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A STUDY OF
SOCIAL BEHAVIOUR RELATING TO
BROOD BREAK-UP AND DISPERSAL IN FRANKLIN'S GROUSE
(*CANACHITES CANADENSIS FRANKLINII*)
UNDER CAPTIVE CONDITIONS

BY

JOHN HENRY ALWAY

A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH

IN PARTIAL FULFILMENT OF THE REQUIREMENTS FOR THE DEGREE

OF MASTER OF SCIENCE

DEPARTMENT OF ZOOLOGY

EDMONTON, ALBERTA

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THE UNIVERSITY OF ALBERTA

FACULTY OF GRADUATE STUDIES AND RESEARCH

The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research, for acceptance, a thesis entitled "A study of social behaviour relating to brood break-up and dispersal in Franklin's Grouse (*Canachites canadensis franklinii*) under captive conditions", submitted by John Henry Alway in partial fulfillment of the requirements for the degree of Master of Science.

Supervisor

Jan O Murie

J S Nelson

Date June 14, 1977

ABSTRACT

The social behaviour of a captive flock of Franklin's Grouse (*Canachites canadensis franklinii*) was studied in an attempt to determine the factor(s) which induce juveniles to leave the brood and move to a different area during autumn and early spring.

It was not possible to distinguish brood break-up from autumn dispersal on the basis of the behaviour of the captive birds, although it is suspected that these events are temporally distinct. Brood break-up appeared to be the combined result of the waning of the parental bond of the brood female and the development of social independance by the juveniles. Brood break-up is therefore dependent upon the complex interaction of numerous internal and external stimuli which determine the behaviour of each individual. No overt aggression occurred during the time when juveniles disperse in the wild, thus suggesting that juveniles are genetically predetermined at hatch to move out of their brood range in the autumn.

Winter was characterised by a linear peck order within the flock and with minimal aggression among birds of the same sex. Relative dominance attained during winter may decide which individuals move from the wintering ground the following spring. The sudden development of overt aggression among birds of the same sex and all age classes in the early spring suggests that intraspecific aggression is the proximate cause of the movements of certain juveniles at this time of year. Therefore it is suggested that the movements should be considered the result of spacing-behaviour and not as dispersal, a term which is defined herein.

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INTRODUCTION

Dispersal is a well established, yet extremely nebulous term in biology. Few studies have focused on dispersal and of these, many have been instigated more because of its significance to other biological problems than by an interest in dispersal per se. Lack of communication between workers studying different organisms and between workers of different specialisations have further retarded a better understanding of this phenomenon. Thus much of the published work on dispersal is applicable only to specific groups whereas it is a phenomenon that occurs in the life cycle of every species of organism. Consequently controversy exists concerning both the definition and evolutionary significance of dispersal.

Dispersal refers to movement and is not to be confused with dispersion, a term which describes the spacing pattern of a group of organisms. The most encompassing definition of dispersal is that of any movement leading to dispersion (Haukioja 1971). Though suitable for non-motile organisms, this is less applicable to motile organisms for which considerable temporal changes in dispersion may occur. Thus most authors limit the term dispersal to movements that result in the dispersion pattern at the time of reproduction. For example, Howard (1960) considering vertebrate populations, defined dispersal as the movement of an individual from its point of origin to the place where it reproduces or would have reproduced had it survived or found a mate.

The mechanism of dispersal will be strongly influenced by the vagility of an organism (Odum 1971). Any movement of a non-motile organism may be classified as dispersal, this being accomplished by the passive movement of propagules by such environmental agents as wind and moving water (eg. Crossland 1903; Wolfenbarger 1946). The situation is more complex when considering motile animals which have highly developed nervous systems and which are capable of directed movement. In such animals, dispersal is typically associated with particular age and sex classes. Thus in insects, dispersal is generally accomplished by winged adults (Johnston 1969). In vertebrates it is characteristically the immature individuals which disperse (eg. Howard 1960; Berndt and Sternberg 1968), but in some species the adults may also disperse as for example in certain rodents (French *et al.* 1968; Myers and Krebs 1971), and the males of some species of *Anatinae* (Sowls 1955).

Howard (1960) suggested that the tendency to disperse is an inherited character. Thus an individual may be genetically predetermined to disperse from the home site ("innate dispersal"), or to remain at the home site unless forced to move in response to some population pressure ("environmental dispersal").

Some authors (eg. Johnston 1961; Berndt and Sternberg 1968; Brown 1975) have argued that the term dispersal should not include the spacing behaviour which results from territorial interactions during the breeding season of some species of animals. In such species an individual presumably develops a 'site attachment' to an area following dispersal and will attempt to breed there but may be forced to move in search of a vacant area by more dominant individuals during the period of territorial establishment (see Meyer 1974, for description of dispersal and territorial establishment of the Black-capped Chickadee, *Parus atricapillus*).

Therefore I propose that dispersal be defined as the movement by an organism from the place in which it becomes physically independant of its parent(s) to the place where it attempts to reproduce, or if applicable, from the place where it attempted to reproduce, irrespective of success, in the previous reproductive season. This does not preclude a dispersal terminating at the point where it commenced. However the effective distance of dispersal will be the distance over which an individual's genetic characteristics are transmitted (Howard 1960).

Dispersal is a mechanism ensuring gene flow within a species, thus promoting outbreeding (Howard 1960; Johnston 1961; Murray 1967). Mayr (1947, 1953) emphasised the genetic consequences of dispersal by recognizing its potential as a factor contributing to the development of new species. Dice (1952) suggested dispersal as the means by which each species colonizes all suitable habitat. This entails both the colonization of previously unoccupied areas and the reinvasion of areas depopulated by catastrophies (Howard 1960). Long distance dispersal is of interest to the biogeographer, for it may result in major range extensions or discontinuous distributions (Rand 1955; Falla 1960; MacArther and Wilson 1967; Brown and Alcala 1970). Dispersal is also a potentially important factor in the regulation of numbers of animal populations (Errington 1956; Lidicker 1962; French *et al.* 1968; Christian 1970; Myers and Krebs 1971).

Thus most authors have accepted that the welfare of the dispersing individual is sacrificed for that of the population. Compliance with this view involves acceptance of many of Wynne-Edward's (1962, 1965) controversial but stimulating ideas on group selection and altruism. Alternatively dispersal might be shaped by natural selection at the individual level with the population consequences being of a 'second-order' effect (eg. Lidicker 1962; Gilbert and Singer 1973).

Thus dispersal would be programmed to take an individual from one locality when the odds favour a greater chance of success by attempting to settle in another locality. Wilson (1975) gives a stimulating review of this problem.

A comprehensive study of dispersal should establish the motivating factor(s) and exact route taken by all dispersing individuals within a population. Field studies thus require that the organism under study be easily caught, marked and recaptured, an impractical combination of requisites in most populations. For these reasons, dispersal has been little studied in avian populations. As it is difficult to accurately delimit the boundaries of a biologically significant population, most field studies refer to dispersal as movement from the study area (Goodbody 1952; Boag 1966; Zwickel and Bendell 1967a; Keppie 1975). Such an assessment is permissable if subsequent conclusions allow for this limitation.

Radio-telemetry enables the movements of birds to be monitored accurately, though as yet is of general use only for larger species (Godfrey and Marshall 1969; Herzog 1977). Logistic problems limit this technique to a relatively small sample, hence generalisations must be made with considerable caution. Capture-recapture methods enable a larger sample to be studied but the importance of individual idiosyncrasies in behaviour may be overlooked. The results will be greatly influenced by the number of 'recapture stations', which should increase with distance from the centrally located 'original capture' station (Haukioja 1971). Further, this method gives little information on the exact route taken by dispersing individuals.

An alternative is to intercept individuals moving into an experimentally depopulated area. Characteristics of dispersing individuals may be assessed by comparing them with 'resident' individuals from a control plot. This has been used in the study of small mammals where the characteristics of dispersing individuals appear to change depending upon the stage of the population cycle (Myers and Krebs 1971). In avian species so far studied, dispersal is mainly by the young some time between independance from their parents and their first breeding season. Thereafter most birds exhibit fidelity to the breeding site (Klopfer 1969; Anderson and Anderson 1973), except in the cases of birds breeding in unstable, fluctuating habitats (McNicholl 1975) and highly nomadic species (Nethersole-Thompson 1975).

Detailed observation of individuals in a population at the time when dispersal is known to occur for that species should provide useful insights to the possible factors motivating this behaviour. Such an approach is justified because if successful, it would help elucidate the biological significance of dispersal for that species. In the present study, I used this approach on a captive flock of Franklin's Grouse (*Canachites canadensis franklinii*). This species was selected for study because Keppie (1975) had already conducted an extensive field study of dispersal on part of the same population from which the captive birds were taken.

Both studies are part of an extensive research programme on the biology of Franklin's Grouse in the vicinity of the R.B. Miller Biological Station, 16 miles west of Turner Valley, Alberta. McCourt (1969) and McLachlin (1970) described habitat selection and dispersion of this race of the Spruce Grouse, whilst MacDonald (1968) described the behaviour of territorial males. Keppie (1975) studied factors which may regulate the age structure of the breeding population. Herzog (1977) followed movements of individual birds throughout the year using radio-telemetry.

The dense habitat, secretive disposition and scattered dispersion of Spruce Grouse makes prolonged and detailed observation of this species extremely difficult in the wild. The only work of this kind has been on territorial males during the breeding season, as at this time they are less secretive and fairly localised (Lumsden 1961; Stoneberg 1967; MacDonald 1968; Hjorth 1970; McLachlin 1970; Anderson 1973). The social behaviour of this species is consequently poorly understood and much of the present information is of an anecdotal nature. I therefore feel fully justified in studying the social interactions of Franklin's Grouse in the captive situation, for although this introduces the possibility of aberrant behaviour patterns, it does enable observation at any time without undue disturbance to the birds which is not feasible in the wild.

Studies of captive animals ('pen studies') frequently permit detailed observation and experimental manipulations which would be unfeasible under natural conditions, for example, Delacour and Amadon (1973) for the *Cracidae*. Providing that the results of such studies are interpreted with caution, work on captive animals can provide a valuable contribution to a more complete comprehension of animal behaviour. Thus it is my firm belief that a comprehensive research programme should involve work in both the wild and captive situations. Unfortunately the intellectual arrogance of many 'field' workers toward pen studies frequently denies access to this valuable source of information. Such an attitude is often coupled with blissful acceptance of extremely dubious experimental manipulations which gain unmerited confidence merely because they were conducted under presumed 'natural' conditions.

Keppie's (1975) study revealed two distinct phases of dispersal, occuring in the autumn and the following spring. The post-dispersal juvenile cohort was qualitatively different from the pre-dispersal cohort in both phases. Only the spring phase resulted in a significant change in numbers.

My major objective in the present study was to attempt to determine the factor(s) which motivate(s) individuals to disperse in both phases, with particular emphasis upon social interaction. Hopefully this research will also contribute toward a better understanding of dispersal *per se*. Further, as the birds were maintained throughout the year, my observations may also answer other questions pertaining to the behaviour of Franklin's Grouse.

METHODS

Maintenance of Grouse

Most attempts at maintaining and breeding grouse in captivity have been instigated because of their popularity as game birds. Emphasis has been placed upon mass-production techniques involving the use of incubators to hatch eggs either laid in captivity or collected from the wild. The results have so far been less successful than for many other gallinaceous birds. McEwan *et al.* (1969) review the literature on this topic.

Relatively few scientific investigations have been conducted using captive grouse. Zwickel (1965) and Lance *et al.* (1970) reared young Blue Grouse (*Dendragapus obscurus*) and compared subsequent mortality in captivity with that observed in the wild, as part of a study on the role of early mortality in the regulation of numbers of the breeding population. Several workers have studied food selection of captive ptarmigan (Moss 1968, for *Lagopus mutus*; Moss 1972, for *L. lagopus scoticus*; Pulliainen and Salo 1973, for *L. lagopus lagopus*). Spruce Grouse have been successfully maintained and bred in captivity by Pendergast and Boag (1971a) who worked on nutrition and diet of this species. Boag (1972) tested the effect of radio packages on the behaviour of captive Red Grouse (*L. lagopus scoticus*). Stirling (1965) and Stirling and Bendell (1970) described the reproductive behaviour of captive Blue Grouse. No work has been published on the social behaviour of captive grouse maintained under semi-natural conditions.

A. Aviary Facilities

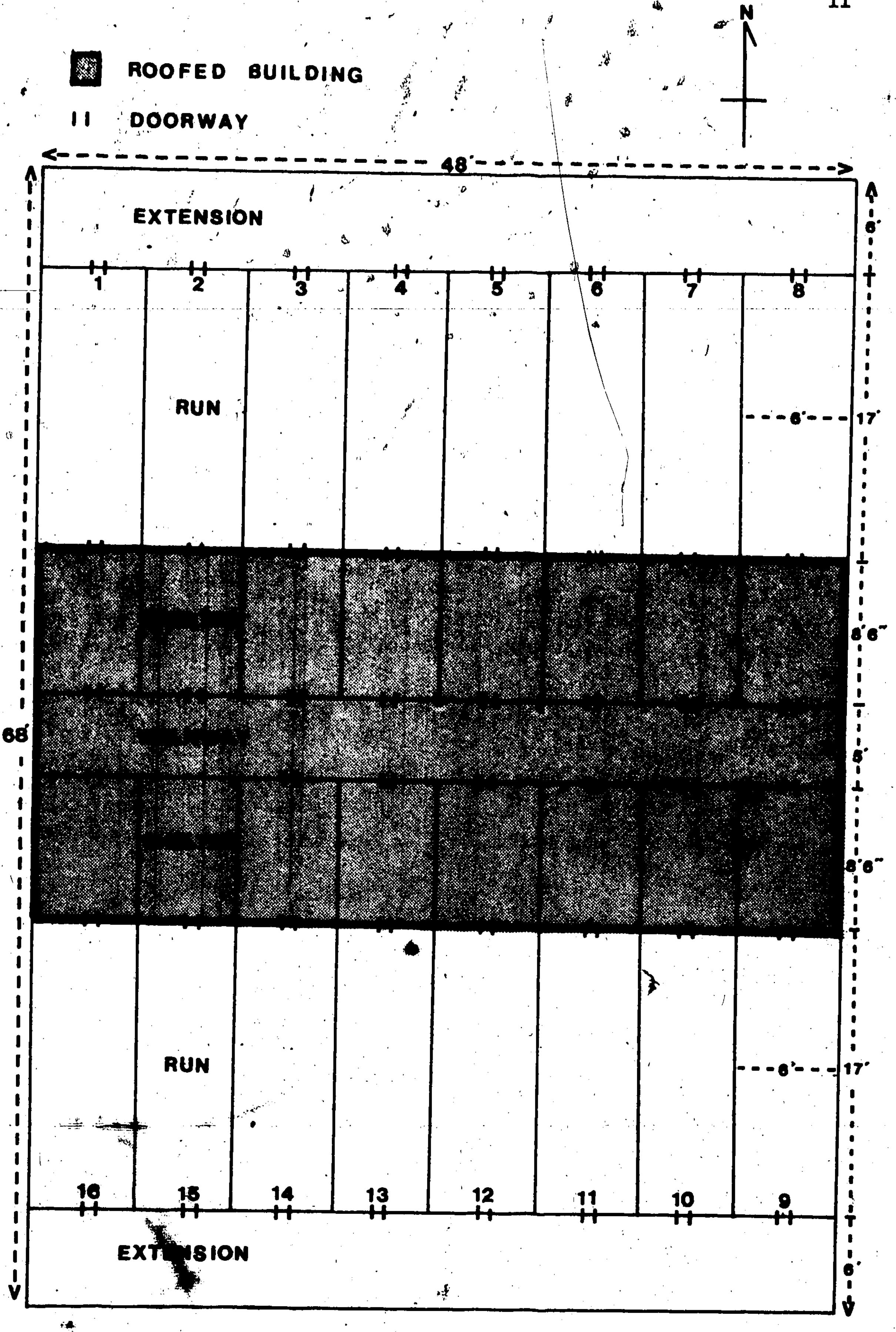
The aviary facilities of the University of Alberta at Ellerslie, 8.5 miles south of Edmonton were used in this study. A diagram of the main aviary used is presented in Fig. 1.

The central building was floored with concrete and consisted of 16 pens (hereafter referred to as 'shelters') in two series of eight on either side of a central walkway, each shelter being 8.5 x 6 x 6 feet high. Access for maintenance duties in each shelter was provided by wire mesh doors opening into the walkway. A single perch was fitted diagonally across each shelter 4 feet above ground level. Food and water were provided in each shelter, care being taken not to place them under the perch, hence avoiding contamination with droppings. Visual contact between birds in adjacent shelters was prevented by wooden partitions and between birds in opposite shelters by hessian sacking stretched across the wire mesh of the maintanance doors. The building had no windows and was provided with electrical illumination. This was connected to a timing device and coincided with the period of daylength. During the winter, temperature was maintained slightly above freezing by two thermostatically-controlled gas heaters.

During part of the study, the maintenance doors were opened allowing the birds access to the central walkway and hence to all other shelters. During these periods, food and water were placed at regular intervals along the walkway, as were perches fixed 4 feet above ground level. Once in the central walkway, birds could fly up to the rafters of the building and perch on top of the maintenance doors.

Each of these shelters communicated with a outside wire mesh run 17 x 6 x 6 feet high (hereafter to be referred to as a 'run') via a

Figure 1. Diagram of the aviary facilities of the University of Alberta at Ellerslie.


ROOFED BUILDING
DOORWAY
N
48'
EXTENSION
1
2
3
4
5
6
7
8
6'
RUN
6'
17'
8'6"
68'
5'
8'6"
RUN
6'
17'
16
15
14
13
12
11
10
9
EXTENSION
6'

small door at ground-level. The aviary therefore consisted of 16 pens, each constituting a shelter and outdoor run. A perch was fixed 4 feet above ground level at either end of each run and the floor was turfed with grass. Partial visual isolation was maintained between adjacent runs by 4 feet high wooden partitions but did not prevent birds using the perches from seeing each other. Higher partitions would have considerably reduced the amount of light in each run thereby making observation of the birds more difficult and preventing growth of vegetation.

During the first summer (1973) of this study, two wire mesh enclosures, both 48 x 6 x 6 feet high (hereafter referred to as 'extensions') were constructed along the outer ends of the runs. Birds had access to the extensions by means of small, ground level doors at the end of each pen. The floors of these extensions were originally covered with gravel but were rapidly colonized by various herbaceous plants. Perches were fixed at regular intervals 4 feet above ground level. When necessary, hessian sacking was stretched across the extensions to provide a physical and visual barrier.

Water was provided in each run and at intervals along the extensions. Food was not placed in these uncovered sections as it would have been spoiled by the rain. All perches were taken from lodgepole pine (*Pinus contorta*) as artificial perches may cause various foot ailments in captive birds. Care was taken to make all the pens equally attractive to the birds. I also tried to simulate the natural habitat as closely as possible by allowing vegetation to grow and by scattering pine and spruce branches throughout the pens and extensions. The latter also gave the birds cover when hiding from dominant individuals or predators attracted to the aviary, and provided nesting cover.

The design of this aviary made it possible to modify the space available to a bird. As there were always more compartments than birds, the birds could flock together or seek isolation. Thus, without reducing the space available to each individual it was possible to maintain many more birds together than would have been possible in a similar sized pen which lacked the partitions.

In 1973, one brood was housed in an adjacent pen, 50 x 12 x 6 feet high. This consisted of a large wire mesh run, at one end of which was a small building which was divided into a small shelter from which the birds had access to the run, and an observation room equipped with one-way glass to the run and shelter.

B. Diet and General Care of the Grouse

The food and nutritional aspects of diet of Spruce Grouse have been studied by Ellison (1966, 1972), Boag and Kiceniuk (1968) and Pendergast and Boag (1970, 1971b). The summer diet consists mainly of vegetation growing on the forest floor with the fruits of *Vaccinium spp.* being especially favoured. Juveniles feed on greater proportions of arthropods and fruit than adults. During the period of permanent snow cover, Spruce Grouse rely solely upon conifer browse; the Franklin's race favouring lodgepole pine. Pendergast and Boag (1973) correlated structural changes in the internal anatomy of Spruce Grouse with this marked seasonal change in diet.

Captive Franklin's Grouse remained in excellent condition on a mixture of commercial turkey and pheasant breeder pellets (North West Feeds Ltd.; minimum crude protein level 20%). This was placed in metal poultry feeding troughs, fitted with swivel bars to prevent the birds perching on the troughs and fouling the food. This diet is of a higher nutritional quality than the natural diet, consequently the captive birds needed to devote less time exclusively to feeding. I agree with Hediger (1950) that the prevention of 'boredom' is extremely important in keeping wildlife healthy. Further, the reduced time required for feeding by captive birds could modify their social behaviour. Therefore, during the period of snow cover, I provided boughs of *Pinus contorta* to supplement the basic diet. During the spring I supplied the new leaders of white pine (*Pinus glauca*) as McCourt *et al.* (1973) found this to be the preferred diet of incubating females. Throughout the growing season, a luxuriant growth of vegetation in the runs and extensions provided browse as well as attracting arthropods.

Fresh water was supplied daily in inverted jar fonts, except during the winter months when the birds had constant access to snow. Grit is extremely important to herbivorous birds as an aid in the mechanical breakdown of food in the ventriculus. Ellison (1974) observed that large numbers of Alaskan Spruce Grouse were attracted to gravel roads during the fall, indicating the need for the birds to store enough grit to cope with their highly fibrous diet throughout the period of snow cover. The captive grouse were provided with granite grit *ad-libitum* in the shelters and during the snow-free period had access to soil and grit in the runs and extensions. Crushed oyster shell was offered in late winter and spring as a source of calcium.

Birds captured in the wild were easily weaned onto the commercial feed by mixing it with berries. Chicks reared in the aviary were initially fed a mixture of hard boiled egg, ground commercial turkey crumbles (North West Feeds Ltd.; minimum crude protein level 28%) and finely chopped dandelion (*Taraxacum officinale*) leaves. To interest the chicks in this diet, I tipped flightless varieties of *Drodophila* over the mixture. I also placed large bundles of herbaceous plants in the rearing pen which provided the chicks with an additional source of invertebrate prey. When available, wild berries were given to older broods.

Franklin's Grouse rapidly accomodated to the aviary conditions and remained in excellent condition. I took care to avoid causing unnecessary disturbance to the birds and they soon became accustomed to my presence. I was able to keep the central building clean by sweeping it out twice a week during the winter and once a week for the rest of the year, as the birds then spent relatively more time in the unroofed sections of the aviary.

Most deaths were the result of collision with the wire mesh, caused when a grouse was frightened by the sudden appearance of a predator and unable to seek cover. Provision of additional conifer boughs substantially reduced the number of mortalities. Several males died in a similar manner whilst attempting to flee from a dominant male during early spring. Disease was not a problem and can be invoked as a possible cause of death in only three instances. This is probably attributable to the avoidance of overcrowding the birds and of the isolation of the aviary from any facilities holding domesticated birds. Ectoparasites were controlled by providing the birds with boxes of sand, placed in the extensions and runs. During the winter months, I occasionally observed the grouse bathing in freshly fallen snow, as noted for Rock Ptarmigan (*Lagopus mutus*) by Watson (1972).

Observational Methodology

This study extended from 5 April 1973 until 16 November 1974. It therefore extended over four periods (April-May 1973, 1974; September-October 1973, 1974) during which Keppie (1975) had recorded the dispersal characteristics of the wild population of Franklin's Grouse from which the aviary birds originated. My main objective was to determine the role that social behaviour plays in the initiation of dispersal in this species. I assumed that the observed seasonal changes in dispersion of wild Franklin's Grouse (Keppie 1975; Herzog 1977) coincide with changes in social behaviour which, being innate, should be manifest within a captive flock. Thus I needed to demonstrate that such changes occurred in the captive flock. Confinement in a pen precluded the possibility of an individual dispersing. Therefore I observed the social interactions between the captive birds in order to determine if any changes in the behaviour of individuals occurred which might indicate the readiness to disperse, or might influence this tendency in other individuals.

This was a pioneer study and hence was extremely descriptive, as experimental manipulations in behavioural studies are succeptible to interpretational error without prior, detailed observation of the research animal under undisturbed conditions (Tinbergen 1953). Hopefully however, this work will suggest fruitful avenues along which future experimental work can proceed.

All birds used in the study were captured in the vicinity of Keppie's (1975) study area, using a noosing pole (Zwickel and Bendell 1976b), or were raised in the aviary. Background information on these birds is presented in Appendix I. Individual birds were recognized by a combination of plumage characteristics, coloured plastic leg bands and patagial wing tags (Rippin 1970). I made every attempt to ensure that the pen conditions resembled 'natural conditions' as closely as possible and particularly that birds were capable of avoiding or associating with individuals of all age and sex classes. Thus I base my results on detailed observation of social behaviour within a group of easily identified individuals and subsequent changes in their social behaviour under simulated natural conditions.

I present here a brief description of the housing arrangement for the birds, to provide perspective. Specific details will be given in the pertinent sections below. At the beginning of the study, eight pairs of grouse were already housed in the main aviary, each pair having access to two adjacent pens via sliding doors between the runs. Following completion of the extensions in late July, the birds were moved to the south side and given access to pens 9 to 16 (Fig. 1) via doorways between the runs and extensions. In early August 1973, five wild broods were brought in, one being housed in the adjacent aviary previously described and the remainder housed one brood per two pens on the north side of the main aviary. During November, the partitions in the extensions were removed, thus allowing the broods access to pens 1 to 8. On 16 February 1974, the maintenance doors between shelters and extensions were removed, thus allowing all birds to move throughout the aviary. On 3 August 1974, the maintenance doors were closed and all non-breeding birds confined to the south side. Two broods (one reared in the aviary and one captured in the wild) were then housed, one brood per four pens, in the south side. Finally in October

1974, shortly before termination of the study, the partition in the southern extension was removed so that the broods had access to pens 1 to 8.

In 1973, I attempted to monitor activity of broods using a series of microswitches, manipulated by depressable treadles and electrically connected to an Esterline Angus recorder. These were placed in the doorways between runs and shelters and between runs and the extensions. Observation showed that these treadles did not accurately represent activity of a brood, for certain individuals underwent periods of marked activity and yet rarely crossed the treadles. This system was not sensitive enough to record periods of intense activity accurately, hence it was frequently impossible to count precisely the number of times that a treadle had been depressed. Furthermore the data gave no indication as to which individuals had been active. For these reasons I abandoned this approach and concentrated entirely on observation.

I did not commence intensive observation until 25 July 1973, as I lacked my own transportation and because the construction of the extensions resulted in considerable disturbance of the birds. Thus from 5 April to 25 July 1973, I visited the aviary five times a week and made only brief observations. During periods of intense observation (mid-August to Mid-November, 1973 and 1974; 16 February to 1 June 1974), I visited the aviary at least twice a day and observed the birds for a minimum of two hours at each visit. For the remainder of the study, I visited the aviary at least four times a week and observed the birds for a minimum of one hour at each visit. Thus I spent a total of approximately 900 hours observing the captive grouse. I did not standardize the times of my observation periods in 1973, as I wished to sample the behaviour of the birds at different times of the day. However this showed that the frequency of social interactions increased with activity and that this species has two daily peaks of activity, ie. several hours after sunrise and several hours prior to sunset, as found by Herzog (1977) for wild birds and by Pauli (1974) for Black Grouse (*Lyrurus tetrix*). Thus in 1974, I made observations for two hours following sunrise and from the two hours preceding sunset until activity had ceased.

Franklin's Grouse proved to be extremely confiding in captivity and rapidly became accustomed to my presence. Upon arrival and just prior to departure of each visit to the aviary, I recorded the position of the birds, in order to gain a measure of dispersion. I did this in a consistent manner, by quietly walking around the aviary in a clockwise direction, beginning at pen 1 and finally opening the west door of the central building and walking along the central walkway. This route minimised the possibility of birds seeing me before I saw them. Birds not seen during this census but subsequently noticed, were not included as it is possible that their location may have been influenced by my activity.

The central walkway and two extensions proved to be particularly favoured by the birds and this enabled me to observe several birds simultaneously. Throughout the winter (November to early April), I made my observations whilst sitting at the western end of the central walkway, as the birds tended to congregate in this section of the aviary during inclement weather. For the remainder of the year, I observed the birds from a vehicle parked at the western end of the southern extension and from the hut located at the western end of the northern extension. The vehicle served as an 'observation hut' and caused only minimal disturbance upon arrival. I observed broods from a vehicle parked adjacent to the extension. These aviary facilities had a disadvantage in that I was unable to guarantee seeing a particular bird during an observation period and that shadows and reflections from the wire mesh often resulted in poor visibility. In 1973, I observed one brood from a hut equipped with one-way glass windows. However this cut out too much light so that it was impossible to observe the birds after sunset, at which time they were still active.

I attempted to record as much information as possible and thus did not adopt any techniques for sampling behaviour on a time basis.

Vocal communication is an integral element of social behaviour, thus I attempted to record each type of vocalisation and produce sonograms of them, with the aid of an audiospectrogram model Kay Electric Co. Missilizer (Model 675). I was not completely successful in this as I was unable to predict when and where an individual would give a particular vocalisation. Difficult light conditions prevented the use of a camera so I recorded postures by making quick sketches.

As female Franklin's Grouse attempt to breed during their first breeding season (Herzog 1977), and males are at least physiologically capable of doing so (this study), I class individuals of this species into three age groups: birds which have not undergone a post-breeding moult are considered to be juveniles, birds which have undergone one post-breeding moult are considered to be yearlings and birds which have passed through two post-breeding moults are considered adults.

I present my data by seasons which reflect the social behaviour of Franklin's Grouse. Specific dates for these seasons will vary between years depending upon weather conditions. Winter is the period of cold weather during which the grouse show a tendency to aggregate in temporary flocks, reflecting low levels of activity and intraspecific aggression. Spring commences with the dissolution of winter flocks as a result of increased levels of activity and aggression. It includes territorial establishment and mating behaviour, and terminates when the females begin laying. Summer follows and includes incubation and brood-care by females; it is a period of relative inactivity and low aggression for males and non-breeding females. Brood break-up, dispersal of juveniles and eventual onset of winter flocking are included in Autumn.

RESULTS AND DISCUSSION

Autumn

My original objective in this season was to determine whether juvenile Franklin's Grouse are "innate" or "environmental" dispersers (see Howard 1960). *A priori*, I believed that a sudden rise in aggression within a brood would suggest "environmental dispersal", whereas a sudden increase in activity without a noticable change in the level of aggression would imply "innate dispersal". However this concept proved far too simplistic. The problem is confounded by the question - is dissolution of a brood (ie. "brood break-up") coincidental in time with dispersal? If indeed these were discrete events, then the enforced proximity of birds beyond the time at which they would have no longer been associated in the wild made interpretation of subsequent social interactions much more difficult. Thus my objective was modified to attempt to determine if brood break-up and dispersal could be distinguished both causally and temporally. As it is necessary to consider the behaviour of a brood prior to break-up and dispersal, I shall include data on the entire "brood season" in this section, and not under Summer where it would more naturally come.

Many logistic problems are inherent in a study of this nature. A large sample size is desirable, particularly as there may be considerable variations between broods, but because of the constraints of the aviary this was impossible to achieve without repeating over many years. It was essential that I observe 'natural' broods (ie. a female with her own chicks). These broods were sought out adjacent to Keppie's (1975) study area and because female Franklin's Grouse with broods are widely dispersed (Herzog 1977) considerable time and effort was required to find and capture them. In 1973, 5 days of search by three parties resulted in the capture of five broods and in 1974, 2 days search by a single party produced only one brood. These 6 broods proved adequate because a larger number of broods would have posed considerable housing and maintenance problems that would have precluded detailed observation. Furthermore, I believe that it is preferable in a pioneer study, to make initial, tentative conclusions based on detailed observation of a small sample, rather than on poorly substantiated evidence derived from less intensive observation of a larger sample. As the behaviour of birds captured in the wild and subsequently held in captivity could conceivably be somewhat aberrant, I attempted to breed birds previously accustomed to captivity. This resulted in one brood (Brood F) being reared to maturity in 1974, by female WO which was captured as a juvenile in 1973. Behaviour of a pen-reared brood might also be aberrant, but at least analysis of behaviour of both pen-reared and wild-caught broods provides a firmer basis for interpretation.

The composition and age of each brood are presented in Table 1. In 1973 I attempted to achieve a reasonable sample by observing five broods. I divided each observation period between the broods as follows:- Brood A, 1 hour; Brood E, 0.5 to 1 hour; and 0.25 hour each on Broods B, C and D. I concentrated on Brood A as I was able to observe it from an observation hut equipped with one-way glass and on Brood E because it was the largest brood. In 1974 I observed only two broods, spending an hour on each brood during each observation period. In this year I was able to provide the two broods with twice the space that had been available to Broods B, C, D and E in 1973, with the result that in 1974 a

Table 1. Composition of broods of Franklin's Grouse observed during the study.

Brood	Brood Females	Male Chicks	Female Chicks	Chick's Age in Days on 22 Aug.[a]
		1973		
A	OF	MY	UM	59
B	BLF	BY	OW PUW	57
C	OO	-	PUO WO	50
D	YF	PO WPU	-	30
E	WP	PUP BLP OP	YBL	58
		1974		
F[b]	WO	-	BLBL YY	50
G	BB	WW	GG RR	53

[a] Based on length of primaries (McCourt and Keppie 1975)

[b] Brood reared in aviary

bird could always obtain visual isolation from its brood mates.

I began intensive observation of broods on 22 August of each year. Broods were captured during early August, at an age of between 30 to 40 days (see Appendix I for specific dates and ages) and given at least two weeks to adjust to captivity. It was originally felt that younger birds would not have survived the rigours of capture and transportation. I now believe this was a mistake as with sufficient care it should be possible to transport chicks of a much younger age. Thus I must rely on the aviary-reared brood for information on early brood behaviour (ie. behaviour prior to 22 August).

1. Early Brood Behaviour

The Spruce Grouse is a promiscuous species, that is, males will mate with more than one female but no pair bond is formed (see Spring). Total care of eggs and young is left to the female. Thus interactions of potential significance to brood break-up and possibly dispersal may occur between a female and her chicks and between the chicks within a brood.

I did not make detailed observation of the pen-reared brood (Brood F) prior to 22 August, as at that time I did not realise the importance of doing so. My results for this period are therefore anecdotal. I now believe that I should have traced the development of social behaviour of the broods from as early an age as possible as has been done by Guhl (1958) for the Domestic Fowl (*Gallus domesticus*) and by Kruijt (1964) for the Red Jungle Fowl (*Gallus gallus*). This would have greatly facilitated interpretation of the behaviour of older broods.

I observed chicks hatched in the aviary feeding for the first time and noticed that the female did not aid them in finding food. Thus this species may be placed into the classification of Nice (1962) among those birds having precocial chicks which follow their parent but which find their own food. The same is true of Blue Grouse (Zwickel 1967).

The first phase of brood behaviour is characterised by the dependence of chicks upon parental brooding and terminates when the chicks are capable of thermoregulation. This lasts for 10 to 12 days in the Domestic Fowl (Wood-Gush 1955) and for approximately 11 days in the Blue Grouse (Zwickel 1967). I am unable to present precise data for Franklin's Grouse as my main concern at this time was to ensure survival of the chicks rather than to obtain behavioural data. No problems were incurred in the rearing of chicks. Thus it would be easy to obtain detailed information on the duration of this phase of brood behaviour from a future study on captive broods. Brooding behaviour occurred frequently until the chicks attained 11 days of age and thereafter infrequently until the chicks were 20 days of age. Thus I tentatively propose that the brooding phase lasts for 20 days in Franklin's Grouse.

Chicks initiated brooding periods by running to the female "cheeping" very rapidly and pushing upwards at her breast, in a manner similar to that described for the Red-legged Partridge (*Alectoris rufa*) by Goodwin (1953). It is not possible to state whether the brood female or chicks terminate brooding periods, as the female may have been responding to auditory or tactile stimuli from the chicks which I could not detect.

Close contact between a female and her brood is maintained by vocal communication. Innate responses to the parent-companion appear to be largely based on auditory signals (Lorenz 1953, cited in Nice 1962).

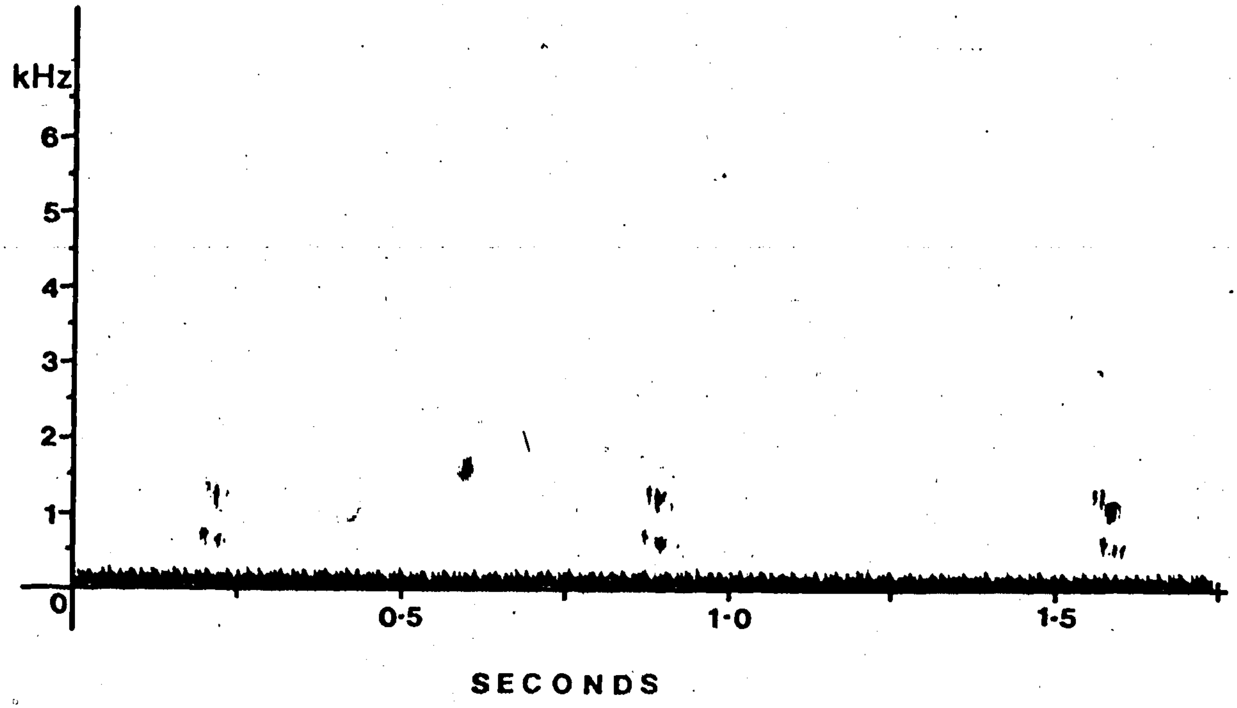
Recognition of the parent is subsequently reinforced by imprinting which occurs when the parent is 'talking' to the hatching or newly-hatched young (Goodwin 1953). It is conceivable that chicks can distinguish volcalisations of their own mother from those of other brood females. This might explain why brood-mixing does not occur when broods occasionally meet in the wild, as mentioned by Keppie (1977). This question could be resolved by experimental manipulations with captive broods.

Whilst foraging, 'contact calls' are uttered frequently by both the brood female (Fig. 2) and the chicks (Fig. 3). When feeding on particularly favoured food items (eg. *Drosophila*), chicks gave "pleasure calls" (Fig. 4), which were characterised by a more rapid sequence and ascending frequency. The pleasure call attracted other chicks to the same location. On one occasion, I attracted fifty-day old chicks (Brood G) into the shelter from the run by imitating this call. Presumably the reciprocal advantages accruing to siblings by having one of them give this call is more than the potential disadvantage that would result through competition for food. This needs further investigation. Harju (1969) described vocal communication of wild Canada Spruce Grouse (*C. c. canace*). When separated from the brood, wild chicks uttered "distress calls" which were loud, repetitive and of descending frequency. The captive chicks did not give distress calls during this period, as the brood was confined to one pen and thus always in visual contact. The call given by chicks wishing to be brooded sounded distinctive to me, but I was unable to record it. The calls of juvenile Franklin's Grouse during this phase have similar characteristics to those of chicks of the Domestic Fowl (Collias 1952).

The brood female therefore affords protection to the chicks:

Figure 2. Sonogram of a "contact call" given by a female Franklin's Grouse while with a brood.

Figure 3. Sonogram of a "contact call" given by a juvenile Franklin's Grouse while with a brood.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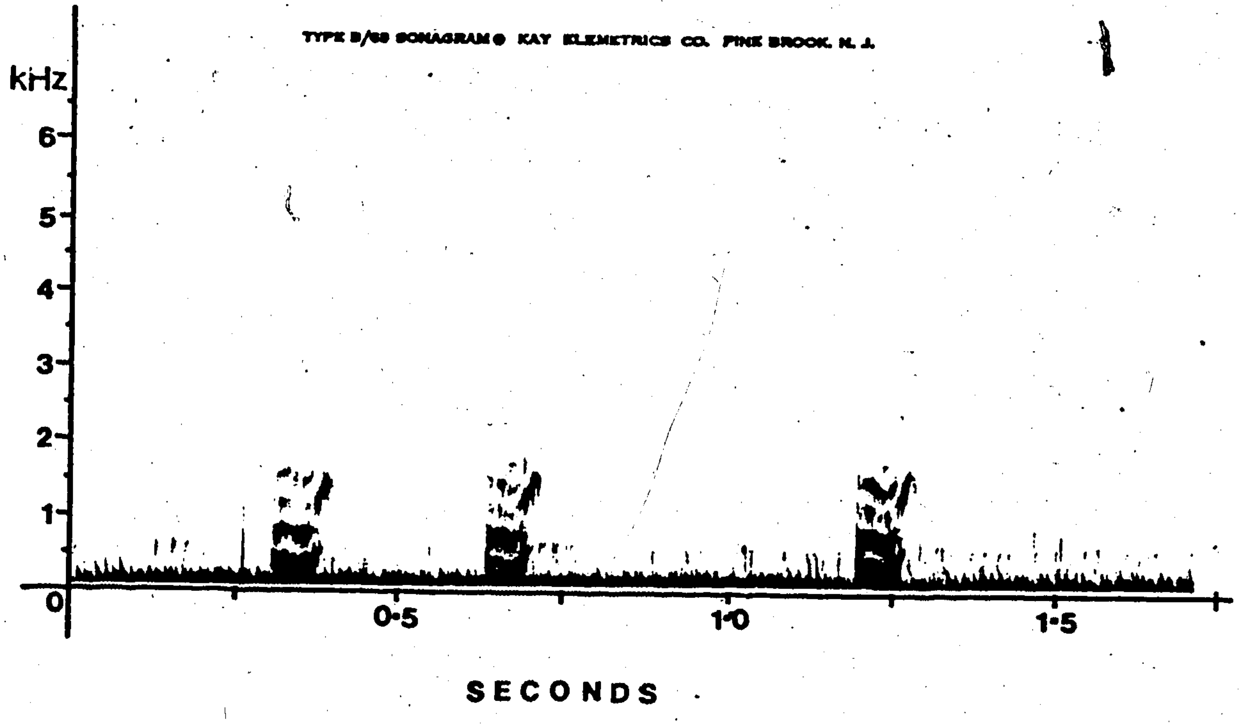
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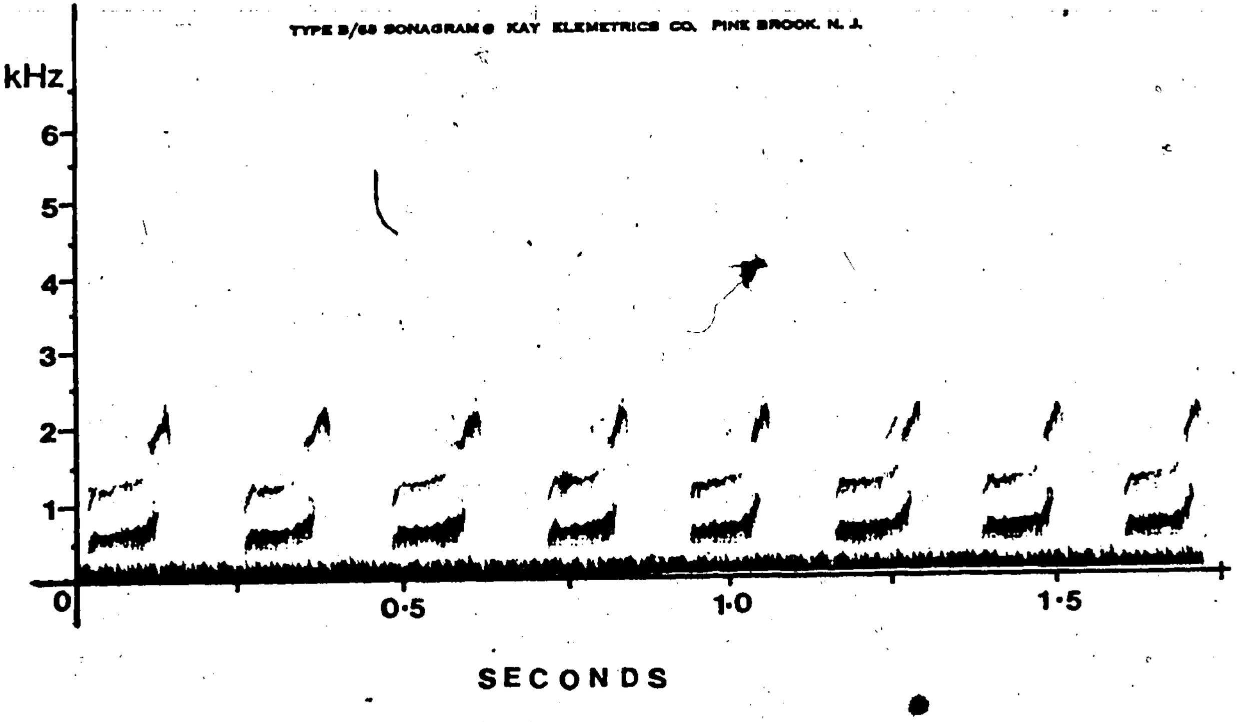
Figure 4. Sonogram of a "pleasure call" of a juvenile Franklin's Grouse given while feeding.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against predators by distraction display and vocal warning; against various environmental factors (eg. rain, hail, cold and heat) by brooding and sheltering them. Until the chicks are capable of flight, at about 2 weeks, the brood females give distraction behaviour to potential terrestrial predators, including humans (Harju 1969; Haas 1974). The captive brood female did not exhibit this behaviour to me, as she was accustomed to my presence.

The significance of this period of brood behaviour to the present study therefore is that survival of chicks is dependent upon their remaining in close contact with the brood female.

2. The Second Phase of Brood Behaviour

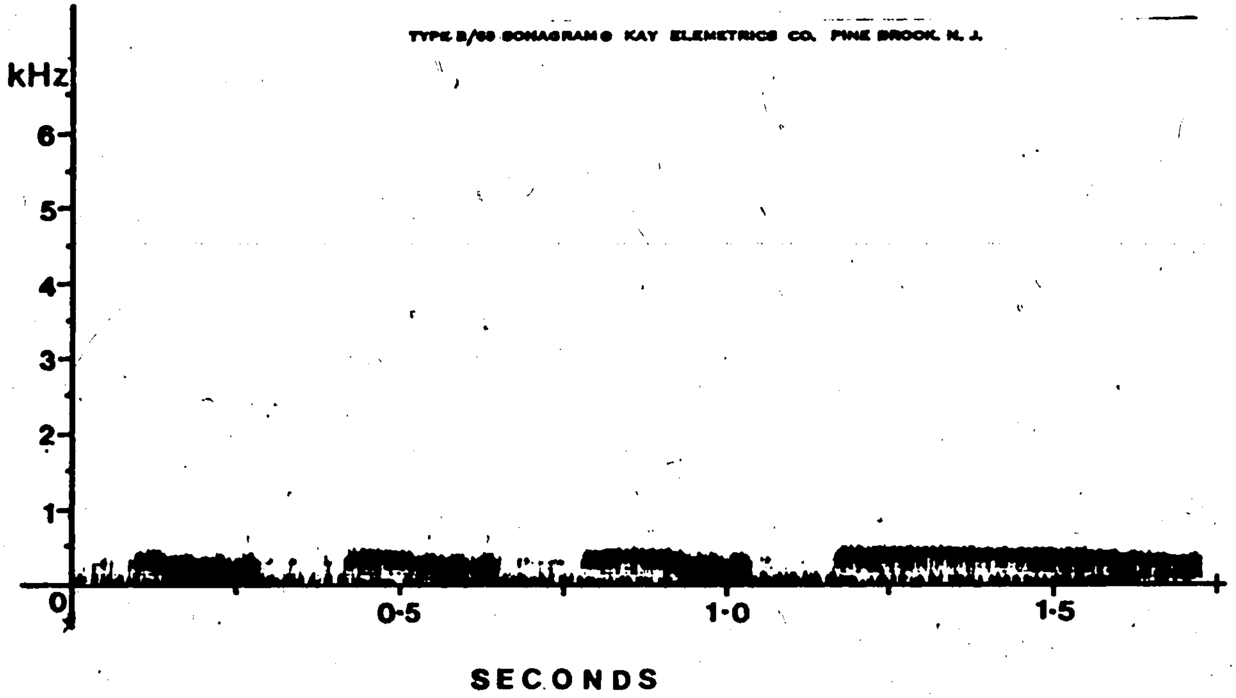
The second phase of brood behaviour commences with cessation of brooding behaviour and terminates with brood break-up. The juveniles are now capable of thermoregulation and therefore theoretically capable of surviving in isolation. That they continue to associate with the brood female indicates that there is a strong selective advantage in them doing so. Keppie (1977) found that 74 percent of the chicks of six "hens" that died during this phase, survived until the end of summer, whereas the chicks of a female that died during the brooding phase ("at 4-9 days post-hatch") were not seen again. He reported that chicks orphaned at less than 40 days of age joined other broods, whereas those orphaned at more than 40 days of age, remained as intact units without a hen (except for one chick which joined a new family). Short term survival was apparently good for juveniles that joined new families and for those that remained orphaned (although no specific data were presented and any statistical comparisons are therefore not possible). This information suggests that although a 'bond' exists between siblings in a brood, juveniles of less than 40 days of age still 'prefer' to be associated with a brood female. I propose that the main proximate advantage of juveniles continuing to associate with brood females at this time is their increased survival as the result of early detection and subsequent escape from predators.

Brood females spent much of their time "keeping watch" from slightly elevated positions whilst the chicks foraged (until at least 60 days) and almost invariably sighted aerial predators before chicks did. If the predator was distant the female would give the "warning call" (Fig. 5) causing her chicks to cease calling and adopt "alert" postures (Fig. 8a). Closer approach by the predator resulted in the female giving the "alarm call" (Fig. 6). Upon hearing the alarm call, all Franklin's Grouse either remained immobile or ran under cover. This alarm call is very different from the alarm call described by Harju (1969), which closely resembles the latter part of the "female aggressive call" (Fig. 11). On 24 August, female WO gave a loud staccato call (not recorded) for about 10 minutes in a sleeked, upright posture, in response to something in the grass outside the aviary. The chicks immediately ceased calling and joined the brood female in alert postures. I interpret this call as indicating the presence of a ground predator. When Harju recorded this call, it was uttered in response to his presence. Other bird species are known to give distinctive alarm calls in response to aerial and ground predators, for example the Chaffinch (*Fringilla coelebs*) (Thorpe 1956).

Female chicks gave alarm calls in response to aerial predators by 22 August and presumably would have done so before this date. I did not

Figure 5. Sonogram of a "warning call" of a female Franklin's Grouse accompanied by a brood, and given in response to sighting an aerial predator.

Figure 6. Sonogram of an "alarm call" of a female Franklin's Grouse accompanied by a brood and given in response to sighting an aerial predator.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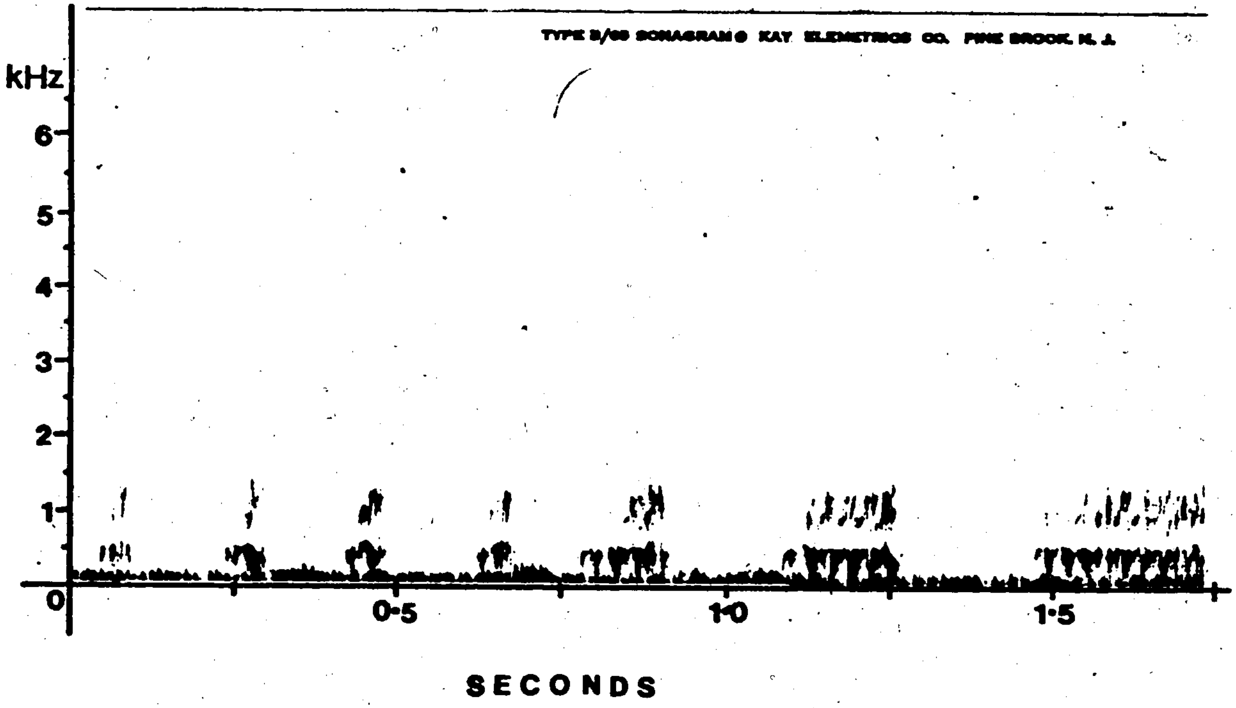
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hear a male Franklin's Grouse of any age give an alarm call in the aviary. Assuming this call is confined to females, perhaps the presence of many females in a brood may increase survival rates for all brood members. I suggest that, although Keppie has shown that juveniles orphaned after 40 days of age can survive, their chances of doing so without a brood female would be considerably reduced.

In the wild, brood females have overlapping ranges; nevertheless they are very rarely found together (Herzog 1977; Keppie 1977). When broods did encounter each other, brood-mixing did not occur. The fact that orphaned chicks had a good prospect of survival when they joined new broods led Keppie to question the purpose of broods remaining discrete. This information indicates to me that juveniles can recognize their own mother's voice (and perhaps that of their siblings) and that natural selection must favour some form of avoidance behaviour between broods, despite the fact that once orphaned, chicks must actively seek out other broods which they will join if less than 40 days of age. The mechanism by which broods avoid each other could be most easily investigated using captive birds. The most obvious selective pressure which could maintain this behaviour is reduced predation. It would seem to be a more advantageous anti-predator strategy to remain dispersed in dense habitat, thus reducing the chance of being detected by a predator. Bird species in which the young may aggregate into creches, typically inhabit open situations where the young are very exposed to predators. For example Thomson (1964) cites this phenomenon for such birds as the Greater Flamingo (*Phoenicopterus ruber*) and the Common Eider (*Somateria mollissima*). Perhaps these aggregations of young reduce the chance of an individual being selected by a predator, or their sheer numbers may intimidate or confuse the predator.

In summary, I believe that there are strong selective pressures in operation which maintain the cohesion of broods. It now remains to determine what causes the broods to eventually break up.

3. Brood Break-up and Dispersal

Brood break-up has been shown to occur in two races of Spruce Grouse during September (Keppie 1972, for *C. c. franklinii*; Ellison 1973, for *C. c. osgoodi*). Keppie noted the first break-up of a brood on 14 September 1970 and on 5 September 1971; he sighted the last complete or 'partial brood' on 2 October and 12 October respectively. I therefore felt justified in commencing my observations on the captive broods on 22 August and continuing them through to early November.

A priori, I assumed that brood break-up would be manifested in the aviary either by sudden development of aggression within a brood, by the brood female towards her chicks and/or between siblings within the brood, or by sudden bursts of activity by the chicks without associated aggression. I observed no aggressive interaction between a brood female and her chicks. Moreover, I observed no overt aggression between siblings which might be postulated as contributing to brood break-up. The only overt aggression that I observed was between the three male chicks in Brood E during October, well after the time that I believe this brood would have broken up in the wild (see below). Thus I conclude that brood break-up of Franklin's Grouse does not result from overt aggression between members of a brood. I make this statement on the strength of approximately 450 hours of observation over a 2 year period, on seven broods of various age, size and sex composition. I feel that the captive condition lends further support to this conclusion as the enforced proximity resulting from captivity would be expected to increase rather than decrease the level of aggression.

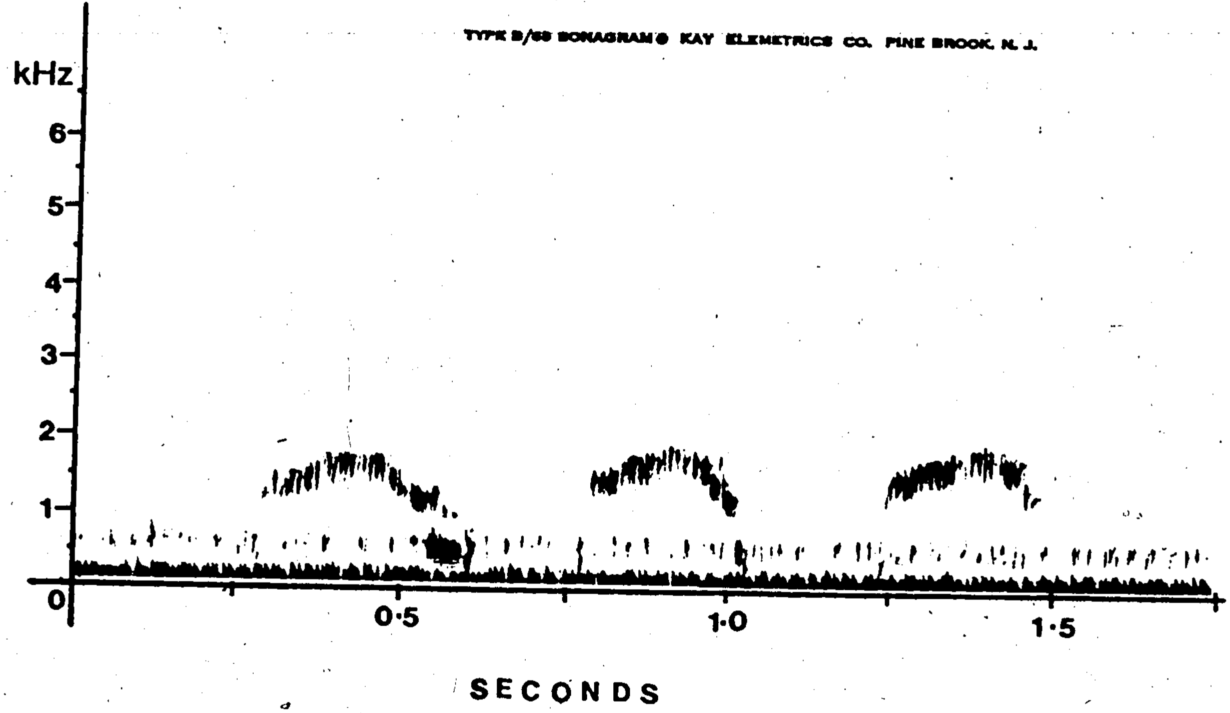
I detected no obvious bursts of activity by individual chicks which might have implied that they were attempting to leave the brood. Nor did any birds appear to actively avoid other members of the brood. I would have expected any tendency towards such behaviour to have been exaggerated in the aviary. However it is conceivable that the presence of physical barriers may have inhibited any 'innate drive' for a bird to make spontaneous movement, though I consider this doubtful. Thus I tentatively conclude that brood break-up does not result from the sudden development of a 'drive' to avoid other members of the brood or to make spontaneous movement *per se*.

Acceptance of the conclusions above implies accordance with the view that the captive broods underwent the same behavioural changes that result in break-up of wild broods. It also requires proof that all broods undergo break-up in the wild during the period that I observed the captive birds. Evidence in favour of the latter is presented by Keppie (1972) and Ellison (1973). Haas (1974) suggests that there was no coordinated or intensive brood break-up during "the early fall period" (September to October) in *C. c. canace*. This statement is based on the evidence that he made numerous sightings of groupings of Spruce Grouse with the age composition of broods during this period and on the fact that only 1 out of 14 broods that he followed "dispersed" at that time. Haas evidently equates brood break-up with dispersal although he fails to substantiate this opinion. Furthermore, without marked individuals, his data cannot be construed as evidence that brood break-up did not occur among the grouse in his study area during this period. I therefore believe that behaviour associated with brood break-up must have occurred and that it must have been of a more subtle nature than I had previously expected.

A possible explanation is that brood break-up results from the gradual weakening of the bonds that must exist between the members of a brood. Thus the brood female might lose her parental attachment toward her chicks and/or the chicks might become increasingly independant of both their mother and their siblings. Such an explanation gains credibility from my observations on the captive broods and from the known facts concerning break-up of wild broods.

In my earlier description of brood behaviour prior to break-up, I stressed the importance of vocal communication in maintaining cohesion of broods. The breakdown of the communication could therefore be regarded as indicating that brood break-up has occurred. I did not systematically collect objective data on vocal communication within broods and the evidence that I present here is admittedly anecdotal. However, all the captive broods maintained almost constant vocal communication until some time between mid-September and early October. Of particular significance here were the loud, three-syllable calls which I term "distress calls" (Fig. 7), given by chicks when visually isolated from their mother. Groups of siblings would give distress calls if visually isolated from the brood female, whereas a chick in visual contact with the brood female but visually isolated from its siblings did not. During the first few weeks, chicks would utter distress calls loudly and persistently when visually separated from the brood female. This would induce the brood female to "cluck" loudly in response, whereupon both birds would approach each other until visual contact was reestablished, at which time distress

Figure 7. Sonogram of a "distress call" given by a Franklin's Grouse of approximately 55 days of age while visually isolated from its mother.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calls ceased. As the chicks matured, the tendency for the chicks and brood female to relocate each other gradually waned. Thereafter the chicks ceased to show distress as long as vocal contact with the brood female was possible.

In 1974, I noticed that female BB (Brood G) (Table 1) no longer responded to calls given by her chicks after 20 September, and from that time on her behaviour appeared to be independent of that of her chicks. Thus I believe that this brood would have broken up at this time in the wild. The two female chicks (GG and RR) in Brood G occasionally gave distress calls for another 10 days and for the first time showed a marked interest in Brood F which was still maintaining vocal communication. This suggests that break-up of Brood G might have been initiated through desertion of the brood female. Although only 3 days younger than Brood G, Brood F maintained vocal communication until 20 October suggesting that the exact timing of brood break-up is independent of the age of the chicks and of extrinsic factors.

Unless chicks were orphaned, there was no apparent vocal communication between different broods, despite the fact that individuals were often closer to birds of a different brood than to their own brood mates. This supports my suggestion that individuals can recognize the voices of their brood-mates, as is well documented for precocial and semi-precocial species (Beer 1970). Orphaned chicks which had apparently ignored broods in adjacent pens prior to the death of their mother, showed a marked attraction to them thereafter. For example, the two chicks in Brood D occupying pens 5 and 6 (Fig. 1, Table 1) seemed to be attracted to Brood E, occupying pens 7 and 8 after the death of female YF (the brood housed in pens 3 and 4 favoured pen 3). Presumably these chicks would have attempted to join Brood E had they been able to do so. The interest in Brood F suddenly shown by the female chicks in Brood G (Table 1) after their desertion by female BB may indicate that juveniles will join other broods after their own broods have disbanded, as suggested by Herzog (pers. comm.) for wild birds.

If contact calls are indeed important in keeping brood mates together through individual recognition, cessation of this vocal communication must indicate that brood break-up has occurred. No indication of intolerance towards brood mates was shown by the birds prior to this cessation of contact calls. This suggests that independence from brood mates is attained gradually through the complex interaction of internal and external stimuli, and not suddenly through agonistic interactions. Brood break-up must be considered as the combined result of two processes: the waning of parental care and the development of social independence by the young. Detailed documentation of both processes is required throughout the entire period that a brood remains intact. Behavioural changes in addition to cessation of overt vocal communication may also indicate the time at which an individual will leave a brood. I observed the emergence of various behaviour patterns in juvenile Franklin's Grouse during the period when break-up of wild broods occurs, which has not been previously described for this species.

I occasionally observed individuals suddenly fly for a few yards with raised wings, sometimes flapping their wings and thus progressing by a series of leaps. This behaviour, which I termed the "flap-run", occurred in all broods throughout September and occasionally into early October. A low intensity form of the "flap-run" (movement in a single direction with little wing flapping) was occasionally given by both brood females and juveniles while in visual isolation from other birds in the apparent absence of any other external stimuli. I interpreted this behaviour as an indication of "surplus energy" (Koford 1953) and thus a possible artifact of captivity although it is possible that this is indeed a part of the behavioural repetoire of wild birds which has so far escaped detection.

A more intense form of the "flap-run" was given by juveniles when in visual contact with siblings. This behaviour was highly contagious and resulted in sudden bursts of uncoordinated activity within the brood. I did not observe brood females give this form of the "flap-run". Birds which initiated this group activity appeared to give the "flap-run" in response to the sudden movement of another individual and in doing so, stimulated the same behaviour in all the juveniles in the group. It is possible that the "flap-run" given by juveniles when in groups is both causally and functionally distinct from the "flap-run" given by visually isolated birds. Similar behaviour ("jumping") has been documented in wild flocks of Red Grouse and Rock Ptarmigan (Watson and Jenkins 1964; Watson 1972). This suggests that the emergence of this behaviour in broods of Franklin's Grouse may be more than an artifact of captivity.

In Domestic Fowl, apparently similar behaviour termed "frolicking" first appears when chicks are a week of age and develops into "sparring" at approximately two weeks of age (Guhl 1958). "Sparring" differs from "frolicking" in that the activity terminates with individuals leaping up at each other in the manner of fighting roosters, although no blows are actually delivered. Nice (1962) reviews the literature on this type of behaviour in birds and suggests that it is characterised by the sharp turns made by the animal. This she argues is part of the inborn movement of fleeing and thus should be denoted as "play-fleeing". I find this explanation difficult to accept for the "flap-run" of Franklin's Grouse as this species responds to ground predators by flying up into a tree and to aerial predators by 'freezing' on the spot, and not by running away conspicuously flapping its wings. Furthermore most of the examples upon which she bases her argument refer to captive animals which were suddenly released into a large enclosure after being closely confined. I feel that these examples are better explained by the hypothesis of "surplus energy".

Watson (1972) classified "jumping" as an agonistic behaviour pattern. It occurs when Red Grouse and Rock Ptarmigan are in groups and is particularly common during the period of brood break-up. Although I observed captive Franklin's Grouse throughout the year, I documented this behaviour only during the period when brood break-up would have occurred in the wild. This strongly suggests that this behaviour is of relevance to the process of brood break-up. I do not imply that this represents the mechanism by which juveniles actually achieve social independence.

Throughout the same period that the "flap-run" was given, I observed another distinctive behaviour pattern which I termed the "nervous crouch". This was performed only by the juveniles in a brood and was elicited by the rapid approach from behind of another individual (most frequently the brood female but occasionally a female chick adopted this behaviour when approached by a male sibling). The "nervous crouch" consisted of an individual suddenly adopting a crouching posture whilst making tramping motions with its feet and rapidly jerking its head up and down and from side to side (Fig. 8b). This behaviour clearly resembles a display given by males during courtship ("head-jerk display", Lunsden 1961; "squatting

Figure 8. Sketches of Franklin's Grouse in various postures.

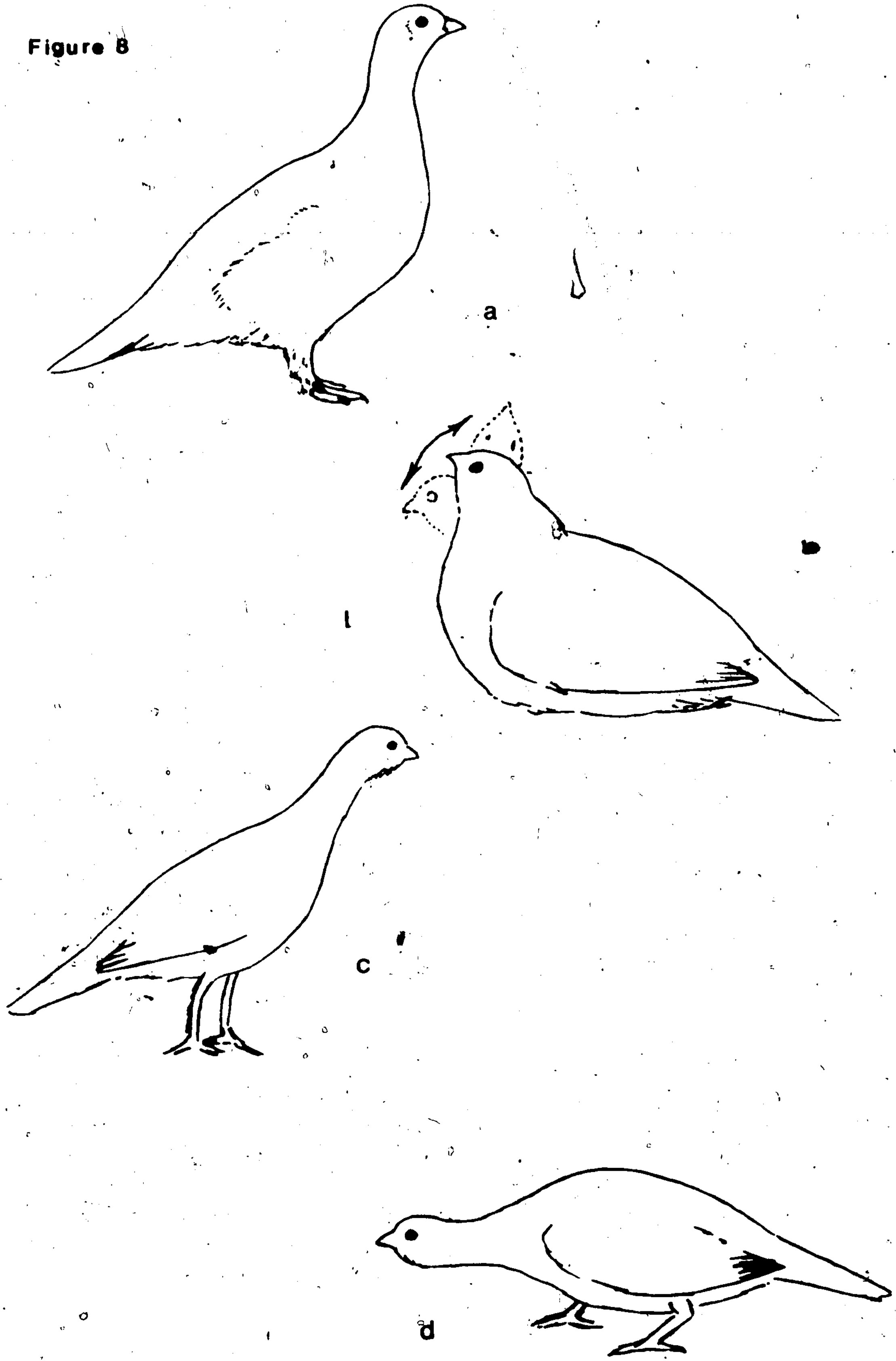
(a) The "alert posture".

(b) Juvenile adopting "nervous crouch".

(c) Juvenile in the "erect stance plus gull call".

(d) The "aggressive posture".

Figure 8



display", MacDonald 1968; "Crouching cum Head-shaking", Hjorth 1970). I shall adopt Hjorth's term as it describes this behaviour the most accurately. Birds giving both behaviour patterns crouch in front of the bird which elicited this display, facing the same direction or obliquely across its path. The "nervous crouch" differs from "Crouching cum Head-shaking" in that the tail in the former is held flat along the ground whereas in the latter it is elevated and flicked half open in synchrony with each head jerk. "Crouching cum Head-shaking" is exclusively a male display whereas the "nervous crouch" was given most frequently by juvenile females. On one occasion (see below) I observed an adult female give the "nervous crouch". The duration of the "nervous crouch" ranged from a few seconds to 2 minutes.

The incidence of the "nervous crouch" is clearly associated with the period during which break-up of wild broods occurs (Table 2). It also appears to be closely related to the age of the juveniles, particularly if only the broods on which I made detailed observations are included (Broods A, E, F and G) (Table 1). This suggests that the "nervous crouch" is given at a certain stage of physical maturity. The early observation of the "nervous crouch" in Brood B on 27 August, was of male BY which very briefly crouched and made tramping motions with its legs but did not give the head jerking motions, perhaps indicating only partial motivation of the behaviour pattern. Brood E is documented as giving the "nervous crouch" over a longer timespan than the other broods. This was because the female juvenile occasionally gave the "nervous crouch" very briefly when approached by the three male siblings which were showing male courtship behaviour during early October.

I consider the "nervous crouch" to be a behaviour pattern not

Table 2. Incidence of "nervous crouch".

Brood	Number of Times Observed	Date First Observed	Age of Chick in Days When First Observed	Date Last Observed	Age of Chick in Days When Last Observed	Timespan Observed in Days
A	12	2 Sep.	70	30 Sep.	98	28
B	2	27 Aug.	62	28 Sep.	93	31
C	1	18 Sep.	77			
E	10	7 Sep.	74	18 Oct.	115	41
F	8	9 Sep.	68	4 Oct.	93	25
G	5	14 Sep.	76	29 Sep.	91	25

previously described for Franklin's Grouse and distinct from "Crouching cum Head-shaking". "Crouching cum Head-shaking" was the last component to emerge in the ontongeny of male courtship behaviour (October) and was given only by males in response to females. The "nervous crouch" was given by birds of both sexes and first appeared at the time when males were exhibiting the first indications of courtship behaviour.

Lumsden (1961) and MacDonald (1968) both suggest that the "Crouching cum Head-shaking" is a precopulatory display, though MacDonald admits that males will occasionally omit it. My own observations of copulations in the aviary suggest that this display is not a precopulatory display and I agree with Hjorth (1970) that this is appeasement behaviour which seems to attract rather than to intimidate females (see Spring). The rapid motions of the legs and head combined with the crouched posture suggests a marked tendency to escape (Hjorth 1970).

The "nervous crouch" can be viewed as showing an even greater escape component as it lacks the potentially intimidating stimulus of an elevated tail. I suggest that the "nervous crouch" is also a more direct expression of the tendency to escape than is "Crouching cum Head-shaking". "Crouching cum Head-shaking" can be considered as the attempt of a more dominant and therefore potentially intimidating individual (the male) to reduce the escape reaction by a more subordinate individual (the female) (see Spring). The "nervous crouch" however is given by a potentially subordinate individual to a potentially more dominant individual (juveniles to brood female; juvenile females to male siblings). This suggests a quite different function for these two behaviour patterns.

My conclusions on the "nervous crouch" are supported by two observations of it occurring between birds other than brood males. On 15

October 1974, the barriers between Broods F and G (Fig. 1, Table 1) were removed and female GG (Brood G) adopted the "nervous crouch" upon encountering female YY (Brood E) for the first time. Female YY subsequently proved to be dominant over female GG. Both were juveniles. The only time that I observed an adult female adopt the "nervous crouch" was during an aggressive encounter between two non-brood females during the autumn. The dominant individual slowly approached the subordinate individual in the aggressive posture (Fig. 8d) thus indicating imminent attack. This prompted the subordinate individual to adopt the "nervous crouch" briefly prior to fleeing.

The "nervous crouch" and "Crouching cum Head-shaking" should therefore be considered as two functionally distinct behaviour patterns. I speculate that it is highly probable that "Crouching cum Head-shaking" has evolved from the "nervous crouch". Hjorth (1970) suggested that the head jerking motion may have originated from backward head bobbing motions characteristic of take-off. I question this idea, as these two types of head movement are quite distinct. Kruijt (1964) described similar "head-shaking" motions which may occur in bouts of fighting between male Red Jungle Fowl and traced their first appearance back to the feeding behaviour of young chicks. Thus he concluded that the head shaking by adult males in an "irrelevant behaviour" given when in a conflict situation. I believe that a detailed study of the ontogeny of social behaviour is a necessary prerequisite before valid conclusions can be formulated on the origin of these displays.

The only other species of grouse for which I have found reference to behaviour resembling the "nervous crouch" are Red Grouse and Rock Ptarmigan (Watson 1972). In both species "head-wagging" occurs in both adults and chicks of both sexes. Captive birds apparently show this behaviour, "when a man suddenly appears beside their cage, and occasionally when another bird of the same or opposite sex comes near" (Watson 1972).

This behaviour has not been described for the other species of grouse despite the fact that many have been the subject of numerous detailed behavioural studies and several have been maintained in captivity. Thus it is tempting to speculate that this behaviour may indicate closer phylogenetic relationship between *Lagopus* and *Canachites*, than has previously been considered. Short's (1967) arguments for merging *Canachites* into *Dandragapus* and for maintaining *Lagopus* as a completely discrete group are far from convincing. Many similarities can be made between *Canachites* and *Lagopus* (eg. natal plumage, general appearance, social behaviour). However, other behavioural, anatomical and developmental similarities and differences among these species need to be examined before any strong conclusions could be drawn.

Thus, I suggest that the appearance of the "nervous crouch" and the "flap-run" in the behavioural repertoire of juvenile birds during the period when brood break-up occurs, is an expression of powerful conflicting agonistic motivations.

I present here a brief review of my observations on the ontogenetic development of male courtship and territorial behaviour, as most of the behavioural components associated with these displays appear during the brood break-up period. I adopt Hjorth's (1970) terminology for behavioural components that have been previously described and refer the reader to that authority, plus the accounts of Lumsden (1961) and

MacDonald (1968), for the descriptions of them. The appearance of these behaviour patterns are of relevance to a better comprehension of brood break-up as they indicate the development of sexual maturity and because the social nature of these displays increased the numbers of interactions occuring between members of a brood.

The chronology of the first appearance of several behavioural components of male courtship and territorial display is presented in Table 3. The chronological sequence of these behaviour patterns is indicated by the order in which they were presented in Table 3, for example, the "Upright" was observed first and the "Crouching cum Head-shaking" was the last to be recorded. I observed two behaviour patterns that have not been previously described for this species: the "erect stance plus gull call" and the "gull call plus flap display".

When giving the "erect stance plus gull call", a bird would adopt a very long-legged stance, with the neck stretched upwards and forwards and then give a fairly loud harsh vocalisation, which was reminiscent to me of the flight call of the Herring Gull (*Larus agentatus*). This posture (Fig. 8c) resembled the crowing posture of the Domestic Fowl. Whilst uttering the vocalisation, the bird would often make a few steps forward and would half fan its slightly elevated tail in synchrony with each syllable. The "gull call plus flap display" strongly resembles the "erect stance plus gull call", with the addition that the bird held the wings horizontally out from the body and immediately after vocalising, would flap the wings stiffly about three times, at the same time hopping forward. It is possible that these behaviour sequences represent different motivational levels for the same display. It was my impression that the vocalisations uttered during the "erect stance plus

Table 3. Phenology of first observation of behavioural components of male courtship behaviour in juvenile Franklin's Grouse.

Brood	"The Upright"	"Erect Stance Plus Gull Call"	"Display Walk Cum Tail-Swaying"	"Gull Call Plus Flap Display"	"The Rush Cum Momentary Tail Fanning and Hiss Cum Squeak Call"	"Crouching Cum Head-Shaking"
A	12 Sep. (MY) 80 days	22 Sep. (MY) 90 days	29 Sep. (MY) 97 days	26 Oct. (MY) 124 days	3 Oct. (UM)[a] 101 days	27 Oct. (MY) 125 days
B			20 Oct. (BY) 115 days	20 Oct. (BY) 115 days		
D	6 Sep. (PO) 45 days	29 Sep. (PO) 68 days		21 Oct. (WPU) 91 days 24 Oct. (PO) 94 days		
E	6 Sep. (BLP) 73 days	18 Sep. (BLP) (PUP) 85 days	23 Sep. (BLP) 90 days	8 Oct. (BLP) (PUP) 105 days	28 Sep. (PUP) 95 days	24 Sep. (PUP) 94 days
	15 Sep. (PUP) 82 days 18 Sep. (OP) 85 days	27 Sep. (OP) 94 days	27 Sep. (PUP) 94 days 15 Oct. (OP) 112 days		6 Oct. (YBL)[a] 103 days 15 Oct. (YBL)[a] 112 days	31 Oct. (BLP) 117 days
G	12 Sep. (WW) 74 days	26 Sep. (RR)[a] 85 days 10 Oct. (WW) 100 days	14 Oct. (WW) 101 days			

[a] Given by females

gull call" were higher pitched than those in the "gull call plus flap display", which clearly resembled the "aggressive call" of mature males (Fig. 9). Unfortunately I was unable to record on tape the "gull call" for sonogram depiction.

I could detect no external stimulus that might have elicited these behavioural patterns. Both were given in close proximity to other birds without any apparent interaction occurring and also when in visual isolation. The vocalisations and movements of the retrices resemble those given by mature males giving the "aggressive call". The upright posture of the juvenile males when giving the "gull call" is however quite unlike the "aggressive posture" of a adult male (Fig. 8d). The wing beats of the "gull call plus flap display" may be related to the drumming behaviour of territorial males documented by MacDonald (1968), but resemble more closely the position of the wings in the "flap-run". Juvenile males had ceased giving brood contact calls prior to the emergence of these behaviour patterns, thus they may not be given by juvenile males while still in contact with a brood.

In the absence of precise information, the phenology of behaviour patterns may be used with discretion, as a crude indication of the type of causal factors which may underlie this behaviour. I intimated above that the emergence of the "nervous crouch" in the behavioural repertoire of juvenile Franklin's Grouse may be related to age and hence physical maturity of a bird, rather than to external factors. As the "nervous crouch" suggests the presence of conflicting agonistic motivations, it is possible that this behaviour is closely associated with the time when a bird gains independence from a brood. This leads to the suggestion that perhaps the timing of brood break-up is also related to the age of the juveniles. However these conclusions were based on broods of comparable ages (all broods except Brood D, Tables 1 and 2). The juvenile males in Brood D gave the various components of these displays on approximately the same date as males in other broods, despite being at least 20 days younger (Table 3). This strongly intimates that this behaviour at least may be strongly influenced by external factors, for example, photoperiod. This might also be true for the "nervous crouch". I made only brief observations on Brood D, thus probably missed this behaviour pattern, although it is most likely that the birds did give this behaviour. A statistical test for analysis of variance based on detailed observation of at least ten broods, to represent as wide a range in age as possible would help clarify this question.

Documentation of behaviour patterns based on detailed observation should be followed by experimental studies designed to analyze the factors responsible for the expression of this behaviour. In particular, the potential role of hormonal control of behaviour needs to be investigated in both the brood female and the juveniles (see Guhl 1962). Hormonal factors might also explain the occasional appearance of characteristically male behaviour patterns in juvenile females (Table 3). A particular physiological state may characterise individuals just prior to the time of emancipation from the brood. Such studies must cover the entire period that broods remain as cohesive units.

In summary, my work suggests that brood break-up of Franklin's Grouse is not the result of aggressive behaviour, as is the case of some species of birds (Howard 1940; Nice 1943: Wood-Gush 1955). Instead I propose that in this species, the dissolution of the family unit involves both the waning of parental care and the increasing development of social independence of the juveniles. Both processes need to be carefully documented and their underlying causal factors analysed. The actual timing of brood break-up will reflect the combined behavioural characteristics of all members of the brood, which in turn are dependent on the complex interaction of internal and external stimuli. Variation among broods in timing of break-up may therefore be expected, as a result of individual differences in behaviour of both brood females and their young, and of differences in the size, age and sex composition of broods. A tho[illegible]tigation of this problem requires work done both in the wild a[illegible]tive conditions. My suggestions are consistent with th[illegible] Bowman and Robel (1977) for the break-up of broods of the Greater Praire Chicken (*Tympanuchus cupido*).

I observed no changes in the behaviour of juveniles, which might have indicated that an individual would have dispersed had it not been confined. Thus I am unable to conclude on the basis of this study, whether or not brood break-up and dispersal are coincident in time, nor to determine which factors might cause an individual to disperse. If these two phenomena are indeed separated in time, then conclusions based on the behaviour of birds still confined together as a family unit after the time when brood break-up had occurred, would be extremely dubious. I believe that only a radio-telemetry study on wild broods could establish whether or not these two phenomena are coincident in time. This is a necessary step before any attempt is made to determine the causal factors of dispersal. Unfortunately, no information has been published on the actual timing of brood break-up and Autumn dispersal of wild Franklin's Grouse.

Studies involving the use of radio-telemetry have shown that brood break-up and dispersal are temporally discrete phenomena in the Ruffed Grouse (*Bonasa umbellus*) (Godfrey and Marshall 1969) and the Greater Praire Chicken (Bowman 1971; Bowman and Robel 1977). This implies that the causal factors responsible for them are different. In the absence of contrary evidence, I speculate that this is probably also true for Franklin's Grouse.

No attempt has been made to date to determine which factors induce an individual grouse to disperse. The first step must be to establish whether or not all juveniles disperse in Autumn. Most field workers have referred to dispersal as movement from the study area (eg. Chambers and Sharp 1958; Keppie 1975), an assessment which contributes little to a better understanding of the biological significance of dispersal, and which gives no more than an extremely dubious estimation of the percentage of birds that disperse. For example, an individual which moves across the boundary of a study area from a point just inside it, would be considered as having dispersed, whereas one that made a larger movement from the centre of the study area to just within the limits of the boundary would be considered as having not dispersed. There is an evident need for more descriptive work to be conducted on precise distances moved by juvenile grouse. The results of such studies should be presented in a manner enabling assessment of the relative effects of such factors as age, sex, genetic relationship and individual differences of behaviour.

Winter

The second part of my main objective was to determine the factor(s) which cause Franklin's Grouse to "disperse" in the spring (Keppie 1975). Three basic explanations are possible: juveniles have an innate tendency to disperse in the spring; juveniles have an innate tendency to disperse in the spring only if stimulated to do so by intraspecific or other environmental factors; juveniles lack an innate tendency to disperse in the spring, but are forced to move from the wintering grounds by intraspecific interactions or other environmental stimuli.

Keppie (1975) documented a non-significant relationship between the size of the overwintering population on his study area and the number of yearlings which became established in the breeding population the following spring. This suggests the possibility that spring movements of juveniles were influenced by intraspecific interactions occurring at some time between the termination of autumn dispersal and the cessation of spring movements of junveiles. During the winter Spruce Grouse frequently aggregate in small transient groups except for the adult males, which generally remain solitary (Ellison 1972; Herzog 1977). Dominance relationships could be established among birds encountering each other in these wintering groups. The relative dominance of a juvenile could influence its probability of moving the following spring.

Adult Franklin's Grouse of both sexes are territorial during the breeding season (Herzog 1977). Males of *C. c. osgoodi* (Ellison 1971), *C. c. canace* (Anderson 1973) and *C. c. franklinii* (Thompson 1972) retain the same territory in subsequent years. This is also generally true of male Blue Grouse (McNicholl MS[1]) and male Ruffed Grouse (Boag 1976).

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[1] McNicholl, M. K. in prep. PhD thesis, University of Alberta.

No information has been published on tenacity to breeding territories by female Spruce Grouse. However, the fact that migrant females tend to return to the same wintering and breeding areas (Keppie 1975; Herzog 1977) indicates that females do show site tenacity. Birds which have previously held a territory appear to have an advantage over newcomers when competing for the same site in subsequent years (Collias and Taber 1951; Hinde 1956; Klopfer 1969). Assuming this to be true of Franklin's Grouse, healthy adults will be dominant over juveniles when territorial interactions occur, irrespective of dominance relationships which may have been established during the winter. Thus social interactions between adults and yearlings during the winter are not likely to have much impact upon movements of juveniles the following spring. On the other hand, the relative dominance of an individual within the juvenile cohort could affect the probability of its moving in the spring. Collias and Taber (1951) documented ~~the~~ existence of dominance hierarchies among transient flocks of Ring-necked Pheasants (*Phasianus colchicus*) during the winter, and found a strong association between the establishment of crowing territories in the spring and ability to dominate other cocks in the winter.

The only aggression that I observed between captive birds occurred between male siblings in those broods with more than one male juvenile, that is Broods D and E (Table 1). I first observed this aggression on 16 October: PO (Brood E) chased WPU: PUP (Brood E) chased BLP and OP but showed no aggression towards females WP and YBL. Interactions occurred among unrelated male juveniles upon first encounter, with relative dominance being established quickly without physical contest. Male BY of Brood B (Table 1) was lowest in social status and male BLP of

Brood E was highest. Prior to allowing the broods to mingle, BLP had become dominant over PUP, thereby reversing their social status. At that time PUP appeared to be injured, the injury possibly caused by colliding with the wire after being suddenly frightened by a predator. A Great Horned Owl (*Bubo virginianus*) was known to have visited the aviary on the two days prior to this dominance reversal. This aggression, which did not appear to be as intense as between males in the breeding season (see Spring), resulted in the establishment of a dominance hierarchy between male siblings within a brood. These interactions occurred after the period when brood break-up and dispersal would have occurred naturally, and therefore indicate that similar interactions between male juveniles may take place in the wild after these processes have occurred.

Aggression between male siblings during this period coincided with the occurrence of male territorial and courtship behaviour in the same birds (Table 3). The dominant adult male, YG in 1973 and BLP in 1974, also showed a resurgence of territorial behaviour at this time. Resurgence of territorial behaviour in the fall has also been demonstrated in the wild for Alaskan Spruce Grouse (Ellison 1973), Red Grouse (Watson 1964) and Sharp-tailed Grouse (*Pedioecetes phasianellus*) (Evans 1969; Brown 1971). Territorial behaviour of male Blue Grouse (Simard 1964) and of male Ring-necked Pheasants (Collias and Taber 1951) correlates with seasonal increases in testicular weight. Implantation of androgens caused a rise in aggression of male Sharp-tailed Grouse (Trobec and Oring 1972), an increase in the size of territory held by male Red Grouse (Watson 1964) and in Domestic Fowl caused an increase in aggressivity which resulted in an individual rising in social status (Guhl 1961).

There must be some selective advantage accruing to male Franklin's

Grouse that exhibit territorial behaviour during late autumn and early winter. I speculate that in exhibiting site tenacity to a breeding territory (see above) and territorial behaviour in the autumn adult male Franklin's Grouse would discourage juveniles and possibly yearling males from attempting to establish themselves on occupied territories. Some adult males migrate between breeding and wintering ranges (Herzog pers. comm.). Information is currently lacking on whether these males assert their territoriality through aggressive behaviour prior to migrating to the winter grounds. Aggression between juvenile males in the early winter might decide which individual would remain in a given area the following spring. A territorial male which is incapacitated in some way might also conceivably be displaced at this time.

No evidence has been published that female Franklin's Grouse show an increase in aggression during the fall. Captive females maintained in a group in the autumn showed no increase in aggression in the autumn, but did show an increase in the following spring. This raises the question: why do only males exhibit aggression in late autumn and early winter? Further field work is needed to solve this problem.

On 15 October 1974, I removed the barrier separating Broods F (pens 1-4) and G (pens 5-8; Fig. 1). Although I had observed no aggression between any females within either brood prior to this date, agonistic interactions occurred between females of different broods at or soon after their first encounter, with the result that all females in Brood F dominated all females including the adult hen in Brood G. The only male juvenile in these broods (WW of Brood G) was aggressive towards females of Brood F but not to either its parent or its siblings. These dominance relationships were established without known physical contest.

In each case, the dominant individual chased the subordinate without opposition.

In 1973 I did not remove the barriers separating Broods B, C, D and E (Table 1) until 25 November, at which time there was already permanent snow cover. Agonistic encounters did not occur between unrelated females upon their first encounter. This may indicate that in late November female-female aggression is lower than during October. Although I did not make detailed observations at the aviary between 25 November and 18 February 1974, I did observe short chases between females during this period, indicating that a dominance hierarchy was eventually established among females.

On 25 July 1973 I moved all non-breeding birds to the south side of the aviary and gave them access to pens 9-16 (Fig. 1). These birds had previously been isolated in pairs, each pair with access to two pens. Many agonistic interactions were observed between birds of the same sex as soon as they were allowed to mingle, and a linear peck order was rapidly attained. Yearling male YG (Appendix 1) proved to be the dominant male, but was excessively aggressive and thus removed from the flock after killing another male, RG. Another yearling male, RY, subsequently became the dominant male. Two yearling females, FY and SW, occupied the two highest positions in the female peck order.

These three sets of observations indicate that captive Franklin's Grouse rapidly establish a dominance hierarchy when individuals are allowed to mix for the first time during the late summer, autumn and early winter. Thus it is possible that social status is established among wild birds during the period of winter flocking, even though associations between particular individuals may be of a very transient nature (Ellison 1972).

On 17 February 1974 I opened the maintenance doorways in the central building (Fig. 1), thereby allowing all birds in the aviary to mingle. Overt aggressive interactions did not occur when birds from opposite sides of the aviary first encountered one another. For example, when the dominant male, RY from the south side of the aviary first encountered the dominant male from the north side, BLP, no interaction occurred. I did not make detailed observations at this time, but a social hierarchy was established subsequent to this date (Table 4, 5). The fact that birds did not interact strongly on their first encounter may indicate that levels of aggression are lower in mid winter than in early winter, and/or that the birds are at first intimidated when entering an "unknown" area, in this case the central walkway (Fig. 1).

I allowed all the birds housed in the aviary to mingle from February to April, as I felt it important that the juveniles be exposed to birds of all sex and age classes prior to the time of spring "dispersal" in the wild (Keppie 1975). I also hoped that freedom to mingle might give some insight as to whether winter flocking in this species is the result of social attraction, or rather simply the congregation of several birds at a period when levels of aggression are low at some favoured resource, for example a particular tree as suggested by Herzog (1977).

In contrast to spring and summer, the central walkway proved to be especially favoured during this winter period, and I frequently observed as many as twelve birds in this walkway at the same time. The level of aggression was very low, resulting in few interactions. Occasionally one bird would chase another briefly, or an individual would move aside at the approach of another, but a few minutes later the same individuals might feed within a few inches of each other. A linear peck order was apparent

Table 4: Number of aggressive-submissive interactions among male Franklin's Grouse, 17 February to 22 April 1974.

Winners		Losers											
		BP	OP	WPU	PUP	RY	YBLY	YBLA	BB	BR	BY	MY	?
BP	(Juv)	-	[illegible]	1[a]	10	3	1	2	6	5	10	4	5
OP	(Juv)	-	-	6	5	-	-	1	1	1	2	2	4
WPU	(Juv)	10[b]	-	-	-	4	1	-	7	3	4	11	-
PUP	(Juv)	-	-	-	-	3	-	3	9	5	4	4	-
RY	(Ylg)	-	-	-	-	-	-	-	1	-	6	-	-
YBLY	(Ylg)	-	-	-	-	-	-	1	-	-	-	1	-
YBLA	(Ad)	-	-	-	-	-	-	-	-	-	-	-	-
BB	(Ad)	-	-	-	-	-	-	-	-	1	-	-	-
BR	(Ad)	-	-	-	-	-	-	-	-	-	-	1	-
BY	(Juv)	-	-	-	-	-	-	-	-	-	-	1	-
MY	(Juv)	-	-	-	-	-	-	-	-	-	-	-	-

? Unidentified male

[a] Dominance reversal occurring on 21 April

[b] Interactions occurring prior to 21 April

Table 5. Number of aggressive-submissive interactions among female Franklin's Grouse, 17 February to 22 April 1974.

	Losers							
Winners	SB	WP	PUO	OO	OW	PUW	WO	?
SB (Ad)	-	2	1	-	3	-	-	3
WP (ad)	-	-	4	-	1	2	1	1
PUO (Juv)	-	-	-	1	-	1	2	-
OO (Ylg)	-	-	-	-	-	1	2	-
OW (Juv)	-	-	-	-	-	1	-	-
PUW (Juv)	-	-	-	-	-	-	-	-
WO (Juv)	-	-	-	-	-	-	-	-

? Unidentified female

among those individuals for which I observed social interactions (Tables 4, 5).

In all cases males were dominant over females, Dominance was more marked among males than females. Adult males of one or more years of age were seen less often than either juvenile males ($\chi^2yc = 22.7; P < 0.005$) or females ($\chi^2yc = 26.7; P < 0.005$) among the other birds in the central walkway, possibly indicating that older males were less sociable than birds of other age and sex classes. Juvenile males were seen there as frequently as females ($\chi^2yc = 0.1; P < 0.5$). Adult male Spruce Grouse are rarely found associated with other grouse in the wild during winter (Ellison 1972, 1973; Herzog 1977). Very few interactions occurred between females during observation periods and when they did, it was often not possible to identify the individuals involved.

This social hierarchy was stable throughout the winter period, and no overt aggression was observed until 15 April. The relative dominance of birds which had encountered each other prior to 17 February 1974 remained the same throughout the rest of the winter period, with the exception that male WPU had become dominant over male BLP. Implicit in the establishment of a stable peck order is the ability to recognize and remember other individuals (Schjelderup-Ebbe cited in Wood-Gush 1955). Schjelderup-Ebbe (op.cit.) found that Domestic Fowl forget other individuals, and consequently their relative social status after 2 weeks separation. Extrapolation of these findings to wild birds is of little value until more information has been documented on the frequency and duration of associations between particular individuals in the wild. The ability of Franklin's Grouse to remember other individuals could be tested easily by experimental manipulations in the captive situation. More information is also required on the movements of wild Franklin's Grouse relative to other individuals. Individuals may have preferred sites for feeding, roosting or other activities in which they become dominant over other individuals to which they are generally subordinate (Thompson 1960).

The captive grouse were noticeably less active during the winter than in either spring or autumn. The fact that they showed a marked preference for the central walkway could be caused by social attraction, attraction to a particularly favoured area (better shelter, more food, etc.) or a combination of these factors. This problem could be studied in the captive situation by maintaining a group of grouse in an aviary that is divided into equally attractive subdivisions. I do not feel that the aviary used in the present study was suitable for such an experiment. I very rarely observed birds together in the shelters although they were often in very close proximity in the central walkway. Perhaps the amount of space available influences individual distance.

In summary, during the winter agonistic interactions between the captive Franklin's Grouse resulted in the establishment of stable social hierarchies. This suggests the possibility that social interactions occur among wild Franklin's Grouse during the winter flocking period, and that these might affect the movements of juveniles in the following spring.

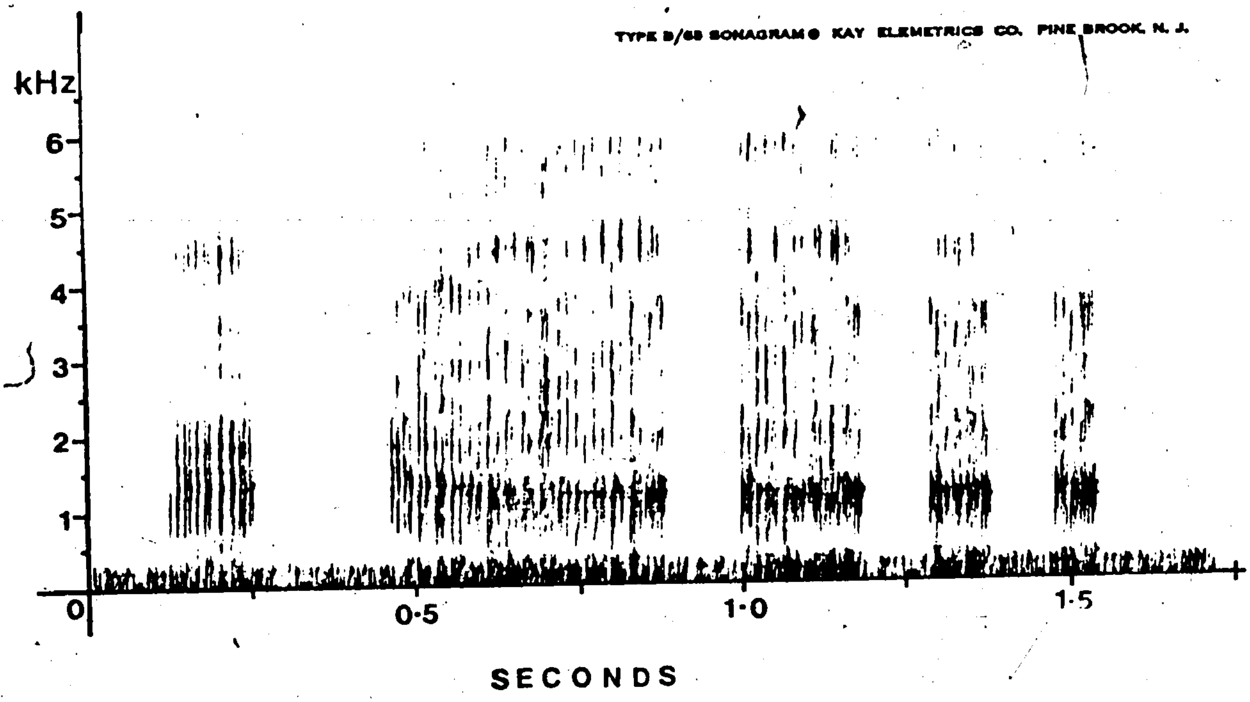
Spring

Keppie (1975) combined totals for three years, showing that 60 percent of overwintering juvenile females and 45 percent of overwintering males emigrated from his study area during the spring. The number of juveniles that eventually settled on his study area following the cessation of "spring dispersal" appeared to be inversely related to the size of the overwintering population. On the basis of these data and in light of apparently good survival for birds of all age and sex classes, Keppie (1975) intimated that "spring dispersal" may act as a density dependent mechanism serving to regulate the size of the breeding population. Herzog (1977) has added support to this hypothesis by showing that both sexes maintain exclusive territories in spring that force non-territorial birds into vacant habitat. Acceptance of this hypothesis must await proof that juvenile birds have an innate tendency to disperse in the spring only if stimulated to do so by some form of population pressure, otherwise the observed spring movements are merely movements in response to social pressure and have nothing to do with dispersal as an innate phenomenon.

I consider the spring season to have commenced on 16 April 1974, as this date marked a radical change in the social organization of the captive birds. Prior to 16 April the captive birds had existed in a state of relative harmony under a stable and apparently linear peck order (Tables 4, 5). On 16 April, I observed male WPU adopt the "aggressive posture" (Fig. 8d) and utter the "male aggressive call" (Fig. 9) toward male MY. Birds adopting the "aggressive posture" lower the body and hold the neck out horizontally. This posture indicates imminent attack, and is the same in both sexes. The "male aggressive call" can be described as a harsh growling sound. During agonistic interactions in the winter, the dominant

Figure 9. Sonogram of the "male aggressive call" given by a male Franklin's Grouse while threatenting another male.

Figure 10. Sonogram of a "moan call" uttered by a female Franklin's Grouse.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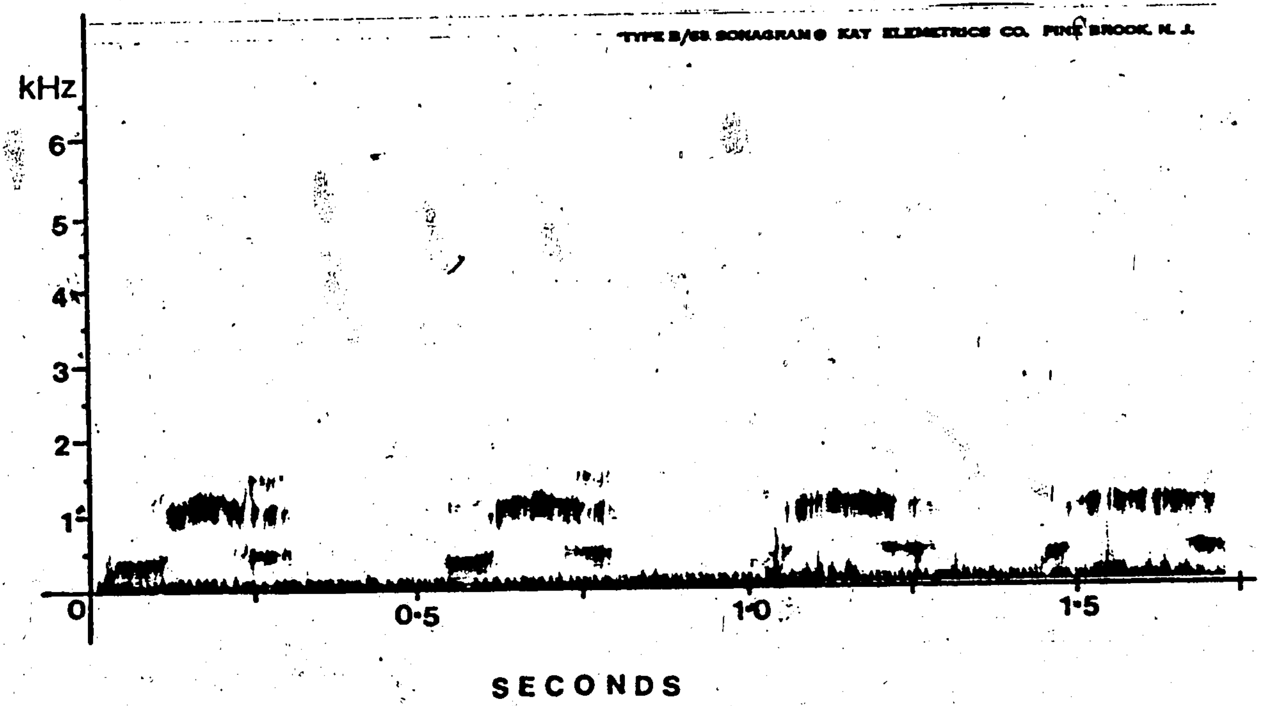
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birds would occasionally adopt the "aggressive posture" towards a subordinate bird, but never gave the "male aggressive call".

The "male aggressive call" has been described previously as given by males towards other males during territorial interactions (MacDonald 1968; Harju 1969). I observed captive males utter this call only during the spring and autumn, suggesting that its occurrence is related to the annual cycle of testicular development (Simard 1964). Similar aggessive behaviour has been described by Stirling and Bendell (1970) for male Blue Grouse and by Watson (1972) for male Rock Ptarmigan.

The period 16 April to 22 April was characterized by the sudden development of extreme intolerance by certain juvenile males (WPU, PUP, BLP, OP) toward subordinate males (Table 4). These dominant males were from broods which included two or more male juveniles (Table 1). Usually visual contact with a subordinate male by these birds elicited the "male aggressive call" prior to attack. When threatened by a dominant male in this manner, subordinate males immediately fled. Thus, 16 April marked a transition from a hierarchical social system among males to a system based on despotism. Males were involved with no overt interactions with females during this period.

On 18 April an adult male (BB) was found dead, presumably having collided with the wire mesh while attempting to escape from an aggressor. I also observed male WPU attack a bird of higher social status (OP) (Table 4) which had not exhibited intense aggressive behaviour prior to this date. Male OP did not retreat and following a very brief encounter, WPU fled with OP assuming the role of aggressor. The following day male BLP gave t[illegible] "male aggressive call" for the first time, and was observed to domin[illegible] both his male siblings PUP and OP (Table 1). Since WPU had been dominant over BLP during the winter but subordinate to OP, a triangular dominance hierarchy evidently existed among males WPU, BLP and PO at this time. Another adult male, BR, was found dead on 19 April.

Thus this period appeared to be a time when certain juvenile males were attempting to assume the role of despot among males in the captive flock. This contest was finally decided on 21 April when BLP was seen to run the entire length of the central walkway to attack male WPU who was chasing male MY. Male WPU fled from BLP immediately, and the latter then assumed male courtship behaviour towards a female. This was the first time that I had observed male courtship behaviour towards any female since the previous October. Thereafter male BLP assumed the role of despot and almost constantly displayed to the females. Other males were attacked whenever seen, with the result that several more died (PUP, WPU, RY, YBLA). Three juvenile males, OP, MY and BY, survived the spring by remaining very secretive and inconspicuous.

The average territory size of adult male Franklin's Grouse at Gorge Creek is 1.0 ha (Herzog 1977). Thus a single male would be expected to include the entire aviary as its "territory". However, I expected this role would be assumed by a yearling or an adult male, rather than a juvenile. In the wild, male Spruce Grouse of more than one year of age exhibit territorial behaviour whereas most yearling males do not, even if they become localised (Ellison 1971; Anderson 1973; Herzog 1977). The most likely candidate for despot in the aviary was a yearling male, RY. This bird was captured as a juvenile in 1972, was housed with a female, and exhibited territorial and courtship behaviour in the spring of 1973. RY was the dominant bird among the flock of adult and yearling males in the autumn of 1973. In fact, male RY was the only male of more than one year of age to show territorial behaviour in the spring of 1974. On 18 April RY uttered the "male aggressive call" towards a juvenile male, MY, and on 21 April he was observed to make a "flutter flight" (Hjorth 1970). However, RY was apparently unable to dominate juvenile male BLP who later killed him.

In the spring of 1973 males were housed with females, each pair having access to two pens. Males of all age classes exhibited territorial and courtship behaviour despite the very close proximity of other territorial males. Aggressive interactions frequently occurred between adjacent males, as they were able to establish visual contact through the wire mesh when using the perches in the runs. These males had been housed in this manner since the previous autumn. This suggests that physical contact must be possible before a dominance hierarchy can be manifest. As birds appeared to recognize their relative dominance status at their first encounter with another individual and did not resort to a physical contest, this raises the question: what factor(s) decide the outcome of the initial encounter between two individuals? Collias (1943) reviewed the factors which affect success in initial encounters between Domestic Fowl.

The fact that the only birds to exhibit any form or territorial behaviour were those of the five highest rank suggests that the other birds were psychologically castrated. Thus the establishment of a peck order during the winter season appears to affect the behaviour of males during the spring.

The fact that a juvenile male became the territorial male in the aviary appears to contradict information known for wild birds. There are two possible explanations: that male BLP would have been able to establish a territory in the wild had it competed with any of the other males which it dominated in the aviary; or that its ability to establish a "territory" is an artifact of the captive situation.

The adult and possibly the yearling males would presumably have held territories had they been in the wild, and thus a juvenile male would not likely have been able to displace them in the early spring. McNicholl (MS) documented a case of gradual displacement of a long established adult male Blue Grouse from its territory by an apparent yearling after the former developed a severe limp, which would have incapacitated this bird in its attempts to display at the "intruder". He also noted several cases in which older males returned to their previous territories early in the spring, but later disappeared with the territories in some cases being occupied by yearlings. The captive adult Franklin's Grouse had been captured as adults or yearlings (Appendi[illegible]), and thus had probably held territories in the wild or, in the cas[illegible] the yearlings, were localised on a unit of habitat. Perhaps removal of these birds from known units of habitat (territories) removed any competetive advantage they would otherwise have held over juvenile birds in agonistic encounters. Information on the ability of adult males to establish a new territory might be attained by a radio-telemetry study of males which are moved in the winter to a different location.

The yearling male cohort has been neglected in field studies of Spruce Grouse. Although few male Spruce Grouse become territorial in their first spring (Herzog 1977), no information has been published on their subsequent behaviour and movements related to establishment of a breeding territory in their second spring. Thus, perhaps the yearling males in the aviary would not have held a territory the previous summer had they been in the wild, and therefore would not be expected to have an advantage over the juveniles. This is unlikely, however, as these males had been captured as juveniles, and they had exhibited territorial behaviour in the aviary in the spring of 1973. I believe, therefore, that the captive males of more than one year of age did not feel "established" as territorial residents in the aviary, and thus were dominated by the more aggressive [illegible] possibly stronger juvenile males of Broods D and E (Table 1).

The fact that aggressive behaviour appeared among captive birds before the appearance of courtship behaviour suggests that this may occur also in the wild. I speculate that a resurgence of territorial defence will occur among resident males in the wild at this time, and also that aggression will occur among the overwintering juvenile males. This aggression may well cause some of the overwintering male juveniles to move in the spring. That male BLP became territorial and successfully bred with several females indicates that at least some juvenile males are physiologically capable of reproducing during their first spring.

There was a marked dichotomy in behaviour between juvenile males that came from broods which included more than one male juvenile and those which lacked male siblings (Table 1). Juvenile males which had male siblings, PUP, BLP, OP, WPU, were aggressive and at the top of the male dominance hierarchy, whereas those without male siblings, MY and BY, were nonaggressive and at the bottom of the male dominance hierarchy (Table 4). This relationship between aggressivity and number of males in a brood may be spurious. However, the possibilities remain that aggression is an inherited character and/or that aggressivity of males is somehow affected by interactions occurring between male siblings in broods. Both possibilities merit further attention and could be pursued in the captive situation. Either possibility would help explain the differences in behaviour of juveniles in the wild.

These data suggest that both aggression among juvenile males and by territorial males towards juvenile males may influence movements of juvenile males in the spring.

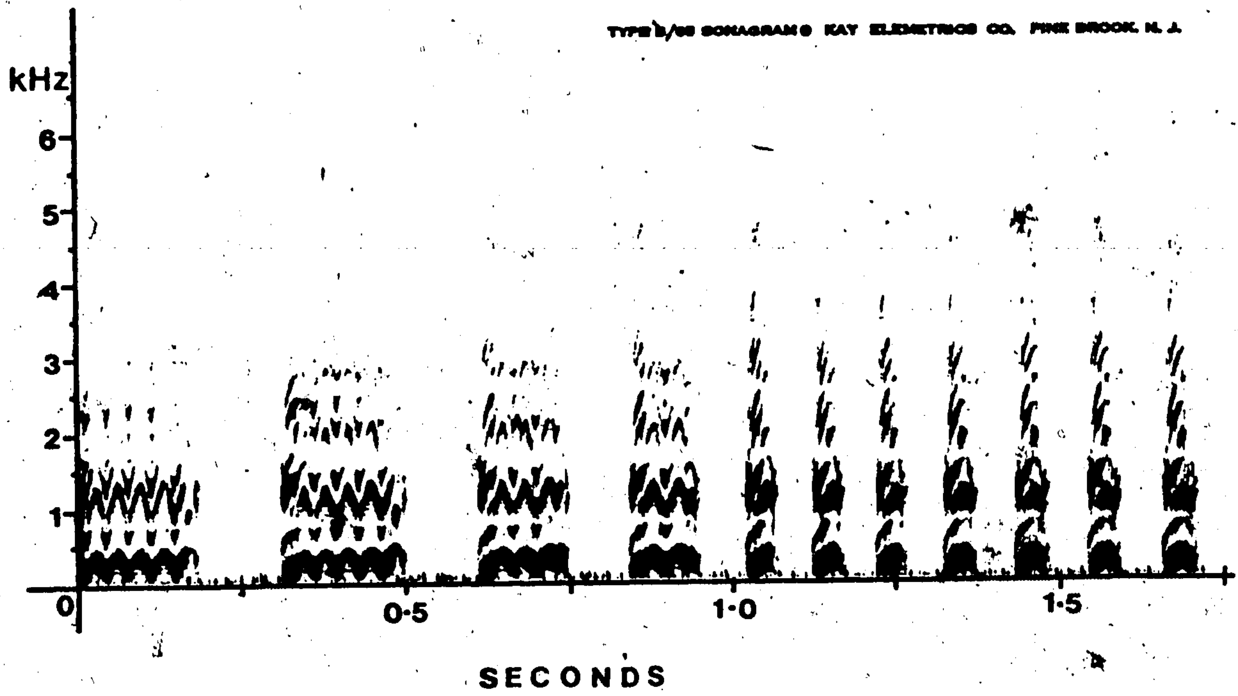
The captive female Franklin's Grouse became extremely vocal in late April, in marked contrast to the winter when they spent most of their time apparently loafing in the central walkway (Fig. 1). During late April and May all females spent considerable time pacing restlessly up and down the extensions and frequently uttering low "clucks" (not recorded). Occasionally one of these birds would stop and adopt an upright, "alert" posture (Fig. 8a), a [illegible] through the wire mesh while giving a distinctive four syllable call which I termed the "moan call" (Fig. 10). Behaviour of females at this time was not obviously influenced by the presence of other females. Herzog (1977) found that wild female Franklin's Grouse, especially juveniles, are also active at this time of year.

Agonistic interactions among females were more frequent in late April than in the winter period, but were generally of low intensity. High intensity threat behaviour by female Spruce Grouse consists of the adoption of a horizontal "aggressive posture" (Fig. 8d) by the aggressor while uttering the "female aggressive call" (Fig. 11). This behaviour has been described for wild birds by MacDonald (1968), McCourt (1969), Harju (1969) and Herzog (1977). Herzog (1977) presents convincing evidence that this vocalisation is associated with territorial defence by female Franklin's Grouse against other females.

I heard the "female aggressive call" in the aviary first on 18 April and infrequently thereafter until mid May, when its frequency increased (Table 6). Thus, captive females exhibited intolerance towards birds of

Figure 11a. Sonogram of a "female aggressive call" uttered by a female Franklin's Grouse while threatening another female.

Figure 11b. Sonogram of the "whine" which sometimes follows the "female aggressive call".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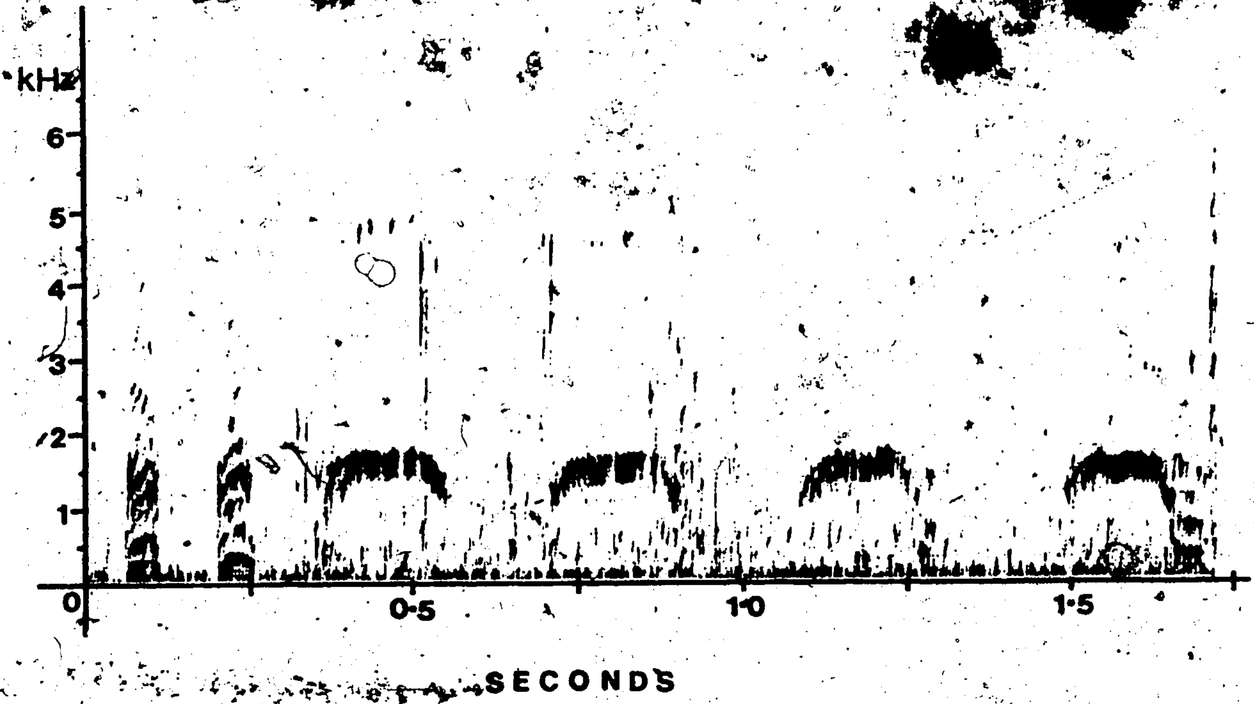
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Table 6. Summary of aggressive behaviour by female Franklin's Grouse towards other females, 18 April to 9 June 1974.

	Occurrence of aggressive behaviour			Occurrence of aggressive calls		
Bird	Total	Prior to Copulation[b]	Post Copulation and prior to Incubation[c]	Total	Prior to Copulation[b]	Post Copulation and prior to Incubation[c]
SB	49	36 (42 days)	13 (10 days)	13	10 (42 days)	3 (10 days)
WP	23	11 (41 days)	12 (10 days)	9	1 (41 days)	8 (10 days)
PUO[a]	39	16 (34 days)	23 (10 days)	23	6 (34 days)	17 (10 days)
WO[a]	11	6 (39 days)	5 (10 days)	5	2 (39 days)	3 (10 days)
OO[a]	3	3 (42 days)	- (10 days)	0	- (42 days)	- (10 days)
PUW	0	-	-	0	-	-
OW	0	-	-	0	-	-

[a] Known nesters

[b] Date of copulation known for SB, PUO, OO; estimated on basis of first egg laid for WO

[c] Date of onset of incubation known for PUO, WO, OO; estimated for SB and WP on basis of time required to lay seven eggs

the same sex during the early spring. However, this aggression was less consistent than that shown among males, and did not occur whenever a dominant individual was in visual contact with a subordinate. The "female aggressive call" was given only to subordinate individuals.

A summary of aggressive behaviour by the captive females towards other females in presented in Table 6. My impression was that females showed a marked increase in aggression at about the time when copulation occurred and throughout the laying period. This statement is based largely on female PUO (Appendix 1), the female for which I have the most precise information on the chronology of breeding behaviour. I observed female PUO copulate with male BLP (Appendix 1) on the evening of 21 May. At sunrise the next morning PUO was making a nest scrape in the western corner of the southern extension (Fig. 1) just in front of my observation hut. Three days later her first egg was laid, then one egg thereafter every 1.4 days until a clutch of seven was attained. This rate of laying corresponds to that documented for wild Franklin's Grouse by McCourt *et al.* (1973). Female PUO showed a marked increase in aggressive behaviour during the laying period (Table 7), but as soon as incubation began PUO no longer responded aggressively towards subordinate females.

Interpretation of the data on other females (Table 6), is confounded by several factors. The existence of a hierarchical system among females during the spring (Table 7) meant that even if a bird was aggressively disposed towards other females, the number of times that this intolerance could be exhibited would depend upon the probability of meeting an individual of lower status. This may explain why females OO and WO were observed to behave aggressively on only a few occasions despite the fact that they both nested. However it is noteworthy that the two birds of

Table 7. Number of aggressive-submissive interactions among female Franklin's Grouse, 18 April to 3 June 1974.

					Loser			
Winners		SB	WP	PUO	OO	OW	PUW	WO
SB	(Ad)	–	8	5	10	5	6	5
WP	(Ad)	–	–	7	6	3	5	4
PUO	[illegible]	–	–	–	16	4	3	14
OO	(Ylg)	–	–	–	–	1	1	2
OW	(Juv)	–	–	–	–	–	–	1
PUW	(Juv)	–	–	–	–	–	–	–
WO	(Juv)	–	–	–	4[a]	–	5	–

[a] Dominance reversal beginning 13 May.

highest social status (SB, WP) did not nest, whereas three birds of lower social status did (PUO, WO, OO). Although based on a few occurrences of aggressive behaviour (Table 6) WO did show an increase in aggressive behaviour at copulation and during laying which subsided rapidly with the onset of incubation. The data for female WP (Table 6) suggests a similar trend in aggressive behaviour, although this bird did not nest an[illegible] was not observed to copulate. However I strongly suspected female WP of "dumping" eggs in OO's nest. Eggs appeared in that nest at twice th[illegible] expected rate and resulted in a final clutch of 14 whereas the usual maximum clutch of wild Franklin's Grouse is six (Keppie 1975) and of captive birds is seven (Pendergast and Boag 1971a; this study). Furthermore, eggs in this clutch were of two distinct colouration types. One day prior to the appearance of the first egg in the clutch, I recorded female WP in OO's nest uttering the "Guinea Pig call" (see Summer); a call which is given only by females on their nests. I also observed female WP utter the "female aggressive call" and chase OO from the vicinity of her nest on 8 June. Why females SB and WP did not nest is a subject of conjecture. Female SB was the dominant female (Table 7) and was observed to copulate with the male BLP three times on 30 May. However each attempt at copulation was very brief and I suspect that none were successful. Moreover SB did not call after copulation as had females PUO and OO, both of which copulated only once and for a longer duration. Nevertheless the data on these females support the conclusion drawn from the behaviour of female PUO, namely that aggressive interactions peak at copulation and during laying to subside rapidly with the onset of incubation.

Herzog (1977) found that wild females occupied exclusive areas which averaged 2.3 ha, and exclusive use of an area was associated with aggressive responses to playbacks of the "female aggressive call". The mechanism(s) by which females are able to establish and maintain large territories in such dense habitat is a subject of conjecture. The "female aggressive call" is the loudest vocalisation that has been documented for females of this species and Harju (1969) suggested that it may serve a territorial function. My impression was that the captive females became particularly aggressive during the twilight conditions following sunset and that the "female aggressive call" was more frequently given at this time. This apparent rise in aggression may be associated with defense of roosting sites, but it is also possible that it represents the manifestation of an endogenous circadian rhythm in aggressivity. If females utter the "female aggressive call" in the absence of other females as suggested by Harju (1969), then dawn and dusk would appear to be the most adaptive times to do so, [illegible] this would reduce the chance of attracting both nocturnal and diurnal aerial predators. This question could be solved by the observation of radio-tracked individuals in the wild. The captive females exhibited aggressive behaviour throughout the spring but this was less intense than among the males and no individual assumed the role of despot. The close proximity of more dominant individuals did not prevent certain individuals of lower status from nesting in the aviary (Table 6, 7). It is noteworthy that the three nests were maximally dispersed in the aviary: PUO nested in the western corner of the southern extension, OO nested in run 8, against the east wall of the run, WO nested in the northern extension between pens 2 and 3 (Fig. 1).

In summary, mid April marked the sudden development of intense agonistic behaviour between captive birds of the same sex, in contrast to the preceding five months of the winter period, when a stable dominance hierarchy existed within the captive flock and agonistic behaviour was minimal. Aggressive behaviour during the spring was exhibited by birds of all age and sex classes. This strongly suggests that movements of juveniles in the spring are in response to intraspecific aggression occurring during the late winter and early spring.

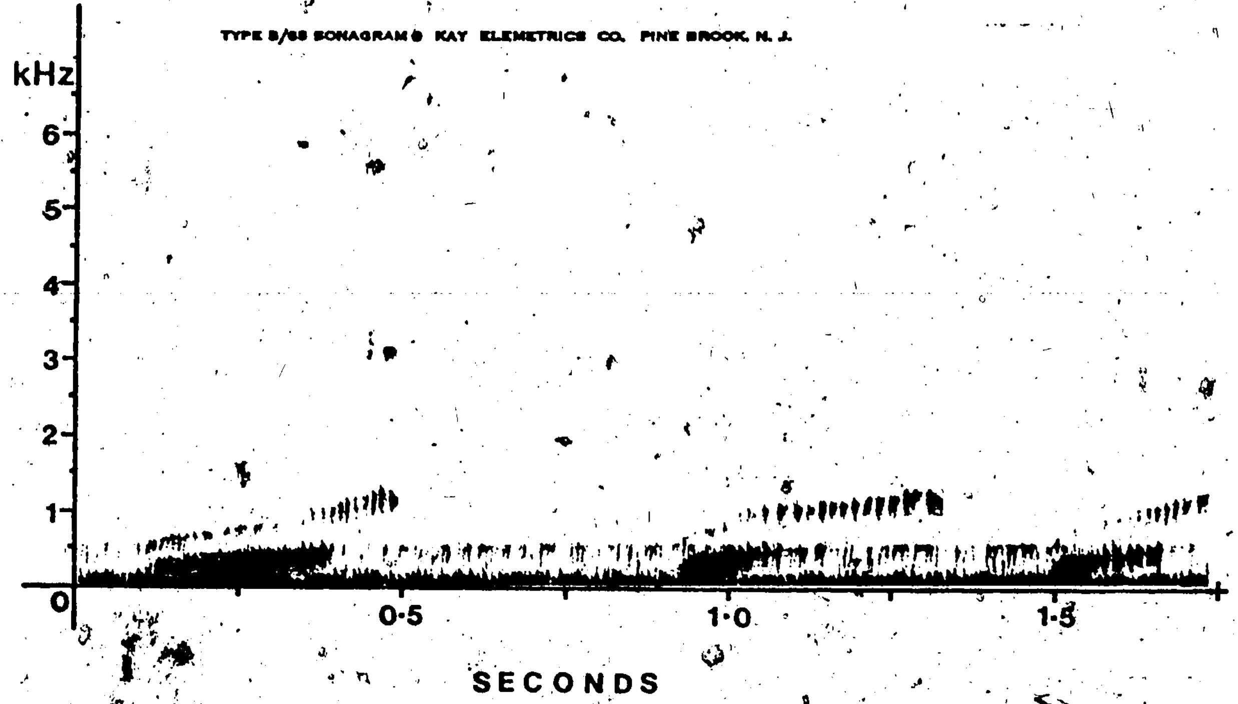
Summer

The summer season encompasses incubation, brood rearing and moult. My data on behaviour of broods during this season are included in the discussion on autumn above. My observations on broods throughout the summer indicated that brood break-up in the fall was not the result of overt aggression by the brood female toward her chicks or between siblings, but rather the combined result of the waning of the parental bond between a hen and her chicks and the gradual attainment of [illegible] independence by the chicks. The apparent association between the number of male siblings in a brood and their subsequent social status during the winter in a flock comprised of both related and unrelated males needs further investigation.

The three females which nested (PUO, OO, WO) uttered a soft, repetitive call (Fig. 12) almost continuously when on their nests. I termed this call the "Guinea Pig call" because of its similarity to sounds uttered by that mammal. I first observed female PUO give this call when she was making a nest scrape prior to the laying period. The "Guinea Pig call" was given both in visual isolation from other grouse and when others were in sight, but not in close proximity to the nest. On several occasions, I was able to enter the observation hut whilst female PUO was away from her nest. Female PUO would immediately utter the "Guinea Pig call" upon returning to her nest although she could not see me. Thus I do not believe that this call was given in response to my presence. Thus the stimulus for a nesting female to give this call appeared to be her location on the nest. I suggest that this call may serve some agonistic function or may help to synchronize hatching and enable the chicks to learn their mother's voice before hatching

Figure 12. Sonogram of the "Guinea Pig call" given by female Franklin's Grouse while sitting on her nest.

Figure 13. Sonogram of the "distress on the nest call" given by a female Franklin's Grouse while sitting on her nest when approached by another Franklin's Grouse.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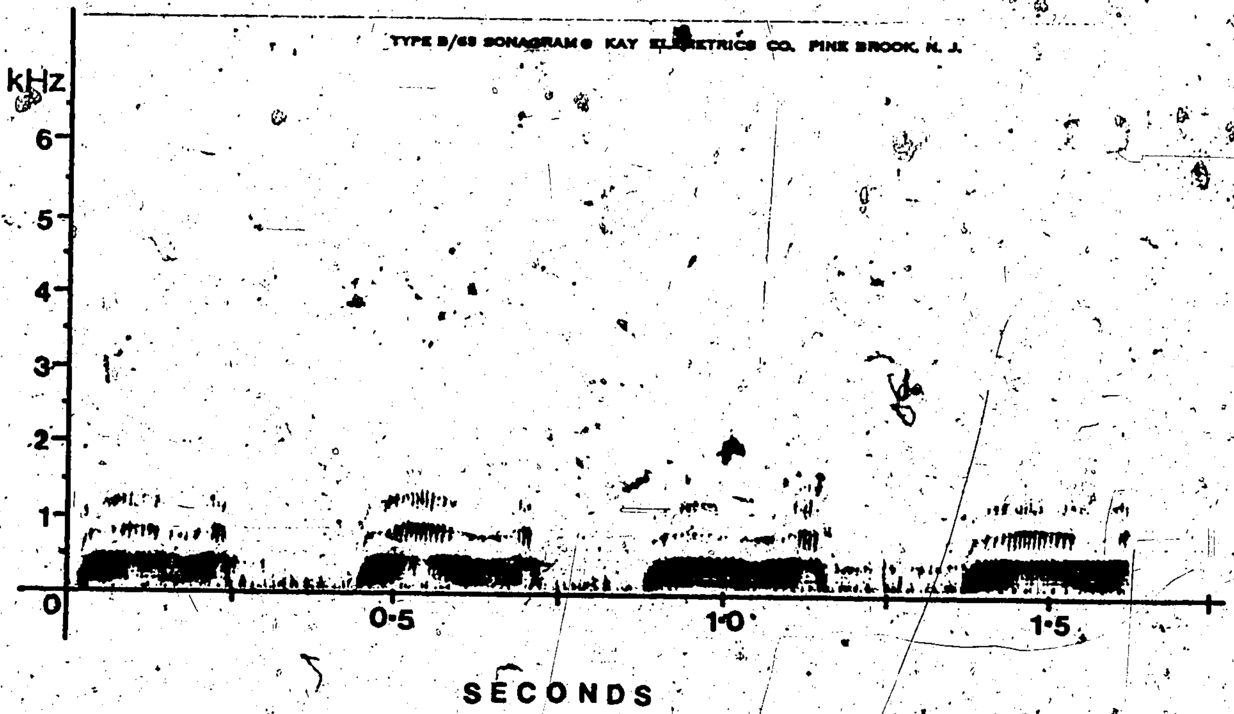
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(e.g. see Beer 1970).

Incubating females gave a slightly different call (Fig. 13) whilst on the nest whenever closely approached by another bird. I termed this call the "distress on the nest call". I speculate that this call may have inhibited any aggression by the approaching bird towards the incubating female and thus may in itself be highly agonistic. Birds of both sexes were often in very close proximity to incubating females on their nests, yet no agonistic interactions were observed. Females of higher social status ignored the incubating females on their nests, even though they would displace these birds when away from their nests and also non-nesting females of lower status when in close proximity. Incubating females showed no overt aggressive behaviour towards other females. Dispersion of females during the incubation period is presumably established earlier in the breeding season and the close proximity of the captive females at this time is an artifact of the penned situation. Aggression between non-nesting females was minimal during the summer and all agonistic interactions observed were of low intensity.

Only female WO successfully reared a brood of chicks. All three females that nested (PUO, OO, WO) showed aberrant behaviour at hatching time. Although all seven chicks hatched from WO's eggs, she continued to brood a "dump" egg that I had placed in her nest, and ignored the chicks which I found in a cluster a short distance from the nest. I confined WO in the shelter of pen 1 with the two surviving chicks and she brooded them immediately. Both were subsequently reared to maturity (YY, BLBL, Appendix I). Female PUO's clutch failed to hatch although subsequent examination showed that all eggs had been fertile. I therefore replaced PUO's clutch with six eggs taken from OO's nest and she continued to incubate. Both PUO and OO appeared to desert their nests at hatching time, and the chicks died during hatching. Two chicks hatched from the foster clutch in PUO's nest but she ignored them, and both died. Torrential rain for several days prior to hatching may have influenced this behaviour. A predator could also have visited the aviary during the night and alarmed the incubating females.

CONCLUDING DISCUSSION

This study was an attempt at determining the factor(s) responsible for inducing the break-up of broods and the dispersal of juvenile Franklin's Grouse. Keppie (1975) documented two periods of movement by juvenile Franklin's Grouse in the wild which he termed dispersal. The number of juveniles dispersing in the autumn was apparently density independent, whereas the spring phase appeared to be density dependent. This implies that the two phases of dispersal are controlled by different factors and also raises the possibility that the adaptive significance of each phase is different.

I was unable to establish whether brood break-up and autumn dispersal are coincident in time. Radio-telemetry studies on Ruffed Grouse (Godfrey and Marshall 1969) and on Greater Prairie Chicken (Bowman and Robel 1977) have shown that these two events are temporally isolated in these species. In the absence of contrary evidence, I suggest that this is also true for Franklin's Grouse. Brood break-up appeared to be the combined result of the waning of the parental bond of, the brood female and the gradual development of social independence of the young, and not the result of a sudden rise in overt aggression by either brood female or young. I observed no overt aggressive interactions either within broods or among non-breeding adults at the time when autumn dispersal of juveniles occurs in the wild. Overt aggression between siblings was not evident until the late autumn, after the time when juveniles would have completed autumn dispersal in the wild. Thus I believe that juveniles do not disperse in response to intraspecific aggression in the autumn. This would be expected if dispersal in the autumn were indeed density independent as suggested by Keppie (1975). I therefore suggest that juvenile Franklin's Grouse are genetically predetermined at hatch to disperse during their first autumn. By Howard's (1960) terminology this would be termed "innate dispersal" as opposed to "environmental dispersal", which infers that an individual is genetically predetermined at hatch to disperse only when stimulated by some facet of population pressure. However, I find Howard's terminology somewhat misleading, as by definition dispersal is an innate phenomenon. I suggest, therefore, that the terms "innate dispersal" and "environmental dispersal" be redefined as "intrinsically determined dispersal" and "environmentally determined dispersal" respectively.

The sudden development of overt aggression among captive Franklin's Grouse of the same sex in the early spring strongly suggests that, in contrast to the autumn, this phase of movement is in response to population pressure. Herzog (1977) showed that movements of juveniles from his study area during the spring coincided with territorial establishment of both sexes. These data may explain why Keppie (1975) found spring dispersal to act in an apparently density dependent fashion. This evidence suggests that movements of juveniles in the spring may be environmentally determined dispersal, or the result of spacing behaviour (Johnston 1961). Keppie (1975) intimated that "spring dispersal" may be a potential mechanism of population regulation. Similarly, Bendell (1972) concluded that autumn to spring losses of juveniles constitutes the major factor affecting recruitment and thereby regulates the populations of most species of grouse.

Keppie (1975) removed all adults and yearlings from a experimental plot during the late winter and found that the proportion of juveniles that emigrated from his area in the following spring was similar to that from a control plot. This evidence seems to contradict his hypothesis that the number of juveniles that emigrate from an area is related to the size of the overwintering population or to territorial aggression by resident birds. If this is the case, then the spring phase of dispersal must be considered as intrinsically determined dispersal. However, it is also possible that aggression among overwintering juveniles forced some of them to leave. It is also conceivable that juveniles forced to emigrate from adjacent areas by older, territorial birds may have immigrated into the experimental area and proved dominant to the individuals that overwintered there. Keppie's (1975) work indicated that emigration and immigration of juveniles on his study area were temporally isolated, but Herzog (1977) showed that this unlikely situation does not occur.

An obvious prerequisite for the formulation of valid conclusions on the biological significance of dispersal is the accurate definition of this process. Keppie (1975) defined dispersal as "movement from the study area" despite the fact that he acknowledged that at least some of the "nondispersing individuals" did make movements within the boundaries of his study area at the time of dispersal. To catagorize individuals as dispersers or nondispersers according to movement across a convenient but biologically meaningless line is totally erroneous. A wide range of dispersal distances by conspecific individuals has been documented for several species (Murray 1967). There is thus an evident need for a more precise deliniation of the distances moved by <u>all</u> juvenile Franklin's Grouse in a particular area. Only then can valid conclusions be formulated as to the biological significance of dispersal in this species.

I question Keppie's (1975) use of the term "dispersal" for movements of juvenile Franklin's Grouse during the spring. Evidence to date suggests that aggressive interactions during the spring are the proximate causes of these movements. The simplest explanation of these movements therefore, is that they are a response to spacing behaviour (Johnston 1961). The use of the term "dispersal" for this phase of movements must await proof that certain individuals are genetically predetermined to disperse in response to population pressure. Environmentally determined dispersal operating below the maximum carrying capacity of the habitat would in this situation avoid the effects of overpopulation (Lidicker 1962) and thus be of advantage to the dispersing individual.

Studies on the mechanisms by which populations may be regulated are hampered by the inherent difficulty of assessing the carrying capacity of an area in a particular year. Herzog (1977) found that the territories of male Franklin's Grouse are aggregated with females holding territories in a zone peripheral to those of the males. This suggests that the location of territories in this species may result from social attraction, although the role of habitat selection is unclear. Long term studies on the characteristics, location and number of territories are needed to help elucidate this problem. If, as I suggest, the spring movements of juvenile Franklin's Grouse documented by Keppie are the result of spacing behaviour, then the question becomes: can territorial behaviour regulate the size of a population in this species? This is an extremely controversial topic that is far from being resolved (Brown 1969; Watson and Moss 1970; Klomp 1972; Watson 1973).

In summary, I speculate that autumn dispersal results in juveniles settling in the area in which they will attempt to establish themselves as breeding residents. However, aggression by more dominant individuals during the spring with the onset of territorial behaviour may cause some of these individuals to move again. Evidence in favour of this hypothesis is provided by the existence of "migrant individuals" (Keppie 1975; Herzog 1977) which appear to remain faithful to their first wintering ground. I suggest that "migrant individuals" represent the group of juveniles which during the spring were forced to emigrate from the area in which they had settled following dispersal in the previous autumn. The fact that these birds return in subsequent years to the same wintering grounds suggests that they establish site adherance to the area in which they settled the previous autumn. This implies but does not prove that these individuals would have remained in the same area during the breeding season. I believe that it is most improbable that Franklin's Grouse can be divided into two behavioural morphs based on a tendency to migrate or to be sedentary and that this suggestion is the result of attributing unwarranted biological significance to movements across the boundaries of a study area. Thus I suggest that the distance that an individual moves between breeding and overwintering areas reflects the distance it was forced to move during the first spring, from its first overwintering area and thus that in reality a complete continuum must exist from so-called migrants to non migrants.

Similar conclusions on dispersal have been reached by Snow (1958) for European Blackbirds (*Turdus merula*) and Meyer (1974) for Black-capped Chickadees. I believe that autumn dispersal by juveniles must be of selective advantage or this trait would not have evolved. I suggest that the most likely advantages of dispersal by juvenile Franklin's Grouse may be the greater possibility of advantageous genetic recombinations resulting from outbreeding and the increased possibility of settling in vacant habitat, particularly as this species is closely associated with fire seres.

I strongly believe that ecological studies must consider the behaviour of the study animal. It is apparent from Wiley's (1974) review of the literature on social organisation of the Tetraonidae that much behavioural information is still needed to provide a firm basis upon which ecological studies can be interpreted. Lumping of ecological data collected from several individuals may result in more convincing statistical samples, but unless these take into account the individuality of behaviour, subsequent conclusions are highly susceptible to interpretational error.

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Appendix I. Information on individual Franklin's Grouse used in the study.

			Males		
Bird	Date When Captured	Age Class When Captured	Date When Died	Age Class When Died	Relationship to Other Birds in this Study
YBLA	13 Dec. 71	Juv.	2 Mar. 74	Ad.	-
RBL	Jun. 72	Ad.	19 Apr. 74	Ad.	-
BB	16 Apr. 72	Ad.	16 Apr. 74	Ad.	-
YBLY	13 Aug. 72	Juv.	9 Apr. 74	Ylg.	Sibling of male YB, female FY
RG	13 Aug. 72	Juv.	27 Jul. 73	Ylg.	Chick of female RB, Sibling of male RY, female YR, FR
RY	13 Aug. 72	Juv.	17 May 74	Ylg.	Chick of female RB, Sibling of male RG, female YR, FR
YG	13 Aug. 72	Juv.	30 Oct. 73	Ylg.	Sibling of male BLY, female FY
SB	8 Aug. 72	Ylg.	28 Jun. 73	Ad.	-
PUP	2 Aug. 73	Juv.	26 Apr. 74	Juv.	Chick of female WP, Sibling of male OP, BLP female YBL
BLP	2 Aug. 73	Juv.	-		Chick of female WP, Sibling of male PUP, OP female YBL

Appendix I. (Cont.)

Bird	Date When Captured	Age Class When Captured	Date When Died	Age Class When Died	Relationship to Other Birds in this Study
				Males	
OP	2 Aug. 73	Juv.	-	-	Chick of female WP, Sibling of male BLP, PUP, female YBL
WPU	19 Aug. 73	Juv.	25 Apr. 74	Juv.	Chick of female YF, Sibling of male PO
PO	19 Aug. 73	Juv.	4 Nov. 73	Juv.	Chick of female YF, Sibling of male WPU
BY	10 Aug. 73	Juv.	-	-	Chick of female BLF, Sibling of female PUW, OW
MY	2 Aug. 73	Juv.	-	-	Chick of female OF, Sibling of female UM
WW	1 Aug. 74	Juv.	-	-	Chick of female BB, Sibling of female GG, RR
				Females	
RB	13 Aug. 72	Ad.	17 Jan. 74	Ad.	Mother of male RY, RG, female RY
BK	10 Jun. 72	Ylg.	3 Aug. 73	Ad.	-
RY	10 Jun. 72	Ad.	9 Aug. 73	Ad.	-

Appendix I. (Cont.)

			Females		
Bird	Date When Captured	Age Class When Captured	Date When Died	Age Class When Died	Relationship to Other Birds in this Study
SW	23 Aug. 72	Juv.	25 Aug. 73	Ylg.	Chick of female SB
YR	13 Aug. 72	Juv.	27 Jun. 73	Juv.	Chick of female RB, Sibling of male RY, RG, female FR
FY	13 Aug. 72	Juv.	25 Aug. 73	Ylg.	Sibling of male YG, YBLY
FR	13 Aug. 72	Juv.	22 Jul. 73	Ylg.	Chick of female RB, Sibling of male RY, RW, female YR
SB	23 Aug. 72	Ad.	15 Nov. 74	Ad.	Mother of female SW
WP	21 Aug. 73	Ylg.	-	-	Mother of female YBL, male PUP, OP, BLP
YBL	2 Aug. 73	Juv.	22 Jan. 74	Juv.	Chick of female WP, Sibling of male PUP, OP, BLP
YF	19 Aug. 73	Ad.	26 Sep 73	Ad.	Mother of male PO, WPU
OO	2 Aug. 73	Ad.	-	-	Mother of female PUO, WO
PUO	2 Aug. 73	Juv.	-	-	Chick of female OO, Sibling of female WO

Appendix I. (Cont.)

			Females		
Bird	Date When Captured	Age Class When Captured	Date When Died	Age Class When Died	Relationship to Other Birds in this Study
WO	2 Aug. 73	Juv.	-	-	Chick of female OO, Sibling of female PUO, Mother of female YY, BLBL
BLF	18 Aug. 73	Ad.	17 Feb. 74	Ad.	Mother of female OW, PUW, male BY
PUW	18 Aug. 73	Juv.	25 Oct. 74	Ylg.	Chick of female BLF, Sibling of male MY, female OW
OW	18 Aug. 73	Juv.	-	-	Chick of female BLF, Sibling of male BY, female PUW
OF	2 Aug. 73	Ad.	2 Mar. 74	Ad.	Mother of female UM, male MY
UM	2 Aug. 73	Juv.	12 Dec. 73	Juv.	Chick of female OF, Sibling of male MY
YY	Hatched in aviary 3 Jul 74		-	-	Chick of female NO, Sibling of female BLBL
BLBL	Hatched in aviary 3 Jul 74		-	-	Chick of female NO, Sibling of female YY
GG	1 Aug. 74	Juv.	-	-	Chick of female BB, Sibling of female RR
RR	1 Aug. 74	Juv.	17 Aug. 74	Juv.	Chick of female BB, Sibling of female GG