STUDIES OF THE HOLDING, BEHAVIOUR AND NUTRITION OF CAPTIVE BLUE GROUSE

by

IAN GROTE STIRLING

B.Sc., University of British Columbia, 1963

A THESIS SUBMITTED IN PARTIAL FULFILMENT OF THE REQUIREMENTS FOR THE DEGREE OF

MASTER OF SCIENCE

in the Department

of

Zoology

We accept this thesis as conforming to the required standard

THE UNIVERSITY OF BRITISH COLUMBIA

November, 1965

In presenting this thesis in partial fulfilment of the requirements for an advanced degree at the University of British Columbia, I agree that the Library shall make it freely available for reference and study. I further agree that permission for extensive copying of this thesis for scholarly purposes may be granted by the Head of my Department or by his representatives. It is understood that copying or publication of this thesis for financial gain shall not be allowed without my written permission.

Department of Zoology

The University of British Columbia
Vancouver 8, Canada

Date Dec 8/65

ABSTRACT

The primary purpose of keeping blue grouse was to learn to keep them in good health and breed them. New data were obtained on the weights, nutrition, survival, diseases, and behaviour of blue grouse in captivity.

They were kept in 3 sizes of pens, 2 feet wide by 4 feet high by 8 feet long, 6 feet wide by 4 feet high by 8 feet long, and 20 feet wide by 10 feet high by 20 feet long. On the basis of plumage condition and reproductive behaviour the medium sized pens were best.

The level of protein of the diet of the hens appeared to affect survival and reproductive behaviour. Grouse that were fed a diet with 18 percent protein had better survival and exhibited more reproductive behaviour than grouse fed a diet with 24 or 28 percent protein. Grouse were unable to survive on a diet of dried and pelleted Douglas fir needles. None of the conclusions reached appear applicable to conditions observed in the field.

Hens exhibiting reproductive behaviour were sexually imprinted upon humans. The only successful method of mating grouse was to take a male exhibiting sexual display to a squatting female. Artificial insemination was as successful as natural matings in the aviary.

The apparent digestibility of the commercial chicken breeder ration varied from 51.2 to 64.9 percent. There was a

relationship between the daily consumption of water and body weight.

The study of behaviour indicated there was a relationship between the hooting of males and the squatting and egg laying of females. Adult males hooted more than yearlings. The female usually gave a pre-copulatory cry when ready to mate. Males became more aggressive during the breeding season and less aggressive through the summer. The females appeared to have two peaks of aggressive behaviour during the reproductive season. Aggressive behaviour of females may serve to space them in the field during the period of nesting. There may be a period of aggressive behaviour in males during the winter.

A partial catalogue of grouse behaviour was made. Photographs of postures and sonographs of calls supplement description.

TABLE OF CONTENTS

	Page
ABSTRACT	i
TABLE OF CONTENTS	ii
LIST OF TABLES	v
LIST OF FIGURES	vii
LIST OF PLATES	viii
ACKNOWLEDGEMENTS	x
PART 1. INTRODUCTION	
Chapter 1. Introduction	1
PART 2. HOLDING AND BREEDING	
Chapter 2. Holding Blue Grouse in Captivity	3
Chapter 3. Mortality of Blue Grouse in Captivity	16
Chapter 4. Breeding Blue Grouse in Captivity	25
Chapter 5. Artificial Insemination of Blue Grouse	35
Chapter 6. Incubation and Brooding	41
PART 3. NUTRITION	
Chapter 7. Experiments on Diets and Viability	44
Chapter 8. Basic Nutrition	54
PART 4. BEHAVIOUR	
Chapter 9. Reproductive Behaviour	61
Chapter 10. Aggression and the Reproductive Cycle	73
Chapter 11. Winter Aggression	84
PART 5. SUMMARY	
Chapter 12. Summary	89

Page

LIST OF REFERENCES 93

APPENDIX 1 99

APPENDIX 2 103

APPENDIX 3 117

LIST OF TABLES

TABLE		Page
1.	Sizes and number of pens in U.B.C. aviary	5
2.	Survival of grouse in each size of pen from December to June of 1963-4 and 1964-5	9
3.	Numbers, age, and sex of grouse held in each size of pen and the proportion that showed reproductive display	12
4.	Numbers, sex, and specific locality of capture of each cohort received in the U.B.C. aviary each August	17
5.	Causes of mortality of blue grouse of each age class at the U.B.C. aviary from August 1962 through August 1965	19
6.	Number of blue grouse at U.B.C. aviary showing reproductive behaviour from 1963 through 1965	27
7.	Results of natural and forced mating attempts in U.B.C. aviary	29
8.	Fertility and hatchability of eggs laid at the U.B.C. aviary	30
9.	Comparative fertility of blue grouse eggs	33
10.	The effect of handling hens for artificial insemination, upon squatting and egg laying	37
11.	Comparison of mean clutch size of blue grouse on Vancouver Island to blue grouse that were naturally mated and artificially inseminated in the U.B.C. aviary	38
12.	Number of hen blue grouse in U.B.C. aviary that showed reproductive behaviour and laying on each ration	48
13.	Survival of hen blue grouse held on each ration at U.B.C. aviary from September, 1963 through December, 1964	50

TABLE Page

14. Caloric values and ratio of calories to percent protein of rations fed to grouse in the U.B.C. aviary from September, 1963 through December, 1964 52

15. Body weights, digestibility and caloric and water requirements of blue grouse held at U.B.C. vivarium 56

16. Weights of grouse, their daily caloric intake and their approximate maintenance energy requirement 59

17. Percent of total observations on adult and yearling male blue grouse upon which males hooted, May 1 through June 20, 1963-65 . . . 64

LIST OF FIGURES

FIGURE		Page
1.	Plan view of the aviary	6
2.	Comparison of body weights of blue grouse in the field and in the aviary	11
3.	Deaths and their cause by age and number . .	21
4.	Survivorship of each age-class of chicks brought to U.B.C. aviary	22
5.	The relationship between the occurrence of male hooting to female squatting and egg laying	65
6.	Indicies of female activity during the breeding season	78
7.	Indicies of male activity during the breeding season	80

LIST OF PLATES

PLATE		Page
1.	U.B.C. aviary from south	117
2.	Inside of a pen at U.B.C. aviary to show position of water faunts, feeders, dividers and roost	117
3.	Electric weighing scale with basket	117
4.	Humidaire incubator	118
5.	Battery incubators	118
6.	Brooder at U.B.C. aviary	118
7.	Posture of a sick grouse	118
8.	Normal stance of a blue grouse	119
9.	Head turn posture	119
10.	Neck-stretch posture, vertical	119
11.	Neck-stretch posture, horizontal	120
12.	Backward stance posture	120
13.	Male sexual display	120
14.	Female giving male sexual display	120
15.	Male presentation of air sac	121
16.	Male fanning tail while exhibiting sexual display	121
17.	Male waltzing	121
18.	Male giving pre-copulatory whoot at termination of pre-copulatory run	121
19.	Female squatting	122
20.	Male exhibiting squatting behaviour	122
21.	Sonogram of male hooting	122

TABLE Page

22. Male in hooting posture 123
23. Sonogram of male cackle aggression call . . 123
24. Male giving aggression call 123
25. Sonogram of male cough aggression cry . . . 124
26. Sonogram of female bleat 124
27. Sonogram of female whinny 124
28. Sonogram of female cry 125
29. Sonogram of female cluck 125
30. Sonogram of female hooting 125

ACKNOWLEDGEMENTS

I am particularly grateful to my supervisor, Dr. J.F. Bendell, who made this study possible. He obtained financial support and made himself constantly available for discussion, criticism of the thesis and general suggestions. Dr. C.W. Roberts of the Department of Poultry Science gave freely of his time for consultation on problems of artificial insemination and statistics. Dr. A.J. Wood provided the facilities at the vivarium and Dr. H.C. Norden gave helpful criticism on the chapters on nutrition. Other members of my committee, Dr. J.R. Adams, Dr. D.H. Chitty, Dr. I. McT. Cowan and Dr. D.J. Randall gave helpful criticism of the thesis.

This work was supported by a grant from the National Research Council of Canada and a scholarship from the Canadian Wildlife Service.

I am also grateful to my fellow students, R.B. Dobson, A.N. Lance, Dr. B.R. Simard and Dr. F.C. Zwickel for their assistance and advice throughout the study.

CHAPTER 1

INTRODUCTION

This work is part of a long range study of the natural regulation of numbers of blue grouse (Dendragapus obscurus fuliginosus) on Vancouver Island, conducted by Dr. J.F. Bendell.

In the study of vertebrates in the field it is often difficult if not impossible to manipulate environmental conditions for experimental purposes. It may also be difficult to obtain quantitative observations.

Alternately, the unnatural environment of animals in captivity may have unobserved effects upon their reactions to a given stimulus. For this reason, conclusions drawn from a study upon captive animals should not be used to explain observations upon the same species in the field without qualification.

There were several objectives in keeping blue grouse in the U.B.C. aviary. One was to learn to keep them alive and in good health. Another was to learn to breed them in captivity. If these two objectives were reached, further studies could provide information applicable to problems encountered in the field. In the course of holding and breeding grouse, many data were gathered that contributed to the understanding of their biology.

Field observations show that the mortality of chicks is higher within some broods than the mean mortality of broods (Zwickel, 1965). This suggests a maternal influence upon the viability of the eggs. One possible explanation is that the quality of the diet of a hen affects the viability of her chicks.

Another possible explanation is that the sperm of some males are inviable, but the importance of this suggestion is diminished by the fact that the hens are polyandrous. If blue grouse could be held and bred successfully in captivity, hens could be fed diets varying in quality and the subsequent viability of their chicks observed. Successful methods of holding and breeding would also permit a study of the basic nutritional requirements of blue grouse.

Holding blue grouse would facilitate the study of behaviour by providing a set of constant conditions under which controlled experiments could be done. Additional descriptive data on postures, displays and calls, difficult to obtain in the field, could be collected.

This thesis describes the methods of holding and rearing blue grouse at the U.B.C. aviary from 1962 to 1965 and the results of nutritional and behavioural studies done there.

The following terms are defined here for use throughout the text.

U.B.C. - University of British Columbia, Vancouver, British Columbia, Canada.

Spring - March, April, May, June

Summer - July, August

Fall - September, October

Winter - November, December, January, February

Juvenile - bird less than 1 year of age

Yearling - bird more than 1 year but less than 2 years of age

Adult - bird over 2 years of age.

CHAPTER 2

METHODS OF HOLDING BLUE GROUSE IN CAPTIVITY

Introduction

Stocks of all North American galliforms have been held in captivity at some time. The Phasianidae and Perdicidae have reproduced many generations in captivity. Hatchability and survival of over 80 percent are recorded for several varieties of pheasants, quail, and partridges (Greenberg, 1949; Delacour, 1959). Hatchability and survival has not generally been as high in the Tetraonidae. After 11 generations of ruffed grouse (Bonasa umbellus) were raised in New York, Hatchability of eggs laid was only 65 percent and survival of chicks was 30 to 50 percent (Bump, 1949). Fay (1963) got 76 percent survival of ruffed grouse chicks raised from eggs collected in the field. Evans (1964) stated that greater prairie chicken (Tympanuchus cupido pinnatus) did not survive well in captivity but no data were given. Sage grouse (Centrocercus urophasianus) raised in captivity had less than 30 percent survival (Pyrah, 1964).

Blue grouse have been held in captivity several time before (Batterson, 1957; Gibson, 1965; Lacher, 1965; Hansen, 1961; Simpson, 1935; Smith, 1963; and Wood, 1957). Most of these attempts were with open air pens 10 to 15 feet wide by 20 to 30 feet long and built on the ground. Gibson (1965) used small wire pens 19 inches square and 16 inches high. None of these attempts produced many grouse compared to productivity in the field.

Disease is the biggest problem with keeping gamebirds. Bump (1949) and Delacour (1959) state the only way to prevent disease is to raise birds in pens with wire mesh floors. Thus birds cannot feed in the feces and become infected with diseases such as enteritis, aspergillosis or coccidiosis. Smith (1960) and Lacher (1965) had disease in their natural-floored pens. Gibson (personal communication) had disease in his wire-floored pens. Sage grouse kept in wire-floored pens had better survival than sage grouse kept on the ground (Pyrah, 1964).

Materials and Methods

Plate 1 is a photograph of the avairy. Note the spaces in the sides to let in light but lack of spaces in the end. Translucent fibreglass sheets were put on the roof to allow extra light and artificial lighting was occasionally used to extend the day length during the reproductive season. The whole unit, with the exception of the outer half of the big pen, was roofed for protection against the excessive rain. Figure 1 gives a plan view of the U.B.C. aviary.

Table 1 gives the size and number of pens in the U.B.C. aviary. The pens of rows A, B, C, and D had a wire mesh (1 inch diameter) floor 2 feet above the ground. There were 2 foot high plywood dividers along the wire mesh walls between pens to prevent interaction (Plate 2). There was a perch in each pen made of a piece of 2 inch square wood (Plate 2). The big pen, E, had a crushed rock (1/2 inch diameter) floor. A few larger rocks (1 foot diameter) and logs were put into the big pen to simulate the natural environment. There was no growing vegetation.

PEN SIZE	PEN ROW	NUMBER	HEIGHT[1]	WIDTH	LENGTH
Small	A	12	4	2	10
	B	10	4	2	8
Medium	C	3	4	6	8
	D	4	4	6	10
Large	E	1	10	20	24

Table 1. Sizes and number of pens in U.B.C. aviary

[1]All dimensions in feet.

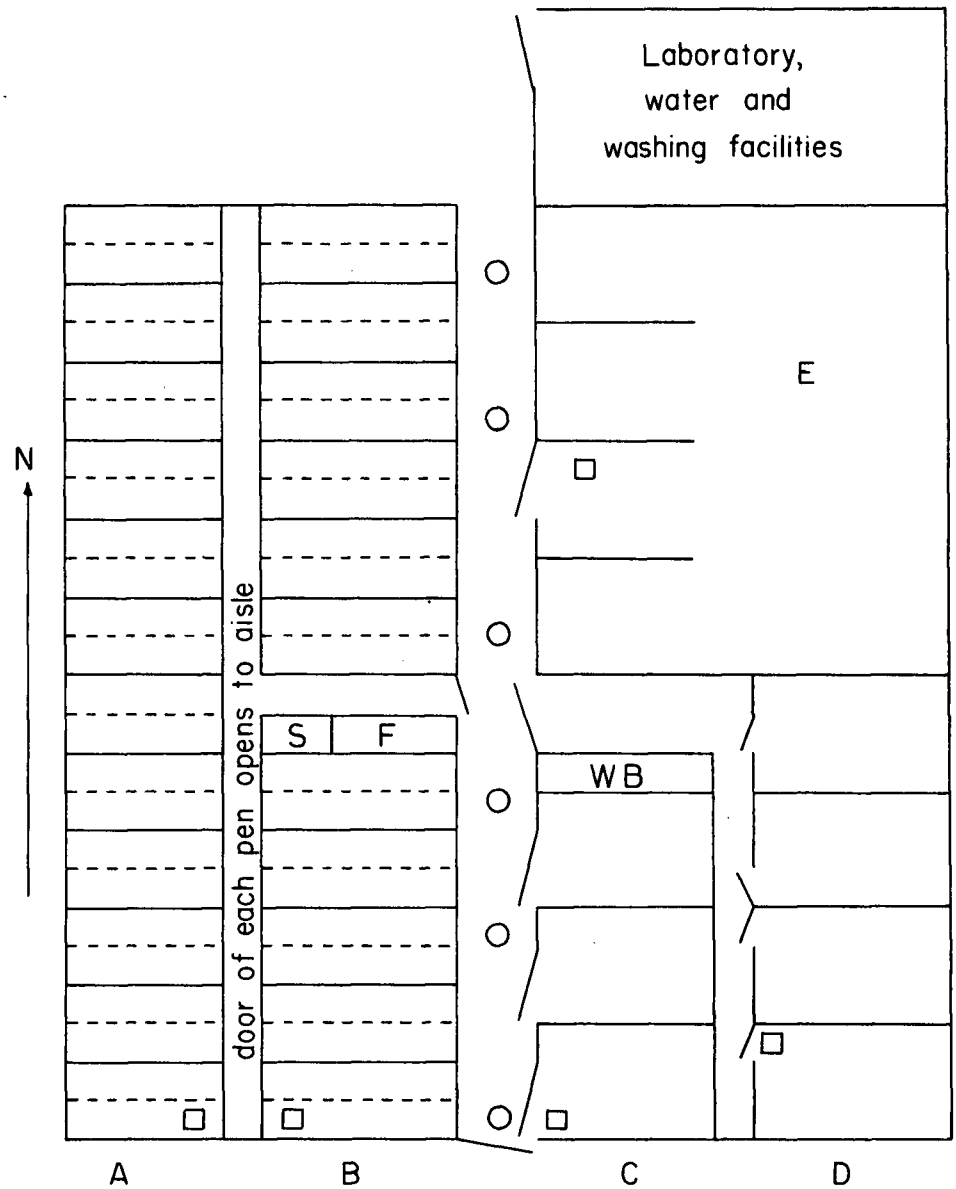

Figure I. Plan view of the aviary
(dimensions given in text)

Legend:
A,B,C,D,E, pen rows discussed in text
—— permanent wire
---- removable wire
□ water and feed
W weighing scale
F feed storage
WB work bench
○ electrical outlet

Combinations of grouse of different ages, sexes and at different densities were tested in the different sizes of pens. One grouse was usually kept in each small pen although 2 grouse were sometimes put in when there was an excess of birds as there was every fall. Two to 3 grouse were normally kept in the medium pens although 6 to 8 grouse were held in the fall. Six grouse were held in the big pen in one year and 4 the second year.

Grouse were fed a commercial chicken breeder ration and #2 crushed grit. Feed was replaced every 2 or 3 days. Plate 2 shows the feeders and water-faunts used. Feed was stored in the Zoology building where it was dry and mold did not form. Nest boxes were provided for females during the breeding season.

Several sanitary measures were used to try to reduce the incidence of disease. Plastic sheets were put underneath the pens with wire floors to catch the droppings. These sheets were replaced every 2 months. Feeders and water-faunts were washed and sterilized with bleach every 2 weeks. A spray of bactericide (brand name Izal) and fungicide (brand name Kleenzade) was used every month on the whole unit. Terramycin, polysol, baciferm, cod-liver oil and aspirin were added to the drinking water of sick birds. Sick birds that stopped eating were force-fed a mixture of water, feed, and medicine to ensure they received some nutrients and medicine.

Birds were weighed once a week during the fall and winter. They were caught by hand and weighed in a basket on an electric scale (Plate 3). They were not usually weighed during the spring or summer.

Four grouse were held in individual wire cages in the vivar-

ium. This vivarium was inside a building and was warm and dry. The pens were 24 inches long, 18 inches wide and 16 inches high. Water and feed were provided in small pans which were weighed daily to measure intake. These birds were weighed daily. The room received natural light from a window on the wall.

Results

Feather picking developed if more than 3 chicks were kept in the medium sized pens, or more than 1 chick in the small pens. Crowding resulted in several deaths due to picking. When Douglas fir (Pseudosuga menziesii) boughs were put into the pens, the picking stopped.

The plumage of birds kept in the small pens was frayed more than birds kept in larger pens. The plumage of birds held in the vivarium was frayed.

The survival of grouse in each size of pen, from December to June of 1963-4 and 1964-5 is given in Table 2. Birds that were moved from one size of pen to another between December and June were not counted. There was no significant difference in the survival of grouse held in any size of pen during either year or between the pooled survival of each group for 1964 and 1965. (Chi-square test at the 5 percent level of probability).

All four grouse held in the vivarium survived from February through August. Survival of grouse in the aviary could only be compared to survival of grouse in the vivarium from February through June because there were no birds in the vivarium during December or January. There was no significant difference in survival during this time (Chi-square test at the 5 percent level of probability). However, the time of heaviest mortality in the

PEN SIZE	1963-4 LIVE IN DECEMBER	1963-4 LIVE IN JUNE	1964-5 LIVE IN DECEMBER	1964-5 LIVE IN JUNE
Small	46	22	46	13
Medium	8	4	13	3
Large	6	3	4	2

Table 2. Survival of grouse in each size of pen from December to June of 1963-64 and 1964-65

aviary was over.

Disease was always present. It was difficult to determine whether medicine in the drinking water was of any benefit. Some sick birds taking medicine returned to good health. These birds were a minority.

Figure 2 compares the body weights of grouse in the aviary to body weights of grouse from Vancouver Island for each month. Data from the same month of different years are considered together. The Vancouver Island data are from Bendell (1955) and Simard (1964). The average weights of grouse from the field and from the aviary are about the same at the same time of the year. The weights of grouse held at the vivarium were comparable.

One factor which could not be controlled in the aviary was moisture. The unit is located in an area of poor drainage. During the rainy winter season, the moisture of the ground gives a damp cold atmosphere to the unit. Air circulation is poor because of the partitions and screens between the pens. The air temperature was noticably lower inside the aviary than outside and the humidity was higher, but no quantitative data on the microclimate of the aviary was collected.

A second unpredicted factor in aviary conditions was the very high population of house mice (Mus musculus). They ate food from the bird feeders and left a mess of powdered feed and feces. Poisoning and trapping were done extensively but with little observed effect.

Table 3 gives the numbers, age and sex of grouse held in each size of pen and the proportion that showed reproductive

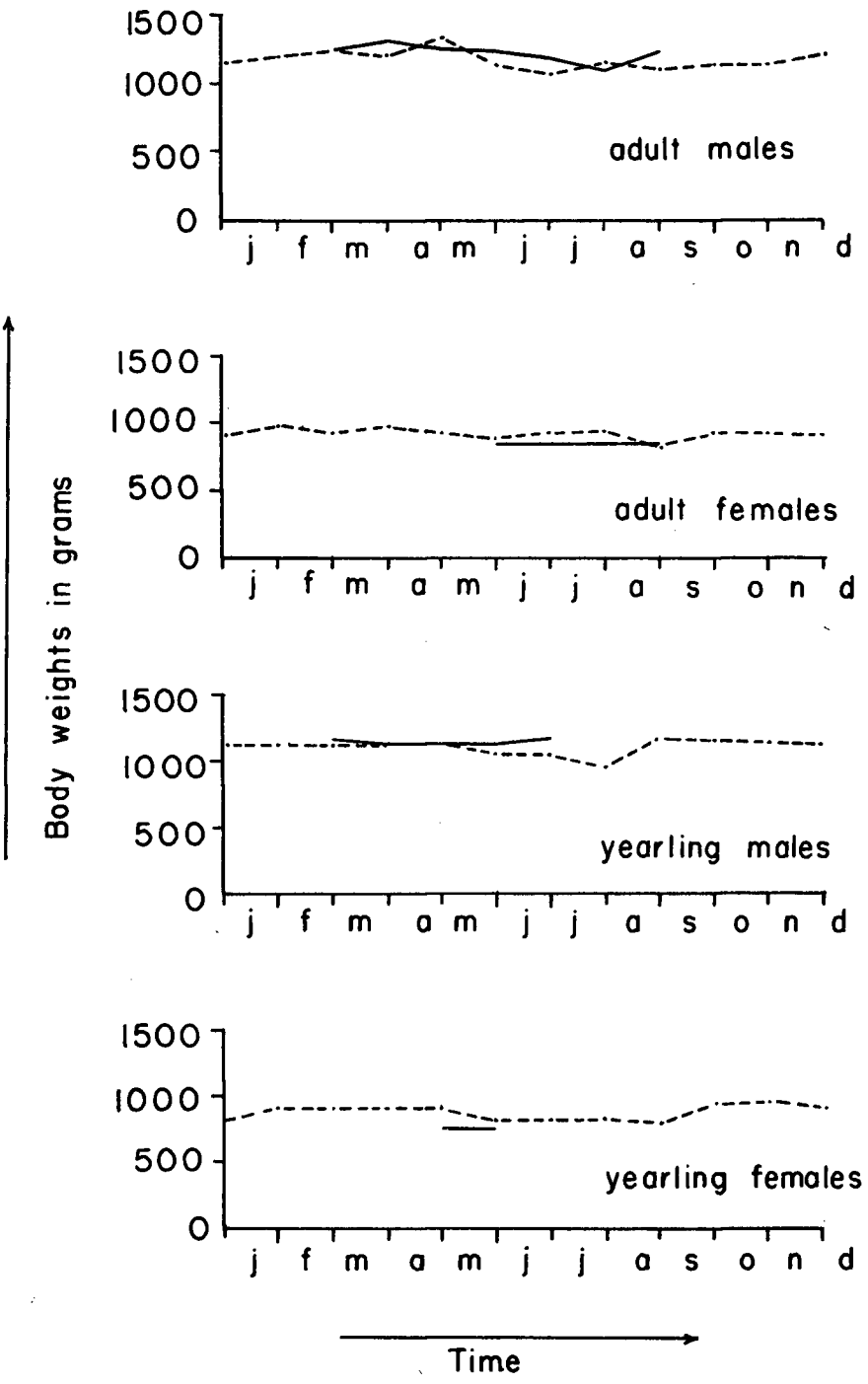

Figure 2. Comparison of body weights of blue grouse in the aviary and the field

Legend: --- weights of grouse in the aviary

—— weights of grouse in the field

CLASS	SIZE OF PEN: SMALL NO. OF BIRDS HELD	SMALL NO. OF BIRDS DISPLAYED	MEDIUM NO. OF BIRDS HELD	MEDIUM NO. OF BIRDS DISPLAYED	LARGE NO. OF BIRDS HELD	LARGE NO. OF BIRDS DISPLAYED
Adult male	15	6	3	3	1	1
Adult female	21	9	0	0	3	0
Yearling male	25	7	5	4	3	2
Yearling female	27	8	5	3	3	1
Total	88	30	13	10	10	4

Table 3. Numbers, age and sex of grouse held in each size pen and the proportion that showed reproductive display

display. Display here is defined as squatting for females and hooting or display for males (Appendix 2).

The proportion of grouse that showed reproductive display in the medium pens was significantly larger than the proportion of grouse that showed reproductive display in the small pens (Chi-square test at the five percent level of probability done on the totals). There was no significant difference between the proportion of grouse that displayed in the small and large pens, or the medium and large pens. No grouse at the vivarium showed reproductive behaviour.

The time that reproductive behaviour began each spring varied. In 1965, hens began to squat and lay eggs 2 to 3 weeks before they did so in 1963 or 1964. The peak of hooting was also earlier in 1965. In all years the beginning of reproductive behaviour in the aviary was later than in the field.

Discussion

The mortality rate of birds in all sizes of pens was equal (Table 2). The fact that birds frayed their plumage badly in the small pens suggests that larger pens are necessary to maintain good plumage.

The weights of aviary birds were comparable to the weights of birds in the field (Figure 2). This suggests that commercial chicken breeder ration met the nutritional requirements of blue grouse for maintenance of body weight. Conversely, it suggests that birds in the field have no difficulty meeting their nutritional requirements.

The damp cool atmosphere of the aviary in the winter apparently provided an ideal environment for the growth of molds. Spraying was of little lasting value. The mice may have acted as mechanical vectors of disease, since they were observed in the feeders many times. It is possible these two factors combined to aggravate the problem of disease.

The pens at the vivarium were adequate for keeping birds alive but plumage was badly frayed. Daily handling for weighing caused additional fraying. Despite the extra handling, plus some sickness, no birds died. The major difference between the vivarium and the aviary was the climate. The aviary was cool and damp while the vivarium was warm and dry. It is likely the environment of the vivarium was less conducive to the growth of mold and bacteria. It was free of mice that might have mechanically vectored diseases from the feces of one grouse to the feed of another.

The small size of pens at the vivarium was probably not the sole reason that none of the grouse exhibited reproductive behaviour. Grouse held in small cages by Gibson, but not handled daily, exhibited reproductive behaviour. By comparison, when weighing of birds at the aviary was stopped well ahead of the breeding season, the reproductive behaviour did not seem to affected. This suggests that the stress of handling of grouse during the breeding season inhibits reproductive display. However, there was no control group at the aviary which was not weighed during the same period.

The fact that birds begin to exhibit reproductive behaviour in the aviary later than they do in the field suggests that some factor or combination of factors may inhibit reproductive behaviour in the aviary. The photoperiod is about the same between the aviary and the field. One possibility is that the lower temperature of the aviary may act to inhibit reproductive behaviour. In 1965, when the grouse in the aviary began to display two weeks earlier than in 1963 and 1964, the average number of hours of sunlight per day in March was about double that of the previous 2 years. The mean monthly maximum and minimum temperature from January through May showed little variation between years. It is possible that this extra amount of sunlight might have had an effect similar to that of a greenhouse and made the aviary warmer.

Summary and Conclusions

Of the pen sizes used, the medium sized pens were best for holding grouse on the basis of plumage condition and reproductive performance. Weights and death rates were the same in all sizes of pens.

The cold damp environment of the aviary during the winter may have been less suitable for holding blue grouse than the warm dry environment of the vivarium because it was more conducive to the growth of disease organisms.

Handling blue grouse during the breeding period may have inhibited reproductive display.

CHAPTER 3

MORTALITY OF BLUE GROUSE IN CAPTIVITY

Introduction

Mortality was high in grouse held at the aviary. This section is to discuss the pattern of mortality in each age class, the variation in the pattern and the causes of mortality.

The mean annual mortality of adult blue grouse in the field is about 30 percent, and most of this occurs during the winter (Zwickel, 1965). Juveniles have a mortality rate of about 70 to 80 percent during the period from spring through fall and about 40 to 50 percent from fall through spring (Zwickel, 1965). From these data it is clear that the highest mortality of a cohort of blue grouse in the field occurs during the first year of life. I wanted to see if this pattern of mortality was repeated in the aviary.

Mortality in the aviary may be divided into two categories, natural and unnatural. A natural death is one caused by disease or the aggressive actions of one bird on another. An unnatural death is one caused by an artifact of captivity such as predators, birds that suffocated in transport, sacrificed birds, birds donated to parasitology, escapes, and birds killed because of physical deformities.

Materials and Methods

Grouse chicks were brought to the aviary from Vancouver

Island each year at the end of August. The numbers, sex and place of capture of each cohort of chicks is given in Table 4. Daily checking of the aviary gave accurate data on the time of mortality. Birds were either autopsied on the day they were found dead, or frozen and autopsied immediately upon thawing.

Two graphic presentations of mortality are given. To show time distribution and causes of deaths, a histogram is given for all deaths of each age class. A survivorship curve for each age class is also given.

Results

Of the 192 birds received, 140 died of natural causes, 31 of unnatural causes and 21 were alive at the termination of the project.

Table 5 gives the causes of mortality of blue grouse of each age class at the U.B.C. aviary from August 1962 through August 1965. The class "other" includes deaths in tramsport, predator kills, sacrifices, escapes, birds given to parasitology and birds killed because of physical deformities. In many (49) cases there were several symptoms of sickness found upon post-mortem examination but the exact cause of death could not be positively determined. The proportion of birds that died of each cause of death was about the same for each sex and age class (Table 5). One exception was aspergillosis which appeared to be more prevalent in males, but this was not statistically significant (Chi-square at the 5 percent level of probability). The number of chicks that died of picking was highest

YEAR	NO. OF MALES	NO. OF FEMALES	SOURCE	TOTAL
1962	21	22	Middle Quinsam Lake, Vancouver Island	43
1963	37	32	16 mi. N.W. Courtenay, Vancouver Island	69
1964	37	43	16 mi. N.W. Courtenay, Vancouver Island	80
Total	95	97		192

Table 4. Numbers, sex and place of capture of each cohort of blue grouse chicks received in the U.B.C. aviary each August

CAUSE OF DEATH	1962 CHICKS MALES	1962 CHICKS FEMALES	1963 CHICKS MALES	1963 CHICKS FEMALES	1964 CHICKS MALES	1964 CHICKS FEMALES
Unknown	5	6	8	10	9	11
Gizzard erosion	4	1	7	5	1	7
Aspergillosis	8	3	3	4	5	1
Enteritis	0	1	7	3	3	4
Picking and aggression	0	0	7	5	3	0
Starved on fir	0	5	0	0	0	0
Predator	0	0	2	0	0	3
Internal hemorrhage	0	1	1	0	0	0
Escaped	0	0	0	0	2	0
Ulcerative gizzard	1	0	0	0	1	0
Proventriculitis	0	1	0	0	0	0
Other	2	1	2	4	8	6
Number starting	21	22	37	32	37	43
Total deaths	20	19	37	31	32	32
Total survivors	1	3	1	0	5	11

Table 5. Causes of mortality of blue grouse of each age class at the aviary from August, 1962 through August, 1965

in the 1963 cohort.

Figure 3 is a histogram of the number of deaths and their causes for each age class from the time they arrived at the aviary through August 1965. Figure 4 gives the survivorship curves of each cohort of grouse from the time they arrived in the aviary through August 1965.

The mortality was generally higher during the winter than the summer in each age class (Figures 3 and 4). The exception was the cohort of chicks from 1963 which had low mortality during the first winter and high mortality during the following summer. The period of greatest mortality for the whole population was during the winter of 1964-5.

The survival of the 1962 and 1963 chicks through the first year of life was significantly better than the survival of the 1964 chicks (Chi-square test at the 5 percent level of probability).

The 1963 chicks were held in the medium pens at densities of 8 to 10 with no cover. They pecked each other until fir boughs were put in for cover. Picking then stopped immediately. Boughs were put in the pens when holding the 1964 chicks and no deaths resulted from picking caused by the stress of crowding.

Discussion

The incidence of disease was usually higher during the winter than the summer. Normally the winters are cool and wet while summers are warm and dry. As discussed in Chapter 2, the warm dry environment is less suitable for growth of mold or

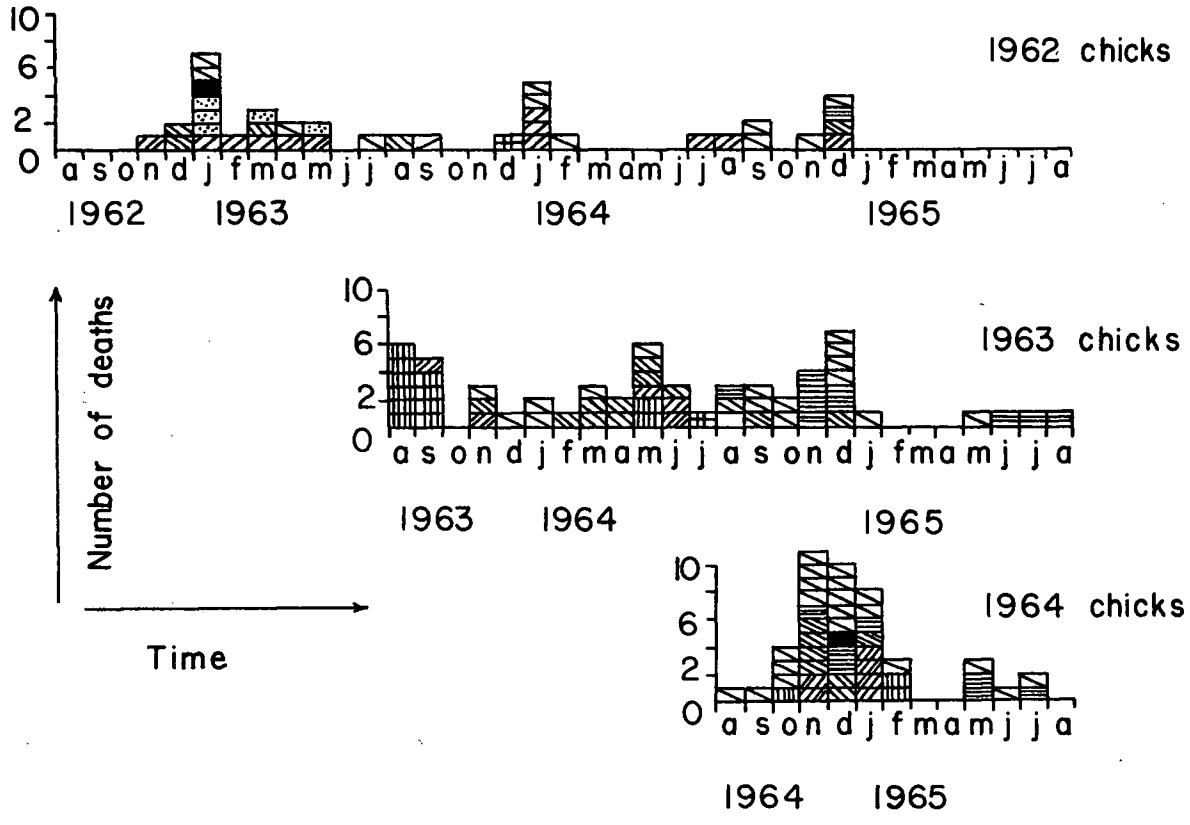

Figure 3. Deaths and their cause by age and number

Legend:
- picking and aggression
- aspergillosis
- gizzard erosion
- enteritis
- starved on fir
- ulcerated gizzard
- internal hemorrhage
- unknown
- proventriculitis

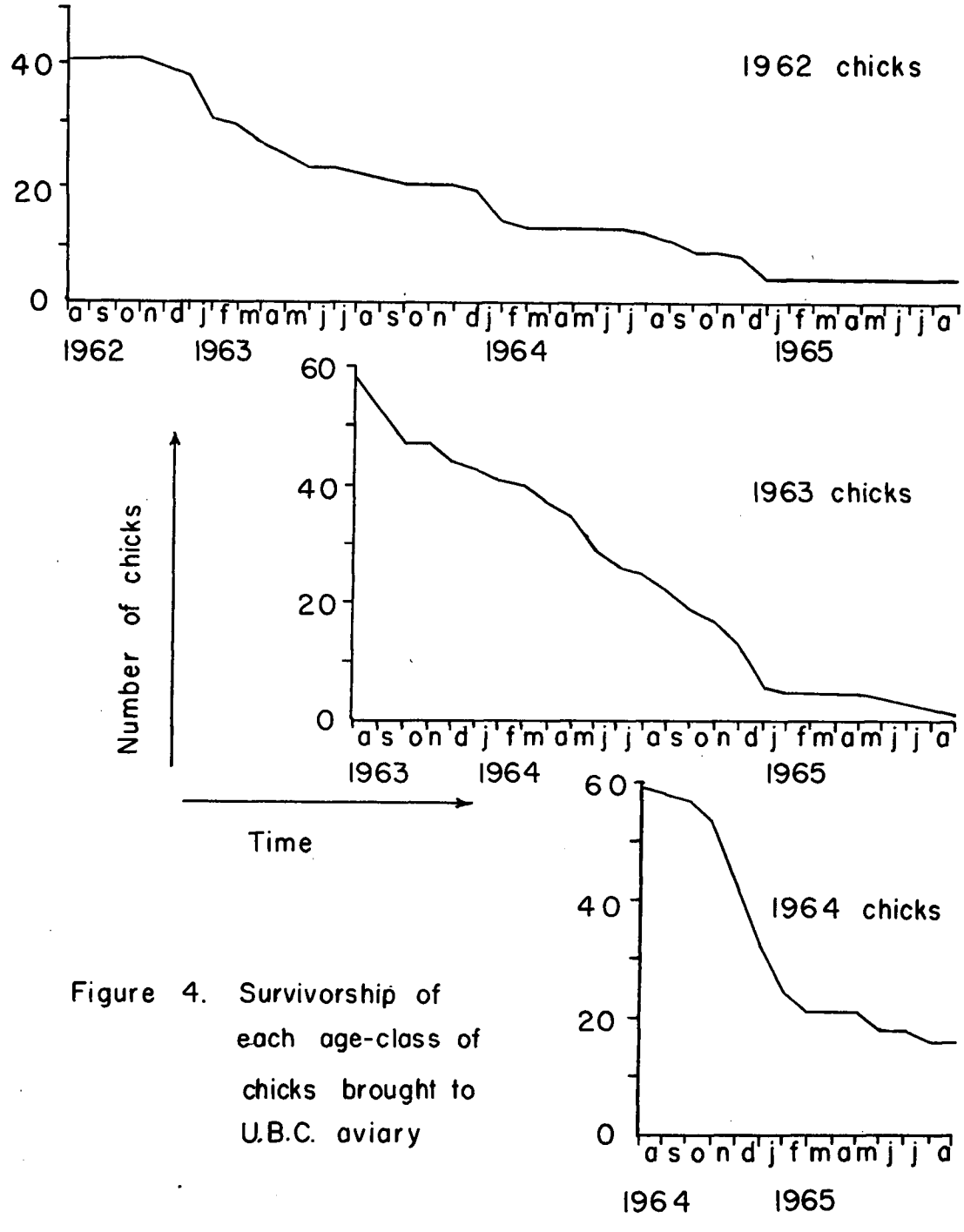

Figure 4. Survivorship of each age-class of chicks brought to U.B.C. aviary

bacteria.

November through January of 1964-65 was particularly cold and wet. Several feet of snow fell in December and remained through half of January. I think this period of excessive cold and wet climate in the aviary was a factor in the particularly high mortality of all age classes during that period.

I cannot explain why the 1963 chicks had a low winter mortality and high summer mortality during their first year in the aviary. They later followed the normal pattern of mortality.

The survival of the 1962 chicks was significantly better than that of the 1964 chicks for the first year of life and significantly better than the 1963 chicks for the first 2 years of life. The 1962 chicks were from Middle Quinsam Lake, Vancouver Island, while the 1963 and 1964 chicks were from 16 miles N.W. of Courtenay, Vancouver Island. Differences in survival may be a reflection of a difference in the stock. However, I think the higher mortality of the 1964 chicks was more likely due to the bad environmental conditions during their first year in the aviary.

I do not think the high incidence of disease affected the subsequent observations upon "healthy" birds. However, none of the "healthy" birds were sacrificed to check for disease that might have inhibited reproduction or behaviour.

Summary and Conclusions

The time of heaviest mortality of grouse in the aviary was usually during the winter. This was probably because the damp

climate during that period was conducive to the growth of disease organisms.

The most common diseases of grouse at the aviary were gizzard erosion, aspergillosis and enteritis.

The differences in survival were more dependent upon climatic conditions of the aviary than upon some difference between the cohorts. Thus, it was unlikely that the 1962 birds had better survival because they were of a more resistant stock.

The proportion of birds of each cohort that died of each natural cause of mortality was about even between years and sexes.

When fir boughs were put into pens in which several chicks were held, they did not peck each other.

CHAPTER 4

BREEDING BLUE GROUSE IN CAPTIVITY

Introduction

Several difficulties are involved in breeding game birds in captivity. The stress of an unnatural environment may inhibit reproductive behaviour. It is difficult to assess the importance of various factors in the natural environment for the stimulation of breeding behaviour. Lighting, external noise, size of pen, age ratios, feed, stock and synchronization of the reproductive behaviour of both sexes may have influenced breeding behaviour in the aviary.

There are two basic methods of breeding game birds in captivity, natural and forced. The natural method involves selection of breeding pairs in the fall or about 2 months before the breeding season occurs and penning the pairs together. Courtship and mating then occurs without human interference. The sex ratio may be monogamous or polygamous depending upon the social structure of the species.

The forced matings, the male and female are put together at the time mating should occur. The female may be taken to the male, the male to the female, or they may both be put into a strange pen at the same time. They may be left together for only a few minutes or for a few days.

Materials and Methods

All 3 sizes of pens described in Chapter 2 were used for breeding experiments.

Several variations of the natural method of mating grouse were tried. In December 1963, 4 pairs of blue grouse were put in medium pens and held there through the breeding season of 1964. Six birds (1 adult male, 2 adult females, 1 juvenile male and 2 juvenile females) were put in the big pen (E, Fig. 1) in February, 1964 and held through the summer. The following year 4 grouse (1 adult male, 1 adult female, 1 juvenile male and 1 juvenile female) were held in the same pen through the breeding season.

Pen rows A and B (Fig. 1) faced each other on a common aisle. During the breeding season, doors were left open overnight to allow breeding pairs to meet in the aisle without human interference. Pens that held males and females on opposite sides of the aisle were joined together and left overnight.

Forced matings were tried several times. Females were taken to males and males to females for short periods of time. Males and females were also penned together overnight.

Results

The number of grouse showing reproductive behaviour in the aviary is given in Table 6.

Of the 4 pairs of grouse penned together in 1964, 3 males exhibited reproductive behaviour. No females were observed

(a) Males

CATEGORY	NUMBER	DISPLAYING[1]	HOOTING
Ad.[2] D.o. fuliginosus	19	10	11
Ad. D.o. pallidus	1	1	1
Yr.[3] D.o. fuliginosus	33	13	9
Total	53	24	21

(b) Females

CATEGORY	NUMBER	SQUATTING	BRED	LAYING
Ad. D.o. fuliginosus	24	9	4	8
Ad. D.o. pallidus	6	4	0	0
Yr. D.o. fuliginosus	36	12	5	7
Total	66	25	9	15

Table 6. Number of blue grouse at U.B.C. aviary showing reproductive behaviour from 1963 through 1965

[1]Appendix 2

[2]Adult

[3]Yearling

exhibiting reproductive behaviour, no matings were observed and no eggs were laid. One male killed his pen mate.

In 1964 the dominant adult male in the big pen displayed and hooted. He was observed displaying to females on several occasions. However no females were observed exhibiting reproductive behaviour, no matings were observed and no eggs were laid. In 1965 the adult male in the big pen again displayed and became dominant. However he killed 2 yearling males put successively into the big pen and had to be removed because of a shortage of males. Of yearling males put into the big pen in February, one became dominant by the end of April. He hooted and displayed to the females. One female was observed squatting but no matings were seen and no eggs were laid.

The only successful method of getting grouse to mate in the aviary was to take a male to a female that was already squatting (Table 7).

Eggs were laid each year. Several were laid by hens that were not mated. Fertility and hatchability of these eggs were low (Table 8).

Discussion

Almost all hens on the breeding range, including yearlings, breed (Zwickel, 1965). Yet at the aviary, only 38 percent of the hens exhibited reproductive display and only 13 percent bred. A slightly higher percent of the males displayed and hooted.

Even though several grouse exhibited reproductive display in the aviary, they did not breed readily. Hens did not squat if

METHOD	1963 TIMES TRIED	1963 TIMES MATED	1964 TIMES TRIED	1964 TIMES MATED	1965 TIMES TRIED	1965 TIMES MATED
Joining pens	7	0	-	-	-	-
Loose in aisle	4	0	-	-	-	-
Penned overnight	8	0	-	-	-	-
Female to male before squatting	16	0	-	-	-	-
Female to male after squatting	4	0	-	-	-	-
Male to female before squatting	11	0	-	-	-	-
Male to female after squatting	23	8	24	1	27	3

Table 7. Results of natural and forced mating attempts in U.B.C. aviary

SOURCE OF EGGS	NO. OF EGGS	NO. POSSIBLY FERTILE	NO. FERTILE	NO. HATCHED	NO. SURVIVED UNTIL FALL
Naturally mated hens	47	39	18	4	2
Artificially inseminated hens	59	41	10	5	2

Table 8. Fertility and hatchability of eggs laid at the U.B.C. aviary

they were handled to be put into the pen of a male. There were only 1 or 2 males each year that would display after being handled, but these males would do so at any time during the reproductive period.

The mating of grouse in the aviary was complicated by 2 additional problems that were difficult to overcome. The first was the fact that females were sexually imprinted upon humans and squatted only in the presence of humans. Males did not become sexually imprinted upon humans. The second was that the males often broke their primaries in the pens and were not able to balance on a squatting female long enough to copulate. In 1965, 5 potential matings were unsuccessful because the male fell off the female.

External noise also seemed to affect the behaviour of grouse. The caribou unit was constructed during the period of reproductive display at the aviary. The birds became extremely restless and very easily frightened. It has been observed since, that the behaviour of the grouse is unsettled and unpredictable upon days of excessive noise made by the caribou and subsequent construction. It is difficult to quantify the effect of such a factor upon the reproductive behaviour of grouse in captivity. However, I feel the influence of external noise was detrimental to breeding success.

Several factors contributed to the low fertility and hatchability of the eggs from the aviary. All embryos in 1963 were killed at about 1 day of age by the overheating of the incubator. As a result, the determination of fertility was

difficult because there was little or no development. Thus the figure for the number of fertile eggs in 1963 is a minimum. These eggs are included in the figures for naturally mated hens (Table 8).

The fertility and hatchability recorded by other workers has also been low (Smith, 1963; Lacher, 1965). However, neither of these workers examined unhatched eggs and thus considered hatchability as fertility. Table 9 compares the hatchability of blue grouse eggs from the data of Smith (1960), Lacher (1965) and the aviary at U.B.C.

The hatchability recorded by Smith is higher than that of U.B.C. or Lacher (Table 8). This difference was statistically significant while the difference in hatchability between the data of Lacher and U.B.C. was not (Chi-square at the 5 percent level of probability).

The fertility and hatchability of eggs in the field are about 90 percent and 80 percent respectively (Zwickel, 1965). Thus only the hatchability recorded by Smith (1960) approached that recorded in the field. However, despite the higher hatchability, the survival of chicks until fall was poor.

Summary and Conclusions

A lower proportion of male and female grouse in the aviary exhibited reproductive display than appeared to do so in the field. This was probably due to the stress of captive conditions. The only successful method of mating grouse at U.B.C. was to put a displaying male into the pen of squatting female. The hens

SOURCE OF DATA	NO. OF EGGS	NO. HATCHED	% HATCH
Smith	30	23	77
Lacher	23	7	30
U.B.C.[1]	54	9	17

Table 9. Comparative hatchability of blue grouse eggs

[1]The clutch of eggs accidentally killed in 1963 is not included in this figure.

were sexually imprinted on humans so that for the female to remain squatting, a human still had to be in sight.

The fertility and hatchability of eggs was low at U.B.C. The data of other workers also indicated difficulty breeding and rearing blue grouse successfully.

CHAPTER 5

ARTIFICIAL INSEMINATION

Introduction

The breeding of blue grouse at U.B.C. aviary was relatively unsuccessful, as discussed in Chapter 4.

In 1964, 3 hens began to lay infertile eggs. These hens had not previously squatted or otherwise indicated arrival into reproductive condition. Attempts to breed them failed. It was decided to attempt artificial insemination as a last possible method to get fertile eggs. Squatting and egg laying were taken as indicative of the time of ovulation and thus the correct time to inseminate.

Materials and Methods

The techniques developed for insemination of chickens and turkeys were used (Taylor, 1949). Dr. C.W. Roberts, Dept. of Poultry Science, U.B.C., further modified the technique as necessary for blue grouse.

For collection of sperm, the male was held with his head and shoulders under the arm of one worker. A second worker massaged the region around the base of the tail. This stimulated the eversion of copulatory protrusions upon which the sperm flowed. The sperm was collected upon a clean slide and transferred to a small syringe.

Sperm was collected from males that hooted or showed

reproductive display. The response varied greatly. The volume collected was always small, varying from .1 to .5 ml. An average collection from a chicken is .5 to 1.0 c.c. (Taylor, 1949). Although no quantitative data were collected, the adults generally produced more seminal fluid than did yearlings and the response of both improved after 1 or 2 collections.

For insemination, the female was held between one worker's knees. Pressure applied to the abdomen with the hands forced the uterus to evert through the cloaca. The syringe was inserted into the uterus and sperm injected.

Touching a squatting female on the back sometimes caused the eversion of the uterus. One squatting hen was stimulated to evert her uterus and then was inseminated.

To prevent contamination of sperm by feces, food was removed from males one day prior to collection of sperm. Care was also taken to prevent fecal contamination of sperm when everting the uterus.

Results

Handling the grouse for artificial insemination caused excitement and stress. The number of hens squatting and laying eggs was reduced after handling for insemination (Table 10). Only hens that laid 2 or more eggs prior to handling for insemination continued to lay.

Table 11 compares the mean clutch size of hen blue grouse from Vancouver Island to the clutch size of hens that were naturally mated and artificially inseminated in the U.B.C. aviary.

YEAR	NO. OF HENS SQUATTING BEFORE INSEMINATION	NO. OF HENS SQUATTING AFTER INSEMINATION	NO. OF HENS LAYING EGGS BEFORE INSEMINATION	NO. OF HENS LAYING EGGS AFTER INSEMINATION
1964	4	2	4	3
1965	4	0	6	2

Table 10. The effect of handling hens for artificial insemination upon squatting and egg laying

GROUP	SAMPLE SIZE	MEAN CLUTCH SIZE	RANGE
Vancouver Island 1964	15	7.00	5-9
Artificially inseminated hens in the aviary	5	9.60	7-13
Naturally mated hens in the aviary	4	10.25	7-14

Table 11. Comparison of mean clutch size of blue grouse on Vancouver Island to blue grouse that were naturally mated and artificially inseminated in the U.B.C. aviary

The clutch sizes from hens in the aviary were larger.

The fertility of eggs laid by artificially inseminated hens was 24 percent. The fertility of eggs laid in the aviary by naturally mated hens was 46 percent (Table 8). The difference was not significantly different (Chi-square at the 5 percent level of probability).

The fertility of eggs from artificially inseminated grouse is low compared with 83 percent fertility obtained by artificially inseminating Japanese quail (Coturnix japonica) (Marks and Lepore, 1965).

Discussion

The stress of handling hens for insemination seemed to affect subsequent squatting and egg laying. Hens usually discontinued laying if handled before dropping 2 or 3 eggs, but continued if handled later. This suggests there may be a critical period after which laying will continue despite a certain amount of stress.

The technique of artificial insemination overcomes the difficulties of trying to get grouse to display and mate naturally. Table 11 suggests that blue grouse are indeterminate layers so that larger clutches than found in the field may be expected if eggs are taken from the nest box daily. It may be possible to maintain an aviary population by selecting males which give a good collection of sperm, selecting females that are good layers and allowing them to lay 2-3 eggs prior to insemination.

Summary and Conclusions

Blue grouse can be artificially inseminated by using the techniques developed for domestic fowl.

For best results in terms of continued egg laying, hens should be allowed to lay 2-3 eggs before insemination.

The fertility and hatchability of eggs from hens that were artificially inseminated in the aviary were comparable to that of hens that were naturally bred in the aviary. The fertility and hatchability of both these sets of eggs was 1/3 to 1/2 of that recorded in the field.

CHAPTER 6

INCUBATION AND BROODING

Introduction

All incubation and brooding were done artificially so that all eggs and all chicks would receive identical treatment. This eliminated possible variation in maternal care.

Materials and Methods

Thirty-four eggs were incubated in a Humidaire 150 egg gravity air incubator, model 10 (Plate 4). This was kept in a small plywood shack. Each egg was collected, individually marked and set the day it was laid. Eggs were incubated as close to 100 degrees F. and 70 percent humidity as possible. They were hand-turned 3 times a day at angle of about 30 degrees from the vertical. Eggs were not turned after the twenty-second day of incubation. The incubation period of blue grouse eggs is about 25 days (Smith, 1960).

Sixty-three eggs were incubated in a large Jamesway incubator, model 2940, with capacity for several thousand eggs (Plate 5). The temperature was kept around 101 degrees. Humidity was high but was not measured. Eggs were automatically turned about 30 degrees from vertical 5 times a day. After 22 days of incubation each egg was put in an individual wire hatching basket and set to hatch in another compartment of the incubator at the same temperature and humidity. Eggs set to hatch

were not turned.

Chicks were left to dry in the incubator for one day after hatching. They were then transferred to the brooder. The brooder was 3 feet square and 1 1/2 feet deep with a wire floor (Plate 6). The mesh was 1/4 inch by 3/4 inch which was large enough for droppings to pass through. The brooder was heated by an infra-red heat lamp suspended so that the temperature at the level of the back of a chick was 98 degrees F.

Chicks were fed for 6 to 8 weeks on Buckerfield's turkey poult ration plus a daily supplement of chopped lettuce and tomato fed in excess. Chicks were then fed Buckerfield's turkey starter ration up to about 3 months of age. They were finally put on Buckerfield's chicken breeder ration for holding.

Results

No eggs hatched in the small incubator. A maximum-minimum thermometer showed that the temperature in the hut varied between 96 and 108 degrees F. The internal temperature of the incubator varied between 98 and 101 degrees F. Examination of the eggs showed that all embryos died after about 1 day in the incubator. It was later found that the thermometer inside the incubator read about 3 degrees low. Thus all the embryos likely had been killed by overheating.

Conditions remained constant between 99 and 100 degrees F. in the battery incubator. Nine chicks hatched.

Conditions in the brooder remained constant. Five chicks died while their 4 pen-mates and brood-mates flourished under

identical conditions at the same time. The dead chicks were not picked and no sign of sickness was found internally.

Discussion

The variation in temperature of the small incubator was due to variation in external temperature and thus indicated poor insulation. Zwickel (1965) used small incubators in a shaded tent where external temperature had minimal fluctuation and found they held fairly constant temperature. Thus the main problem in using the small incubator is keeping it at a relatively constant temperature. The overheating of the incubator probably killed the embryos in 1963.

Summary and Conclusions

The combination of incubating grouse eggs in the battery incubators and brooding chicks by Zwickel's procedures was satisfactory.

CHAPTER 7

EXPERIMENTS ON DIETS AND VIABILITY

Introduction

This chapter presents data from experiments designed to test the effect of the diet of the hen upon the viability of her chicks.

As discussed in the introduction, field observations on blue grouse have shown that the mortality of chicks is higher within some broods, that the mean mortality of broods (Zwickel, 1965). One possible explanation is that a difference in the quality of the diet of the hen may be reflected in the viability of her chicks. The quality of the diet of the hen apparently determines the viability of the chicks of the red grouse (Lagopus lagopus scoticus) and the peafowl (Legumus galli) (Allen, 1964; Jenkins, 1963).

The protein level of the diet of the hen is important because of the heavy drain upon protein reserves for egg production. The protein level of the diet of female rats is critical to reproductive success in the laboratory (Nelson and Evans, 1953).

The main part of the diet of blue grouse on the winter range is fir needles (Beer, 1943; Hoffmann, 1961; Marshall, 1946; Stewart, 1944). A chemical analysis of Douglas fir (Pseudosuga menziesii) needles at U.B.C. indicated a crude protein level of 6 percent. A similar analysis by Hoffmann of needles of white

fir (Abies concolor) indicated a protein level of 5 to 7 percent. By comparison to recommendations in the literature for poultry diets, 6 percent would seem to be far too low for maintenance let alone successful breeding.

After arrival on the breeding range in the spring, hens eat succulent greens almost exclusively. Cocks still eat fir needles as well as greens (Bendell, personal communication). This suggests that the fir diet of the winter range is not suitable for egg production and a supplement of greens, higher in protein, is needed.

Materials and Methods

The plan in 1963 was to hold females over the winter on diets that differed in levels of protein. In the spring, these hens were to be bred and the subsequent viability of their chicks compared.

Two groups of 12 hens were selected at random. The first group was held on a commercial chicken breeder ration which was theoretically as complete in nutritive requirements as possible. The protein level was 18 percent. The second group was held on a diet of dried and pelleted fir needles. In 1962, Zwickel held a group of blue grouse for two months on a diet of dried and pelleted fir needles (personal communication). I hoped to do the same and breed the hens to study the effect of this low quality diet on the viability of the chicks.

Four diets were designed to condition the grouse to a gradual change from chicken breeder ration to fir. These diets con-

tained 25 percent, 50 percent, 75 percent and 100 percent fir. The remainder of the diet was made up of the commercial chicken breeder ration. The level of fir in the diet was increased at two week intervals to allow time for the hens to adjust to the change.

To compare the effect of different localities on the quality of the fir, pellets were made from stands at U.B.C. and the Haney forest. A ration was also made with needles from all parts of the tree to compare with one from only the growing tips of the branches.

In the spring, when greens were available to hens in the field, 1/2 of the group of hens still on the fir diet and 1/2 the group of hens on the breeder ration diet received a supplement of greens which was in excess at all times. This was to test if the availability of succulent greens had a significant effect upon the reproductive success of the hens. The grouse were weighed twice a week to follow weight changes.

In 1964, 3 randomly selected groups of hen blue grouse were selected to be held on 3 commercial rations with varying levels of protein. The percent protein of the 3 rations fed to hen blue grouse at U.B.C. aviary from September, 1963 through December, 1964 was as follows.

RATION	PERCENT PROTEIN
Chicken breeder ration	18
Turkey starter ration	24
Turkey poult ration	28

Hens were held on this diet through the winter of 1963-4 to be bred in the spring of 1964.

In 1965, hens were held on chicken breeder ration only. The sole objective was to hold them over the winter under the most favourable conditions and breed them in the spring.

Results

The grouse survived and maintained weight on a diet of up to and including 75 percent fir and 25 percent commercial breeder ration. By observation, the food intake was higher on this diet than on other rations. When the birds were placed on a pure fir diet they began to lose weight in 3 days. Within 2 weeks they reached a weight of 750 grams from a healthy weight of 850 to 900 grams or more. At this point they were again fed the chicken breeder ration. However, 5 of these hens continued to lose weight and eventually died.

No birds exhibited reproductive behaviour while on any of the four diets, and all birds were back on chicken breeder ration by the time the breeding season was over. No additional breeding behaviour was exhibited by hens with a diet supplement of greens. In 1963, all embryos were killed in the incubator as discussed in Chapter 6, so that there was no information on viability.

In 1964, only females held on chicken breeder ration showed a significant amount of reproductive behaviour (Table 12). This difference is statistically significant (Chi-square test at the 5 percent level of significance). In addition, 2 adult

RATION	NO. OF HENS ON RATION DURING BREEDING SEASON	NO. OF HENS EXHIBITING REPRODUCTIVE BEHAVIOUR	NO. OF HENS LAYING EGGS
Chicken breeder ration	13	6	5
Turkey starter ration	14	0	1
Turkey poult ration	9	1	0

Table 12. Number of hen blue grouse in U.B.C. aviary that showed reproductive behaviour and laying on each ration

females that displayed and bred while held on the chicken breeder ration in 1963 did not display or breed while held on turkey poult ration in 1964. One female that displayed and bred in 1963 while held on chicken breeder ration did so again in 1964 while on the same ration.

The mortality rates of birds held on the turkey starter and poult rations are higher (Table 13). These are not statistically significant (Chi-square test at the 5 percent level of probability). However, I feel the differences are still biologically significant.

Discussion

I do not know why the grouse lived on Zwickel's pelleted fir but not on mine. It was suggested by Buckerfield's agent who supervised on the making of the pellets that they might have been contaminated with other feed residues that were still in the pelleting machine. It may have been due to variation in processing and pelleting procedures, the time of year, portion of tree used, location of stand, annual variability, or another factor of which I am not aware.

The 1964 experiments compared 3 high quality diets. They did not provide any information upon the viability of chicks from hens on different diets.

The excessively high protein content of the turkey starter and poult rations was the most important difference between them and the chicken breeder ration. Bump (1949) stated that excessive protein in the diet will stop laying and bring on moult.

RATION	NO. BIRDS ON EACH RATION	NO. BIRDS DIED ON EACH RATION
Chicken breeder ration	23	13
Turkey breeder ration	14	12
Turkey poult ration	9	7

Table 13. Survival of hen blue grouse held on each ration at U.B.C. aviary from September, 1963 through December, 1964

The recommended dietary protein level for chickens is 18 percent (Ewing, 1963); turkeys, 20 percent (Ewing, 1963); and pheasants, 18 percent (Greenberg, 1949). Delacour (1959) recommends 24 percent protein for pheasants. However, animals eat to meet a caloric requirement so that percent protein is of less importance.

The caloric values of rations used to hold female blue grouse at U.B.C. aviary, September, 1963 through December, 1964 are given in Table 14. Note the ratio of calories to percent protein. By simple ratio it may be seen that a hen on turkey starter ration is taking in a greater amount of protein than a hen on chicken breeder ration, to meet the same caloric requirement, by not 1/3 greater. The same applies to the turkey poult ration. Thus, comparison of the effect of different dietary levels of protein was invalid. However, a difference in reproductive behaviour and laying was still demonstrated between groups of hens on different diets.

The hypothesis was that the quality of the diet of the hen would be reflected in the viability of her chicks. Thus, the quality of the diet of the hen would ultimately control the number of grouse produced. However, to date there is no evidence from the field to indicate that birds arrive onto the breeding range in poor condition. There is no evidence of any shortage of nutritious food for hen grouse on the breeding range. The aviary experiments in 1963 and 1964 showed a difference in reproduction and survival between hens on different diets. However, I cannot conclude that these experiments have produced any results which are meaningful to natural conditions.

RATION	% PROTEIN	CALORIC VALUE	CAL./% PROTEIN
Chicken breeder ration	18	1172 cal./gr.	63.0
Turkey starter ration	24	1404 cal./gr.	56.8
Turkey poult ration	28	1371 cal./gr.	46.7

Table 14. Caloric values and ratio of calories to percent protein of rations fed to grouse in the U.B.C. aviary from September, 1963 through December, 1964

Summary and Conclusions

Blue grouse were not able to survive in the U.B.C. aviary on a diet of dried and pelleted fir needles for longer than 2 weeks.

Hen blue grouse held on chicken breeder ration (18 percent protein) had better survival and exhibited more reproductive behaviour than hen blue grouse held on turkey starter ration (24 percent protein) or turkey poult ration (28 percent protein.

No conclusions applicable to natural conditions were made.

CHAPTER 8

BASIC NUTRITION

Introduction

Once the basic parameters of the nutritional requirements of blue grouse are known, then experiments may be designed to test the effect of the quality of the diet upon growth, survival, egg production, and viability of chicks.

Materials and Methods

Four grouse (3 females and 1 male) were held in the vivarium for nutritional studies. The conditions of holding were described in Chapter 2.

The grouse were fed Buckerfield's chicken breeder ration. This ration has a protein level of 18 percent and a caloric value of 2578 calories per kilogram, or 2.58 calories per gram. Feed and water intake were measured daily. Two water pans were kept in empty cages and weighed daily to record evaporation. Droppings were collected on plastic sheets underneath the pens, dried in an oven and weighed until the weight was constant. This point occurred after 2 days in the oven.

The apparent digestibility of the feed was calculated as follows:

Apparent % digestibility equals

$$\frac{\text{dry weight of feed consumed - dry weight of feces}}{\text{dry weight of feed consumed}}$$

The energy for maintenance was the number of digestible calories required by a bird of a particular weight per day at a particular temperature. The temperature at the vivarium when these data were collected was 72 to 75 degrees F.

The basic water requirement was calculated as the number of grams of water consumed per digestible calorie. The daily intake of dry weight of feed and water for individual body weights was also calculated.

Results

Table 15 presents a summary of the data collected on body weights, digestibility of feed and the daily caloric and water consumption of grouse held at the vivarium. This data was collected in four series July 9 to 16, July 20 to 24, July 28 to 30, and August 2 to 6, 1965. The variation in digestibility from 51.2 to 64.9 percent was not statistically significant (analysis of variance at the 5 percent level of probability). There was a 6 percent variation from the mean body weight but a 30 percent variation from the mean digestible calories. The daily intake of digestible calories was not significantly related to body weight (linear regression at the 5 percent level of probabliity).

Analysis of the daily water consumption showed it was not directly related to the intake of digestible calories except for yearling male 1215 (linear regression at the 5 percent level of probability). The daily consumption of grams of water was directly related to body weight in all birds except adult female 1002 (linear regression at the 5 percent level of probability).

BIRD	NO. OF SAMPLES	AVERAGE BODY WEIGHT[1]	AVERAGE DAILY CALORIC INTAKE	AVERAGE DIGEST-IBILITY OF FEED (%)	AVERAGE DAILY WATER CONSUMP-TION	AVERAGE DIGESTIBLE CALORIES RECEIVED DAILY	RATIO OF WATER CON-SUMPTION TO DIGESTIBLE CALORIES
Yearling female 1105	19	864.2	69.7	51.8	45.8	36.2	1.25
Yearling female 1109	20	946.1	82.0	51.2	54.8	41.8	1.30
Adult female 1002	19	915.3	74.3	64.9	37.9	48.3	.79
Yearling male 1215	19	965.5	98.5	61.9	57.2	61.1	.86

Table 15. Body weights, digestibility and caloric and water requirements of blue grouse held at U.B.C. vivarium

[1]All weights in grams.

Discussion

There was variation in the results of the digestibility study. Although the methods were fairly crude, they were constant. Birds showed some variation in daily food consumption. They appeared healthy at all times during the collection of these data. There were no diarrhetic feces which might indicate sickness although some days they consumed only a few grams of feed. The average digestibility of 57.4 percent is fairly low compared to the 71 percent digestibility calculated using the same technique on rats (Schurch, Lloyd, and Crampton, 1950).

The daily water requirement varied. I do not feel that error was incurred by the technique of measurement. If birds were at all sick, water consumption might change. There is also the possibility that the water consumption may not be directly related to the daily intake of apparent digestible calories since only 1 of 4 showed a statistically significant relationship.

The significant relationship between the number of grams of feed and the number of grams of water taken in per day, but the lack of a significant relationship between the intake of water and apparent digestive calories or the intake of apparent digestible calories to body weight suggest an error in calculation of the digestibility. I do not know what caused the error, since as nearly as I was able to determine, the methods were constant.

From Brody (1945:375) the basal metabolic rates for chickens of weights comparable to grouse are as follows:

WEIGHT	BASAL METABOLISM, CAL/24 HR.
.85 Kg.	65
.90 Kg.	70
.95 Kg.	75

The basal metabolic rate is equivalent to 85 percent of the maintenance energy (Brody, 1945:470). The weights of grouse, their daily caloric intake and their approximate maintenance energy requirement (as calculated from Brody's metabolic requirements) are given in Table 16.

From Table 16, the measured caloric intake for the grouse was lower than that required for maintenance according to Brody.

As discussed before, the grouse in the vivarium were kept in small pens and were inactive. Possibly due to this lack of activity, they did not require as many calories for maintenance as Brody's figures suggest. It is also possible that the chickens tested might have had a higher metabolic rate. This comparison suggests that the calculated digestibility was low.

Summary and Conclusions

The apparent digestibility of the chicken breeder ration by the 4 grouse ranged from 51.2 to 64.9 percent. The mean was 57.4 percent. The variation was not statistically significant.

The range of the daily requirements of apparent digestible calories at about 72 to 75 degrees F. was 35.8 to 66.0. The range in body weight was 864.2 to 965.0 grams.

The range of the calculated daily requirement of water was 37.9 to 57.2 grams. The consumption of water was directly

AVERAGE WEIGHT OF GROUSE (in grams)	AVERAGE MEASURED CALORIC INTAKE	CALCULATED MAINTENANCE REQUIREMENT
864.2	69.7	70.5
915.3	74.3	82.3
946.1	82.0	88.2
965.5	88.2	98.5

Table 16. Weights of grouse, their daily caloric intake and their approximate maintenance energy requirement

related to the body weight of 3 of the 4 chickens.

The consumption of water per digestible calorie varied from .79 to 1.30 grams. The consumption of water per digestible calorie was significantly related in only 1 of 4 birds. That ratio was .86 grams water per digestible calorie.

CHAPTER 9

REPRODUCTIVE BEHAVIOUR

Introduction

This chapter is to present data on the breeding behaviour of blue grouse in the aviary and compare it to the behaviour of blue grouse in the field. The 3 main areas of investigation were visual communication, auditory communication, and the mating display.

Materials and Methods

Observations on wild and captive blue grouse were recorded descriptively. The aviary was visited daily for at least 2 hours from May through August. It was visited at least every 2 days through the remainder of the year. Fred Gornall made films of the mating display of grouse in the field which were used for comparison to the display of captive birds. Vocalizations were recorded on a Wollensack tape recorder at a tape speed of 7 1/2 feet per minute. The Wollensack microphone was either held by hand in the pen of the grouse, or fixed to the wall. The recordings were played to captive and wild grouse to observe their response.

Results

Visual Communication

The sexual display (Appendix 2) of the male blue grouse is described in the literature (Bendell, 1954; Bendell and Elliott,

1965; and Smith, 1960). Plate 7 is a photograph of the display.

The sexual display was given only during the spring and early summer. There was no difference observed between the sexual display of adults and yearlings, between different years, between varying daily weather conditions, or between the sexual display in the aviary and that described in the literature. Males in the aviary sometimes displayed on the roost. However, most display was on the floor of the pen.

On a few occasions females were observed giving the same sexual display as the males. Plate 8 is a photograph of the female display. The caruncle of the eye was yellow. The air sacs were not visible although the feathers on the neck were turned back.

Auditory Communication

Several vocalizations of blue grouse were recorded in the aviary.

Territorial males hoot during the reproductive season (Bendell and Elliot.1965). The males in the aviary also hooted during the spring. There was no hierarchy observed between the hooting males, in that one male did not stop hooting if a second male began. If anything, the hooting of one male stimulated the hooting of other males since groups of males were often heard hooting together in the aviary. Bendell and Elliott (1965) also observed in the field that the hooting of one male seemed to stimulate males on adjacent territories to hoot.

For the period of May 1 through June 20 of each year the

aviary was visited daily, and at different times of the day. The number of males hooting each day were counted and summed. Table 17 presents the total number of observations of hooting by adult and yearling birds as a percent of the possible observations of adults and yearlings hooting.

From Table 17, the adult males hooted more frequently than yearlings. This difference was statistically significant (Chi-square test at the 5 percent level of probability).

The incidence of hooting was calculated by summing the number of males hooting each day for 5 days and dividing by 5. This was done through the period April 20 through June 30 for 1963-65.

The relationship of the occurrence of male hooting and female squatting and egg laying during the spring is given in Figure 5. Note that the period of squatting coincides with the period of peak hooting each year. In 1963 and 1965, an adult male began to hoot about a week before yearling males, while in 1964, a yearling male hooted for a week before the first adult.

The first aggressive calls of males (Appendix 2) were observed about a week before the first hooting was heard each spring. The sexual display began and ended at the same time that hooting began and ended.

The flutter-jump described for males in the field (Bendell and Elliott, 1965; Blackford, 1963; and Wing, 1946) was not observed in the aviary.

In the spring, yearling and adult hens usually gave a distinct pre-copulatory cry, the whinny (Appendix 2), when ready to

	1963		1964		1965		TOTAL	
	AD[1]	YR[2]	AD	YR	AD	YR	AD	YR
No. males available	3	15	14	9	2	9	19	33
No. of visits	51	51	51	51	51	51	153	153
No. possible observations	153	765	714	459	102	459	969	1683
No. actual observations	46	33	53	13	36	5	135	51
Percent of observations on which males hooted	30	4	7	2	35	1	14	3

Table 17. Percent of total observations on adult and yearling male blue grouse upon which males hooted, May 1 through June 20, 1963-65

[1]Adults

[2]Yearlings

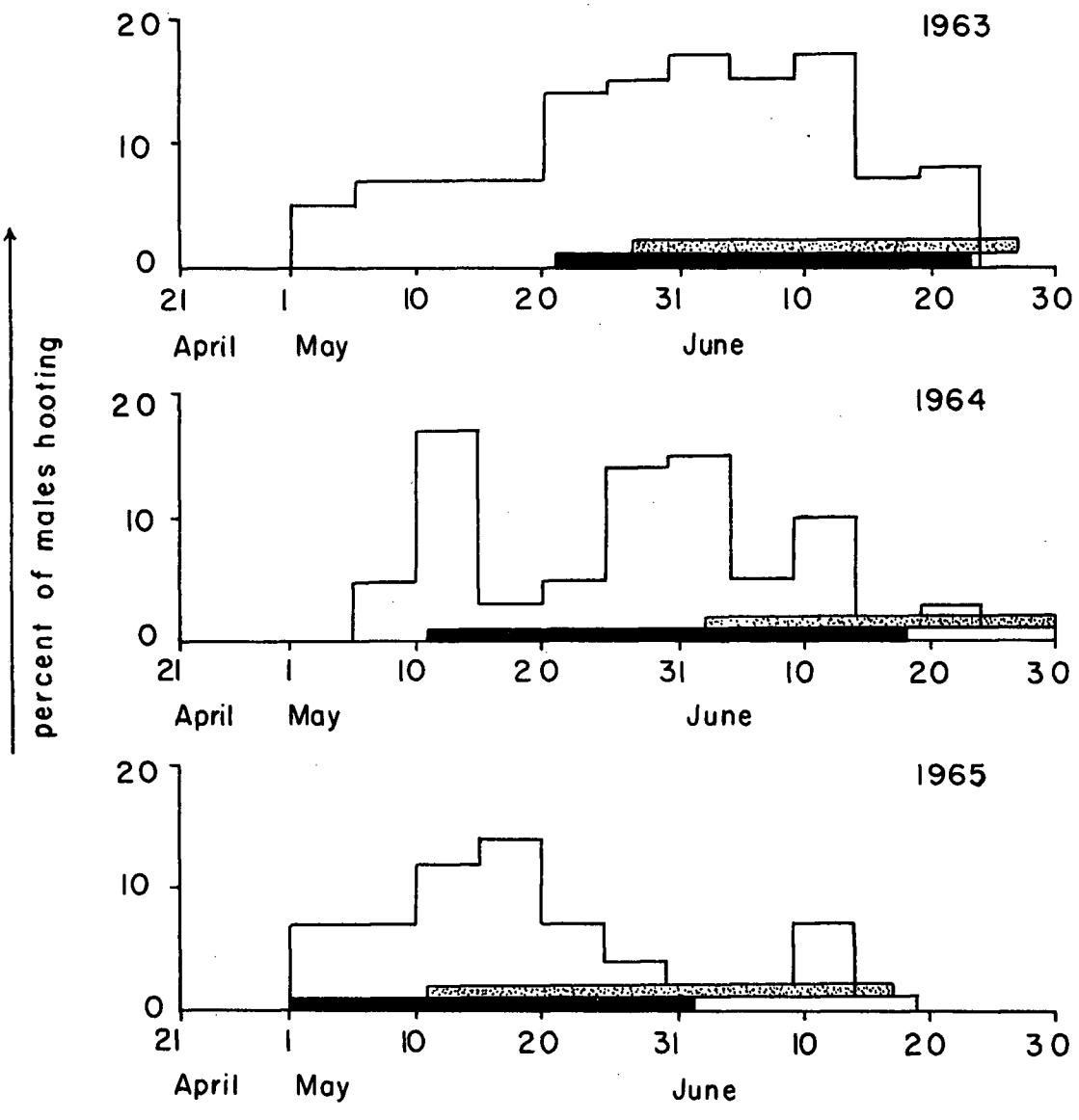

Figure 5. The relationship between the occurence of male hooting to female squatting and egg laying

Legend: —— percent of males in aviary population hooting
period of squatting of females
period of egg laying

squat for copulation. It could be heard at any time during daylight hours.

Whenever a female gave the whinny, reproductively active males immediately began to hoot or display or both.

The whinny was played on the tape recorder to aggressive males in the aviary. In every instance, reproductively active males began to hoot or give sexual display or both. One male was continuously aggressive. However, every time the whinny was played during the display of intense of intense aggressive behaviour, the male exhibited sexual behaviour and hooted.

Hens in the aviary immediately stopped all movement and listened whenever a hen gave a whinny, or a whinny was played on the tape recorder. They looked in the direction of the source but rarely replied.

Male grouse in the field responded to the whinny by hooting and advancing in sexual display toward the speaker (Stirling and Bendell, 1966). It did not cause known individually banded males to leave their previously observed territories.

Adult and yearling females that squatted or laid eggs without squatting often gave a staccato cry during the breeding season. It was called the female cry (Appendix 2). It was sometimes heard when females were squatting, but more often when females exhibited aggressive behaviour. Females in reproductive condition quickly gave the cry in response to another hen or a tape recording of the cry. Males responded to the female cry by hooting, but with less intensity than they responded to the whinny.

No other calls related to breeding were observed.

Mating Displays

The sequence of acts of the male during the actual mating display observed in the U.B.C. aviary was essentially the same as described by Bendell and Elliott (1965). In the aviary, the female either remains squatting through the series of male acts leading up to copulation, or walks around the pen very slowly. If the hen squats later, she does so when the male makes the short pre-copulatory run and gives a distinct pre-copulatory hoot. The pre-copulatory hoot sounds a little like a single syllable of the hoot, but because the function is completely different it is onomatopoetically called the "whoot" (Appendix 2). Otherwise she runs or flies away from the male when he begins the pre-copulatory run.

If the female remains squatting after the male gives the pre-copulatory whoot, the male begins to tread her. He may first bob his head 1 to 10 times over a period of 5 seconds to 3 or 4 minutes, or he may tread immediately.

The male takes 4 to 8 or 9 steps and settles with his feet approximately over the scapulae. The nape of the hen's neck is taken in the cock's bill. The wings of the male clasp the sides of the female for balance. The male tips his tail to one side, the female tips her tail to the other side. In the matings observed, the tail of the male was always tipped to the left and the tail of the female to the right. The male lowers himself so that the cloacae may come together for copulation. The uterus

protrudes from the cloaca of the female and from the cloaca of the male protrude two copulatory papillae upon which sperm is carried. These are applied together. Copulation lasts about 2 to 5 seconds.

Then, either the male steps off the back of the female or the female runs from underneath. Both birds stand still and ruffle their feathers for about 30 seconds. The male then becomes extremely aggressive and viciously attacks the female. In the aviary, the grouse were always separated at this point. About half the naturally mated hens squatted again after copulation. Two naturally mated hens laid 9 fertile eggs after only one mating. One of these hens laid a fertile egg 17 days after mating.

Some of the following variations and peculiarities were observed. The male did not always give the pre-copulatory whoot prior to mating if the female was already squatting at the time the male was introduced to the pen to begin his display. Females squatted in the presence of humans. Males in single pens sometimes gave the pre-copulatory whoot when alone. Some pairs mated after a minute of display or less while some required forty minutes of display or more before copulation took place.

One female was selective about which male she mated with. Consistently she squatted only when a particular male was put in to her pen. In successive years the males were both yearlings.

Discussion

The reproductive behaviour observed in the aviary was

essentially the same as reproductive behaviour observed in the field. This suggests that the basic pattern of displays and calls related to reproductive behaviour are innate.

The main function of the display of birds that come together only for mating is sex recognition (Marler, 1961). Display is also indicative of the bird's physiological condition (Marler, 1961). Blue grouse associate during the spring only for mating. Thus the primary function of the display would seem to be for sex recognition. The display also indicates the physiological states of both sexes.

It has been demonstrated that the size of the eye caruncle of a male chicken partially determines the success of initial encounters, that is, the male with the larger comb is more successful (Guhl, 1953). The eye caruncle of blue grouse changes from yellow to scarlet and expands as reproductive display becomes intense. This suggests that the intensity of the color of the caruncle and the size may function in reproductive display to indicate the physiological condition of the male.

Hamerstrom and Hamerstrom (1960) suggest that male territorial calls in the prairie chicken (Tympanuchus cupido pinnatus) serve 3 functions, to advertise the general territory, to threaten other males, and to attract females. Observations on the hooting of male blue grouse support this general suggestion. The hooting of male grouse is of low frequency and difficult to locate precisely by ear. The assumption is made that it is equally difficult for a grouse to locate exactly by ear. The hooting of an individual male has been observed to affect the hooting and

movements of males in adjacent territories (Bendell and Elliott, 1965). The fact that males begin to hoot immediately upon hearing the female whinny supports the suggestion that one function of hooting is to attract females.

The whinny is a call of high frequency and easy to locate accurately by ear. The variation in pitch may also aid location. When the whinny was played in the field, males responded quickly and were able to locate the source of the sound accurately. This suggests the function of it may be to direct the male to the female when she is ready to mate.

Thus I suggest the following relationship between the hooting of the male and the whinny of the female. Hooting advertises the presence and general location of the male. The female is attracted to the non-specific location of the male when she is ready to mate. The hen then gives the whinny, which directs the male to her.

The function of the female cry is uncertain. It was heard in the aviary when hens were ready to squat and also immediately prior to the attack of a hen upon its mirror image. It may be given as a result of conflicting drives or it may have a function in reproductive and aggressive behaviour.

The pattern of the mating display was essentially the same as recorded by Bendell and Elliott (1965) and filmed by Gornall. Some of the peculiarities such as a male treading a female without giving the pre-copulatory whoot may have been artifacts of captivity since it has not been observed in the field. There was no difference observed between treading with or without the whoot.

Male chickens with a high reproductive drive and no releaser sometimes display and ejaculate while penned alone (C.V. Roberts, personal communication). Similarly, male grouse giving the pre-copulatory whoot while alone in their pens probably had a high reproductive drive and no releaser. This behaviour has not been observed in the field.

The squatting of hen grouse for a human is similar to sexual imprinting described for domestic fowl (Guiton, 1959; Guiton, 1961; and Klopfer, 1965). Some of these imprinted grouse mated with a cock if a human was present. Hens squatted in response to the waving of a human hand. Imitation of the whoot was not as effective for stimulating the female to squat. Possibly because the hen faces forward while squatting, any movement sufficient to be seen from the corner of the eye is sufficient to act as a releaser for squatting behaviour.

The hooting of males always began before any female reproductive behaviour was observed. In 1965 the first hooting and squatting were both observed on May 1 (Figure 5). Male aggressive behaviour was observed before May 1 in 1965 and it is possible that hooting may have occurred earlier but was not heard. It is also possible that males may not hoot for extended periods at first and thus have less chance of being heard.

Most squatting behaviour is synchronized with the peak of hooting. This, plus the fact that hooting was usually observed first, suggests that hooting may be an ultimate stimulus to female reproductive behaviour.

Summary and Conclusions

The data suggest that the reproductive displays are innate.

The data suggest the hooting of the male serves to attract females to the territory of the male. Once attracted to the general area, the female gives a whinny call to direct the male to her.

Hooting may be an ultimate stimulus that releases reproductive behaviour in hens.

Hen blue grouse imprint sexually upon humans but will often mate with a cock grouse if a human is present.

Movement immediately behind a hen may be the stimulus necessary to cause that hen to squat.

CHAPTER 10

AGGRESSION AND THE REPRODUCTIVE CYCLE

Introduction

The behaviour of territorial male blue grouse has been described in detail (Bendell and Elliott, 1965). In short, males advertise their territories by hooting and defend them by threat displays and physical attack. Most non-territorial males are yearlings and do not contribute significantly to the breeding population.

Females occupy a home range during the pre-nesting and nest-in periods and these home ranges are spaced (Bendell and Elliott, 1965). It is uncertain whether or not these home ranges are mutually exclusive. If the home range of the hen is exclusive and thus homologous to the territory of the cock, then I would make the hypothesis that hens would show some aggressive behaviour homologous to the aggressive behaviour of the cocks. Thus, I wanted to test hens in the aviary for aggressive behaviour that might function in the field to space them during the reproductive season. The function of spacing of the home ranges of hens is discussed.

Materials and Methods

Data on aggressive behaviour was collected in several ways. Photographs, tape recordings and written descriptions were made.

As a test for aggressive behaviour, male and female grouse

in single pens were presented with a mirror in which they could see their own image. Grouse reacted as much to their own mirror image as to a dummy, and dummies were too quickly mutilated to be used for extended periods. Live birds were not used because they were too frightened after being handled to act normally.

The test were done in mid-morning once a week during the late winter and spring and twice a week from May through August. Since grouse are most active during the early morning and evening (Bendell, 1955) the tests were done in mid-morning to avoid recording this diurnal movement. Activity for the remainder of this chapter is defined as any movement, posture, or call given by a grouse in response to the mirror image.

The number of hens tested was as follows.

YEAR	NO. OF ADULTS	NO. OF YEARLINGS
1964	10	15
1965	9	11

The number of cocks tested was as follows.

YEAR	NO. OF ADULTS	NO. OF YEARLINGS
1964	14	9
1965	2	9

A shorthand system of assigning a 1 or 2 letter symbol to

each posture, movement or call was used to record each action the bird made while the mirror was in the pen. Every 5 seconds during the tests, an electric interval timer buzzed and a check-mark was made in the notes. Thus all movements were recorded chronologically and at known intervals of time.

Data was collected for 3 minutes after the mirror was presented to the grouse. This length of time was chosen after several extended tests indicated that a grouse reacted to its image within a maximum of 3 minutes. Usually grouse reacted within a few seconds. All activity was recorded.

The symbols used for females were as follows. They are listed in functions I think they serve. There is some duplication. A detailed description of each is included in Appendix 2.

Class	Act	Symbol
Investigative	head turn	ht
Threat	neck stretch	ns
	backward stance	bs
	croak call	cr
	peck mirror image	pk
	cluck call	cl
Conflict	male sexual display	dis
	walk	wa
	bleat call	bl
	puk-puk call	puk
	scratch	scr
	stretch	str

Class	Act	Symbol
	conflict pecking	pkc
Fear	walk	wa
	bleat call	bl
Reproductive	whinny call	wh
	cry call	cy
	squat	sq

The symbols used to record male behaviour were as follows.

Class	Act	Symbol
Investigative	head turn	ht
Threat	neck stretch	ns
	backward stance	bs
	cackle call	ca
	cough call	co
	peck mirror image	pk
Conflict	female sexual display	dis-f
	walk	wa
	scratch	scr
	stretch	str
	conflict pecking	pkc
Fear	walk	wa
Reproductive	display	dis
	hoot call	ho

The data were analyzed by scoring one point for each symbol recorded. The total number of observations upon each type of movement, for all hens (or cocks) on each day was divided by

the number of grouse tested. This gave a numerical average that could be graphed from day to day. The total of all observations of all movements on one day was divided by the total number of birds tested, to give an overall mean number of movements for each grouse in the tested population. This totalled mean was used because all movement represented a reaction to the mirror image, whether it was investigative, threat, conflict, fear, or reproductive. For convenience the totalled mean of the activity of the population is referred to as the "index" in the following discussion.

The daily indicies were graphed. The values were tested with an analysis of variance and Duncan's Multiple Range Test for significant differences between points at the 5 percent level of significance. The periods during which hens squatted and laid eggs were plotted on the graph to check for correlation of periods of activity in reaction to the mirror image. The data for males was treated identically.

Results

Figure 6 gives the graphs of the daily indicies for the females through the breeding seasons of 1964 and 1965. The level of activity changed through the breeding season and it was highest when the females squatted and laid eggs. The range of higher values (marked by horizontal dashed line) were significantly different from the range of lower values (marked by horizontal dashed line). The values between these lines were not significantly different from each other.

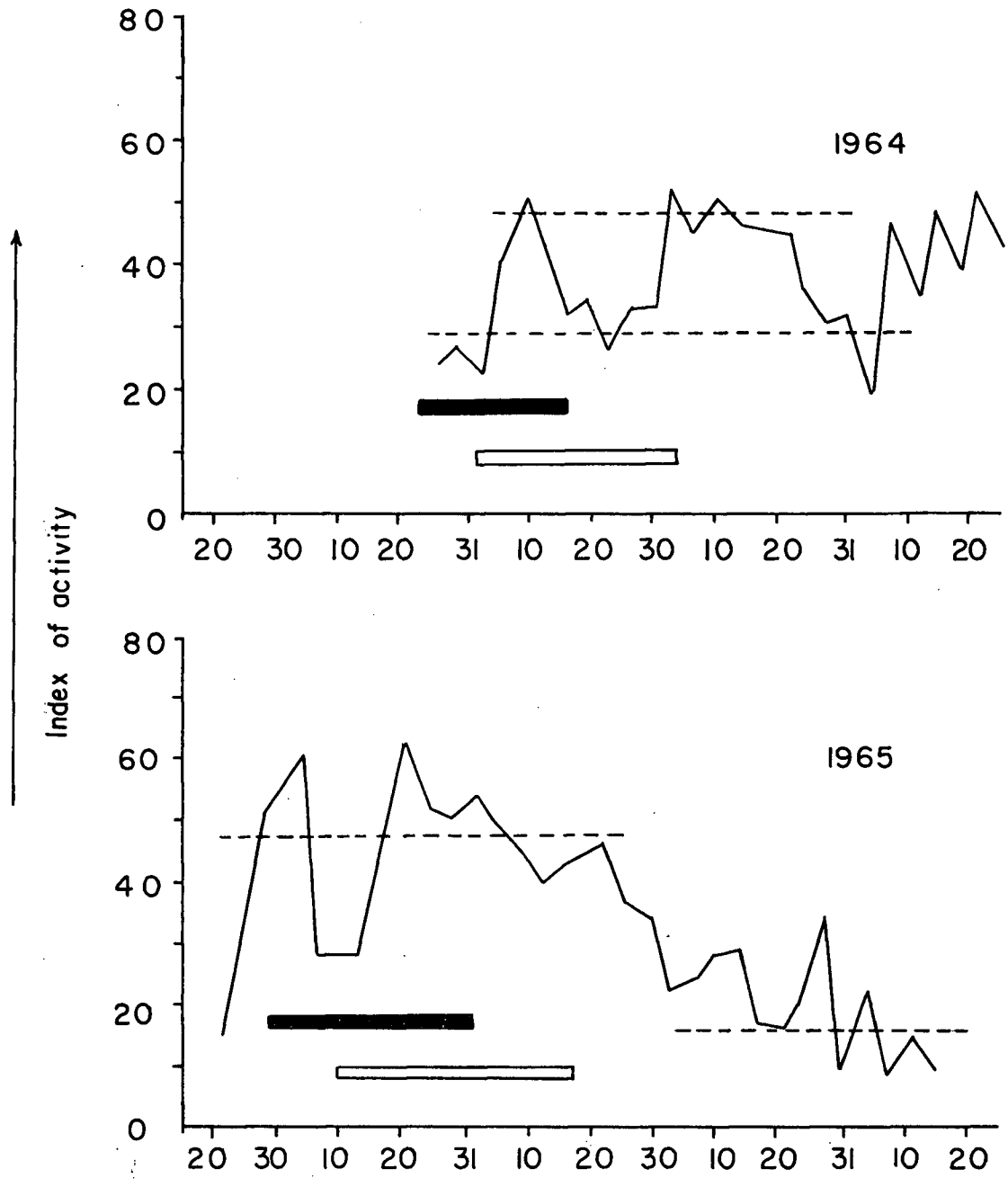

Figure 6. Indices of female activity during the breeding season

Legend: ▬ period of squatting

▭ period of egg laying

The mirror test was first developed and used to test the activity level of the population 3 days after squatting behaviour began in 1964. Note the rise in activity in August, 1964 compared to August, 1965. The tests done in August, 1964 were done early in the morning when the grouse were more active. Because the August 1964 data was not collected in the standard manner it was not considered in a comparison of the 2 graphs. Thus the 2 graphs were compared for the period from 3 days after squatting behaviour began through 30 days after egg laying ceased (68 days). They were not significantly different (Sign test at the 5 percent level of probability).

All behavioural characters were analyzed to determine which ones occurred in a repeatable pattern. The characters that showed a pattern all showed the same pattern as the graph. These characters were: head turn, neck stretch, backward stance, walk, and cluck. The incidence of the rest of the characters varied at random.

Figure 7 gives the graphs of the daily indicies for the males through the breeding seasons of 1964 and 1965. The August, 1964 data was not considered because it was collected at a different time of day than the earlier data of that year. As in Figure 6, the horizontal dashed lines indicate the ranges of significant difference between indicies.

The graphs of male indicies of 1964 and 1965 were tested over the same period as the graphs of female indicies were compared. They were statistically different (Sign test at the 5 percent level of probability).

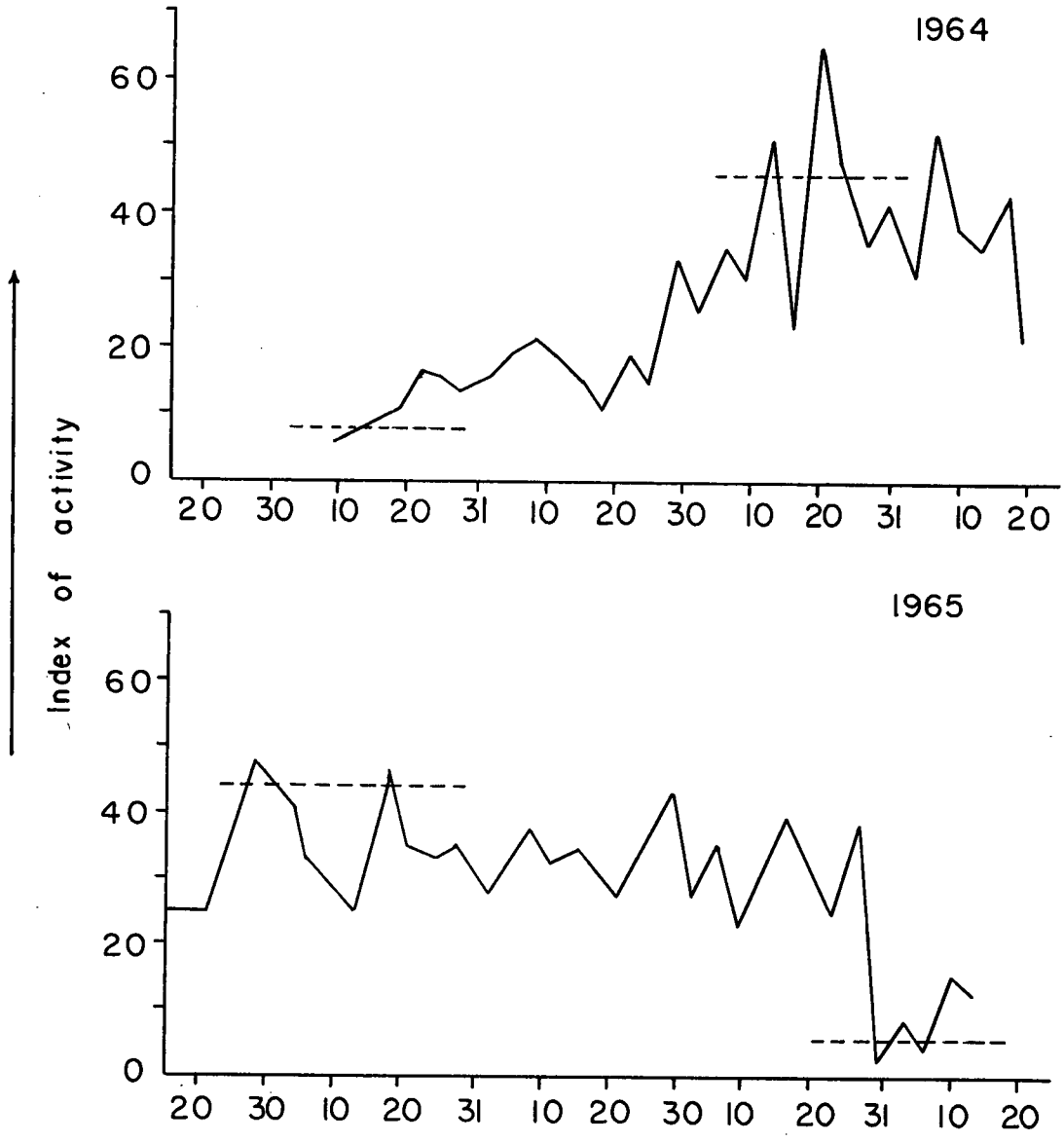

Figure 7. Indices of male activity during the breeding season

Discussion

Hens show fidelity to a specific area for nesting (Zwickel, 1965). As previously mentioned, hens occupy a home range during the pre-nesting and incubating period but it is uncertain whether these home ranges are exclusive or defended. After the clutch hatches, hens and broods are observed at widely separated points and at times mixed with other broods (Bendell, 1955). The greatest reaction of hens to their mirror image was during the time that hens in the field would occupy a home range (Figure 6).

The index decreased past the end of egg laying to the lowest point 25 to 30 days after the last egg was laid. This coincided with the time the last egg would have hatched. After that period, the index fluctuated slightly but remained low.

The possibility remains however that the index might have remained high if hens had been allowed to incubate and hatch clutches. The index may have dropped from the lack of stimulus. I cannot deny this possibility as there was no control, but the evidence from the field suggests that interaction between hens at this time is low.

A strong dip in the value of the index during the squatting and laying period of 1964 was repeated in 1965. There was no change in weather that might effect activity. As mentioned before, these graphs are not different statistically. This suggests there may be a biological function for a lack of aggressive behaviour at this time. The only suggestion I can make is that hens may be aggressive during the period of selecting a

nesting site, then become more docile for a period to allow a male to copulate, and then become more aggressive when laying and defending the nest site. There are data contrary to this reasoning. First, all hens do not exhibit the same display at the same time, that is, some hens may be laying eggs when others begin to squat. Thus, one would not expect the population to give such a low index. secondly, the one natural mating that occurred in 1964 and 2 in 1965 all took place during the first peak of activity, not during the depression.

The patterns of aggressive behaviour exhibited by cocks in the aviary are observed in the field at the corresponding time in the reproductive cycle. Correspondingly, the aggressive behaviour exhibited by hens in the aviary during the reproductive period may also occur in the field. If it does, then the home ranges of hens may be mutually exclusive during the nesting period and possibly defended.

The nests of hens in the field are spaced rather than clumped. It has been shown in the wood pigeon (Columba palumbus) that spacing of nests functions for protection against predation (Murton, 1962). Thus the spacing of nests of blue grouse may serve the same function.

The range of indicies of male behaviour show little statistical significance. This is because there is more individual variation between males than there is between females. The difference between the graphs of the male indicies of 1964 and 1965 is thus partly caused by individual males that were exceptionally aggressive. I cannot explain why the index for males in July,

1964 was so high. It was not as high in 1965. The July, 1964 index for females was not high. The lack of statistically significant results and lack of repeatable data between years reduced the value of the male aggression tests.

Descriptive data on aggressive behaviour of cocks was the same as observed in the field and thus acted as a partial control. This was valuable since it is difficult to obtain observations on female behaviour in the field for comparison to behaviour observed in the aviary.

Summary and Conclusions

A relationship between the aggressive behaviour of females and the reproductive cycle was demonstrated in the aviary. The aggressive behaviour of males in the aviary and in the field was the same. Thus, the data suggest that the behaviour of females in the field may be the same as observed in the aviary.

On the basis of aggressive behaviour observed in the aviary, ti seems possible that the home ranges of females in the field are mutually exclusive and may also be defended until the clutch has hatched.

CHAPTER 11

WINTER AGGRESSION

Introduction

Blue grouse have a seasonal migration. They winter in the subalpine forests and breed on open alpine areas and lowland burns and logging slashes. Present data on the natural regulation of numbers of blue grouse show that more chicks leave the breeding range at the end of the summer than are required to compensate for adult mortality (Zwickel, 1965). This suggests either heavy mortality of chicks on the winter range or high dispersal, since a surplus of yearlings is not observed on the breeding range in the spring.

It has been suggested that winter territoriality of red grouse (Lagopus lagopus scoticus) regulates the number of red grouse available for breeding in the spring. Surplus birds are forced into marginal habitat and die there (Watson, 1964).

The behaviour of blue grouse was studied at the aviary during the winters of 1963 through 1965 for evidence of winter aggression.

Materials and Methods

The big pen described in chapter 2 (Fig. 1, E) was used to study interactions of blue grouse. The number, age, and sex of birds put into the big pen in February 1964, were as follows.

SEX	AGE	NUMBER
female	yearling	2
female	adult	2
male	yearling	1
male	yearling	1

Birds which died were replaced as required.

The number, age, and sex of birds put into the big pen in October, 1964 for the winter of 1965 were as follows.

SEX	AGE	NUMBER
female	yearling	1
female	adult	1
male	yearling	1
male	adult	1

Birds which died were replaced as required.

Results

In all 3 years, 1 or 2 adult males in the aviary population showed aggressive behaviour and hooted from about the end of January through February of each year. After this period, there was no hooting until April or May, prior to the normal breeding season.

In 1965, the adult male in the big pen quickly became

dominant. He was unable to fly so that the yearling male was safe from attack while roosting. The yearling male was subordinate although he gave aggression calls from the roost, where he was most frequently seen. His sperm was viable but the adult male prevented him from displaying to the females. This yearling male was dead in September, 1964. He was emaciated and there was no food in the crop or stomach. He probably starved to death.

Yearling male 1286 was introduced to the big pen in October, 1964. The adult male followed the yearling for a few minutes but made no attack. The yearling was submissive. The adult remained dominant but allowed the yearling to feed.

The adult male was first observed giving aggression calls on January 5, 1965. This was the last day the yearling was observed on the ground. By the end of January, the yearling was so hungry he flew from the roost to my arm to feed from my hand. He was dead of starvation on February 2, 1965. His crop and stomach were empty and all body fat was gone. He weighed 998 grams.

A second yearling male was placed in the big pen on February 6. He was selected because of large size. The adult male attacked the yearling male immediately. He was badly pecked during the next 2 days and was dead on February 9.

Males were never observed to interact with the females during the winter. No interaction between females was observed during the winter.

There was also no interaction observed during the fall.

Discussion

Aggressive behaviour exhibited by males in the aviary during the spring has been observed in the field. Correspondingly, the aggressive behaviour observed in the aviary during the winter may also occur in the field.

In the aviary, winter aggressive behaviour was only exhibited by adult males. Male red grouse are territorial during the winter. Non-territorial males are excluded to marginal habitat and die (Watson, 1964). However, it is difficult to see how juvenile male blue grouse could be excluded to marginal habitat during the winter since there is no evidence of any shortage of winter range.

The fact there was no interaction during the fall suggests that simple crowding did not cause the interactions between grouse in the spring.

The hens showed no aggressive behaviour during the winter. In late spring, 1964, one hen became very aggressive for several days, chased the adult male around the pen and viciously pecked him. No other interaction between the hens in the big pen was observed.

Summary and Conclusions

Aggressive behaviour was studied during the winters from 1963 through 1965. Each year adult males were observed giving aggression calls or hooting during late January to February. One adult male in the big pen killed 2 yearling males in early February.

This suggests the possibility of a period of winter aggression similar to that observed in red grouse.

No similar behaviour was observed in females.

CHAPTER 12

SUMMARY

1. Blue grouse were held in captivity over a period of 3 years to find the best methods of holding and rearing them. In addition, data were obtained on the weights, survival, behaviour, nutrition, and diseases of captive blue grouse.
2. Grouse were held in wire pens that measured 2 feet by 4 feet by 8 feet, 6 feet by 4 feet by 8 feet, and 20 feet by 10 feet by 24 feet. On the basis of plumage condition and reproductive performance the medium sized pens were most suitable. Weights and death rates were the same in all sizes of pens.
3. Captive grouse fed on commercial chicken breeder ration lived and maintained weight indefinitely. The weights of the grouse in the aviary were comparable throughout the year to weights of grouse in the field.
4. The cold wet weather of winter affected the survival of grouse in that the number of deaths in the winter was double the number of deaths in summer.
5. The mortality of 1965 was exceptionally severe and correlated with the exceptionally cold wet winter of that year.
6. Death rates were the same among, (a) the three groups of chicks brought to the aviary, (b) birds of both sexes, and (c) birds of each age group.

7. The diseases that caused the greatest mortality were gizzard erosion, aspergillosis, and enteritis.
8. Feather-pecking by chicks was stopped by placing fir boughs in the pens.
9. Reproductive display of males and females was less in the aviary than in the field.
10. The only successful method of mating grouse in the aviary was to put a displaying male into the pen of a squatting female.
11. Hens that exhibited reproductive behaviour were sexually imprinted upon humans.
12. The fertility and hatchability of blue grouse eggs in the aviary was 1/3 to 1/2 of that recorded from the field.
13. The mean clutch size of hens in the aviary was larger than the mean clutch size of hens in the field.
14. Blue grouse can be artificially inseminated by using techniques developed for domestic fowl. Hens should be allowed to lay 2 or 3 eggs before insemination for best results in terms of continued egg laying.
15. The fertility and hatchability of eggs from hens that were artificially inseminated were comparable to that of eggs from hens that were naturally bred in the aviary.
16. The combination of incubating grouse eggs in the battery incubators and brooding chicks by the methods of Zwickel (1965) was satisfactory.
17. Blue grouse were unable to survive in the aviary on a diet of dried and pelleted Douglas fir needles.

18. Grouse that were fed a diet with 18 percent protein had better survival and exhibited more reproductive behaviour than grouse fed a diet with 24 or 28 percent protein.
19. The apparent digestibility of commercial chicken breeder ration by four grouse varied from 51.2 to 64.9 percent. The mean was 57.4 percent. The variation was not statistically significant.
20. The range of the calculated daily water requirement was 37.9 to 57.2 grams. The consumption of water was directly related to body weight in 3 of the 4 birds.
21. Adult males in the aviary hooted more than yearling males.
22. The fact that males in the field are attracted so quickly and accurately to the whinny suggests it directs the male to the female.
23. The stimulus to squat in the female is likely movement behind and at the same level as the hen.
24. A relationship between the aggressive behaviour of females and the reproductive cycle was demonstrated in the aviary. This pattern of behaviour may also occur in the field as a mechanism of spacing during the period of nesting.
25. Males became more aggressive during the breeding season and less aggressive through the summer.
26. Aggressive behaviour was observed during the winter in adult males. This suggests the possibility of a period of winter aggression similar to that observed in red grouse.
27. The following postures and calls were more frequent during the reproductive season; females, head-turn, neck-stretch,

backward stance, walk, cluck, whinny, cry, and squat; males, head-turn, neck-stretch, backward stance, peck, walk, cackle, cough, hoot, and whoot.

28. The following grouse calls were analyzed with sonograms: male hoot, female hoot, male cackle, male cough, female bleat, female whinny, female cry, and female cluck.

LIST OF REFERENCES

Allen, A.A., 1929, Ten years experiments in the rearing of ruffed grouse in captivity, Trans. Am. Game Conf., 16:3-21.

Allen, G.A., 1964, Green Peafowl (Pavo muticus), Game Bird Breeder's Gazette, 8(1):10-14.

Armstrong, E.A., 1950, The nature and function of displacement activities, Symp. Soc. Exp. Biol., 4:361-384.

_____., 1963, A Study of Bird Song, Oxford University Press, New York, 335 pp.

Banks, E.M., 1954, Social organization in red junglefowl hens, Ecology, 37:239-248.

Batterson, W.M., 1957, The propagation of grouse, Game Bird Breeder's Gazette, 7(10):12-17, 50-51.

Beer, J.B., 1943, Food habits of the blue grouse, Jour. Wildl. Mgmt., 7(1):32-43.

Biely, J., E.A. Lloyd and I.W. Moynihan, 1950, Poultry Diseases, Province of British Columbia, Dept. of Agriculture, Bull. No. PB 108, 109 pp.

Bendell, J.F. 1955a, Age, molt and weight characteristics of blue grouse, Condor, 57(6):354-361.

_____., 1955b, Age, breeding behaviour and migration of sooty grouse, Dendragapus obscurus fuliginosus (Ridgway) Trans. N. Am. Wildl. Conf. 20:367-381.

_____., and P.W. Elliott, 1965, Territorial behaviour and the regulation of breeding density in blue grouse, Can. Wildl. Service Series (in press).

Blackford, J.L., 1958, Territoriality and breeding behaviour of a population of blue grouse in Montana, Condor, 60(3):145-158.

_____., 1963, Further observations on the breeding behaviour of a blue grouse population in Montana, Condor, 65(6):485-513.

Borror, D.J., 1960, The analysis of animal sounds, Animal sounds and communication, A.I.B.S. publication No. 7m 26-37.

_____., and C.R. Reese, 1953, The analysis of bird songs by means of a vibrilizer, Wilson Bulletin, 65(4):271-276.

Brody, S., 1945, Bioenergetics and Growth, Hafner Publishing Co., New York, 1023 pp.

Bump. G., R.W. Darrow, F.C. Edminster, and W.P. Crissy, 1947, The Ruffed Grouse, Holling Press Inc., Buffalo, New York, 915 pp.

Buss, I.O., and B.A. Schottelius, 1954, Breeding age of blue grouse, Jour. Wildl. Mgmt., 18(1):137-138.

_____., R.D. Conrad and J.R. Reilly, 1958, Ulcerative enteritis in the pheasant, blue grouse and california quail, Jour. Wildl. Mgmt., 22(4):446-449.

Collias, N.E. and M. Joos, 1953, The spectrographic analysis of sound signals of the domestic fowl, Behaviour, 5:175-187.

Cowan, J.M., 1959, Rearing grouse, a challenge to the game breeder, Game Bird Breeder's Gazette, 10(2):49-54.

Dalke, P.D. et al., 1960, Seasonal movements and breeding behaviour of sage grouse in Idaho, Trans. N. Am. Wildl. Conf. 25:396-407.

Davis, D.E., 1963, The hormonal control of aggressive behaviour, Proc. Int. Ornith. Cong., 13:994-1003.

Davis, I.L., 1964, Biological acoustics and the use of the sound spectrograph, Southwestern Naturalist, 9(3):118-145.

Delacour, J., 1959, Pheasant Breeding and Care, All-Pets Books, Fond du Lac, Wisconsin, 108 pp.

Edminster, F.C., 1947, The Ruffed Grouse, Its Life History, Ecology and Management, The MacMillan Co., New York, 385 pp.

Etkin, E.T., 1964, Social Behaviour and Organization Among Vertebrates, University of Chicago Press, Chicago, 307 pp.

Evans, K.E., 1964, Habitat requirements of the greater prairie chicken in Colorado, Unpublished M.Sc. Thesis, Colorado State University, 50 pp.

Ewing, W.R., 1963, Poultry Nutrition, 5th Edition, Ray Ewing Co., Pasadena California, 1475 pp.

Fay, L.D., 1963, Recent success in raising ruffed grouse in captivity, Jour. Wildl. Mgmt., 27(4):642-647.

Fowler, R.G. and D.I. Meyer, 1961, Physics for the Engineer and

Scientist, Allyn and Bacon, Inc., Boston, 553 pp.

Gibson, G.G., 1965, The taxonomy and biology of Splendidofilariine Nematodes of the Tetraonidae of British Columbia, Unpublished Ph.D. Thesis, University of British Columbia, 235 pp.

Grange, W.B., 1948, Wisconsin Grouse Problems, Wisconsin Conservation Department, Madison, Wisconsin, 318 pp.

Greenberg, D.B., 1949, Raising Gamebirds in Captivity, D. Van Nostrad Co. Inc., New York, 224 pp.

Guhl, A.M. and L.L. Ortmann, 1953, Visual patterns of recognition of individuals among chickens, Condor, 55(4): 287-298.

_____., 1962, The Behaviour of Chickens, CHapter 17 of The Behaviour of Domestic Animals, E.S.E. Hafez, London, 857 pp.

Guiton, P., 1959, Socialization and imprinting in brown leghorn chicks, Animal Behaviour, 7(1-2):26-34.

_____., 1961, The influence of imprinting on the agonistic and courtship responses of the brown leghorn cock, Animal Behaviour, 9(3-4):167-177.

Hamerstrom, F. and Frances Hamerstrom, 1960, Comparability of some social displays of grouse, Proc. 7th Ornith. Cong. 274-293.

Hansen, N., 1961, Raising blue grouse, Game Bird Breeder's Gazette, 10(2):49-54.

Hart, D., 1964, Propagation of game birds, Gamebird Breeder's Gazette, 13(1):18-22.

Hill, R., 1962, Raising prairie chickens, Game Bird Breeder's Gazette; 11(6):11-13

Hoffman, R.S., 1961, The quality of the winterfood of the blue grouse, Jour. Wildl. Mgmt., 25(2):209-210.

Jenkins, D., 1961, Social behaviour in the partridge, Ibis 103: 155-188.

_____., A. Watson and G.R. Miller, Population studies on red grouse, Lagopus lagopus scoticus (Lath.) in Northeast Scotland, Jour. Anim. Ecol., 32:317-376.

Kirkpatrick, C.M., 1964, Age vs. environment as conditions for

reproduction in caged bobwhites, Jour. Wildl. Mgmt., 28(2): 240-243.

Klopfer, P.H., 1965. Imprinting: a reassessment, Science, 147(3655):302-303.

Koivisto, I., 1965, Behaviour of the black grouse Lyrurus tetrix (L.) during the spring display, Finnish Game Paper 26, Helsinki, 60 pp.

Lacher, J.R. and D.D. Lacher, 1965, Blue grouse in captivity, Jour. Wildl. Mgmt., 29(2):404-405.

Lancaster, D.A., 1964, Biology of the brushland tinamou, Nothoprocta cinerascens, Bull. Am. Mus. Nat. Hist., Vol. 127, Article 6, 314 pp.

Lehmann, V.W., 1941, Attwater's prairie chicken, its life history and management, N. Am. Fauna 57, U.S. Govt. Printing Office, 63 pp.

Li, J.C., 1964, Statistical Inference, Edwards Brothers, Inc., Ann Arbour, Michigan, 657 pp.

Lumsden, H., 1961, Displays of the spruce grouse, Can. Field Nat., 75(3):152-160.

Marks, H.L., and P.D. Lepore, 1965, A procedure for artificial insemination of Japanese quail, Poultry Science, 44(4): 1001-1003.

Marler, P., 1955, Characteristics of some animal calls, Nature, 176:6-8.

_____., 1961, The evolution of visual communication, A University of Texas Symposium, pp. 96-121.

_____., and D. Isaac, 1960, Physical analysis of a simple bird song as exemplified by the chipping sparrow, Condor, 62(2): 124-135.

Marshall, W.H., 1946, Cover preferences, seasonal movements and food habits of Richardson's grouse and ruffed grouse in southern Idaho, Wilson Bulletin, 58(1):42-51.

Moynihan, M., 1955a, Remarks on the original sources of displays, Auk, 72(3):240-246.

_____., 1955b, Types of hostile display, Auk, 72(3):247-259.

Murton, R.K. and A.J. Isaacson, 1962, The functional basis of some behaviour in the wood pigeon Columba palumbus, Ibis, 104:503-521.

Nelson, M.M. and H.M. Evans, 1953, Relation of dietary protein levels to reproduction in the rat, Journal of Nutrition, 32:71-83.

Pyrah, D., 1961, Sage grouse investigations, Job completion report, Idaho Dept. of Fish and Game, mimeo. 20 pp.

Ralston Purina Co., 1963, Commercial game bird raising, Game Bird Breeder's Gazette, 12(5):10.

_____., 1964, Ulcerative enteritis in quail and grouse, Game Bird Breeder's Gazette, 13(2):10-11.

Ripley, S.D., 1962, Important news about aspergillosis, Game Bird Breeder's Gazette, 11(7):20.

Schaller, G.B. and J.T. Emlen, 1962, The ontogeny of avoidance behaviour in some precocial birds, Animal Behaviour, 10(3-4):370-381.

Schurch, A.F., L.E. Lloyd and E.N. Crampton, 1950, The use of chromic oxide as an index for determining the digestibility of a diet, Journal of Nutrition, 43:629-636.

Simard, B.R., 1964, The testicular cycle of blue grouse (Dendragapus obscurus fuliginosis) and its relation to age, breeding behaviour and migration, Unpublished M.Sc. Thesis, University of British Columbia, 113 pp.

Simpson, G., 1935, Breeding blue grouse in captivity, Trans. Am. Game Conf., 21:218-219.

Smith, N., 1960, Molt patterns and breeding behaviour in captive blue grouse, M.S. Thesis, Washington State University, 93 pp.

Smith, N., and I.O. Buss, 1963, Age determination and plumage observations of blue grouse, Jour. Wildl. Mgmt., 27(4): 566-578.

Smith, W.J., 1963, Vocal communication of information in birds, American Naturalist, 47(893):117-125.

Stewart, R.E., 1944, Food habits of blue grouse, Auk, 46(2): 112-120.

Stirling, I. and J.F. Bendell, 1966, Census of blue grouse with recorded calls of a female, Jour. of Wildl. Mgmt., 30(1): (in press).

Stokes, A.W., 1961, Voice and social behaviour of the chukar partridge, Condor, 63(2):111-127.

_____., 1963, Agonistic and sexual behaviour in the chukar partridge, Animal Behaviour, 11(1):;2;-;34.

Taylor, W.L., 1949, Fertility and Hatchability of Chicken and Turkey Eggs, John Wiley and Sons, Inc., New York, 423 pp.

Tinbergen, N., 1953, Social Behaviour in Animals, Methuen and Co. Ltd., London, 150 pp.

_____., 1959, Comparative studies of the behaviour of gulls, Behaviour, 15(1-2):1-70.

Watson, A., 1964, Aggression and population regulation in red grouse, Nature, 202:506-7.

_____., and D. Jenkins, 1964, Notes on the behaviour of the red grouse, British Birds, 57:137-170.

White, J.C., 1957, The American Grouse, Game Bird Breeder's Gazette, 6(2):14-18, 53.

Wing, L., 1946, Drumming flight in the blue grouse and courtship characters of the Tetraonidae, Condor, 48(2):154-157.

_____., 1947, Seasonal movements of the blue grouse, North Am. Wildl. Conf., 12:504-510.

Wood, E.D., 1956, Blue grouse, Game Bird Breeder's Gazette, 6(4):16-17.

Wood-Gush, D.G.M., 1955, The behaviour of the domestic chicken: a review of the literature, British Journal of Animal Behaviour, 111(3):81-110.

_____., 1956, The agonistic and courtship behaviour of the brown leghorn cock, British Journal of Animal Behaviour, 4:133-142.

_____., 1957, Aggression and sexual activity in the brown leghorn cock, British Journal of Animal Behaviour, 5:1-6.

Zwickel, F.C., 1964, Early mortality and the numbers of blue grouse, Unpublished Ph.D. Thesis, University of British Columbia, 153 pp.

APPENDIX 1

DISEASES OF GROUSE IN U.B.C. AVIARY

Introduction

This appendix is to catalogue the diseases identified in blue grouse held at the U.B.C. aviary. The signs and treatments for each disease are discussed.

Sick grouse exhibited several external signs. A hunched posture was most characteristic (Plate 7). Sick grouse exhibited little movement. Breathing was often forced and had a rasping sound. White diarrhetic feces were characteristic.

Post mortem internal examination of many grouse showed several signs of disorder but none severe enough to have caused death. Several birds were taken to the Animal Pathology Laboratory of the Federal Department of Agriculture but nothing definite was isolated.

The following is a list of the diseases recognised in the aviary.

Aspergillosis

Aspergillosis is a fungal disease of the lungs and air sacs, caused by the fungus Aspergillus fumigatus or, rarely, A. niger. In extreme cases it spreads throughout the viscera also.

External symptoms are a hunched stance, loud rasping breathing and white diarrhetic droppings. Internally, cream coloured nodules are found throughout the lungs and air sacs. The air

sacs may become a solid lump of mold and nodules of fungus may occur throughout the viscera. Death occurs by suffocation when the fungi block the trachea.

Treatment of aspergillosis has not been very successful. Biely et al. (1950) state treatment is of no value. Ripley (1962) used Amphoteracin B (Squibb) mixed with Alevaire in a spray to cur waterfowl. One gosling was successfully treated by spraying it four times a day for 10 days in a plastic tent with an auxillary supply of oxygen. This method was impractical for use at U.B.C. W.G. Ford, Supervisor of Washington State Game Farms, found that zinc bacitracin, marketed under the brand name of Baciferm, reduced the incidence of aspergillosis on the State Game Farms (personal communication). This product was used at U.B.C. although no difference in the number of deaths due to aspergillosis was observed.

The mechanism of infection is inhalation of spores from moldy feces and feed. The aviary was sprayed regularly to reduce the mold.

Gizzard Erosion

Gizzard erosion is a degeneration of the lining of the gizzard. The gizzard stones eventually go into the muscle. The bird stops eating and death is by starvation. The causative organism has not been isolated.

External signs are hunched stance, white diarrhetic droppings and bad smelling breath. Internal examination reveals brown pussy scars of earlier infections that have healed. The

gizzard smells foul.

Treatment was with Terramycin and Polysol in drinking water.

Ulcerative Enteritis

Ulcerative enteritis is an inflammation and hemorrhaging of the mucous membrane of the intestine. It is not a specific disease in itself but is the most common general condition observed in poultry diseases (Biely et al., 1950). It has been recorded previously from captive blue grouse but no causative organism has been isolated (Buss, et al., 1958).

The same external signs described for other diseases are observed. Internally, the intestines are flaccid and watery. Upon sectioning, the lining is found sloughing and often bleeding.

Terramycin and Polysol were used in the drinking water. Success was fair where birds were kept in a laboratory free of mechanical vectors of disease, otherwise reinfection occurred.

Ulcerative Gizzard

This is the formation of a large pus-filled ulcer in the gizzard. The bird stops eating and death is by starvation. I have only found it twice (Table 3). No mention of this condition is made in the literature on poultry science.

External signs were the same as for enteritis and I could not diagnose it specifically. Consequently the treatment was the same as described before.

Proventriculitis

Proventriculitis is characterized internally by excessive swelling of the proventriculus. The membranes and glands are inflamed. It is prevalent in chickens raised in confinement (Biely et al., 1950). No causative organism has been isolated.

This condition results in poor digestion and the bird becomes emaciated. No definitive external symptoms are observed so that diagnosis can only be post-mortem. Proventriculitis was observed several times, particularly in chicks which had been badly pecked when held under crowded conditions. Death was only attributed to proventriculitis once.

The stress which seems to cause proventriculitis may be prevented by raising birds in less confinement.

Internal Hemorrhage

Internal hemorrhage is diagnosed by loose clots of blood in the body cavity. It cannot be diagnosed externally. Hemorrhaging is usually due to the rupture of blood vessels in the liver, spleen, ovaries, or kidney (Biely et al., 1950). It occurs in birds which are nervous and fly into things when startled.

Prevention is twofold, to avoid startling the birds and to handle them gently.

APPENDIX 2

BEHAVIOUR

Introduction

The purpose of this appendix is to describe the displays and calls of blue grouse observed in the U.B.C. aviary. This is not intended to be a complete catalogue of blue grouse behaviour. Only the behaviour discussed in the thesis is explained. Photographs and sonographs are used for illustration. The sonographs were made on a Kay missilyzer, Audio and Sub-audio Spectrograph. The methods are given by Borror (1960), Davis (1964) and Marler and Isaac (1960). An attempt to understand the function is given whenever possible.

Investigative, agonistic and reproductive displays

Normal Stance (Plate 8)

In the normal or neutral posture of blue grouse the body is upright, head slightly forward, bill horizontal, wings beside the body and tail down. There is no display of air sacs or eye caruncle. This is the posture blue grouse are observed in most of the time. It is not associated with any particular movements and no sounds are emitted.

Head turning (Plate 9)

Head turning is done by both sexes. The grouse stands in an upright position with the wings beside the body and tail down while watching the mirror image or other grouse. The head is

moved up, down or to the side and held there. It may occur as rapidly as one turn per second. The bird continues to watch. Usually there is no sound given although males may give the cackle and females may bleat or cluck.

It is the most common movement seen in the aviary besides the normal stance and is seen at all times of the year. It seems to be mainly investigative.

Neck stretching (Plates 10 & 11)

This is the most common threat posture. The body may be upright with the neck vertical (Plate 9) or it may be tipped forward with the neck horizontal (Plate 10). The tail is down and the wings are held close to the body. No sound is given while this posture is held. Male aggression cries and female clucks may be associated with neck stretching. It is often exhibited immediately prior to direct attack. It is observed most often during spring and early summer.

The posture functions as a threat to other grouse. Similar postures are taken by red grouse (Lagopus lagopus scoticus) (Watson and Jenkins, 1964) and several species of gull (Larus sp.) (Tinbergen, 1959).

Backward stance (Plate 12)

This is a very intense threat display used by both sexes. The body is upright and the neck is arched over the back. The bill is level, tail down, wings close to the body and neck feathers flattened. This threat display is used less than others. It is most often seen during spring and early summer. No sounds

are given while standing in this posture. Male aggression calls and the female cluck are associated with it.

Sexual display (Plate 13)

The male display is mainly for sex recognition. It is only seen during the spring and early summer. It is given during the courting of a female. The head is erect, wings slightly drooped, tail fanned, and air sacs expanded. The skin of the air sac is orange and the feathers are white giving the general effect of a fried egg. The eye caruncle is expanded and yellow, changing to bright red as display becomes more intense. No sound is given. Males stand on sexual display for several minutes at a time. Very similar displays have been described for the prairie chicken (Tympanuchus cupido pinnatus) (Hamerstrom and Hamerstrom, 1960; Lehman, 1941) and sage grouse (Centrocercus urophasianus) (Dalke, et al., 1960). Display has been observed twice in female grouse (Plate 14). I do not understand the function in this instance.

Head nodding

This display is given by the male during courtship. The male stands on full display with his head in an upright position and looks at the female. He then quickly nods his head almost to the ground and back to the upright position. No sound is given. Individual nods may be from 5 seconds to a minute apart. A similar behaviour pattern was observed in the brushland tinamou (Nothoprocta cinerascens) and it was suggested that it might be a visual stimulatory mechanism for the female (Lancaster, 1964).

The function may be similar in the blue grouse since the nod is often given laterally or on an angle to the hen and displays the air sac.

Presentation of air sac (Plate 15)

The male displays laterally to the hen. The head and neck lower and go slightly forward. The eye is just visible above the feathers surrounding the air sac. The air sac is then slowly expanded and retracted. No sound is emitted. It is a display of presentation and functions in sex recognition. Prairie chicken give a similar display (Hamerstrom and Hamerstrom, 1960).

Tail fanning (Plate 16)

While displaying, the male sometimes turns and stands with his tail fanned toward the hen. This makes the black and white pattern very striking. No sound is emitted. The function seems to be sex recognition. It exemplifies the observation of Stokes (1961) that most of the male reproductive display is presentation.

Strutting

Strutting is a series of slow deliberate steps taken by the male while in full sexual display. The male may strut when alone but more frequently does so before a female. The feet are raised about 2 inches off the ground and set down firmly. No sound is given. The wings and tail do not usually move from the normal display position. The cock may look around while

strutting. The function of strutting would seem to be sex recognition and possibly to stimulate the female to exhibit reproductive behaviour.

Waltzing (Plate 17)

This is a term used to describe chicken behaviour (Wood-Gush, 1955). It refers to a displaying male drooping his wings slightly and making short runs of a few feet, toward or past a female. No vocal sounds are emitted but the primaries rattle as they drag on the ground. The function seems to be to stimulate the female to begin reproductive display. The waltz usually ends behind the female so that it may be to stimulate her to squat. It is only seen during the spring and early summer. Waltzing has been noted in chukar partridge (Alectoris graeca) (Stokes, 1961) and prairie chicken (Hamerstrom and Hamerstrom, 1960).

Pre-copulatory run (Plate 18)

This is a short run the displaying male makes toward the female, immediately prior to or while the female is squatting. The run is usually on a curved path to behind the female. The male suddenly stops behind the female, tips forward with the momentum, and a cry called the pre-copulatory whoot is given. The cry itself is described later. The eye caruncles are red. Prairie chickens have a similar run and call (Hamerstrom and Hamerstrom, 1960). The function seems to be to stimulate the female to squat.

Sqaut (Plate 19)

This is the posture the female assumes when ready to mate. It is only seen during the spring. The legs are bent causing the body to lower, the wings are lowered with the tips on the ground for balance and the neck is extended slightly forward. No sounds are given. The function seems to be to stimulate the male to mount. A male was observed squatting once (Plate 20). I do not know what the function of this was.

Tread

This is the advance of the male upon the back of the female to copulate. The male takes 2 to 5 steps onto the center of the back of the female, takes the nape of her neck in his bill and clasps her sides with his wingtips for balance. The tails of the male and female are tipped to opposite sides to allow the cloacae to meet for copulation.

Pecking

This is an act of direct aggression exhibited by grouse of both sexes, but more by males than females. The pecks are usually delivered on the head or neck. The neck stretch and backward stance are usually associated. The male usually gives aggression calls. The female may cluck or give the croak call. The function is to drive the opponent away.

Conflict pecking

This was exhibited by grouse of both sexes when there was no stimulus for a specific behaviour pattern. They would stand

erect or walk slowly around the cage pecking the walls, floor or water faunt. No sounds are emitted. This seems to be displacement behaviour.

Wing attack

This is an act of direct aggression which may be given by grouse of either sex but predominantly by males. The grouse usually does a vertical neck stretch, takes a little hop into the air and delivers the blow with the wing. It is of sufficient strength to be painful to a human. No vocal sounds accompany this action. It may be preceded in the case of the male by aggression calls. No sounds have been heard emitted by the female at this time.

Grouse calls and cries

All frequencies are in cycles per second and all time lengths are in seconds. The fundamental and harmonics are defined as follows: "The lowest frequency mode is called the fundamental. Higher modes are referred to as harmonics," (Fowler and Meyer, 1961:376).

Male hoot (Plate 21)

The hoot is heard mainly in the spring during the reproductive period. The male assumes an upright stance, tail down, head forward and air sacs filled (Plate 22). The suggested function is to advertise the territory to other males and attract females, as discussed in chapter 9.

The song consists of 7 syllables and last about 2.90

seconds (mean of 5 samples). The first syllable is the loudest and longest. The last 2 syllables are run together and are difficult to distinguish. The fundamental and harmonics are run together so only the maximum and minimum frequencies of each syllable are given. These are as follows.

	SYLLABLE					
	1	2	3	4	5	6-7
Frequency range	50-708	50-913	50-1000	50-831	50-675	50-530
Length of syllable in seconds	.43	.20	.20	.20	.21	.23
Length of time between syllables	.46	.44	.35	.27	.41	

Male pre-copulatory cry

The male pre-copulatory cry is heard only in the spring. It is given to a female by a male exhibiting reproductive behaviour. The male makes a short run toward the female, stops suddenly just behind the female, tips forward with the momentum and gives a low pitched "whoot." The function seems to be to stimulate the female to squat. It was not recorded on a tape so that no sonogram was made.

Male cackle (Plate 23)

The male cackle is heard only during the spring and summer. It sounds like a staccato repetition of "ca-ca-ca-. . . ." It is given from an upright position (Plate 24) or while walking,

and functions as a threat call.

The call has 8 to 10 syllables and lasts for about .87 seconds (mean of 20 samples). The frequency of the fundamental and first harmonic, length of time of each syllable and length of time between syllables are given on page 112.

Male cough (Plate 25)

The male cough is heard only during the spring and summer. It is a throaty, rough sounding, slower form of the cackle. It is also given as a threat. It is not given as often as the cackle. It is given from the same stance as the cackle. Upon analysis of the 1965 aggression tests it was found given in a ratio of 1:6.27 to the cackle. It has 7 to 8 syllables and lasts about 11.29 seconds (mean of 11 samples). The frequency of the fundamental and first harmonic, length of time of each syllable and length of time between syllables are given on page 13.

Female bleat (Plate 26)

The bleat may be given by a hen in any stance except aggressive and at any time of the day or year. Very intense bleating may occur prior to egg laying or when startled. Largely, I feel it is a result of conflicting drives and possibly fear.

The bleat is about .26 seconds long (mean of 25 samples) and may occur about .47 to .56 seconds apart. The fundamental and four harmonics are consistently plain. The frequency of these in cycles per second are as follows (mean of 25 samples).

	SYLLABLE									
	1	2	3	4	5	6	7	8	9	10
Frequency of fundamental	50-650	50-680	50-640	50-635	50-630	50-635	50-620	50-595	50-543	50-453
Frequency of harmonic 1	1347-2512	1640-2667	1710-2707	1802-2822	1885-2795	1895-2850	1897-2780	2077-2692	1950-2517	1650-1850
Time length of each syllable	.16	.08	.06	.06	.05	.05	.05	.05	.05	.04
Time length between syllables	.11	.02	.02	.02	.02	.02	.02	.01	.01	

The frequency of the fundamental and first harmonic, length of time of each each syllable, and length of time between syllables of male cackle.

	SYLLABLE							
	1	2	3	4	5	6	7	8
Frequency of fundamental	50-600	50-620	50-620	50-597	50-607	50-600	50-596	50-500
Frequency of harmonic 1	807-1432	812-1595	992-1585	825-1515	817-1474	805-1442	827-1452	900-1425
Time length of each syllable	.18	.07	.07	.07	.06	.06	.06	.05
Time length of period between syllables	.06	.05	.05	.06	.07	.09	.09	

The frequency of the fundamental and first harmonic, length of time of each syllable, and length of time between syllables of male cough.

NOTE	CYCLES/SECOND
Fundamental	460-955
Harmonic 1	1107-1352
2	1592-2060
3	2322-2660
4	2859-3217

Female whinny (Plate 27)

The whinny is heard only during the spring or early summer. It may be given at any time within a day of squatting and often immediately prior to squatting. Ths sound resembles the whinny of a horse but is much higher pitched. Males in the aviary and in the field immediately respond to the whinny by hooting and giving reproductive display. A possible function is suggested in Chapter 10.

The fundamental and at least 4 harmonics are broken up into several subnotes which make the sonograph difficult to measure. Thus only the length of the song, minimum and maximum frequencies and a photograph of the sonograph are given. The frequency ranges from 88 to 2105 cycles per second and the cry is about 10.5 seconds long (mean of 10 samples.

Female cry (Plate 28)

The female cry is only heard during the spring and early summer. It is a staccato repetition of one basic note and sounds like "ka-ka-ka-. . . ." Note from Plate 26 that the intensity rises and falls. It is sometimes associated with reproductive behaviour and sometimes with aggressive behaviour. I am uncertain

of its function. It is of no definite length and has been recorded from 9 to 32 syllables. The length of the syllables is about .7 to .8 seconds and the time between syllables about .06 and .12 seconds (based on means of 7 calls). The frequency of the fundamental is between 450 to 850 cycles per second and the first harmonic is between 1375 to 2100 cycles per second.

Female cluck (Plate 29)

The cluck is heard mainly during the spring and summer but has occasionally been recorded during the winter. It is given by a female during aggressive display. It is often given prior to a direct attack. It sounds like the written word "cluck."

It has at least 4 harmonics above the fundamental but because the peculiar shape of the note makes a normal measurement impossible, only the minimum and maximum frequencies and a photograph of the sonograph are given. The call ranges between 50 and 2270 cycles per second and is about 2.34 seconds long (mean of 10 samples).

Female puk

The puk call may be heard at any time of year. It is given by a female sitting or standing still. It is a low call which sounds like "puk-puk-puk-. . ." rapidly repeated for several seconds. It has been recorded from 5 to 20 seconds. I was unable to make a tape recording. It was normally only heard when someone looked into the pen or filled the feeder. This suggests it may be a fear reaction or possibly conflict.

Female croak

The female croak was only heard during the spring. It is low pitched sound much like the purr of a cat. It was only given during periods of aggressive behaviour when a female attacked her mirror image. It was not recorded on tape.

Female hoot (Plate 28)

Hooting by a female was only observed twice. Both occasions were in the spring. It sounded like the male hooting but had a higher pitch. One female did it with no observed stimulus and one did it on 3 separate occasions when she saw her mirror image. The female takes the same stance as a male but the eye caruncles do not become inflated and the air sacs are not exposed. Only 2 series of female hooting were recorded. It lasted about 1.7 to 2.1 seconds. The frequency range is from about 50 to 2250 cycles per second. The syllables were from .09 to .39 seconds long and from .20 to .39 seconds apart (mean of 2 samples).

APPENDIX 3

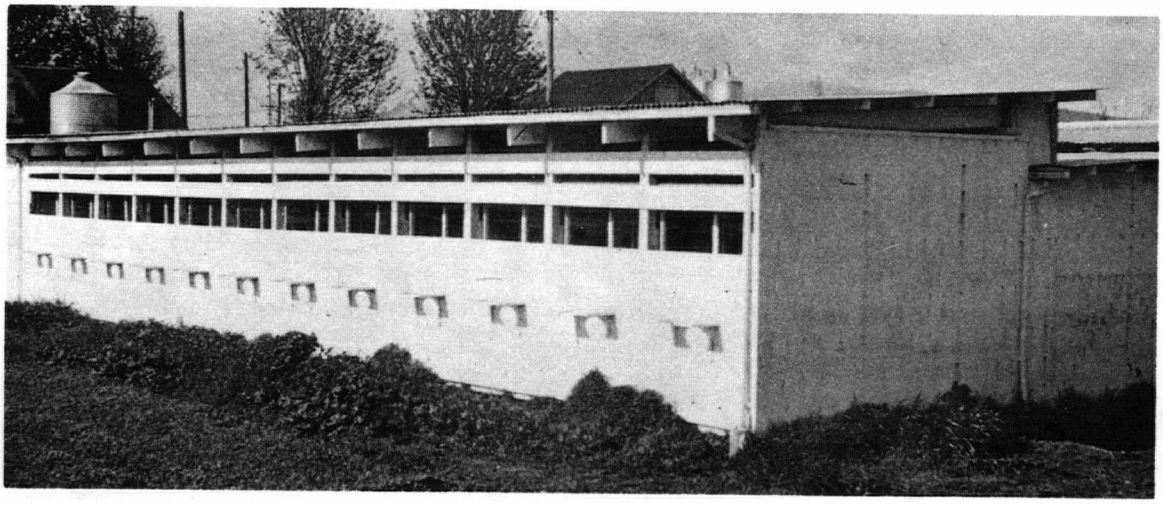

Plate 1. U.B.C. aviary from south.

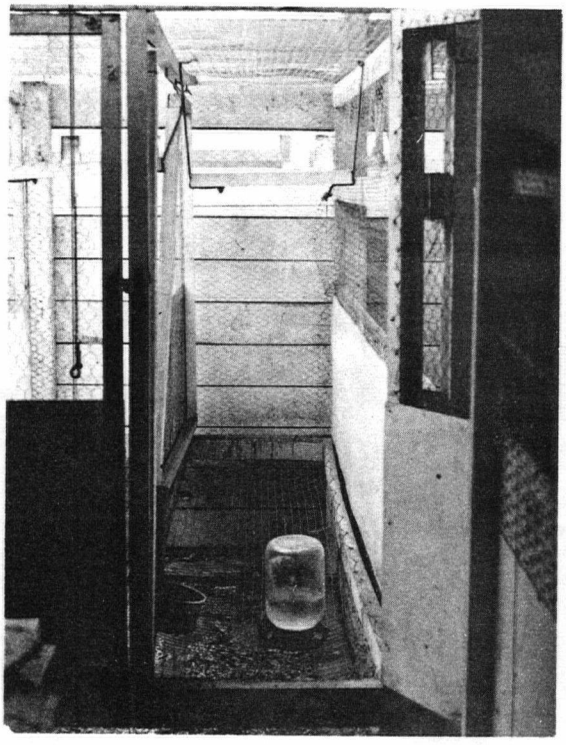

Plate 2. Inside of a pen at U.B.C. aviary to show position of water faunts, feeders, dividers and roost.

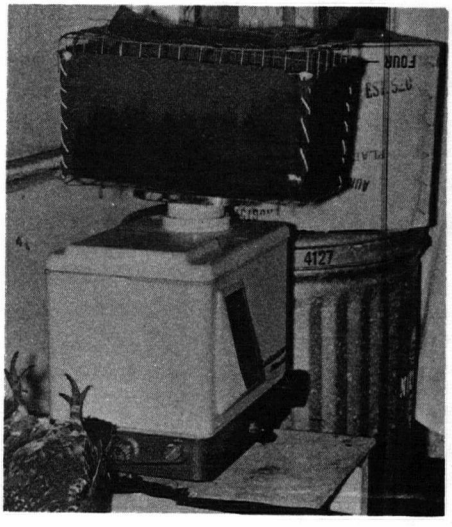

Plate 3. Electric weighing scale with basket

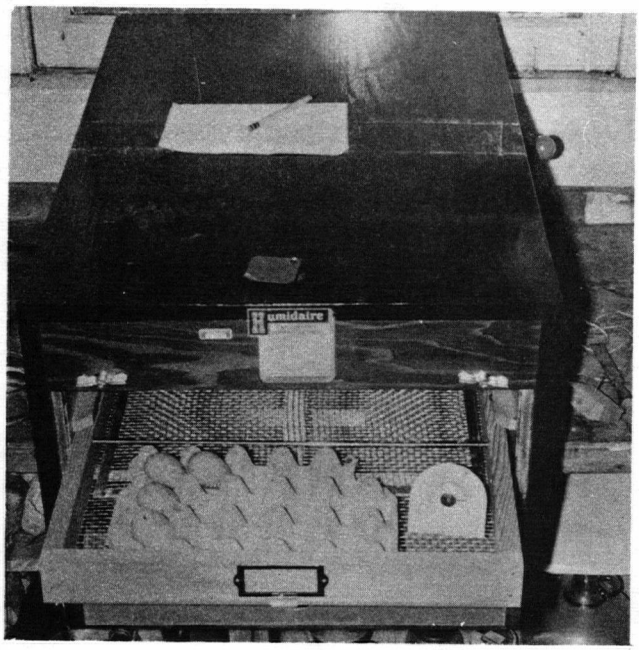

Plate 4. Humidaire incubator

Plate 5. Battery incubators

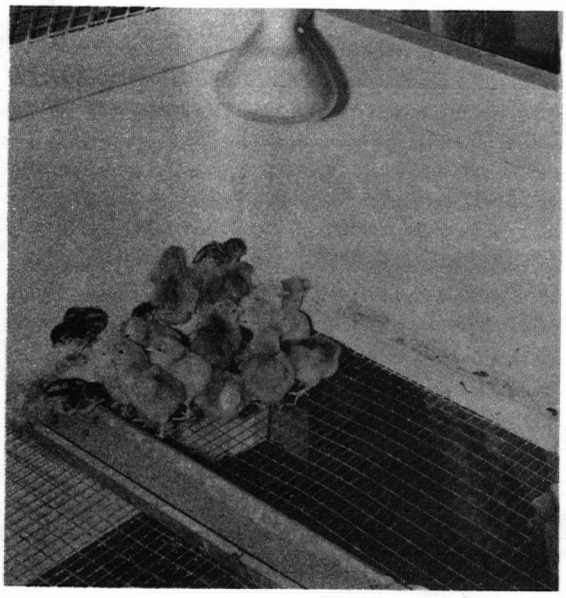

Plate 6. Brooder at U.B.C. aviary.

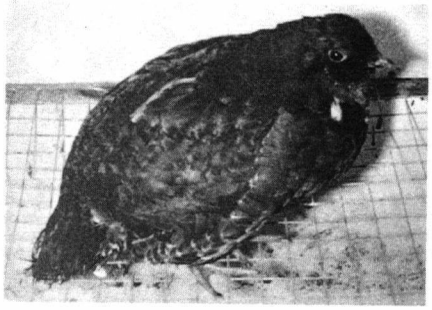

Plate 7. Posture of a sick grouse.

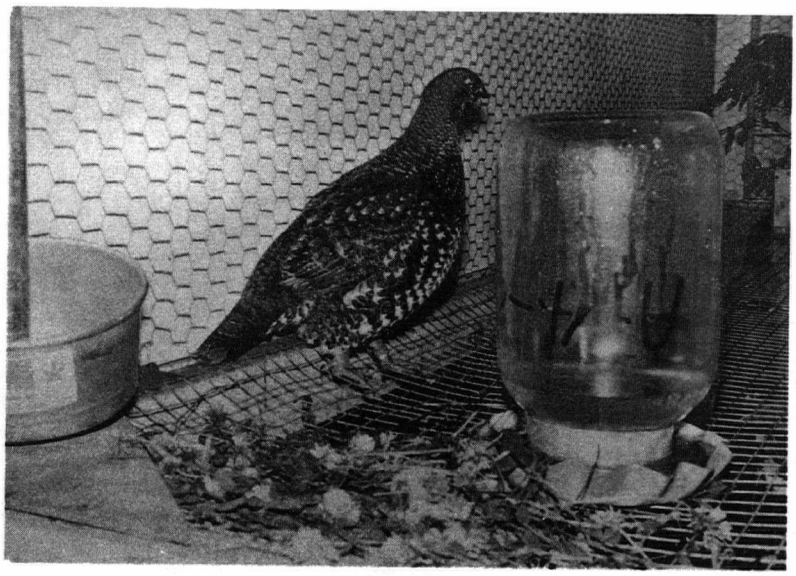

Plate 8. Normal stance of a blue grouse.

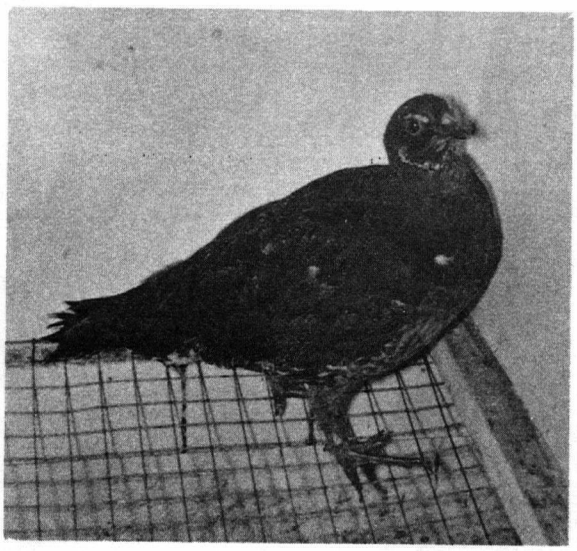

Plate 9. Head turn posture.

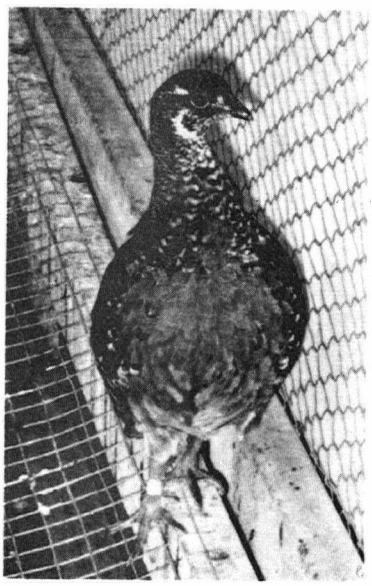

Plate 10. Neck-stretch posture, vertical.

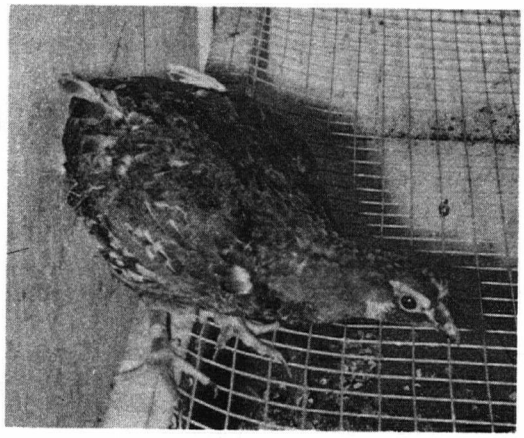

Plate 11. Neck-stretch posture, horizontal.

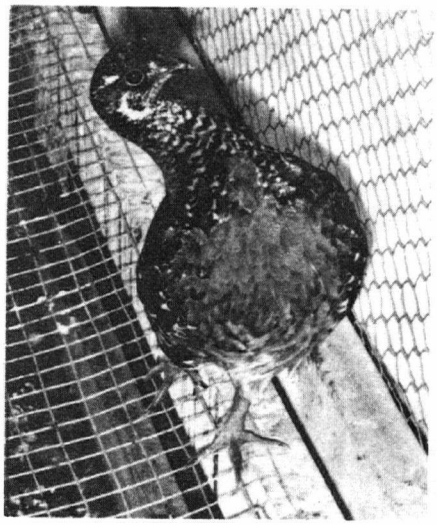

Plate 12. Backward stance posture.

Plate 13. Male sexual display.

Plate 14. Female giving male sexual display.

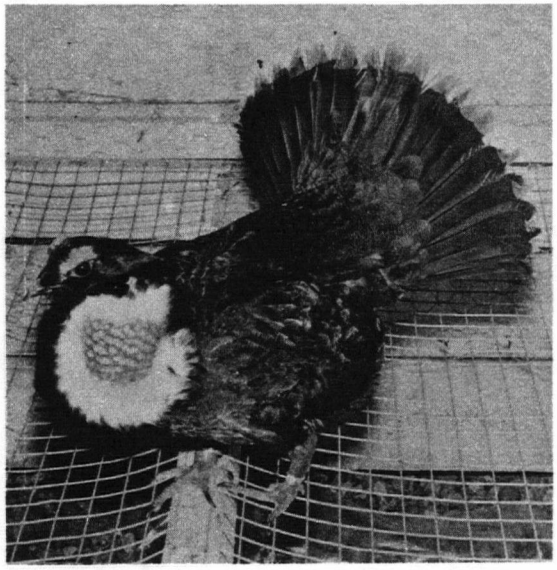

Plate 15. Male presentation of air sac.

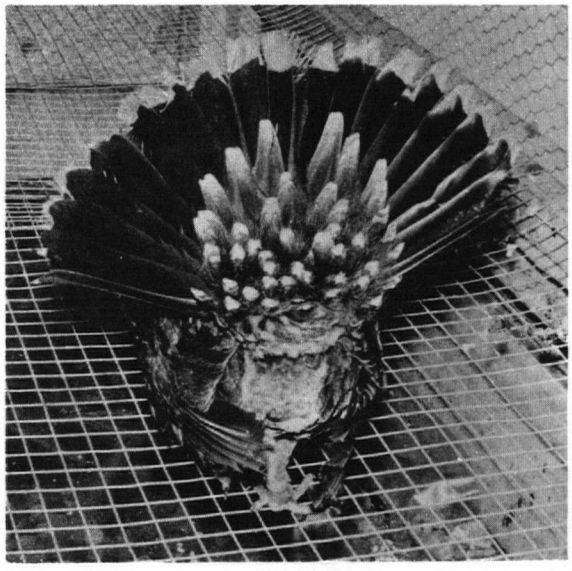

Plate 16. Male fanning tail while exhibiting sexual display.

Plate 17. Male waltzing.

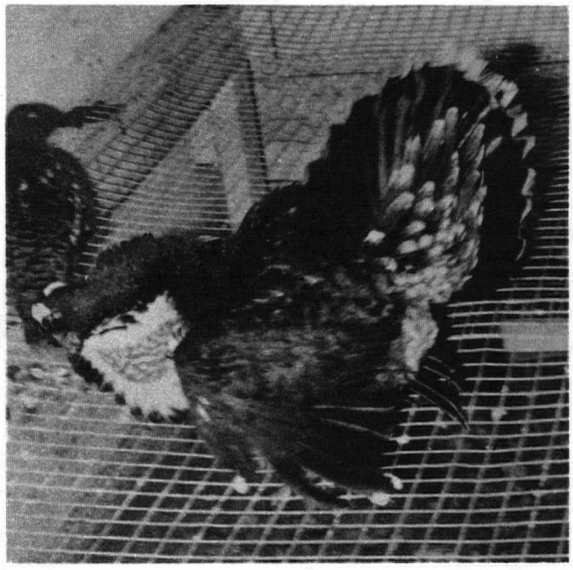

Plate 18. Male giving pre-copulatory whoot at termination of pre-copulatory run.

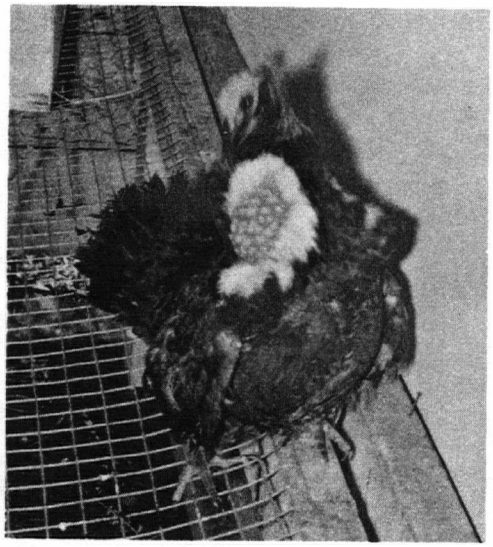

Plate 19. Female squatting.

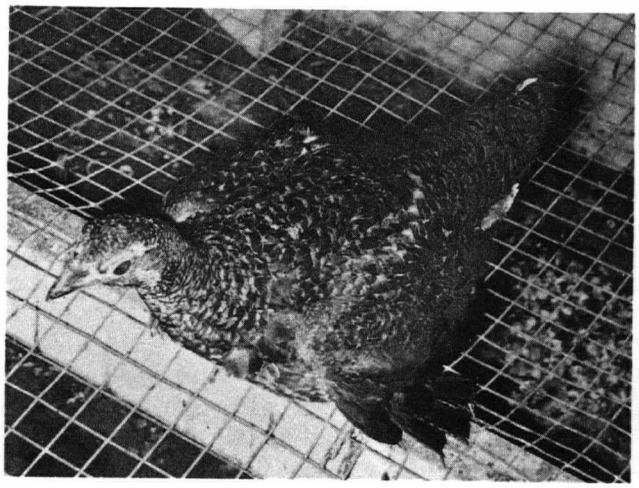

Plate 20. Male exhibiting squatting behaviour.

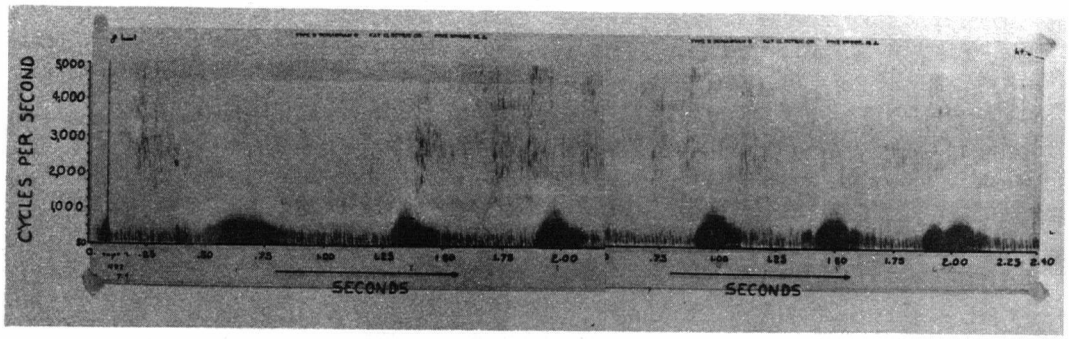

Plate 21. Sonogram of male hooting.

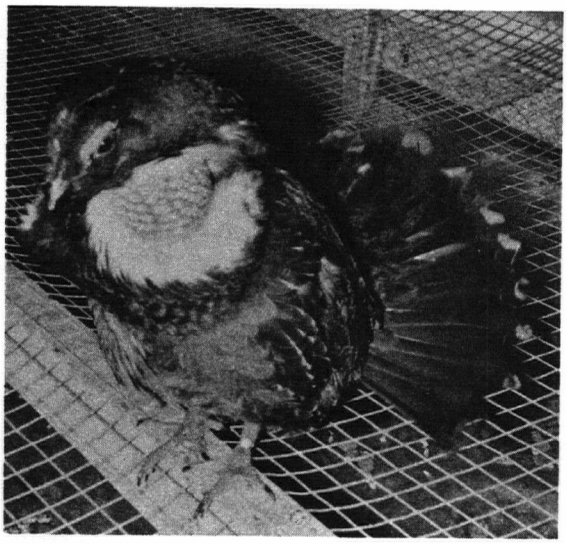

Plate 22. Male in hooting posture.

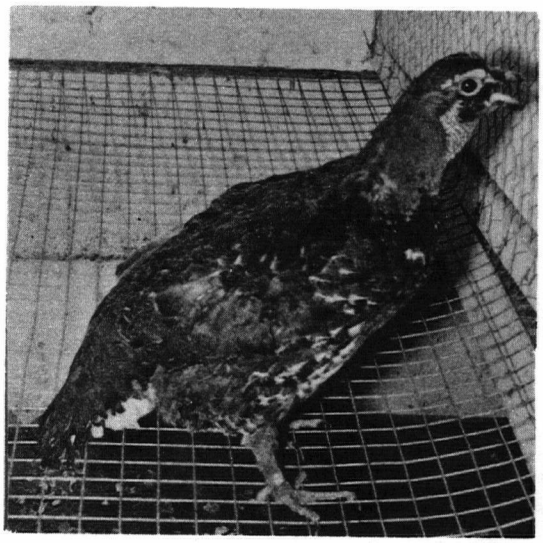

Plate 24. Male giving aggression call.

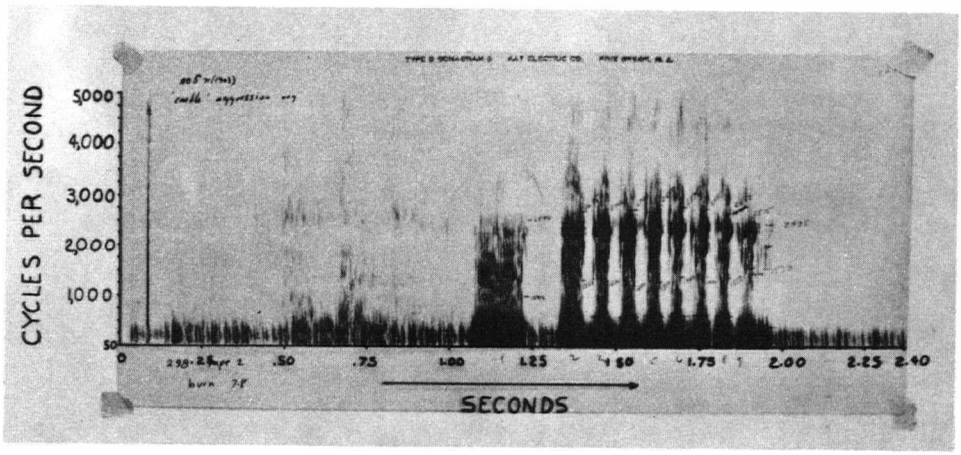

Plate 23. Sonogram of male cackle aggression call.

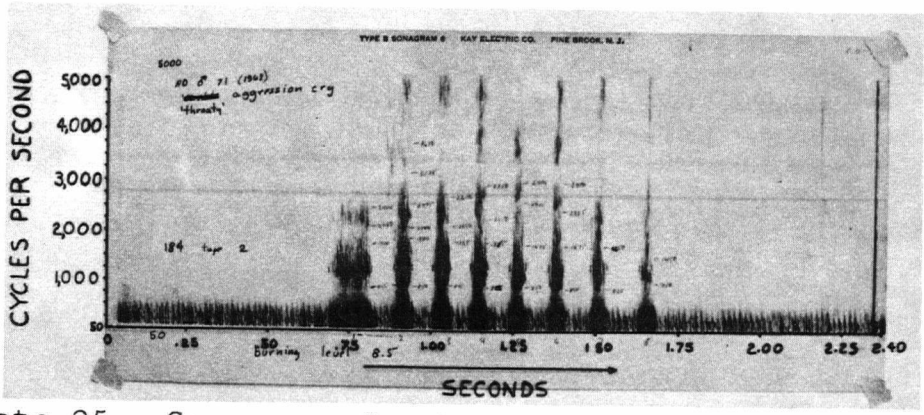

Plate 25. Sonogram of male cough aggression cry.

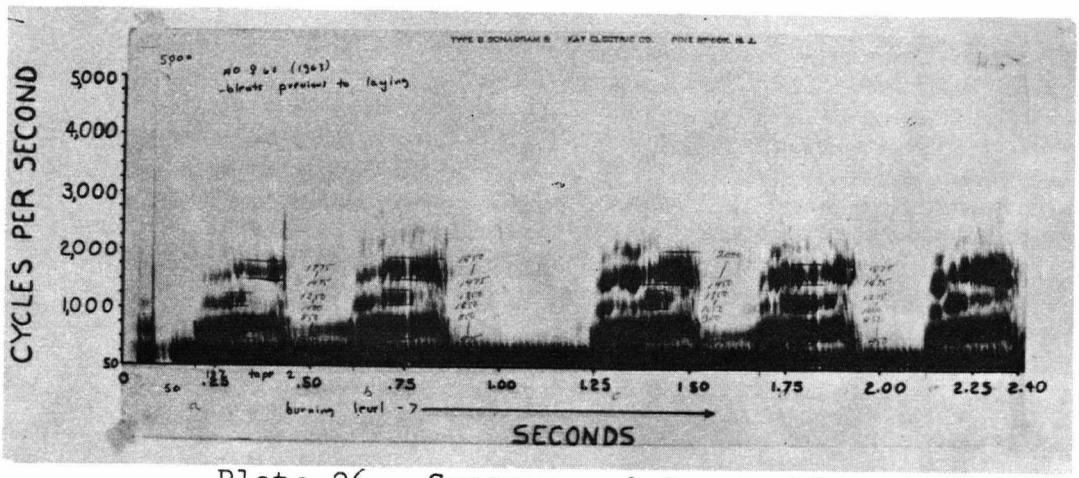

Plate 26. Sonogram of female bleat.

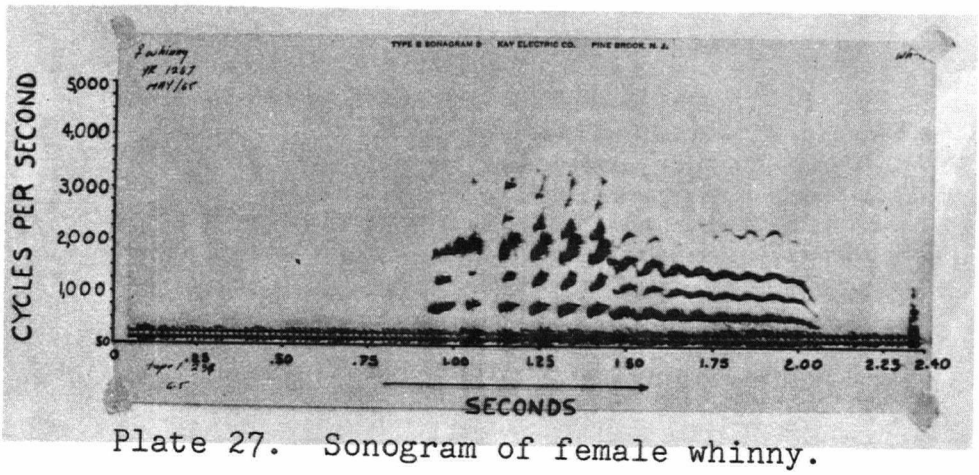

Plate 27. Sonogram of female whinny.

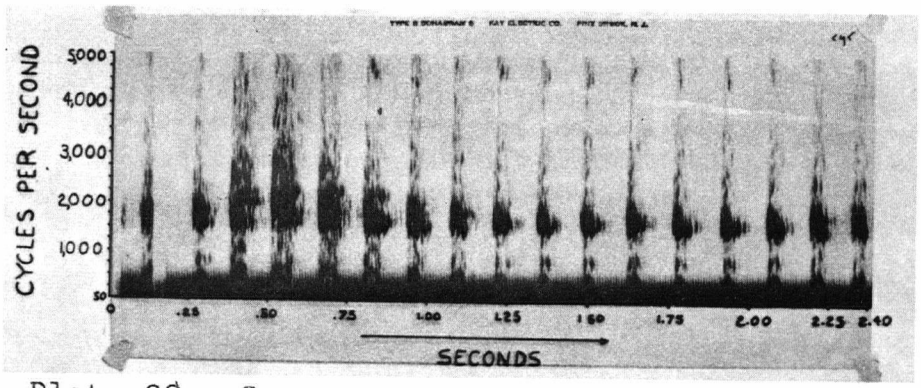

Plate 28. Sonogram of female cry.

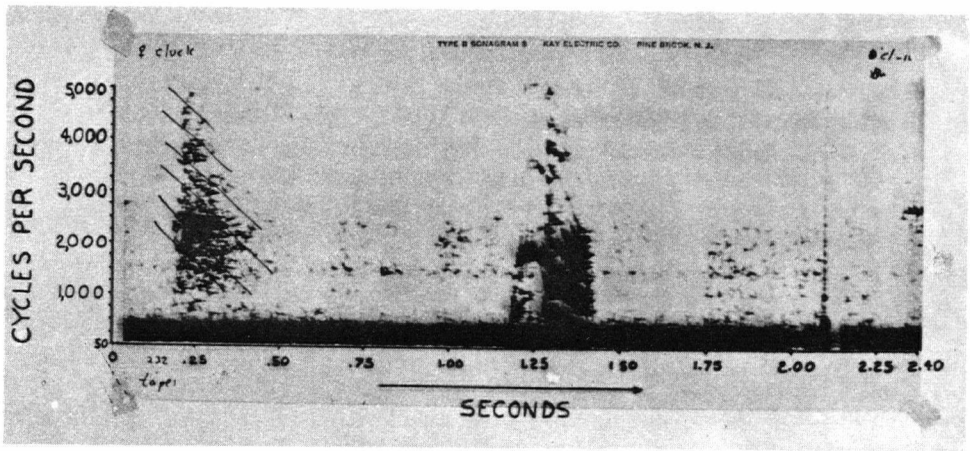

Plate 29. Sonogram of female cluck.

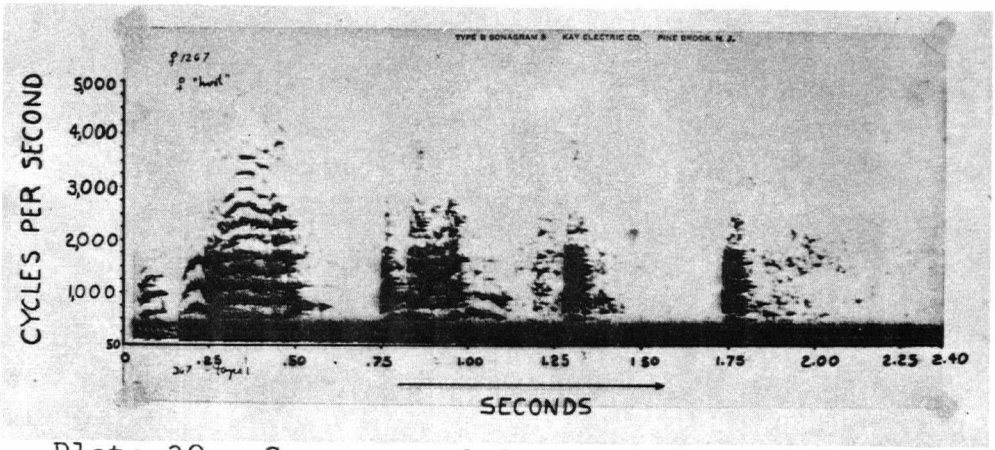

Plate 30. Sonogram of female hooting.