing cohort.

A rate of emigration in autumn was obtained from the juveniles present before break-up of broods and the number of these individuals absent in winter. A rate of emigration in spring was obtained from the number of overwintering juveniles that were absent from the study area in the next breeding period. All analyses exclude birds known to have died.

Dispersal in Autumn

Dispersal in autumn is summarized in Table 10. In each year considerably more females dispersed from the study area than males. Differences were significant in 1970 and 1972. Over the entire study, emigration of females (75 percent) was significantly greater ($\chi^2 = 14.70$) than that of males (41 percent). Concurrent with emigration was the immigration of other juveniles; in all years females again predominated. Numbers of males and females coming onto the study area in autumn were, respectively, 50 and 44 percent greater than the number that emigrated (all years combined). Not all new birds remained however; 29 percent of these males and 32 percent of the females were not seen at Gorge Creek in winter. Of these juveniles that disappeared from autumn to winter (transients;

Table 10. Dispersal of juvenile spruce grouse in autumn at Gorge Creek, 1970-72.

	Year and sex					
	1970		1971		1972	
	Males	Females	Males	Females	Males	Females
No. juveniles before dispersal	25	18	34	28	14	21
No. not seen on area in winter	10	14	14	18	6	18
% emigration	40^A	78^A	41	64	43^B	86^B
No. immigrants, remaining in winter	8	15	14	18	10	16
No. transients through area	1	6	8	11	4	6
Total juveniles present in winter	23	19	34	28	18	19
Net change: before to after dispersal						
No.	-2	+1	0	0	+4	-2
%	8	6	0	0	29	10

13 males, 23 females), 28 percent died from natural causes or handling, 11 percent emigrated, and the fate for 61 percent was unknown.

The resulting number of juveniles that wintered each year was very similar to the number present before dispersal, ranging from a 10 percent decrease (two birds) to a 29 percent increase (four birds). Combining the data of all years, the number of juveniles in winter was only 3 percent (two birds) and 2 percent (one bird) different, males and females respectively, from the number present in late summer. Clearly, in each year dispersal in autumn did not reduce numbers of juveniles.

There were several similarities in between-year comparisons of dispersal data. For both males and females, the number present before dispersal, the number of immigrants in autumn, and the total number of birds present in winter were all greatest in 1971 (and 1971-72 winter) (Table 10). Within each sex, but especially for males, emigration rates were similar each autumn in spite of considerable differences in numbers of juveniles present in late summer.

Dispersal in Spring

There were only small reductions between numbers of juveniles present before dispersal in autumn and overwintering juveniles present before dispersal in spring (a maximum of five birds or 19 percent; row 1, Table 10 and row 3, Table 11). Summing all years, males and females present

Table 11. Dispersal of spruce grouse in spring at Gorge Creek, 1971-73.

	Year and sex					
	1971		1972		1973	
	Males	Females	Males	Females	Males	Females
No. overwintering juveniles before dispersal						
Raised on area	15	3	17	8	7	3
Autumn immigrant	8	12	12	18	6	14
Total	23	15	29	26	13	17
No. not seen on area in summer						
Raised on area	4	1	12	6	2	3
Autumn immigrant	3	6	8	10	3	9
Total	7	7	20	16	5	12
% emigration						
Raised on area	27	33	71	75	29	100
Autumn immigrant	38	50	67	56	50	64
Total	30[A]	47	69[A]	62	39	71
No. immigrants, recorded in breeding period	5	13	6	9	4	8
No. transient yearlings	0	4	0	1	1	2
Total yearlings in breeding period	21	21	17[1]	19	14[1]	13
Net change: before to after dispersal						
No.	-2	+6	-12	-7	+1	-4
%	9	40	41	27	8	24

[1] Total exceeds by two the sum of non-emigrating birds plus row 10; both were present until late autumn but returned in spring.

before dispersal in spring were, respectively, only 11 percent (73 - 65 = 8 birds) and 13 percent (67 - 58 = 9 birds) lower than the number the previous autumn. However, there were many different juveniles in the counts at those two times because of emigration and immigration in autumn.

A summary of dispersal in spring is given in Table 11. Within years, emigration of females generally exceeded that of males. Over all years, 60 percent of the females and 49 percent of the males ($P > 0.05$) emigrated in spring. The differences between sexes within years were often small compared to those in autumn. Emigration was not significantly different between birds raised at Gorge Creek and those that immigrated in autumn.

Immigration of females also exceeded that of males. Over all years, yearling males arriving in spring-summer were 50 percent fewer than the number that emigrated; the number of new females was 6 percent greater than the number that emigrated. Most new birds either remained for or were first seen in the breeding period: 94 percent for males and 81 percent for females. Only eight birds were recorded as transients; four emigrated and were alive elsewhere, one died from handling, and the fate of three was unknown.

The overall influence of dispersal in spring was measured by comparing the number of overwintering juveniles before dispersal with the total number of yearlings in the next breeding period. Differences between these two counts, within sexes and years, varied from a 41 percent decrease (12 birds) to a 40 percent increase (six birds) (Table 11). The changes in numbers of birds in spring were greater than the changes that resulted from dispersal the previous autumn in four of six instances within years (row 8, Table 10 and row 14, Table 11). For all years combined, the net changes from dispersal in spring were reductions of 20 percent (13 birds) for males and 9 percent (five birds) for females.

The number of overwintering juvenile males present before dispersal was greatest in 1972; this high count followed the high number of juveniles in late summer of 1971. Emigration among total males was significantly greater in 1972 than in 1971. Since the number of immigrant males in spring-summer was similar each year it follows that emigration was the most influential component in how dispersal modified numbers of overwintering males.

The number of females present in late winter was also greatest in 1972. Dispersal in spring of 1972 reduced considerably the number of potential female recruits, a sharp contrast to the net increase in 1971. The reduction in 1972 resulted from both reduced immigration and increased emigration.

The most notable change between 1972 and 1973 was the decreased emigration of males in 1973 which largely caused the equal pre- and post-dispersal numbers.

Survival

Birds were initially classed as emigrating if there were no further sightings of them on the study area. It is critical though to know whether the loss was due to emigration, as previously implied, or death.

Thir[illegible]s and 50 females, data of 1970-72 combined, were said [illegible] dispersed from the study area in autumn. Sixteen p[illegible] these birds (13/80) were seen alive during (of[illegible]udy [illegible]r after (on or off study area) the following [illegible]er. [illegible]at is, I lost contact with at least 16 percent [illegible] th[illegible] juveniles in autumn because they emigrated.

S[illegible]l is documented for birds classed as emigrating in spri[illegible] Table 12. A total of 32 male and 35 female overwint[illegible]ng juveniles were absent in the next breeding period o[illegible]e study area. Of this total, 66 percent of the males and [illegible] percent of the females were seen alive after dispersal [illegible] spring. These birds survived at least into summer and, for most, into autumn. Eighty percent of the resightings [illegible]re of birds that returned for the following winter(s). [illegible]d work stopped in early autumn of 1973 and I was less able to determine survival of birds that emigrated that spring. The known short-term survival of spring emigrants becomes 72 percent (36/50, males and females) with the data of 1973 excluded.

I compared known survival of spring emigrants and non-emigrants for an approximate 12-month period following 1 April (used as a starting date for dispersal). Survival into March following dispersal (1971 and 1972 only) was 72 percent (31/43) for non-emigrants and 52 percent (26/50) for

Table 12. Survival of spruce grouse that dispersed from the Gorge Creek study area in spring, 1971-73. Survival was documented through the dispersal period and at least into summer.

	Year and sex					
	1971		1972		1973	
	Males	Females	Males	Females	Males	Females
Raised on study area						
No. emigrated	4	1	12	6	2	3
% known survival	100	100	75	67	0	0
Autumn immigrants						
No. emigrated	3	6	8	10	3	9
% known survival	100	83	50	60	33	44
Total						
No. emigrated	7	7	20	16	5	12
% known survival	100	86	65	63	20	33

emigrants. Differences are significant ($\chi^2 = 4.83$). But I am certain the estimate for emigrants is low because of the unknown fate of many that did not return for their second winter on the study area. Hence, spring emigrants survived well through the dispersal period itself and their subsequent survival for nearly a year was probably close to that of birds not emigrating in spring. The annual survival of those spring immigrants that were present in the immediate breeding period (1971 and 1972) was 69 percent (20/29). The survival rate of these latter birds reflects that of dispersers that have successfully recruited into the breeding population.

At least 257 juveniles (all years) were found on the study area in autumn. These birds were either raised there or had immigrated and they subsequently either remained, emigrated, or died there. Only two juveniles, 1 percent of the total, were found dead during autumn. In spring, at least 157 yearlings (all years) were recorded on the study area; they were overwintering juveniles and new yearlings before 1 June. Again, mortality was insignificant as only four deaths (3 percent) were recorded. Probably not all dead birds were found, but if mortality were a common fate of dispersers many more dead birds would have been present and some of them should have been found.

Summary of Dispersal, and Survival, Autumn Through Spring

At this point it is appropriate to reiterate the key points on dispersal and survival of juveniles from autumn through spring. The patterns of change in numbers were quite consistent each year.

Emigration of juvenile female grouse was greater than that of males in each autumn. Concurrent with emigration was the immigration of other juveniles, and again females predominated. Late summer counts of juveniles varied between years but rates of emigration were quite constant. Because of the compensatory effect of immigration, numbers of juveniles seen in winter were almost identical to numbers present before break-up of broods.

Little mortality was recorded during dispersal in autumn. Survival through the ensuing winter was high and little emigration occurred then. Hence, numbers attained in late summer through reproduction were carried through to the end of winter with little change.

Beginning in March a second period of dispersal began. Evidence indicated that the disappearance of some overwintering juveniles in spring resulted from emigration. As in autumn, mortality during the period of movement was slight. Many birds that dispersed in spring were seen later, indicating that their survival was good. Females again predominated among dispersing individuals; differences between sexes were slight compared with those in autumn.

In autumn, dispersal produced only a very slight net effect on numbers. But in spring there was a greater change, as measured by the difference between the numbers of juveniles in late winter and total yearlings in summer. Consequently, dispersal in spring seemed to have a greater and a more variable impact on numbers of yearlings in the breeding population.

Numbers of yearlings in the breeding population were determined from the interaction of three factors: the number of wintering juveniles, spring emigration, and immigration in spring-summer. Emigration in autumn was nearly constant and numbers of wintering juveniles varied directly with the numbers present in late summer. Spring emigration, therefore, acted upon a group of juveniles whose size was directly dependent on production during the previous summer. The effect of production on dispersal in spring was most obvious for males in 1973. Immigration of males in 1972 was similar to that in 1973. But even though the rate of emigration in spring of 1973 was low the number of overwintering (1972-73) juveniles was also low and thus the yearling count in summer of 1973 decreased. The influence of production on yearling recruitment seems to have been only indirect. For production to have directly influenced the number of breeding yearlings the rate of emigration in spring would have to be constant, which did not occur. Immigration in spring further modified the relationship between production and recruitment (discussed later).

Time of Dispersal in Spring

An approximation to the time of emigration in spring is given in Figure 2; it is based on the dates overwintering juveniles were seen last on the study area. There were no significant differences between years in the proportions of birds remaining on each successive date, and all data were combined. Most of the study area was covered in a 7-day period. I suspect most birds emigrated within 7 days of the last sighting. I was not aware of behavioral differences among birds in spring that would account for one sex being more secretive than the other and, thus, more difficult to locate.

There was a steady disappearance of males from early March to mid May. In sharp contrast, almost all emigrating females were still present in early April; the single exception was a known movement on 14 March. Emigration of females accelerated about mid-April, and consequently, proportions of males and females still present at the end of April were similar.

During field work it was obvious that I lost contact with many overwintering juveniles long before new birds were seen. Although 68 percent of the emigrants (sexes combined) were seen for the last time before 30 April 83 percent of the immigrants were not seen until at least 7 May; 29 percent were not seen until after 1 June. Five birds (three females) were sighted first in March but four were close to a boundary and may have moved just a short distance from a winter site off the study area (known for one bird). Four of the five new birds in March moved further later in the spring. Hence,

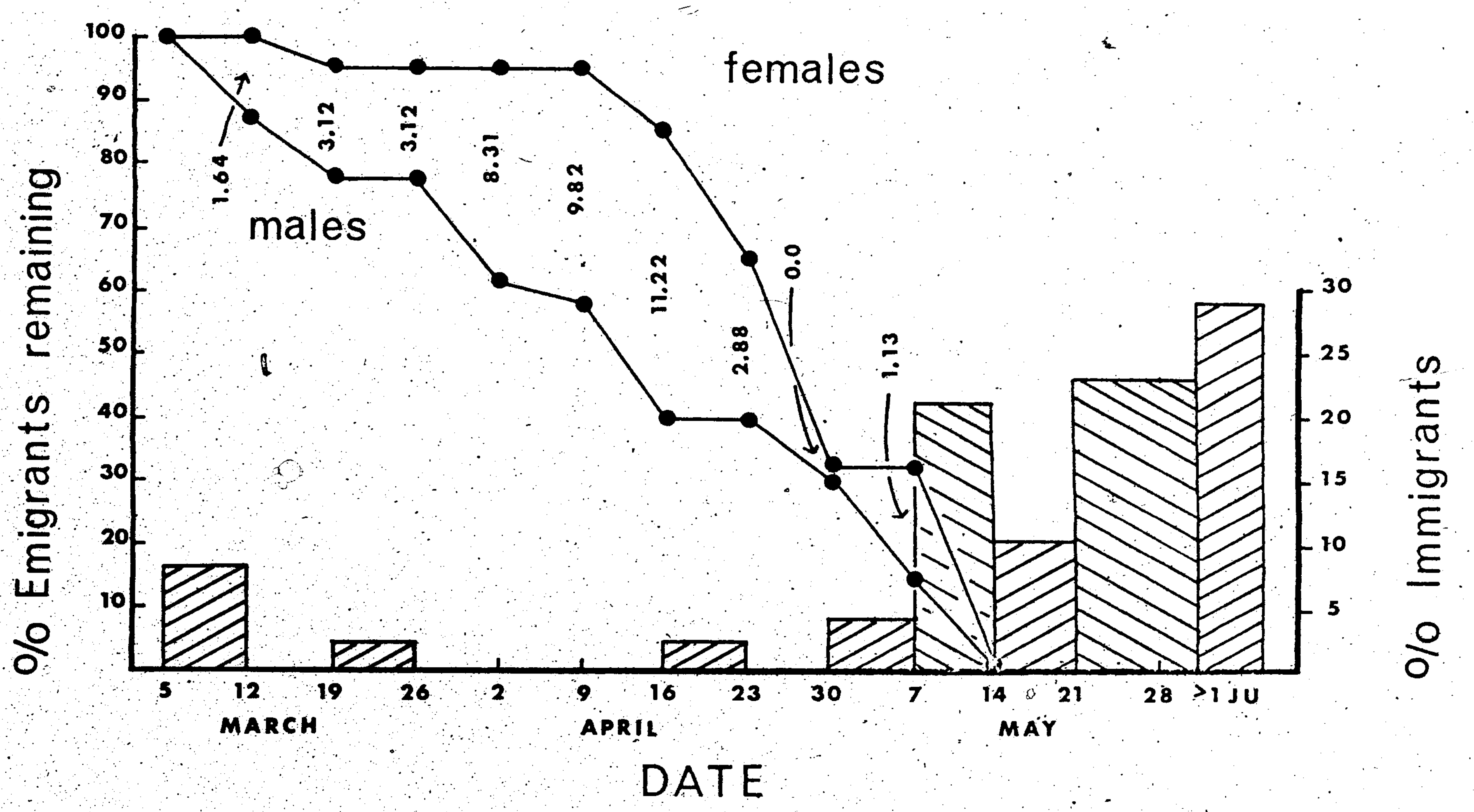

Figure 2. Time of dispersal of spruce grouse in spring at Gorge Creek, 1971-73 (all years combined; 1973 experimental section excluded). Percentages of emigrants (27 males, 30 females) indicate birds seen on or after the given date. Percent immigrants (n = 48, sexes combined) are those seen for first time. Calculated χ^2 values are given for the difference between sexes of emigrants ($\chi^2_{0.05, 1\ df} = 3.84$).

immigration of yearlings was not apparent until after the bulk of emigration.

Immigration shown in Figure 2 includes the earliest sightings of unmarked birds. With one exception there were no significant differences in timing of immigration between sexes or years. The exception was barely significant ($T = 31.5$ whereas $T_{0.05} = 32$; rank test, White 1952) and was between males and females in 1972, when females were seen earlier.

Density and Emigration

Many factors could affect dispersal and all may interact. Only density was investigated here. Results may be meaningful because density is the pivotal force in regulation theory. Although population size per se may not induce dispersal it may be indicative of the level of effect of some proximal factor.

Emigration in autumn was plotted against the number of adults and yearlings present and the number of juveniles present for each sex (Figure 3). I used adults-yearlings counted during the late brood period (between 1 August and the last date a complete or partial brood was sighted: 2, 12, and 4 October 1970, 1971, and 1972 respectively); juveniles used were those present before dispersal.

There was no obvious positive trend between emigration of either sex in autumn and numbers of adults-yearlings or

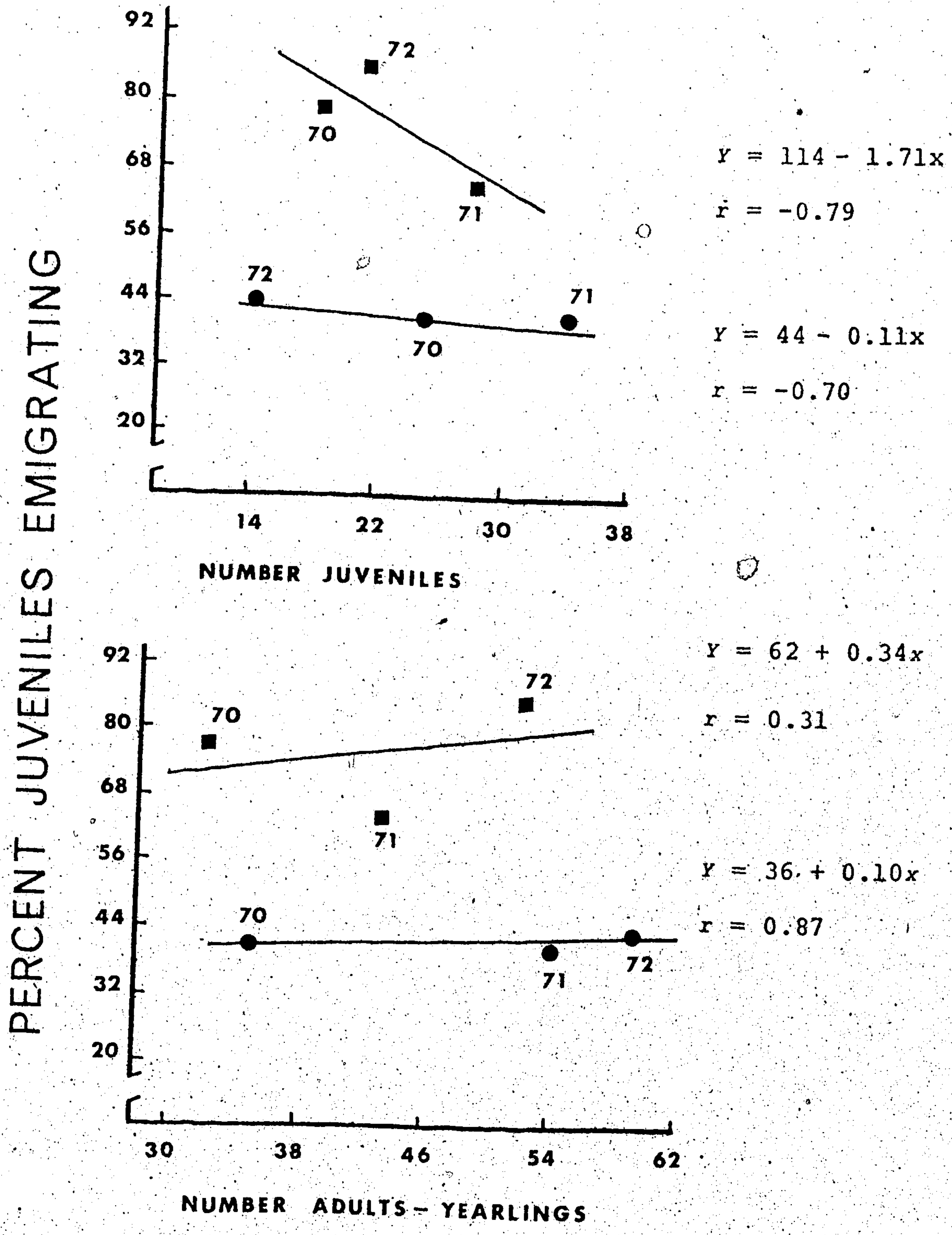

Figure 3. Dispersal of juvenile spruce grouse from the study area at Gorge Creek in autumn, 1970-72. Emigration is plotted against numbers of adults and yearlings present from 1 August to the end of the brood period and juveniles present before dispersal (males = ●, females = ■).

juveniles. Emigration of males was similar each year but numbers of adult and yearling males increased 69 percent through the study and juveniles decreased 59 percent between two successive years. Adult and yearling females increased 63 percent during the 3 years but emigration increased only 10 percent. Proportions of females that left the study area were, in fact, inversely related to juvenile numbers. Recall that for each sex there were no significant differences in proportions emigrating between years (Table 10).

I analyzed emigration in spring according to the number of adults and yearlings present during 1 March to 15 May and the number of overwintering juveniles present before dispersal (sexes separately)(Figure 4). The 1 March date confines the interpretation to the possible effects of population size only during late winter. All emigrants except one apparently moved by 15 May.

Emigration of both sexes in spring increased as the number of wintering adults-yearlings increased, and emigration of males was correlated equally well with wintering juveniles. The population was high in 1971 and the highest count of juveniles before dispersal in autumn occurred then. High numbers in 1971 did not induce an immediate increase in mortality of juveniles in summer or emigration in autumn. There was no apparent response to high numbers until dispersal in spring, 1972. But emigration, of males at least, was not extremely responsive to population size. Numbers of adult and yearling males were constant from 1972 to 1973 but emigration decreased from 69 to 39 percent. No

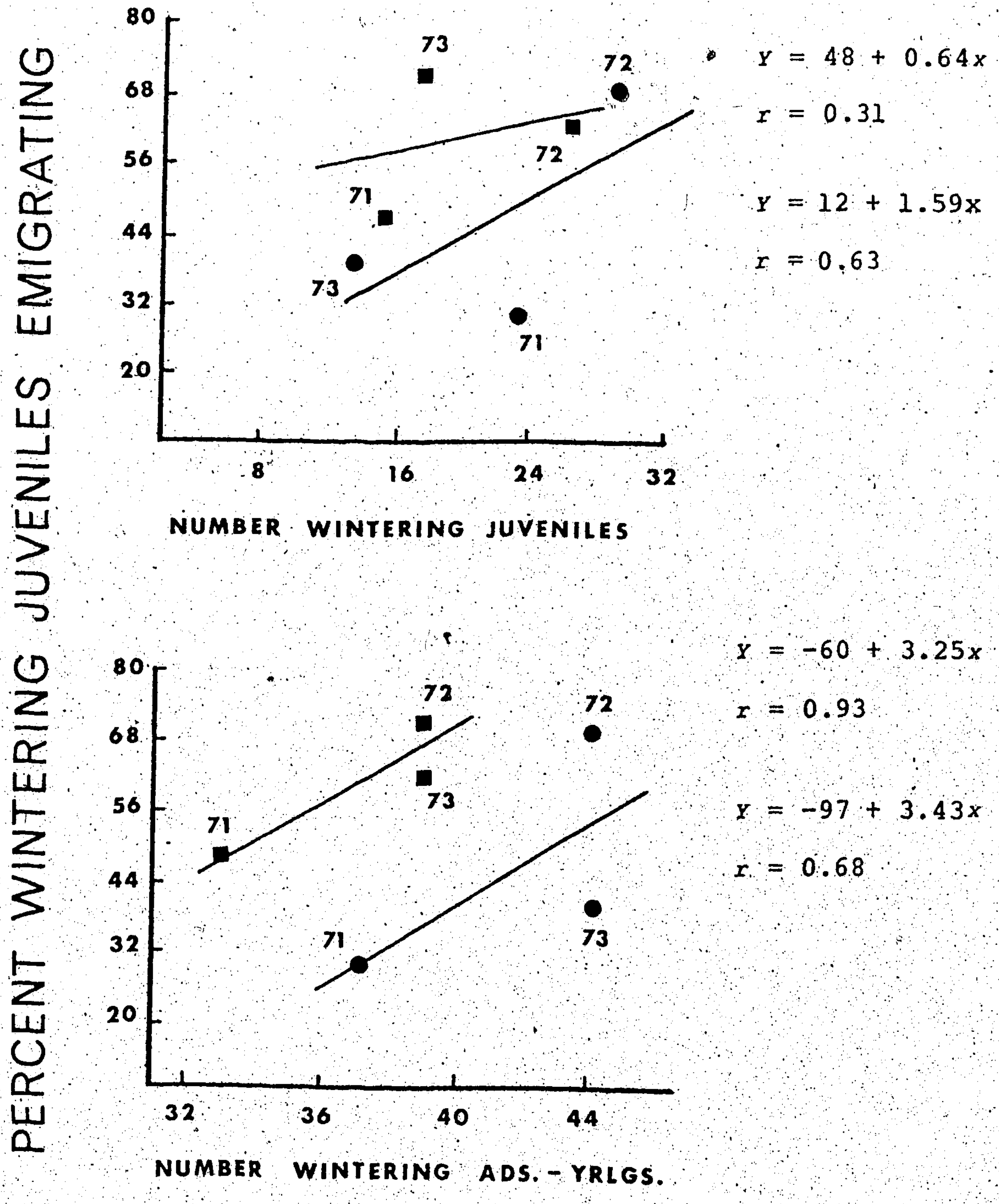

Figure 4. Dispersal of spruce grouse from the study area at Gorge Creek in spring, 1971-73. Emigration is plotted against numbers of overwintering adults and yearlings present from 1 March to 15 May and overwintering juveniles present before dispersal (males = ●, females = ■).

regressions of density on emigration were significant.

There is at least one factor to consider in the relation between adults and yearlings in late winter and emigration in spring. Twenty-two percent (51/236, all years) of the adults and yearlings seen between 1 March and 15 May were not present in the breeding period. Percentages for females were 37 (41/111) and for males were 8 (10/125). Mortality was slight and the losses mainly represent migration to breeding sites elsewhere. Considering the 41 females only, the last sighting of individuals extended from 21 February to 30 April; 34 percent were not seen after 1 April, 44 percent were not seen after 9 April, and 71 percent were not seen after 16 April. The data suggest that many of these females were not present when younger birds actually dispersed (Figure 2).

Certain small parts of the study area were used by grouse mainly in winter. For all years combined, 47 percent of the 32 adult and yearling males and 88 percent of the 17 adult and yearling females in these sites were not present in summer. Emigration of overwintering juveniles from these sites in spring was 71 percent of 35 males and 65 percent of 26 females. Although wintering juveniles undoubtedly contacted other older birds in late winter (known in a few cases) they were predominantly associated with older birds located in those sites, many of which were there only temporarily.

Migration was common and population size was not static in either autumn or spring. The flux of adult and yearling numbers and the period over which emigration took place make it difficult to obtain a single density figure that is meaningful. Certainly, many adult females present through the winter were apparently not there when most young females emigrated in spring. Many adults were resident only in winter and if they did influence the tendency to disperse it was not made in the context of defense of their breeding site. Hence, investigations of effects of population size need to be more explicit than solely a count of gross numbers.

Effect of a Manipulation of Density on Emigration

After the first 2 years of study I realized that emigration was an important form of loss. I then decided to test a possible cause of the movement. Data on hand suggested that emigration in spring was variable, in contrast to that in autumn, and that it may have influenced the size of the breeding population because it occurred just before breeding.

Results from 1971 and 1972 suggested a possible effect of adults and yearlings in late winter on emigration in spring. Therefore, in late winter of 1972-73 I removed the adults and yearlings from part of the study area to test the hypothesis that emigration was determined by their presence. Specifically, would a decrease in adult-yearling density in late winter reduce emigration of wintering juveniles?

There was no other site in the region similar to that at Gorge Creek in terms of density and history of marked birds. Manpower available was also insufficient to monitor more than one area. The only alternative was to divide Gorge Creek into experimental and control sections. Reduced numbers of birds resulted but I anticipated that the removal could be complete and movements for all potential emigrants monitored.

The experimental section was a 60 hectare tract at one end of the study area, surrounded on two sides by contiguous spruce grouse habitat that was not part of the study area. The control section consisted of the remaining 459 hectares at Gorge Creek, separated from the removal section by 200 meters of uninhabited creek bottom. I felt that to get the clearest picture of the effects of reduced density on emigration the removal had to be completed before dispersal. Accordingly, I began to shoot birds on 27 February 1973.

A summary of the removal and subsequent dispersal is presented in Figure 5 and Table 13. Twenty-two birds were removed, 11 of each sex; of these, only 12 were resident there the previous summer. Sixteen of the 22 birds were removed by 2 March, and all but two by 19 March. The remaining two birds, males, were taken when first seen in that section, 29 March and 20 April. Both males were at the boundary of the experimental section and their histories

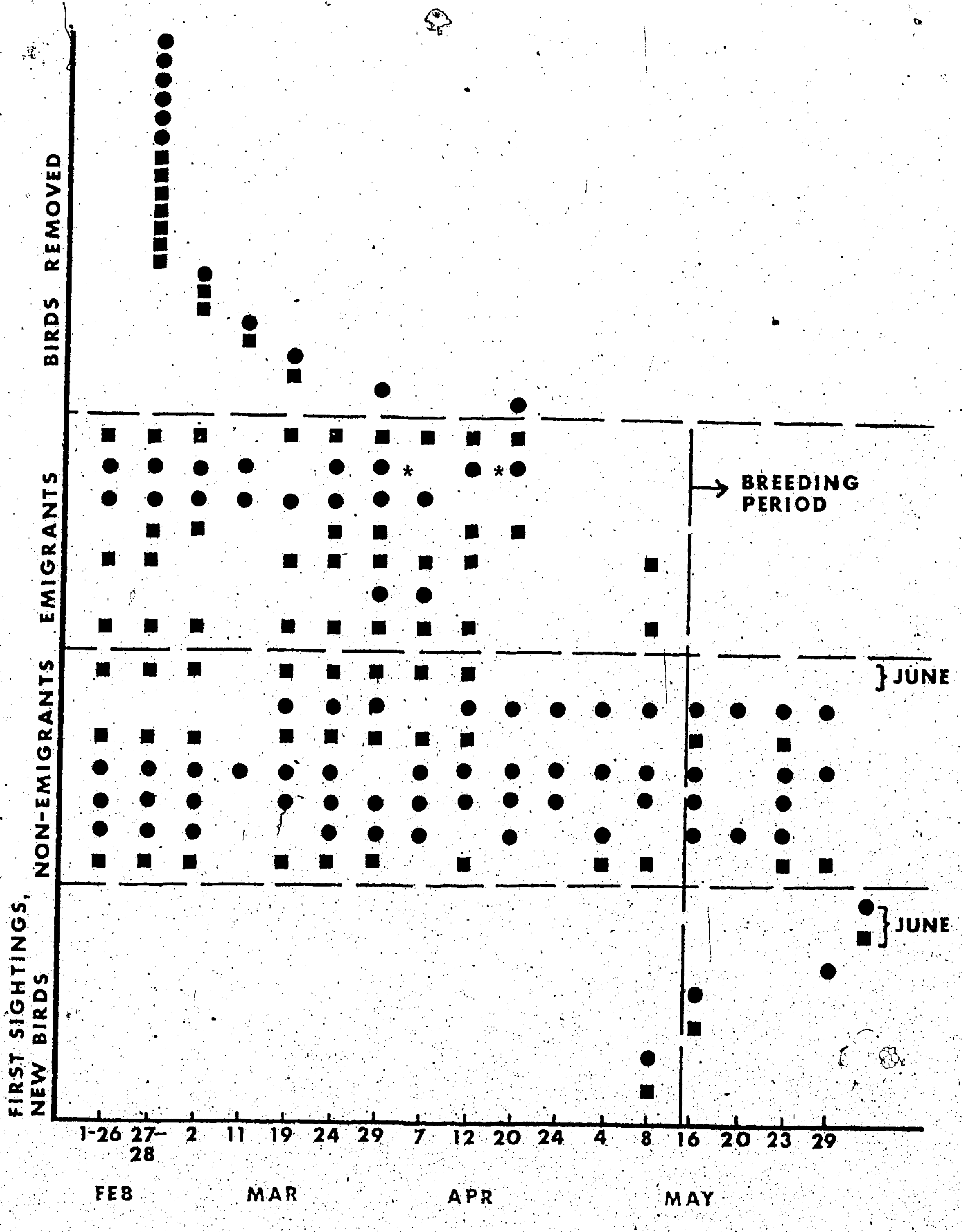

Figure 5. Sightings of spruce grouse during and after a removal of overwintering adults and yearlings on part of the study area at Gorge Creek, February - May 1973. (Each row equals one bird; males = ● ; females = ■ ; * = bird found 1/2 - 1 km away.)

Table 13. Summary of a removal of overwintering adults and yearling spruce grouse and the subsequent dispersal in spring; Gorge Creek, 1973.

	Sex	
	Males	Females
No. overwintering adults-yearlings removed	11	11
No. overwintering juveniles present before dispersal	7	7
No. emigrated	3	4
% emigration	43	57
No. Immigrant yearlings, recorded in breeding period	3	2
No. transient yearlings	1	1
Total yearlings, breeding period	7	5

suggested little association with that area. Hence, all known adults and yearlings except one (20 April) were removed before any evidence of dispersal. No adults were observed on the experimental section after 20 April.

Seven juveniles of each sex wintered on the experimental site and were available for emigration. Of these, four males and three females were seen there in the 1973 breeding period; 43 percent of the males and 57 percent of the females emigrated. Corresponding emigration from the control section was 50 percent for males and 80 percent for females (six males and 10 females available), not significantly different from those of the experimental section.

Although the experimental section held similar numbers of yearlings in summer (12) and juveniles in winter (14) dispersal changed the individuals involved. Forty-two percent (5/12) of the yearlings in the experimental section in summer immigrated after the removal. Immigrants onto the control area equalled 47 percent (7/15) of the total yearlings in summer; these proportions of immigrants were not significantly different.

All future emigrants were seen on the experimental section on 29 March. The first emigration was recorded on 2 April, a male found 1 km away. This male subsequently returned, made another long move, returned again, and then vacated the experimental section after 20 April. The next earliest movements were also made by males, two last seen on 7 April. Dispersing females remained longer than males; the earliest emigration was after 12 April and two were still present on 8 May. There is additional evidence that the social organization of grouse during winter changed earliest among males. On 12 April 1973 four males were found on the experimental section, three of which remained into summer, and all were well separated. All seven females that overwintered were seen on 12 April and all were seen in a single flock.

I calculated the probability of seeing a given bird at least once during any 7-day period between 27 February and 15 May. The purpose was to determine if non-emigrants and emigrants differed in their chances of being found, as one index to differential behavior. Probabilities were obtained by partitioning the 27 February-15 May period into 7-day intervals and tallying the intervals in which each bird was seen at least once. I assumed the emigrants were not present in the 7-day period after the final sighting. Sightings in Figure 5 reduce to the following mean probabilities (sexes combined): 0.69 (0.55 - 0.91) for non-emigrants and 0.71 (0.33 - 1.0) for emigrants. At the time when older birds were absent, emigrants, until they presumably dispersed, were located equally well as non-emigrants.

The time that dispersal from the removal section began and the fact that males disappeared before females were both similar to events on the control section in 1973 and the entire study area in earlier years (Figure 2).

New birds were seen first on the experimental section on 8 May (two which had wintered adjoining this area); two more were located on 16 May. Therefore, the earliest known arrivals of grouse were considerably later than the earliest emigration, similar to that on the control section and for the entire study area in earlier years.

In summary, several grouse dispersed from the experimental site where overwintering adults and yearlings were absent at the time of dispersal. The removal did not significantly alter the proportions of grouse emigrating nor the timing of dispersal. Results did not support the hypothesis that the presence of overwintering adults and yearlings (density) influenced the tendency to disperse.

Relative Effects of Various Losses

The various types of loss after hatching and until recruitment have been considered independently. At this time we can use the information presented heretofore to determine how much of the total loss resulted from each component.

The maximum number of juveniles known to be hatched over the three summers of 1970-72 was 208 (Table 4). I calculated the difference between this sample of juveniles and the number of these recruited as yearlings in the next breeding period (Table 14). Total loss between these two counts was separated into: mortality in summer, mortality in autumn, emigration in autumn, winter loss, mortality in spring (before 15 May), and emigration in spring. Losses attributable to each component are expressed in two ways: as a percent of the birds alive at the start of the interval, the method employed previously, and as a percent of the total loss from the maximum count of juveniles to yearling recruitment. These calculations are possible only with birds raised on the study area.

Three results are of particular interest. First, although considerable emigration occurred in autumn it was not a greater proportion of total loss (40 percent, females and 33 percent, males) than was mortality in summer (50 percent, females and 48 percent, males). Undoubtedly many more juveniles hatched than were seen and the real summer mortality would have been a still greater proportion of total loss. Second, there was no known mortality during the autumn and spring periods of dispersal, and loss in winter was a minor contribution (3 percent, sexes combined) to total loss. Third, although many birds emigrated in spring they were a small part of the total loss before recruitment. For example, 80 percent of the females and 36 percent of the males present in late winter emigrated in spring, but they equalled only 8 and 15 percent, respectively, of the total loss the cohort encountered.

I then examined the loss incurred by juveniles that

Table 14. A sequence of losses of juvenile spruce grouse from the study area between their first and second summer, Gorge Creek, 1970-73. A comparison of the proportional losses from mortality and emigration. Total loss is the difference between the maximum number of juveniles recorded in summer and the number of those recruited within the study area the next summer. Data of all years combined.

	Sex	
	Males	Females
Maximum recorded juveniles	104	104
% mortality in summer	39	49
as % of total loss	48	50
No. juveniles alive end of summer	64	53
% known mortality in autumn	0	0
% emigration in autumn	42	77
as % of total loss	33	40
No. juveniles remaining start of winter	37	12
% loss in winter	11	17
as % of total loss	5	2
No. juveniles remaining at start of dispersal in spring	33	10
% known mortality in spring	0	0
% emigration in spring	36	80
as % of total loss	15	8
No. juveniles recruited (yearlings) into breeding population	21	2
Total loss (%)	83 (80)	102 (98)

Data are from only those birds known or assumed to have been produced on the study area; juveniles in broods seen first in late summer are excluded.

had been raised to independence. I calculated the emigration in spring as a proportion of the total loss between early autumn (juveniles alive end of brood period) and summer (Table 15). In each year, emigration in spring was a more important cause of loss when the mortality in the first summer was excluded from the analysis. But this emigration still was not the primary cause of loss. As shown below, emigration in spring accounted for less of the total loss, autumn to summer, than emigration the previous autumn (data from Tables 10 and 15).

Percentages of total loss, autumn to summer, that resulted from emigration in autumn and spring respectively:

	1970-71	1971-72	1972-73
males	71,29	48,41	67,22
females	88,6	69,23	86,14

All differences are significant except for males in 1971-72.

Although fewer birds were removed from the study area by emigration in spring than by emigration in autumn it seemed to have a more important effect on the breeding population. Emigration of overwintering birds varied between years (Table 11), most noticeably 1971 to 1972. But more importantly, from 1971 to 1972 the emigration in spring became a greater component of the total loss encountered by the juvenile class.

Table 15. Emigration in spring of overwintering juvenile spruce grouse as a proportion of total loss encountered by the juvenile class. The analysis shows how much the emigration in spring contributed toward removing juveniles from the study area. Total loss is expressed two ways: the difference between the maximum number of juveniles recorded and the number of these recruited as yearlings; and the difference between the juveniles present before dispersal in autumn and the number of these recruited. Gorge Creek, 1970-73.

	Year 1971		1972		1973	
	Males	Females	Males	Females	Males	Females
Emigration in spring as a part of total loss from the juveniles counted the previous summer						
Maximum no. juveniles	33	33	37	38	34	33
No. yearling recruits	11	1	5	1	5	0
Total loss	22	32	32	37	29	33
No. emigrants in spring	4	1	6	4	2	3
Emigration as % of total loss	18	3	19^A	11	7	9
Emigration in spring as part of total loss from the juveniles present before dispersal the previous autumn[1]						
No. juveniles	25	18	34	28	14	21
No. yearling recruits	11	2	5	2	5	0
Total loss	14	16	29	26	9	21
No. emigrants in spring	4	1	12	6	2	3
Emigration as % of total loss	29	6	41^A	23	22	14

[1] Juveniles in broods arriving in late summer (not produced on area) are included in these calculations; hence, the differences in numbers in rows 2 and 7, and rows 4 and 9.

Net Change in Numbers, Autumn to Summer

Emigration reduced the potential number of juveniles that could be incorporated into the breeding population. Yet many birds immigrated and their effect was to compensate for loss. Factors that determine recruitment into a population might affect immigration as well as emigration. The net change in numbers was the difference between juvenile production, measured before dispersal in autumn, and total yearlings in the population the next summer (Table 16).

The time at which the changes in numbers occurred has been dealt with in part earlier (Summary of Dispersal, and Survival, Autumn Through Spring) but this point is elaborated here. For both sexes, dispersal in autumn did little to reduce numbers, and although winter loss varied between years (Table 9) it was not greatest during the year of the greatest change in numbers from autumn to summer. Most of the overall change in numbers of the juvenile class occurred in spring (Table 16). Increased emigration of males in spring of 1972 (Table 11) accounted for the high loss from autumn of 1971 to summer of 1972. Among females, the net increase in numbers over 1970-71 was unique; in spring of 1971 emigration was lowest and immigration was highest.

I investigated the relationship between net change from autumn to summer and numbers of adults-yearlings and

Table 16. Changes in numbers of juveniles from before dispersal in autumn to the following breeding season (yearlings recruited); Gorge Creek, 1970-73. Data are extracted from Tables 10 and 11, and show the net change from autumn to summer and the percent of this change that occurred during dispersal in spring.

	Number of birds present					
	Before autumn dispersal	Winter	Before spring dispersal	Breeding period, total yearlings	% net change	% of change occurring during spring dispersal
Males						
1970-71	25	23	23	21	-16	50
1971-72	34	34	29	17	-50	71
1972-73	14	18	13	14	0	-
Females						
1970-71	18	19	15	21	+17	100
1971-72	28	28	26	19	-32	78
1972-73	21	19	17	13	-38	50

juveniles in early autumn (as in Figure 3). These analyses might help show whether population size affected both loss and immigration. Resulting coefficients of correlation with adult-yearling counts were $r = 0.93$ for females and 0.01 for males; with counts of juveniles they were 0.66 for females and 0.97 for males. Net change of females was best correlated with adult-yearling numbers in autumn. Since most of the change in numbers actually occurred in spring I also related the autumn to summer changes with population counts in late winter (as in Figure 4). The maximum difference between numbers of adult and yearling females in autumn and the succeeding late winter was 25 percent (13 birds). The coefficient of correlation between net change and numbers of adult-yearling females in late winter was $r = 0.99$. The best correlation between net change of males and early autumn numbers was with juveniles. The number of juvenile males in late winter differed by a maximum of 15 percent (five birds) from the count before dispersal in autumn. The coefficient of correlation between net change and numbers of juvenile males in late winter was $r = 0.94$.

Results clearly show that net changes in numbers of the juvenile class from autumn to summer were correlated equally well with population size in late winter and the preceding early autumn. Hence, *if* density did affect the overall change in numbers it becomes difficult to identify the time at which the influence was mediated, even though most of the change actually occurred in spring.

Immigration in spring-summer greatly reduced the potential impact that emigration then could have had on recruitment. Males that immigrated in spring-summer were equal to at least 30 percent and as high as 80 percent of the wintering birds that emigrated, and 47 percent for all years combined (Table 11). Immigrant females in spring-summer were equal to at least 56 percent of those that emigrated in spring, and in 1971 the influx was 86 percent greater than the number of emigrants. For all years combined, female immigrants in spring-summer equalled 86 percent of the number that emigrated in spring. In 1972, emigration in spring was compensated less by immigration (both sexes) than in other years; this compounded the effect of a high level of emigration on recruitment.

Composition of Yearling Breeding Cohort

Dispersal had a profound effect on *which* yearlings were incorporated into the breeding population (Table 17). Yearlings were either raised on the study area, or they immigrated the previous autumn or during spring and summer of the given year.

Over 3 years of this study only 7 percent of the yearling females in the breeding population were produced on the study area compared to 44 percent for males ($p < 0.05$). A greater proportion of males than females remained in all years; differences between sexes were

Table 17. Proportions of the yearling spruce grouse in the breeding population at Gorge Creek that were raised within the study area or that immigrated; 1971-73.

	Year and sex					
	1971		1972		1973	
	Males	Females	Males	Females	Males	Females
Total yearlings	21	21	17	19	14	13
Raised on area previous year	52^{A}	$9^{A,B}$	30	11^{C}	50^{D}	$0^{D,E,F}$
Immigrated previous autumn	24	29	35	42	21	38^{E}
Immigrated present year	24^{G}	$62^{B,G}$	35	47^{C}	29	62^{F}

significant in 1971 and 1973. The greater similarity between sexes in 1972 resulted largely from more emigration of males in that spring than in other years. Proportions of yearlings that immigrated as juveniles the previous autumn were similar for both sexes among years. Over all years, autumn immigrants composed 36 percent of the females and 27 percent of the males in the breeding population. By contrast, 57 percent of the yearling females had immigrated during spring-summer but only 29 percent of the yearling males immigrated then ($P < 0.05$).

Distances of Dispersal

I calculated individual distances of dispersal to determine if differences existed between sexes and years and how densities were related to distances moved. In this section I treat movements from brood and winter ranges as dispersing movements even though most were within the study area, and hence the population, and do not agree with my previous definition of dispersal (page 6). Data can be compared with earlier results on movements across fixed boundaries. A knowledge of distances that animals move ultimately helps to define the area a population occupies and the limits to gene flow.

Three distances were calculated: 1) in autumn - from perimeter of brood range to geographic center of winter range; 2) in spring - from perimeter of winter range to center of breeding range; 3) from the perimeter of brood range to the center of breeding range. I used only those birds whose brood or winter range was on the study area.

Summaries of individual distances are given in Tables 18-20. Medians are the best single measure of distances obtained; they are more informative than means when data give a skewed distribution from a small sample. The following two procedures were used to test for differences in the frequency distributions between sexes and years: 1) a non-parametric rank test (Mann-Whitney *U* test); and 2) individual distances were grouped into discrete intervals and χ^2 values (*G* test) were calculated for each interval and then totaled for the entire frequency distribution. Results of both procedures were identical. I conducted 27 tests between sexes and years by each method; both tests produced two significant differences, the same for each test. Although I have no evidence I assume survival was not affected by the distance moved yet data obtained were biased in favor of short movements. Hence, distances recorded probably were not representative of all birds. I use the proportion of the cohort present at the beginning of dispersal that subsequently moved a maximum of 2 km to show gross changes in distances for the total initial cohort. This particular distance is somewhat arbitrary, but I assume that major changes in proportional sightings at less than 2 km were real rather than caused by changes in effort and efficiency of searching.

I obtained dispersing distances in autumn (Table 18) for 44 males and 17 females. There were no significant

Table 18. Distance moved by juvenile spruce grouse in autumn at Gorge Creek, dispersing from brood range to winter range; 1970-72.

	Year and sex					
	1970		1971		1972	
	Males	Females	Males	Females	Males	Females
% (No.) of birds relocated, that moved:						
< 100 meters	25(4)	25(1)	30(6)	40(4)	25(2)	33(1)
100 - 500	19(3)	0	15(3)	20(2)	13(1)	0
500 - 1000	25(4)	50(2)	35(7)	10(1)	50(4)	33(1)
1000 - 1500	19(3)	0	15(3)	10(1)	13(1)	33(1)
1500 - 2000	6(1)	0	5(1)	0	0	0
> 2000	6(1)	25(1)	0	20(2)	0	0
Total birds	16	4	20	10	8	3
Median distance	698	787	562	382	698	585
% of *original* cohort moving < 2 km	60^A	17^A	59^B	29^B	57^C	14^C

Table 19. Distances moved by spruce grouse in spring at Gorge Creek, dispersing from winter range to first breeding site; 1971-73.

	Year and sex					
	1971		1972		1973	
	Males	Females	Males	Females	Males	Females
% (No.) of birds relocated, that moved:						
< 100 meters	7(1)	25(2)	7(1)	44(4)	75(6)	60(3)
100 - 500	47(7)	50(4)	29(4)	11(1)	13(1)	20(1)
500 - 1000	13(2)	13(1)	29(4)	0	0	20(1)
1000 - 1500	27(4)	0	21(3)	22(2)	0	0
1500 - 2000	0	13(1)	0	0	13(1)	0
> 2000	7(1)	0	14(2)	22(2)	0	0
Total birds	15^{A}	8	14^{B}	9	$8^{A,B}$	5
Median distance	450	213	877	225	45	90
% of *original* cohort moving < 2 km	61	53	41	27	62	29

Superscript letters: frequency distributions are significantly different at $P < 0.05$; both χ^2 and rank tests.

Table 20. Distances moved by juvenile spruce grouse at Gorge Creek from brood range to first breeding site; 1970-73. Movements were made in autumn, spring, or both.

	Year and sex					
	1970 to 1971		1971 to 1972		1972 to 1973	
	Males	Females	Males	Females	Males	Females
% (No.) of birds relocated, that moved:						
< 100 meters	8(1)	0	9(1)	0	17(1)	0
100 - 500	42(5)	0	18(2)	0	17(1)	0
500 - 1000	25(3)	100(2)	9(1)	0	50(3)	0
1000 - 1500	17(2)	0	18(2)	33(1)	17(1)	0
1500 - 2000	0	0	18(2)	33(1)	0	50(1)
> 2000	8(1)	0	27(3)	33(1)	0	50(1)
Total birds	12	2	11	3	6	2
Median distance	562	765	1170	1890	652	4195
% of original cohort moving < 2 km	44[A]	11[A]	24	7	43	5

differences among the frequency distributions between sexes or years. But the proportion of total males relocated within 2 km was significantly greater than that for females in each year, suggesting longer movements of females.

Individual distances in spring were obtained from 37 males and 22 females (Table 19). Earlier results (Table 11) showed a greater reduction of potential yearling recruits in 1972 than in 1971. The median distances for males in spring increased substantially between the same years, but not significantly so. There was no significant change from 1971 to 1972 in the frequency distributions recorded for both sexes. But smaller proportions of males (41 percent) and females (27 percent) were relocated after dispersal within 2 km of winter range in 1972 than in 1971 (61 percent, males and 53 percent, females). These differences were not statistically significant but suggest longer movements by both sexes in 1972.

Median distances were lowest in spring for both sexes in 1973. The frequency distribution of distances for males in 1973 was significantly different from that recorded in 1971 and 1972. Distances in 1973 were obtained for only 13 birds, and eight were from the experimental section. But the removal of adults and yearlings did not seem to reduce distances in that section and was not responsible for the overall reduced medians. Median distances (sexes combined) in the experimental and control sections were 0 and 90 meters, respectively. I do not consider the 90 meter difference to be important. The proportion of the original cohort of males that moved less than 2 km increased from 1972 (41 percent) to 1973 (62 percent), paralleling the decreased medians. A similar pattern did not exist for females.

Distances between brood range and first breeding range are summarized for 29 males and seven females in Table 20. These are straight-line distances without regard to when the bird moved. The median distance for males hatched in 1971 was much greater than the medians in 1970 and 1972, reflecting longer movements in spring 1972. There was no significant difference in any comparison of frequency distributions. Samples of distances between brood range and breeding site were small, particularly among females, and not much should be inferred from them. In each year a greater proportion of males than females were relocated as yearlings within 2 km of their brood range, suggesting females dispersed farthest overall. Recall that in both autumn and spring of each year proportionally more females than males apparently moved over 2 km.

I attempted to determine if population size was related to distances dispersed. For this I employed regressions between proportions of birds that moved less than 2 km and numbers of individuals of the same sex. I used the numbers of adults-yearlings and juveniles present in early autumn (Figure 3) and late winter (Figure 4); distances are given in Tables 18-20.

Distances for both sexes in autumn were not related positively to population size. Numbers of juveniles relocated in winter less than 2 km from their brood range did not decrease as population size increased. Regression equations for males were $Y = 64-0.11x$ ($r = -0.87$) for numbers of adults-yearlings, and $Y = 56+0.11x$ ($r = 0.70$) for numbers of juveniles; and for females they were $Y = 24-0.11x$ ($r = -0.13$) for numbers of adults-yearlings, and $Y = -11+1.37x$ ($r = 0.88$) for numbers of juveniles. None of these regressions was significant. I calculated supplementary regressions of density on median distances; all slopes were negative, likewise indicating that distances recorded did not increase as population size increased.

Negative regression slopes of density on proportions of birds relocated within 2 km of winter range suggest that movements beyond 2 km in spring did increase as population size increased. Regression equations for males were $Y = 111-1.36x$ ($r = -0.46$) for numbers of adults-yearlings, and $Y = 80-1.19x$ ($r = -0.81$) for numbers of juveniles; and for females they were $Y = 191-4.17x$ ($r = -0.998$) ($P < 0.05$) for numbers of adults-yearlings, and $Y = 69-1.71x$ ($r = -0.69$) for numbers of juveniles.

Proportionally fewer juveniles moved less than 2 km from brood site to first breeding site as population size in autumn increased. Regression equations for males were $Y = 53-0.32x$ ($r = -0.36$) for numbers of adults-yearlings, and $Y = 59-0.91x$ ($r = -0.81$) for numbers of juveniles;

and for females they were $Y = 20-0.30x$ ($r = -0.991$) for numbers of adults and yearlings, and $Y = 14-0.28x$ ($r = -0.47$) for numbers of juveniles. None of these regressions were significant.

Distances moved by males in spring were correlated best with numbers of juveniles in late winter, and distances moved by females then were correlated best with numbers of adults-yearlings. Numbers of juvenile males and adult and yearling females in late winter differed, respectively, by a maximum of 15 percent (five birds) and 25 percent (13 birds) from numbers the previous autumn. Since distances dispersed in autumn were not related positively with population size in autumn the above correlations for brood to breeding site distances mostly reflect the correlations for movements in spring.

Some general comments should be noted about the preceding analyses. I used two sorts of methods to study individual distances: medians and tests on actual distances obtained; and percentages of the potential dispersers that moved a given critical distance. Both procedures have disadvantages. Although medians reflect real distances they probably are not representative for the total population since I put little effort into locating long-distance dispersers. On the other hand, percentages of birds that moved a specified distance should reflect gross changes of the entire cohort. But calculations with a 2 km demarcation are not sensitive to changes within th[illegible] "less than" or "more than" 2 km categories. This could make it especially difficult to identify small changes, particularly between years within a sex. Conclusions based on statistical tests among the actual distances obtained (frequency distributions) often differed from those that used a 2 km critical distance.

Distances from the center of the study area to the nearest and farthest boundaries were only 675 meters and 2 km, respectively. Yet I recorded one move of 9.5 km while spending only 10 percent of the field effort outside the study area. Because of the biased spatial effort I obtained records of distances for only 46 percent (120/263) of all birds. Both general methods of analyses used here are really affected by the same basic problem, a lack of long-distance records.

Proportions of birds that moved a given critical distance can be compared with earlier results on emigration. For example, distances over 2 km were recorded for nine birds in autumn and spring, and seven of these emigrated beyond the study area. Further, there were 111 movements of less than 2 km, and 104 (94 percent) of these birds also remained within the study area. Another comparison involved the tests for significant differences among emigration rates and among proportions of birds relocated within a 2 km distance. I conducted 18 tests for each of these two methods of analyzing dispersal (Tables 10 and 11, 18 and 19). Each method produced only three significant differences and two were common to each. Rates of emigration and the index to distances moved (using a 2 km critical distance) both revealed that: in autumn and spring, females dispersed more than males; from the viewpoint of the local population at Gorge Creek, the effect of dispersal in spring on recruitment was the most lax, particularly for females, in 1971 - proportionally fewer birds emigrated and more were relocated a short distance from winter range; and the effect of dispersal in spring on recruitment was the most restrictive, particularly for males, in 1972 - proportionally more birds emigrated and fewer were relocated within a short distance from winter range.

DISCUSSION

DISPERSAL AND EXISTING POPULATION THEORY

Dispersal, along with natality and mortality, is frequently suggested to be a major force in determining population size. Although the need for an analytical approach to movement data was promoted long ago (Park et al. 1941) we have not learned much about dispersal in free-living populations. The present study was an attempt to evaluate the effects of dispersal on population size.

Most work on population control with birds has centered on two principal views. Lack (1954,1966) proposed that populations of most species are regulated by post-breeding season mortality, effected by the food supply, and operating in a density-dependent manner. In my study, a considerable loss of juveniles raised on the study area did occur in autumn and winter. But these losses, mostly emigration, were not very important numerically because of compensation through immigration. Numbers of juveniles present in late winter were only about 12 percent lower than numbers present before dispersal the previous autumn. Survival of all sex and age classes over autumn and winter approximated 87 percent. Herein I restrict the post-breeding season to autumn and winter, and for those periods I conclude there was no support for Lack's hypothesis.

Wynne-Edwards (1962) submits that social behavior is responsive to population size and that changes in competition directly or indirectly control reproductive output, which in turn can limit population growth. Wynne-Edwards emphasized that synchronized, communal displays (epideictic) are one way to give the population information on its size relative to resources. Although spruce grouse flock together in winter I doubt that it is a good example of epideictic behavior. But changes from flocking to individual status occur in late winter and spring, prior to and concurrent with the start of dispersal. Emigration, particularly just before breeding, is one way to control recruitment, thereby adjusting density (Wynne-Edwards 1965). My results support Wynne-Edwards' hypothesis only to the extent that dispersal was a form of behavior that affected recruitment. The important issues remain: to determine the proximal cause of dispersal and whether population size is involved.

My results are mostly about dispersal in a local population, which Lack and Wynne-Edwards gave little attention to or considered it to be less important than other effects on population size. Krebs and his coworkers (Krebs et al. 1969, Krebs 1970, Myers and Krebs 1971) have made the strongest case that dispersal could determine population size. Their early work on voles demonstrated that when emigration was prohibited overpopulation resulted and habitat severely deteriorated. Subsequent work showed genetic and behavioral polymorphisms between dispersing and resident voles. Aggression by voles also changed during phases of the population cycle and Krebs (1970) suggested that if such changes regulate numbers they likely operate via dispersal. Results obtained by Krebs support Lidicker's (1962) speculation that dispersal could prove to be a primary way of regulating numbers.

I related population size to the proportions of grouse that dispersed from the study area and to the distances moved. A summary of results on dispersal and population size is given in Table 21. The clearest results were in autumn - movements were independent of my measurements of density. In spring, the relationships between population size and dispersal were less consistent and there were differences between sexes. In particular, results from an experiment did not support other data on the effect of numbers of adults-yearlings on emigration. Although emigration from the experimental site was, proportionally, slightly less than that on the control area the important conclusion from the experiment is that emigration *did occur* in spite of the absence of adults-yearlings; and the number of birds that emigrated exceeded the net difference between overwintering juveniles and yearlings in summer. In general, it was clear that changes in rates of emigration and distances moved occurred only in spring. It is more difficult to understand whether density *in* late winter might have caused the variable dispersal or if dispersal was predisposed by a similar density at an earlier time. In this regard, adults and yearlings in the experimental section, prior to late winter, might have stimulated a pattern of

Table 21. Summary of major relationships between dispersal of spruce grouse at Gorge Creek and population size. The time of season at which the counts of birds were obtained is given in text.

<table>
<tr><th rowspan="2"></th><th colspan="2">Sex</th></tr>
<tr><th>Males</th><th>Females</th></tr>
<tr><td>Autumn</td><td></td><td></td></tr>
<tr><td></td><td colspan="2">No positive relationship between no. adults and yearlings and no. juveniles on both the percent of juveniles emigrating and the distances juveniles moved.</td></tr>
<tr><td>Spring</td><td></td><td></td></tr>
<tr><td></td><td colspan="2">Percent of juveniles emigrating was positively correlated with no. adults and yearlings; emigration of males was correlated equally well with juvs.</td></tr>
<tr><td></td><td>Distances moved by juveniles best correlated, positively, with no. juveniles.</td><td>Distances moved by juveniles best correlated, positively, with no. adults and yearlings.</td></tr>
<tr><td></td><td colspan="2">In an experimental removal of adults and yearlings the percent of juveniles emigrating and the distances moved during the absence of adults and yearlings were not significantly less than results on a control section.</td></tr>
<tr><td>Distances moved, brood range to breeding site</td><td></td><td></td></tr>
<tr><td></td><td>Distances best correlated, positively, with no. juveniles. This was accounted for by the relationship between no. juveniles and distances in spring.</td><td>Distances best correlated, positively, with no. adults and yearlings. This was accounted for by the relationship between no. adults and yearlings and distances in spring.</td></tr>
<tr><td>Net changes in numbers, autumn to summer</td><td></td><td></td></tr>
<tr><td></td><td>Change best correlated, positively, with no. juveniles, equally well in late winter as early autumn.</td><td>Change best correlated, positively, with no. adults and yearlings, equally well in late winter as early autumn.</td></tr>
</table>

dispersal, which then occurred in spring even though they were absent at the time. The possibility also arises that some overwintering juveniles in the experimental section became dominant over others after older birds were removed, causing some subordinates to emigrate.

Although the relationships between population size and emigration and distances are illustrated best as correlations I am very reluctant to place much confidence in the predictability implied by some slopes of density on dispersal because of the small samples. Further, movements of migrant adults and yearlings concurrent with dispersal of juveniles, and the long period over which dispersal itself occurred make it difficult even to be confident that the counts of adults and yearlings used were the most appropriate ones. There also is little benefit from concluding simply that dispersal is density-dependent. Population size itself probably cannot cause emigration; rather it is an index to the magnitude of some intraspecific process. I agree with Eberhardt (1970) that our understanding of population processes will result only from great effort on studying the possible mechanisms themselves, rather than superficial tests of relationships. However, analyses of density and dispersal were of value by showing that futher work on their possible association should be conducted first in late winter and spring.

Krebs (1970) concluded that dispersal could be the mechanism by which behavioral changes operate to regulate density. I agree that dispersal is an important way of adjusting numbers but it is not the basic mechanism involved; something must stimulate animals to move. We should also keep in mind that emigration is not the only way that breeding and production can be limited. Successful recruitment into a population, especially among promiscuous species, does not guarantee that the individual will breed.

Given the carryover of a high population through winter, dispersal in spring is the final opportunity for restricting or permitting recruitment. If emigration of some individuals always occurs, then there will be selection for *which* yearlings are recruited, even without a net change in numbers. This agrees with Myers' and Krebs' (1971) contention that a genetic or behavioral polymorphism may act on dispersal. Such polymorphisms are the essence of Chitty's (1967) hypothesis on population change. The alternative would be that dispersal among individuals is random.

It is significant that there is agreement on the general timing of the proximate causes of change in numbers for spruce grouse and the closely related blue grouse. Results of my work support Ellison's (1973[illegible]ulation that important changes in numbers of spruce grouse occur in spring. Bendell et al. (1972) and Zwickel (1972) conducted removals in summer of resident blue grouse; repopulation by yearlings the next spring suggested to them that the number of birds added to the population was determined in spring. Bendell et al. (1972) indicate that numbers are determined during a period of little overt courtship. Similarly, emigration recorded here for spruce grouse was before obvious courtship behavior. On another point, Zwickel (1972) speculated that the number of *potential* yearling recruits (alive in late winter) may be dependent on the previous year's production, and this seemed conclusive in my study.

I have stressed that dispersal is an important means for changing numbers of spruce grouse, but this conclusion may not apply in all cases. On certain small islands successful emigration and immigration may not be possible, for example, with small mammals. At these sites there may be only one homogeneous population and only natality and mortality interact to determine population size. The importance of dispersal is also relative to the area of study. At some point as we increase our perspective from a local site to a larger region emigration decreases and mortality increases in relative importance in elimination of *total* excess individuals. Hence, the quantitative effects of dispersal are most relevant only to localized populations and where inter-population exchange is possible. However, dispersive movements would always seem to have qualitative effects, by changing the distribution of individuals with different traits.

Some work with tetraonids elsewhere suggests dispersal did not have an important effect on numbers of birds. For example, Jenkins et al. (1964:190) reported that dispersal of red grouse did not occur in some years, and that breeding densities resulted simply from locally raised chicks (Jenkins et al. 1967:105; Watson and Moss 1972:137). But their data do not clearly show that dispersal did not normally occur or how they could identify locally raised birds as distinct from immigrants. I do accept their point, though, that the mortality of birds unsuccessful in obtaining a territory in autumn (potential dispersers?) is irrelevant to population control. Other authors (Rusch and Keith 1971, Myrberget 1972) report that predation is an important influence on population size.

In spite of the instances noted above there could be much generality for the case made here with dispersal and recruitment. There is little evidence to negate the possibility that dispersal has an important effect on local population size and that emigrants survive well. There has been too little work done with dispersal. The work by Krebs and coworkers (Krebs et al. 1969, Krebs 1970, Myers and Krebs 1971) and this study have attempted to investigate intensively the phenomenon. Significantly, both studies conclude that dispersal was variable (during spring, this study) and that it was an important proximal means for adjusting numbers.

RELEVANCE OF OTHER RESULTS

Many of the specific results in this study are relevant to the findings and interpretations of other workers and are discussed here.

A high rate of mortality early in life is common to many animals (reviews by Lack 1954, Zwickel 1965; and Calef 1973 for quite a different example), but usually there is still great loss over the non-breeding season. Where data are available for forest grouse, production autumn always exceeded the total number of birds recruited as yearlings in the local site (Boag 1966, Bendell and Elliott 1967, Zwickel and Bendell 1967a, Rusch and Keith 1971, Redfield 1972, Ellison 1974). Exceptions may occasionally occur in increasing populations, such as during a part of this study. These same patterns of change can probably be seen in species other than forest grouse if good counts of production and the age composition of breeding individuals are available. I have stressed the importance of yearling *recruitment* in the fluctuation of total breeding numbers. This is probably a general case as others have concluded that changing age ratios characterize changes in total numbers (Dhondt 1971:542, Bendell et al. 1972, Watson and Moss 1972:141, Weeden and Theberge 1972, Zwickel 1972).

I separated mortality from emigration as components of loss where it was possible, and there were great differences in the impact of each factor. We see that in such diverse species as song sparrows and roe deer (*Capreolus capreolus*) (Tompa 1964 and Strandgaard 1972, respectively) emigration also was considered an important part of local loss. A knowledge of the relative importance of mortality and emigration is critical if we try to expand results from a local site to a large region. Iwao (1971) gave similar advice for the general application of local results. On a related point, *loss* is the appropriate term when death and movement cannot be separated (Weeden and Theberge 1972).

Survival was high in autumn and winter for all sex and age classes of spruce grouse; this may be more common among tetraonids than assumed. Results that show poor overwinter survival are often from circumstantial evidence. Watson (1965), Jenkins et al. (1967, among others), and Rusch and Keith (1971) made periodic counts through winter on rock ptarmigan, red grouse, and ruffed grouse, respectively. In the first two studies survival was high throughout winter (territorial red grouse only) or over long periods. Bendell et al. (1972) and Zwickel (1972) did not document survival rates for blue grouse over winter but observed that survival of juveniles was at least good enough for complete repopulation of vacant breeding range in spring. Expanding this case, Errington (1945) noted that bobwhite quail (*Colinus virginianus*) in the northern limits of its range, and with characteristically high mortality, showed high survival in some winters.

Smith (1967) provided an excellent documentation of good survival of black-capped chickadees (*Parus atricapillus*) in winter. The point here is that autumn and winter are not necessarily always a critical period for survival, even in nothern evironments.

Rates of loss are usually calculated on the initial population at the time the loss occurs. I also calculated the different sorts of loss as percentages of the total loss incurred by that age class. This approach differs slightly from the calculations proposed by Thompson (1928) and Morris (1957) but uses their reasoning. For example, using Thompson's terminology, the *apparent loss* of emigrating females (raised on study area) in spring was 80 percent but the *real loss* was only 8 percent (Table 14). Emigration rates alone, derived from individuals present at the start of the dispersal period, will overestimate the relative importance of emigration as a means of removing individuals from an area or population. Only a small portion of total loss was accounted for by emigration in spring but this was important in determining final breeding numbers because of its variation. This is the kind of variation needed to show that population size is regulated since it is implicit that the power of the regulating mechanism must be flexible.

An important need in this study was to document survival of dispersing birds. Annual survival of birds that emigrated in spring was not much less (52 percent, perhaps a low estimate) than that of overwintering juveniles that did not disperse from the study area in spring (72 percent). Survival of immigrants (69 percent) for 1 year after their arrival in spring-summer was about the same as overwintering juveniles that did not disperse in spring. I acknowledge that these immigrants mostly represent birds that were successful in locating a place to settle and thus may be expected to show good survival. The problem is one of documenting a survival rate for dispersers that were unsuccessful in locating a permanent breeding site, if such birds existed. This is a difficult point to resolve with the data available. But even if all emigrants whose survival was not documented (100 - 72 = 28 percent, spring, 1971 and 1972 only) did not settle but had died they were still a small portion of total emigrants. Further, the fact that so little mortality was recorded in autumn and spring suggests that mortality was not concentrated at the time dispersers were moving most and perhaps subjected to greater stress from unfamilar habitat and aggressive residents.

My results do not support the frequent contention, either stated or implied (for example, Howard 1960, Lidicker 1962, Christian 1970, Gadgil 1971), that dispersing animals are subjected to greater mortality than individuals that do not disperse. The supposed greater mortality of dispersers is an important element in the agrument that dispersal is primarily of selective advantage to the population and not the individual (Howard 1960, Mayr 1966:198, Van Valen 1971).

If mortality of emigrants was not greater than non-emigrants then numbers of spruce grouse elsewhere might have been increasing. The alternative is that net losses elsewhere were greater than at Gorge Creek, and emigrants only replaced those lost. The necessary data are not available but, in fact, my impression is that the study area at Gorge Creek was optimal habitat. Therefore, statistics at Gorge Creek may not be wholly representative, but only intensive work elsewhere can answer this point.

I do not believe there was necessarily lower survival of dispersers in autumn than in spring. Differences in recorded survival (16 percent, autumn and 61 percent, spring, sexes and all years combined) can probably be explained by the observation that many birds spent successive winters in the same site as their first winter. Only rarely did an emigrant in autumn return to the study area in summer. A juvenile that emigrates in autumn may never return to its natal site and, hence, it is more difficult to document its survival than for spring emigrants that return for winter to the area being censused.

I know of only one other study on higher vertebrates that gives data on the fate of dispersers versus residents. A central point in the work with red grouse (Jenkins et al. 1963, 1967) is that birds which do not acquire a territory in autumn are expelled into marginal habitat. Predation on non-territorial red grouse was heaviest just after dispersal (Jenkins et al. 1964). The two following points slightly weaken their conclusion that dispersers suffer the greatest mortality. First, in several years the difference between August (minus hunting) and spring counts was used as the number dispersing. It is not clear if mortality of non-dispersers was included. Second, only 14 percent of the dispersers were found dead. These problems may be minor, however, and perhaps do not affect their main conclusion.

Two other studies provide relevant data on dispersal and survival. Myers and Krebs (1971) reported that 30 - 40 percent of *Microtus pennsylvanicus* lost from control trapping grids had successfully emigrated to outlying grids. This index to survival caused them to modify an earlier conclusion (Krebs et al. 1969) that emigrants suffered high mortality. The vole study may be criticized in that distances between control and recapture grids were very short. This logic parallels a potential criticism of my study since I do not know the distance moved by most surviving emigrants. Carl (1971) reported that arctic ground squirrels (*Spermophilus undulatus*) unsuccessful in obtaining territories were expelled and established refugee colonies in marginal habitat. All refugees subsequently died. Carl believed the refugees were exploring to colonize new habitat. This interpretation agrees with that for red grouse; in both studies, mortality was the normal fate after being excluded from secure (territory) and good quality habitat, and these individuals were termed dispersers. For spruce grouse, resident and dispersing individuals shared common habitat; it was difficult to determine criteria for good and poor habitat. In spite of the exceptions noted above I maintain that as yet there is little evidence that dispersing individuals are subject to higher mortality than those that remain settled.

Although distances moved are unavailable for most spruce grouse that emigrated there is evidence that movement beyond the study area was a meaningful loss to the group of birds remaining within the study area. Only seven birds (6 percent, 7/111) known to disperse less than 2 km also settled beyond the study area. Only 5 percent of the emigrants (8/147) were relocated within 1 km of the study area. The important point is that so few emigrants settled nearby (<1 km). Dispersal beyond the boundaries effectively terminated association between emigrants and residents, at least during spring and summer. Hence, there is some reason to consider the group of birds within the study area as a population because the probability of contact between those individuals, for breeding or other activities, must have been greater than that between residents and previous emigrants. But such a population was not entirely discrete because of contact between peripheral residents and external individuals. I also assume survival of dispersers was high and although most off-area searching was conducted only up to a 1 km distance the maximum known dispersal was much farther (9.5 km). These two points suggest that the areal extent of influence, genetic and otherwise, of birds from Gorge Creek could have been quite large. I presently use distances moved within and away from the study area to help identify the spatial limits to the population. But this approach may not be sufficient; for example, information on the reinvasion by progeny of the emigrants, which is presently unavailable, would help show whether dispersal is really effective in controlling inbreeding, and its possible consequences on population dynamics over the long term.

I am not convinced that the methods I used to define dispersal and to distinguish a population would be correct for all studies. A single criterion for these parameters may not be realistic. In each case, consideration must be given to these problems and the decision justified according to the individual circumstances. But particularly, some appraisal is necessary of the contact between individuals within and outside the main area of work.

One ultimate reason for dispersal could be to increase the probability of breeding. Yet if aggression by residents is keen then emigration to reduce injury or death may be the real proximal stimulus to disperse, as Beer and Meyer (1951) and Errington (1963) infer for certain individual muskrats (*Ondatra zibethica*). Gruys (1971) was more convinced on this point, by stating that dispersal of pine loopers (*Bupalus piniarius*) was an adaptation to avoid density-related mortality. Murray (1967) and Myers and Krebs (1971) comment that subordinate animals will maximize their chance of settling and reproducing only by moving away from dominant individuals at their birth site. But, of course, emigration does not necessarily put a subordinate individual into a better social rank. According to Myers' and Krebs' thinking (1971:72) yearling male spruce grouse that did not emigrate would be dominant, but at least there is no evidence that they were reproductive any earlier than immigrants, termed subordinates because they emigrated from elsewhere.

These problems are even more difficult with female grouse. Almost all females dispersed, and there may be too few individuals remaining near their birth site to study how dominance and reproductive potential might vary according to dispersal. Even if emigrating females were subordinate where raised to non-emigrants they were reproductively capable when they settled: 91 percent (30/33) of the yearling females known to nest at Gorge Creek in 1971-73 were immigrants. Perhaps maximization of reproduction does not hinge on the age of first breeding but on total reproductive output during the lifespan. The difficult questions here will remain until dominance can be measured for juveniles that disperse and those that do not. If behavior is important to dispersal, are immigrants simply equal in dominance to those that emigrated, or are they able to settle because of a higher ranking than emigrants? The influence of genetics and experience would seem to be critical to these problems. In summary, I believe field data are not available to support much of the contemporary theory on dispersal.

Immigration is of interest in two ways: its numerical effect on recruitment, and the possible differences in behavior between birds that dispersed and those that did not. I did not gather data systematically on aggressive behavior but Stirling and Bendell (1970) reported seasonal changes in aggressive behavior of blue grouse in spring and summer. Aggression among spruce grouse might have peaked before most courtship activity in spring and, perhaps, many immigrants arrived only after the (supposed) aggressive level of residents had subsided. This generates the question of what really constitutes a breeding population. Present results may reflect Dhondt's (1971) report that there is only a short period of territorial defense among great tits (*Parus major*), and "floaters" are later able to settle in undefended areas. The present practice of counting all individuals as breeders even if seen only once may be too rough. On the other hand, all birds may have been physiologically capable of breeding. Yearling females commonly breed; yearling males on the experimental site probably also bred as they were quite localized, exhibited courtship behavior typical of adults, and yearling females there produced broods.

I envision three possible explanations for the apparent differential in timing of emigration and immigration. First, the separation is real. Proximal causes of emigration might occur earlier in a premium habitat or dense population, if such were characteristics of Gorge Creek. Second, dispersal is very slow. Hence, the arrival times of immigrants are delayed though they left their winter site at similar times as those from Gorge Creek. Third, the differential was not real. Dispersers suddenly become secretive; emigrants are still present on the study area after last seen and immigrants are present before first seen. That most immigrants (those known) remain for summer means they have found a general place to settle. They suddenly become less secretive and are seen in mid to late May, about the time breeding starts. Relevant data are scarce and subjective impressions conflict with all three possibilities. I have no real evidence that emigrants were more secretive than non-emigrants in spring. There was no temporal separation in autumn. But differential behavior might be expected most in spring since it was only then that dispersal affected numbers. I have no guess as to why I lost sight of males before females but did not see a difference in first sightings of immigrants. Males may become solitary and emigrate before females in accordance with earlier courtship and aggressive displays.

Some workers have assumed that immigration in autumn equalled emigration (Rusch and Keith 1971:811, Ellison 1974: 390). The marked population in this study provided a chance to document the possible equality of the flux. But there is no reason to *expect* equality among emigration and immigration on a local basis. For example, the immigration of female spruce grouse in spring was not greatest when emigration rates were highest. The number of immigrants is, of course, affected by population size and emigration rates elsewhere, and by the extent of the area from which they come. Immigration could not be calculated as percentages like emigration, and it may simply have been that a much larger geographical area supplied immigrants to the small Gorge Creek site. A known move of 9.5 km from Gorge Creek supports this possibility.

CONCLUSIONS

The purpose of this study was to evaluate the hypothesis that mortality and dispersal, primarily of juveniles, in autumn and winter determine the size of the breeding population. Results did not support this hypothesis.

Major year to year changes are summarized here. The breeding population of spruce grouse increased greatly from 1970 to 1971. Yearlings accounted for most of the increase, which in turn was caused by a high retention (low emigration) of wintering birds and high immigration (females only). Production was high in 1971 and the subsequent wintering count of juveniles was high. Following the high winter population, emigration in spring of 1972 increased greatly over that in 1971 and fewer females immigrated. Both factors produced fewer yearlings in 1972, which slowed potential growth of total numbers. Production was low in 1972 and the 1972-73 wintering count of juveniles was also low. These low counts, modified by dispersal in spring of 1973 contributed to another reduced yearling count in 1973.

The major conclusions follow.

1. Most changes in total numbers of the breeding population resulted from changes in numbers of yearlings. Annual survival of adults and yearlings was similar and, hence, the increment of yearlings to the population was the primary factor in determining changes in total numbers.

2. Disappearance of many juveniles in autumn and

overwintering juveniles in spring was judged to be due to emigration. The survival rate of dispersing individuals approximated that of non-dispersers, at least in spring.

3. Quantitatively, dispersal in autumn was not a reducing factor: immigration compensated for almost all emigration. Proportions of juveniles emigrating each year were similar. Dispersal in autumn did not have a direct, numerical effect on recruitment.

4. Survival of all birds was high in autumn and winter. Clearly, autumn and winter were not critical times for survival in this population and mortality then did not have an important effect on numbers of breeding individuals.

5. Proportions of birds emigrating in spring were variable between years. Immigration compensated for much of the loss from emigration. The number of yearlings present in summer was a direct result of emigration and immigration beginning in spring.

6. Production did affect dispersal in spring by setting the population base upon which emigration in spring would act; numbers of junveniles in late summer and late winter were very similar. Production did not determine recruitment because of variation in emigration rates in spring. Nesting success and production varied between years; adults and yearlings were both affected, but yearlings more so. The poorest reproductive output occurred in the same year as the highest emigration.

7. Proportions of birds that emigrated and distances moved during dispersal were analyzed according to population size. Data in autumn were consistent: emigration and distances were independent of density. Dispersal in spring was variable and was correlated positively with either (different between sexes) the numbers of adults-yearlings or juveniles in late winter. But results from an experimental removal of adults and yearlings in late winter did not support the interpretation of other data that emigration in spring was dependent on their numbers. Some inconsistencies in the data in spring do not weaken the conclusion that if population size affected dispersal it was manifested in spring rather than in autumn.

8. Population size may be only one of several interacting forces on dispersal. Three factors made it difficult to study how population size affected emigration in spring: 1) many adults and yearlings present in winter were not resident breeders; we require information on the dominance scheme of individuals not on breeding sites; 2) some birds might have emigrated in spring because the immediate habitat was unsuitable for use in summer, regardless of density; and 3) changes in numbers and composition of adults and yearlings present because of migration and the long period over which dispersal occurred make it difficult to evaluate the reliability and usefulness of a single density figure.

From the results of this study I envision that the following events might occur in the annual cycle to account for population size. Production of spruce grouse is low, at least relative to some other tetraonids. This is compensated by very high survival after about 2 months of age; a long life span is suggested by a high annual survival rate. Density does not seem to influence the tendency to disperse in autumn and dispersal then has no numerical importance. Dispersal in autumn might result from some behavioral or genetic polymorphism whose purpose is simply to redistribute birds with different traits and genetic makeup. This scrambling effect might increase the homogeneity of quality of individuals over large regions and directly or indirectly affect subsequent survival and dispersal in local areas. With high survival over autumn and winter the level of production is predictive of the wintering cohort of juveniles. Dispersal in spring is the final opportunity to alter the *size* of the breeding population. However it is accomplished, there is also a selection for *which* yearlings will be present in summer. Recruitment does not depend on a "first-come" basis; occupancy of summer habitat in winter does not assure that the bird will remain in summer. Birds that disperse in spring probably do not suffer greater mortality, at least immediately, than those that do not disperse. But if such dispersing individuals are at a disadvantage relative to non-dispersers it may be in terms of other subtle differences, as long term survival or reproductive success throughout life. The tendency to disperse in spring may be governed by an interaction of factors; density may reflect the magnitude of effect of a factor. A genetic basis could be at least a partial cause to disperse in spring. This seems particuarly so because much habitat is unused but (subjectively) appears suitable and birds emigrate further. Completely different factors may determine production. Changes in production could cause further restriction or increase of population growth by indirectly affecting dispersal in spring.

Some replication of this study on other intensively worked, well marked populations is necessary to evaluate the general application of these results. Advancements with many species will be made if effort is expanded from autumn through spring; continued work solely during the breeding season will not be as helpful.

I recommend that priority be given to studying if and how social contact between individuals promotes dispersal from wintering sites. Extending this, we need to know if aggressive levels decrease over time and if some immigrant yearlings successfully recruit simply because of this. For spruce grouse, these objectives require, in part, an intensive study, say from 1 February into June, to monitor changes in behavioral patterns *with a concurrent* study of the precise times of emigration and immigration. In more general terms these objectives agree with priorities for other species as well (Krebs 1970, Bendell et al. 1972, Zwickel 1972). We need refined work on the possible association of population size and dispersal, and especially on the timing of a possible influence by population size. Present gross counts of density may be too superficial. Manipulations of population parameters will help; but to be really helpful they must be well controlled and very well timed.

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Appendix 1. Summary of sightings of adult and yearling male spruce grouse [illegible] Gorge Creek, September 1970 - August 1973.

Month	Total sightings[1]		Unmarked birds			Total individuals	
	Encounters	Individuals	Encounters	Individuals		Seen previous month (%)[3]	Marked by end of month (%)
					No. still unmarked end of month[2]		
1970							
Sept.	35	20	0	0	0	85	100
Oct.	34	26	1	1	0	54	96
Nov.	30	23	1	1	0	61	100
Dec.	26	17	2	2	0	65	100
1971							
Jan.	9	7	1	1	0	83	100
Feb.	28	21	2	2	1	19	95
Mar.	41	23	0	0	0	57	100
Apr.	68	40	1	1	1	83	98
May	151	56	4	4	0	64	100
June	138	48	1	1	0	92	100
July	91	38	0	0	0	95	100
Aug.	129	51	1	1	0	69	100
Sept.	56	36	1	1	0	92	100
Oct.	52	31	1	1	0	71	100
Nov.	50	32	1	1	0	59	100
Dec.	62	34	1	1	1[A]	71	97
1972							
Jan.	32	24	2	1	1[A]	75	96
Feb.	34	24	0	0	0	29	100
Mar.	45	28	0	0	0	57	100
Apr.	67	48	0	0	0	67	100
May	174	52	4	2	0	81	100
June	152	49	2	2	0	82	100

(continued)

Appendix 1. Continued

Month	Total sightings[1]		Unmarked birds			Total individuals	
	Encounters	Individuals	Encounters	Individuals	No. still unmarked end of month[2]	Seen, previous month (%)[3]	Marked by end of month (%)
July	113	45	0	0	0	89	100
Aug.	137	49	1	1	0	76	100
Sept.	104	50	0	0	0	78	100
Oct.	95	44	0	0	0	73	100
Nov.	78	40	1	1	0	80	100
Dec.	60	38	0	0	0	82	100
1973							
Jan.	59	37	0	0	0	78	100
Feb.	42	27	0	0	0	78	100
Mar.	67	36	0	0	0	47	100
Apr.	95	46	1	1	0	85	100
May	118	45	1	1	0	82	100
June	66	36	0	0	0	83	100
July	84	36	0	0	0	78	100
Aug.	83	31	0	0	0	81	100
Total	2705		30			$\bar{x}$ = 74%	

[1] Numbers change between months for many reasons, related to birds present and time searched. March to April increases reflect increment of juveniles to yearlings.

[2] Superscript letters: same individual.

[3] Percentages show consistency of locating individuals. A low % means a greater % of birds seen that month (*x*) were not seen in month *x*-1. Low %'s resulted from: (a) few birds seen in *x*-1 (poor efficiency) though assumed present in *x*-1 and *x*, or (b) immigration during *x*. For adult and yearling males, low %'s in February 1971, February 1972, and March 1973 resulted from (a). Other low %'s probably resulted from differences in allocation of time among parts of area.

Appendix 2. Summary of sightings of adult and yearling female spruce grouse at Gorge Creek, September 1970 - August 1973.

Month	Total sightings[1]		Unmarked birds			Total individuals	
	Encounters	Individuals	Encounters	Individuals		Seen previous month[3] (%)	Marked by end of month (%)
					No. still unmarked end of month[2]		
1970							
Sept.	32	18	2	2	0	61	100
Oct.	32	20	4	3	1	60	95
Nov.	24	12	3	2	0	83	100
Dec.	27	17	6	4	1^A	41	94
1971							
Jan.	19	12	0	0	1^A	83	92
Feb.	20	14	1	1	1^A	50	93
Mar.	37	20	3	1	1^A	50	95
Apr.	62	34	0	0	0	76	100
May	69	36-38	15	11-13	1-3	41	92-97
June	59	30	6	4	0	73	100
July	64	29	1	1	0	83	100
Aug.	75	30	0	0	0	70	100
Sept.	72	33	5	3	0	70	100
Oct.	45	25	4	2	1^A	72	96
Nov.	32	21	2	1	1^A	81	95
Dec.	42	21	2	1	1^A	71	95
1972							
Jan.	22	18	2	1	1^A	78	94
Feb.	22	15	1	1	1^A	60	93
Mar.	35	24	1	1	1^A	58	96
Apr.	63	44	0	0	0	64	100
May	108	47	9	8	0	54	100
June	51	32	2	2	1^B	72	97

(continued)

Appendix 2. Continued

Month	Total sightings[1]		Unmarked birds			Total individuals	
	Encounters	Individuals	Encounters	Individuals		Seen previous month (%)[3]	Marked by end of month
					No. still unmarked end of month[2]		
July	95	34	1	1	1[B]	74	97
Aug.	118	39	3	2	0	79	100
Sept.	79	42	4	4	1[C]	79	98
Oct.	96	50	4	3	2[A,C]	54	96
Nov.	80	44	4	3	1[A]	84	98
Dec.	73	41	2	1	1[A]	78	98
1973							
Jan.	50	30	3	1	0	70	100
Feb.	58	32	0	0	0	50	100
Mar.	63	37	0	0	0	57	100
Apr.	75	45	0	0	0	93	100
May	59	36	4	4	0	64	100
June	43	28	4	4	0	79	100
July	80	26	1	1	0	81	100
Aug.	57	26	0	0	0	88	100
Total	2038		99			$\bar{x}$ = 69%	

[1] Footnote 1, Appendix 1.

[2] Superscript letters: same individual

[3] See general comments of footnote 3, Appendix 1. For adult and yearling females, low %'s in February 1971 and February 1972 resulted from (a); low %'s in May 1971, May 1972, October 1972, and May 1973 resulted from (b). Other low %'s probably resulted from differences in allocation of time among parts of area.

Appendix 3. Summary of sightings of juvenile male spruce grouse at Gorge Creek, September - March, 1970-73. Sightings commence with departure from the brood.

Month	Total sightings		Unmarked birds			Total individuals	
	Encounters	Individuals	Encounters	Individuals		Seen previous month[2] (%)	Marked by end of month (%)
					No. still unmarked end of month[1]		
1970							
Sept.	3	3	1	1	0	-	100
Oct.	33	21	4	3	1	-	95
Nov.	28	14	1	1	0	-	100
Dec.	32	17	8	2	1[A]	65	94
1971							
Jan.	21	12	0	0	1[A]	92	92
Feb.	24	19	2	2	1[A]	53	95
Mar.	41	21	1	1	1[A]	76	95
Sept.	3	3	2	2	0	-	100
Oct.	62	29	11	11	1[B]	-	97
Nov.	34	24	3	3	2[B]	-	92
Dec.	91	35	8	6	1[C]	60	97
1972							
Jan.	38	27	0	0	1[C]	100	96
Feb.	30	17	0	0	1[C]	94	94
Mar.	32	22	1	1	0	55	100
Sept.	1	1	0	0	0	-	100
Oct.	48	23	9	9	0	-	100
Nov.	36	19	2	2	0	-	100
Dec.	37	17	0	0	0	82	100
1973							
Jan.	24	14	0	0	0	100	100

(continued)

Appendix 3. Continued

Month	Total sightings		Unmarked birds			Total individuals	
	Encounters	Individuals	Encounters	Individuals		Seen previous month (%)[2]	Marked by end of month (%)
					No. still unmarked end of month[1]		
Feb.	26	9	0	0	0	78	100
Mar.	40	15	0	0	0	53	100
Total	684		53			$\bar{x}$ = 74%	

[1] Superscript letters: same individual. In January and March 1971 and January and February 1972 a bird was not seen but assumed present.

[2] Percentages not calculated for September-November because of great flux. See general comments of footnote 3, Appendix 1. For juvenile males, low %'s in February 1971, March 1972 and March 1973 resulted from (a). The low % in December 1971 resulted from (b).

Appendix 4. Summary of sightings of juvenile female spruce grouse at Gorge Creek, September - March, 1970-73. Sightings commence with the departure from the brood.

Month	Total sightings		Unmarked birds			Total individuals	
	Encounters	Individuals	Encounters	Individuals	No. still unmarked end of month[2]	Seen previous month (%)[3]	Marked by end of month (%)
1970							
Sept.	2	2	2	2	1[A]	-	50
Oct.	22	18-20	15	13-15	3-5[A]	-	75-83
Nov.	21	16-17	10	8	1-2[A]	-	88-94
Dec.	31	13	2	1	0	69	100
1971							
Jan.	7	6	0	0	0	83	100
Feb.	16	12	0	0	0	42	100
Mar.	32	16	2[1]	2	0	63	100
Sept.	14	9	5	5	2	-	78
Oct.	51	31	15	14	0	-	100
Nov.	38	23	4	3	0	-	100
Dec.	74	28	5	3	0	68	100
1972							
Jan.	37	27	0	0	0	100	100
Feb.	19	16	0	0	0	100	100
Mar.	28	19	0	0	0	63	100
Sept.	9	8	2	2	0	-	100
Oct.	33	18	12	11	0	-	100
Nov.	37	19	7	7	0	-	100
Dec.	28	17	0	0	0	88	100
1973							
Jan.	32	17	1	1	0	88	100

(continued)

Appendix 4. Continued

Month	Total sightings		Unmarked birds			Total individuals	
	Encounters	Individuals	Encounters	Individuals		Seen previous month^3 (%)	Marked by end of month (%)
					No. still unmarked end of month^2		
Feb.	38	13	0	0	0	92	100
Mar.	49	19	1	1[1]	0	68	100
Total	618		83			$\bar{x}$ = 78%	

[1] Immigrant in late winter.

[2] Superscript letters: same individual.

[3] Percentages not calculated for September-November because of great flux. See general comments of footnote 3, Appendix 1. For juvenile females, low %'s in February 1971, March 1972, and March 1973 resulted from (a); the low % for December 1971 resulted from (b).