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DEMOGRAPHY AND GENETICS IN COLONIZING POPULATIONS OF BLUE GROUSE *(DENDRAGAPUS OBSCURUS)*

by

© JAMES ALLEN REDFIELD

A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH

IN PARTIAL FULFILLMENT OF THE REQUIREMENTS FOR THE DEGREE

OF DOCTOR OF PHILOSOPHY

DEPARTMENT OF ZOOLOGY

EDMONTON, ALBERTA

SPRING, 1972

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FACULTY OF GRADUATE STUDIES AND RESEARCH

The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research for acceptance, a thesis entitled Demography and Genetics in Colonizing Populations of Blue Grouse *(Dendragapus obscurus)* submitted by James Allen Redfield in partial fulfillment of the requirements for the degree of Doctor of Philosophy.

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ABSTRACT

Demography and genetics of increasing populations of blue grouse *(Dendragapus obscurus)* were studied by combining intensive field observations with analysis of genetic structure of the populations. This research was designed to test the hypothesis that genetic structure of populations changes with changes in population density.

Blue grouse colonize newly logged regions rapidly and, in this study, density of breeding birds increased for at least seven years following logging. The age-structure of colonizing populations changed from 70% to 45% yearlings in the first three years after logging and stabilized thereafter.

The *Ng* locus appears as white bands on gels stained for serum esterase, following electrophoresis. The *Ng* locus was polymorphic and was used as a marker. The three alleles at this locus were widespread spatially and stable temporally. Frequency of the most common allele, *NgM*, was higher in birds in one-year-old habitat than in birds on older-aged habitats. Frequency of heterozygotes as well as the observed frequency of heterozygotes/expected frequency (O/E ratio) among yearlings were significantly positively regressed on age of habitat. Correlation between population density and both frequency of heterozygotes and the O/E ratio among yearlings was positive and significant, i.e., the higher the population density, the higher the frequency of both heterozygotes and the O/E ratio among yearlings. These results support the original hypothesis that changes in genetic structure occur with changes in density. The cause of these relationships is not known but experiments were suggested to investigate two possible alternatives. A conceptual model, based on the idea of total heterozygosity of individuals conferring competitive advantage, was described to account for the observed results.

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"No population ecology can succeed that is not also population genetics."

Richard C. Lewontin (1968) in
Population Biology and Evolution

INTRODUCTION

Populations of blue grouse on Vancouver Island increase rapidly following logging or burning of mature forest (Hatter 1955) suggesting a surplus of grouse is available for colonization. If rapid expansions are possible in these situations, what are the mechanisms which stop these increases? Chitty (1965, 1967) proposed that changes in the genetic quality of populations associated with changes in abundance were both necessary and sufficient to stop increases. Much recent research in population biology has attempted to see if genetic changes are associated with changes in abundance.

The objectives of the research reported in this thesis were twofold: a) to describe the mechanism of population increase following logging, and b) to test the hypothesis that genetic changes are associated with changes in abundance. (The null hypothesis is that genetic changes are not associated with changes in density.) Demography was studied via intensive field observation and genetics were studied using electrophoresis to differentiate genetic variants at a marker locus. An experimental approach was made possible because logging of mature forest continually creates new habitat.

BACKGROUND

The Experimental Approach

The creation of new, previously unoccupied, breeding habitat may present ecological opportunities for certain species and can be used as an experimental approach to induce population increases. Often, new breeding habitat is an unexpected by-product of man's alteration of the ecosystem (Bustard 1969, Tevis 1956a,b). Logging on Vancouver Island, for example, induces rapid population increases in blue grouse by creating favorable breeding habitat. Present day logging patterns on Vancouver Island involve the complete removal, i.e. clear-cutting, of blocks of forest. Often adjacent blocks of forest are cut in successive years creating a mosaic of habitat types within a restricted region. This experimental manipulation is not the only way to create new breeding habitat but it is the most practical and probably simulates fire in earlier times, at least to grouse.

The approach used was to choose three large areas containing sub-units which were logged in several previous years. I will, throughout this thesis, speak of age of habitat synonymously with years since logging. The number of grouse on these areas was ascertained and habitat-specific densities were calculated by associating each grouse with the habitat type. All areas logged in the same year were combined for analysis.

The Animal

Blue grouse are endemic to mountains of western North America. On Vancouver Island, in spring and summer, they occur in openings in the forest and in winter they occur in mature or old second-growth forest (Bendell and Elliott 1967). In spring, adult males (2-year-olds and older) are territorial and live solitarily. Yearling males (1 year old) are not usually

territorial, roam over extensive areas in spring and probably do not contribute to breeding. Females, both adults and yearlings, do not appear to be territorial in spring or summer. Both adult and yearling females breed. Most breeding occurs in May and chicks usually hatch in June. Grouse appear polygamous and males do not participate in nesting, incubation or care of the young. Once chicks hatch, females and broods move rather extensively.

Grouse are suitable for study since they are diurnal, conspicuous and easily captured, banded and resighted. One drawback associated with studies on blue grouse is their migration off breeding range into dense forest in late summer and autumn which makes it difficult to study them in winter (King 1971). Other problems involve overlapping generations, secretive nature of 1-year-old males and difficulty in finding nests. However, these are of minor hindrance to this study.

Research on population dynamics of grouse on logged regions of Vancouver Island has been relatively intense since the early 1950's. Bendell (1955) studied grouse near Campbell River and concluded that parasites were limiting his very dense, but stable, population. In later studies he was unable to confirm this. A new study, started in 1958, was aimed at seeing if surplus grouse were available to colonize depopulated areas. These new studies were on a stable population, but densities were less than half those found in the earlier study. Basically, from this study Bendell concluded that there were no surplus adult grouse (Bendell and Elliott 1967).

Zwickel (1965) and Zwickel and Bendell (1967a) studied the relationship between nutrition, chick survival and subsequent population density. They concluded that survival of chicks was predetermined in the mother but that the level of production in any one year was more than adequate to explain

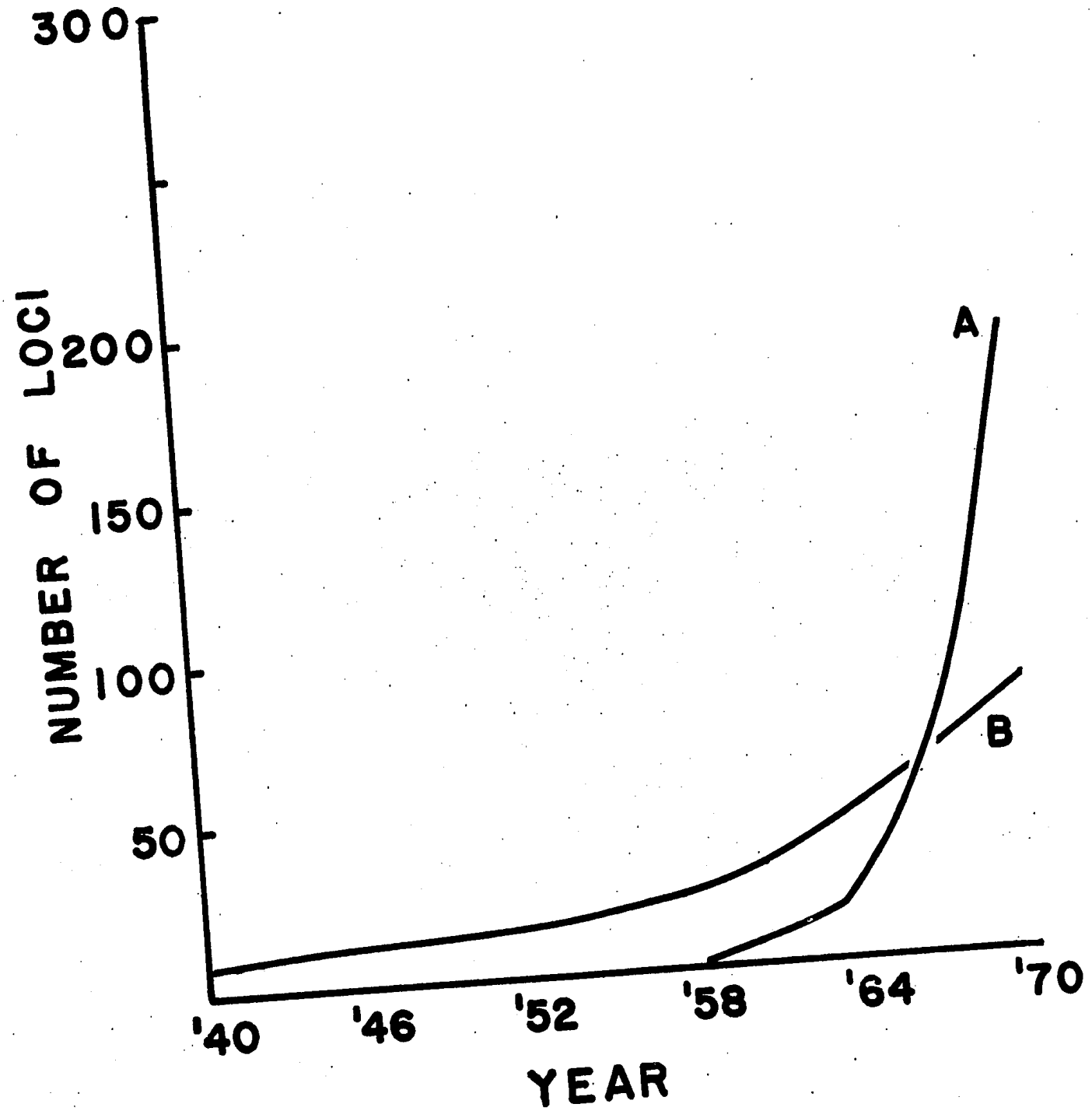
recruitment the following year. Like the earlier studies, populations in this study were stable but at a lower density.

Thus, population densities of grouse appeared stable, indicating they were regulated, even though no substantial surplus of potentially breeding grouse could be found. But surpluses are also indicators of regulated populations (Brown 1969, Watson and Moss 1970). Reproduction varied between years whereas recruitment did not, suggesting recruitment was regulated, at least in stable populations. Food seemed adequate and disease was uncommon. Most external limiting factors seemed inadequate, either by themselves or in combination, to explain numbers of grouse (Zwickel and Bendell 1967a, 1970). That leaves, as one possibility, the interactions of the grouse themselves as a regulatory mechanism.

Chitty (1967) has pointed out the problem of discovering a regulatory mechanism in a stationary population. Since stationary populations can offer no comparative information on the causes of increases and decreases, they are of limited value in the study of population regulation. That is why the experimental approach used in this study seemed necessary in an attempt to explain population regulation in blue grouse.

The Genetic Marker

Studies involving the interaction of genetics with ecology require a suitable genetic marker(s). Criteria most often used in choosing markers are that they be a) variable, b) easily identified, c) simply inherited, and d) stable. In the past, studies of ecological genetics such as this one were not possible with most species since these criteria could not be met. Even though morphological variants were known to occur in some species [e.g., banding in *Cepaea memoralis* (Cain and Sheppard 1954); melanism in *Biston*


300
200
150
100
50
NUMBER OF LOCI
A
B
'40
'46
'52
'58
'64
'70
YEAR

betularia (Kettlewell 1956); spot patterns in *Maniola jurtina* (Ford 1965a); *T*-locus in *Mus musculus* (Lewontin and Dunn 1960)], it was not until the development of electrophoresis that a tremendous amount of cryptic genetic variation was revealed in virtually all species (Lush 1966, 1970, Manwell and Baker 1970). When I initiated this research nothing was known about genetic variation within populations of blue grouse. However, several proteins and enzymes of other vertebrates were characteristically polymorphic (Figure 1; Lush 1967, 1970, Manwell and Baker 1970).

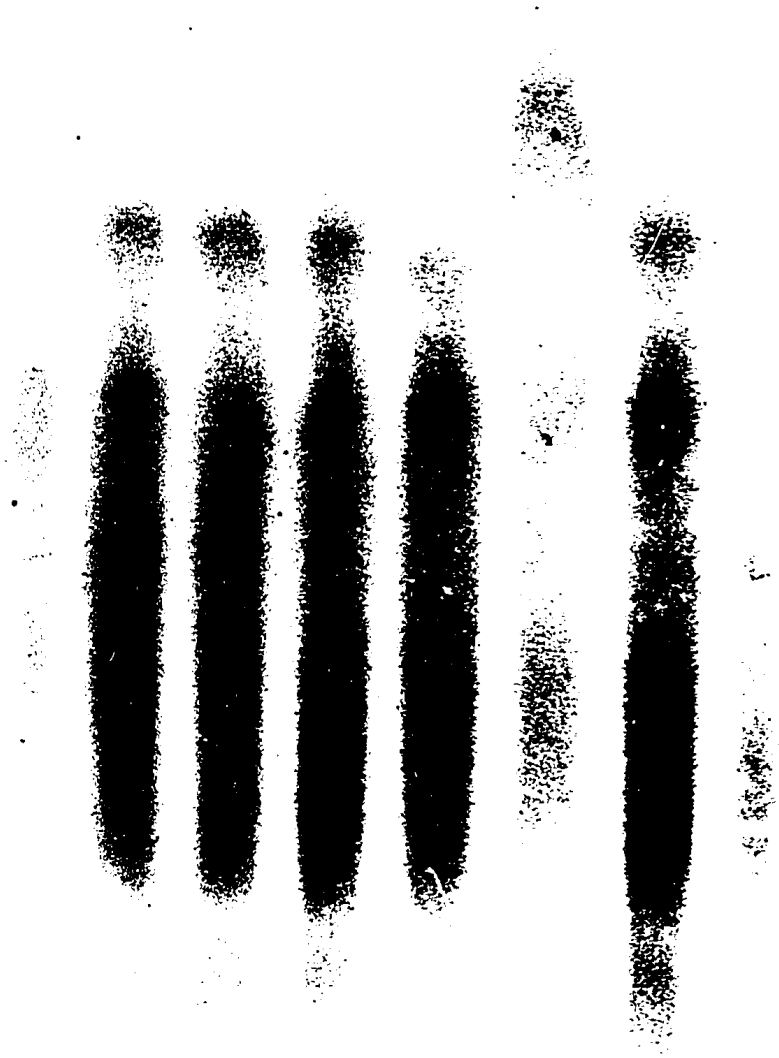
My aim, at first, was to survey several proteins and enzymes to see which showed electrophoretic variation. Of those surveyed, transferins and lactate dehydrogenase were not polymorphic while some others (including acid phosphatase, alkaline phosphatase and leucine amino peptidase) gave consistently poor resolution. Esterases were variable but the genetics of this variation seemed too complex. Baker *et al.* (1966) reported a similar complexity in the esterases of pheasants *(Phasianus colchicus)* in North America. Since I was searching for genetic variation which could be investigated without an elaborate breeding program, I disregarded esterases.

However, during a routine stain for serum esterase, early in this study, a gel was accidentally overstained, and when washed in the normal manner (see Methods), revealed a series of white bands (Figure 2) on a blue or grey background. These bands (*Ng* locus) were variable and of apparent simple inheritance (Birdsall *et al.* 1970) and were chosen for study on this basis. Thus, the marker was chosen more or less at random. The biochemical significance of the substance is unknown. However, this matters little to the analysis, since the hypothesis was stated in general terms to cover any genetic variation.

Figure 2. Starch-gel showing the three white bands and four genotypes at the *Ng* locus in blue grouse.

1. *NgM/NgM;* 2. *NgS/NgM;* 3. *NgS/NgM;* 4. *NgS/NgM;*
5. *NgS/NgF;* 6. *NgM/NgF;* 7. *NgS/NgM;* 8. *NgM/NgM.*


+
F
S
M
Ng
ALBUMIN
ORIGIN
1 2 3 4 5 6 7 8


+
F
S
M
Ng
ALBUMIN
ORIGIN
1 2 3 4 5 6 7 8

Genetics and Demography

There has been an increasing interest for the past several years in considering demography and genetics simultaneously (Birch 1960, Cavalli-Sforza 1962, Cavalli-Sforza and Bodmer 1971, Charlesworth 1971, Chitty 1960, Crow and Kimura 1970, Ford 1965a,b, King and Anderson 1971, Kojima 1971, Lewontin 1970, MacArthur and Wilson 1967, Roughgarten 1971, Wallace 1968a,b, 1970, and many others). This interest has been especially spurred by recent technical advances in the use of electrophoresis which makes the detection and differentiation of genetic variation in most species relatively easy (Hunter and Markert 1957, Poulik 1957, Smithies 1955).

Among numerous recent hypotheses (e.g. Ford 1965a,b, Howard 1960, etc.) involving the interaction of genetics and demography, Chitty's (1960, 1964, 1965, 1967, 1970) is one of the more interesting and has some evidence in favor of it. For example, Ford (1965a) showed that during periods of rapid population increase in butterflies (Lepidoptera) selection pressure was relaxed and resulted in a burst of genetic variability. This was countered by increased selection during declines. Wellington (1960) demonstrated shifts in proportions of different types of tent caterpillars *(Malacosoma pluviale)* during changes in abundance. Baltensweiler (1968) and Clark *et al.* (1967 p.124-136) argued for qualitative shifts in populations of the Larch tortix *(Zeiraphera grisearia)* with changes in abundance. Although Wellington and Baltensweiler did not demonstrate the genetics of the types examined, it seems unlikely that the changes in types were totally induced by the environment, since they existed at all population densities examined.

Perhaps the most outstanding works on demography and genetics of vertebrates are those being done on several species of small rodents in North America (Canham 1969, Gaines and Krebs 1971, Gaines, Myers and Krebs 1971,

Myers and Krebs 1971, Rasmussen 1964, 1970, Selander 1970a,b, Selander and Yang 1969, Tamarin and Krebs 1969). Rasmussen and Selander aimed their research at the genetic structure of populations and how genetic structure was affected by demography and behaviour, while the other studies cited above attempted to study demography and behaviour as affected by genetics.

STUDY AREAS

In 1968 a brief survey was conducted on three regions and more intensive work was confined to two other main regions. Since 1968, grouse on the latter two regions, plus one new area, were studied. Since the only information used from the three general regions studied in 1968 is allelic frequencies, further descriptions of these plots are not necessary. Generally, all areas were in a relatively young stage of vegetative regeneration following logging or burning. The intensive study areas are described below. All are in the Ash River Valley near Elsie Lake, midway between Courtenay and Port Alberni, Vancouver Island (Figure 3). Sizes and logging histories of each study area are given in Table 1.

Area 104 is on a steep southwest-facing slope ranging in elevation from 270 to 1070 meters. Most of it was logged since 1962 but only part of the debris left after logging was burned. This area probably has the best soil (J. Holm, Chief Forester, MacMillan-Bloedel Sproat Lake Division, *pers. comm.*) of all the intensively studied tracts.

Area 107 is the largest of the study plots and its size has continuously increased since 1968, through the addition of newly logged regions adjacent to the study area. This region is characterized by a series of parallel rocky ridges running east and west with elevations from 200 to 600 meters.

Area 108e was added to the study in 1969 and is the smallest study area. It has the most uniform logging history and the least relief, but is similar in topography to 107.

The Ash River Valley would be classed in the Coastal Western Hemlock Zone (Krajina 1969). Most of the natural forest in the Ash River Valley was

Figure 3. Map of the Ash River Valley, Vancouver Island, British Columbia, showing the locations of the three main study areas.

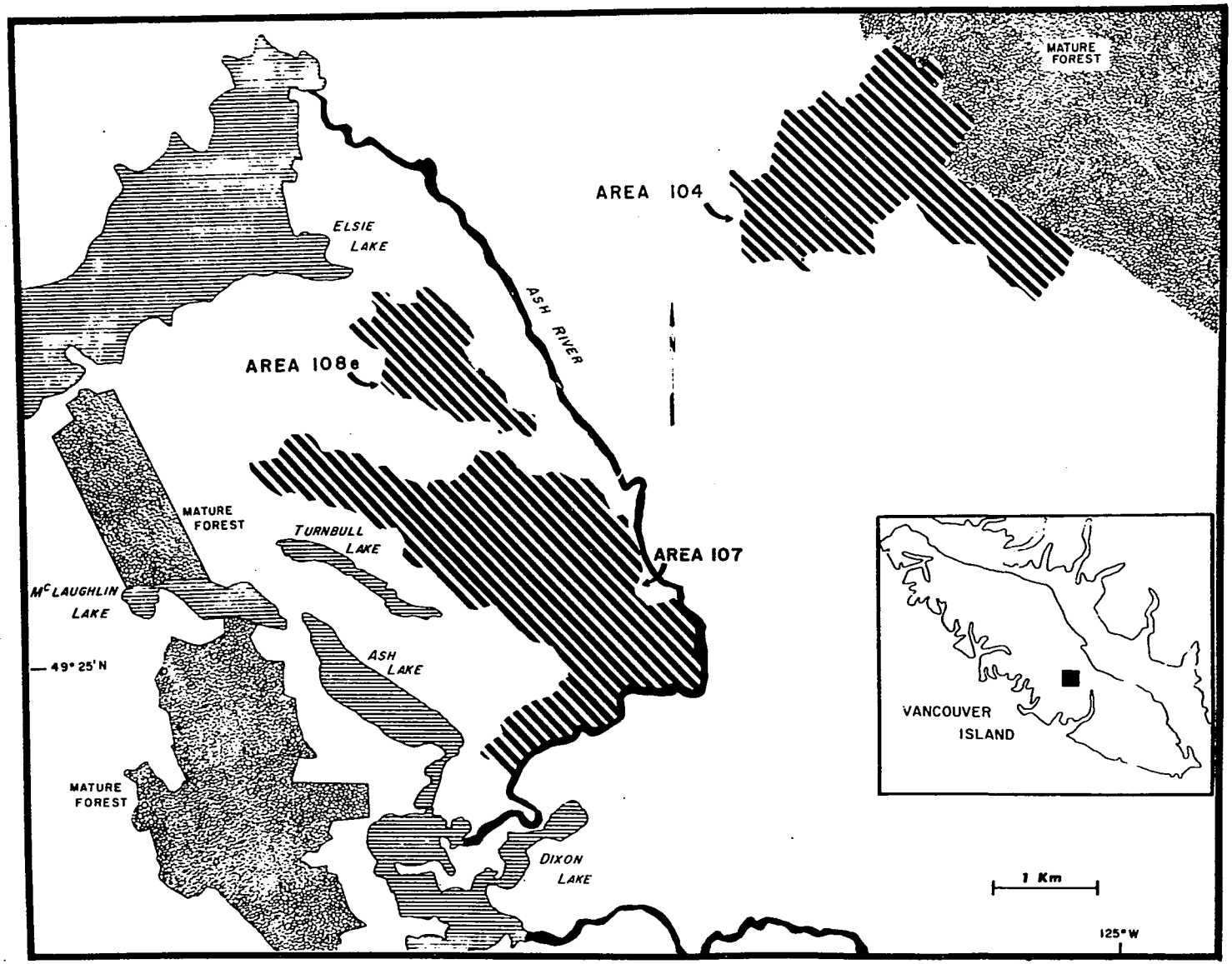

MATURE FOREST
AREA 104
ELSIE LAKE
ASH RIVER
AREA 108e
MATURE FOREST
TURNBULL LAKE
AREA 107
McLAUGHLIN LAKE
ASH LAKE
49° 25' N
MATURE FOREST
DIXON LAKE
VANCOUVER ISLAND
1 Km
125° W

Table 1. History of logging of the study areas (in km^2). Data were compiled from maps of logging patterns supplied by MacMillan Bloedel, Ltd., Sproat Lake Division.

Year	Area		
	104	107	108e
pre-1961	0.943	0.826	-
1961	-	0.198	-
1962	0.413	-	-
1963	-	-	-
1964	0.287	0.429	0.457
1965	0.376	0.696	-
1966	0.405	0.413	0.583
1967	0.324	0.304	0.134
1968	0.708	0.494	-
1969	-	0.822	-
1970	-	0.267	-

removed (Figure 4). The logging history of the valley, as compiled from maps, is presented in Table 2. In recent years, 15 to 40 hectare stands of trees were logged using clear-cut methods, creating a patchwork of various habitat types. It was not unusual, for example, to have 20-, 10-, 5- and 1-year-old areas immediately adjacent to each other. Since 1960, logging activities increased in the valley, especially when compared to the decade starting with 1950. Almost all of the logged region was replanted with Douglas fir and these plantations were in various stages of regeneration.

Although vegetation was not studied in detail some general statements can be made. Fireweed *(Epilobium angustifolium)* was probably the most prominent herbaceous plant in summer. Douglas fir *(Pseudotsuga menziesii)* and western hemlock *(Tsuga heterophylla)* were the predominant conifers. Judging from published results of other studies on Vancouver Island (Bendell and Elliott 1967, Zwickel and Bendell 1967), vegetation on the areas I studied was more luxuriant with less willow *(Salix* spp.*)*.

Weather in the Ash River Valley is influenced by the Beaufort Mountains to the east. Rainfall is over 250 cm annually with snow common in winter. Summers are pleasant with hottest days over 40 C and coolest nights near 0 C (as measured in weather screens at ground level). Long periods of very hot and dry weather are frequent between May 1 and September 1.

Figure 4. Photograph of the Ash River Valley looking east towards the Beaufort Mountains. Trees in most of the valley bottom were removed prior to 1945 while the more open areas on the upper slopes have been logged since 1960. Note the clear-cut logging pattern. Crest of these mountains is near 1800 meters.

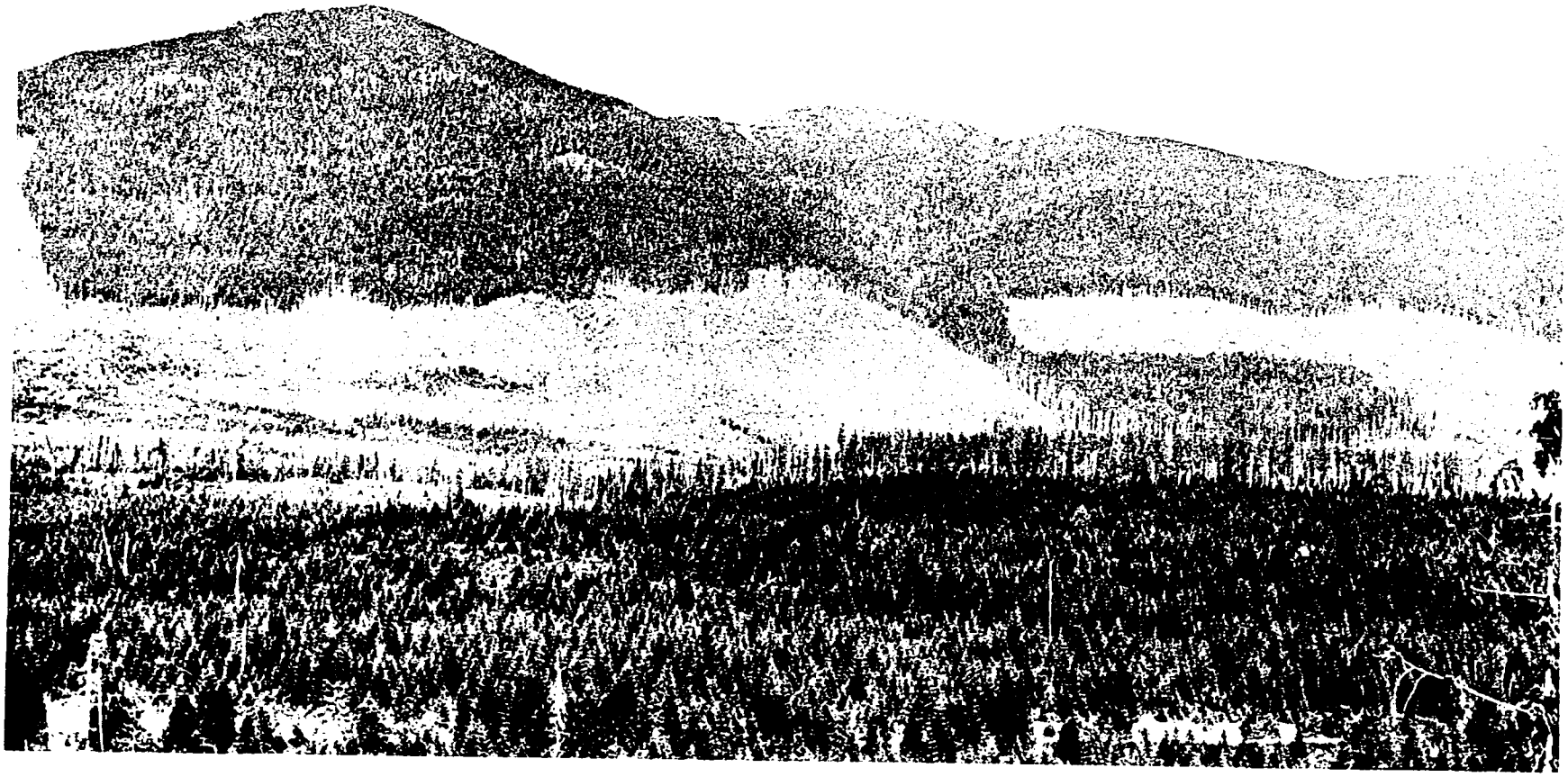


Table 2. History of logging in the Ash River Valley. Data were compiled from maps of logging patterns provided by MacMillan Bloedel, Ltd., Sproat Lake Division.

Year	Size (km^2)	% logged	cumulative %
Pre-1940	38	21	21
1940	5	3	24
1941	6	3	27
1942	11	6	33
1943	3	2	34
1944	4	3	37
1945	5	3	39
1946	7	4	43
1947	3	2	44
1948	4	3	47
1949	3	2	48
1950	4	2	50
1951	2	2	51
1952	2	1	52
1953	4	3	55
1954	2	1	55
1955	2	1	56
1956	3	2	58
1957	1	1	59
1958	3	2	60
1959	1	1	61
1960	2	2	62
1961	3	2	63
1962	5	3	66
1963	3	2	68
1964	3	2	69
1965	6	4	72
1966	6	4	76
1967	4	3	78
1968	4	3	80
1969	3	2	81
Unlogged	35	20	100

METHODS

Finding and Marking Grouse

Field work began in late April in 1968 and in late March or early April in other years. In all years field work terminated near September 1. A systematic search with trained dogs was conducted daily. Grouse were located by one of three methods: 1) the dogs pointed a majority of the silent birds, 2) in spring and early summer males on territories were conspicuous and often located because of their displays and calls, and 3) once eggs hatched, hens with chicks were often located by their response to an artificial chick call given by the observer.

An attempt was made to capture and band all unmarked grouse. Grouse were captured with a 7-meter telescoping noose pole (Zwickel and Bendell 1967b). Birds in the hand were weighed, bled, marked with unique color combinations of leg bands, and released. Chicks less than 25 days of age were too small to be marked with leg bands. Most of the information in this thesis comes from marked grouse. For purposes of analysis, the point of first sighting in a given year was used to assign a bird with a habitat of known age.

Estimating Density

Adult males were relatively easy to count in spring and early summer since they occupy territories from which they display and mate (Bendell and Elliott 1967). Most territorial males were captured and marked but some were difficult to capture because they were wild or usually located in tall trees. If unmarked males with characteristic behaviour were consistently found in a specific region, I included them in the estimate of density.

Yearling males, unlike adults, were more difficult to count since they

were usually not territorial and did not display. Thus, I used an indirect method of analysis based on the sex-ratio of yearling males and yearling females counted prior to the onset of hatching of eggs (a period when this ratio is least likely to be biased). (If this ratio was 1:1, I assumed that the numbers of yearling males and females were equal.) During the four years of this study, 142 yearling females and 121 yearling males were captured in this period (1.18♀:1♂). This ratio was not different from an expected 1:1 ratio ($\chi^2(1)=1.67$; $p=0.1$) and I conclude that there were the same number of yearling males as yearling females. Thus, density of yearling males was considered the same as for yearling females.

Like most yearling males, females had few displays and activities in spring which made them conspicuous. Likewise, they did not appear to be territorial. However, once chicks hatched, females with broods were easy to count and most brood hens were probably found in all years (except perhaps 1968). But not all females had broods which made females more difficult to count. Zwickel and Bendell (1967a) used number of females seen per hour of search during the period May 14 to June 3 as an index of density, but noted that this was potentially biased. I developed a method, modified from the common Lincoln model (Lincoln 1930), for estimating density which circumvented most of the biases of the method of Zwickel and Bendell (1967a).

Estimation formulae. Numbers of adult and yearling females were estimated separately, N_a and N_y: For purposes of illustration, consider only adults, N_a:

Let

N_p = the number of adult females resighted or newly banded prior to hatching of eggs;

P_b = the number of N_p that were later seen with broods; and

B = the total number of marked adult brood hens sighted in a given year.

Assuming that the same proportion of brood hens were among hens located prior to broods hatching (N_p) as among those not seen prior to hatching (N_a-N_p) and that the same proportion of brood hens was found among N_p as among N_a-N_p, then

$$B = (P_b/N_p) \cdot N_a;$$

therefore,

$$N_a = B \cdot (N_p/P_b).$$

An analogous calculation yielded an estimated number of yearlings, N_y.

Biologically, this formula will overestimate if the ratio of P_b/N_p is abnormally low, as might happen for example, if, by capturing a bird, one reduces its chances of successfully nesting. This may have been the case with some new bandings in May, especially yearlings nesting for the first time, but there is no way, at present, to test the bias. Regardless of biological biases, this formula overestimates the number of females (Ricker 1958) and a correction could be added to compensate for this overestimate. Corrections were calculated but they made little difference to the estimates. I feel that corrections were unwarranted, given the nature of the data. Thus, both statistically and biologically, this formula will likely overestimate the number of females and the estimates of densities based on these calculations are maximums.

I first tested the null hypothesis that there were no differences in the ratio P_b/N_p between years or age-classes (Table 3). Among adults, a greater proportion may have had broods in 1971 than in 1969 ($0.1>p>0.05$) but among yearlings, there were no differences between years. Between age-classes, adults were more successful in 1971 than yearlings ($p<0.05$) but all other

Table 3. Data used to compare the ratio P_b/N_p among adult and yearling female blue grouse. †

Year	Adults		Yearlings	
	Number	Proportion	Number	Proportion
1968	2/3	0.67	4/9	0.45
1969	16/33	0.49	19/37	0.51
1970	19/34	0.56	13/28	0.46
1971	24/32	0.75	36/69	0.52
Totals	45/69 (without 1969)	0.65	72/143	0.50

†P_b is the number of hens located before broods hatch and then later seen with a brood. N_p is the total number of hens located before broods hatch. The ratio among adults in 1969 was nearly significantly different from adults in other years ($p \leq 0.1$), hence it was not used to calculate the total ratio.

comparisons showed no differences. Thus, the ratio P_b/N_p, was estimated as 0.5 for adults in 1969 and 0.65 in other years. For yearlings the estimate was 0.5 in all years.

Collection of Blood

For genetic studies a sample of blood was collected from all birds handled. Blood was collected by clearing about 3 cm of feathers from the distal end of the humerus on the ventral surface of the wing and puncturing a vein that crosses the humerus at this point. As blood formed a pool it was drawn into a syringe which had been rinsed with 4% sodium citrate. A 1 cc disposable tuberculin syringe with 27 gauge, 1/2 inch needle was used with small chicks. Otherwise, a 2-1/2 or 3 cc syringe with 22 gauge 1 inch needle was used. (Syringes found to work best in the field were those with a heavy plastic case which prevented damage to the syringe and needle.) The amount of blood collected varied from 0.05 to 2 cc depending on the size of the bird. Samples were successfully collected from chicks that had just hatched as well as all older ages. Since 1968, no more than 1 cc of blood was taken from any one individual.

While in the field, blood was stored in 1 cc centrifuge tubes on ice in a 1/2 liter vacuum bottle. Upon arrival at camp, usually within 10 hours, blood was centrifuged and the plasma was separated and frozen. Plasma was usually frozen for 2 to 9 months at -20 to -60 C. Longer storage appeared to have had little effect on the protein examined. I obtained the same qualitative results with 14 samples run after 4 months' storage and again 3 years later.

Electrophoretic Techniques

All samples were analyzed for variation at the *Ng* locus (see The Genetic

Marker) using starch-gel electrophoresis. The buffer systems used for detection of these bands were modified from Fujino and Kang (1968). Starch-gel electrophoresis (Smithies 1955, 1959) of plasma was carried out in a discontinuous system of buffers (Poulik 1957). Bridge buffer contained 23.6 g boric acid, 4.0 g lithium hydroxide, and 1 liter of water (pH 7.8); gel buffer contained 2 g citric acid, 7 g Tris, 170 ml bridge buffer, and 1 liter water (pH 8.1). Vertical electrophoresis was conducted at 2 C with a constant 400 volts and a starting current of 2 ma/cm of gel for about 4 hours but it was allowed to proceed until the borate buffer had migrated 16 cm. This was important since the *Ng* system was not clear until the borate buffer had migrated through it.

Gels were stained for 2 hours in the dark in a solution commonly used for detecting esterases: 0.05 g α-napthyl acetate (dissolved in 2.5 ml acetone), 10 ml 0.1 molar Tris-HCl buffer (pH 7), and 250 mg Fast-blue RR salt were added to 90 ml water and mixed for about two minutes immediately prior to staining. Destaining was for 24 to 48 hours in methanol, water and acetic acid (5:5:1). Bands at this locus were visible anodal to the major albumin esterase activity as white areas on a grey or blue background (Figure 2). This method is modified from that reported in Birdsall *et al.* (1970). All questionable readings were rerun until definitive results were obtained. Less than 1% of all samples could not be classified, but this was due to smearing, not to an absence of the white bands.

Statistical Analysis

The specific statistical tests made on the data are mentioned in the text. However, all χ^2 tests were done with a G-test (Sokal and Rohlf 1969). Where appropriate, Yate's correction for continuity was applied.

All statistical analyses were done with an IBM/360 computer using the APL language. Most of the programs are documented in Library 160 in Armitage (1971). The level of significance is 5%, but I may refer to trends in the data when the probability value is less than 10%.

RESULTS

Demography

Demography is the study of populations, their density, age structure, dispersion, birth and death rates, and dispersal. Within the limitations of this study, only density and birth rates (i.e., breeding success) with respect to colonization were analyzed.

Density

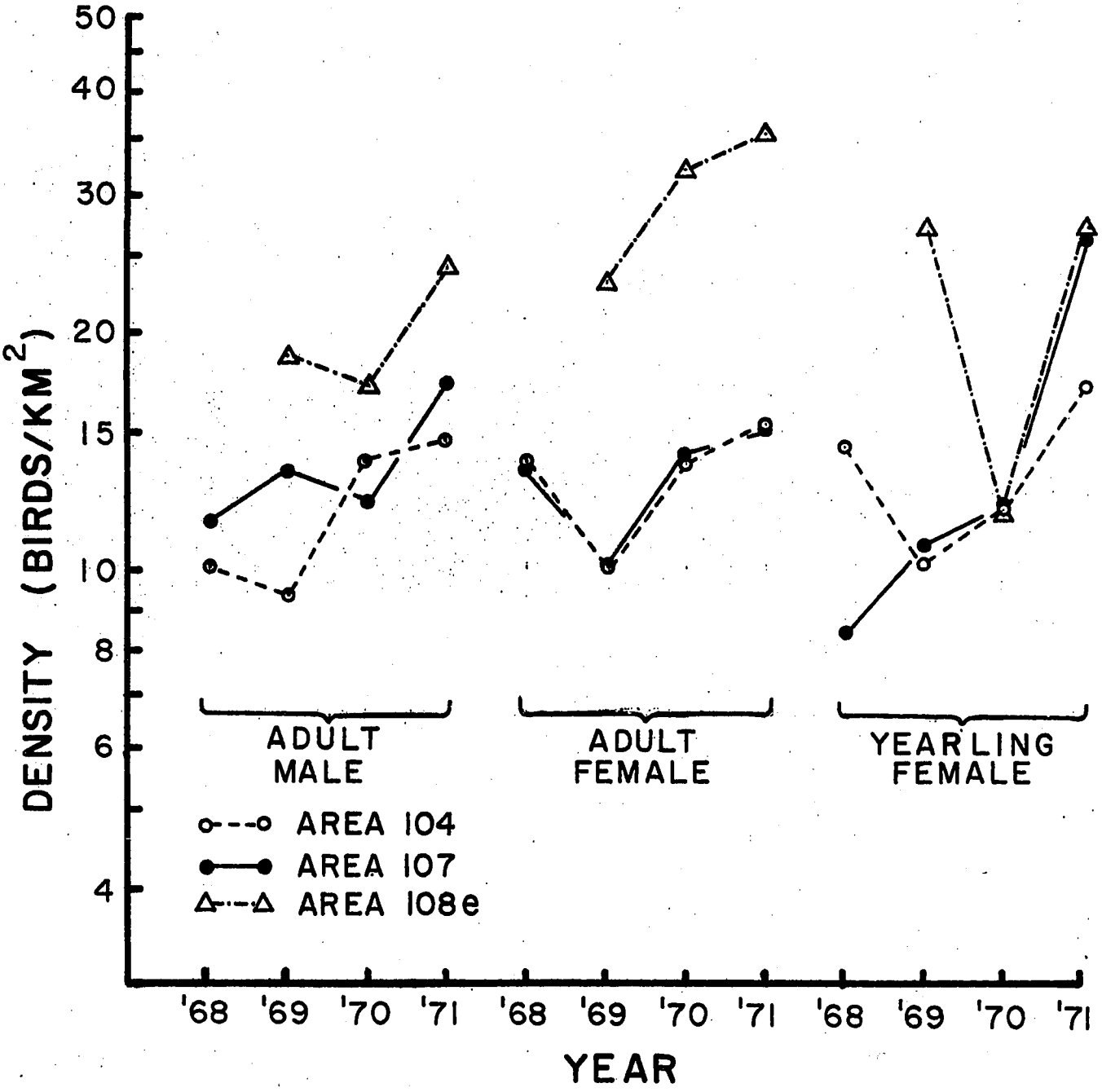
General Considerations. Before looking at changes in density associated with colonization, the general changes in density are given. These patterns may help interpretation of colonization and are also valuable comparisons with other studies. Since I consider the density of yearling males to be the same as for yearling females (see METHODS) I will discuss the results for adult males, adult females and yearling females (Figure 5). Following this section changes in density associated with colonization are examined.

Area 108e had a consistently higher density of adult males and females than either of the other areas, at least since 1969. Area 107 had a higher density of adult males than 104, except in 1970, when the relationship was reversed. Both 104 and 107 had nearly the same density of adult females in all years.

Recruitment of yearlings in 1969 was higher in 108e than in the other areas. In 1970 and 1971 108e had recruitment rates essentially identical to those in 107. In 1968, 104 had a higher rate of recruitment of yearlings than 107, while in 1969 and 1970 these two areas had nearly identical rates of recruitment. In 1971, 107 had a higher rate of recruitment than 104.

Comparisons within areas but between years gave the following results: In 104 all segments of the breeding population declined between 1968 and

Figure 5. Density of adult male, adult female and yearling female blue grouse on the three main study areas, 1968 to 1971.


50
40
30
20
15
10
8
6
4
DENSITY (BIRDS/KM^2)
ADULT MALE
ADULT FEMALE
YEARLING FEMALE
AREA 104
AREA 107
AREA 108e
'68
'69
'70
'71
YEAR

1969 but after 1969 there was a general increase. In 107, adult males increased from 1968 to 1969, decreased slightly in 1970 and increased markedly in 1971. Adult females in 107 decreased between 1968 and 1969, and increased in both 1970 and 1971. Recruitment of yearlings into 107 increased steadily since 1968 with a sharp increase in 1971. Density of grouse in 108e was higher than in 107 but densities of both adult males and females paralleled those in 107. In 1970 and 1971, recruitment of yearlings in 108e was the same as in 107.

In general, populations increased since 1969 with increases in 1971 being most marked. Recruitment of yearlings increased most markedly, especially in 108e and 107 in 1971. Because of the high recruitment rates in 1971, populations in the Ash River Valley appear to still be increasing.

Using these estimates of density, I calculated the minimum percentage of birds banded in each area for each year (Table 4). In most years and areas, greater than 50% of all sex-age classes, except yearling males, were marked. In all years higher percentages of adult males were marked than yearling males. This was due to behavioural differences between the two age groups. The percentage of females banded was as high or higher than for adult males, suggesting I was equally successful at locating and marking females and adult males. The low percentage of adult males tagged in 104 in 1971 (42%) was probably due to two factors: 1) The increase in total density of birds on all study areas in 1971 made complete coverage of all areas difficult, especially early in spring and early in the year less effort was expended on 104 than on 107 or 108e. 2) Many of the birds on 104 seemed wild in 1971, making resighting and capture difficult. The wildness was found in birds on 104 in other years but it was more distinct in 1971.

Changes in Density Associated with Colonization. The data on density

Table 4. Percentage of blue grouse banded on the study areas, 1968 to 1971. The percentage of adult males is based on the number of territories counted and the number of marked territory holders. The yearling male percentage was based on the estimated number of females (yearling) and the actual number of yearling males banded. Female percentages were based on the actual number of females marked and the total number estimated to be alive. The numbers in brackets represent actual number banded/total estimated number.

Area	Age	Sex	1968	1969	1970	1971
104	Adult	♂	46 (13/28)	70 (23/33)	75 (28/37)	42 (21/50)
	Yearling	♂	15 (5/34)	46 (15/32)	17 (8/48)	30 (17/58)
	Adult	♀	72 (23/32)	64 (27/42)	70 (32/46)	71 (34/48)
	Yearling	♀	71 (24/34)	85 (27/32)	54 (26/48)	57 (33/58)
107	Adult	♂	55 (17/31)	59 (25/42)	70 (32/46)	70 (44/63)
	Yearling	♂	28 (5/18)	50 (15/30)	29 (14/49)	38 (42/101)
	Adult	♀	66 (24/36)	88 (30/34)	77 (44/57)	72 (41/57)
	Yearling	♀	78 (14/18)	100 (30/30)	71 (35/49)	76 (81/101)
108e	Adult	♂	--	86 (19/22)	90 (17/19)	82 (22/27)
	Yearling	♂	--	31 (9/29)	29 (4/14)	29 (10/35)
	Adult	♀	--	68 (22/32)	94 (30/32)	76 (29/38)
	Yearling	♀	--	80 (23/29)	72 (10/14)	69 (24/35)

presented in the previous section did not show changes occurring on different age habitats. Since a mosaic of habitat types existed within each study area, and since each habitat type represented different years since logging, it is of interest to know if birds were distributed at random over these various habitat types, or whether they were more dense on some areas than others.

In order to calculate density of birds on each age habitat, I calculated the size of each habitat (Table 5), the number of resightings on that habitat (Table 6), and the percentage of the total number of birds banded (Table 4). Samples for each area (104, 107 and 108e) were too small for between-area comparisons, hence data for all areas were combined. Even with data combined between areas, samples were usually too variable for between-year comparisons and all years were combined for final analysis (Table 7).

Density of adult males and adult and yearling females for all age-habitats are given in Figure 6. Density of adult males and females increased steadily from one through at least seven years after logging. Age-class ≥ 8 is composed of all habitat 8 years old and older and includes some habitats which were unsuitable (according to Bendell and Elliott 1966). Regression on these points (excluding point ≥ 8) showed that adult males and adult females were increasing at about 2.9 to 3.4 birds/km^2/age of habitat during this seven year period ($Y_{males}=1{\cdot}52+2.89X$ [$p\leq 0.01$]; $Y_{females} = 1{\cdot}71+3.38X$ [$p\leq 0.01$]) while density of yearling females did not increase as rapidly as adults ($Y = 7{\cdot}51+2{\cdot}23X$ [$p\leq 0.01$]). These density figures show a sharp increase in density of adults and smaller increases in density of yearlings in the first seven years following logging.

Density of yearling females did not fit a linear model well. There appeared to be, among yearlings, a two stage period of colonization.

Table 5. Size (in km^2) of each age habitat studied, 1968 to 1971, for all areas combined.

Year	Age of Habitat							
	1	2	3	4	5	6	7	>8
1968	0.63	0.82	1.07	0.72	--	0.41	0.12	1.77
1969	1.20	0.76	1.40	1.10	1.20	--	0.41	1.96
1970	0.82	1.20	0.76	1.40	1.10	1.20	--	2.26
1971	0.27	0.82	1.20	0.76	1.40	1.10	1.20	2.26
Totals	2.92	3.60	4.43	3.98	3.70	2.71	1.73	8.25

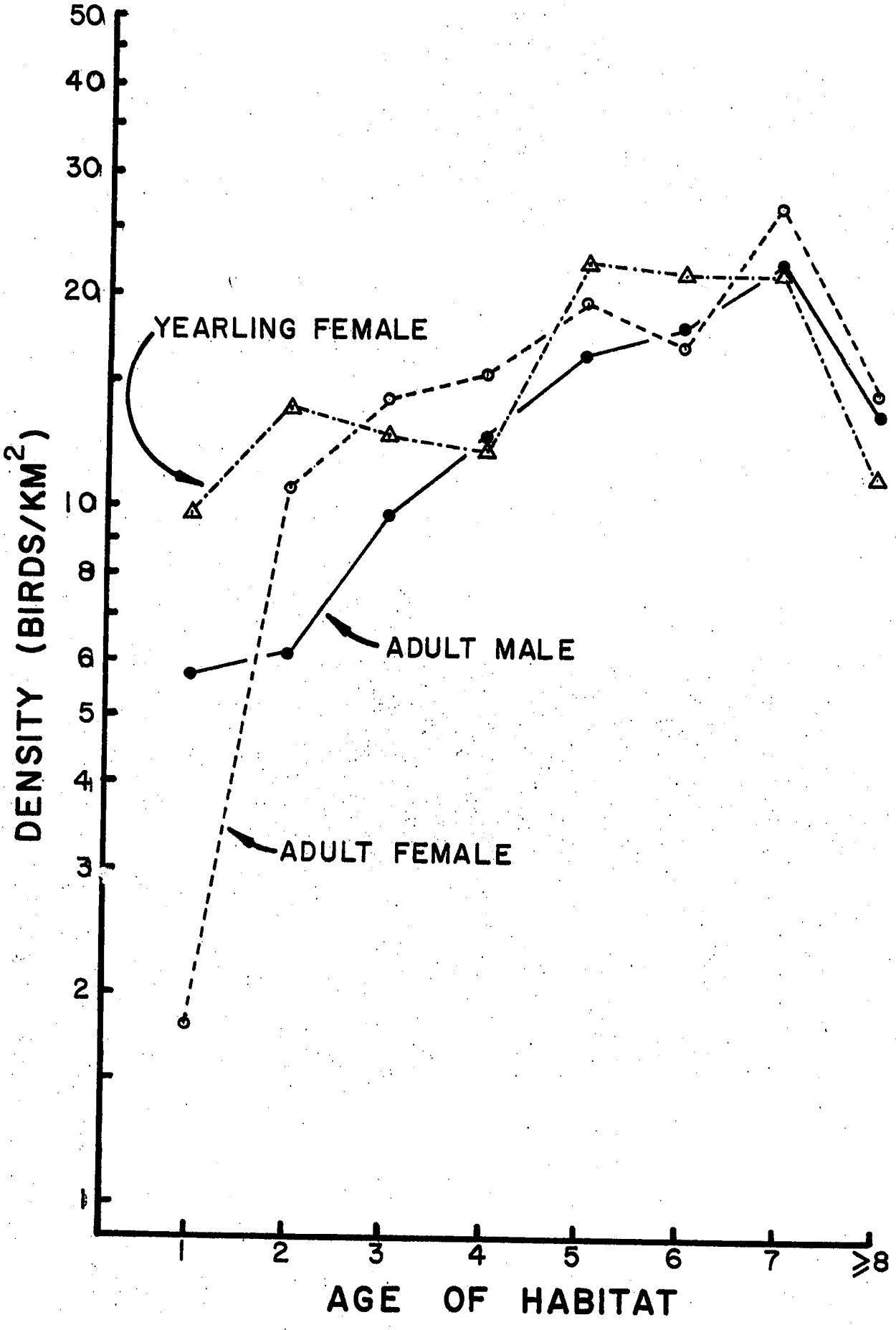
Table 6. Number of blue grouse captured or registered on each age of habitat, 1968 to 1971.

Year	Age	Sex	Age of Habitat								Total
			1	2	3	4	5	6	7	≥8	
1968	Adult	♂	0	3	5	6	--	6	0	10	30
	Yearling	♂	0	0	2	3	--	2	0	3	10
	Adult	♀	0	3	5	11	--	4	0	24	47
	Yearling	♀	1	6	6	7	--	10	0	8	38
1969	Adult	♂	4	6	14	8	18	--	7	10	67
	Yearling	♂	5	3	6	2	13	--	7	4	40
	Adult	♀	2	8	14	11	24	--	8	12	79
	Yearling	♀	4	12	15	9	21	--	4	16	81
1970	Adult	♂	1	7	4	19	7	17	--	22	77
	Yearling	♂	3	5	3	5	0	4	--	6	26
	Adult	♀	2	9	13	21	9	24	--	28	106
	Yearling	♀	5	7	6	12	10	13	--	18	71
1971	Adult	♂	6	0	4	4	17	9	22	25	87
	Yearling	♂	9	6	4	8	8	3	11	19	68
	Adult	♀	0	9	8	9	19	9	26	25	105
	Yearling	♀	11	16	10	9	30	17	24	22	139
Total	Adult	♂	11	16	27	37	42	32	29	67	261
	Yearling	♂	17	14	15	18	21	9	18	32	144
	Adult	♀	4	29	40	52	52	37	34	89	337
	Yearling	♀	21	41	37	37	61	40	28	64	329

Table 7. Density of blue grouse/km^2 on various age habitats for 1968 to 1971 combined. (Yearling males are considered the same as yearling females.)

Years	Age	Sex	Age of Habitat							
			1	2	3	4	5	6	7	≥8
Total	Adult	♂	5.7	6.2	9.7	12.7	16.6	18.2	22.5	13.9
	Adult	♀	1.8	10.8	14.3	15.6	19.7	17.3	27.3	14.8
	Yearling	♀	9.8	13.9	12.9	12.2	22.4	21.7	22.2	11.4

Figure 6. Density of adult male, adult female and yearling female blue grouse on each age habitat for all years combined. Age of habitat is equivalent to years since logging.


50
40
30
20
10
8
6
5
4
3
2
1
DENSITY (BIRDS/KM²)
YEARLING FEMALE
ADULT MALE
ADULT FEMALE
1
2
3
4
5
6
7
≥8
AGE OF HABITAT

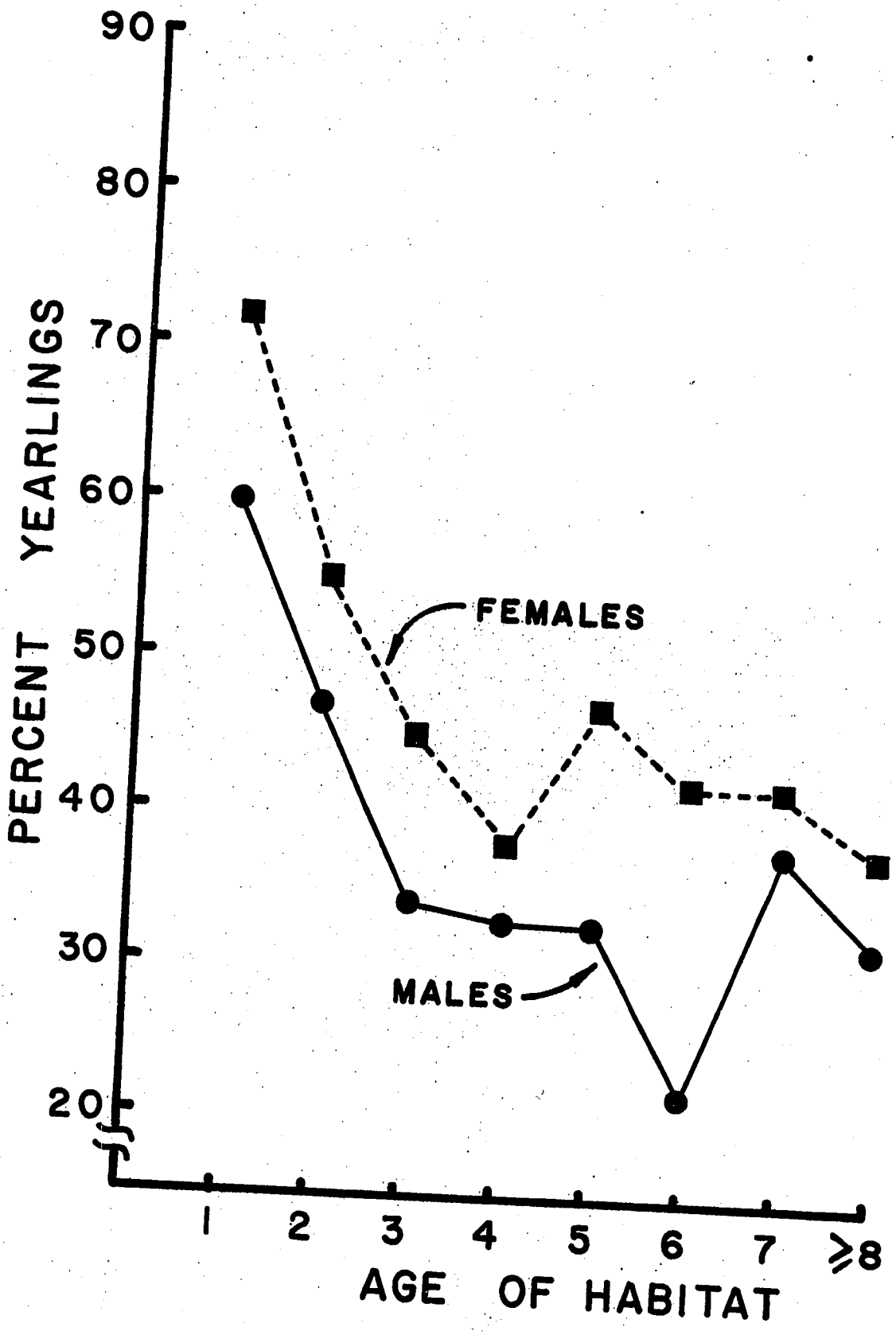
Populations were fairly stable at about 10-13 yearling females/km^2 during the first four years after logging but five years after logging populations increased about 70% to a new level of about 22 yearling females/km^2. This new level was stable for at least three years.

All groups declined in age-class ≥8. Since age-class ≥8 was a composite and included some habitat which, according to Bendell and Elliott (1966), could be called unsuitable, it is difficult to say what happened in older, but suitable, habitat. However, densities probably stabilized shortly after year seven.

Age-specific density and age structure of grouse living on each habitat type were closely related. For analysis of age structure, only birds known to be alive were used. As the data on density would suggest, there was a high proportion of yearlings on age-classes 1 and 2 (Figure 7). Age structure of birds on one-year-old habitat was about 70% yearlings and was significantly different from age structure of birds on all other habitat types ($p \leq 10^{-5}$). Age structure of birds on two-year-old habitat was about 55% yearlings and was significantly different from age structure of birds on older habitat types ($p \leq 0.01$). Age structure relationships on all other habitat types show no differences or trends, suggesting age structure stabilized at about 45% yearlings by three years after logging.

Recruitment onto one- and two-year-old habitat was related with production the previous summer. For example, 1970 was a year of very high reproductive output and in 1971 recruitment onto one-year-old habitat was higher than had been recorded previously. The total number of yearlings captured in 1971 was nearly double the number captured in any previous year, but χ^2 analysis suggested that recruitment was significantly higher in one- and two-year old habitat than in other habitat types. In order to test the null

Figure 7. Percentage of yearling male and female blue grouse among all banded grouse on each age habitat, all years combined. The male percentage is lower than the female percentage because yearling males are more difficult to locate than yearling females.


90
80
70
60
50
40
30
20
PERCENT YEARLINGS
FEMALES
MALES
1
2
3
4
5
6
7
≥8
AGE OF HABITAT

hypothesis of no differences in recruitment into all age habitats between years, χ^2 goodness-of-fit values were calculated. These calculations show number of yearlings on age-class 1 and 2 habitat in 1971 was significantly larger than in the other three years (Table 8). Other habitat types had smaller values, except age-class ≥8.

In summary, density of adult males and females increased for at least seven years following logging. Yearlings occurred in higher absolute densities than adults on younger age habitats but did not increase as rapidly as adults. Yearlings seemed to have a two stage pattern of settlement. The first stage was at about 10 to 12 yearling females/km^2 and lasted four years. The second stage was at about 22 yearling females/km^2 and lasted at least three years. All segments of the population declined in habitat ≥8 years old but this may have been due to some of this old habitat being unsuitable. There were signifcant shifts in age structure of colonizing populations from about 70% to 45% yearlings in three years. Recruitment of yearlings onto young habitat (one and two years old) was significantly higher in 1971, a year following very high production, than in other years.

Breeding Success

General Considerations. Several calculations associated with breeding may be needed for an evaluation of population changes. Three of these are the percentage of females with broods, the average size of broods and the total estimated chick production (which may be important in evaluating the number of colonizers available for the following year).

I assume all females were capable of and attempted to breed each year (Zwickel and Bendell 1967). However, not all females were successful at completing the nesting cycle. The proportion which was successful was part

Table 8. Results of χ^2 analyses of captures of yearling blue grouse on various age habitats in 1971. A significant departure means that there were a greater number captured in that age habitat in 1971 when compared to the years 1968 to 1970 combined.

Age of Habitat	Yearling Males		Yearling Females		Totals	
	χ^2	$p\leq$	χ^2	$p\leq$	χ^2	$p\leq$
1	39.30	0.00	47.3	0.00	86.50	0.00
2	3.18	0.07	6.11	0.01	9.20	0.00
3	0.01	0.90	0.01	0.92	0.02	0.88
4	7.34	0.01	0.61	0.44	4.79	0.02
5	0.00	0.98	3.02	0.08	2.21	0.14
6	0.18	0.67	0.09	0.77	0.01	0.93
7	0.17	0.68	4.96	0.03	2.19	0.14
8	15.00	0.00	1.53	0.22	10.70	0.00

of the *effective breeding number* (Kimura and Crow 1963). Effective breeding was analyzed by two methods: First, I calculated the total percentage of all females with broods. This overestimated the percentage with broods since successful hens with broods were easier to locate than unsuccessful, lone hens. About 50% of the hens were first located after broods hatched. Thus, this calculation likely gave maximum estimates. Alternatively, the proportion of females found prior to broods hatching that later had a brood was calculated. This estimate was a minimum and was previously calculated in connection with estimating numbers (Table 3). These two estimates set limits on what I called effective breeding.

Both sets of data are presented in Table 9. Data for 1968 are weak since at that time I did not spend the necessary time on the intensively worked study areas, especially early in the year, to make large enough counts of females. Thus, most of my conclusions are based on data for the latter three years.

In most years between 50 and 90% of adults and between 45 and 85% of yearlings were effective breeders. There seemed to be a smaller percentage of effective breeding among adults in 1969 than in either 1970 or 1971. Between age-classes and within years, adults were more successful than yearlings only in 1971.

Zwickel and Bendell (1967a) suggested a maximum of 50% of females were broodless in a given year in their study. Their calculations were based on total counts of females on breeding range. Using these criteria (maximum estimates), my data suggest that less than 30% of females were unsuccessful in a given year. The difference between the two studies was significant and two explanations are possible: First, perhaps I was more efficient at finding females, especially females with broods. I used an imitation chick

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Table 9. Maximum and minimum percentages of female blue grouse with broods on all study areas combined, 1968 to 1971. The minimum percentages are from Table 3 and the maximum percentages are based on the method of Zwickel and Bendell (1967a).

Year	Age	Actual No. of Females	Actual No. of Broods	% with Broods	
				Maximum	Minimum
1968	Adult	46	44	96	67
	Yearling	38	26	69	45
1969	Adult	79	55	68	49
	Yearling	80	46	56	51
1970	Adult	106	88	83	56
	Yearling	67	53	79	46
1971	Adult	104	95	91	75
	Yearling	138	100	73	52

call extensively during searches once broods hatched and this caused many females to respond, thus identifying their location. Zwickel *(pers. comm.)* did not use this call. Alternatively, perhaps this was a case of selection for genotypes with a high reproductive rate in an expanding population. In the study of Zwickel and Bendell (1967a), the population was relatively stable, whereas populations which I studied increased rapidly after 1969. Selection for high and early reproduction in rapidly expanding populations has been hypothesized on theoretical grounds (Cole 1954, Lewontin 1965, MacArthur and Wilson 1967).

Among females with broods, I calculated average brood size by counting the number of chicks in broods known to be older than 15 days [by backdating of captured chicks (Zwickel and Lance 1966)] or estimated older than 20 days (by size of chicks). A one-way analysis of variance with unequal sample sizes was used to ascertain if there were differences between parental age-classes, years, or areas (Steel and Torrie 1960, Sokal and Rohlf 1969). The means and standard errors for all counts are presented in Table 10.

Adults had significantly larger brood sizes than yearlings in all years except 1968 (1968: $F=0.04$, $df=1,66$, $p\leq0.75$; 1969: $F=5.23$, $df=1,95$, $p\leq0.05$; 1969: $F=5.23$, $df=1,95$, $p\leq0.05$; 1970: $F=16.56$, $df=1,164$, $p\leq0.001$; 1971: $F=13.14$, $df=1,164$, $p\leq0.001$). Thus, parental ages were considered separately in further analyses. Brood sizes of adults between areas showed no significant differences (1968: $F=0.03$, $df=1,41$, $p\leq0.75$; 1969: $F=0.22$, $df=2,50$, $p\leq0.75$; 1970: $F=2.63$, $df=2,99$, $p\leq0.1$; 1971: $F=0.67$, $df=2,90$, $p\leq0.75$). Brood sizes of yearlings between areas showed significant differences only in 1968 (1968: $F=6.89$, $df=1,23$, $p\leq0.001$; 1969: $F=1.09$, $df=2,41$, $p\leq0.5$; 1970: $F=0.25$, $df=2.61$, $p\leq0.75$; 1971: $F=0.93$, $df=2,70$, $p\leq0.5$). In 1968 the difference stemmed from a homogeneous set of six brood counts and I disregarded

Table 10. Average (±1 standard error) brood sizes for adult and yearling female blue grouse, 1968 to 1971, in all study areas.

Year	Age		Area 104	Area 107	Area 108e	Totals
1968	Adult	N	21	22	--	43
			3.5±0.4	3.6±0.3	--	3.5±0.2
	Yearling	N	19	6	--	25
			4.2±0.7	1.7±1.2	--	3.6±0.8
1969	Adult	N	20	20	13	55
			3.5±0.5	3.8±0.5	3.9±1.2	3.7±0.4
	Yearling	N	11	23	10	41
			2.9±1.0	3.2±0.3	2.4±1.0	2.9±0.4
1970	Adult	N	33	44	25	102
			4.2±0.6	5.0±0.2	5.2±1.0	4.8±0.3
	Yearling	N	29	30	5	64
			3.8±0.6	3.7±0.6	3.2±4.6	3.7±0.5
1971	Adult	N	24	40	29	93
			5.1±1.0	4.7±0.4	4.4±0.6	4.7±0.4
	Yearling	N	23	36	14	73
			4.0±0.8	3.3±0.3	3.6±1.5	3.6±0.4

this difference. Areas were combined and between-year analyses calculated. These calculations showed highly significant between-year fluctuations in average brood size of adults ($F=8.04$, $df=3,287$, $p \leq 0.001$) but not for yearlings ($F=1.96$, $df=3,202$, $p \leq 0.1$).

The between-year difference among adults was reduced to a difference between 1968+1969 and 1970+1971. Adults in these latter two years had large brood sizes for grouse on Vancouver Island. Thus, average brood size of adults seemed more variable than for yearlings.

Average brood sizes for both yearlings (2.9 to 3.7) and adults (3.5 to 4.8) was high when compared to data from other studies on Vancouver Island. Bendell (1955) reported an average brood size of 2 to 2.7 in late summer, 1950 to 1952. Zwickel and Bendell (1967a) reported an average brood size of 2.2 to 2.9 for late summer during 1962 to 1964 (adults and yearlings combined). It is not easy to explain this difference as artifact. Once chicks can fly (at about 7 to 10 days of age), they were relatively easy to count and both Zwickel *(pers. comm.)* and I feel that our counts were accurate. A possible explanation is that, as for the percentages of females breeding, there was recent selection for high reproductive genotypes in the population. Whether this hypothesized selection was the cause of population increases or the result of them is not known. In support of this hypothesis, Zwickel reopened his studies of blue grouse on Vancouver Island and found that the population at his old study area was increasing; the average brood size was also higher than in his earlier studies (Zwickel, *pers. comm.*).

Zwickel and Bendell (1967a) concluded that recruitment in a stable population was not dependent on the previous year's production. I compared these two variables by estimating total production on each study area in a given year and calculating correlation coefficients between production and

number of yearlings captured in the following year (Table 11). There was a nearly significant correlation between these two variables for all data combined ($r=0.970$, $p<0.2$) and for areas considered separately ($r=0.679$, $p\approx0.05$) suggesting that recruitment in an expanding population may have been related to the previous year's production.

Summarizing, a high percentage of females was successfully breeding in the Ash River Valley. Adults were slightly more successful than yearlings. Among successful hens, average brood size was also high. Adults had larger broods than yearlings in all years except 1968 but there was little variation between areas. Brood sizes of adults, but not yearlings, varied significantly from year to year. The variation was reduced to a difference between 1968+1969 and 1970+1971. In the latter two years brood sizes of adults were large. Correlation between recruitment in one year and production in the previous one was found. The data support the hypothesis that in expanding populations there is selection for high reproductive rate.

Breeding Success and Colonization. In the previous section I presented evidence suggesting higher breeding success in expanding populations of grouse. Now I ask the question: Does breeding success vary with birds on different age habitats? Since population densities were increasing with age of habitat it was reasonable to suppose that there would be a systematic change in breeding success. As in the previous section, percentage of females with chicks and average brood size were used as a measure of breeding success.

Since data were too few to compare minimum estimates, I compared maximum percentages of females known to have had broods for adults and yearlings on different age-habitats (Table 12). Females on older age-habitats tended to have a higher percentage with broods than females on younger age habitats.

Table 11. Estimates of production for blue grouse in year X-1 and recruitment in year X.

Year	Age of Hen	Area	Total No. of Broods	Brood Size	Estimated Total Production Year X-1		Year	Total No. of Yearlings Captured Year X	
1968	Adult	104	21	3.5	73	243	Adjusted* 328 (for 108e)	43	120
		107	23	3.6	83		1969	45	
	Yearling	104	17	4.2	72			32 (108e in 1969)	
		107	9	1.7	15				
1969	Adult	104	21	3.5	73	334		35	98
		107	17	3.8	65		1970	49	
		108e	17	3.9	66			14	
	Yearling	104	16	2.9	46				
		107	15	3.2	48				
		108e	15	2.4	36			45	192
1970	Adult	104	30	4.2	126	566	1971	113	
		107	37	5.0	137			34	
		108e	21	5.2	109				
	Yearling	104	24	3.8	91				
		107	22	3.7	81				
		108e	7	3.2	22				

*This adjustment is based on a predicted percentage contribution from area 108e based on the contributions in the following two years.

Table 12. Maximum proportion of female blue grouse on each age habitat with and without broods.

Age	Status	Age of Habitat							
		1	2	3	4	5	6	7	≥8
Adult	With	2	21	33	38	38	26	33	76
	Without	2	8	8	11	14	9	2	8
Proportion with broods		0.50	0.69	0.80	0.78	0.73	0.74	0.94	0.90
Yearling	With	13	29	23	24	37	27	19	69
	Without	8	11	11	14	25	12	8	13
Proportion with broods		0.62	0.73	0.67	0.63	0.60	0.69	0.70	0.84
Totals:	With	15	50	56	62	75	53	52	145
	Without	10	19	19	25	39	21	10	21
Proportion with broods		0.60	0.71	0.74	0.71	0.66	0.72	0.84	0.87

I first tested the null hypothesis that there were no differences between adults and yearlings within a habitat type. Only age-class 7 had a significantly higher proportion of adults than yearlings with broods ($p \leq 0.03$). Since there were no other obvious trends in these data, all data were combined. When χ^2 was calculated on pairs of samples, the results indicated that age-class 7 and ≥ 8 had a significantly larger percentage of successfully breeding females than other age habitats.

These results are potentially biased, however. If in older habitats it was more difficult to resight a female before broods hatch due to the structure of vegetation, then the estimated percentage of females with broods would be too high. Secondly, Mossop (1971) suggested that birds in populations at high densities were wilder than birds in populations at low densities. If true, then it may have been more difficult to resight females without chicks, and this would increase the observed percentages with broods. At any rate, the data do not support the hypothesis that birds in low density populations would be more successful breeders than birds in higher density populations.

I calculated the average number of chicks per brood hen on each age habitat (Table 13). There were no significant differences in the relationship between age of habitat and brood size in 1968, 1969, or 1971. In 1970, among yearling females there were significant differences in brood sizes between habitat types. Although there were differences, there were no trends in the data, with brood sizes of females on 2-, 4- and 8-year-old habitat being larger than those on 1-, 3-, 5- and 6-year-old habitat ($F=4.18$, $df=6,57$, $p \leq 0.005$). These data indicate that number of chicks raised per hen was independent of age of habitat.

Both the data for percentage of females breeding and number of chicks

Table 13. Average size of broods for blue grouse located on each age habitat, 1969 to 1971. Brood counts include broods older than 15 days of age. Sample sizes in 1968 were too small to consider in this analysis. F is the result of analysis of variance between ages of habitats; N is sample size; $\bar{x}$ is mean; and se is the standard error of the mean.

Year	Age		Age of Habitat 1	2	3	4	5	6	7	≥8	F
1969	Adult	N	3	1	14	4	15	1	10	7	0.36
		$\bar{x}$	3.5		3.7	4.3	3.9		3.9	3.0	
		se	0.5		0.02	0.5	0.01		0.04	0.08	
	Yearling	N	-	12	3	7	7	-	-	12	2.4
		$\bar{x}$	-	3.0	2.0	4.1	2.1	-	-	2.9	
		se	-	0.01	0.5	0.1	0.04	-	-	0.01	
1970	Adult	N	1	4	10	11	9	24	-	42	0.44
		$\bar{x}$	4.6		5.3	4.8	4.6	5.2	-	4.6	
		se	0.6		0.1	0.1	0.1	0.01	-	0.00	
	Yearling	N	6	3	5	9	9	7	-	25	4.18**
		$\bar{x}$	3.3	6	2.2	4.2	3	2.6	-	4.2	
		se	0.2	2.2	0.2	0.1	0.1	0.1	-	0	
1971	Adult	N	-	12	7	4	17	2	37	13	1.23
		$\bar{x}$	-	5.4	3.4	3.3	4.7		4.7	5.2	
		se	-	0.01	0.2	0.7	0.01		0.0	0.1	
	Yearling	N	2	7	2	8	19	6	18	10	1.25
		$\bar{x}$	3.4		3.7		3	3	4.2	4	
		se	0.1		0.04		0.01	0.14	0.01	0.04	

**p≤0.01

per successful female show no increases in younger age habitats as hypothesized. These results do not necessarily negate the hypothesis as stated, however, since the population has been increasing since 1969. There was a high average brood size and a high percentage of females successfully breeding throughout these increasing populations, and this may be overriding the hypothesis. As noted earlier, both the average brood size and percentage of females successful at nesting was larger in this study than reported for other recent studies on Vancouver Island. Thus, when these data from expanding populations are compared to data from other, more stable, populations the general hypothesis was substantiated.

Genetics of the *Ng* Locus

The *Ng* locus was previously described only in a note (Birdsall, *et al.* 1970). Therefore, it is appropriate to discuss the inheritance of the bands detected, the spatial and temporal distribution of the alleles and the fitness of the genotypes before considering changes in this system associated with colonization.

Inheritance of the bands is essential since, in order to test a genetic hypothesis, one must be sure he is working with a genetically determined character. Inheritance was studied by comparing the pattern of variability to other systems with similar characteristics and known inheritance, and also by the method of incomplete family data (Cooper 1968); i.e., where the genotype of one parent and one or more offspring are known.

Understanding spatial and temporal distribution of the alleles is necessary, since potentially the most useful genetic markers in the study of interaction between genetics and demography are those which are spatially widespread and temporally stable. Spatial and temporal variation was studied

by comparing frequencies of alleles and genotypes between samples from different parts of Vancouver Island and from the adjacent mainland, by comparing allele frequencies between years within areas, and by Hardy-Weinberg calculations [see Falconer (1960) or Li (1955) for discussion of implications of Hardy-Weinberg calculations]. Fitness calculations are needed to help understand *if* and *how* the various genotypes may be affecting genetic structure and demographic events. Also, fitness calculations may shed some light on the mechanism of maintenance of the polymorphism. Reproductive success and survival of different genotypes was used to calculate fitness of various genotypes.

Inheritance

General Considerations. Three white bands were detected after electrophoresis of plasma from blue grouse. All individuals scored had at least one band, but none had more than two bands. In addition, plasma from the same birds bled at two different times produced the same pattern. Since bands with similar characteristics have been found to be inherited as codominant alleles at a single autosomal locus (Manwell and Baker 1970) and since there was close agreement to Hardy-Weinberg expectations based on this hypothesis, it was reasonable to suppose that these bands were products of three codominant, autosomal alleles, *NgF*, *NgM*, and *NgS* for the fastest, intermediate and slowest band, respectively (Figure 2, p.7). All six genotypes from these three alleles were found. Homozygotes were characterized by having a single band and heterozygotes by having two bands.

NgM was by far the most common allele with a frequency of near 0.8 in most populations. Because of the rarity of *NgF*, it was considered equivalent to *NgS* for some analyses. Most populations examined were in Hardy-Weinberg

equilibrium and the three alleles were widespread in blue grouse on Vancouver Island (see Hardy-Weinberg Calculations and Distribution). Thus, the polymorphism appeared stable (Ford 1965a).

Incomplete Family Data. Incomplete family data (IFD) were used to examine the genetics of the *Ng* locus. IFD are genetic data where the genotype of one parent and one or more offspring are known. Cooper (1966, 1968) and Cooper and Rendel (1968a) pointed out the utility of IFD in the analysis of genetics of populations. IFD have the advantage over population data in that they allow one to test hypotheses about inheritance and detect the effects of selection and population subdivision (the Wahlund effect, Wahlund 1928). Additionally, IFD are easier to collect than complete family data and may be the only data available from most natural populations.

Cooper (1968) urged the collection of IFD from marsupials and domestic species of mammals. Manwell and Baker (1970, p.24) state that IFD can *only* be collected from viviparous or ovoviviparous vertebrates. These authors seem to have overlooked the possible source of information obtainable from birds. In many birds, including blue grouse, a mother and young are closely associated for some time which leads to the possible collection of IFD.

The method using IFD is based on the fact that among parents of known genotypes there are certain expectations for the ratios of offspring. These expectations are presented in Table 14, as an idealized IFD table with no selection or population subdivision. In this table there are two alleles, A and B, at a single autosomal locus, with frequencies p and q in the parent generation. Offspring are represented as O and subscripts are used to denote parent genotype and offspring genotype, respectively. Thus, $O_{A.AB}$ denotes an AB offspring born from an AA parent. From this table it can be shown that the following conditions hold:

Table 14. Idealized incomplete family data table when there is no population subdivision or selection. O represents offspring. Subscripts appended to O signify parental and offspring genotype respectively. This table is for two allele case only.

Parental Genotypes and their Frequencies		Frequencies of Genotypes among Offspring			Total
Female	Male	AA	AB	BB	
AA p^2	AA p^2	p^4	-	-	
AA p^2	AB $2pq$	p^3q	p^3q	-	
AA p^2	BB q^2	-	p^2q^2		
AA p^2	?	p^3 $[O_{A.A}]$	p^2q $[O_{A.AB}]$		p^2 $[O_{A.}]$
AB $2pq$	AA p^2	p^3q	p^3q	-	
AB $2pq$	AB $2pq$	p^2q^2	$2p^2q^2$	p^2q^2	
AB $2pq$	BB q^2	-	pq^3	pq^3	
AB $2pq$	?	p^2q $[O_{AB.A}]$	pq $[O_{AB.AB}]$	pq^2 $[O_{AB.B}]$	$2pq$ $[O_{AB.}]$
BB q^2	AA p^2	-	p^2q^2	-	
BB q^2	AB $2pq$	-	pq^3	pq^3	
BB q^2	BB q^2	-	-	q^4	
BB q^2	?	-	pq^2 $[O_{B.AB}]$	q^3 $[O_{B.B}]$	q^2 $[O_{B.}]$
Total		p^2 $[O_{.A}]$	$2pq$ $[O_{.AB}]$	q^2 $[O_{.B}]$	1

$$1)\quad \frac{(O_{AB\cdot A} + O_{AB\cdot B})}{O_{AB\cdot AB}} = \frac{1}{1}$$

$$2)\quad \frac{O_{A\cdot A}}{O_{A\cdot AB}} = \frac{O_{AB\cdot A}}{O_{AB\cdot B}} = \frac{O_{B\cdot AB}}{O_{B\cdot B}} = \frac{p}{q}$$

The first ratio is the 1:1 ratio and the next three the gametic gene ratios (Cooper 1968). Using these ratios, several different χ^2 goodness-of-fit tests can be carried out on data collected from blue grouse to detect selection or population subdivision.

The 1:1 ratio will only be affected by selection operating on zygotes, while the gametic gene ratios will be affected by gametic selection, zygotic selection, and population subdivision (Cooper 1968).

IFD collected from blue grouse from 1969 to 1971 are presented in Table 15. No other breeding data in blue grouse were available. Cooper (1968) pointed out that in calculating heterogeneity χ^2 values for the gametic gene ratios, the usual χ^2 test must be corrected for multiparity (Table 16). The corrected formula for heterogeneity χ^2 is given in Cooper (1968).

Frequency of genotypes among mothers showed no significant departures from Hardy-Weinberg expectations (Table 17). Frequency of genotypes among chicks, however, had two significant departures: in 1969 there was a significant deficiency of heterozygotes and in 1970 there was a significant excess (Table 17). There were no departures from expectations in 1971, nor were there any significant departures from expectations when the data were combined for all years. The two deviations found in chicks in 1969 and 1970 cancelled each other so that totals for chicks were in equilibrium.

Results of tests made on IFD for agreement with the 1:1 ratio are given in Table 18. In all years heterozygous mothers produced an excessive number

Table 15. Incomplete family data collected from female blue grouse and their offspring on Vancouver Island, 1969 to 1971. The allele *NgF* is combined with *NgS* to avoid small numbers.

Year	Mother's Genotype	Offspring Genotype		
		NgS/NgS	*NgS/NgM*	*NgM/NgM*
1969	*NgS/NgS*	3	3	-
	NgS/NgM	4	4	7
	NgM/NgM	-	8	25
1970	*NgS/NgS*	1	7	-*
	NgS/NgM	3	19	27
	NgM/NgM	-*	61	88
1971	*NgS/NgS*	3	7	-*
	NgS/NgM	9	42	58
	NgM/NgM	-	41	195
Totals	*NgS/NgS*	7	17	-
	NgS/NgM	16	65	92
	NgM/NgM	-	110	308

*The single offspring which belonged to each of these cells was not compatible with genetic theory. These individuals have been excluded from all further analyses.

Table 16. Distribution of the number of young scored from each mother. These are the data used to correctly calculate heterogeneity χ^2 values based on a formula given by Cooper (1968). *NgF=NgS.*

Year	Mother's Genotype	Number of young typed						
		1	2	3	4	5	6	≥7
1969	*NgS/NgS*	2	0	0	2	0	0	0
	NgS/NgM	10	1	2	1	0	0	0
	NgM/NgM	14	9	1	1	0	0	0
1970	*NgS/NgS*	1	1	0	0	1	0	0
	NgS/NgM	8	2	2	1	4	0	1
	NgM/NgM	17	11	6	5	8	1	3
1971	*NgS/NgS*	1	1	0	2	0	0	0
	NgS/NgM	13	5	7	8	3	3	0
	NgM/NgM	31	17	16	8	3	5	6
Totals	*NgS/NgS*	4	2	0	3	1	0	0
	NgS/NgM	31	8	11	10	7	3	1
	NgM/NgM	62	37	23	13	11	6	9

Table 17. Observed and expected genotypic frequencies of mothers and offspring. Expectations were based on Levene's exact formulae for Hardy-Weinberg proportions (Dobzhansky and Levene 1948). N is the sample size, n_e the effective number of alleles (Crow and Kimura 1970), p the frequency of *NgM*, and probability is the exact probability of observing this distribution by chance alone. *NgF=NgS*.

Year	Group		N	*NgS/NgS*	*NgS/NgM*	*NgM/NgM*	p	n_e	probability
1969	Adults	Obs.	41	0.073	0.341	0.585	0.756	1.58	0.52
		Exp.		0.055	0.378	0.567			
	Chicks	Obs.	54	0.130	0.278	0.593	0.731	1.65	0.02
		Exp.		0.068	0.400	0.531			
1970	Adults	Obs.	72	0.042	0.250	0.708	0.833	1.38	0.32
		Exp.		0.026	0.282	0.692			
	Chicks	Obs.	206	0.019	0.422	0.558	0.769	1.55	0.001
		Exp.		0.052	0.357	0.591			
1971	Adults	Obs.	129	0.031	0.302	0.667	0.818	1.42	0.94
		Exp.		0.032	0.300	0.668			
	Chicks	Obs.	355	0.034	0.254	0.713	0.839	1.37	0.24
		Exp.		0.025	0.270	0.704			
Totals:									
	Adults	Obs.	242	0.041	0.293	0.665	0.812	1.44	0.50
		Exp.		0.035	0.307	0.659			
	Chicks	Obs.	615	0.037	0.312	0.650	0.807	1.45	0.97
		Exp.		0.037	0.313	0.650			

Table 18. Results of χ^2 goodness-of-fit tests for the 1:1 ratio at the *Ng* locus in blue grouse. Ratio tested: $O_{AB \cdot AB} : O_{AB \cdot A} + O_{AB \cdot B} = 1:1$.

Year	Observed Numbers	χ^2	P≤
1969	4:11	2.4	0.12
1970	19:30	2.0	0.15
1971	42:67	5.3	0.02
Total	65:108	10.2	0.001

of homozygous offspring. In 1971, and in the totals for years combined, these differences were significant. The excess of homozygotes was due to zygotic selection against heterozygous offspring from heterozygous mothers.

Gametic gene ratios were tested and results are presented in Table 19. These tests were testing the gametic ratios of *male* parents. There were no significant departures from expectations in 1969 or 1971. In 1970 rare homozygotes from heterozygous parents were significantly different. In all years heterozygotes tended to produce too few rare homozygotes, resulting in the totals being significantly different from expectations. That this was not consistent through all genotypes was shown by significant heterogeneity in the gametic gene ratios for the totals.

Based on these results, departures from expectations in both the 1:1 tests and the gametic gene ratio tests were caused by selection against heterozygous and, perhaps, rare homozygous offspring of heterozygous females. Segregation distortion can be eliminated as a possibility, since it can be shown that segregation distortion will not alter the expectations in the 1:1 tests.

Analogous tests to those above can be done on the columns and diagonals of Table 14. Using these ratios, the following should hold:

$$1)\quad \frac{(O_{A\cdot AB} + O_{B\cdot AB})}{O_{AB\cdot AB}} = \frac{O_{A\cdot AB}}{O_{AB\cdot A}} = \frac{O_{B\cdot AB}}{O_{AB\cdot B}} = \frac{1}{1}$$

and

$$2)\quad \frac{O_{A\cdot A}}{O_{AB\cdot A}} = \frac{O_{A\cdot AB}}{O_{B\cdot AB}} = \frac{O_{AB\cdot B}}{O_{B\cdot B}} = \frac{p}{q}$$

Also, offspring from AA, AB and BB parents should be in Hardy-Weinberg equilibrium with respect to each other (last column of Table 14). These tests measure not the viabilities of offspring but the reproductive output of mothers.

Table 19. χ^2 tests for heterogeneity of male gametic gene ratios at the *Ng* locus in blue grouse.

Year	Ratio Tested	Observed Numbers	χ^2	df	p	Heterogeneity corrected for multiparity 2 df
1969	(1) $0_{A.A}:0_{A.AB}$	3:3	1.1	1	0.3	
	(2) $0_{AB.A}:0_{AB.B}$	4:7	0.2	1	0.7	
	(3) $0_{B.AB}:0_{B.B}$	8:25	0.5	1	0.5	
	(4) Heterogeneity	-	1.8	2	0.4	1.5 $p \leq 0.47$
1970	(1)	1:7	2.1	1	0.15	
	(2)	3:27	9.9	1	0.002	
	(3)	61:88	2.5	1	0.12	
	(4)	-	14.4	2	0.001	9.3 $p \leq 0.01$
1971	(1)	3:7	1.0	1	0.3	
	(2)	9:58	0.6	1	0.4	
	(3)	41:195	0.0	1	0.9	
	(4)	-	1.7	2	0.4	1.3 $p \leq 0.52$
Total	(1)	7:17	0.3	1	0.6	
	(2)	16:92	5.7	1	0.02	
	(3)	110:308	1.1	1	0.3	
	(4)	-	7.1	2	0.03	5.7 $p \leq 0.06$

Results from the auxiliary 1:1 ratio tests are presented in Table 20. The first 1:1 ratio test showed a consistent deficiency of heterozygous offspring produced by heterozygous parents. All cases with significant departures from the expected ratio were a result of too few heterozygous offspring being produced by heterozygotes. This result effectively eliminates misclassification as the cause of the earlier heterozygote deficiency and also shows that selection was occurring only against heterozygous offspring from heterozygous mothers. There was only one other significant departure in the 1:1 ratio tests. In 1970, heterozygous females produced too few common homozygous offspring when compared to the production of heterozygotes by the common homozygotes.

Results of the auxiliary gametic gene ratio tests showed no consistent trends (Table 21). Among the totals, rare homozygotes produced fewer heterozygous offspring than would be expected when compared to the output of the more frequent homozygote.

Summarizing, the three bands found on starch gels after electrophoresis have characteristics similar to other analogous systems, suggesting the bands were gene products of three codominant, autosomal alleles. Incomplete family data supported this hypothesis and also showed selection acting against heterozygous offspring from heterozygous mothers. These results validate the white bands as a *genetic* marker.

Hardy-Weinberg Calculations and Distribution

Hardy-Weinberg Calculations. The Hardy-Weinberg model relates observed frequency of alleles to expected genotype frequencies and makes comparisons of observed results with expectations possible. The model is particularly useful in the empirical study of population genetics and is the basis for

Table 20. Results of χ^2 goodness-of-fit tests on auxiliary 1:1 ratios at the *Ng* locus in blue grouse.

Year	Ratio Tested	Observed Numbers	χ^2	p≤
1969	(1) $O_{AB.AB}:O_{A.AB}+O_{B.AB}$	4:11	2.4	0.1
	(2) $O_{A.AB}:O_{AB.A}$	3:4	0.0	1.0
	(3) $O_{B.AB}:O_{AB.B}$	8:7	0.0	1.0
1970	(1)	19:68	26.5	10^{-4}
	(2)	7:3	0.9	0.3
	(3)	61:27	12.4	10^{-4}
1971	(1)	42:48	0.3	0.6
	(2)	7:9	0.1	0.8
	(3)	41:58	2.6	0.1
Total	(1)	65:127	19.4	10^{-4}
	(2)	17:16	0.0	1.0
	(3)	110:92	1.4	0.2

Table 21. χ^2 tests for heterogeneity of auxiliary gametic gene ratios at the *Ng* locus in blue grouse.

Year	Ratio Tested	Observed Numbers	χ^2	p≤
1969	(1) $0_{A.A}:0_{AB.A}$	3:4	0.5	0.5
	(2) $0_{A.AB}:0_{B.AB}$	3:8	0.0	0.8
	(3) $0_{AB.B}:0_{B.B}$	7:25	1.1	0.3
	(4) Heterogeneity	-	1.2	0.5
1970	(1)	1:3	0.2	0.7
	(2)	7:61	21.8	10^{-4}
	(3)	27:88	6.9	0.001
	(4)	-	5.4	0.07
1971	(1)	3:9	0.5	0.5
	(2)	7:41	0.2	0.7
	(3)	58:195	6.0	0.01
	(4)	-	1.9	0.4
Total	(1)	7:16	0.5	0.5
	(2)	17:110	9.1	0.003
	(3)	92:308	0.3	0.6
	(4)	-	7.0	0.03

the development of most theoretical population genetics. It is also one of the most useful ways to reduce data and search for patterns of deviations from expectations. Observed and expected allelic and phenotypic frequencies for the *Ng* locus were calculated for all sex and age groups for all intensive study areas in all years (Tables 22, 23, and 24). There were few deviations from Hardy-Weinberg expectations (using Levene's exact expectations for small samples [Dobzhansky and Levene 1948, Crow and Kimura 1970]) among either adults or yearlings. However, all significant or near-significant deviations were in the direction of too few heterozygotes.

Often the actual number of alleles was greater than the effective number, n_e (Crow and Kimura 1970). n_e has also been presented in these tables and was calculated using the relationship

$$n_e = \frac{1}{\Sigma\, p_i^2}$$

where p_i is the frequency of the i^{th} allele (Crow and Kimura 1970). In this system n_e had limits of 1 and 3. Most values were between 1.5 and 1.7, making the effective number of alleles about 50% of the actual number. Frequency of alleles between populations showed no consistent differences. The frequency of the most common allele, *NgM*, ranged from a low of 0.636 to a high of 1 (in a small sample of 4) but nearly all values clustered around 0.8. *NgS* varies from 0.1 to 0.15 (Figure 8).

Spatial and Temporal Distribution. The same three alleles were found in approximately the same frequencies in populations of blue grouse on Vancouver Island from 40 km south, 100 km southeast, 30 km north, 70 km northwest, of the Ash River Valley, and from mainland British Columbia, 110 km northeast of the Ash River Valley (Figure 9). There was no heterogeneity in these allele frequencies between areas. The widespread occurrence of this

Table 22. Genetic parameters at the *Ng* locus in blue grouse on area 104, 1968 to 1971. N is sample size; SS, SM, and MM are the observed frequencies of *NgS/NgS*, *NgS/NgM*, and *NgM/NgM* respectively; p, q, and r are the frequencies of the three alleles *NgS*, *NgM*, and *NgF* respectively; n_e is the effective number of alleles; O/E is the observed number of heterozygotes (without combining of genotypes) divided by the expected number; probability is the probability of deviations from Hardy-Weinberg expectations. For computation of fit-to-Hardy-Weinberg conditions, *NgF=NgS*.

Year	Age	Sex	N	SS	SM	MM	p	q	r	n_e	O/E	probability
1968	Adult	♂	12	0.17	0.33	0.50	0.21	0.67	0.13	1.99	0.84	0.22
	Yearling	♂	4	0.00	0.50	0.50	0.13	0.75	0.13	1.68	1.23	1.00
	Adult	♀	23	0.09	0.26	0.65	0.13	0.78	0.09	1.57	0.72	0.16
	Yearling	♀	25	0.00	0.28	0.72	0.10	0.86	0.04	1.33	1.10	0.50
Total			64	0.06	0.30	0.64	0.13	0.79	0.08	1.55	0.88	0.30
1969	Adult	♂	21	0.10	0.38	0.52	0.19	0.71	0.10	1.80	0.96	0.58
	Yearling	♂	12	0.00	0.25	0.75	0.13	0.88	0.00	1.28	1.14	0.78
	Adult	♀	25	0.08	0.32	0.60	0.12	0.76	0.12	1.65	0.81	0.39
	Yearling	♀	25	0.00	0.40	0.60	0.12	0.80	0.08	1.51	1.18	0.27
Total			83	0.05	0.35	0.60	0.14	0.78	0.08	1.59	0.98	0.97
1970	Adult	♂	28	0.11	0.29	0.61	0.14	0.75	0.11	1.68	0.79	0.13
	Yearling	♂	8	0.00	0.38	0.63	0.06	0.81	0.12	1.47	1.17	0.72
	Adult	♀	30	0.07	0.37	0.57	0.17	0.75	0.08	1.67	0.91	0.75
	Yearling	♀	26	0.00	0.35	0.65	0.12	0.83	0.06	1.43	1.16	0.35
Total			92	0.05	0.34	0.60	0.14	0.78	0.09	1.59	0.94	0.71
1971	Adult	♂	21	0.05	0.38	0.57	0.14	0.76	0.10	1.64	0.98	1.00
	Yearling	♂	16	0.00	0.63	0.38	0.13	0.69	0.19	1.91	1.31	0.11
	Adult	♀	35	0.03	0.29	0.69	0.09	0.93	0.09	1.43	1.05	0.88
	Yearling	♀	32	0.09	0.38	0.53	0.22	0.72	0.06	1.76	0.87	0.54
Total			104	0.05	0.39	0.57	0.14	0.76	0.10	1.65	1.00	0.65

Table 23. Genetic parameters at the *Ng* locus in blue grouse on area 107, 1968 to 1971. (Symbols as in Table 22).

Year	Age	Sex	N	SS	SM	MM	p	q	r	n_e	O/E	probability
1968	Adult	♂	15	0.00	0.20	0.80	0.07	0.90	0.03	1.23	1.08	0.81
	Yearling	♂	6	0.00	0.33	0.67	0.17	0.83	0.00	1.39	1.20	1.00
	Adult	♀	25	0.12	0.40	0.48	0.14	0.68	0.18	1.94	0.91	0.53
	Yearling	♀	15	0.07	0.33	0.60	0.03	0.77	0.20	1.59	0.90	0.56
Total			61	0.07	0.33	0.61	0.10	0.77	0.13	1.61	0.91	0.48
1969	Adult	♂	27	0.00	0.41	0.59	0.07	0.80	0.13	1.52	1.19	0.23
	Yearling	♂	14	0.00	0.14	0.86	0.00	0.93	0.07	1.15	1.08	1.00
	Adult	♀	30	0.07	0.89	0.60	0.17	0.77	0.07	1.61	0.88	0.56
	Yearling	♀	32	0.06	0.28	0.66	0.16	0.80	0.05	1.51	1.02	0.33
Total			103	0.04	0.31	0.65	0.12	0.81	0.08	1.50	1.00	0.86
1970	Adult	♂	34	0.00	0.27	0.74	0.06	0.87	0.07	1.31	1.11	0.44
	Yearling	♂	15	0.07	0.27	0.67	0.13	0.80	0.07	1.51	0.79	0.31
	Adult	♀	47	0.06	0.23	0.70	0.11	0.82	0.07	1.45	0.75	0.10
	Yearling	♀	34	0.09	0.24	0.68	0.13	0.79	0.07	1.53	0.68	0.06
Total			130	0.05	0.25	0.70	0.10	0.82	0.07	1.44	0.80	0.06
1971	Adult	♂	43	0.00	0.23	0.77	0.07	0.88	0.05	1.27	1.10	0.44
	Yearling	♂	42	0.07	0.24	0.69	0.10	0.81	0.10	1.49	0.80	0.09
	Adult	♀	42	0.05	0.26	0.69	0.13	0.82	0.05	1.44	0.86	0.38
	Yearling	♀	77	0.03	0.30	0.68	0.10	0.83	0.08	1.44	0.98	0.85
Total			204	0.03	0.27	0.70	0.10	0.83	0.07	1.41	0.93	0.45

Table 24. Genetic parameters at the *Ng* locus in blue grouse for sex and age groups sampled on area 108e, 1969 to 1971. (Symbols as in Table 22).

Year	Age	Sex	N	SS	SM	MM	p	q	r	n_e	O/E	probability
1969	Adult	♂	14	0.00	0.50	0.50	0.21	0.75	0.04	1.64	1.28	0.31
	Yearling	♂	8	0.00	0.25	0.75	0.13	0.88	0.00	1.28	1.14	1.00
	Adult	♀	22	0.05	0.36	0.59	0.18	0.77	0.05	1.58	0.99	0.95
	Yearling	♀	22	0.23	0.27	0.50	0.25	0.64	0.11	2.08	0.61	0.03
Total			66	0.09	0.35	0.56	0.21	0.74	0.06	1.71	0.88	0.32
1970	Adult	♂	17	0.00	0.29	0.71	0.12	0.85	0.03	1.35	1.14	0.59
	Yearling	♂	4	0.00	0.00	1.00	0.00	1.00	0.00	1.00	1.00	1.00
	Adult	♀	30	0.10	0.23	0.67	0.10	0.78	0.12	1.57	0.74	0.05
	Yearling	♀	10	0.00	0.10	0.90	0.05	0.95	0.00	1.11	1.05	1.00
Total			61	0.05	0.21	0.74	0.09	0.84	0.07	1.38	0.84	0.10
1971	Adult	♂	20	0.00	0.35	0.65	0.18	0.83	0.00	1.41	1.21	0.43
	Yearling	♂	10	0.00	0.30	0.70	0.10	0.85	0.05	1.36	1.13	0.76
	Adult	♀	29	0.03	0.21	0.76	0.09	0.86	0.05	1.33	0.84	0.33
	Yearling	♀	22	0.00	0.13	0.82	0.05	0.91	0.05	1.20	1.07	0.75
Total			81	0.01	0.25	0.74	0.10	0.86	0.04	1.32	1.02	0.72

Figure 8. Frequency of the two most common alleles, *NgM* and *NgS*, in blue grouse on the three main study areas, 1968 to 1971.

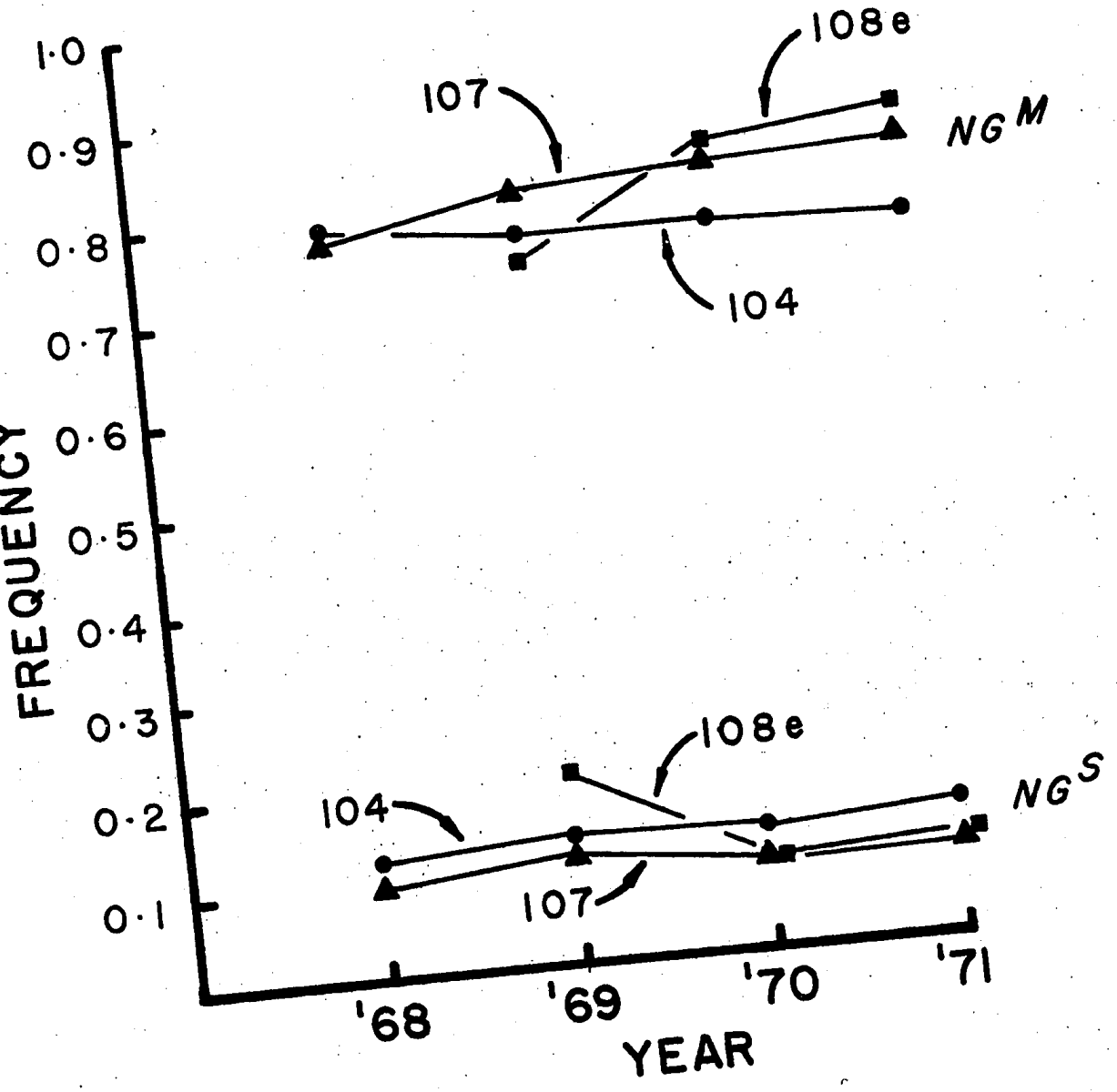
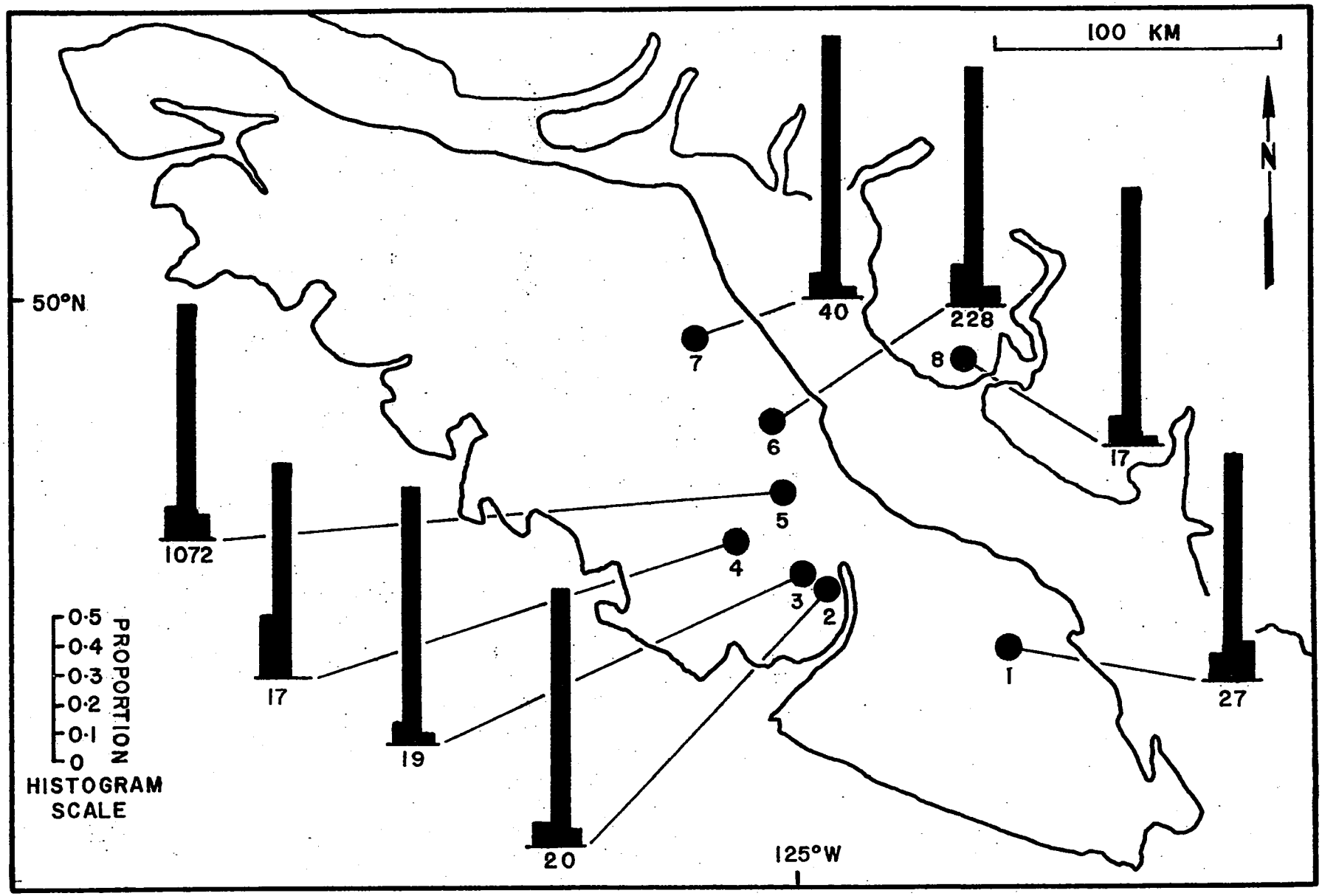

1·0
0·9
0·8
0·7
0·6
0·5
0·4
0·3
0·2
0·1
FREQUENCY
108e
107
NG M
104
108e
104
NG S
107
'68
'69
'70
'71
YEAR

Figure 9. Frequency histograms of the three alleles, *NgF*, *NgM* and *NgS*, in blue grouse from populations on Vancouver Island and from the adjacent mainland of British Columbia. The three bars in the histograms represent, from left to right respectively, *NgS*, *NgM* and *NgF*. Sample sizes are given under the histogram.

Sample locations: 1. Copper Canyon (on Boulder Creek); 2. Cous Creek; 3. Stirling Arm of Sproat Lake; 4. Taylor River (Taylor River Burn); 5. Ash River Valley; 6. Comox Burn near Brown's River; 7. Middle Quinsam Lake; and 8. Pasha Lake near Powell River.


100 KM
N
50°N
125°W
40
228
17
1072
17
19
20
27
7
8
6
5
4
3
2
1
0·5
0·4
0·3
0·2
0·1
0
PROPORTION
HISTOGRAM
SCALE

polymorphism and the relationship of allele frequencies suggest that the system was balanced (Ford 1965a).

There were some differences in allele and genotype frequencies between areas, years, and sex-age groupings in the Ash River Valley (Tables 22, 23, and 24). In 1971, 104 was significantly different from the other two areas ($\chi^2[2]=8.5$, $p\leq0.01$) because the frequency of *NgM* in 104 was significantly lower than in either 107 ($\chi^2[1]=4.17$, $p\leq0.05$) or 108e ($\chi^2[1]=5.9$, $p\leq0.01$). For areas combined, in 1969 there was significant heterogeneity ($\chi^2[3]=11.36$, $p\leq0.001$), because of a high frequency of *NgM* among yearling males. Summing all data for areas in a given year and comparing between years showed no differences ($\chi^2[3]=6.3$, $p\leq0.093$). All other comparisons showed no differences.

Similar calculations to those above were done for juveniles (Table 25). Since 1968, juveniles on 104 had a lower frequency of *NgM* than juveniles on either 107 or 108e. The frequency of *NgM* among juveniles increased steadily in 108e. Phenotypic ratios among juveniles in 1970 ($\chi^2[2]=20.3$, $p\leq0.0001$) and 1971 ($\chi^2[2]=14.7$, $p\leq0.0006$) were significantly different. The difference was caused by a low frequency of *NgM* among juveniles on 104 and a high frequency on 108e. Comparisons of phenotypic ratios within areas but between years showed significant heterogeneity ($\chi^2[3]=10.99$, $p\leq0.05$) (104); ($\chi^2[3]=9.17$, $p\leq0.03$) (107); ($\chi^2[2]=5.9$, $p\leq0.05$) (108e). In 104 the heterogeneity was a result of a significant deficiency of heterozygotes in 1971 ($\chi^2[1]=6.32$, $p\leq0.01$); in area 107 this was caused by a low frequency of *NgM* in 1968 ($\chi^2[1]=4.69$, $p\leq0.03$); and in area 108e this resulted from a low frequency of *NgM* in 1969 ($\chi^2[1]=4.48$, $p\leq0.03$).

Various genetic parameters for adults and yearlings combined were compared to density of birds to see if there was a relationship between density

Table 25. Genetic parameters at the *Ng* locus for juvenile blue grouse banded in all the study areas, 1968 to 1971. (Symbols as in Table 22).

Year	Area	N	SS	SM	MM	p	q	r	n_e	O/E	probability
1968	104	28	0.04	0.39	0.57	0.09	0.77	0.14	1.62	1.12	0.72
	107	13	0.15	0.46	0.39	0.12	0.62	0.27	2.15	0.86	0.70
1969	104	20	0.15	0.35	0.50	0.20	0.68	0.13	1.96	0.82	0.30
	107	24	0.04	0.21	0.75	0.10	0.85	0.04	1.35	0.97	0.26
	108e	10	0.10	0.30	0.60	0.20	0.75	0.05	1.65	1.01	0.27
1970	104	52	0.04	0.50	0.46	0.19	0.71	0.11	1.82	1.15	0.15
	107	71	0.03	0.35	0.62	0.14	0.80	0.06	1.52	1.02	0.55
	108e	37	0.03	0.08	0.89	0.04	0.93	0.03	1.15	0.08	0.004
1971	104	23	0.22	0.22	0.57	0.20	0.67	0.13	1.96	0.62	0.007
	107	23	0.00	0.26	0.74	0.13	0.87	0.00	1.29	1.15	0.56
	108e	22	0.00	0.09	0.91	0.02	0.96	0.02	1.10	1.04	1.00

and genetics on a general level. There was no correlation between adult male density and frequency of heterozygotes (r=-0.307), effective number of alleles (r=-0.0442), O/E ratio (observed number of heterozygotes/expected number) (r=-0.282) or frequency of *NgM* (r=-0.25) (all with 11 pairs).

Summarizing, nearly all Hardy-Weinberg calculations showed no significant deviations from expectations. The frequency of the three alleles at the *Ng* locus were widespread geographically and stable temporally. There were no correlations between genetic parameters and density. Thus, the *Ng* locus is not only a *genetic* marker, it is a stable marker. Potentially, at least, this increases the generality of genetic statements concerning demographic events.

Components of Fitness

Various components of fitness were analyzed in two segments: reproduction and survival.

Reproduction. Fitness for breeding was analyzed in two ways: by comparing success of different genotypes at completing nesting (only 50-80% of females were usually successful at nesting), and by comparing brood size by maternal genotype.

First, comparisons of genotypic frequencies of females with broods to genotypic frequencies of those without broods (Table 26) showed no trends or significant differences between successful and unsuccessful breeders; (1968--$\chi^2[2]=0.996$, $p\leq0.617$; 1969--$\chi^2[2]=1.03$, $p\leq0.59$; 1970--$\chi^2[2]=1.40$, $p\leq0.496$; 1971--$\chi^2[2]=1.09$, $p\leq0.58$). Nor were there any differences when adults were considered separately from yearlings or when all years were combined. Thus, success at nesting was not selective, at least at the *Ng* locus.

Table 26. Number of female blue grouse of each *Ng* genotype with and without a brood in all years. For computations, *NgF=NgS*.

Year	Age	Status	*NgS/NgS*	*NgS/NgM*	*NgM/NgM*
1968	Adult	with	4	14	25
		without	1	2	2
	Yearling	with	1	10	15
		without	0	3	12
1969	Adult	with	3	18	30
		without	2	8	16
	Yearling	with	5	17	26
		without	2	8	21
1970	Adult	with	6	23	57
		without	2	6	13
	Yearling	with	1	15	36
		without	2	3	13
1971	Adult	with	3	23	68
		without	1	4	7
	Yearling	with	3	31	64
		without	2	8	23
Total	Adult	with	16	78	180
		without	6	20	38
	Yearling	with	10	73	141
		without	6	22	69

Second, comparisons of average brood size by genotype and year were made using a two-factor analysis of variance with unequal and disproportionate sample sizes by fitting constants (Steel and Torrie 1960, p.257f.). Adjusted average brood size by age and genotype of mother are presented in Table 27 (adjustments made by fitting constants). Interaction was insignificant. There were no significant differences either between years or between genotypes within age-classes (Table 28). Thus, the number of chicks raised to fledgling stage was independent of maternal genotype at the *Ng* locus.

Survival. Overwinter survival of juveniles and older birds was analyzed in the following manner:

For juveniles, the observed ratio of each genotype in year X was used as the expectation among yearlings in year X+1. This assumed that yearlings in year X+1 came from a population of juveniles which was statistically like those sampled in year X. It was not possible to follow survival of marked juveniles since few grouse marked as juveniles were found again. For older birds, overwinter survival of each genotype was calculated by following survival of tagged yearlings and adults. This assumed that I found marked birds in the following year at random with respect to genotype. Since a high percentage of birds was found each year, this was probably not invalid.

Fitness (W) values were calculated by the formula:

$$W_{ij} = \frac{O_{ij}}{E_{ij}} \; X \left[\frac{1}{\text{MAX } \frac{O_{ij}}{E_{ij}}} \right]$$

where O_{ij} and E_{ij} are the observed and expected proportions, respectively, among genotype ij. The term in brackets scales all fitness values to 1 and below. For juveniles, the significance of these values was tested using χ^2

Table 27. Adjusted average brood size of blue grouse by genotype and year for adults and yearlings considered separately. The adjusted means were calculated by the method of fitting constants (Steel and Torrie 1960, p.257f.). For computation *NgF=NgS*. These adjustments were necessary for the analysis of variance presented in Table 28.

Age	Year	Genotype			Yearly Means
		NgS/NgS	*NgS/NgM*	*NgM/NgM*	
Adult	1968	2.99	3.32	3.70	3.34
	1969	3.16	3.48	3.86	3.50
	1970	4.29	4.62	5.00	4.64
	1971	4.10	4.40	4.80	4.40
	Genotype Averages	3.63	3.96	4.33	3.98
Yearling	1968	3.39	3.73	3.44	3.52
	1969	2.84	3.18	2.89	2.97
	1970	3.52	3.85	3.56	3.64
	1971	3.54	3.88	3.58	3.67
	Genotype Averages	3.32	3.66	3.37	3.45

Table 28. Results of two-way analysis of variance with unequal, disproportionate sample sizes on brood sizes and genotypes from Table 27. The method used is that of fitting constants. Interaction is negligible.

Age	Source	df	SS	MS	F
Adult	Genotype and Year	11	135.70	12.34	0.52
	Years adjusted for genotype	3	79.99	26.66	1.13
	Genotypes adjusted for years	2	15.14	7.57	0.32
	Error	267	6513.30	23.59	
Yearling	Genotype and Year	11	31.10	2.83	0.18
	Years adjusted for genotype	3	13.95	4.65	0.29
	Genotypes adjusted for years	2	3.75	1.87	0.12
	Error	188	3018.90	16.06	

goodness-of-fit, while for yearlings and adults, significance was tested with contingency χ^2.

There were no significant differences in overwinter survival among juvenile genotypes for 1969 to 1970 or for 1970 to 1971, but there was a significant difference in overwinter survival for juveniles in 1968 to 1969 with *NgM/NgM* homozygotes, the most common genotype, also the most fit (Table 29). Thus, juveniles of the most common genotype survived best over one winter.

Among yearlings and adults, rare homozygotes, *NgS/NgS*, survived poorest and heterozygotes *NgS/NgM* survived best over two winters (1968 to 1969 and 1970 to 1971) (Table 30). The winters 1968 to 1969 and 1970 to 1971 were severe, with the former being one of the hardest on record. In contrast, the winter 1969 to 1970 was mild. In these two severe winters, survival depended on *Ng* genotype but in the mild winter survival was random with respect to the *Ng* locus.

Summarizing, selection did not operate on reproductive events, at least at the *Ng* locus, but selection occurred in overwinter survival of both juveniles and older birds. Juveniles of *NgM/NgM* genotype survived best over one winter. In older grouse, heterozygotes, *NgS/NgM*, had a selective advantage with respect to overwinter survival, especially in years of severe winter weather.

Genetic Changes During Colonization

Three methods were used to examine genetic structure of colonizing populations: allelic frequencies, frequency of heterozygotes and an observed/expected (O/E) ratio of heterozygotes. If populations are in Hardy-Weinberg equilibrium, allelic frequencies may give the most pertinent genetic information. Frequency of heterozygotes was calculated by summing the

Table 29. Overwinter survival of juvenile blue grouse. Fitness was based on observed and expected frequencies of each genotype among yearlings. Expectations were calculated from the genotype frequencies found among juveniles the previous summer. χ^2 goodness-of-fit tests were calculated (2 df) on the observed and expected numbers. *NgF=NgS* for computation.

Year		N	*NgS/NgS*	*NgS/NgM*	*NgM/NgM*	χ^2	p≤
1969	Obs.	116	0.052	0.267	0.680	13.30	0.001
	Exp.		0.073	0.415	0.512		
	W†		0.536	0.484	1		
1970	Obs.	97	0.041	0.258	0.701	3.74	0.15
	Exp.		0.093	0.278	0.630		
	W†		0.396	0.834	1		
1971	Obs.	198	0.04	0.313	0.646	0.95	0.62
	Exp.		0.031	0.338	0.631		
	W†		1	0.718	0.793		
Total	Obs.	411	0.044	0.287	0.670	8.98	0.01
	Exp.		0.057	0.346	0.597		
	W†		0.683	0.740	1		

† - Overwinter fitness

Table 30. Overwinter survival of yearling and adult blue grouse. Observed numbers of each genotype which survive and die over winter; these counts are based on individually tagged birds. *NgF=NgS* for computation.

Period		*NgS/NgS*	*NgS/NgM*	*NgM/NgM*	χ^2	p≤
1968-69	Sur.	2	25	31	6.99	0.03
	Die	6	14	43		
	W†	0.39	1	0.65		
1969-70	Sur.	7	47	87	0.01	1.00
	Die	6	40	76		
	W†	1	1	0.99		
1970-71	Sur.	3	45	93	7.02	0.03
	Die	13	40	91		
	W†	0.35	1	0.95		
Total	Sur.	12	117	211	7.00	0.03
	Die	25	94	210		
	W†	0.58	1	0.90		

† - Overwinter fitness

observed frequencies of all heterozygous genotypes within each habitat type. Finally, O/E ratios for each habitat type were calculated. The O/E ratio of heterozygotes is a measure of departure from Hardy-Weinberg expectations. If the ratio is less than 1, there is an overall deficiency of heterozygotes and if the ratio is greater than 1, there is a heterozygous excess. The null hypothesis being tested, in each case, was that there were no changes in genetic parameters associated with age of habitat or population density.

Genetic statistics on composition of populations on different age habitats since 1968 are presented in Table 31. There were no significant differences between sexes, ages, or areas; all data were combined for these comparisons. For years combined, there was a high frequency of *NgM* allele (0.9) in birds on one-year-old habitat, but the frequency of this allele decreased to about 0.8 by age-class 2 and did not fluctuate thereafter. Among totals, frequency of *NgM* among birds on age-class 1 was significantly different from all other age classes (Table 32) but none of the other age-class comparisons were different from each other.

As mentioned in the discussion on the density of birds on habitats of various ages, 1971 seemed to be a year of large numbers of birds moving onto one- and two-year-old habitat. The surplus of birds available to colonize seemed to be larger in 1971 than in other years. There was, likewise, in 1971, a significantly higher number of birds carrying the *NgM* allele on age-class 1 habitat than on other habitat types. Of 25 birds captured on one-year-old habitat in 1971, only one was not an *NgM/NgM* homozygote, being an *NgM/NgS* heterozygote. Thus, I conclude that grouse on one-year-old habitat were more likely to be carriers of the most common allele than are grouse inhabiting older age habitats.

Next, the observed frequency of heterozygotes was plotted against age of

Table 31. Statistics on the genetic structure at the *Ng* locus of populations of blue grouse on different age habitats. Adults and yearlings, males and females are combined. N is sample size; q is the frequency of the most common allele; O/E is the ratio of the observed number of heterozygotes to the expected number; and p is the probability of the observed distribution of phenotypes based on the Hardy-Weinberg model (using Levene's formulae for small samples). *NgF=NgS* in calculation of fit-to-Hardy-Weinberg conditions.

Year		Age of Habitat							
		1	2	3	4	5	6	7	≥8
1968	N	2	12	29	27	-	21	-	44
	q	1.0	0.79	0.79	0.76		0.76		0.80
	O/E	-	0.95	0.79	0.85		0.73		0.85
	p≤	-	0.19	0.27	0.50		0.21		0.21
1969	N	15	28	50	31	76	-	26	42
	q	0.80	0.77	0.79	0.79	0.79		0.75	0.83
	O/E	0.78	0.84	1.00	0.82	0.91		1.05	1.15
	p≤	0.31	0.07	0.53	0.36	0.58		0.64	0.23
1970	N	11	28	26	58	27	59	-	74
	q	0.82	0.75	0.87	0.82	0.80	0.85		0.79
	O/E	0.59	0.36	0.90	0.93	0.97	1.01		0.92
	p≤	0.05	0.001	0.22	0.92	0.95	0.80		0.51
1971	N	25	30	26	27	72	35	80	91
	q	0.98	0.87	0.83	0.82	0.84	0.71	0.82	0.80
	O/E	1.00	0.84	0.90	0.47	0.94	0.91	1.12	1.08
	p≤	1	0.31	0.58	0.002	0.79	0.77	0.26	0.30
Total	N	53	98	131	143	175	115	106	251
	q	0.9	0.8	0.81	0.80	0.81	0.79	0.80	0.80
	O/E	0.69	0.68	0.89	0.80	0.93	0.93	1.09	1.00
	p≤	0.02	0.001	0.17	0.07	0.64	0.51	0.23	0.75

Table 32. Probability table for comparisons of the number of *NgM* alleles vs. *NgF+NgS* alleles occurring in blue grouse on different age habitats. When age-class 1 was compared to other areas, Fisher's Exact Test was used (due to small sample sizes). For all other comparisons, a 2 x 2 contingency χ^2 was calculated.

Age of Habitat	Age of Habitat						
	1	2	3	4	5	6	7
2	0.02						
3	0.05	0.61					
4	0.03	0.767	0.89				
5	0.06	0.46	0.91	0.70			
6	0.02	0.97	0.70	0.878	0.53		
7	0.04	0.77	0.93	0.93	0.76	0.88	
≥8	0.02	0.74	0.84	0.95	0.62	0.86	0.96

habitat for all years and for the combined totals (Figure 10). Since 1969, frequency of heterozygotes had a significant positive regression on age of habitat. Clearly, not only was the frequency of alleles shifting during colonization, frequency of genotypes was also shifting. The slopes of these regression lines were not significantly different from each other.

To further test the regression of heterozygosity on age of habitat, I recalculated the regression statistics, excluding age-class 1 samples, since age-class 1 had a higher frequency of the most common allele which lowered the frequency of heterozygotes. When these calculations were done, there were still significant positive regressions of heterozygosity on age of habitat (total sample: $b=0.02$, $p \leq 0.01$), suggesting that the changes in genotype frequencies were more than a manifestation of changes in allele frequencies.

Shifts in frequency of heterozygotes may have resulted from differential survival of genotypes, selective recruitment of different genotypes into the population, or both. Thus, genetic statistics for each age of habitat were calculated for adults and yearlings considered separately (Table 33). Regression of the observed frequency of heterozygotes on age of habitat was not significant among adults (Figure 11). A similar calculation for yearlings gave significant regression of the frequency of heterozygotes on age of habitat. However, the slopes of these two regression lines were not different from each other.

O/E ratios on age of habitat were plotted separately for adults and yearlings (Figure 12). Among adults the O/E ratio and age of habitat were not related. For yearlings, the O/E ratio had a significant positive regression on age of habitat. Again, however, the slopes of these regression lines were not different from each other. Among yearlings, there was a significant

habitat for all years and for the combined totals (Figure 10). Since 1969, frequency of heterozygotes had a significant positive regression on age of habitat. Clearly, not only was the frequency of alleles shifting during colonization, frequency of genotypes was also shifting. The slopes of these regression lines were not significantly different from each other.

To further test the regression of heterozygosity on age of habitat, I recalculated the regression statistics, excluding age-class 1 samples, since age-class 1 had a higher frequency of the most common allele which lowered the frequency of heterozygotes. When these calculations were done, there were still significant positive regressions of heterozygosity on age of habitat (total sample: $b=0.02$, $p \leq 0.01$), suggesting that the changes in genotype frequencies were more than a manifestation of changes in allele frequencies.

Shifts in frequency of heterozygotes may have resulted from differential survival of genotypes, selective recruitment of different genotypes into the population, or both. Thus, genetic statistics for each age of habitat were calculated for adults and yearlings considered separately (Table 33). Regression of the observed frequency of heterozygotes on age of habitat was not significant among adults (Figure 11). A similar calculation for yearlings gave significant regression of the frequency of heterozygotes on age of habitat. However, the slopes of these two regression lines were not different from each other.

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Figure 10. Regression of observed frequency of heterozygotes at the *Ng* locus in blue grouse on age of habitat, 1968 to 1971.

*$p \leq 0.05$
**$p \leq 0.01$

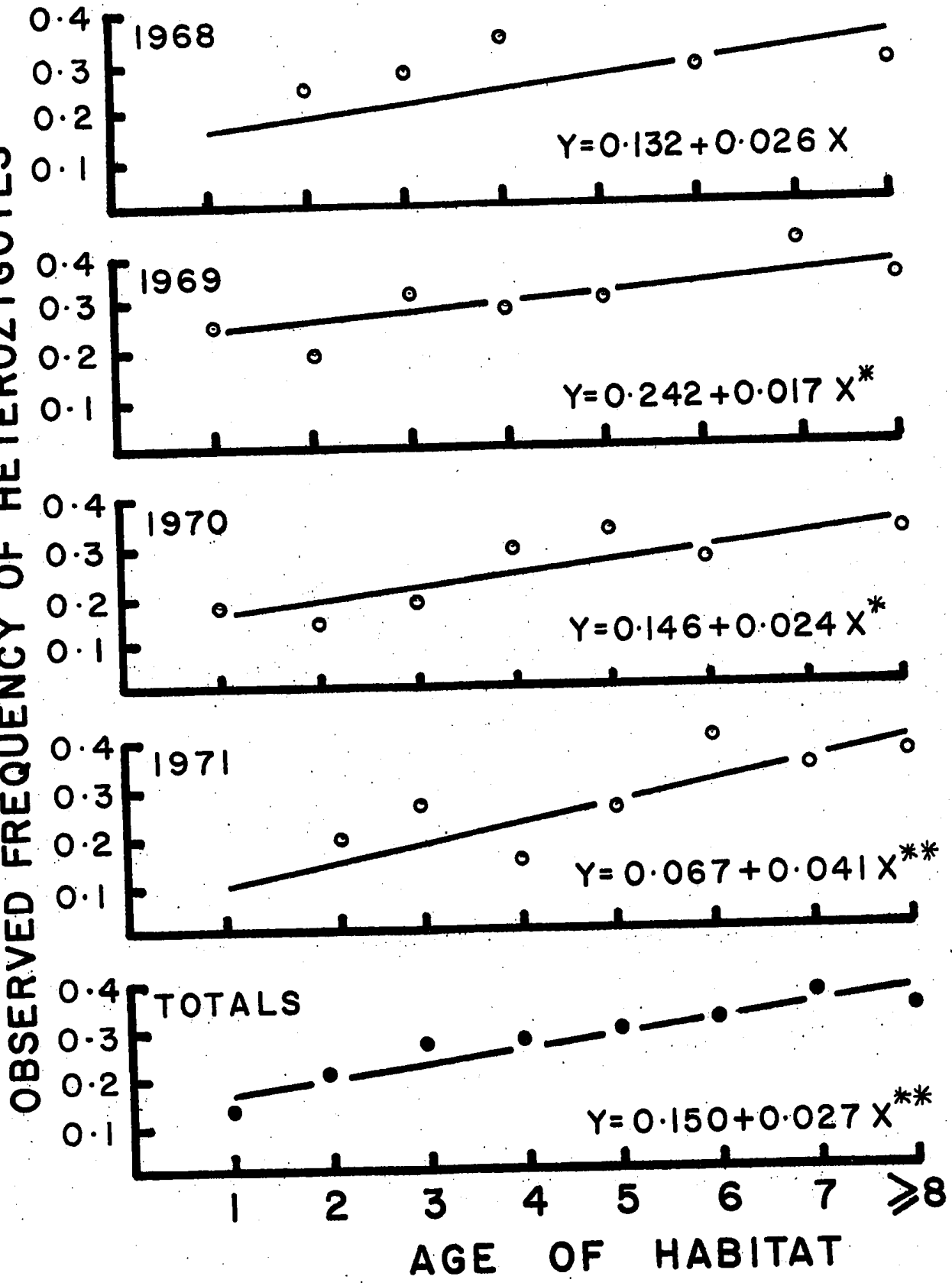

OBSERVED FREQUENCY OF HETEROZYGOTES
0·4
0·3
0·2
0·1
1968
Y=0·132+0·026 X
1969
Y=0·242+0·017 X*
1970
Y=0·146+0·024 X*
1971
Y=0·067+0·041 X**
TOTALS
Y=0·150+0·027 X**
1 2 3 4 5 6 7 ⩾8
AGE OF HABITAT

Table 33. Statistics on genetic structure at the *Ng* locus of adults and yearlings separated on different age habitats. Years were combined. (The symbols are the same as in Table 31.)

Age		Age of Habitat							
		1	2	3	4	5	6	7	≥8
Adult	N	16	45	73	88	96	71	63	154
	q	0.94	0.74	0.81	0.79	0.80	0.78	0.84	0.81
	O/E	1.07	0.75	0.89	0.79	0.89	0.95	0.98	0.97
	p≤	1	0.07	0.26	0.10	0.44	0.69	0.59	0.71
Yearling	N	37	53	58	55	79	44	43	97
	q	0.88	0.84	0.81	0.81	0.83	0.82	0.74	0.78
	O/E	0.61	0.61	0.90	0.83	0.98	0.88	1.24	1.05
	p≤	0.01	0.0001	0.35	0.30	0.89	0.46	0.03	0.41

Figure 11. Regression of the observed frequency of heterozygotes at the *Ng* locus in blue grouse on age of habitat for adults and yearlings considered separately, all years combined.

**$p \leq 0.01$

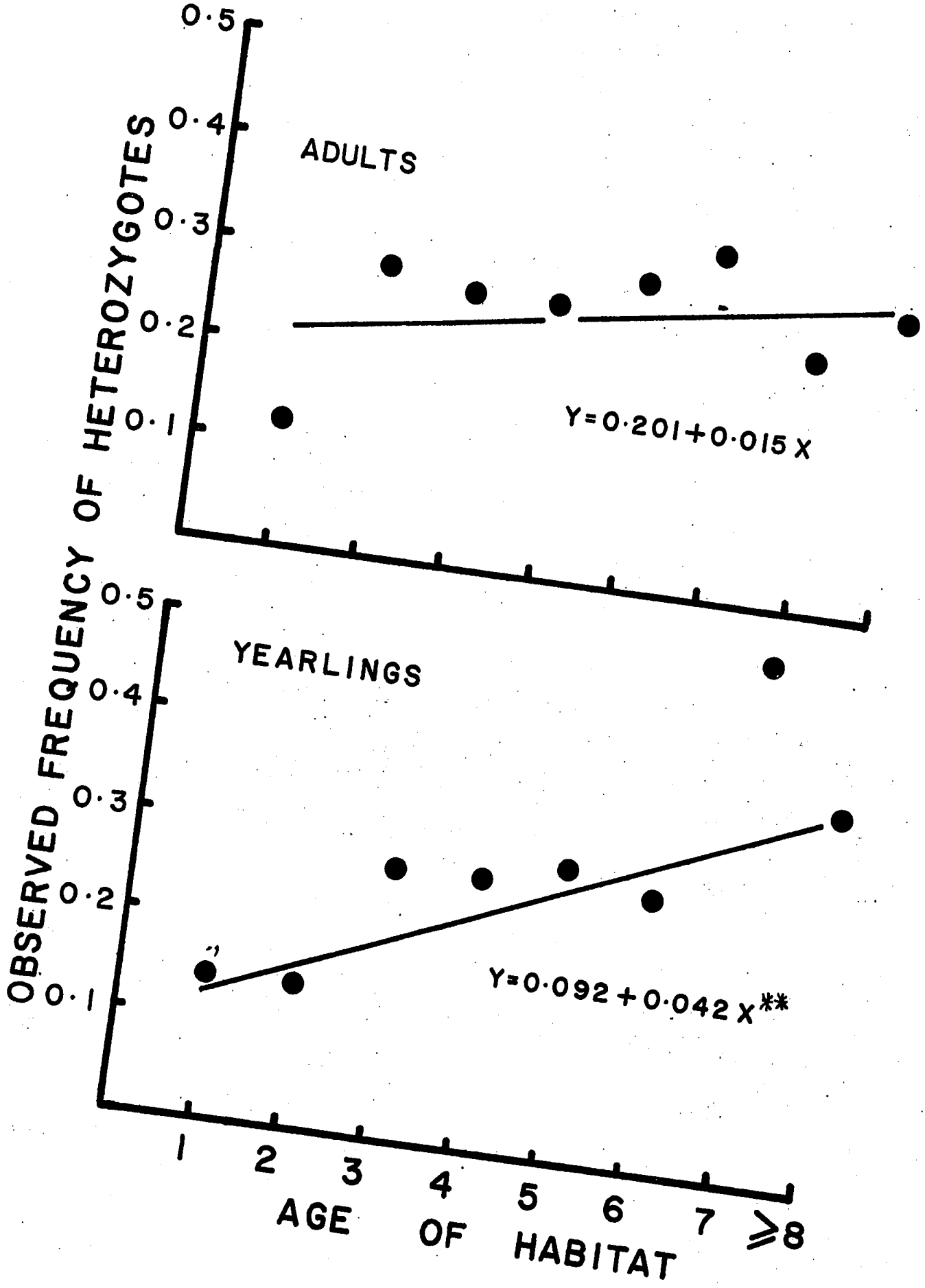
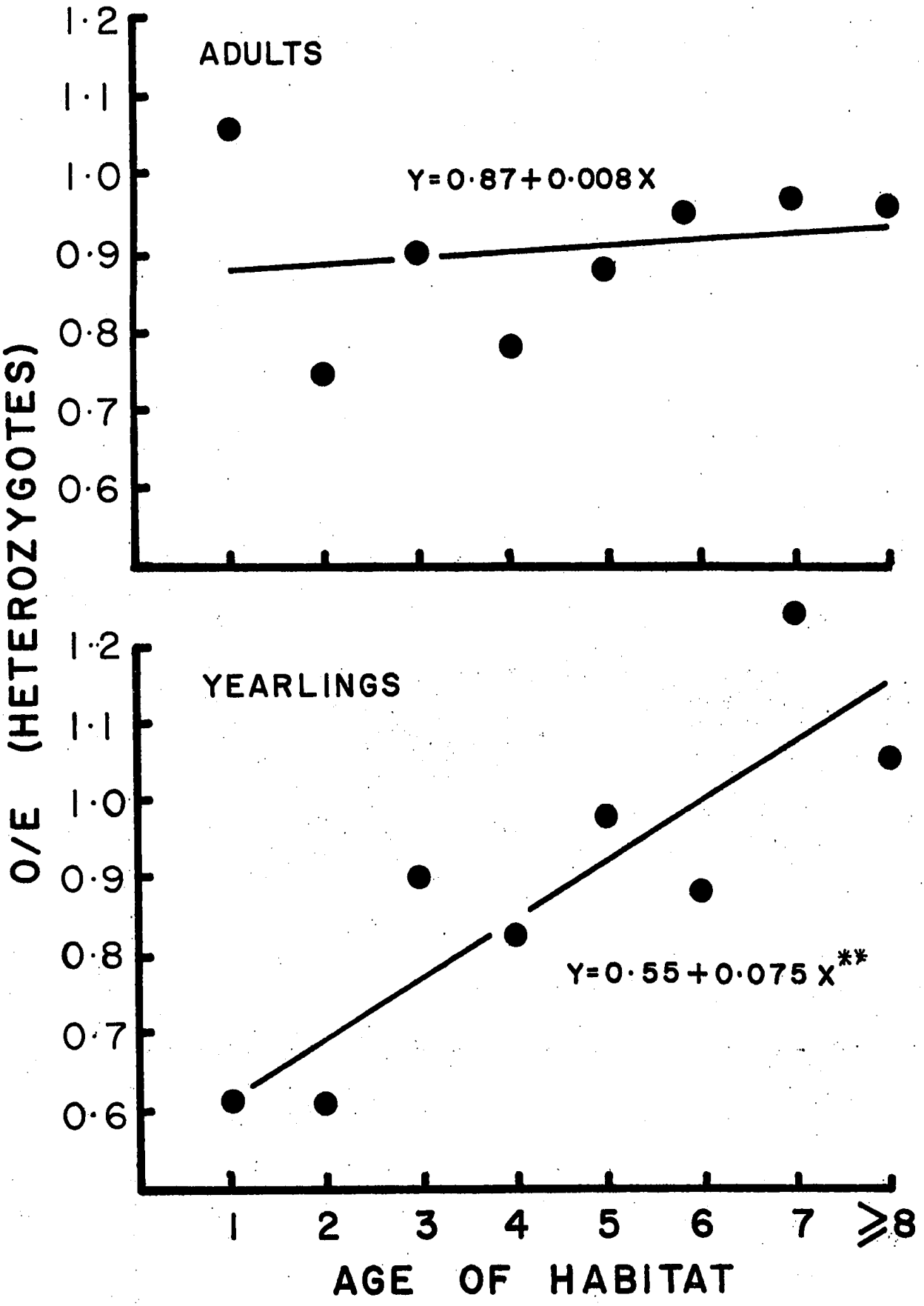

OBSERVED FREQUENCY OF HETEROZYGOTES
0·5
0·4
0·3
0·2
0·1
ADULTS
Y=0·201+0·015 X
YEARLINGS
Y=0·092+0·042 X**
1
2
3
4
5
6
7
≥8
AGE OF HABITAT

Figure 12. Regression of the O/E ratio (i.e., observed frequency of heterozygotes/expected number) at the *Ng* locus in blue grouse on age of habitat for adults and yearlings considered separately, all years combined.

**$p \leq 0.01$


ADULTS
Y=0·87+0·008X
YEARLINGS
Y=0·55+0·075X**
O/E (HETEROZYGOTES)
1·2
1·1
1·0
0·9
0·8
0·7
0·6
1
2
3
4
5
6
7
≥8
AGE OF HABITAT

deficiency of heterozygotes in habitats 1 and 2 and a significant *excess* in habitat 7.

Population density increased with increasing age of habitat for seven years after logging (Figure 6). Thus, both density and heterozygosity were increasing with age of habitat. As expected, total heterozygosity and population density were positively correlated ($r=0.820$, $p \leq 0.01$). Frequency of heterozygotes for adults and yearlings considered separately was plotted against population density (Figure 13). Among adults these two variables were not correlated ($r=0.430$, $p \leq 0.05$) but among yearlings these variables were significantly correlated ($r=0.838$, $p \leq 0.05$). When analogous plots were made for the O/E ratio and density among adults and yearlings considered separately, yearlings, but not adults, had a significant positive relationship (Figure 14). These patterns were consistent whether total density, adult density, or yearling density was correlated with observed numbers of heterozygotes or with the O/E ratio (Table 34). Whether changes in population density were causing changes in allele and genotype frequencies is not known; nor is the converse known. Perhaps both were caused by some other common factor such as changing quality of vegetation or habitat selection. There can be little question that there were genetic shifts associated with changes in abundance during colonization.

The regression of frequency of heterozygotes and the O/E ratio on age of habitat among yearlings shows that yearlings were selectively recruited into populations on different habitat types. The mechanism of selection is not known, but it seems unlikely that the birds were selecting some environmental variable regardless of population density. Population density consistently changed through the first seven years after logging. These results are evidence in favor of the view that cryptic genetic polymorphisms

Figure 13. Correlation, for adults and yearlings considered separately, between the observed frequency of heterozygotes and total density of blue grouse. Circles are points for adults and triangles are for yearlings.

**$p \leq 0.01$

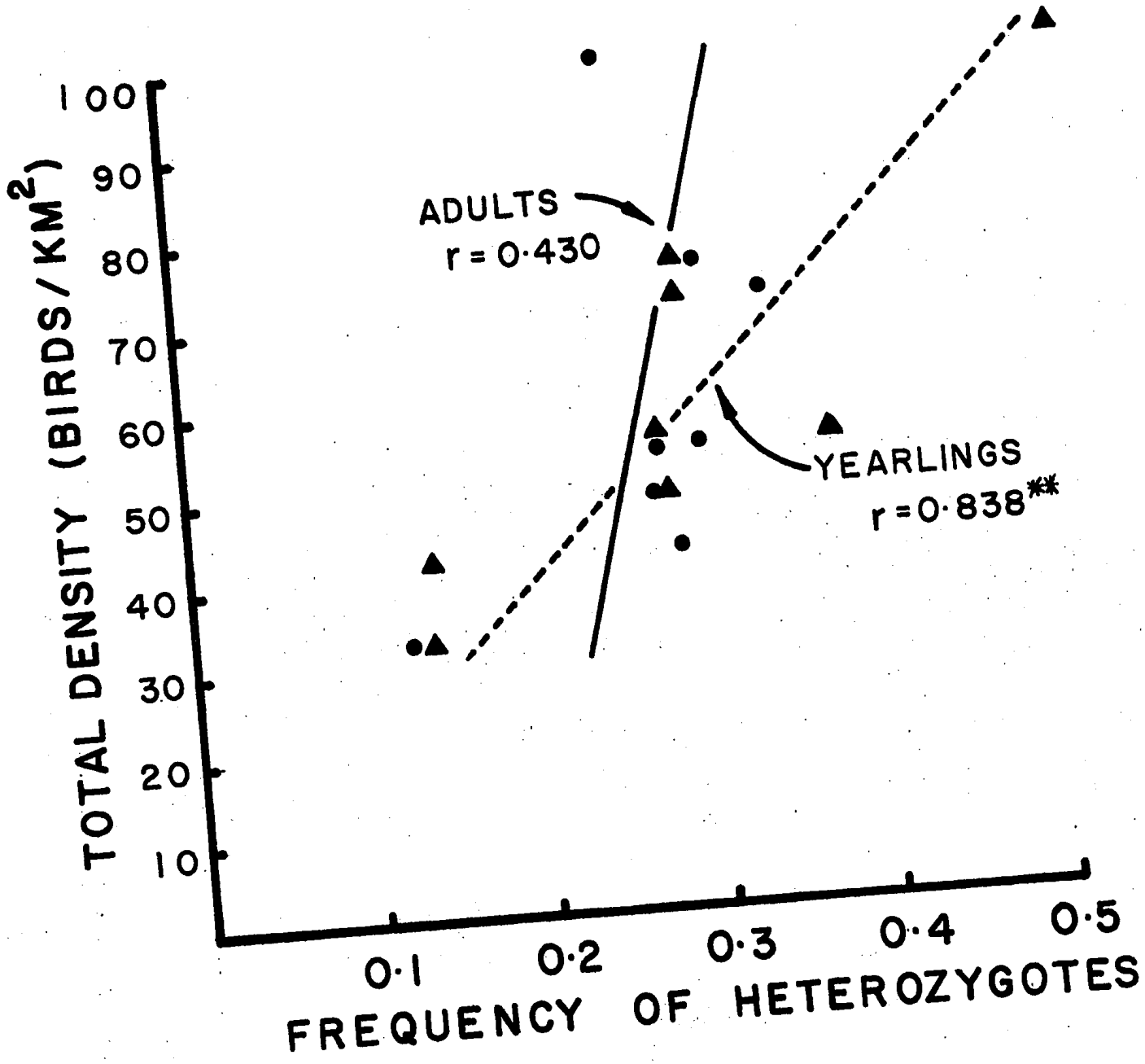

100
90
80
70
60
50
40
30
20
10
TOTAL DENSITY (BIRDS / KM²)
ADULTS
r = 0·430
YEARLINGS
r = 0·838**
0·1
0·2
0·3
0·4
0·5
FREQUENCY OF HETEROZYGOTES

Figure 14. Correlation, for adults and yearlings considered separately, between the O/E ratio and total density of blue grouse. Circles are points for adults and triangles are for yearlings.

**$p \leq 0.01$

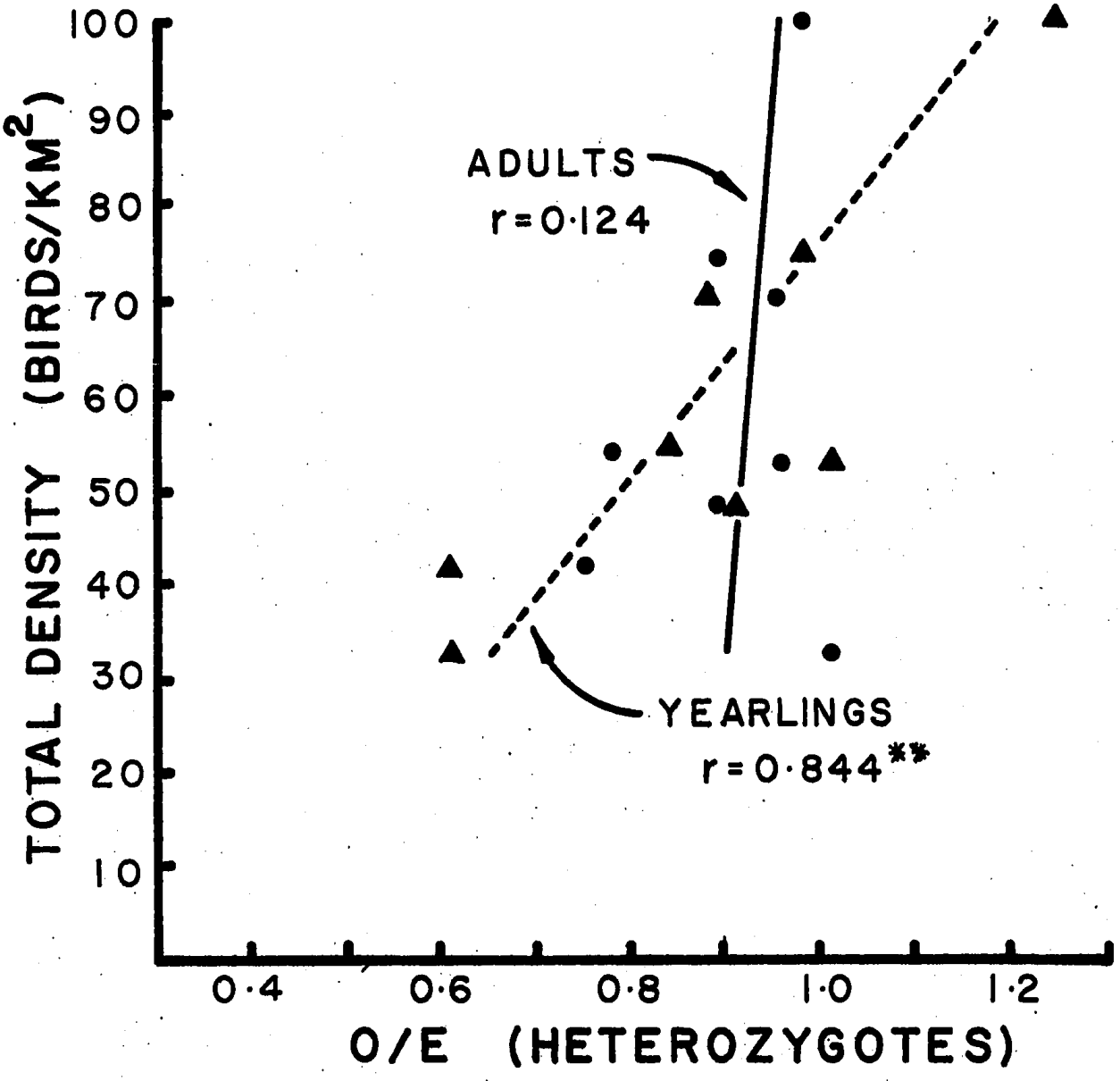

TOTAL DENSITY (BIRDS/KM²)
100
90
80
70
60
50
40
30
20
10
ADULTS
r=0·124
YEARLINGS
r=0·844**
0·4
0·6
0·8
1·0
1·2
O/E (HETEROZYGOTES)

Table 34. Correlation coefficients for comparisons between frequency of heterozygotes and the O/E ratio compared to total, adult and yearling density, all with 11 pairs compared.

	Frequency of Heterozygotes		O/E Ratio	
	Adult	Yearling	Adult	Yearling
Total Density	0.426	0.838**	0.124	0.844**
Adult Density	0.533	0.861**	0.148	0.891**
Yearling Density	0.214	0.693*	0.248	0.694*

*$p \leq 0.05$
**$p \leq 0.01$

are not selectively neutral.

Summarizing, the frequency of *NgM* was significantly higher in birds on one-year-old habitat than on other age habitats. The observed frequency of heterozygotes had a positive regression on age of habitat among yearlings but not among adults. The same was true of the O/E ratio of heterozygotes. Population density was correlated with both heterozygosity and the O/E ratio in yearlings but not in adults. These results are in agreement with the original hypothesis that there would be genetic changes associated with changes in population density.

DISCUSSION

Colonization and Population Regulation

This study was designed to describe colonization by blue grouse of newly logged regions (a period when populations of grouse are rapidly expanding) and to test the hypothesis that genetic structure of populations would shift during this episode. The hypothesis stems directly from Chitty's (1967) suggestion that genetic changes occur during changes in population density.

A fundamental question in population biology is why do most populations tend to remain stable, i.e., why are rates of increase over long periods near to zero? Generally, animals produce more offspring than necessary to replace adult mortality (Lack 1954, 1966, and others). This production is a constant driving force away from equilibrium. Population regulation is the process which counteracts this force and promotes stability (Chitty 1960, Krebs 1964, Schwerdtefeger 1968).

Several theories have been advanced to account for the regulation of numbers of animals in natural populations. Lack (1966) and others suggest that population regulation is brought about by external factors, especially the amount of food available outside the breeding season. In their view, animals are reproducing as rapidly as possible and population regulation occurs because of factors beyond control of the population. This has been called extrinsic regulation of numbers.

Wynne-Edwards (1962) suggests that animals limit their reproductive output by means of social behaviour and assessment of resources. This is a self-imposed birth control system, geared to external factors and involves the concept of *group selection*.

Chitty (1967), arguing in a somewhat similar vein but not involving the group selection of Wynne-Edwards, suggests that numbers are regulated by genetically controlled behaviour, i.e., populations are self-regulating because certain genotypes have an advantage when populations are sparse but not when they are dense. Both Chitty's and Wynne-Edwards' hypotheses have been called intrinsic regulation of numbers. However, both Chitty and Wynne-Edwards recognize the need for external factors to act as environmental cues.

The results of extrinsic vs. intrinsic control are quite obvious. If a population is regulated by extrinsic mechanisms, breeding surpluses never exist. Thus, the colonization of new habitat should be by drifters away from established populations and the populations which colonizers leave should decline. However, intrinsic regulation allows for a breeding surplus to be generated, since the behavioural interactions usually thought to regulate numbers take place with the onset of breeding. Kluiver and Tinbergen (1960) demonstrated a behavioural surplus in great tits *(Parus major)* and, using Chitty's hypothesis, these surpluses should be genetically different from non-surplus.

In several more recent field studies on the ecology and genetics of small mammals (rodents), attempts were made to relate genetic composition to changes in density. Semeonoff and Robertson (1968) reported a change in the frequency of an esterase allele (*Es* locus) related with population changes in *Microtus agrestis*. Others also reported genetic changes associated with demographic events. Canham (1969), Gaines, *et al.* (1971), Gaines and Krebs (1971), Myers and Krebs (1971) and Tamarin and Krebs (1971) all showed a relationship between population increases or decreases and genetic structure in several species of mice.

All studies outlined above were concerned with changes in genetic structure of populations with changes in density. Some have shown that fitness and density cannot be considered separately, i.e., fitnesses of genotypes change with changes in density, supporting Kojima's (1971) conclusion that no single set of fitness values can be attached to a particular locus.

Thus, Chitty's hypothesis, originally formulated to explain numbers of small rodents, but broadened to include all animals (Chitty 1967), has been tested on only a few populations of small rodents. Clearly, the need is to go beyond this limited scope and test the hypothesis on a wider variety of organisms.

In blue grouse the *Ng* locus is polymorphic and apparently of simple inheritance. The three alleles at this locus were widespread in similar frequencies among birds on Vancouver Island and among birds on the adjacent mainland. Three lines of evidence suggest that this locus (or a closely linked one) was of some biological significance in the life of grouse.

First, selection acted against heterozygous offspring from heterozygous mothers. While no mechanism is known to account for this phenomenon, a similar finding was reported for domestic cattle *(Bos taurus)* at the *Tf* locus (Ashton 1965, Cooper and Rendell 1968). Second, after one year of age heterozygotes survived better than homozygotes during harsh winters. Finally, birds of different genotypes selectively recruited onto habitats of various ages. Selective recruitment was correlated with population density, but it was not known if the relationship was cause and effect.

The locus used in this study was chosen in a nearly random manner. The same locus was found in all species of birds I examined (robins, *Turdus migratorius;* ruffed grouse, *Bonasa umbellus;* white-tailed ptarmigan, *Lagopus leucurus;* spruce grouse, *Canachites canadensis;* and sharp-tailed grouse,

Pedioecetes phasianallus) as well as a variety of mammals (see Birdsall *et al.* 1970). Even though nothing is known about the biochemical significance of the *Ng* locus, this does not invalidate it as a genetic marker. My original hypothesis was stated in general terms to cover changes in genetic structure during increases in density. In many respects the random choosing of this locus generalizes the results.

In order to test a hypothesis that genetic structure changes with changes in density, two experimental approaches could be used to induce rapid population increases in normally stable populations. Classically, the method used to induce population increases has been the removal of resident breeders (Bendell and Elliott 1967, Harris 1970, Hensley and Cope 1951, Krebs 1970, 1971, Myers and Krebs 1971, Stewart and Aldrich 1951, and Watson and Jenkins 1968). Essentially, removal experiments involve the creation of depopulated areas in suitable habitat and their subsequent repopulation. A second means to induce rapid population increase is to create suitable habitat out of formerly unsuitable habitat.

Colonization of unoccupied habitat is a problem in evolutionary theory (Mayr 1963, 1965, Simberloff and Wilson 1969) and population dynamics. The specific details concerning the mechanisms of colonization have not been examined in many instances, but the results of such examinations are important to population and evolutionary biologists alike. As population biologists, the types of questions we must answer are: What is the rate of movement onto unoccupied regions? What is the sex and age composition of colonizing populations? How long is a colonizing episode for a particular species? Are colonizers behaviourally distinct from non-colonizers? Are there genetic differences between colonizers and non-colonizers? Are colonizers surplus to other populations?

Density of blue grouse increased steadily for at least seven years following logging. Densities of adult males and adult females increased more rapidly than those of yearlings. Yearlings seemed to have two stages of colonization. The first was a four year period of stability at about 12 females/km^2 and the second was for at least 3 years at about 22 females/km^2. Because populations of grouse in the general vicinity were increasing, at least since 1969, I cannot say whether colonization would always take seven years. In fact, if colonization is that period when age structure of populations is unstable, then colonization was over in three to four years, since this was the length of time it took the age structure to stabilize. It may be difficult to distinguish between a colonizing population and one that is increasing. In fact, the two phenomena are similar and the mechanisms causing both may be similar. Both involve the recruitment of young, both have increasing densities and both may involve genetic changes.

The origin of colonizing populations was not known, since few grouse banded as juveniles were seen later. On the basis of banding, it seems safe to conclude, however, that most colonizers were produced outside the study areas.

Throughout the period of population increase there were systematic shifts in the genetic structure of populations. These shifts involved changes in both allele and genotype frequencies. Birds on one-year-old habitat had a higher frequency of *NgM* than birds on all older age habitats but there were no other changes in allele frequencies. Heterozygosity also increased with increases in density. In addition to these changes in allele and genotype frequencies, genetic structure changed with increases in density from populations with a heterozygote deficiency, to ones with a balanced genetic structure, to ones with a heterozygote excess. Thus, genetic structure

One possible way to resolve this problem might be the following hypothetical model: Individuals with the greatest degree of heterozygosity have the greatest competitive advantage. Ignoring the *Ng* locus, for the moment, individuals will have a certain average heterozygous background. For example, say an average individual has 200 heterozygous loci, excluding the *Ng* locus. Then individuals heterozygous at the *Ng* locus are, on average, slightly more heterozygous than homozygotes at this locus (201 vs. 200). If overall heterozygosity gives a competitive advantage, then *Ng* heterozygotes, on average, would be competitively superior to *Ng* homozygotes.

Now, imagine that the quality of the habitat of blue grouse increases for several years following logging. Individuals compete in the highest quality habitat first, but because of the superiority of heterozygotes, the highest quality habitat would be filled by an excess of heterozygotes. The next best habitat would be filled in a similar manner but since there would be fewer heterozygotes available there would be relatively fewer selecting this habitat. This process would continue until all available habitat was filled, or until no more birds were left. This stepwise settling of habitat potentially could create a relationship between overall heterozygosity and age of habitat like observed. The *Ng* locus, then, becomes not necessarily important in itself but a marker in relation to a whole genetic background.

Others have shown that colonizers are more homozygous than non-colonizers. As pointed out by Anderson (1970), Semeonoeff and Robertson (1968) found that *Microtus agrestis* inhabiting temporarily suitable habitat (due to periodic flooding) had a higher frequency of an *Es* allele (which also meant there were more homozygotes) than animals in more stable areas. Also, Myers and Krebs (1971) found, most consistently, in *M. ochrogaster* and *M. pennsylvanicus*, homozygous genotypes dispersed more frequently than heterozygous genotypes,

maintained by selection, and if there are several thousand polymorphic loci (Lewontin 1967), a genetic load is placed on a population which is too great to bear (Kimura and Crow 1964).

The issues in this debate seem clear cut. Either most polymorphisms are maintained by selection or most are not. If most are not, then the probability of choosing a polymorphism at random and showing any differential survival and/or reproduction is vanishingly small. Intensive genetic and demographic studies, such as this one, provide useful data to this debate. Canham (1969), Gaines and Krebs (1971), Gaines *et al.* (1971), Myers and Krebs (1971), Semeoneoff and Robertson (1968), Tamarin and Krebs (1969) and this study showed differential survival and/or reproduction associated with a variety of relatively randomly chosen cryptic enzymatic and protein polymorphisms. This seems, on the surface, to be conclusive evidence against the neutral allele hypothesis.

To circumvent the problem associated with genetic load arising from non-neutral loci, King (1967), Milkman (1967) and Sved *et al.* (1967) argued for truncation selection of individuals, not loci. Wallace (1968a,b, 1970) proposed the concept of hard and soft selection to account for the observed facts.

Another way to maintain large amounts of genetic variability without genetic load is through multiple-niche polymorphism. The theoretical development of this mechanism has been developed by Levene (1953, 1967) and Prout (1968). For example, if animals of different genotypes select habitat at random, but survive differentially according to genotype on each habitat, it is possible to have a stable polymorphism without heterozygous advantage. In a species such as blue grouse, adapted to living in temporarily suitable habitat, this might be a means of adding stability to a polymorphism without

especially during periods of population increase.

The observed relationship between survival value and *Ng* genotype among adult and yearling blue grouse depended on the severity of winter weather. During two harsh winters heterozygotes survived best, while during one mild winter all genotypes survived equally well. Selection dependent on weather may be a means of causing population increases or declines. For example, several harsh winters in succession might change the genetic structure of populations by continual favoring of heterozygotes. If heterozygotes are competitively superior and able to tolerate crowding, a population increase may follow. On the other hand, several mild winters may mean that less tolerant homozygotes would become more abundant and populations might decline.

Evolutionary Implications of Experimental Population Genetic Studies

Harris (1966), Lewontin and Hubby (1966), O'Brien and MacIntyre (1969), Prakash *et al.* (1969) and Selander *et al.* (1969) have shown that a large proportion of the genome of animals is polymorphic with the same sets of alleles widespread at relatively constant frequencies. One of the more interesting outgrowths of the demonstrations of large amounts of genetic variation is the continuing discussion on the maintenance of such variability. Manwell and Baker (1970), Prakish *et al.* and others have argued that such variability has biological patterns suggesting maintenance by selection. Kimura (1968, 1969), Kimura and Maruyama (1971), and Kimura and Ohta (1971) argue that most polymorphisms are neutral and that mutations, drift and movement are enough to maintain the same allelic states over wide areas (Kimura and Ohta 1971, Maruyama 1970a,b). Population genetics today is concerned largely with explaining the maintenance of genetic variability (Wallace 1970). The problem arises because if most polymorphic loci are

increasing the genetic load.

It is likely that grouse are selecting habitat according to genotype rather than being selected against once they arrive onto a habitat. The mechanism of habitat selection by blue grouse is not known. What is it about the *Ng* locus that makes it important in this type selection? Is it quality or quantity of food? Or are there behavioural interactions involved? Perhaps older habitat is most suitable and heterozygotes are able to preempt a spot to live. Homozygotes, on the other hand, may not be able to tolerate high density populations and move to lower density regions.

This discussion illustrates one of the ways that detailed demographic and genetic studies can aid in our understanding of events occurring in evolution and help resolve problems arising in theoretical development of population biology.

Validity of the Data

In any field study, a wide variety of uncontrolled variables can be disturbingly annoying and this study is not unique in that respect. The experimental design left something to be desired. However, I had no control over logging patterns and, therefore, no control over the size, shape or placement of new habitat. The size of openings ranged from 15 to over 40 hectares. Some of the openings were created in autumn or winter while others were created in spring and summer. Sometimes these new regions were burned after logging; sometimes they were not. However, burning appeared to have little effect on density of blue grouse (Redfield *et al.* 1970). These uncontrolled experimental variables probably made the results less clear cut. Thus, the patterns that emerged were probably indicative of the overriding pattern of colonization.

For purposes of analysis of colonization, I counted birds only once in a given year and each bird was assigned to the habitat type on which it was first found. A bird could have been counted on a given type of habitat when it belonged to another. For adult males, who occupy a small territory in spring and summer, this was probably insignificant. For other segments of the population, however, misclassification was potential. I assumed that any misclassification would be balanced by an opposite misclassification. Again, this might add variability to the results and obliterate some not so obvious trends. Thus, any relationships that emerge must be fairly indicative of what is actually happening.

Another source of variation was the possibility of misclassification of genotypes. While there may have been some misclassification of genotypes (both because of clerical errors, which are impossible to eliminate completely, and also because of leakage, or misreading), of over 600 chicks whose mothers were known, only three were not compatible with genetic hypothesis and it is possible to account for these by mixing of broods. Also, most samples of blood were classified more than once. Even if some misclassification occurred, it should have been at random over all the samples regardless of the habitat type from which the bird was taken.

One might question the conclusion that, based on a single locus, genetic structure changes during a colonizing episode. If this is the only locus which shows the effect claimed, then indeed, genetic structure has changed. If, however, other loci show changes (of any nature), then the results are even more striking. These results force one to say that genetic structure has indeed changed during colonization.

The Future

The results of this study are consistent with Chitty's genetic hypothesis,

CONCLUSIONS

What has this research accomplished and revealed?

1) Blue grouse colonized newly logged regions rapidly and increased in density for at least seven years after logging. The increase was brought about by increases in adult and yearling density. Age structure of colonizing populations shifted significantly from 70% to 45% yearlings in the first three years after logging, but stabilized after that.

2) Reproductive output was high and early colonizing populations did not appear to be any more successful at reproduction than late colonizers.

3) A series of white bands from serum of grouse were identified with starch-gel electrophoresis. These bands were inherited as codominant alleles at a single autosomal locus. Incomplete family data analysis demonstrated that heterozygous mothers produced too few heterozygous offspring. No mechanism was known which could account for this, but segregation distortion was ruled out.

4) Birds of the various genotypes at the *Ng* locus did not show any differential reproduction but survival was selective. First year survival favored the common homozygote, *NgM/NgM*, over one winter and survival of older birds favored heterozygotes, *NgS/NgM*, during two severe winters.

5) Frequency of heterozygotes and the O/E ratio (observed/expected heterozygotes) among yearlings had a significant positive regression on age of habitat.

6) Correlation between population density and both frequency of heterozygotes and the O/E ratio among yearlings was positive and significant.

relationship between habitat and populations is to be fully understood, we must directly manipulate the habitat in a predetermined manner. Thus, the second experiment is every bit as vital to these studies, but may involve cooperation on a larger scale than ever before in grouse research. This cooperation may need to be between biologists, logging companies and provincial governments.

In addition to these experimental approaches, new genetic markers must be studied. As many more loci as feasible should be studied in the future. We need, in short, a large survey of the genome, as done by Lewontin and Hubby (1966), Prakish *et al.* (1969) and Selander (1970a,b), coupled with an intensive population study. Only then will the full interaction of the genome and density begin to be revealed.

Whether these shifts were caused by changes in population density or changes in habitat is not known, but it is difficult to imagine that the shifts were occurring independently of population density. Suitable experiments were briefly outlined which could be used to approach this problem.

7) The results of this study, along with those of other field studies, are not in agreement with Kimura's (1968) neutral allele hypothesis, since, if Kimura is right, the probability of choosing a locus whose genotypes have any differential significance to the life of an individual is small.

8) These results lend some credibility to the hypothesis concerning genetic changes associated with changes in density, but at the same time raise some even more perplexing problems, not the least of which is the suggestion that several hundred or several thousand polymorphic loci must be related with changes in population density.

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