A STUDY OF
DEMOGRAPHY AND BEHAVIOUR OF RUFFED GROUSE
IN BRITISH COLUMBIA

by

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B.Sc., University of Victoria, 1968

A THESIS SUBMITTED IN PARTIAL FULFILLMENT
OF THE REQUIREMENTS FOR THE DEGREE OF
MASTER OF SCIENCE
in the Department
of
Biology

ACCEPTED
FACULTY OF GRADUATE STUDIES
[redacted]
DEAN
DATE 27 Apr/73

We accept this thesis as conforming
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UNIVERSITY OF VICTORIA

April 1973

Supervisor: Dr. A. T. Bergerud

ABSTRACT

A demographic and behavioural study of ruffed grouse was carried out in the central interior of British Columbia to test the null hypothesis that there was no difference in behaviouristic and demographic parameters between red and grey colour phases.

The density of the breeding population increased during the years 1968 to 1971 and decreased in 1972. The survival rates of red and grey phase males were similar. However, the abundance of red phase birds in the breeding population increased throughout the study period. Chick production varied independently of population density, being lower in late hatch years than early hatch years. Chick survival was correlated with mean maximum temperature in June. Further, the survival of broods hatched by red hens was lower than that of broods hatched by grey hens.

A comparison of three indices of behaviour: agonistic behaviour of males directed at a mirror image; approachability or flushing distance; and brood defence behaviour of hens suggested significant differences between behaviour of red and grey phases. Red phase birds interacted more vigorously with their mirror image, were more approachable, and defended their broods more vigorously than grey phase birds.

The results suggest that red and grey phase ruffed grouse differ intrinsically in certain behavioural and survival characteristics which can potentially be related to ruffed grouse population fluctuations.

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ACKNOWLEDGMENTS

I am grateful to Dr. A. T. Bergerud for the generous assistance he has given me during the writing of this thesis. His help and guidance has been invaluable. My appreciation is also expressed to Dr. E. M. Hagmeier for his constructive criticism of this thesis.

I also acknowledge the assistance of my fellow students, H. J. Barclay and J. Donaldson, who engaged in many helpful discussions. I also acknowledge D. Lowe, of the B.C. Fish and Wildlife for his assistance with field work.

I am indebted to Mr. R. W. Ritcey, biologist of the B.C. Fish and Wildlife, for use of his study areas and access to his project data. I also acknowledge the financial assistance of the B.C. Fish and Wildlife Department.

I would like to thank my wife, Karen, for her patience and understanding, while I was engaged in field work and in writing this thesis. I am extremely grateful for the time spent by my two sisters, Deirdre and Beverly, in typing and compiling vegetation data.

INTRODUCTION

A basic problem in ecology is to determine how animal numbers in natural populations are regulated. In recent years several studies of tetraonid ecology have emphasized the role of behaviour in the self-regulation of numbers (Bendell and Elliott, 1967; Watson, 1964, 1967 a, b; Jenkins, 1963; Jenkins *et al*., 1963, 1967; Mossop, 1971; Theberge, 1971; Bergerud, 1970). Furthermore, both the Wynne-Edwards and Chitty schools of population regulation feel that behaviour plays a key role in population regulation. Chitty has recently argued that such behaviour may have a genetic basis and that we need to know more about the genetics of populations to understand population regulatory processes (Chitty, 1967).

In this study I compared demography and behaviour of two colour phases of ruffed grouse populations (*Bonasa umbellus affinis*) in central British Columbia from 1968 to 1972. Work by Gullion and Marshall (1968) indicated that the two colour phases differed in survival of males; also, the differences they found, appeared correlated with population fluctuations. My null hypothesis was that there was no difference in behaviour and demographic parameters between red and grey phases.

Ruffed grouse populations appear to be polymorphic, based on colour of tail retrice. These colour morphs are persistent in time, and are geographically widespread (Bump *et al*., 1947; Gullion and Marshall, 1968). The phenotypes of the red and grey morphs appear to be discontinuous (Gullion, 1972, pers. comm.). Mayr

(1963) has argued that discontinuous phenotypes normally result from a genetic polymorphism. No breeding experiments have been carried out to determine the inheritance of tail colour. However tail colour appears to be constant for individual grouse throughout their lives (successive molts) (Gullion, 1972, pers. comm.). Also, both red and grey phase chicks are found in the same broods in any one year - same mother and same environment. These two facts argue for genetic determination of tail colour rather than colour being a response to environmental conditions. In this study, I have assumed that colour phases are genetically determined and likely to result from a stable polymorphism.

STUDY AREAS

I gathered data from two study areas located at Watch Lake, British Columbia (51^{o} 28' N, 121^{o} 04' W) (Fig. 1). Study area I (270 acres) was established in 1968 and Area II (318 acres) in 1970. Both areas were situated on south-east slopes extending from low ridges (3900 ft. elev.) to flat meadow land (3600 ft. elev.). Both areas had topography that was gently rolling.

Climate of the area is characterized by long, cold, dry winters (snow from November to April) and short, hot, dry summers. Frost free days vary from 50 to 70 per year. Annual precipitation is 20 to 25 inches, most falling as snow. Seasonal distribution of precipitation follows a regular pattern. March and April are typically dry while June and December/January are periods of maximum precipitation. Seasonal changes are abrupt.

Vegetation of the general region has been described as a Montane Douglas Fir Zone by Halliday (1937), or as a Cariboo Aspen-Lodgepole Pine-Douglas Fir Parkland Zone by Krajina (1965) and Beil (1969). Vegetation of both study areas is essentially a mosaic of mixed and pure stands of Aspen (*Populus tremuloides*), Lodgepole pine (*Pinus contorta*), Douglas fir (*Pseudotsuga menziessii*), and White spruce (*Picea glauca*) with numerous openings of pasture area and willow swamps (*Salix* spp.). The vegetation patterns have been strongly influenced by past disturbances: selective logging for Douglas fir in 1950's, patch-burning in 1890's and 1930's, seasonal grazing, and

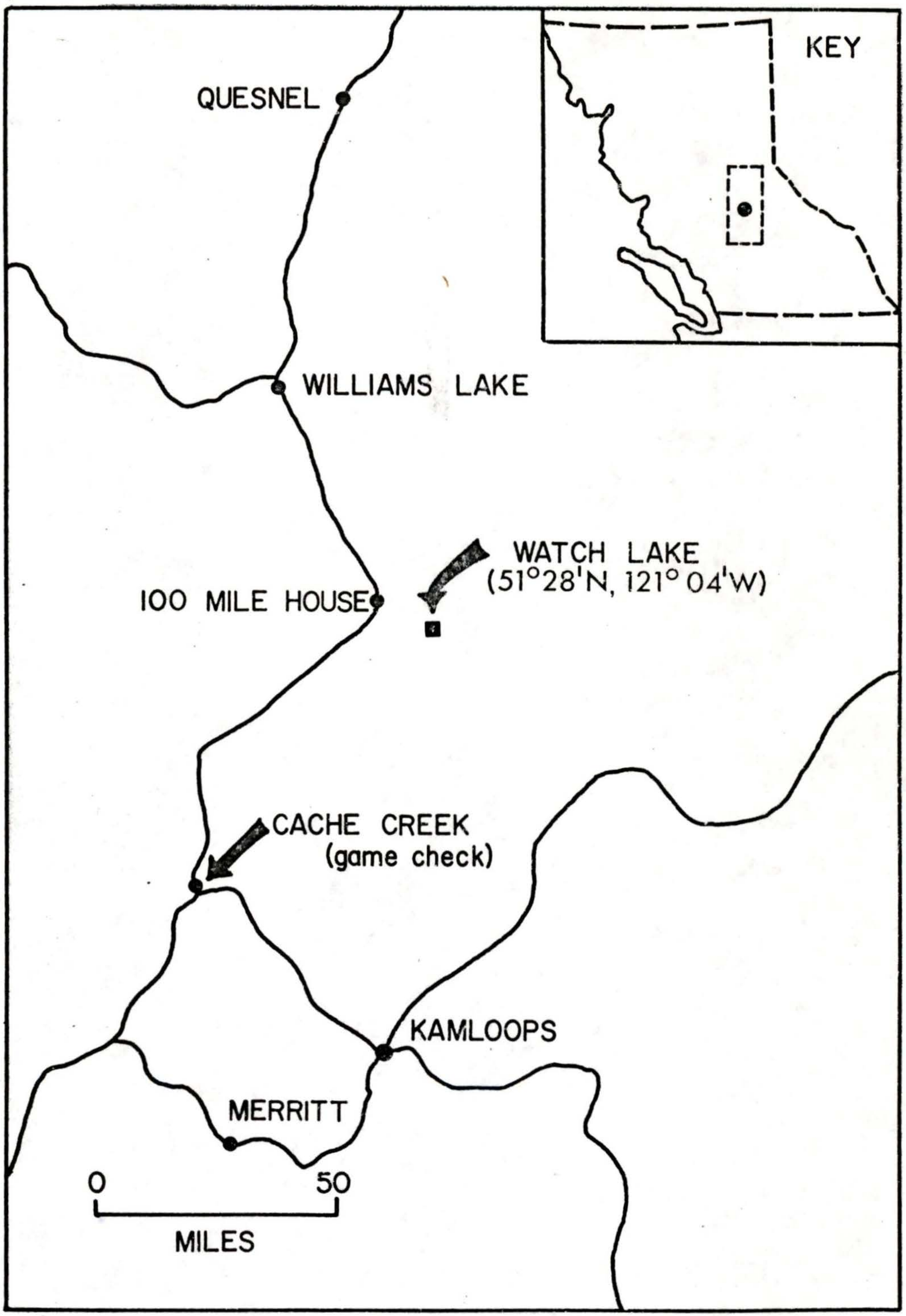

Fig. 1. Watch Lake, British Columbia and surrounding region showing location of study area.

pole-cutting (Area I). Vegetation descriptions are given in Appendix 5 of this thesis.

METHODS

Estimation of numbers

Drumming transects were conducted each spring, April 27 to May 10, along a 15 mile section of the Watch Lake-Bridge Lake road (Fig. 2) in order to estimate trends in cock density. This task was shared with biologists from the Kamloops Fish and Wildlife Branch. Listening posts were spaced at one mile intervals. At each listening post the number of 'different' drumming grouse was recorded during a 3 minute interval between hours 0500-0800.

Each spring, drumming males on both study areas were counted. Also, known drumming logs were visited and examined for signs of occupancy. Repeated visits were made to all occupied logs throughout season. Locations of drumming logs of all territorial males were plotted on large scale aerial photographs (1:5000).

Each August, 1969 to 1971, a drive-type census was carried out on Area I by 6-10 men (with dogs) of the B. C. Fish and Wildlife Branch. These workers covered the area walking straight line transects with an interval of 75 feet between men.

Brood counts were conducted from June to September of each year within a 20 mile radius of the study areas. Information such as time, date, location, vegetation type, hen colour, brood size, and age of chicks was recorded on standardized observation cards (Appendix 1). Broods were aged from the development of wing feathers of captured chicks and flight and size characteristics after Bump *et al*. (1947).

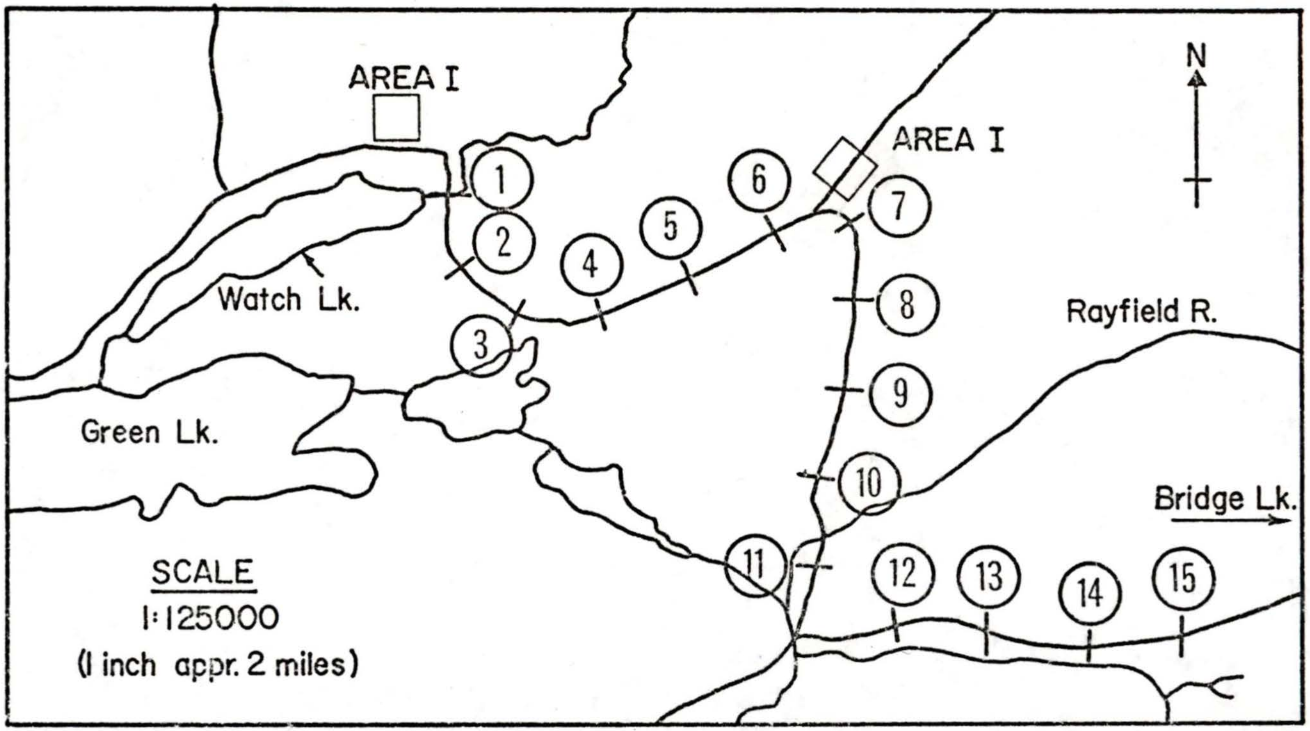

Fig. 2. Watch Lake drumming transect and listening posts.

Capture and collection of birds

Each spring drumming grouse on the two study areas were captured using mirror traps placed on the drumming logs (see Gullion, 1965). The traps accounted for 89 birds in 203 trap days from 1968 to 1972. The birds were aged by primary feather contour and sheathing, and retrice dimension after Dorney (1956) and Gullion (1964). Colour phase was based on retrice colour, mixtures of red and grey (brown variations) being classed as grey phase. Birds were weighed, banded, and released. Further, a number of birds were shot each spring to obtain additional information on weights and colour phases.

Chicks were both captured and collected in areas adjacent to the study areas. These chicks were aged by wing feather development after Bump *et al*. (1947), the ages being used to construct hatch curves.

Each fall, wing and tail feathers of grouse were collected by the B. C. Fish and Wildlife Branch from birds killed by hunters in Management Area 14, the region in which this study was conducted. I determined age, sex, and colour phase of their samples using procedures outlined by Dorney (1966) and Gullion (1964). This data provided a comparitive check on population parameters that I secured from my study areas.

Weather recording

A continuous record of temperature and humidity readings May to September during 1968 to 1972 was obtained from a hygro--thermograph located on Area I. A summary of temperature means is given in Table 1. The hygrothermograph was not operated during

Table 1. Mean minimum and maximum temperatures (F°) at Watch Lake, B. C., May to August, 1968 to 1972.

Year	May Mean		June Mean		July Mean		August Mean	
	min.	max.	min.	max.	min.	max.	min.	max.
1968	29.4	62.4	37.8	64.8	41.5	73.9	40.0	64.8
1969	36.6	70.4	45.9	78.9	——	——	——	——
1970	32.6	61.0	42.7	74.4	44.0	76.9	42.7	76.0
1971	34.3	65.9	39.9	64.1	42.5	76.0	39.2	76.0
1972	——	——	39.9	63.1	——	——	——	——

winter. Precipitation was measured using a standard rain gauge but measurements were not complete in all years thus are not included in this report.

Measurement of behaviour

In the interval May 1 to 25, 1970 and 1971, drumming males were presented with their mirror image (see Mossop, 1971; Theberge, 1971; and Appendices 3 and 4 for a critical evaluation of this technique). The mirror was placed on the drumming log and the grouse observed from a blind nearby. Detailed procedures are described in Appendix 2. Tests were conducted between the hours 0400-0700. Each male was tested twice during May for a total of 1 hour of observation per bird. Each bird was tested, trapped, then retested a second time approximately 10 days later. In addition several males were tested 4 to 6 times to assess consistency in behaviour relative to time and dates of observation (Appendix 3). Observations were recorded on a portable cassette recorder. The behaviour of the males was quantified according to the number of hard pecks and jump-attacks (Mossop, 1971) directed at the mirror image of the bird.

The flushing distance (distance from observer when bird flushes) of brood hens and single grouse was recorded. Further, it was noted whether a hen with a brood: (1) rushed towards the observer (2) attempted to lead him away from the brood, or (3) simply flushed. The intensity of these actions was rated as 2 for vigorous action, 1 for a medium to weak response, and 0 for no response.

DEMOGRAPHIC RESULTS

Density trends

The total density of the breeding population increased from 1968 to 1971, based on 4 indices (Table 2). However, the number of males in 1972 did not increase on Area I and decreased on Area II. Further, adults in the fall kill also decreased in 1972. I conclude that a decline occured in 1972.

The density of the breeding population prior to this study can be inferred only from birds reported killed on fall hunting returns (Fig. 3). These kill statistics likely reflect production rather than breeding density (brood survival section). Only years of extremely high or low kill tend to correlate well with density trends in Minnesota (Gullion, 1970). Based on the harvest statistics, I believe breeding densities were low from 1963 to 1965 and were likely increasing when this study began in 1968 (Fig 3).

Production trends

Production of chicks increased from 1968 to 1969, then decreased from 1969 to 1971, based on mean August brood size and the juvenile per adult ratio in the fall kill (Table 3). Brood sizes were not available for August 1972, however the juvenile per adult ratio in that year indicated an increase (Table 3). August brood size and the juvenile per adult ratio appeared to be correlated ($r = 0.926$, $0.10 > P > 0.05$).

Table 2. Population trends of the breeding population, 1968 to 1972, based on spring census of territorial males, fall drive census of Area I, estimated number of adults in the fall kill, and the number of grouse heard on spring drumming transect.

Census Method	1968	1969	1970	1971	1972
Counts of drumming males[a]					
Area I (270 acres)	10(3.7)	10(3.7)	10(3.7)	13(4.8)	13(4.8)
Area II (318 acres)	—	—	24(7.5)	28(8.8)	24(7.5)
Fall drive of Area I					
No. of grouse flushed	—	13	17	21	—
No. of adults in fall kill[b]	323	343	376	583	402
Road drumming transect					
Max. No. of grouse heard	—	29	34	41	31

[a] Density of males per 100 acres in parenthesis.

[b] Estimated from first six weeks of fall hunter kill.

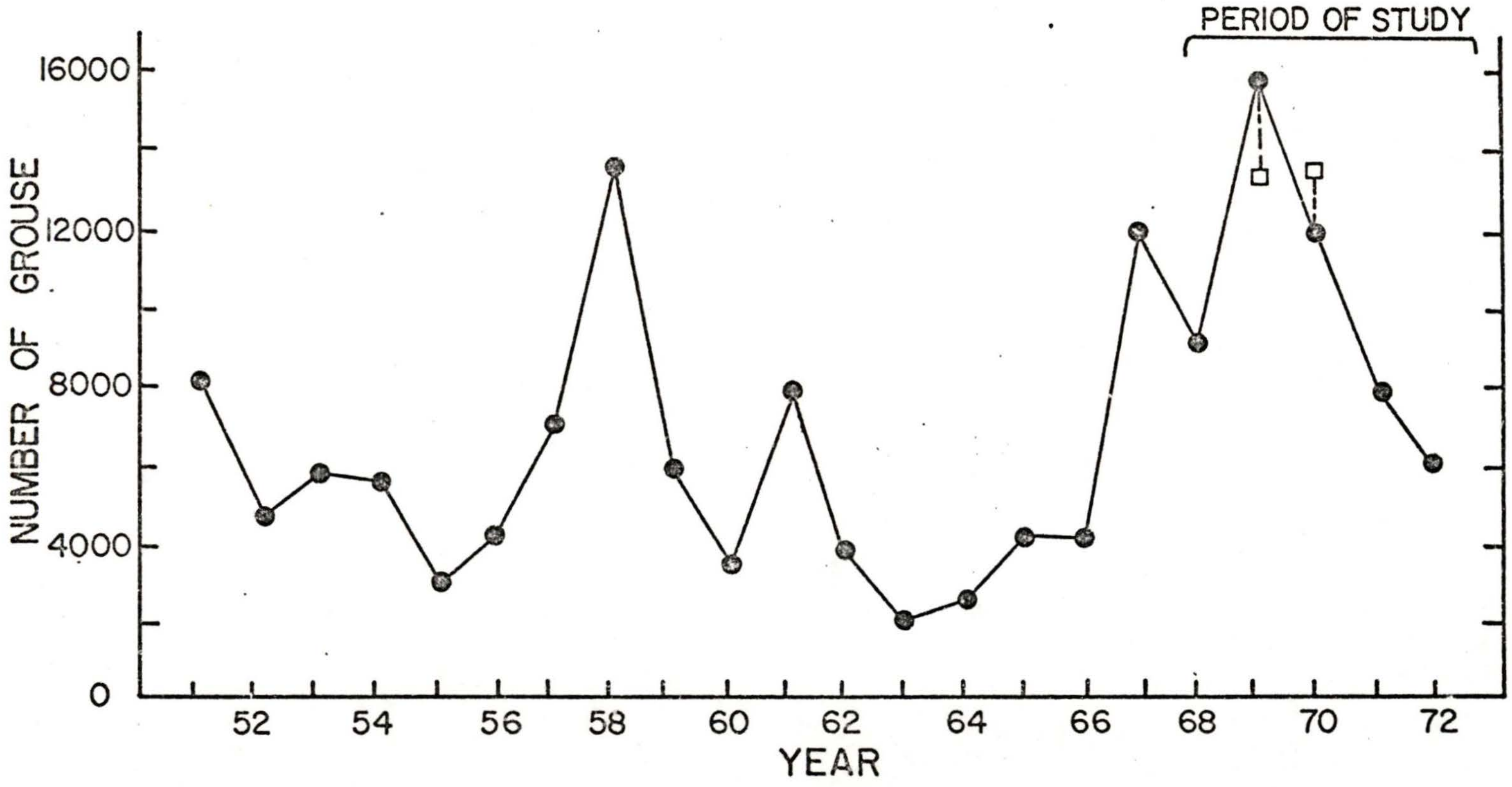

Fig. 3. Total ruffed grouse harvest recorded at B.C. Fish and Wildlife Game check station, Cache Creek, British Columbia, from 1952 to 1972. Additional road check data included in Cache Creek totals in 1969. Opening of 1970 season delayed two weeks. Adjusted kill totals indicated by squares.

Table 3. Production of young, 1968 to 1971 based on mean August brood sizes and the number of juveniles per adult estimated from fall kill, 1968 to 1972.

Indice	1968	1969	1970	1971	1972
Mean August brood size[a]	4.1	4.8 ± 0.24	4.5 ± 0.32	3.9 ± 0.16	——
sample size	——	(18)	(35)	(51)	——
Number of Juveniles per adults in fall kill[b]	2.85	6.65	3.51	1.93	2.13
95 % C. L.	(1.51-5.73)	(3.52-11.56)	(3.04-4.11)	(1.51-2.72)	(1.70-2.85)
sample size	(50)	(102)	(794)	(376)	(234)

[a] 1968 brood size obtained from Fish and Wildlife Branch. Sample size not available. Brood counts not done in 1972.

[b] Estimated from hunter sample of first six weeks of hunting season.

Drumming male survival

Mean annual survival of breeding males, 1968 to 1972, was based on a survivor series of males banded on Area I (Table 4). No corrections were used for surviving males not recaptured. The mean survival rate of 44.7 percent compares favorably with mean values of 0.41 given by Rusch and Keith (1971) in Alberta and the 6 year mean of 0.47 reported by Gullion and Marshall (1968) at Cloquet, Minnesota. Survival rates of red and grey phase males, 0.43 and 0.45, were not significantly different.

The percentage of the total birds that were red phase in both the spring male and adult fall population increased, 1968 to 1972 ($P < 0.01$, Table 5 and Fig. 4). The percentage of reds increased, in spite of the apparent similar survival of red and grey males on drumming logs (Table 4). Gullion and Marshall (1968) reported an increase in red phase birds in the juvenile segment of the drumming male population despite an apparent lower overwinter survival of red phase males. They also found, in contrast to my findings, that grey phase males survived significantly longer than red phase males. Thus, the observed increase in red phase birds in my study may mean that red juvenile males obtained a greater proportion of the available territories each year. All males were not trapped each year, however, and since males must be trapped to determine age, my data is insufficient to resolve the above question.

Table 4. Survivor series of males banded on Area I, 1968 to 1971.[a]

			Number Recaptured			
Year Banded	No. Banded		1969	1970	1971	1972
1968	Grey	6	3	1	-	-
	Red	3	2	1	-	-
	Total	9	5	2	-	-
1969	Grey	3	-	1	-	-
	Red	1	-	1	-	-
	Total	4	-	2	-	-
1970	Grey	7	-	-	3	3
	Red	1	-	-	-	-
	Total	8	-	-	3	3
1971	Grey	7	-	-	-	3
	Red	2	-	-	-	1
	Total	9	-	-	-	4

[a] Calculated survival rates: Grey phase= 0.45; Red phase= 0.43; Both phases= 0.447.

Table 5. The increase in abundance of red phase birds in the breeding population, 1968 to 1972, based on the number of red birds in both the spring male population and fall adult population.

	1968	1969	1970	1971	1972
Percent red males on logs	20.0	20.0	23.5	26.8	32.4
sample size	(10)	(10)	(34)	(41)	(37)
Percent red adults in fall kill[a]	18.2	20.6	25.0	29.8	34.5
95 % C. L.	(8.6-31.4)	(13.5-30.3)	(19.2-31.6)	(22.8-35.8)	(24.8-44.5)
sample size	(44)	(102)	(192)	(188)	(64)

[a] Average percentage red phase adults occuring in weekly samples for first six weeks of hunting season.

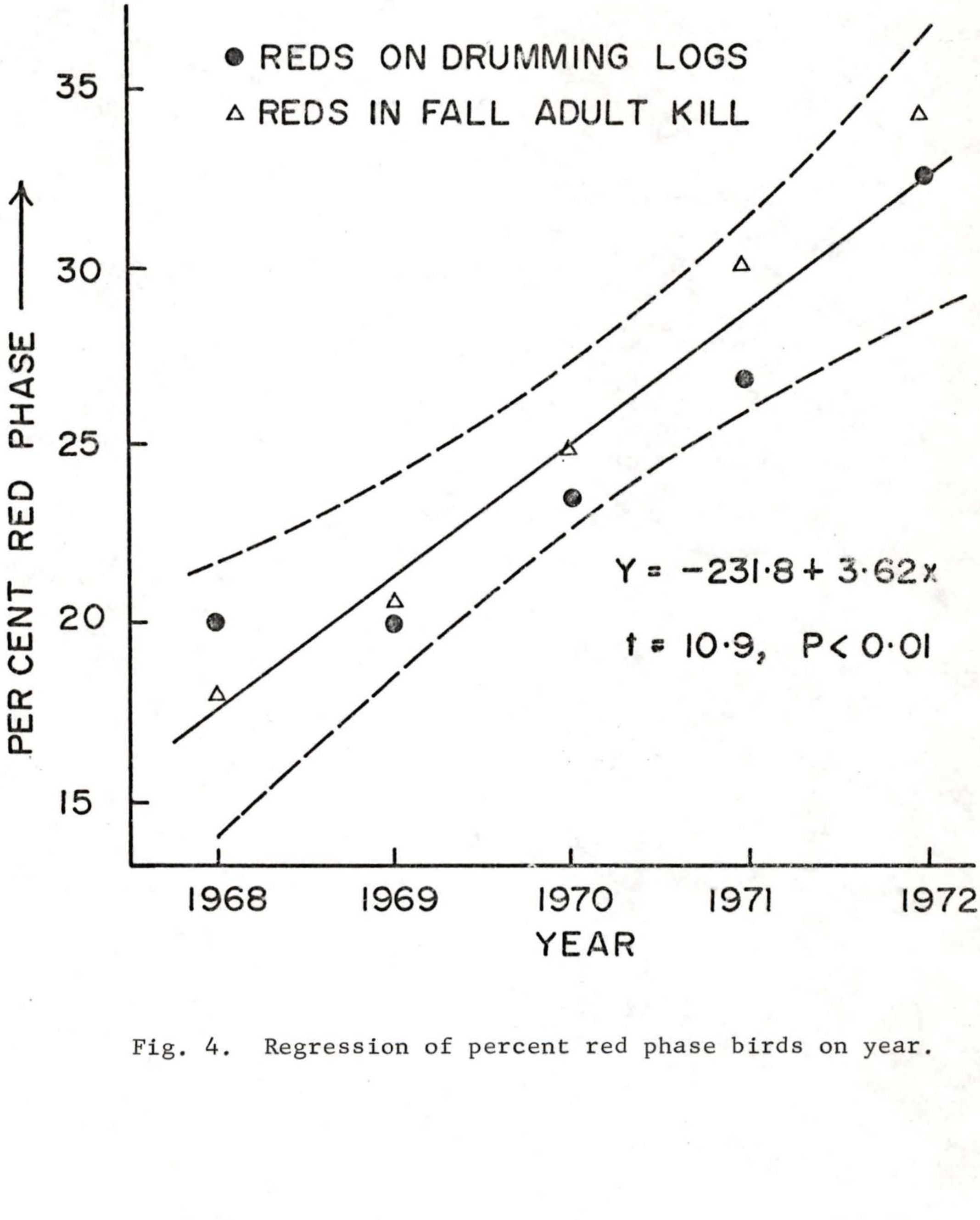

Fig. 4. Regression of percent red phase birds on year.

Brood survival

Mean survival of broods was calculated from the observed decline in mean brood sizes from hatching till the end of August. Only broods thought to be completely counted were included. I had insufficient data to determine annual changes in clutch size - only six nests (9.4 chicks per nest).

Brood survival from hatch to August was low in 1968 and 1971 (0.44 and 0.42), and higher in 1969 and 1970 (0.51 and 0.49) (Table 6). Mean brood survival based on all four years was 0.47. This figure is similar to the 0.51 survival estimated by Rusch and Keith (1971) for ruffed grouse in Alberta, and higher than the figure reported by Bump *et al*. (1947) in New York State (0.34) and lower than survival given by Dorney and Kabat (1960) for Wisconsin of 0.67.

Brood survival during July to August was similar in all years (0.79 to 0.85). Thus the annual differences in brood survival hatch to August (Table 6) were likely due to survival differences that occurred within one month of hatch. A high early mortality of chicks is typical of tetraonids. Rusch and Keith (1971) found similar late summer survival rates for ruffed grouse; Bergerud (1970) found little mortality occuring in summer in willow ptarmigan (*Lagopus lagopus alleni* L.); Mossop (1971) working with blue grouse (*Dendragapus obscurus fuliginosus*) found that June survival varied between years and populations but July and August survival was similar.

I compared the survival of chicks in broods accompanied by red and grey hens (red broods and grey broods) between the months

Table 6. Mean number of chicks in broods observed during June, July, and August, 1968 to 1971; plus calculated survival rates of young, June to August. Sample sizes in parenthesis.

	Mean Brood Sizes			Survival			
Year	June	July	August	Hatch to July	July to August	Hatch to August	No. of Broods
1968[a]	6.7	4.4	4.1	0.50	0.85	0.44	
	( )	( )	( )				(24)
1969	6.8 ± 0.79	5.7 ± 0.47	4.8 ± 0.34	0.61	0.84	0.52	
	(05)	(07)	(18)				(30)
1970	7.3 ± 0.35	5.7 ± 0.36	4.5 ± 0.33	0.61	0.79	0.49	
	(17)	(26)	(24)				(67)
1971	6.1 ± 0.31	5.0 ± 0.25	4.0 ± 0.16	0.53	0.80	0.42	
	(23)	(30)	(50)				(103)
Means	6.7	6.3	4.4	0.56	0.82	0.47	(224)

[a] Monthly sample sizes not available for broods in 1968.

of June, July, and August and between the years 1970 and 1971. The relationship between hen colour and chick colour was not known. There were significantly more chicks in broods with grey hens than in broods with red hens (Table 7 and 8). The difference between colour phases in chick survival appeared to be mainly due to differences in chick survival from hatch to June, based on assumption of equal clutch size between red and grey phases (Table 8). Grey hens had 7.4 chicks in June 1970 and 6.6 chicks in June 1971 whereas red hens had 7.0 chicks in June 1970 and 5.1 chicks in June 1971 (Table 8). Also, it appeared that the survival of chicks of red broods was lower than that of grey broods from hatch to August (Table 8). I could not document this difference statistically, however, since a comparison of slopes of the regression of brood sizes on month between red and grey broods showed no significant difference (Fig. 5).

Histograms of brood sizes for August 1969 to 1971, showed approximately normal distributions of sizes in all years (Fig. 6). Data was not available for 1968. The peak brood size was one chick lower in the year of low production, 1971, than in two years of good production, 1969 and 1970 (Fig. 6). There were fewer red hens than grey hens with large broods in 1970 and 1971 (Fig. 6).

I felt that any explanation of brood mortality would have to account for the large loss of chicks shortly after hatch and differential mortality of red and grey broods. Further, the severity of the mortality factor involved would have to be correlated with the number of chicks per hen.

Table 7. Analysis of variance showing effects of color phase of hen, year, and month on brood size.

Source of Variation	df	MS	F	P less than
Hen color	1	32.82	17.363	0.001
Year	1	28.50	15.077	0.001
Month	2	70.93	37.526	0.001
Hen color x year	1	4.84	2.562	0.111
Hen color x month	2	0.83	0.226	0.798
Year x month	2	1.14	0.604	0.548
Hen color x month x year	2	0.46	0.242	0.785
Error	158	1.89		

Table 8. A comparison of brood production and survival parameters between broods hatched by red and grey phase hens, 1970 and 1971. Sample size in parenthesis.

		Mean Brood Sizes			Survival			
Year	Hen Color	June	July	August	Hatch to July	July to August	Hatch to August	No. of Broods
1970	Grey	7.4 ± 0.38	5.8 ± 0.36	4.8 ± 0.33	0.61	0.83	0.51	
		(13)	(21)	(20)				(54)
	Red	7.0 ± 0.91	5.8 ± 0.86	4.0 ± 0.90	0.62	0.69	0.43	
		(04)	(05)	(04)				(13)
1971	Grey	6.6 ± 0.30	5.4 ± 0.26	4.4 ± 0.19	0.57	0.83	0.47	
		(16)	(18)	(34)				(68)
	Red	5.1 ± 0.63	4.3 ± 0.50	3.3 ± 0.24	0.46	0.77	0.35	
		(07)	(12)	(16)				(35)

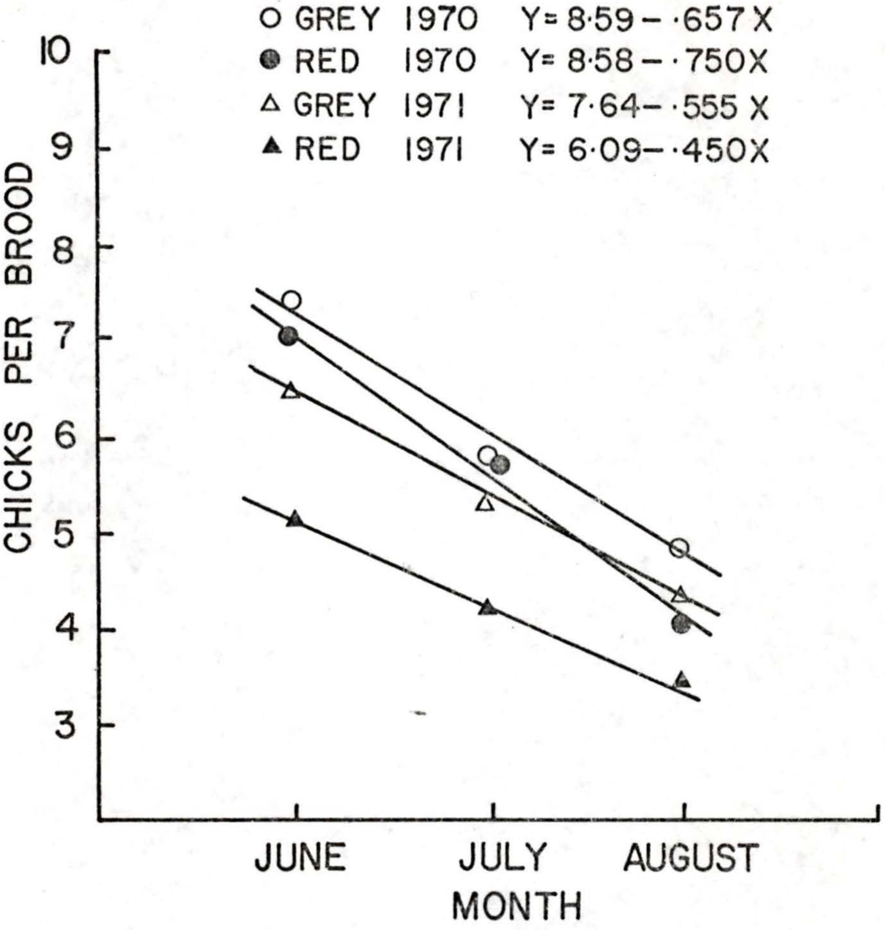

Fig. 5. Regression of mean brood sizes of red and grey hens, on month, 1970 and 1971.

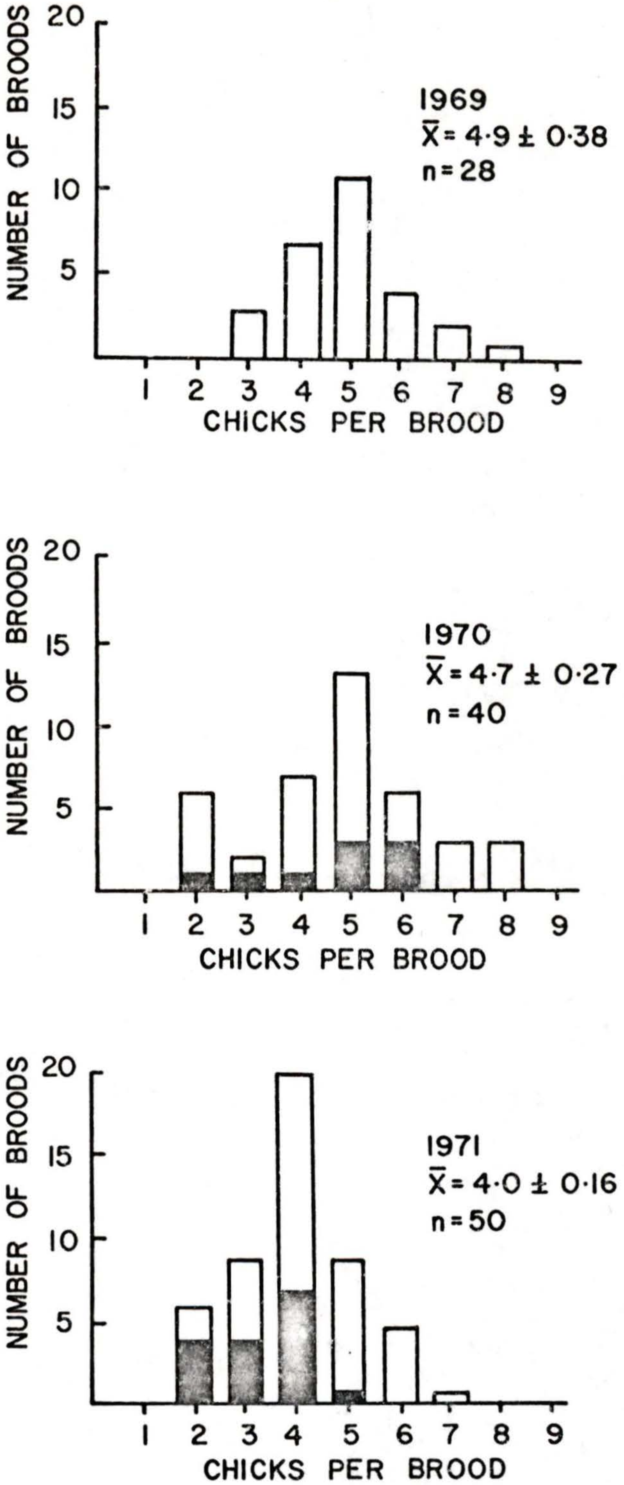

Fig. 6. Comparison of August brood sizes, 1969 to 1971, at Watch Lake, B.C. Number of red broods indicated by black shading and grey broods by white bars.

I found that August brood sizes were negatively correlated with date of mean hatch in four years ($r = -0.964$, $P < 0.05$, Fig.7). Hatch curves were derived from collected and captured chicks aged to the nearest 1/2 week and fall juveniles aged to the nearest week (Fig. 8). Samples collected in fall were not collected on similar dates year to year. Nevertheless, I feel that a one week difference in mean hatch date such as exists between 1968 and 1969 is indicative of an actual difference.

Either a decrease in clutch size or lower survival of chicks in late hatch years could account for the correlation of August brood size and date of hatch. Insufficient clutches were found to investigate yearly clutch size variation but other workers have found decreases in mean clutch size in years of late hatch. Clutch size was found to be negatively correlated with date of hatch in Newfoundland willow ptarmigan for 9 years (Bergerud, 1970) and in Scottish red grouse (*Lagopus lagopus scoticus*) in 5 years (Jenkins *et al*., 1963). Bump *et al*. (1947) found yearly variations in clutch size of ruffed grouse in New York State but did not relate decrease to hatch date. The possibility that red and grey phase hens produce different size clutches has not been reported in the literature, but it cannot be eliminated.

More hens hatched broods in July in the low production (late hatch) years, 1968 and 1971, than in years of good production (early hatch) 1969 and 1970 (Fig. 8). These July broods may have resulted from renesting. Bump *et al*. (1947) found first clutches to contain an average of 11.6 eggs, and second clutches 7.5 eggs, but they felt renesting was not a major factor determining yearly production.

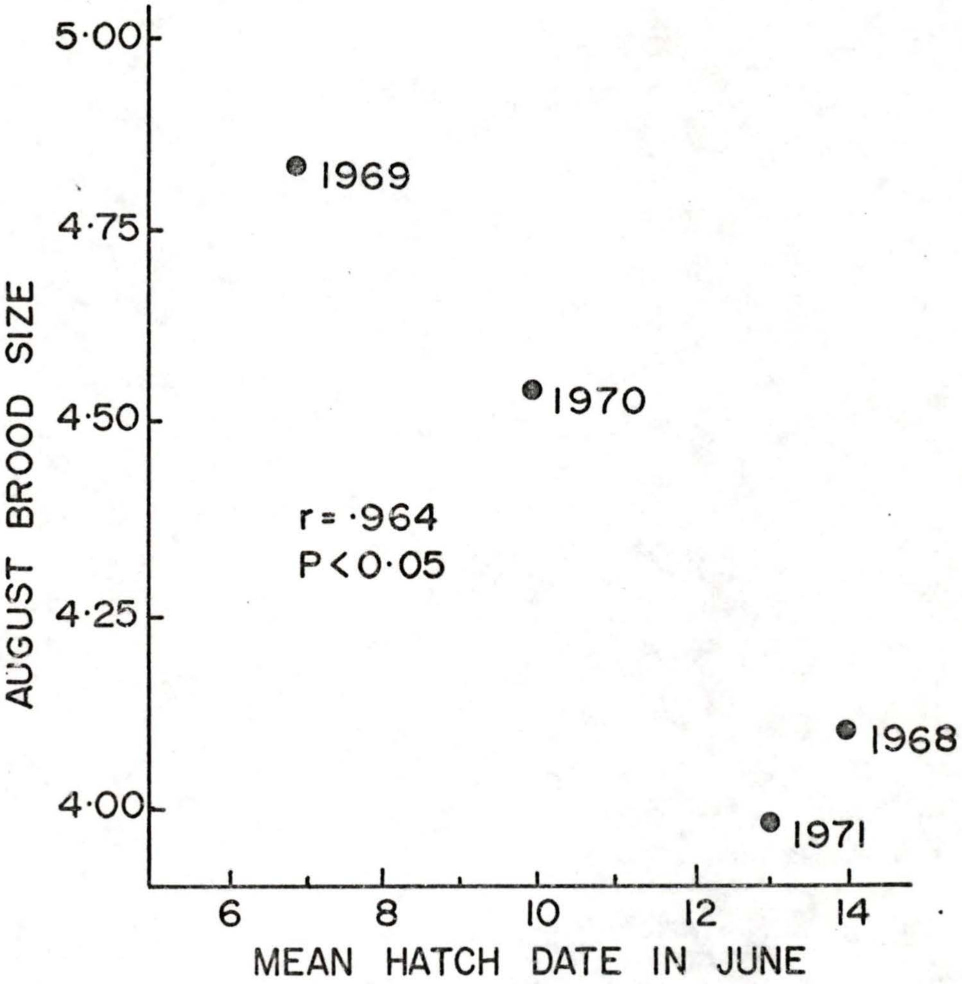

Fig. 7. The correlation between number of chicks per brood in August and mean hatch date in June.

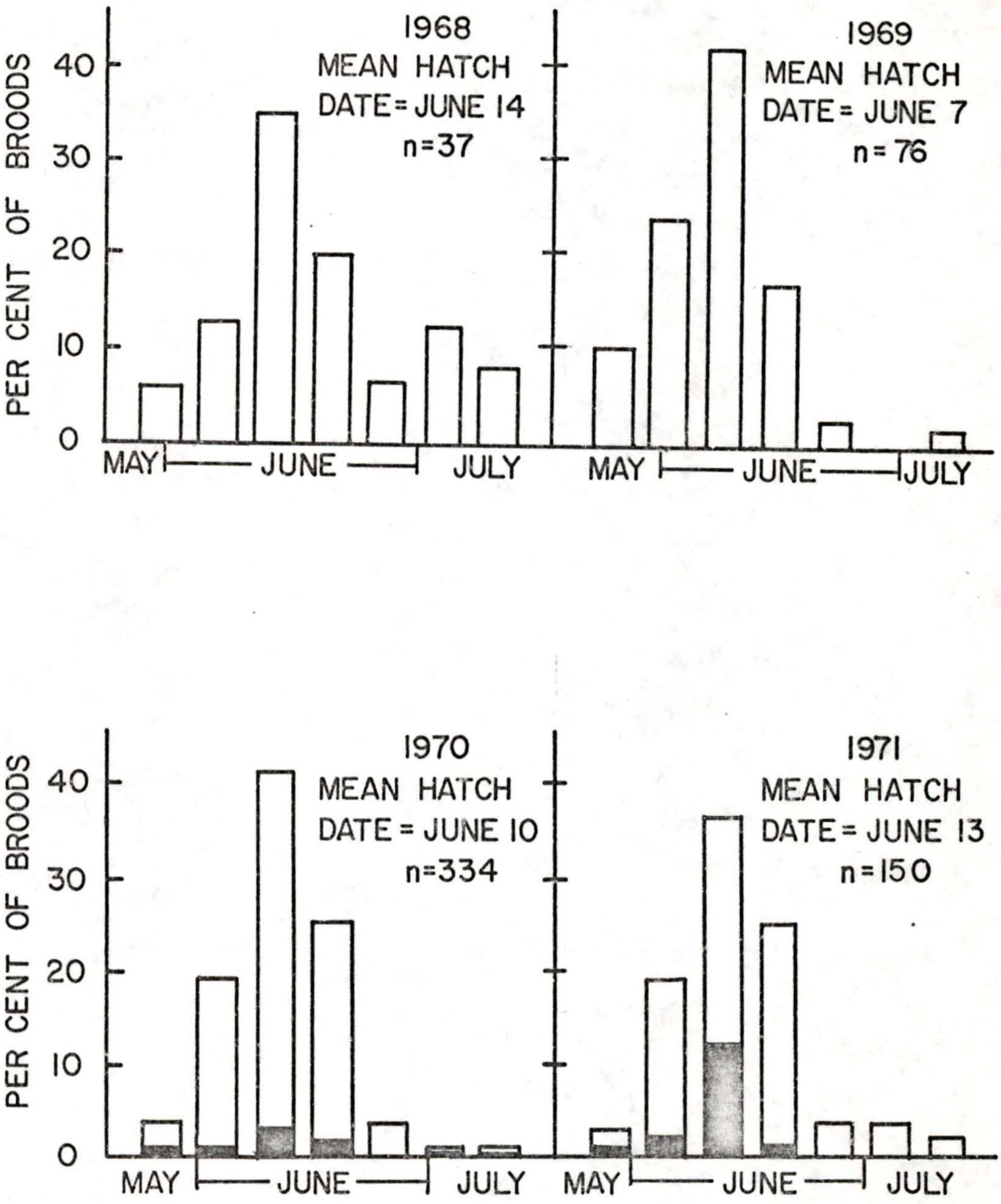

Fig. 8. Hatch curves for broods at Watch Lake, B.C., 1968 to 1971. The percentage of red young indicated by shaded bars, grey young by white bars.

Another possible explanation for smaller brood sizes in the late hatch years, 1968 and 1971, is that late hatched chicks had a lower survival than early hatched chicks. Wagner *et al*. (1965) have shown that late hatched pheasant chicks (*Phasianus colchicus*) have reduced survival. Also, studies of Scottish red grouse have suggested this possibility (Jenkins *et al*., 1963 and 1967). Zwickel and Bendell (1967) working with Vancouver Island blue grouse, found that all chicks, both early and late hatch chicks, survived less well in late hatch years.

Severity of weather, both prior to laying and following hatch, has often been suggested as an extrinsic variable affecting chick survival. Siivonen (1957) postulated that the mean temperature three weeks prior to laying determined quantity or quality of food available to hens; thus differences in maternal nutrition were reflected in viability of young. Gullion (1970) suggested that physiology of the hen was dependent upon winter weather rather than weather immediately prior to laying. Some workers have shown that low temperatures during the early brood period were correlated with brood survival or yearly production (Bump *et al*., 1947; Ritcey and Edwards, 1963). May mean daily temperature was not correlated with brood survival indices. June mean maximum temperature was significantly correlated with brood survival from hatch to August ($r = 0.998$, $P < 0.05$), with August brood size ($r = 0.996$, $P < 0.01$), and juveniles per adult in fall kill ($r = 0.914$, $P < 0.05$, Fig. 9). Mean maximum temperature was used in these computations since the mean minimum temperature occurs during the night, an inactive period for grouse. Hens are usually

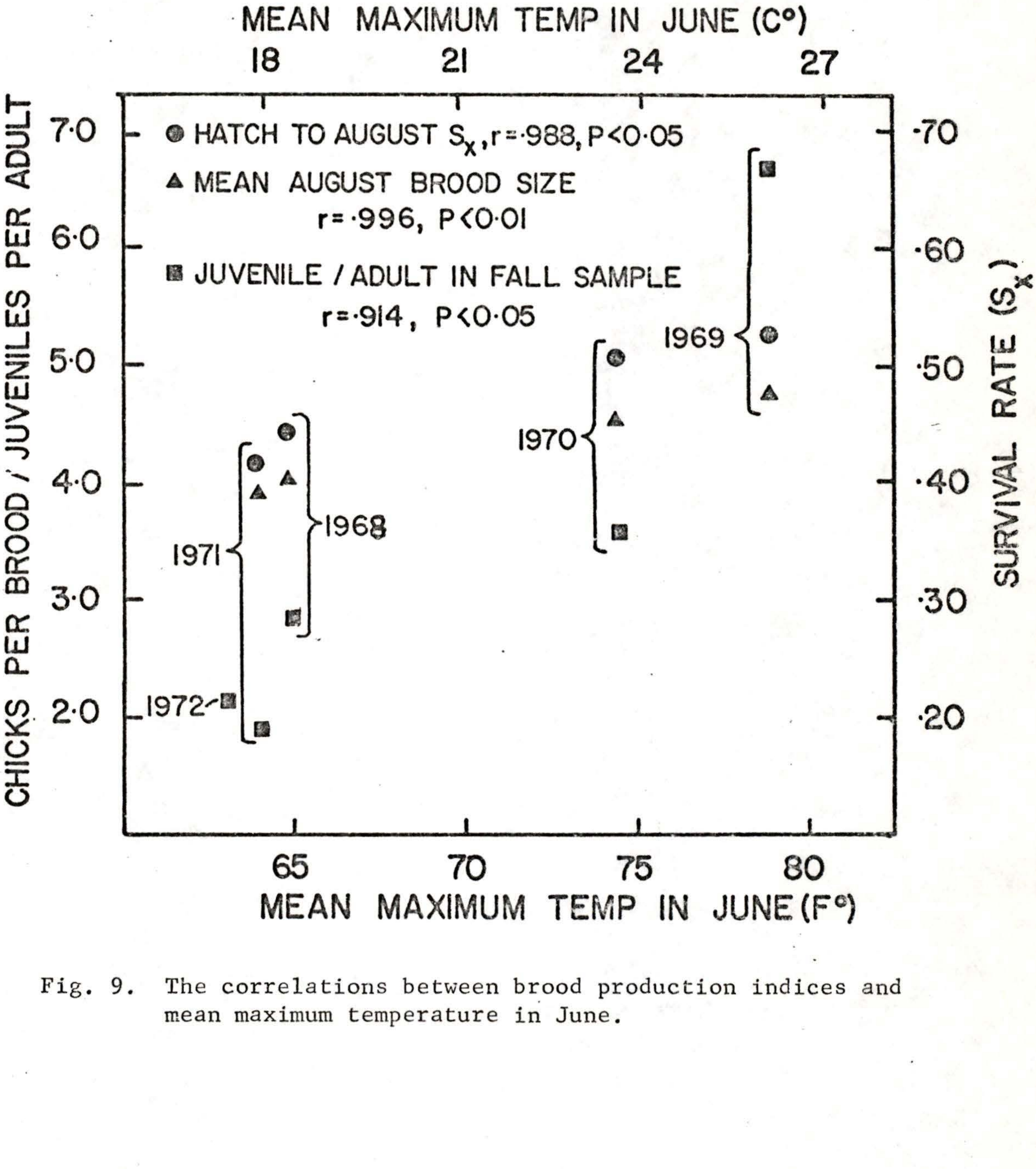

Fig. 9. The correlations between brood production indices and mean maximum temperature in June.

brooding at this time. These correlations suggest that weather following the hatch was an important determinant of chick survival. The fact that its depressant effects were greater on red broods than grey broods suggests that viability of chicks was dependent to some degree on the intrinsic quality of the hen.

Brood production decreased from 1970 to 1971 and 1972 during this study while density of the breeding population increased during this time suggesting that density per se and production are unrelated (Table 9). Chicks per brood in August was not significantly correlated with total fall kill ($r = 0.841$). However the correlation coefficient was sufficiently high to suggest that changes in production accounted for most of the yearly variation in kill ($r^2 = 71$ %). Fall kill was not correlated with densities the following spring ($r = -0.491$). This last finding agrees with other ruffed grouse studies (Gullion, 1970; Bump et al., 1947; Rusch and Keith, 1971). Since there was no correlation between fall populations (as reflected by kill figures) and the breeding population the next spring, it appears likely that the changes in spring density resulted from changes in overwinter survival. Further, since spring densities did not reflect prior production a greater proportion of juveniles may have died during the years of high production (1969 and 1970) than in years of poor production (1968, 1971, and 1972).

Mortality trends based on grouse killed by hunters

Birds killed by hunters provided data to compare sex, age, and colour phase ratios during the hunting season. Some workers

Table 9. Summary of density and production indices, 1968 to 1972.

Year	No. of Drumming Males on Area I	Brood Size in August[a]	J/A Ratio in Fall Kill[b]	Total Fall Kill MA 14[c]
1968	10	4.1	2.85	2500
1969	10	4.8	6.65	4300
1970	10	4.5	3.53	4200
1971	13	3.9	1.93	2700
1972	13	—	2.13	2100

[a] brood counts not carried out in 1972

[b] estimated from fall kill for first 6 weeks of hunting season.

[c] MA 14 is region in which study areas are located.

have concluded that susceptibility to hunting may vary according to the sex and age of the bird (Rusch and Keith, 1971; Dorney and Kabat, 1960). Thus my analysis was an evaluation of mortality relative to hunting and may not be an index of changes occuring in the population.

In both the adult and juvenile kill, 1970 and 1971, the percentage of red phase birds increased progressively throughout the hunting season (Fig. 10). This trend was significant in both years for the juvenile kill ($P < 0.05$) and approached significance in the adult sample ($P < 0.10$). This increase was not related to total weekly kill of grouse since the percentage of red phase birds continued to increase after the weekly kill declined (total weekly kill peaked approximately during the fifth to sixth week of the season in both years, 1970 and 1971).

To determine if this increase in reds and corresponding decrease in greys was equal in both males and females, the distribution of all age, sex, and colour classes was plotted for the first six weeks of the hunting season in 1971 (Fig. 11). Only birds judged to be accurately sexed and aged were used. Sample sizes of red adults in early weeks of 1970 hunting season were not adequate for this analysis; thus, only 1971 data is presented here.

In the adult sample, an increase of red males accounted for the increase in red phase birds ($P < 0.05$). Changes in other sex and colour classes (adult sample) were not significant based on regression analysis of the slope coefficients. Small individual sample sizes resulted in large confidence limits and any conjecture about indicated trends would be suspect.

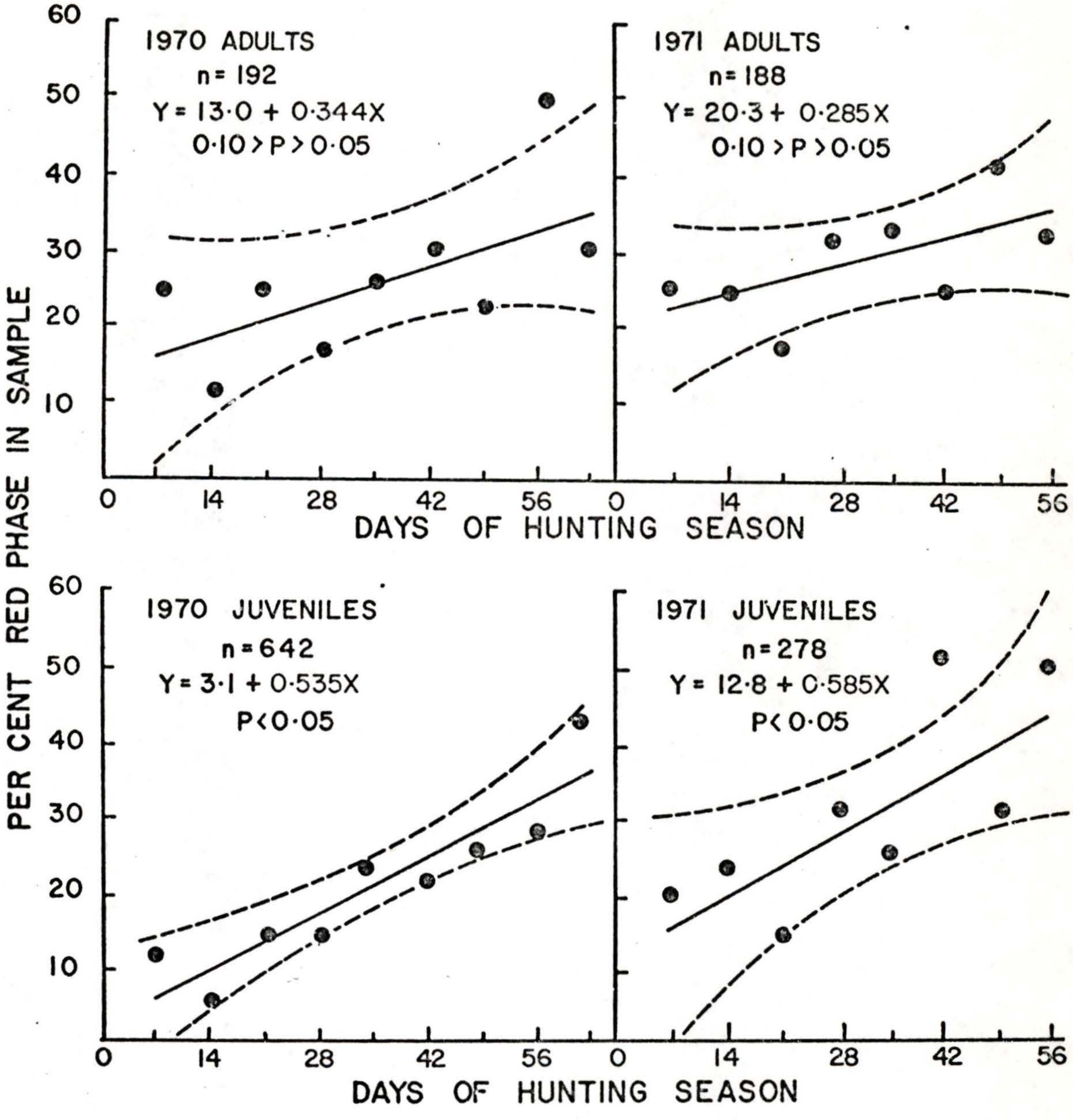

Fig. 10. The regression of percent red phase grouse on days of the fall hunting season for juvenile and adult samples of fall hunter kill, 1970 and 1971. Weekly samples obtained from B.C. Fish and Wildlife check station located at Cache Creek, British Columbia.

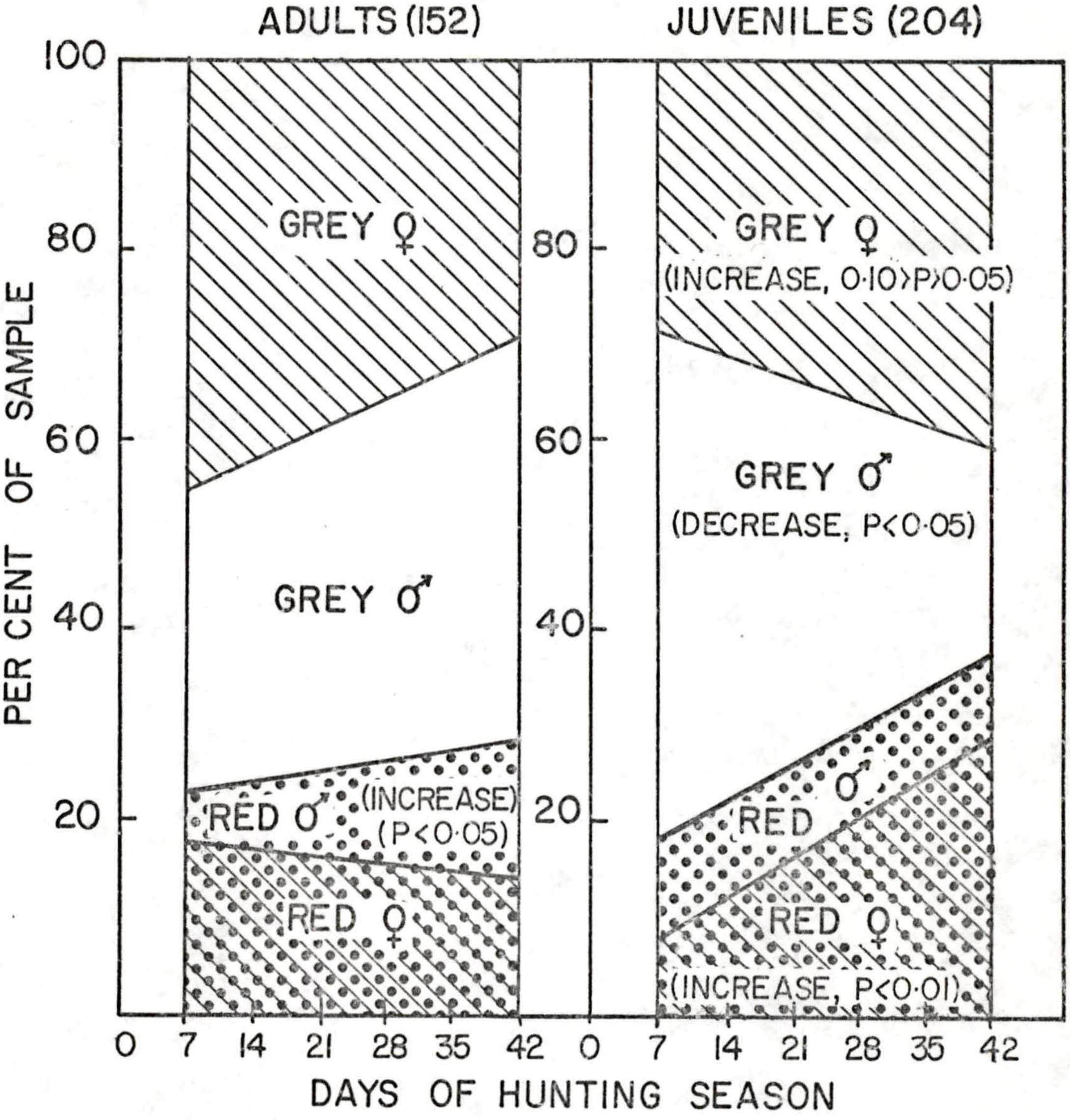

Fig. 11. Sex and colour phase composition of juvenile and adult kill samples plotted for first 6 weeks of fall hunting season, 1971.

In the juvenile sample a large increase in red females accounted for the change in percentage reds ($P < 0.05$). The percentage of juvenile red males remained fairly constant in each weekly sample. Grey males decreased significantly ($P < 0.05$) while grey females increased ($0.10 > P > 0.05$). The overall trend was a decrease in males and a corresponding increase in females throughout the six weeks ($P < 0.05$).

In previous studies of kill data differential vulnerability to hunting has been attributed to differences in mobility and wariness of bird (Dorney and Kabat, 1960), and territorial behaviour of males and brood defence behaviour of hens (Rusch and Keith, 1971). Thus red and grey phase grouse may differ in respect to the above mentioned attributes, any of which could conceivably influence fall survival

BEHAVIOUR RESULTS

Flushing distances

A statistical analysis of flushing distances, which is an index of the approachability of grouse (Mossop, 1971), was carried out on a multivariate analysis of variance program (MANOVA). Independent variables in the analysis were colour phase (red or grey), area (Area I or II), and year (1970 or 1971).

Drumming males could be recognized because of flushing locale but the sex of other birds could not be distinguished; thus only drumming males are included in the following analysis. Separate anovas were run for males flushed in aspen and aspen/conifer habitats.

The analysis of flushing distances of drumming males in aspen indicated significant differences between colour phases, years, and areas (Table 10). The analysis of flushing distances in the aspen/conifer habitat gave results similar to those above (Table 11). In general the flushing distances of grey males was greater than that of red males (Fig. 12). The flushing distance of grey males decreased 1970 to 1971 (Fig. 12) whereas the flushing distances of red phase males decreased only slightly or remained the same (Fig. 12). Mean flushing distance of both phases was greater on Area II which had a higher density of males than Area I (see Table 2).

Table 10. Analysis of variance showing effects of study area, color phase, and year on flushing distances of males in the aspen vegetation type.

Source of Variation	df	MS	F	P less than
Area (I or II)	1	3261.11	43.361	0.001
Color phase	1	2664.75	35.165	0.001
Year	1	415.54	5.525	0.021
Area x color	1	238.68	3.174	0.078
Area x year	1	41.94	0.558	0.457
Color x year	1	17.65	0.235	0.629
Area x color x year	1	3.76	0.050	0.824
Error	83	75.21		

Table 11. Analysis of variance showing the effects of study area, color phase, and year on flushing distances of males in aspen/conifer vegetation type.

Source of Variation	df	MS	F	P less than
Area (I or II)	1	890.94	14.546	0.001
Color phase	1	305.25	4.984	0.033
Year	1	272.85	4.445	0.043
Area x color	1	39.80	0.650	0.427
Area x year	1	35.11	0.573	0.455
Color x year	1	32.65	0.553	0.471
Area x color x year	1	17.23	0.281	0.600
Error	30	61.25		

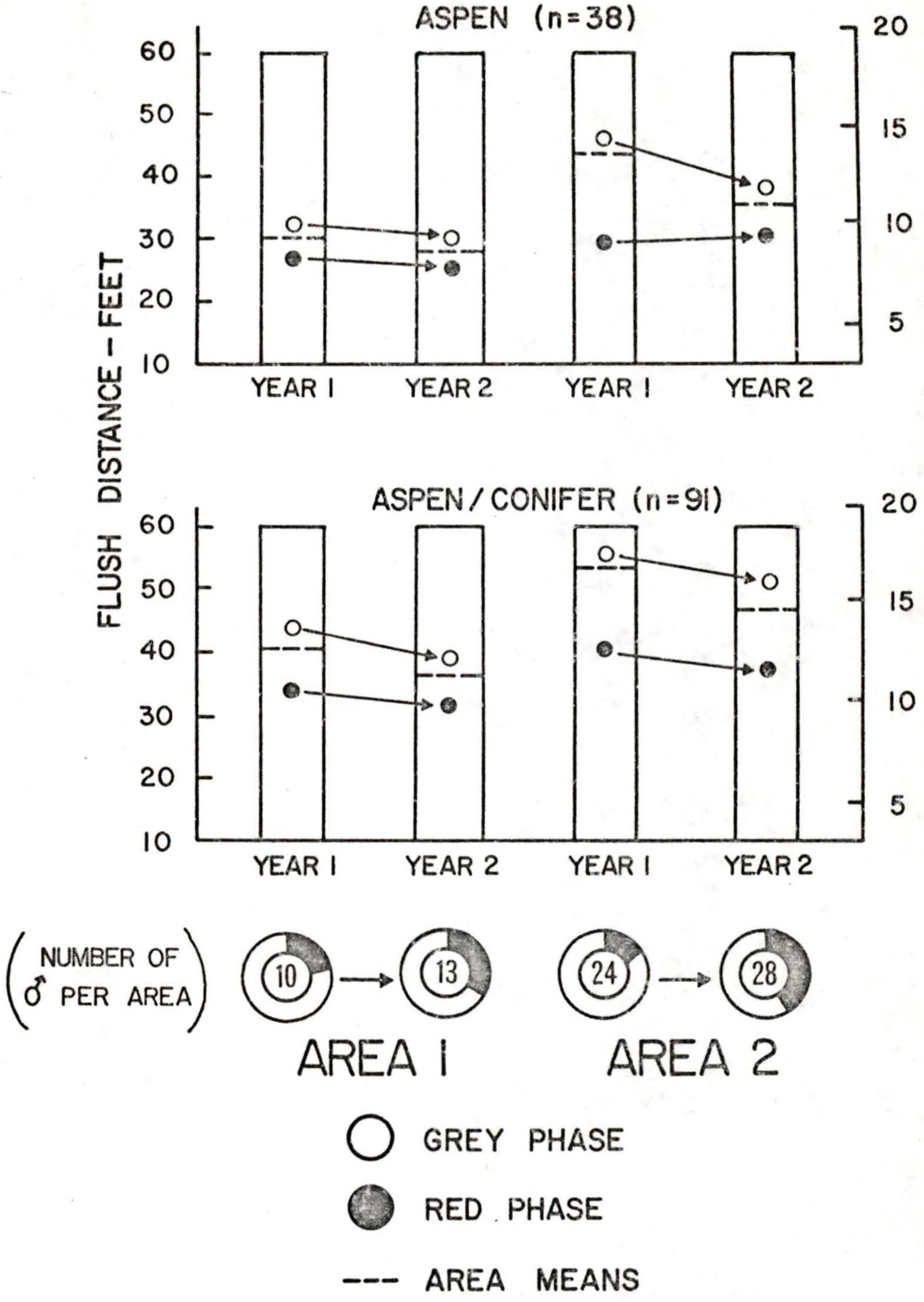

Fig. 12. Comparison of flushing distances of males between colour phases, area, years, and between aspen and aspen/conifer habitat types. Years 1 and 2 are 1970 and 1971. Numbers of males are indicated in large circles. Shaded portion of circles represents percentage of males which were red phase.

I also compared the flushing distances of all single birds (females or sex unknown) flushed during May field work on both areas and in the surrounding region. Again, there were significant differences between colour phases and vegetation types (Table 12). In general, red phase grouse were more approachable - had a shorter flush distance (Fig. 12).

A third analysis of flushing distances of single birds flushed only in the summer (June, July, August) showed only significant differences between vegetation classes (Table 13). I believe that many of the flushed birds recorded in the spring as sex unknown were males, since (1) females would be incubating at this time, and (2) demographic work involving the male population was being carried out at this time. In the summer I likely observed non-territorial males, lone females, and some territorial males.

Mirror tests

The measure of agonistic behaviour of drumming males when confronted with their mirror image was analyzed using the same multivariate analysis of variance program. In this analysis colour phase (red or grey), study area (Area I or II), and year (1970 or 1971) were the independent variables. Pecks per hour and attacks per hour, and weights were the dependent variables.

The analysis indicated significant differences between areas for both pecks per hour and attacks per hour (Table 14). Colour phases differed in the number of attacks and pecks per hour, red phase birds appearing to be more agonistic (Table 15). Weight differences were not significant, but a significant interaction between years and colour phase for attacks was indicated (Table 14).

Table 12. Analysis of variance showing effects of color phase, year and vegetation type on flushing distances of single birds (sex unknown) during May.

Source of Variation	df	MS	F	P less than
Color phase	1	5238.99	41.156	0.001
Year	1	175.93	1.382	0.241
Vegetation[a]	5	10826.32	85.049	0.001
Color x year	1	73.85	0.580	0.447
Color x vegetation	5	199.75	1.569	0.169
Year x vegetation	5	199.00	1.508	0.187
Color x year x vegetation	5	69.64	0.547	0.741
Error	299	127.30		

[a] Vegetation classes were Aspen, Aspen/conifer, conifers, willow swamps, logging slash or regeneration, road edges.

Table 13. Analysis of variance of flushing distances of all birds encountered in summer, 1970 and 1971, showing effect of color phase, year and vegetation type on flushing distances.

Source of Variation	df	MS	F	P less than
Color phase	1	448.02	1.960	0.162
Year	1	141.38	0.619	0.432
Vegetation[a]	5	43438.11	190.481	0.001
Color x year	1	4.75	0.021	0.885
Color x vegetation	5	53.69	0.235	0.947
Year x vegetation	5	860.36	3.764	0.002
Color x year x vegetation	5	456.72	1.998	0.007
Error	733	228.57		

[a] Vegetation classes were Aspen, Aspen/conifer, conifers, willow swamps, logging slash or regeneration, road edges.

Table 14. Probabilities derived from analysis of variance of agonistic scores of males tested 1970 and 1971 showing effect of color phase, study area, and years on pecks and attacks directed at mirror image. Effects on weights is also given.

Factor[a]	Probabilities of Dependent Variables (P)		
	Pecks per Hour	Attacks per Hour	Male Weights
Color Phase (Red or grey)	0.019	0.095	0.630
Area (I or II)	0.004	0.019	0.152
Year (1970, 1971)	0.521	0.004	0.551
Year x color phase[b]	0.158	0.005	0.268

[a] All main effects and interactions had one degree of freedom.

[b] No significant interaction between color x area, area x year, color x area x year.

Table 15. Summary of mean agonistic scores of males tested with mirrors in 1970 and 1971. Sample size in parenthesis.

Area	Year	Color phase		Pecks per hour	Attacks per hour
Area I	1970	Grey	(07)	488.0 ± 64.7	6.7 ± 0.9
		Red	(02)	448.0 ± 249.1	5.0 ± 1.0
	1971	Grey	(10)	468.5 ± 82.6	2.9 ± 0.8
		Red	(02)	712.0 ± 10.6	7.0 ± 1.0
Mean 1970 and 1971		Grey	(17)	475.3	4.5
		Red	(04)	580.0	6.0
Area II	1970	Grey	(10)	263.5 ± 65.8	5.0 ± 0.8
		Red	(01)	333.0 ± ——	3.0 ± ——
	1971	Grey	(14)	268.1 ± 50.1	2.5 ± 0.3
		Red	(05)	541.0 ± 89.6	5.4 ± 1.5
Mean 1970 and 1971		Grey	(24)	265.8	3.5
		Red	(06)	506.3	6.0

Peck and attack ratings for all males, 1970 and 1971, were combined, ranked, and tested using the Mann-Whitney U Test (Sokal and Rohlf, 1969). Red phase males had a higher combined rating than grey phase males ($P < 0.05$); Area I males had a higher combined rating than Area II birds ($P < 0.05$); there was no significant difference in intensity of agonistic behaviour between years. The interaction between colour phase and year for attacks was likely caused by attacks of red birds increasing 1970 to 1971 and attacks for grey birds decreasing (Fig. 13).

Basic results of the mirror tests are illustrated graphically (Fig. 13). Red phase males, on both areas, showed an increase in attacks and pecks from 1970 to 1971. Grey phase ratings decreased or remained the same. Both colour phases on the high density area, Area II, had lower ratings than their counterparts on the low density area, Area I (see Table 2 for area densities).

I found that peck per hour ratings and flush distance ratings of individual males were negatively correlated ($r = -0.681$, $P < 0.01$) (Fig. 14). This correlation suggests that the more agonistic birds were more approachable.

I ranked males on both areas according to their test scores and designated the upper 50 percent as high score birds, and the bottom 50 percent as low score birds, and then compared whether the drumming locations of high and low score birds were proportionally distributed in (1) aspen dominated areas, and (2) conifer stands. These two vegetation types were considered to be optimum and marginal habitat, respectively, in Alberta (Rusch and Keith, 1971) and in Minnesota (Gullion, 1970). High score birds occured in the

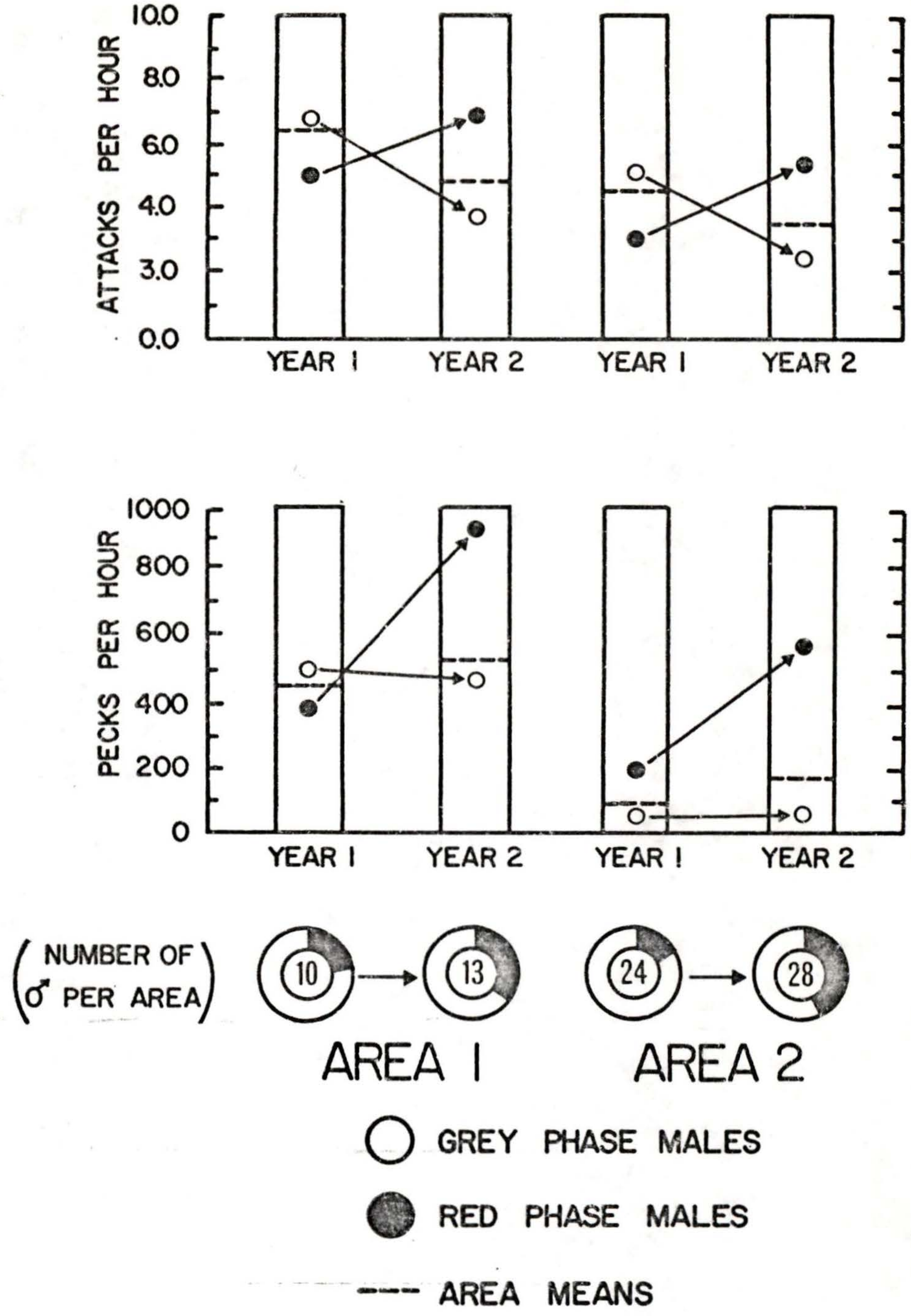

Fig. 13. Comparison of mean agonistic scores of mirror tested males between color phases, areas, and years. Years 1 and 2 are 1970 and 1971. Number of males per study area are indicated in large circles. Shaded portion of large circles represents percentage of males which are red phase.

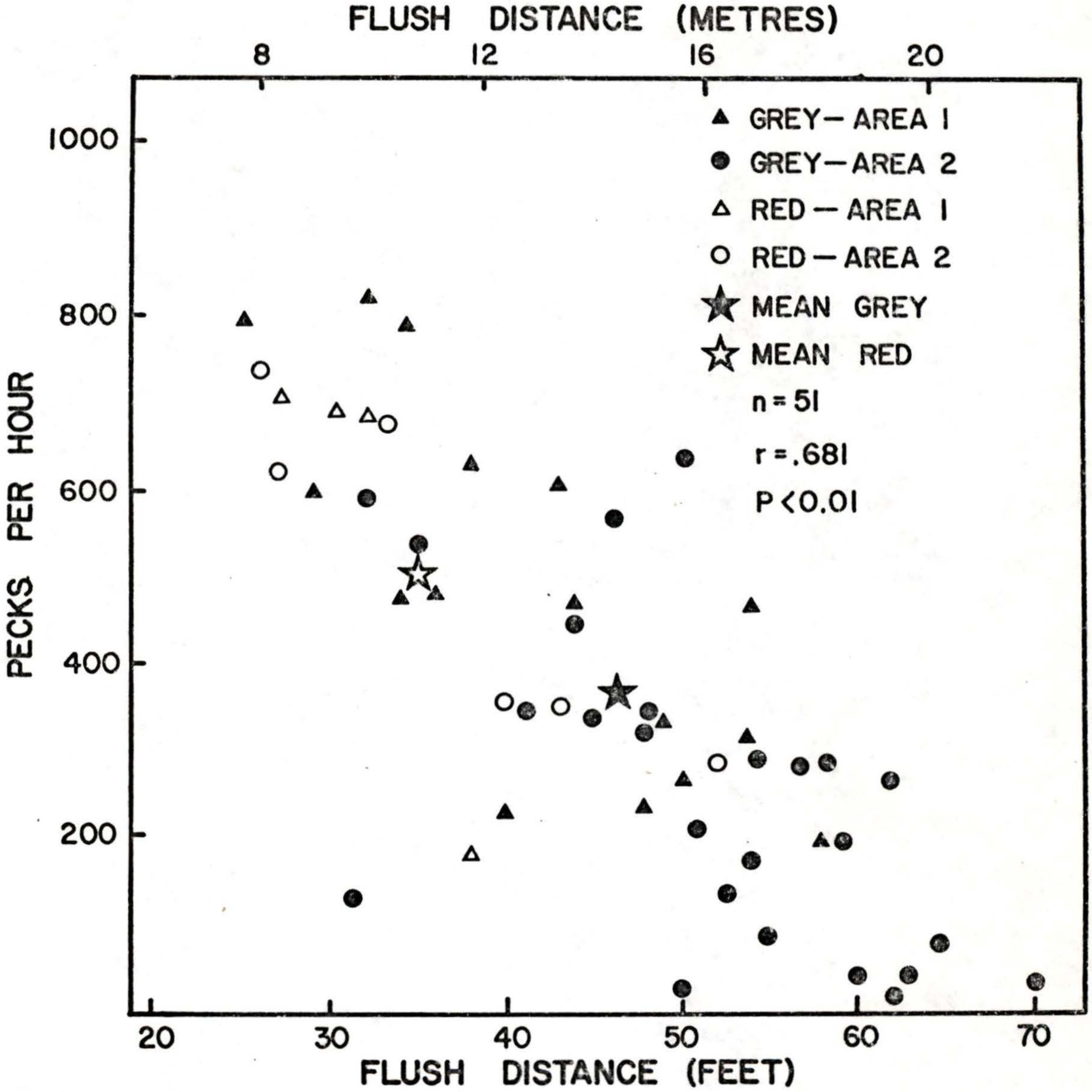

Fig. 14. The correlation between mirror test score (pecks/hour) and flush distances of territorial males on Area I and Area II. Data from 1970 and 1971 combined.

aspen dominated areas in greater numbers than expected based on total acreages of the two vegetation types ($P < 0.05$). Low score birds were distributed in both vegetation types close to expected numbers (Table 16). The basic assumption that grouse would be expected to occur in numbers proportional to the acreages of vegetation types is likely not valid, but the analysis does still suggest that distribution of low and high score birds was considerably different: more aggressive birds being found in the optimum habitat.

Brood defense behaviour of hens

Brood defense behaviour (Mossop, 1971) of hens was analyzed using the MANOVA program. The frequency of intensity of rushing, leading, and flushing behaviour of hens were the dependent variables. Month (June, July, August, and September) was the independent factor. There were significant differences in flushing and rushing (both $P < 0.05$) (Table 17). Hens with young broods more often rushed the observer, while hens with older broods more often flushed (Fig. 15). Red and grey hens differed in the amount of leading ($P < 0.10$) and the amount of flushing ($P < 0.05$). Grey phase hens flushed considerably more than red phase hens, especially in June; while reds attempted to lead observer away from broods more than greys. The two colour phases did not appear to differ in the amount of rushing behaviour exhibited except in June 1971, where reds rushed more than greys (Fig. 15).

Table 16. A comparison of the distribution of high and low score birds between aspen dominated stands and conifer stands. Area I and Area II males, 1970 and 1971, combined.

Habitat Types	Observed No. of Males with[a]		Expected No. of Males[b]
	High Mirror Score	Low Mirror Score	
Aspen stand and Aspen/conifer	21	14	15
Conifer stand	4	11	10
	25	25	25

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[a] 51 birds were tested. The 25 birds above the median were arbitrarily called high score birds and the 25 birds below the median were called low score birds.

[b] expected prorated on basis of 352 acres of aspen and aspen/conifer available (approx. 60 %) and 224 acres of conifer available (approx. 40 %).

Table 17. Probabilities of rushing, flushing and leading behaviour of hens encountered during June, July, August and September, 1970 and 1971 (derived from multivariate analysis of variance) showing effects of month, year and color phase.

	Dependent Variables		
Factor	Rushing	Flushing	Leading
Month[a]	0.001	0.010	0.617
Year	0.668	0.200	0.894
Color phase	0.122	0.023	0.059

[a] June, July, August and September.

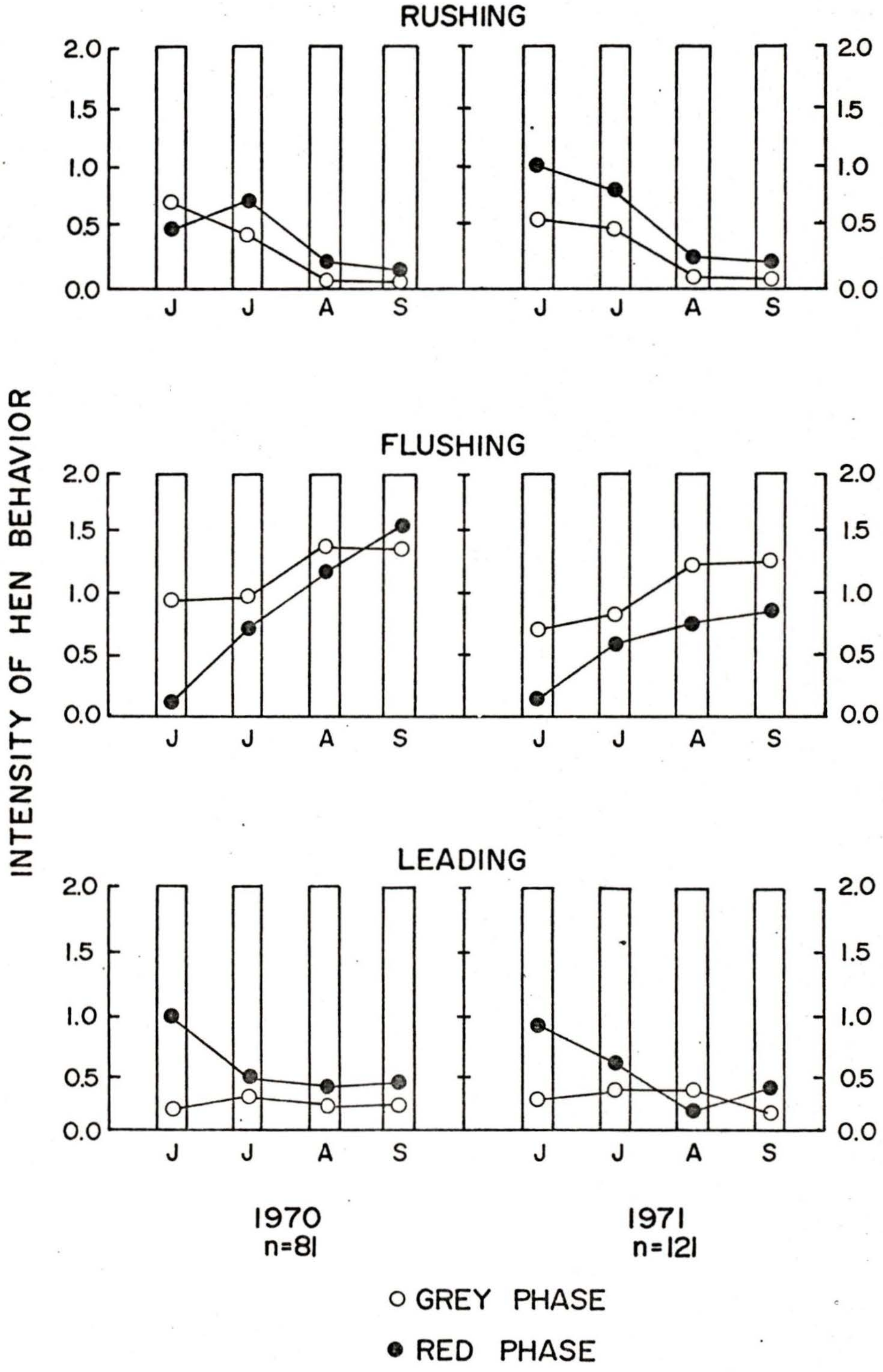

Fig. 15 A comparison of brood defense behaviour of hens between colour phases, months, and years.

DISCUSSION

The general conclusion drawn from this study is that the null hypothesis is not always true. Red and grey phases were found to differ in certain of their demographic and behaviour characteristics.

During this study the density of the breeding population increased 1968 to 1970 or 1971 and declined in 1972. The survival of red and grey phase males was similar. However, the percentage of red phase birds in the breeding population increased throughout the study suggesting that selection for red phase males was occuring. Chick production was lower in two late hatch years 1968 and 1971, than two years with an earlier hatch, 1969 and 1970. No correlation existed between spring densities and subsequent chick production. Further, there was no correlation between production in one year and the density of the breeding population the following spring. August brood survival was correlated with mean maximum June temperature. Mortality of red broods was higher than that of grey broods suggesting that chick viability was influenced by intrinsic qualities of hen. The kill analysis indicated that sex, age, and colour phase classes differed in vulnerability to hunting.

A comparison of three indices of behaviour (1) agonistic behaviour directed at mirror image (2) approachability or flushing distance, and (3) brood defence behaviour of hens suggested significant differences between behaviour of red and grey phases.

Red phase interacted more vigorously with their mirror image, were more approachable and defended their broods more vigorously than grey phase birds.

The grouse species involved in this study appears to be genetically polymorphic based on tail colour. This polymorphism occurs to some degree in all ruffed grouse populations in North America (Gullion and Marshall, 1968), and was reported as early as the 1800's (Bump _et al_. 1947). Such persistence in time and space indicates its stability. This stability enhances the value of these morphs as genetic markers.

The difference in population parameters between red and grey morphs observed during this study was not unexpected. Mayr (1963) points out that even seemingly insignificant genes (such as those affecting coat or plumage pigment) often effect other characteristics of great evolutionary importance such as longevity, sexual vigor, fertility, fecundity, and tolerance of environmental extremes. Some behaviour of individuals is genetically determined (Ford, 1964; Caspari, 1958). This being so a change in the frequency of the two colour morphs has the potential of being related to population change.

During this study the percentage of red phase birds increased. I had insufficient data to detect survival differences between red and grey phase males. I obtained some evidence of lower survival of chicks in broods with red hens, and fairly strong evidence of higher mortality of red phase juveniles to hunting. Gullion and Marshall (1968) found that red phase breeding males survived a significantly shorter time than grey phase breeders.

Further, they found that late summer to spring mortality of red juvenile males was much higher than that of grey juvenile males in most years. They attributed both of these to higher mortality of red phase birds relative to predation and a lower tolerance of the red phase to severe winters. I had no data to support or refute the latter idea but my behaviour studies of flushing distances suggest that reds being more approachable may be more vulnerable to predation.

Lower production was coincident with increase in red phase birds. The percentage of red males on logs increased 1970 to 1972 (Table 5) whereas production decreased 1969 to 1971 and 1972 (Table 3). My results suggest that low production was correlated with weather following the hatch. If red phase hens also increased as did the males, the increased number of red hens may have effected productivity levels. My data suggest that red phase hens were less successful in raising chicks, especially in years of poor weather (1971). Red phase hens exhibited more brood defence behaviour. Mossop (1971) found increased brood defence behaviour to be correlated with poor production in a declining population of blue grouse. I suspect that weather was the dominant factor although the increased presence of red hens may have increased the depressant effect of weather. Gullion (1970) found a series of years of low production both during and following an increase of red phase birds in the population but attributed the lower reproductive success to the severity of prior winter weather affecting the physiology of the parents which was reflected in lower nesting success and lower viability of young. He felt that red birds were intrinsically less viable in respect to cold winter weather; thus I assume red birds in my population would be more affected by severe weather conditions and this could be reflected in relative reproductive success of red and grey hens. Our ideas are not at odds, and differ only in that he does not consider behavioural influences between red and grey phases. Further, I do not have winter mortality data or winter weather data from the study areas and therefore cannot refute or support his ideas.

Apparently red phase birds have a higher mortality and raise fewer young than grey birds, yet in this study they increased in frequency when the population was at a high density. One explanation for this apparent paradox might be that red phase birds were more successful than grey phase birds in securing territories and possibly in attracting hens when densities were high.

Other work has shown that success in territorial competition and attraction of hens is contingent on aggression of contenders (Watson, 1964, 1967 a, b; Watson and Moss, 1970). My studies indicated that red phase males pecked and attacked the mirror image more often than grey phase males. These two actions have been interpreted as acts of direct aggression(Stirling, 1965; Mossop, 1971). Bump *et al*. (1947) described captive ruffed grouse displaying such behaviour as wing strikes, foot and bill slashing, jump-attacks, and hard pecks in grouse to grouse conflicts when hierarchies were being established. I have witnessed a few encounters between male grouse in my own field work. The most vigorous action seen was a rush and jump-attack. The action terminated with the other grouse retreating. The other encounters terminated before actual contact occured but still support the theory that aggressive tendencies determine the outcome of grouse-grouse conflicts.

The mean level of aggression was different on the two study areas. The most aggression was observed on Area I which had the lowest density and greatest distance between birds; thus the differences in aggression could not simply be a phenotypic response to increased density. The fact that red and grey phase grouse differed in mean aggression suggests that a component of the observed aggression was intrinsically determined.

Watson (1964, 1967 a, b) found, in Scottish red grouse, that aggressive males tended to obtain the best territories; had larger territories, and had more hens within these territories. In this study red phase males in Area I were more aggressive and the greater distance between territories occured on the low density area, Area I. In ruffed grouse, like red grouse, the most aggressive bird may have the largest territory.

Watson (1964, 1967 a, b) also suggested that the more aggressive individuals appeared to exclude less aggressive individuals from breeding by preventing them from obtaining territories, or by excluding them to marginal areas where presumeably they incurred high mortality, due to weather, predation, or starvation. In this study more of the aggressive birds were found in aspen dominated areas than in conifer areas than I predicted on the basis of available habitat types. Aspen is a preferred habitat compared to conifers (Gullion, 1970). This sequence is additional evidence that aggressive birds were more successful in establishing territories.

I suggest that the increase in red males and lower production of red hens may be related to Chitty's behavioural and genetic polymorphism theory (Chitty, 1967). He argued that as populations increase, mutual interference increases so that natural selection favors the more aggressive genotypes. Densities might decline if aggressive animals occupied more space, produced less viable young, and adversely affected the physiology of the docile animals (Chitty, 1967). The increase in red phase birds would produce more aggressive juveniles to enter the breeding population next spring. Such a system could lead to still more aggression. This could possibly bring about greater spacing of territories and decreased density of breeders. Further, since reds produce fewer chicks, the population would decrease in abundance. Although my study does not cover a period of low population density, it is possible that at low density territorial competition is not severe; thus the more viable grey birds would have a selective advantage. Grey hens would produce more chicks and the population would expand. Gullion and Marshall (1968) found that red phase birds were low during the beginning of a population increase. Chitty (1967) includes such a switchover in selective advantage of genotypes depending upon the trend of the population - increasing or decreasing. Such a switchover may help explain the stability of the polymorphism.

Major theories of ruffed grouse population regulation dwell on extrinsic mortality factors such as predation and weather (Gullion, 1970; Rusch and Keith, 1971). Gullion's studies strongly suggest that red birds are less viable in respect to winter weather.

Lower viability to weather extremes is also suggested by clinal geographic distribution of the two colour phases. Red phase birds are more prevalent in areas of milder climate (Gullion and Marshall, 1968; Gullion, 1970; Aldrich and Friedmann, 1943; Ridgeway and Friedman, 1946; Weeden, 1965). Gullion (1964) suggested that red males possibly suffer higher predation loss; Rusch and Keith (1971) suggest predation as the dominant factor causing grouse mortality. I suspect that these theories that suggest weather or predation as causing population declines could possibly be mistaking the accontuated effects of regular population loss due to high numbers of red phase birds or progeny - mistaking effect for cause. This hypothesis needs testing.

In summary I conclude that red and grey phase ruffed grouse differ intrinsically in survival and behavioural parameters which can potentially be related to population fluctuations and population regulation. This hypothesis can be disproven if future studies show (1) that the red and grey colour phases do not have a genetic basis and (2) that these two colour phases do not differ in behaviour and demographic characteristics.

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APPENDIX I. Observation card.

CARD # ______

Date __________ Time __________ Observer ___________

Weather ____

Species ______ Bird: M,S,H,Brood : Trapped, Flushed.

Phase __________ Tail Band __________ Leg Bands ____

Flushing distance from: Obs. ________ Dog __________

Direction travelled by: Obs. ________ Dog __________

Direction flushed _________ Distance flushed _______

Trapped Male: wt _______ Age ________ Bands ________

Broods: #chicks _____ Age _____ definite, indefinite

Behav: before flush _________________________________

____

: after ____

____

Cover and location : on back

Legend:

Species	ruffed, spruce, or sharp-tailed grouse
M	male
S	single (sex unknown)
H	hen
Phase	red or grey phase ruffed grouse
Tail band	plastic band on tail (present)
Leg band	plastic or metal band (present)
Obs.	name of observer
Definite, indefinite	complete or incomplete brood count

APPENDIX II. Method of mirror testing males.

The following procedure was followed when testing males in the mirror test situation:

1. Drumming logs of all males to be tested were located prior to being tested. My field observation in other years indicated that males were faithful to particular logs. Also, they usually displayed from a particular spot on the log (termed a drumming platform or stage). This spot could be ascertained by accumulations of droppings and worn spots on the log.

2. In the evening (2000-2200 hours), one mirror (9 x 12 inches) was placed upright, on the short edge, approximately 4 feet from the drumming stage. The mirror was supported by a rough frame constructed from nylon fish line and branches (Fig. A2-1). The mirror was covered completely with a cover constructed of fir branches. A nylon line was attached to the mirror cover and run to a blind set up approximately 40 to 60 yards from the drumming log. The blind was constructed of sacking and rope supports and camouflaged with vegetation taken from the immediate area.

I arranged the mirror in the evening because my experience in trapping birds with mirror traps had shown that the best and most consistent trapping success was obtained if the trap was set up in the evening. Males, if flushed in the evening, returned to their logs sometime before dawn and were subsequently trapped. Apparently, they did not notice the trap till daylight. Setting traps up during the day gave poor results; apparently birds were reluctant to return to log during the day if a trap was present.

3. The following morning (0400-0700) I entered the blind taking care not to disturb male on the drumming log (I kept the blind between the bird and myself to avoid bird sighting me).

4. Prior to test, I recorded wind speed and direction, temperature, and precipitation falling.

5. After remaining quiet for 10 minutes, I removed the mirror cover (via string from blind to cover).

6. Tests commenced when the cover was removed (all males noticed the mirror or the cover motion immediately). I then dictated a continuous recording of all behaviour (see Appendix 4 for interpertation of behaviour). A 'Phillips' portable cassette recorder was used.

7. Tests were terminated after 1/2 hour. I then flushed the bird and dismantled the apparatus. I was able to test 2 to 4 birds per morning.

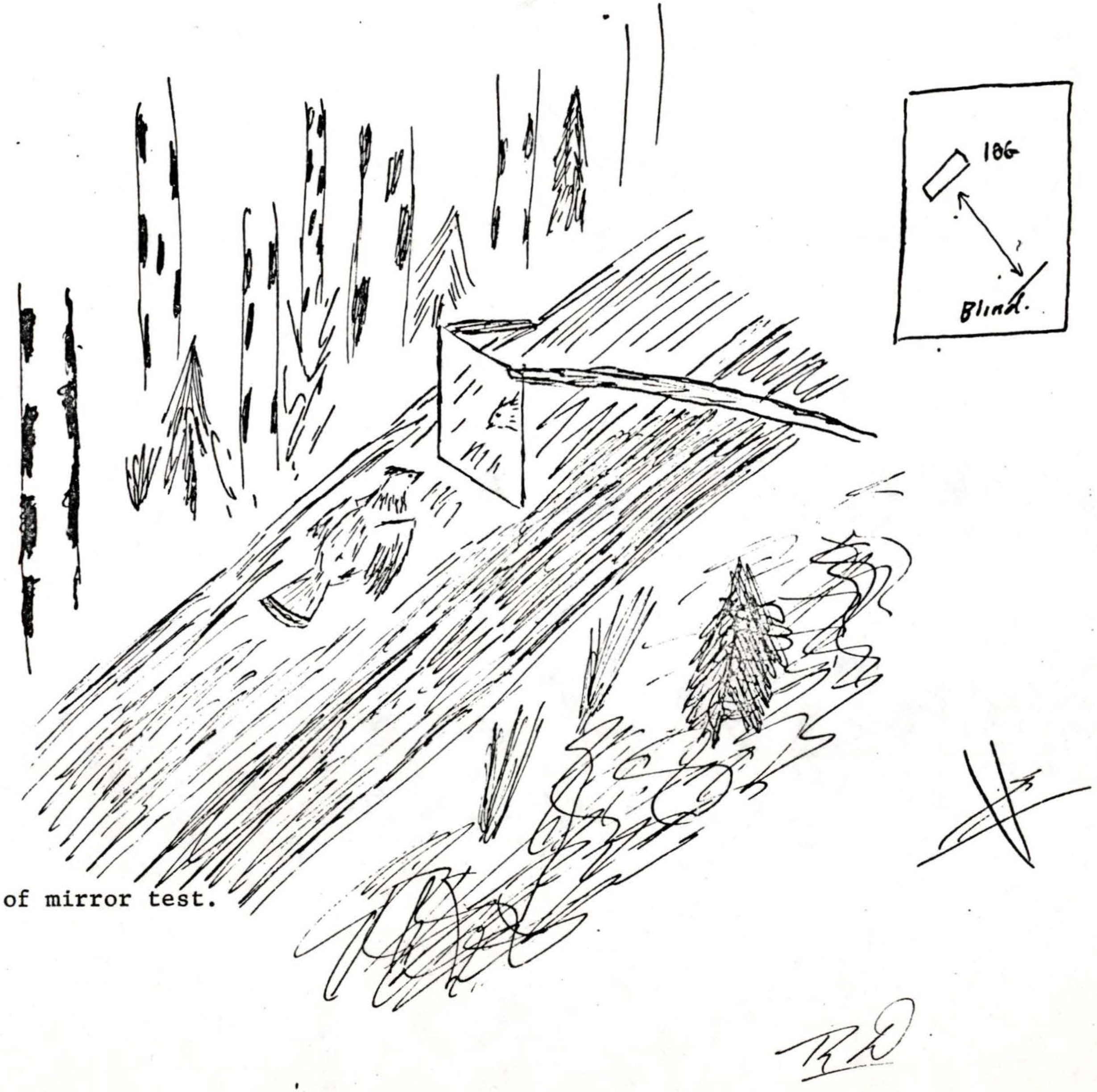


Fig. A2-1. Rough sketch of mirror test.

APPENDIX III. Repeat tests on same male.

Prior to the main analysis of the response of males to the mirror, I evaluated whether the agonistic scores of birds were consistent with time by repeat observations of individual birds within years (Table A3-1), and between years (Table A3-2). The two way anova of repeat observations on individual birds within the same year (Table A3-3) indicated that pecks per hour ratings were consistent between days ($F = 1.448$, 5 df, $P > 0.25$). Attacks per hour were consistent between days ($F = 1.106$, 5 df, $P > 0.40$). However, the analysis also suggested that attacks per hour were not significantly different between birds ($P < 0.10$). Thus, the use of the latter indice was questioned. Attacks per hour and pecks per hour were significantly correlated ($r = 0.687$, $P < 0.05$) (Fig. A3-1), thus I feel that both ratings are valid but pecks per hour is the more useful index.

A similar two way anova of repeat observations on individual birds over two years indicated that pecks per hour ratings were consistent between years for the same bird ($F = 0.194$, 3 df). Thus in main analysis the rating of a bird was based on his mean score averaged for the two years.

In addition, I compared pecks per hour before and after a bird was trapped to evaluate effects of trapping. Trapping did not significantly effect scores ($t = 0.158$, 50 df, $P < 0.70$).

Table A3-1. Six repeat tests on 5 males. All tests conducted in same month.

		Days					
Bird #	Behaviour	1	2	3	4	5	6
1	Pecks/hr	178	171	186	180	161	177
	Attacks/hr	2	1	1	3	1	1
33	Pecks/hr	308	352	301	312	306	282
	Attacks/hr	1	3	3	2	1	4
24	Pecks/hr	617	629	616	600	564	601
	Attacks/hr	4	6	2	4	2	5
2	Pecks/hr	304	316	281	300	308	284
	Attacks/hr	3	1	3	2	2	3
5	Pecks/hr	381	364	398	351	359	372
	Attacks/hr	3	6	4	2	4	3

Table A3-2. Repeat tests of four males in two years.

	Male Number	1970 Pecks per hr	1970 Attacks per hr	1971 Pecks per hr	1971 Attacks per hr
Area I	5	722	8	697	6
	8	317	6	276	2
Area II	11	187	5	211	2
	1	331	7	351	3

Table A3-3. Analysis of variance of <u>pecks/hr</u> scores obtained from repeat observations of individuals within same year.

Source of variation	df	MS	F	P less than
Male	4	134704.500	757.224	0.001
Days	5	257.600	1.440	0.250
Error	19	177.900		

Table A3-4. Analysis of variance of attacks/hr scores obtained from repeat observations of individuals within same year.

Sou4ce of Variation	df	MS	F	P less than
Male	4	5.292	3.226	0.100
Days	5	1.813	1.106	0.400
Error	19	1.643		

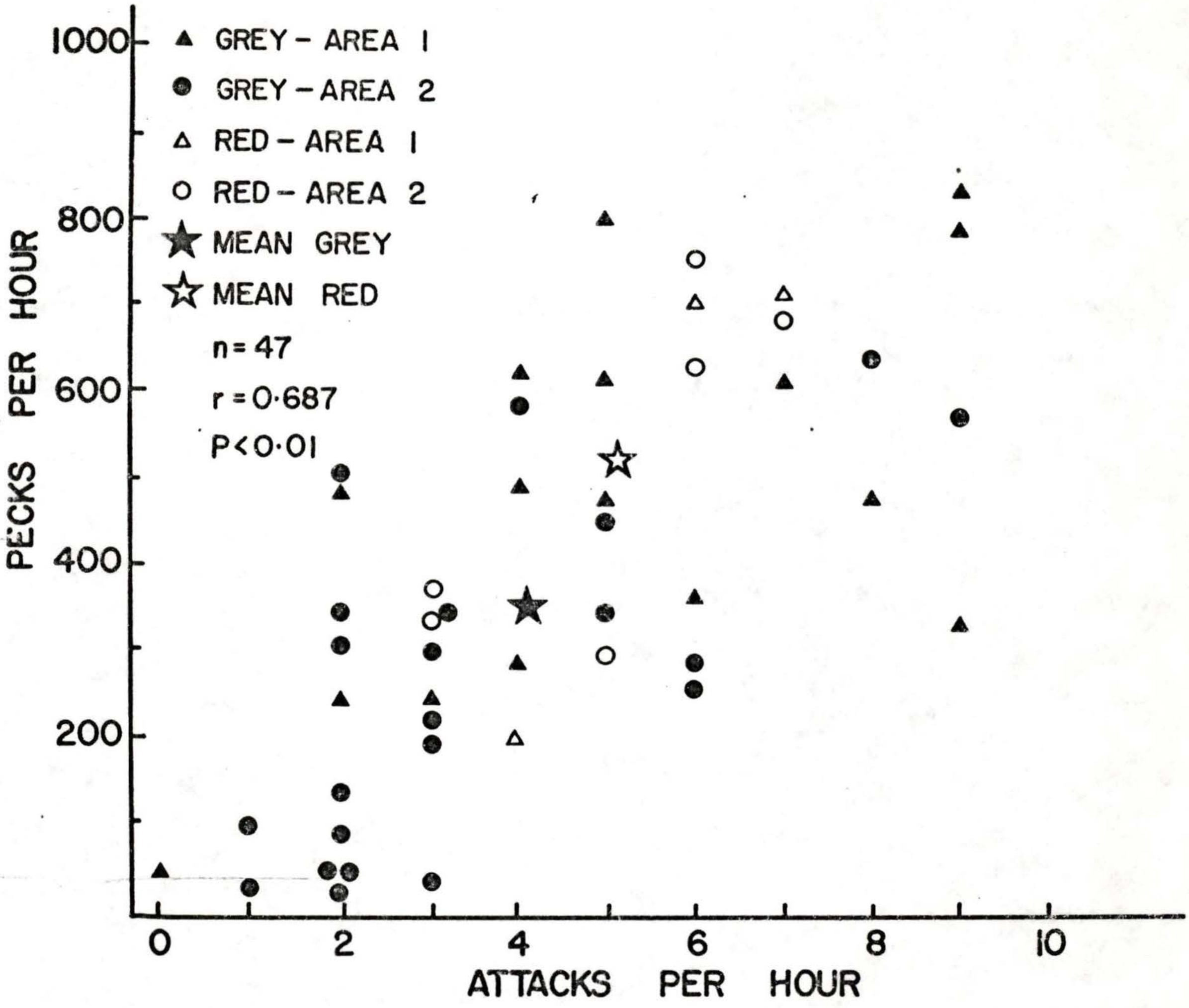


Fig. A3-1. The correlation between two mirror test scores, attacks per hour and pecks per hour. 1970 and 1971 data combined.

APPENDIX IV. Interpretation of mirror tests.

During tests all behaviour of male grouse was noted (see Aubin, 1970, for comprehensive descriptions of male ruffed grouse behaviour). To avoid situations where subjective decisions on interpretation or rating of intensity of behaviour were required (Aubin's study had not been completed when this study was started) only discrete "aggressive" acts were used to rate birds. The two most intensive actions, hard pecks and jump-attacks were used. These two actions could be easily counted and have been interpreted as acts of direct aggression by several authors (Stirling 1965; Mossop, 1971; and Theberge, 1971). These acts have also been observed both in the aviary and the field in grouse-grouse encounters (Bump _et al._, 1947). Thus the agonistic score of male grouse was determined solely on basis of number of pecks and attacks directed at mirror image per hour.

The interpretations of the mirror test results could possibly be questioned on the basis that they are an artifact. The mirror test situation was not similar to grouse-grouse encounters in several respects - the opposing movements in the mirror and the edges of the mirror where an image could not be seen. Further, I am not certain as to whether the grouse were aware of my prescence in the blind.

Such arguements can be levelled at any studies where mirrors or models are presented to animals (Lisman, 1932; McBride, 1958; Tinbergen, 1951, 1959). These authors felt that conclusions they drew from test situations would hold true in real situations. Theberge (1971) used mirrors to test ptarmigan chicks and concluded that the method was reliable to measure aggressive tendencies and possibly simulate actual chick to chick encounters.

The grouse in my study definitely appeared to be directing their actions at the mirror image and were not simply "attacking or exploring" a foreign object. I feel this conclusion is justified for the following reasons: (1) Males in this study hit the mirror forcibly, sometimes bloodying their beaks. This suggests that the grouse were aiming beyond the face of the mirror - at their mirror image (Dr. C. W. Tolman, University of Victoria, pers. comm.). If the pecking motions were simply ingestive or exploratory they would have been more precise and well aimed, and forward motion would likely have stopped at the point aimed at. (2) Many males literally wore grooves in the rotten wood of some drumming logs, by going behind the mirror and returning to the front again to attack image. Moving in a partial circle around an intruding grouse is a common action of territorial males (Aubin, 1970). (3) When a mirror was presented backwards with the brown backing facing the drumming stage, the bird left the log when sighting it. This appears to be analagous to mirror trapping where the tin trap door and fresh wood on traps had to be camouflaged to obtain good trap success. Uncamouflaged traps were often avoided by males.

APPENDIX V. Vegetation characteristics of the study areas.

Introduction

The ruffed grouse population studies at Watch Lake were carried out on two separate study areas. Gullion and Marshall (1968) found grouse abundance, distribution, and survival to be strongly influenced by vegetation characteristics. The two study areas were intended to be used as replicate areas; thus, I thought it necessary to compare general vegetation characteristics of these two areas.

None of the vegetation classifications for the central interior of British Columbia by Halliday (1937), Krajina (1965), or Beil (1969) were suitable. These classifications proved to be far too general, i.e., the major portion of both study areas would fall into the Pseudotsuga menziessii Calamagrostis association (Beil, 1969). Further, forestry classifications were useful only for dominant tree cover.

A classification, to be relavent to the grouse study, had to give some indication of vegetation parameters important to grouse survival. These are (1) prevalence of aspen (tree species composition), (2) availability of drumming sites and roosting cover (understory species composition and density), (3) brood cover and food availability (herbaceous vegetation species and density), and predator protection (tree species composition, density, and edge cover). The classification presented in this study has been developed with these factors in mind. Further, it must be stressed that the classification was developed solely to outline major vegetation differences between areas, and to serve as a guide in delineating grouse distribution. The study should not be construed as a detailed vegetation analysis, despite the fact that typical forestry procedures are used throughout.

Methods

Delineation of basic cover types was based on aerial photos (1:5000), forestry cover maps, ground surveys, plus an intimate knowledge of the two study areas gained by working on areas in four years (1969 to 1972). Within all cover types the dominant and subdominant trees of each stand were assessed for percent canopy coverage, density, height, d.b.h., age, and basal area. Also, in all stands general notes on shrub and ground vegetation, topographic features such as slope and exposure, moisture regime, and cattle and logging disturbance were taken. Two types of cover maps were compiled. The first was simply dominant tree cover. The second was an expansion of this to include general assessments of age, height, density, species composition, and shrub and ground cover of stands. Acreages of vegetation types were derived from these maps using a dot-grid overlay. Edge cover was measured with a planimeter.

In addition, I had originally intended to obtain indices of site quality and productivity within Douglas fir, spruce, aspen, and pine cover types. Selective logging of fir areas in the 1950's, and the small area of spruce precluded use of these two types. Aspen was also excluded. Unreliable and time consuming sampling methods caused by clonal distribution and variation (Barnes, 1966; Zahner and Crawford, 1966; Maini and Coupland, 1964) plus lack of adequate forestry yield tables for use with aspen negated sampling of this species. Finally, pine stands were sampled to obtain site indices of quality and productivity. All trees within 1/10 acre plots were measured for height, d.b.h. and age. From these data Average D.B.H., total basal area, average height of stand, and average height of dominants and codominants were obtained using procedures outlined by Illingworth (1958). Site index was derived from B. C. Forest Service Yield Tables (1947). Total Volume of mean tree species was obtained from the B. C. Forest Service, surveys and Inventories Division-Interim Standard Cubic Foot Volume Tables. The resulting stand parameters from the plots (expanded to 100 acre basis) were used to estimate site quality and productivity by comparison with site criteria developed by Illingworth (1958).

Results and Discussion

Dominant tree cover, synthesized classification of cover types, calculated acreages of vegetation types, assessment of edge cover, and summaries of pine site data are presented in Figures A5-1 to A5-4, and Tables A5-1 to A5-6 (pages 81 to 99).

General vegetation differences between the two study areas are: (1) a predominance of pure stands (one tree species composes greater than 75 percent of stand) on Area I and a predominance of mixed stands (all species less than 75 percent of stand) on Area II, (2) a greater amount of aspen dominated stands on Area II and conversely a greater amount of conifer dominated stands on Area I, (3) a greater amount of spruce on Area II both in understory and in tree canopy, (4) more lush herbaceous growth and denser stands on Area II, and (5) a greater prevalence of both lowland Aspen-Salix and open types on Area I.

An assessment of the vegetation maps compiled from stand analysis suggested that most of these area vegetation differences could be accounted for by differences in succession, possibly site quality differences, plus influences of topography and various forms of disturbance.

Succession was more advanced on Area II. Aspen stands were approximately 100 plus years of age and pine stands approximtely 80 years of age on Area II. On Area I these two types were approximately 75 and 45 years of age. This probably accounts for the area discrepancy between amounts of pure and mixed stands. Many trees of a particular species present in the understory on Area I formed part of the upper canopy on Area II. More advanced succession could, also, partially account for the prevalence of spruce on Area II. Spruce is more shade tolerant than either fir or pine and tends to dominate understory in older stands.

Site quality appeared to be higher on Area II. High incidence of aspen with spruce is indicative of moist conditions (Beil, 1969). The greater amount of closed canopy aspen, high density understory, and lush herbaceous growth on Area II suggest that this area was the richer site. Site data obtained from pine stand sampling was not sufficient to warrant statistical treatment. Site index values tended to be higher on Area II, but other stand parameters when compared to site criteria outlined by Illingworth (1958) were not sufficiently different to separate Area I and Area II pine stands on the basis of site quality.

The greater amount of lowland Aspen-Salix vegetation type on Area I was likely due to the topography of this area. The south-east corner of Area I was flat and transected by a swamp area. The Aspen-Salix type was largely confined to this corner. All but a few acres of Area II was within a slope area thus suitable soil and moisture conditions were likely not available for growth of this vegetation type.

The influence of selective logging for Douglas fir was roughly comparable on both areas as indicated by similar amounts of fir and pine regeneration. Cattle grazing effects were very noticeable on Area I. The south half of this area was grazed moderately to intensively each summer (10 to 20 head of cattle on 135 acres). Grazing tends to suppress herbaceous growth and sometimes results in a reversal of herb succession (Krajina, 1965). Further, grazing tends to keep stands more open. Thus some of the area differences in density of herbaceous vegetation and amount of open areas indicated by vegetation maps were likely maintained by this grazing.

Edge cover assessments indicated that amount and type of edge situations on both areas were similar. This was surprising considering the differences in area vegetation. This suggests that although actual acreages of vegetation types were different on the two areas, the distribution and shapes of these types was such, that similar lengths of vegetation type interfaces were found between areas.

Conclusions

Although the study was general and results nonspecific, I feel evidence was sufficient to warrant conclusion that Area I and Area II should not be considered replicate study areas. Basic differences in vegetation characteristics should be included in evaluation of parameters of grouse populations on these two study areas.

Fig. Fig. A5-1 . Dominant tree cover on Area II.

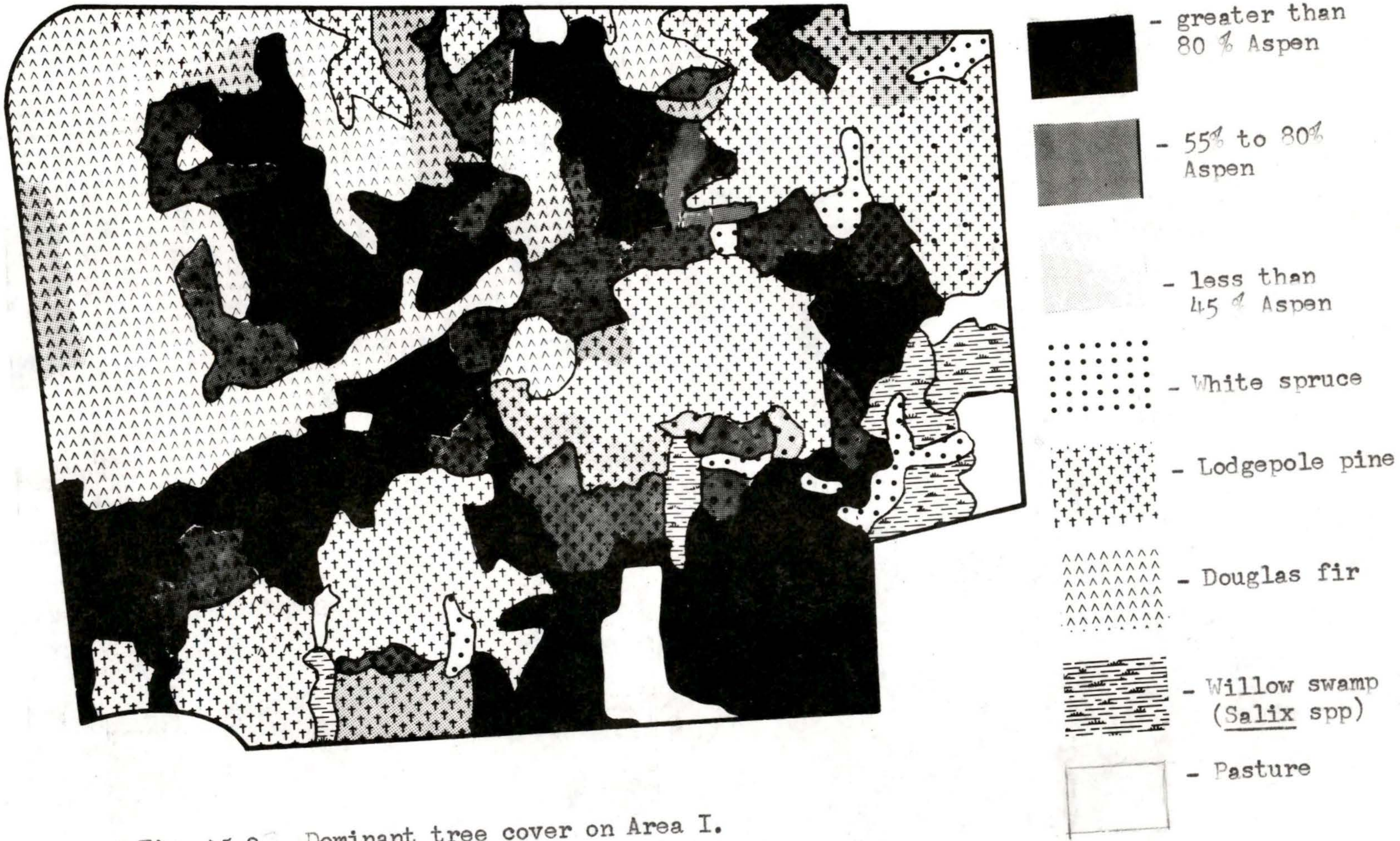


Fig. A5-2. Dominant tree cover on Area I.

Table A5-1 A comparison of the acreages of dominant tree cover between Area I and Area II, based on Fig. A5-1 and Fig. A5-2

Dominant Tree Cover	Area I Acres	Area I % of Total	Area II Acres	Area II % of Total
Aspen	81.72	30.26 %	60.18	18.13 %
Aspen/pine	17.18	6.36	56.63	17.07
Aspen/fir	16.32	6.04	31.83	9.68
Aspen/spruce	4.79	1.77	18.75	5.65
Subtotal	120.01	44.43 %	168.69	50.53 %
Pine	41.97	15.49	12.49	3.76
Pine/aspen	13.87	5.14	22.03	6.64
Pine/fir	9.89	3.66	15.40	4.64
Pine/spruce	10.40	3.85	16.42	4.95
Subtotal	76.13	28.14 %	66.34	19.99 %

(continued)

Table A5-**1** (continued)

	Area I		Area II	
Dominant Tree Cover	Acres	% of Total	Acres	% of Total
Fir	39.06	14.41 %	48.45	14.59 %
Fir/aspen	9.13	3.38	18.41	5.55
Fir/pine	2.86	1.06	9.69	2.92
Subtotal	52.05	18.85 %	76.55	23.06 %
Spruce	5.92	2.19	11.22	3.38
Spruce/pine	0.61	0.23	0.00	0.00
Spruce/aspen	0.00	0.00	1.00	0.36
Subtotal	6.53	2.42 %	12.22	3.74 %
Open areas	9.53	3.52	1.50	0.48
Salix areas	7.14	2.64	7.30	2.20
Totals	270.39	100.00 %	331.60	100.00 %

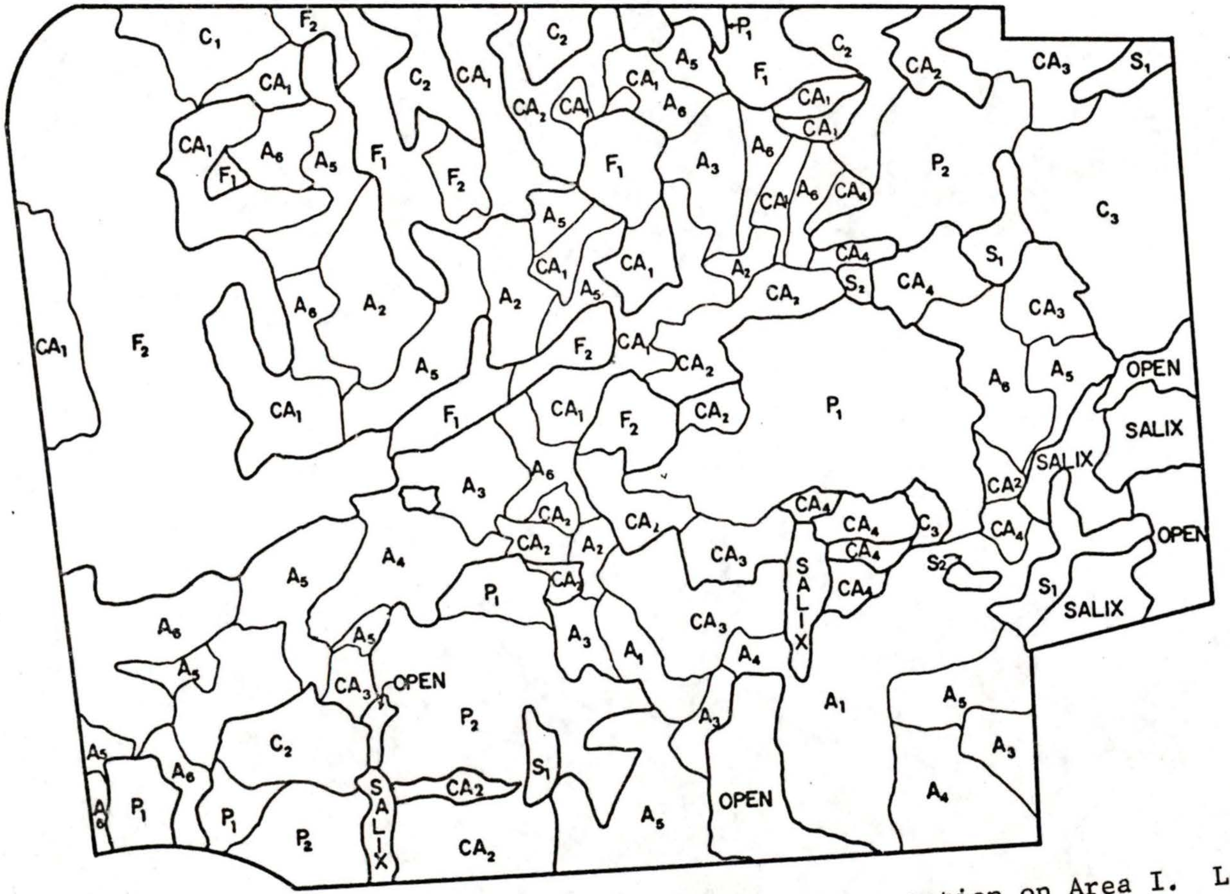
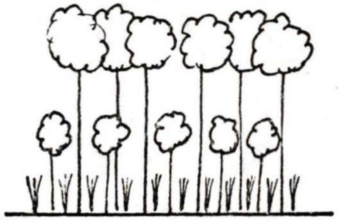
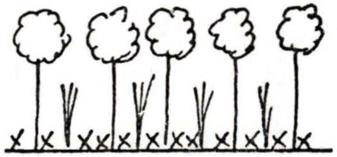
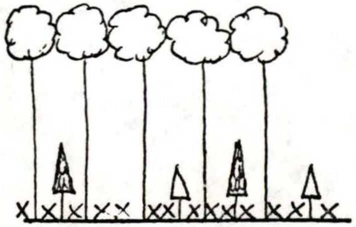
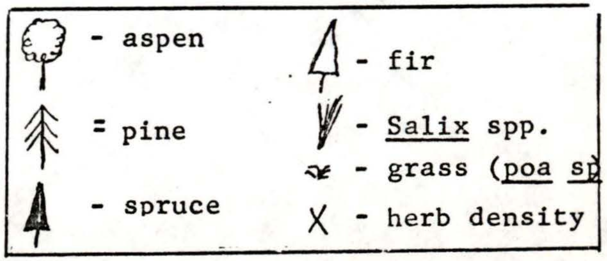
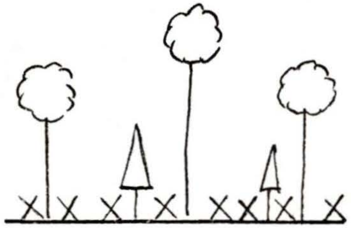


Fig. A2-3. Synthesized classification of Vegetation on Area I. Legend pp. 87-93.

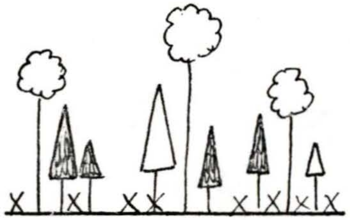
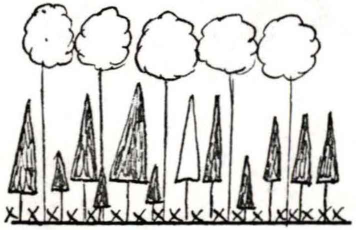
Fig. A-2-4. Synthesized classification of vegetation for Area II. Legend pp. 87-93.

No.	Stand Type	Description	Canopy Coverage	Tree Height	Moisture Regime
ASPEN - BRUSH UNDERSTORY					
A_1	Lowland aspen/salix 	Dense aspen, vigorous understory of salix and aspen saplings. Few conifers present in understory. Occurs in swamp or seepage areas.	75 - 100 %	to 70 ft.	moist-wet
A_2	Upland aspen/salix 	Medium density aspen, understory of salix clumps and dense rose. Some conifers present. Occurs in seepage gullies. Differentiated from A_1 by poorer growth of aspen, less dense understory.	50 - 75 %	to 50 ft.	moist
A_3	Aspen/calamagrostis closed canopy 	Fairly dense aspen, a few conifers present in understory. Lush herbaceous and shrub growth dominated by pine grass and rose. Fireweed and/or solidago reach high dominance.	75 - 100 %	to 80 ft.	mesic to moist

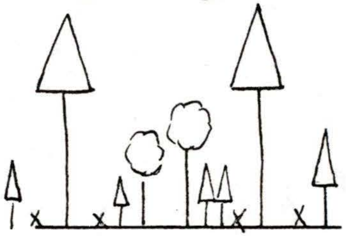
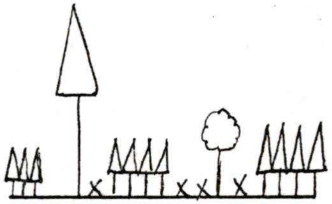


A_4	Aspen/calamagrostis 	Open aspen, a few conifers present. Ground cover less dense than A_3, but dominated by same species. Differentiated from A_3 by lower density aspen, sparser understory.	25 - 50 %	to 80 ft.	mesic

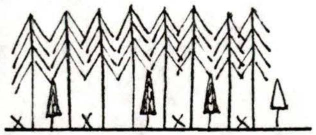
ASPEN - CONIFER UNDERSTORY

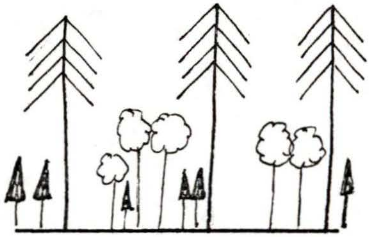
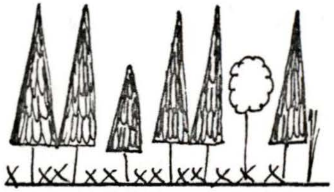
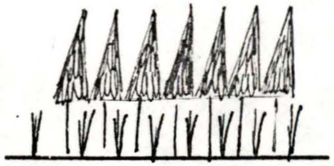
A_5	Aspen - open canopy Conifer understory 	Essentially A_4, with conifer understory. Medium age, to mature, low density aspen. Rose and pine grass dominate ground cover. Tree understory, second growth aspen and conifers of low to medium density.	25 - 50 %	to 80 ft.	mesic
A_6	Aspen - closed canopy Conifer understory 	Essentially A_3, with understory of medium to high density conifers. Spruce prevalent. Herbaceous growth dense - same species as A_3.	75 - 100 %	to 80 ft.	mesic to moist

DOUGLAS FIR STANDS

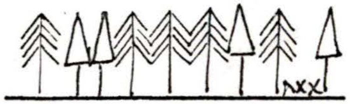
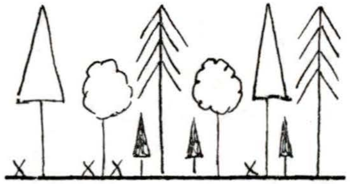
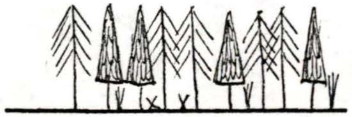
F_1	Mature Douglas fir 	Large Douglas fir trees, open understory of Douglas fir regen. and sporadic aspen. Ground cover sparse, mostly pine grass. Occurs on ridges, in small areas left by logging outfits.	10 - 25 %	to 120 ft.	dry-mesic
F_2	Douglas fir regen. 	Dense fir occuring in continuous or "thicket-opening" type of cover, on areas selectively logged. A few large seed trees usually present. Ground cover fir needle litter with pine grass, rose, sheperdia, and aspen in openings.	25 - 100 %	to 40 ft.	dry-mesic

LODGEPOLE PINE STANDS

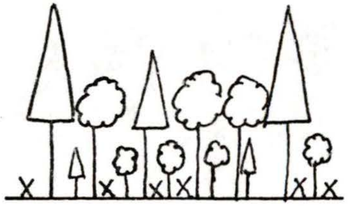
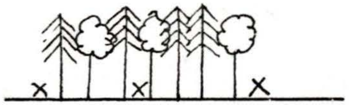
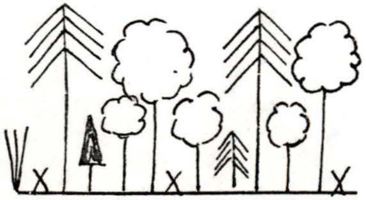
P_1	Pine regeneration 	Dense stand of usually one-age pine. Understory contains fir, or spruce, and aspen. Sheperdia prevalent. Ground cover pine grass with some arcto-staphylos. Stands tend to open up with maturity, conifers and aspen become more prevalent. Occurs on mesic sites - usually established by fire.	50 - 100 %	to 50 ft.	mesic

P_2	Mature pine 	Fairly open mature pine, light density conifer understory plus young aspen clones. Pine grass ground cover.	25 - 50 %	to 80 ft.	mesic
SPRUCE STANDS					
S_1	Lowland spruce 	Dense to medium density spruce, few aspen present. Understory pine grass plus vigorous epilobium and/or solidago with rose. Clumps of salix present in some areas. Usually occurs in depressions and cold air drainage areas, especially in close proximity to swamp areas.	25 - 100 %	to 80 ft.	moist-wet
S_2	Swamp spruce 	Dense spruce only tree species present. Understory varies from sparse to vigorous salix. Ground cover mosses and esquisetum. Occurs in seepage areas and flooded areas.	50 - 100 %	to 80 ft.	wet

MIXED CONIFERS

C_1	Pine/fir regeneration 	Dense fir and pine mixture - continuous to patch cover. Very little shrub or ground cover except in openings where rose and pine grass dominate. Usually occurs on areas selectively logged or burned.	50 - 75 %	to 30 ft.	mesic
C_2	Pine/fir 	Any medium age to mature mixture of pine and fir if neither species composes better than 75 % of stand. Understory variable mixture of aspen and conifers. Ground cover is pine grass.	25 - 50 %	to 80 ft.	mesic
C_3	Pine/spruce 	Dense pine spruce mixture occuring in cold air drainage areas, seepage flats, usually on areas disturbed by pole cutting or logging. Aspen present in all tree layers. Understory and ground cover varies from litter in dense stands, to salix in wet areas, to pine grass and rose in drier areas.	50 - 100 %	variable	fresh to moist

ASPEN - CONIFER MIXTURES

CA_1	Fir/aspen 	Variable mixture of fir and aspen occuring either as mosaic of aspen and fir clumps or clones of aspen in fir area. All gradations occur. Stands single to mixed ages. Understory fir and aspen saplings. Ground cover variable, pine grass and rose dominate. Solidago and/or epilobium prevalent in aspen clumps.	variable	variable	mesic
CA_2	Immature pine/aspen 	Dense pine and aspen mix-even age. Calamagrostis understory. Usually established by burning.	75 - 100 %	to 40 ft.	mesic
CA_3	Mature pine/aspen 	Open pine/aspen mixture. Occurs where pine has overtaken aspen in height growth. Either mosaic or aspen clump type of distribution. Understory conifers and aspen plus salix. Pine grass dominant ground cover.	25 - 50 %	to 80 ft.	mesic

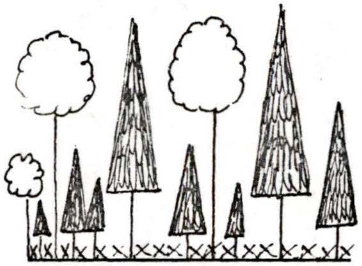
CA$_4$	Aspen/spruce 	Old age aspen stand in which spruce understory has reached top tree layer to produce heterogeneous mixture of aspen and spruce. Ground cover and understory similar to closed canopy aspen with much higher density of conifers in understory.	50 - 100 %	to 100 ft.	moist
SALIX		Swamp areas - used for any extensive areas of either salix varieties, and salix/swamp-birch mosaics. Ground cover usually sedges.			
OPEN		Grazing areas predominately grass.			

Table A5-2. A comparison of acreages and percent of area covered of vegetation types between Areas I and II, based on Fig. A2-3, and Fig. A2-4 (cover maps of synthesized classification).

		Area I		Area II	
Code	Vegetation Type	Acres	% of Total	Acres	% of Total
A_1	Lowland aspen/salix	11.95	4.43 %	0.85	0.26 %
A_2	Upland aspen/salix	7.76	2.87	1.29	0.38
A_3	Aspen/calamagrostis closed canopy	7.33	2.71	10.33	2.91
A_4	Aspen/calamagrostis open canopy	9.26	3.43	1.07	0.34
A_5	Aspen/conifer understory closed canopy	26.67	10.24	8.74	2.61
A_6	Aspen/conifer understory open canopy	17.75	6.58	37.90	11.52
F_1	Douglas fir - mature	8.96	3.31	4.60	1.29
F_2	Douglas fir - regeneration	30.10	11.10	43.85	13.16
P_1	Lodgepole pine - regeneration	20.51	5.57	11.39	3.57
P_2	Lodgepole pine - mature	21.46	7.92	1.10	0.35

Table A5-2 (continued)

Code	Vegetation Type	Area I Acres	Area I % of Total	Area II Acres	Area II % of Total
S_1	Lowland spruce	4.49	1.66 %	5.25	1.55 %
S_2	Spruce swamp	1.43	0.53	5.97	1.80
C_1	Pine/fir - regeneration	2.85	1.06	8.14	2.49
C_2	Pine/fir - mature	9.90	3.66	16.95	5.19
C_3	Pine/spruce	11.01	4.08	16.42	4.95
CA_1	Fir/aspen	25.46	9.42	50.24	15.04
CA_2	Pine/aspen - immature	15.02	5.56	1.14	0.34
CA_3	Pine/aspen - mature	16.03	5.94	78.82	23.75
CA_4	Aspen/spruce	4.79	1.77	18.75	5.75
Salix	Salix varieties	7.14	2.64	7.30	2.20
Open	Pasture and openings	9.53	3.52	1.50	0.45
Totals		270.39	100.00 %	331.60	100.00 %

Table A5-3. Summary of selected vegetation types, areas and percentages of Area I and II.

	Area I		Area II	
General Type	Acres	% of Area	Acres	% of Area
Aspen with brush understory	36.30	13.4 %	13.54	3.9 %
Aspen with conifer understory	45.42	16.8	46.64	14.1
Total Aspen	81.72	30.3	60.18	18.0
Aspen/conifer mixs	61.30	22.6	148.95	45.1
Aspen with open canopy	44.69	16.5	11.10	3.4
Aspen with closed canopy	37.03	13.7	49.08	14.7
Conifer stands (total)	110.71	40.8	113.67	34.4
Spruce mixs	21.72	8.0	43.39	13.0

Table A5-4. Assessment of edge cover on Area II and I.

Edge between:	Area I Miles	 % of Total	Area II Miles	 % of Total
Aspen and road or open	1.28	11.0 %	1.21	10.2 %
Conifers and road or open	1.37	11.7	2.19	18.5
Aspen/conifer and road or open	0.96	8.2	0.74	6.3
Aspen and salix swamp	0.03	0.3	0.20	1.7
Conifer and salix swamp	0.16	1.4	0.33	2.7
Aspen/conifer and salix swamp	0.28	2.4	0.15	1.5
Aspen and conifer	1.67	14.3	2.20	18.5
Aspen/conifer and aspen	2.50	21.4	2.07	17.5
Aspen/conifer and conifer	3.42	29.3	2.73	23.1
Totals	11.67	100.0 %	11.82	100.0 %

Table A5-5. Summary of pine stand data for Area I.

Plot No.	Species	Age Yrs.	Stems #	Av. DBH	Av. Ht.	Av. Ht. Dom.	BA	Total Vol.	Site Index
I-1	Pl	44	1246	4.2	41 ft.	44 ft.	124.6	2664	65
I-2	Pl	43	1320	4.1	40 ft.	44 ft.	119.0	2522	65
I-3	Pl	44	1020	4.0	40 ft.	42 ft.	110.0	2364	63
I-4	Pl	44	1170	4.6	42 ft.	46 ft.	134.2	3124	62
	F		10	2.6			3.7	43	
			1180				137.9	3167	
I-5	Pl	45	952	4.3	44 ft.	48 ft.	136.0	2742	67
	F		54	2.6	12 ft.		1.8	27	
	A		102	3.1	15 ft.		2.0	56	
			1108				139.8	2825	

Table A5-6. Summary of pine stand data for Area II.

Plot No.	Species	Age Yrs.	Stems #	Av. DBH	Av. Ht.	Av. Ht. Dom.	BA	Total Vol.	Site Index
II-1	Pl	79	1464	5.0	64 ft.	64 ft.	178.0	6854	65
	S		32	3.2	22 ft.		1.1	13	
	A		19	4.2	41 ft.		1.8	32	
			1515				180.9	6899	
II-2	Pl	77	660	6.3	54 ft.	60 ft.	128.4	4230	62
	F		350	5.3	56 ft.		54.6	1134	
			1010				183.0	5364	
II-3	Pl	78	420	7.4	65 ft.	71 ft.	120.0	4108	73
	A		5	5.1	31 ft.		.7	9	
			425				120.7	4117	
II-4	Pl	81	680	6.9	67 ft.	73 ft.	169.5	6835	71
	S		25	3.1	22 ft.		.3	2	
			705				169.8	6837	
II-5	Pl	78	415	7.3	68 ft.	74 ft.	128.0	4108	76
	S		8	4.9	36 ft.		10.1	8	
			423				138.1	4116	

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IN BRITISH COLUMBIA

Author [redacted]

RICHARD GLENN DAVIES

April 26/72