FEMALE AGGRESSIVENESS, BREEDING DENSITY, AND MONOGAMY IN WILLOW
PTARMIGAN
by
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ABSTRACT

In this thesis I investigate the influence of aggression by females in setting breeding density and maintaining monogamy in a population of willow ptarmigan (Lagopus lagopus). The aims of the study were: 1) to test the hypothesis that female willow ptarmigan determine their own breeding density by spacing behaviour, independently of male density; 2) to evaluate the effect of interactions between the sexes on final breeding density; and 3) to examine factors which may constrain willow ptarmigan populations to monogamy.

Sex ratio of the population was altered in spring by continuous removal of most males and females from separate plots. The effect of removals on numbers of the same and the opposite sex was monitored. The following results were obtained and conclusions reached:

1) Females and males defend territories against individuals of the same sex, and this behaviour prevents some potential recruits from breeding. Physiologically mature yearling females and males settled in response to the removal of territorial birds of like sex.

2) Density of territorial males may not determine the number of females that breed. Females settled at high density, despite a reduction in the density of males, defended territories against each other within the enlarged territories of the remaining males, and mated polygynously.

3) Settlement patterns and subsequent territory sizes of males may affect density of both males and females. Females
preferred territories of medium to large size, and males with smaller territories often remained unmated. Competition by yearling males for limited space on the breeding area may reduce territory size below that acceptable to females. Females may also alter settlement patterns of males by ignoring territorial boundaries of males and inciting interactions between neighboring cocks.

4) Unshared male vigilance is not essential to, but may improve, female reproductive success in years of high predation. Polygynous females had similar breeding success and survived as well as monogamous females, except in a year of high nest predation when they suffered higher nest loss.

5) The aggressive behaviour of females may prevent polygyny from occurring in unmanipulated populations, if a polygyny threshold exists. Females are able to defend territories which are similar in size to those of males and thus can prevent secondary females from settling.

Results of this study indicate that aggressive behaviour of females in a monogamous species may be an important factor in regulating population density. Future studies should examine physiological and ecological factors influencing agonistic behaviour of females and should attempt to manipulate female aggressiveness to test whether changes in this behaviour can cause changes in population density.
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CHAPTER ONE: GENERAL INTRODUCTION

Female-female agonistic or aggressive behaviour is a widespread but relatively undiscussed phenomenon. Interfemale aggression has been documented in fish (Pottle and Green 1979), lizards (Rand 1967, Bustard 1970), birds (Howard 1920, Nero 1956, Watson 1965, von Haartman 1969, Smith 1978, Brown 1979) and mammals (Downhower and Armitage 1971, Strandgaard 1972, Floody and Pfaff 1977, Gleason et al. 1980). Early studies on dominance hierarchies in flocks of domestic hens pointed out the importance of high social status to reproductive output (reviewed by Guhl 1962), but, until recently, the functions and consequences of female agonistic behaviour have largely been ignored.

Females may interact agonistically for one or all of the following reasons:
1. To acquire resources and to prevent other females from sharing them;
2. To gain access to the 'best' male and to monopolize his vigilance, and/or parental care; or
3. To improve relative reproductive output by reducing, delaying, or inhibiting reproduction by other females.

Whatever the evolutionary reasons for the development of interfemale agonism, this behaviour has the ecological consequence of regulating population size. Since females are usually the limiting sex (Trivers 1972), the reproductive output of a population is determined by the number of females that breed. The importance of female spacing behaviour (which
includes dominance, territoriality, and agonistic behaviour) in limiting population growth has now been recognized for some promiscuous and polygynous species (e.g. Robel 1970, Zwickel 1972, 1980, Redfield et al. 1978) but as yet has not been discussed for monogamous species.

Predictions of current hypotheses on the evolution of mating systems are based on the differential energy investment of males and females in the production of germ cells and the development of young (Trivers 1972). The type of mating system that develops depends on whether male or female reproductive interests are favoured by environmental factors (Wittenberger and Tilson 1980). A second ecological consequence of interfemale agonism, if it delays or prevents some females from breeding, is that it may reduce the degree of polygyny (Holm 1973), or completely prevent its occurrence (Wittenberger 1979). There has been little discussion of what factors would allow aggressive behaviour by females to enforce monogamy on males.

The purpose of this thesis is to consider the ecological consequences of spacing behaviour in females of a monogamous grouse species, the willow ptarmigan (*Lagopus lagopus*). In Chapter Two I ask the question, "What form of spacing behaviour do female willow ptarmigan display?", and test the hypothesis that female spacing behaviour determines the number of females that breed, independently of the density of males. I then discuss how interactions between females and males can influence the breeding density. In Chapter Three I evaluate the effects of monogamous versus polygynous mating by females on their
reproductive success and survival and discuss the role of female aggression in maintaining monogamy in the population. Chapter Four is a brief, general discussion.

**Study animal**

I chose the willow ptarmigan as a study animal because it is a predominantly monogamous species, individuals are easy to capture and mark, can be observed readily in the field, and are sexually dimorphic.

Ptarmigan males begin to set up territories on the breeding area in April. Females arrive soon after and move about in small groups before settling and pairing with a male in late April or early May. Females lay eggs in a rudimentary nest during late May and incubate for about 21 days. Dates of hatch of individual nests span the period from late June, through July. The male remains on the territory during this time and accompanies the hen and brood when they leave the territory a few days after hatch. Juveniles begin to fly at 11 or 12 days of age. Ptarmigan spend the winter in large flocks usually on areas away from the breeding range, and the sexes winter separately (Weeden 1964).

The diet in winter and early spring consists primarily of willow (*Salix* spp.) twigs and buds (West and Meng 1966, Weeden 1969). During summer the birds forage on the catkins, buds, and leaves of willow, as well as flowers and seeds of other herbaceous plants (Williams *et al.* 1980). Potential predators of ptarmigan that are present on my study area are the golden
eagle (*Aquila chrysaetos*), gyrfalcon (*Falco rusticolus*), goshawk (*Accipiter gentilis*), marsh hawk (*Circus cyaneus*), short-eared owl (*Falco rusticolus*), coloured fox (*Vulpes vulpes*), short-tailed weasel (*Mustela erminea*), wolf (*Canis lupus*), and wolverine (*Gulo luscus*).

*Lagopus lagopus* populations undergo cyclic fluctuations in abundance (Buckley 1954, Williams 1954, Keith 1963). Numbers of willow ptarmigan in North America and Iceland peak every 10 years (Gudmundsson 1960, Bergerud 1970); the willow grouse (*L. l. lagopus*) in northern Europe every 3 to 4 years (Myrberget 1972), and the red grouse (*L. l. scoticus*) in Scotland every 6 years (Watson and Moss 1979).

Hypotheses invoked to explain fluctuations in abundance of grouse (Tetraonidae) are similar to those proposed for small mammals (reviews: Keith 1963, Krebs 1964, Keith 1974, Krebs and Myers 1974, Krebs 1978) and are summarized by Watson and Moss (1979). These include cyclic changes in abundance of predators (Lack 1954, Rusch and Keith 1971, Myrberget 1972, Bulmer 1974, Hörnfeldt 1978), variations in quality of food (Watson and Moss 1972), and changes in behaviour that are intrinsic genetic (Chitty 1967) or phenotypic (Christian and Davis 1964, Christian 1978, Watson and Moss 1972). Although ptarmigan populations cycle, my study was done at high and constant density (varying from 32 to 36 breeding pairs per km²), therefore I was not able to test any of these general hypotheses.
CHAPTER TWO: FEMALE TERRITORIALITY AND BREEDING DENSITY OF WILLOW PTARMIGAN.
INTRODUCTION

Spacing behaviour and its effects on the regulation of vertebrate population density have been discussed extensively (e.g. Brown 1969, Watson and Moss 1970, Clarke 1970, Klomp 1972, Philobosian 1975, Krebs 1979, Watson and Moss 1979, Patterson 1980). Historically, descriptive and experimental studies have centered on male aggressiveness, implying that spacing behaviour of males determines both male and female breeding density. This emphasis was based first on the observation that males of many species are often more aggressive than females, and second, on the conclusion of early removal experiments (e.g. Stewart and Aldrich 1951, Hensley and Cope 1951) that "surplus" females (i.e. potentially reproductive females prevented from breeding by territorial behaviour of residents) did not exist. However, females behave aggressively toward one another during the breeding season (e.g. Howard 1920, Welter 1935, Nero 1956, Watson and Jenkins 1964, MacDonald 1970, Crawford 1977, Morton et al. 1978), and surplus females have now been identified for several species (e.g. Watson 1965, Holmes 1966, Watson and Jenkins 1968, Harris 1970, Young 1970, Zwickel 1972, 1980, Manuwal 1974), which suggests that an evaluation of the effect of female spacing on breeding density is overdue.

The main purpose of this study was to determine whether the spacing behaviour of females in a monogamous species could determine the number of females that breed, independently of male density. In some promiscuous or polygynous species,
Spacing behaviour is sex-specific. For example, in voles interaction with mature animals of the same sex inhibits sexual maturation of juveniles (Bujalska 1973, Boonstra 1978, Saitoh 1981), and females of some bird species defend territories against intruders of the same sex (e.g. Nero and Emlen 1951, Nero 1956, Herzog and Boag 1977, 1978). Sex-specific removal experiments on Microtus townsendii indicate that juvenile survival and recruitment in both sexes are inversely related to the density of mature females (Redfield et al. 1978, Boonstra 1978), which suggests that female density is more important than male density in determining population size. Manipulations of sex ratio to test if spacing behaviour is sex-specific in birds have not previously been attempted.

The experiments presented here were designed to test whether spacing behaviour in spring determines breeding density of both sexes in a sex-specific way. I altered the sex ratio in spring of a population of willow ptarmigan, Lagopus lagopus alexandreae Grinnell, by simultaneously removing most males and females from separate plots. I then monitored the effect on the same and opposite sex. The predictions tested were:

1) that if resident birds prevented potential recruits from breeding, then when residents are removed, individuals of the same sex will settle and attempt to breed (Watson and Moss 1970); and

2) that if each sex sets its density independently of the density of the other, then reduction in density of one sex will not lower density of the other.
I had observed that females were aggressive to one another and thus was particularly interested in testing whether female willow ptarmigan are territorial during the breeding season, and whether this behaviour could determine numbers of breeding females and males.
METHODS

Study area

The study was conducted in the Chilkat Pass area, northwestern British Columbia, Canada (59° 50'N, 136° 20'W) from April to August each year from 1979-1981. Study plots were situated on the flats of the pass at an elevation of approximately 880m, near km 128, Haines Road (Fig. 1). Vegetation here is composed of an overstory of dwarf shrubs, mainly willow (Salix spp), birch (Betula glandulosa) and shrubby cinquefoil (Potentilla fruticosa); and an understory of bryoids, graminoids and perennial forbs (Weeden 1959, 1960). Vegetation on the plots was generally very open, and willows, the predominant shrubs, averaged about 1m tall. Experimental work was conducted in April and May when snow covered the study area. Snow was approximately 1.5 m deep in April and usually melted completely by the last week of May. Vegetation provided little cover when snow was deep, thus birds were relatively easy to observe and count. The climate is characterized by heavy snowfall in winter, frequent light to moderate rain the rest of the year, and moderate to high winds year round. A more detailed description of the weather and vegetation of the area can be found in Weeden (1959, 1960).
Figure 1. Location of the study area and study plots on the Haines Road, northwestern British Columbia. Shaded areas indicate plots used in 1979 (C=Control, HR=Haines Road plot, KL=Kelsall Lake plot).
General Methods

In 1979 three 50ha rectangular plots (Kelsall Lake plot (KL), Haines Road plot (HR), and a Control), each at least 1 km apart, were gridded into 100m squares (Fig. 1). In 1980, I established a new 50ha Control plot because of low density of birds on the 1979 Control. KL and HR were enlarged in 1980 to 80 and 90 ha respectively in order to increase sample size for the experiments.

Birds were captured by gently driving them into 1m high white gill nets strung through the willows or by noosing with a 6m collapsible noose pole. Sexes were distinguished by differences in plumage, voice, and wing length (Bergerud et al. 1963). Birds were categorized as yearling (hatched the previous summer) or adult, by comparing pigmentation of the ninth and eighth primaries (Bergerud et al. 1963). Each bird received a numbered aluminum band and 3 coloured plastic bands (2 bands per leg) in a unique combination.

Density of territorial birds was determined by skiing or walking in a zig-zag pattern between grid lines and marking the position of each bird on a map. Two observers were present throughout most of the study, 3 were present in May. In spring of 1979 before experiments began, few birds were colour-marked, so density was estimated from 3 complete censuses in which the entire plot was surveyed in one day. In 1980 and 1981, all birds on territories were either marked or recognized individually by plumage characteristics before experiments began, so a complete count was made. Birds were also censused
on a 100m wide strip around each plot. We pushed birds to the edges of their territories to initiate boundary disputes or to determine the point at which the bird turned back. Territories were plotted by marking these positions and by noting the places where birds called or engaged in natural border disputes on a map. Boundaries were drawn by connecting the outermost points.

A bird (male or female) was considered to be territorial if it was consistently seen on the same area and if it advertised vocally in the air or on the ground within that area, or if it engaged in border disputes with neighbours, or chased intruders from the area. I defined a female to be territorial or to be mated with a male if she was seen on the territory in more than two spring censuses; advertised vocally, engaged in border disputes, or chased other females from the area; was found on a nest or with one-day-old chicks on the territory; or was seen with a brood and accompanied by the male on or off the territory.

Hatch dates were determined by estimating age of chicks in each brood by the method of Bergerud et al. (1963), and backdating. Date of laying the first egg was estimated by subtracting incubation time (21 days) and time to lay a clutch of mean size (8 days) from date of hatch.

Nonparametric statistical tests (Siegel 1956) were used if the assumptions of parametric tests were violated, or if the sample size was very small. Probabilities greater than 0.05 were judged not significant. All tests were two-tailed unless otherwise specified.
**Behaviour of females**

To determine whether females were aggressive towards territorial intruders, the behaviour of females in interactions with other hens or with a female model was observed. In 1981, we described all natural cases of female-female interaction that were observed at close quarters. In spring 1980 and 1981 I placed a stuffed female model mounted in alert posture (Watson and Jenkins 1964) onto 23 territories and as a control, a stuffed female bufflehead (*Bucephala albeola*) onto 5 territories. I pushed the female in the direction of the model until she had seen it. The behaviour of the female in response to the model was recorded for 5 minutes.

**Removal experiments**

The removal experiments were designed to answer the following questions: 1) Is there a surplus of birds of both sexes that is prevented from breeding by the behaviour of residents in spring, and that can settle and breed when resident birds are removed? 2) Is the final breeding density of either sex determined by the density of the opposite sex, or are numbers determined by within-sex influences? To address these questions simultaneously, I removed males and females from separate plots as outlined below.
Slow pulsed removal

On 5 and 6 May 1979, 22 of 29 males on KL and 15 of 20 females on HR were removed by shooting. Removals were from territories located uniformly across the plot. Since most birds were unmarked at the time of the experiment, a numbered card was placed on each removal territory, and any unmarked birds seen within 50m of the card were removed on 14 and 15 May and again on 23 May. The male removal was initiated after females had settled on the plot.

Rapid pulsed removal

In 1980 the experiments were repeated on the same areas, but the rate of removal was increased to every 2 or 3 days. All resident birds were individually identified, and the territorial boundaries of the males were mapped before the removal began. Birds on territories in the 100m strip around the plots were also marked.

Females were removed from 15 of 28 randomly chosen territories of males on HR on 12 May 1980. Males were removed randomly from 16 of 32 territories on 8 and 9 May 1980 on KL. Replacements, except for neighbouring males expanding their territories, were removed every 2 or 3 days until the first week of June. Replacement birds were only removed if they appeared to have settled on the plot: i.e. for males if they moved about openly on the territory and did not fly off it when approached; for females if they were accompanied by the male and did not fly
off the territory when approached. The rapid pulsed male removal experiment was repeated on 15 of 31 territories on HR in 1981 starting 30 April. The male removals in 1980 and 1981 were initiated before females had settled on territories.

**Single session female removal**

During the pulsed removals, replacement females were not allowed to settle long enough to breed. In order to test whether replacement females were physiologically capable of breeding, 10 females were removed from 9 territories on KL on 14 and 15 May 1981. Replacement females were allowed to settle and were then captured and colour-marked. The plot was censused regularly to determine whether these females nested and produced broods.

Table I summarizes the schedule and location of each removal experiment.

To compare body size and condition of replacement birds to those of residents, a necropsy was performed on each bird that was removed. I predicted that residents would be larger or in better condition since they were able to maintain territories against intruders. Pectoral muscle mass and volume have been used as indicators of body condition in birds (Evans and Smith 1974). I used length of keel as an index of body size because it is not subject to wear (as is wing length), and was rarely damaged by shot (as were the long bones). Pectoralis muscles were excised and weighed to the nearest g. Length of keel was measured with vernier calipers to the closest 0.1mm. To correct
Table I. Schedule of experiments conducted on Haines Road and Kelsall Lake plots in 1979, 1980, 1981.

<table>
<thead>
<tr>
<th>Year</th>
<th>Haines Road (HR)</th>
<th>Kelsall Lake (KL)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1979</td>
<td>slow pulsed female removal</td>
<td>slow pulsed male removal</td>
</tr>
<tr>
<td>1980</td>
<td>rapid pulsed female removal</td>
<td>rapid pulsed male removal</td>
</tr>
<tr>
<td>1981</td>
<td>rapid pulsed male removal</td>
<td>single session female removal</td>
</tr>
</tbody>
</table>
for possible differences in body size, I expressed pectoralis weight as a function of length of keel and used this as an index of body condition.
RESULTS

Female-female interactions

Female and male willow ptarmigan advertise their presence on territories by flying up in an arc, and at the apex singing or "becking" (nomenclature of Watson and Jenkins 1964). They give a similar call from the ground as advertisement or threat: ground becking or the "ko-ko-ko-ko-krrr". The "krrow" and "kohway" are used as threat calls in interactions with other birds (Watson and Jenkins 1964). Calls of willow ptarmigan are similar to those of the conspecific red grouse, L. l. scoticus.

Interactions among females were recorded during 15 intruder chases and 16 border disputes. Actual fighting occurred in only one intruder chase, usually the interloper ran or flew off the territory when chased by the resident. Vocalizations commonly given during chases were the krrow (9 cases), ground becking (5), and the kohway (2). Resident males interfered in 5 chases: in 3 of these, males ran between the 2 females and gave krrow calls to their mates; in one case the male attempted to display to the intruder; and once the male helped his mate chase the intruder.

Females also fought infrequently during border disputes with neighbouring hens: in only 2 of 16 disputes. The usual pattern was for females to stand side by side (11) or to walk in line (5) while giving repeated krrow calls (12), ground becks (3), or kohways (1). Males interfered in 10 border disputes; 7 of these were between 2 mates of polygynously mated males. In
the polygynous groupings, the male attempted to stay between the 2 females, giving krow calls if one of them approached the other. In the border disputes between monogamously mated females, the male either chased the neighbouring hen, chased his own mate back onto the territory, or displayed between the 2 females.

Twenty-three resident females were presented with the stuffed female model between 11 and 24 May 1980, 1981. All advanced towards it, thirteen gave an aerial beck or ground beck, and 17 of 23 gave repeated krow calls. Ten of the females attacked the dummy by flying at it and hitting it with the feet, running toward it and bumping it with the shoulder or wing, and/or pecking at the head and neck. One female neither vocalized nor attacked the model. Males were present during 20 experiments and 16 of them interfered with the female by keeping between her and the dummy or chasing her while giving krow calls. In these cases, 9 of the females attempted to lead the male away from the dummy by crouching and giving a head-wag accompanied by krow calls. Twelve males attacked the dummy by pecking it and 4 displayed and attempted to copulate with it. In one case where the female was unable to interact physically with the dummy because of male interference, after I noosed the male, the female approached the dummy and attacked it. In the five control experiments with the model of the duck, females looked at the model but showed no further interest in it.

Clearly, these observations and experiments suggest that female willow ptarmigan do defend territories by chasing or
attacking female intruders, and engage in border disputes with neighbours in a similar way to males. I did not collect detailed information to compare amount of time spent in territorial advertisement and defence by males and females, a question which requires further study. However, aggressive behaviour of females was less apparent than it was in males, partly because in females it was less frequent diurnally and more restricted seasonally. A complete description of male territorial behaviour is given in Watson and Jenkins (1964).

Removal experiments

Female removal

Slow pulsed removal: At least 11 hens settled on the 15 removal territories within a week after the first removal period. Ten of these were shot. Six additional females settled on the plot and were not removed. The final breeding density of females on HR was 12, and eight of these were later located with broods, indicating that at least some of the replacement females had bred. The origin of the replacements was unknown because not all females were banded prior to the experiment.

Rapid pulsed removal: Fifty-six females settled and were subsequently removed from the 15 removal territories between 12 May and 4 June 1980 (Fig. 2). Some females appeared on territories within 4 to 6 hours of the previous removal.
Figure 2. Number of females removed from 15 territories during 11 removal periods on HR in 1980 (inset is a histogram of date of first egg laid for non-experimental hens on the plot). Dots represent removal periods when no hens were removed.
Replacement rate was high until 26 May (Fig. 2), then declined suddenly, coinciding with the period when hens on unmanipulated territories began to lay eggs.

Some territories had more replacements than others (Fig. 3). Number of replacements was positively correlated with territory size of the male (Spearman's rank correlation coefficient=0.69, N=15, p<0.01). To investigate whether females chose larger male territories or simply settled randomly, I tested the null hypothesis that females settled in proportion to the amount of area taken up by all males with small (1-1.9ha), medium (2-3.4ha) and large (3.5-6ha) territories. The null hypothesis was rejected ($\chi^2=6.08$, p<0.05). Females settled less frequently on small territories, most frequently on medium territories, and as expected on large territories (Table II). Neither age of male (adult or yearling) nor position of his territory (either on the outer edge of the plot or in the core) had a significant effect on the number of females that settled on his territory (Table III) (Mann-Whitney U-test, U=17.5, p=0.57; U=18.0, p=0.23 respectively).

Single session female removal: Seven new females settled on the 9 territories after the removal on 14 and 15 May 1981. Four of these were later seen with broods, one other was probably in laying condition at capture as she had an enlarged cloaca and wide pubic symphysis, and two were not seen during the brood season. This experiment indicated that at least half of the replacement females were physiologically able to breed.
Figure 3. Number of female replacements removed from individual territories during the female removal.
Table II. Number of females that settled on small, medium, and large removal territories compared with the expected number that would have settled at random.

<table>
<thead>
<tr>
<th>Territory size</th>
<th>Number of female replacements</th>
<th>Observed</th>
<th>Expected</th>
<th>$\chi^2$</th>
</tr>
</thead>
<tbody>
<tr>
<td>small (N=5)</td>
<td></td>
<td>6</td>
<td>10.9</td>
<td>2.2</td>
</tr>
<tr>
<td>medium (N=5)</td>
<td></td>
<td>23</td>
<td>15.5</td>
<td>3.6</td>
</tr>
<tr>
<td>large (N=5)</td>
<td></td>
<td>27</td>
<td>29.7</td>
<td>0.3</td>
</tr>
</tbody>
</table>

6.1
Table III. Mean numbers of females that settled on removal territories of adult and yearling males, and males with territories at the edge (outer) or in the core (inner) of the removal plot.

<table>
<thead>
<tr>
<th></th>
<th>Mean</th>
<th>SE</th>
<th>N</th>
<th>range</th>
</tr>
</thead>
<tbody>
<tr>
<td>Adult males</td>
<td>4.4</td>
<td>1.08</td>
<td>5</td>
<td>1-7</td>
</tr>
<tr>
<td>Yearling males</td>
<td>3.4</td>
<td>0.70</td>
<td>10</td>
<td>0-6</td>
</tr>
<tr>
<td>Inner territories</td>
<td>3.2</td>
<td>0.79</td>
<td>6</td>
<td>0-5</td>
</tr>
<tr>
<td>Outer territories</td>
<td>4.1</td>
<td>0.82</td>
<td>9</td>
<td>0-7</td>
</tr>
</tbody>
</table>
Age structure, origin, and condition of recruits: Most replacement females in all removals were yearlings (Table IV). Of the 63 females identified as replacements in 1980 and 1981, 3% moved from other territories on the plots, 10% were nonterritorial banded birds (seen in small groups of females, or alone and not regarded as territorial or mated (p. 13)), and 87% were of unknown origin. Clearly the vast majority of birds came from areas off the plot and not from the territories directly surrounding it (i.e. from the 100m wide strip). Removal of females did not affect the density of females the next spring nor did the age ratio (% yearlings) change significantly from one spring to the next (Table IV).

I compared a body size (length of keel) and condition index (pectoralis weight divided by length of keel) among resident females, females who replaced birds shot during the first removal period, and females replacing birds removed in later removal periods (see Table V and Fig. 2 for dates of removal periods). All classes of females were similar in terms of body size (ANOVA, F=0.35, p=0.79) (Table V). Mean condition indices of females in the four groups varied (F=3.19, p=0.03). The condition index of replacement females in the first group was not significantly different from that of residents, although the index was higher than those of later replacements (Student-Newman-Keuls test, p<0.05, Sokal and Rohlf (1969), p. 242). This analysis indicates that replacements are of the same body size as residents, but, except for the earliest replacements, were in poorer body condition.
Table IV. Number of resident females before and after the female removal, number breeding the next spring, and number of replacement females (% yearlings in brackets).

<table>
<thead>
<tr>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>Number before</td>
<td>20</td>
<td>13</td>
<td>28</td>
<td>26</td>
<td>23</td>
<td>22</td>
</tr>
<tr>
<td>removal</td>
<td>(60%)</td>
<td>(64%)</td>
<td>(59%)</td>
<td>(39%)</td>
<td>(57%)</td>
<td>(50%)</td>
</tr>
<tr>
<td>Number of</td>
<td>11</td>
<td>--</td>
<td>56</td>
<td>--</td>
<td>7</td>
<td>--</td>
</tr>
<tr>
<td>replacements</td>
<td>(91%)</td>
<td>(87%)</td>
<td>(67%)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Number after</td>
<td>12</td>
<td>14</td>
<td>13</td>
<td>26</td>
<td>20</td>
<td>22</td>
</tr>
<tr>
<td>removal</td>
<td>(64%)</td>
<td>(38%)</td>
<td>(63%)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Number the</td>
<td>19</td>
<td>14+</td>
<td>28</td>
<td>22</td>
<td>--</td>
<td>--</td>
</tr>
<tr>
<td>next spring</td>
<td>(59%)</td>
<td>(56%)</td>
<td>(50%)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>(\chi^2)</td>
<td>0.04</td>
<td>--</td>
<td>0</td>
<td>0.26</td>
<td>--</td>
<td>--</td>
</tr>
<tr>
<td>(p&gt;0.8)</td>
<td></td>
<td></td>
<td>(p&gt;0.9)</td>
<td>(p&gt;0.5)</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

* in 1980 HR plot size was increased to 90 ha.
+ birds were not banded, result of two censuses.
Table V. Comparison of mean length of keel and ratio of pectoralis weight to length of keel among female residents, early replacements, and later replacements.

<table>
<thead>
<tr>
<th></th>
<th>Residents</th>
<th>Replacements*</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>First</td>
<td>Second</td>
</tr>
<tr>
<td>Length of keel (mm)</td>
<td>66.5</td>
<td>65.5</td>
</tr>
<tr>
<td>Mean</td>
<td>66.5</td>
<td>65.5</td>
</tr>
<tr>
<td>SE</td>
<td>0.84</td>
<td>1.19</td>
</tr>
<tr>
<td>N</td>
<td>9</td>
<td>8</td>
</tr>
</tbody>
</table>

Pectoralis to keel ratio (g/mm)

<table>
<thead>
<tr>
<th></th>
<th>Residents</th>
<th>Replacements*</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>First</td>
<td>Second</td>
</tr>
<tr>
<td>Mean</td>
<td>0.68</td>
<td>0.71</td>
</tr>
<tr>
<td>SE</td>
<td>0.011</td>
<td>0.021</td>
</tr>
<tr>
<td>N</td>
<td>9</td>
<td>8</td>
</tr>
</tbody>
</table>

* first=removal sessions 2,3; second=removal sessions 4,5; third=removal sessions 6-10 (see Fig. 1).
Male response to removal of females

Removal of females from HR in 1979 and 1980 had little effect on the number of males (Table VI). Eleven males that had their mates removed in 1979 were banded: four of these left the plot. In 1980, despite the more rapid rate of removal, only 4 of 15 males on female removal territories left the plot. Thus a total of 11 banded males in the 2 years left HR: 7 were not seen again, 2 moved to the male removal area (KL), one gained a territory on the edge of HR and mated with a female, and one remained nonterritorial and unmated. All of these males had remained on their territories up to the end of the second week of May before leaving. Most left during the last week of May, a period when resident hens had begun to lay eggs, and when female replacement rate had dropped (Fig. 2).

Unmated males

During all years, some territorial males were unmated, and hence served as natural counterparts to males on female removal territories. These males remained unmated despite an excess of females being available in the population (as indicated by the female removal). On the Control in 1981, 3 males were unmated, 2 males with adjacent territories shared a female (i.e. she was seen with both males throughout the spring), and one male lost his female to a previously unmated male with an adjacent territory. On KL in 1981, one male lost his mate and did not attract another, one remained unmated, and one took over an
Table VI. Numbers of males on removal plots and Control in the period before the female removal experiment and the period after removals had ceased.

<table>
<thead>
<tr>
<th></th>
<th>1979 HR</th>
<th>1979 Control</th>
<th>1980 HR</th>
<th>1980 Control</th>
</tr>
</thead>
<tbody>
<tr>
<td>Before</td>
<td>26</td>
<td>15</td>
<td>28</td>
<td>24</td>
</tr>
<tr>
<td>After</td>
<td>19</td>
<td>14</td>
<td>24</td>
<td>24</td>
</tr>
</tbody>
</table>
adjacent territory and mated with that female when her previous mate was killed by a predator. In 1979 on KL, 2 previously unmated males moved onto removal territories, mated, and raised broods, which indicates that this class of males can breed.

Unmated, and monogamously or bigamously mated males on the Control had territories of different sizes (Kruskall-Wallis one way analysis of variance by ranks, $H=13.94$, $N=7,9,3$, $p=0.001$) (Table VII). Unmated males appeared to have smaller territories than other males (Table VII). They also had shorter wings (unmated: $\bar{x}=183.9$ mm, SE=1.09, $N=9$; mated: $\bar{x}=188.1$, SE=1.09, $N=17$, unpaired t-test, $T=2.5$, $p<0.05$) and weighed less (unmated: $\bar{x}=486.7$ g, SE=7.15, $N=6$; mated: $\bar{x}=525.0$, SE=3.35, $N=6$, $T=2.5$, $p<0.05$) than mated yearling males (weight comparison made between birds caught between 24 and 29 April 1981). All unmated males except 2 remained on territory at least until females were on nests: one was killed by a predator, another left his territory around 15 May and was seen skulking on another's territory. All unmated males that were individually identified were yearlings ($N=15$).

The female removal experiments indicated that a large number of females, primarily yearlings, were available to replace residents. These females were physiologically able to breed. Most replacements did not come from territories on or directly surrounding the removal plot. This large reduction in female density did not result in a similar reduction of male density. "Widowed" males and naturally unmated males stayed on
Table VII. Mean territory size (ha) of males of three mating types on Control.

<table>
<thead>
<tr>
<th></th>
<th>unmated*</th>
<th>monogamously mated</th>
<th>bigamously mated</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Mean</strong></td>
<td>1.5</td>
<td>2.2</td>
<td>4.1</td>
</tr>
<tr>
<td><strong>SE</strong></td>
<td>0.11</td>
<td>0.08</td>
<td>0.34</td>
</tr>
<tr>
<td><strong>N</strong></td>
<td>7</td>
<td>9</td>
<td>3</td>
</tr>
</tbody>
</table>

* includes males that 'shared' a female.
their territories through most of May and the few that left did so after female replacement rate had dropped.

**Male removal**

**Slow pulsed removal:** After the first removal of 22 males from KL, 16 males settled on vacant areas by 13 May 1979. After a second removal of 8 males on 14 and 15 May, 5 more males settled and were subsequently removed on 23 May. One more settled but did not mate. Sixteen territorial males remained after the experiment. At least 8 of these were replacements that settled, mated, and raised young (only 7 residents remained after the first removal).

**Rapid pulsed removal:** Sixteen males replaced removed birds on 16 territories on KL in 1980, and 10 on 15 territories on HR in 1981 (Fig. 4). Replacement rates for males were much lower than those for females (Fig. 2 and 4) (females: 7 birds per removal session; males: 1.6 per session). Remaining males quickly moved onto the vacant ground, in some cases within a few hours, and began to defend it, thus probably excluding potential replacements. For example, on KL in 1980 on the day following the removal, 5 males whose territories abutted removal territories were sighted on these removal territories. In 1981, on the Control, a territorial male was accidentally killed during capture, and within 30 minutes his neighbour was calling on his territory.
Figure 4. Number of males removed from 16 territories on KL in 1980, and from 15 territories on HR in 1981, during the rapid pulsed removal.
Territorial boundaries were plotted for each male on the plot, before and after the removal. Territory size of the remaining males expanded dramatically when male density was reduced (Fig. 5) (Wilcoxon's matched pairs signed ranks test, KL1980: T=0.0, N=9, p<0.01; HR1981: T=0.00, N=8, p<0.01). Territory size on Control remained constant during the same time period (1980: T=55.0, N=16, p>0.05; 1981: T=16.0, N=8, p>0.05). Males situated at the edge of the removal plots expanded significantly their territorial boundaries onto the plot after the removal (Fig. 5) (1980: T=0.0, N=8, p<0.01; 1981: T=0.0, N=9, p<0.01) but those the Control kept within their former boundaries (1980: T=4.0, N=4, p>0.05; 1981: T=3.0, N=4, p>0.05).

Some males increased their territory sizes more than others. Percent increase in size ranged from 11% to 449%. The number of females mated to a male was correlated with his territory size after the removal (Spearman's rank correlation coefficient=0.64, N=17, p<0.01) but not (rs=0.26, N=17, p>0.20) with the percent increase in his territory size (i.e. his capacity to gain more area).

Nonterritorial males were also seen on the other plots throughout spring until late June, alone or in small groups (2-7 birds), skulking on territories and being chased by territorial males.
Figure 5. Mean territory size (±SE) of males before (clear) and after (hatched) the male removal, and mean area extending onto the plots of territories of males along the edge (solid).
Age structure, origin, and condition of recruits: Replacement males in all years were mainly yearlings (Table VIII). For 1980 and 1981 combined, 3 replacements were non-territorial banded birds, one came from the female-removal plot, and 18 were unbanded and of unknown origin.

Removal of males in 1979 did not alter the age ratio (% yearlings) of resident males in 1980. However, the age ratio in 1981 on KL was biased towards yearlings and was different from the age ratio in 1980 (Table VIII). This bias may have occurred because 12 of the 17 males left on the plot after the 1980 removal were adults and 8 of these were at least 3 years old. The high proportion of older males contributed to a low overwinter survival of adult males from KL in 1980-1981 (16% compared to 54% on the Control (N=24)). The number of males holding territories on KL decreased from 1979 to 1981.

Males resident on the plot before the removal were not significantly larger than males that immediately replaced them (before the next removal session) nor than males who replaced them later in the season (Table IX) (ANOVA, F=0.08, p=0.92). However, resident males were in better condition than either of the groups of replacement males (Table IX) (F=3.77, p=0.03, Student-Newman-Keuls test). Data from all years of the study were lumped, since pectoralis to keel ratios for residents were identical for the 3 years. This analysis suggests that replacement males were prevented from obtaining a territory because they could not compete effectively with males in better condition.
Table VIII. Number of resident males before and after the male removal, number breeding the next spring, and number of replacement males (% yearlings in brackets).

<table>
<thead>
<tr>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>Number before</td>
<td>29</td>
<td>15</td>
<td>32</td>
<td>24</td>
<td>31</td>
<td>24</td>
</tr>
<tr>
<td>removal</td>
<td>(42%)</td>
<td>(69%)</td>
<td>(31%)</td>
<td>(50%)</td>
<td>(48%)</td>
<td>(46%)</td>
</tr>
<tr>
<td>Number of</td>
<td>21</td>
<td>--</td>
<td>16</td>
<td>--</td>
<td>10</td>
<td>--</td>
</tr>
<tr>
<td>replacements</td>
<td>(73%)</td>
<td></td>
<td>(87%)</td>
<td></td>
<td>(90%)</td>
<td></td>
</tr>
<tr>
<td>Number after</td>
<td>16</td>
<td>14</td>
<td>17</td>
<td>24</td>
<td>17</td>
<td>24</td>
</tr>
<tr>
<td>removal</td>
<td>(88%)</td>
<td>(29%)</td>
<td>(35%)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Number the</td>
<td>20</td>
<td>14+</td>
<td>26</td>
<td>24</td>
<td>--</td>
<td>--</td>
</tr>
<tr>
<td>next spring</td>
<td>(35%)</td>
<td>(80%)</td>
<td>(46%)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>( \chi^2 )</td>
<td>0.02</td>
<td>--</td>
<td>12.22</td>
<td>0</td>
<td>--</td>
<td>--</td>
</tr>
<tr>
<td>( p \geq 0.9 )</td>
<td>p&lt;0.001</td>
<td>p&gt;0.99</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

* In 1980 KL plot size was increased to 80 ha.
+ Birds were not banded, results of two censuses.
Table IX. Comparison of mean length of keel and ratio of pectoralis weight to length of keel among male residents, first replacements, and later replacements.

<table>
<thead>
<tr>
<th></th>
<th>Residents</th>
<th>First replacements</th>
<th>Later replacements</th>
</tr>
</thead>
<tbody>
<tr>
<td>Length of keel (mm)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Mean</td>
<td>70.4</td>
<td>70.8</td>
<td>70.4</td>
</tr>
<tr>
<td>SE</td>
<td>0.59</td>
<td>0.93</td>
<td>0.89</td>
</tr>
<tr>
<td>N</td>
<td>24</td>
<td>11</td>
<td>13</td>
</tr>
<tr>
<td>Pectoralis to keel ratio (g/mm)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Mean</td>
<td>0.72</td>
<td>0.67</td>
<td>0.67</td>
</tr>
<tr>
<td>SE</td>
<td>0.011</td>
<td>0.014</td>
<td>0.024</td>
</tr>
<tr>
<td>N</td>
<td>24</td>
<td>11</td>
<td>13</td>
</tr>
</tbody>
</table>
Female response to male removal

Slow pulsed removal: Females did not leave their territories when male density was reduced. Twenty-two females had settled on KL prior to the removal experiment and 21 remained after 23 May when removals ceased. On Control, 13 females were identified before the removal period, 14 after. Females on KL were banded and their mating status was assessed. Thirteen females mated polygynously: 6 of these were later seen with their broods accompanied by males, and seven reared broods without male assistance. Eight of the 21 were monogamously mated: 2 of these to formerly unmated territorial males that had moved onto removal territories.

Rapid pulsed removal: Females settled at high densities on both areas in both years even though male density had been substantially reduced earlier (Table X). Breeding sex ratio was skewed on the removal plots but not on the Control.

Since the removal of males caused an increase in polygynous matings, males on removal plots divided their attention between their mates. This allowed me to plot the territorial boundaries of females with a minimum of male interference. On Control this was impossible because males chased their mates when I attempted to plot their territories. On HR in 1981, females occupied exclusive areas that overlapped little with other females and these areas were not always congruent with the territories of males (Fig. 6).
Table X. Numbers of territorial males before and after the male removal experiment, and numbers of females settling on KL, HR and Control.

<table>
<thead>
<tr>
<th></th>
<th>1980</th>
<th>1981</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>KL</td>
<td>Control</td>
</tr>
<tr>
<td>No. males before*</td>
<td>32</td>
<td>24</td>
</tr>
<tr>
<td>No. males after</td>
<td>17</td>
<td>24</td>
</tr>
<tr>
<td>No. females</td>
<td>29</td>
<td>26</td>
</tr>
<tr>
<td>Sex ratio</td>
<td>1:1.7</td>
<td>1:1.1</td>
</tr>
</tbody>
</table>

* males that had at least part of their territory on the plot before the removal.
Figure 6. Territorial boundaries of males (solid lines) and females (shaded) on HR 1981 after the removal of males.
The male removals indicated that excess males, primarily yearlings, were available to replace residents. However, there were substantially fewer male replacements compared with female replacements in the parallel female removal, even though nonterritorial males were seen on other areas. Replacements were physiologically able to breed. Remaining residents expanded their territorial boundaries soon after the removal and obtained much larger territories. The density of females was not reduced whether males were removed before or after hens had settled. When male numbers were low, females mated polygynously and defended territories against each other within the larger territories of the males.

**Territory sizes of females and males**

The distribution of territory sizes of females had the same mode, but a more limited range than that of males (Fig. 7). No females on HR in 1981 defended territories smaller than 1.5ha, and the smallest territory of a mated male on all plots in 1980 and 1981 was 1.6ha. Nor did a female defend a territory larger than 5ha. Females appeared to prefer territories of medium size: as reported previously, more females settled on medium than on small or large territories during the female-removal experiment. Thus males on small territories likely remain unmated, while those on larger territories could attract two females. The 3 bigamous males on Control in 1981 had territories of 3.6, 3.9, and 4.8ha in size.
Figure 7. Ranges of territory sizes used by females and males in 1981 (males on HR hatched).
DISCUSSION

Female territoriality and female numbers

Wilson (1975, p. 256) defined territory as "an area occupied more or less exclusively by an animal or group of animals by means of repulsion through overt defense or advertisement." Female willow ptarmigan are territorial: they occupy and vocally advertise on areas from which they repel intruders of the same sex, and defend borders against encroachment by neighbours. Does the territoriality of females limit the number of females that can breed? To determine this I had to demonstrate that a substantial part of the population was prevented from breeding by the territorial behaviour of residents and that these surplus birds were physiologically able to breed (Watson and Moss 1970). When I removed females from 15 territories, 56 females settled and were subsequently removed (Fig. 2). These replacement birds did not come from other territories on the plot, nor from the 100m wide strip around the plot, indicating that they were not immediate neighbours. I conclude that these birds had been prevented from breeding on my study plot by the territorial behaviour of the resident females. Replacement females were able to breed: most of those that settled and were not removed, were later seen with broods. Replacement birds were similar in body size to residents and the earliest replacements were equal in condition to residents. Thus it is unlikely that body size or condition affected the initial probability of gaining a territory.
Removal experiments on other avian species have also demonstrated that replacement females exist that can breed if residents are removed (Watson 1965, Holmes 1966, Watson and Jenkins 1968, Harris 1970, Young 1970, Bendell et al. 1972, Zwickel 1972, Manuwal 1974, Knapton and Krebs 1974, Krebs 1977, Zwickel 1980, Saether and Fonstad 1981). Many population studies, including this one, are conducted in good habitat where density of animals is high. Replacement individuals may be nonterritorial surplus birds or they may have moved from territories in marginal habitat, as in the the Great tit (*Parus major*) (Krebs 1971). Most replacement females in this study appeared within a few hours of the removal, suggesting that if they had settled previously in marginal habitat, then this habitat must have been nearby. The Control in 1979 was located in poorer habitat than the other plots: breeding density was much lower here and vegetation was taller and denser. There was no decrease in density of females on this Control during the female removal on HR in 1979 or 1980. This suggests that females did not leave Control and move to HR, or if they did, they were replaced by other females.

If replacement females had not settled prior to their appearance on HR, then it is unlikely that they would have settled at all. Females become territorial soon after they arrive: in 1980 all females on HR and 86% of those on the Control had settled by 13 May, and by 20 May all territorial females had settled on my plots. However, I was still removing females from HR until 2 June. If they had not settled by 20
May, then it is unlikely that they would have settled anywhere, at least in the immediate area. Timing of settlement of females on the 1979 Control (poor habitat) was similar to that on KL and HR (at least 80% of territorial females had settled on each plot by 1 May 1979), indicating that settlement on poor habitat is similar in time to that on better habitat. Therefore, I conclude that these replacement birds had been prevented from breeding on my study area by the territorial behaviour of resident females, and that at least some of them were surplus birds.

Replacement of removed females declined markedly in late May, around the period when resident females began to lay eggs. This phenomenon has also been observed in blue grouse, *Dendragapus obscurus*, (Hannon and Zwickel 1979) and white throated sparrows, *Zonotrichia albicollis* (Falls 1978). Either the number of surplus individuals has been depleted by frequent removal or by high predation rates (as in surplus red grouse (Jenkins et al. 1964), some females may have settled elsewhere, or there may be a physiological block that prevents recrudescence of the gonads after this point in time. For example, if female willow ptarmigan had settled after 2 June, their eggs would not have hatched until 13 July at the earliest. No first nests hatched after 8 July in 1980, although renests did hatch after that time. Perhaps the ovaries become refractory if hens have not settled before a certain time. This could explain why removal experiments conducted on a species after laying has begun have yielded no female replacement (eg.
Stewart and Aldrich 1951, Holcomb 1974). Harris (1970), however, found that female oystercatchers (Haematopus ostralegus) were replaced when removal was done after laying.

Male territoriality and male numbers

There were 2 types of nonbreeding males: those with territories on the area and those without. Territorial males without mates were able to move onto removal territories and breed. Some nonterritorial males gained territories during removals, and when left to settle, were able to breed. Unmated territorial males were smaller and younger than mated territorial males, which may account for their smaller territory size (Table VII). Replacement males were in poorer condition than residents (Table IX), but whether this was the cause or effect of not gaining a territory is not clear. I do not know whether these males moved from marginal habitat; however, the arguments presented above for females apply to males.

Replacement rate of males was much lower than that of females, probably because the experiment was done later in terms of tenure on the breeding range for males than females, and secondly because neighbouring males reacted quickly to removal by expanding their borders, an illustration of Huxley's (1934) "elastic disc" model of territoriality. When a higher proportion of males on the plot was removed (as in 1979) proportionately more replacements settled, possibly because the few remaining males were unable to expand their boundaries to cover the whole plot. Replacement by females on the female
removal plot was so rapid, that this, and interference by their mates, probably deterred the remaining females from monopolizing adjacent empty territories.

**Interactions between the sexes**

The removal experiments suggested that female territoriality determined the number of females that settled, and male territoriality, the number of males that settled. Did this sex-specific territoriality in any way determine the number of the opposite sex that bred?

**Female behaviour and male breeding density**

Females could potentially influence density of breeding males at two points: during the initial competition for territories; or after males have settled. When females arrive on the breeding area, they may choose a territory from the existing array of male territories, or they may settle independently, choose their own territories and the males then readjust their boundaries. The end result is the same: territories of males and females largely overlap. My data are not sufficient to distinguish between these two possibilities, however some evidence indicates that the latter is plausible. Females on the male removal plot defended their own territories and did not always remain within the boundaries of their mates' territories (Fig. 6). I have seen both monogamously and polygynously mated females fly spontaneously, call, and land
several metres over the boundaries of their mates' territories. This usually incites a dispute between her mate and the neighboring male. An aggressive female may be able to enlarge her mate's territory in this way, and as a consequence force other males onto smaller territories or out of the area completely. This hypothesis could be tested by increasing a female's aggressiveness by implanting her with testosterone and determining whether territorial boundaries changed. A second test would be to map the territories of males before and after females arrived.

If a female simply chooses a territory of a male, after the number of territorial males on the area stabilizes, then factors influencing the acceptable territory size to the female could determine the number of males that breed. Unmated territorial males occur despite a surplus of females (this study, Jenkins et al. 1963, Watson and Moss 1980) and have smaller territories than mated males (Table VII, Choate 1963, Watson and Miller 1971). In populations that cycle in density, the proportion of unmated males increases at the peak and during the early decline phase (Jenkins et al. 1963, Watson 1965, Myrberget 1972) and territories of these males are larger during a decline in numbers than they are in years of high density (Watson and Miller 1971). If spring densities of males and females are similar (i.e. overwinter mortality of each sex is equal), then males probably remain unmated because they are rejected as mates by females because their territories are too small. Increases in the minimum territory size acceptable to females, because of
a decrease in resources or an increase in the inherent aggressiveness of females, could precipitate declines in breeding density. Thus, choice of territories by females could influence the number of males that breed.

**Male behaviour and female breeding density**

If females adjust their territory boundaries to those of males, instead of the other way around, then the settlement patterns of males in spring could influence the number of hens that breed. High competition by recruiting males for limited space on the breeding range may result in many of them holding small territories that will not support a female. Differences in survival and aggressiveness of successive cohorts of males may result in varying amounts of space becoming accessible to potential recruits and thus affect their territory size. For example, chicks produced during the peak and decline of a rock ptarmigan (L. mutus) population survived longer and were more aggressive than those hatched the year before the peak (Theberge and Bendell 1980). Watson and Miller (1971) reported that cohorts of males produced during a population decline survived better, were more aggressive, and defended larger territories than cocks produced during the increase phase. A particular cohort could defend the majority of the breeding range for one or two years, leaving successive cohorts to compete for the remaining space. High competition could lead to a reduction in territory size below the minimum acceptable to females and thus these males would be excluded from breeding. Thus the final
breeding density of the population is determined by the settlement patterns of males, factors affecting minimum acceptable territory size in females, and within-sex spacing behaviour. In Fig. 8 I summarize the effects of within-sex spacing behaviour and interactions between the sexes on breeding density of the population.

Cyclic declines in density of grouse

Variations in chick production have been related to fluctuations in population size (Jenkins et al. 1963, Bergerud 1970, Gullion and Marshall 1968, Myrberget 1972, Weeden and Theberge 1972). In my removal experiments, I identified a surplus of yearlings of both sexes in spring, indicating that survival of juveniles to spring was high. Thus spacing behaviour in spring, not overwinter loss of juveniles, appeared to regulate the breeding density. However, my study was conducted on a population at high and stable density, and whether chick mortality would become a significant factor during a decline in density is unknown. Low chick production may be caused by increased predation on nests, higher rates of nest desertion, nutritionally-related changes in viability of chicks, intrinsic phenotypic or genetic changes in vigour or behaviour of chicks, and variations in the quality of parental care (Watson and Moss 1979). Most work has focussed on extrinsic causes of production loss and overwinter mortality of juveniles. In the future it would be of interest to determine whether high levels of female aggressiveness are related to survival of
Figure 8. Postulated influences of within-sex spacing behaviour (solid lines) and between-sex interactions (dotted lines) on the breeding density of willow ptarmigan.
WITHIN-SEX

Females arrive

Non-breeding females

♀-♀ competition for territories

BETWEEN-SEX

♂-♂ competition for territories

♀'s choose territories independently of males & alter ♂ settlement

Settlement patterns of males

♀'s choose ♂ territories, exclude those on small territories

Final settlement density

WITHIN-SEX

Males arrive

Non-breeding males

BREEDING DENSITY
juveniles and their subsequent territorial behaviour.

If changes in spacing behaviour cause cyclic changes in the density of grouse populations as suggested by Watson and Moss (1979, 1980), then level of aggressiveness must be inherited either due to maternal effects, which can be related to nutrition of the hen (Watson and Moss 1972) or to overcrowding (Christian 1978), or be genetically inherited (Chitty 1967). Studies on dominance and aggressiveness of red grouse in the field and in captivity have been devoted solely to males (e.g. Watson and Miller 1971, Moss et al. 1979, Watson and Parr 1981). These studies indicate that in males aggressiveness and dominance are related to levels of androgen (Moss et al. 1979) and that they can be inherited (Moss and Watson 1980, Moss et al. 1982). I have shown that aggressiveness of females may be important in determining breeding density and suggested that changes in female spacing behaviour may be related to changes in population density. Future studies could investigate factors affecting territory size of females, the inheritance and hormonal basis of aggressiveness in females, and whether changes in female aggressiveness are related to changes in breeding density.
**Sex-specific population regulation in other grouse species**

Can a mechanism, such as I have suggested for willow ptarmigan be generalized to other grouse species? Workers on other species or subspecies of *Lagopus* have not considered that female territoriality has an effect on breeding density. However, in these species, females are aggressive towards one another during the breeding season (Watson and Jenkins 1964, MacDonald 1970) and unmated territorial males are present (Choate 1963, Watson 1965, Bergerud 1970, Watson and Miller 1971, Myrberget 1972). These similarities among monogamous species indicate that breeding density may be determined in a similar way.

A major difference is that numbers of breeding Scottish red grouse and willow grouse (*L. l. lagopus*) in Norway (Blom and Myrberget 1978) appear to be determined proximately by overwinter mortality, which is socially induced by fall territorial behaviour in red grouse (Jenkins et al. 1963). My removal experiments demonstrated an excess of birds available to occupy territories in spring. This difference in the timing of regulation may be related to whether a particular population is migratory or not. Migratory ptarmigan in North America are not territorial in fall (Weeden 1959) although males of non-migratory willow ptarmigan (*L. l. alleni*) in Newfoundland exhibit territorial behaviour at this time (Bergerud 1970).

The spacing of females of promiscuous tetraonids has been described in only one species, the spruce grouse (*Canachites canadensis franklinii*). Females maintain non-overlapping
territories separate from males in late spring (Herzog and Boag 1978) and react aggressively to other females (Herzog and Boag 1977). A similar dispersion is possible for female blue grouse (D. o. fuliginosus) which are evenly spaced on the breeding range (Bendell and Elliott 1967) and aggressive in spring (Stirling 1968, Hannon 1980), and for female ruffed grouse (Bonasa umbellus) that occupy spring home ranges with little overlap (Maxson 1978). Among lekking species, females have been reported to interact aggressively on the lek (Lumsden 1965, 1968, Kruijt and Hogan 1967, Robel 1970) but whether this intolerance continues after mating and serves to space hens on the summer range is unknown. In promiscuous species, females apparently do not depend on resources on a male's territory, and appear to live independent lives except for a brief period during copulation. In these species, breeding density is determined by the number of females that breed, and this number may be determined by female-female interactions independently of male density. Unfortunately few removal experiments have been attempted to determine whether surplus birds of both sexes exist (but see Bendell et al. 1972, Zwickel 1972, Zwickel 1980), nor has the effect of removal of one sex on the density of the other been investigated.

I have investigated the effect of female spacing behaviour on the breeding density of the monogamous willow ptarmigan. Resident females are territorial during spring prior to incubation, and this behaviour prevents non-territorial females
from settling. Spacing behaviour by males determines the initial settlement density of males. However the number of females that settle is not always equal to the number of males on territories, since females do not mate with males on small territories. Since most birds are monogamous, more descriptive and experimental studies are necessary to assess whether the results from this study can be generalized to other monogamous species.
CHAPTER THREE: FACTORS MAINTAINING MONOGAMY IN WILLOW PTARMIGAN POPULATIONS
INTRODUCTION

Willow ptarmigan are usually monogamous (Hjorth 1970), but polygyny occurs occasionally: in my study population only 9% (N=57) of males present on Control areas paired polygynously (Table XI). Why is polygyny not more prevalent in willow ptarmigan populations? In a recent review, Wittenberger and Tilson (1980) presented three hypotheses to explain why most noncolonial bird species with multipurpose territories are monogamous:

1. Male parental care is nonshareable and indispensable to female reproductive success;
2. Territories of males do not vary enough in quality to make it advantageous for a female to mate with an already mated male rather than with an available unmated male (i.e. the polygyny threshold (Orians 1969) is not exceeded); and
3. Aggression by females prevents males from acquiring additional mates, even though the polygyny threshold is exceeded.

Males of monogamous grouse species provide more investment in female reproductive success than do males of promiscuous species (Wittenberger 1978). In the three ptarmigan species, males defend territories until the end of incubation (Weeden 1963, Watson 1965, Giesen and Braun 1979) and appear to provide vigilance against predators for the hen during foraging (Choate 1963, MacDonald 1970, Wittenberger 1978). Male rock ptarmigan (L. mutus) (MacDonald 1970) and willow ptarmigan (personal observation) protect the nest from potential predators, and male
willow ptarmigan accompany the female and defend the brood against predators. Is this male investment essential to female reproductive success and survival in monogamous grouse?

In this chapter I test Wittenberger and Tilson's first hypothesis by comparing the breeding success and survival of polygynous and monogamous female willow ptarmigan. By continuous removal of males from certain territories, I altered part of the population (48%, N=48, Table XI) from monogamy to polygyny (Chapter One). Since mean male territory size doubled on the male removal area and polygynous females divided the territories of males and defended subterritories against each other, I concluded that polygynous females had the same access to resources as monogamous females, but had less male investment time allotted to them. If males are important as predator detectors in the prelaying and laying periods, then a female foraging without male vigilance should either be more susceptible to predation, or should forage less efficiently and hence lay a smaller clutch, or lay and hatch eggs later than a monogamous female. Low food availability has been related to reduced clutch size and later laying date in some species of birds (e.g. Klomp 1970, Moss et al. 1971, Källander 1974, Greenlaw 1978). If male vigilance at the nest or with the brood is important, then polygynous females would be expected to suffer higher rates of nest predation and lower brood sizes respectively.

After considering the first hypothesis, I will then evaluate the applicability of the second and third hypotheses to
Table XI. Number of males breeding with one, two, three, or four females on the male removal and Control plots.

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<tbody>
<tr>
<td>One</td>
<td>8</td>
<td>14</td>
<td>9</td>
<td>22</td>
<td>8</td>
<td>16</td>
</tr>
<tr>
<td>Two</td>
<td>5</td>
<td>0</td>
<td>4</td>
<td>2</td>
<td>8</td>
<td>3</td>
</tr>
<tr>
<td>Three</td>
<td>1</td>
<td>0</td>
<td>4</td>
<td>0</td>
<td>0</td>
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</tr>
<tr>
<td>Four</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>0</td>
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the maintenance of monogamy in willow ptarmigan using data presented in Chapter One.
METHODS

Experimental removal of males was conducted during spring of 1979, 1980 and 1981 on plots located in the subalpine tundra of the Chilkat Pass, northwestern British Columbia, Canada (59° 50'N, 136° 20'W). The study area, general methods and removal schedule are described in more detail in Chapter One. Three plots were used: a 50ha Control, and 2 removal areas: 90ha Haines Road plot (HR); and 80ha Kelsall Lake plot (KL). The final density of breeding males and females, and the number of polygynous matings on each plot are summarized in Table XI.

I located nests by searching around roosts of males to a radius of 80 paces. A few nests were found by a pointing dog during routine census. Nests of most females were not located, and hatch dates of nests for these females were determined by estimating age of chicks in the brood by the method of Bergerud et al. (1963), and backdating.

Counts of fledged chicks were made by locating broods with a trained pointing dog, and then searching the immediate area thoroughly, counting the number of chicks that flew away. Additional counts were made off the plots by searching on foot with or without the dog, and by counting broods along the road from a vehicle. Only those counts in which I was present before chicks began to flush were used to estimate brood size. Chicks began to fly at about 11 or 12 days of age and those used in the analysis varied from 11 to 33 days of age. Zwickel and Bendell (1967) found that 90% of juvenile mortality occurred prior to fledging in blue grouse and I assumed that once fledged, willow
ptarmigan juveniles experienced similar levels of mortality to adults, at least in the period of my study.

Statistical comparisons of breeding success and survival of monogamous and polygynous females were based on the null hypothesis that there was no difference between the two groups, and the alternative hypothesis that polygynous females would do worse. Thus these tests were one-tailed. Probabilities greater than 0.05 were judged not significant.
RESULTS

Male vigilance

Males that mate polygynously appear to spend time with more than one of their females during the prelaying and laying periods (Fig. 9). During incubation, a monogamous male sits close to the nest (usually within 50m) and distracts intruders by calling and bringing attention to himself. Nests are difficult to find, and in only one case were both nests of a polygynous group located. The male was seen close to both nest sites which were located about 80m apart. I did not collect data on how much time a male spent with each female during the prelaying, laying, and incubation periods, however, it is likely that each female of a polygynous group receives less male vigilance compared with monogamously mated females.

Birds with broods leave their territories 3 or 4 days after the eggs hatch, and males in polygynous groupings accompany and defend the chicks of only one hen. The male usually accompanies the female whose young hatch first (7 of 8 males where hatch dates were known for both hens). I term polygynously mated females that are accompanied by the male during the brood season, primary females; and those defending the brood alone, secondary females.
Figure 9. Number of polygynous males that were seen during routine census with each of their hens, at least two hens, or with only one hen prior to hatch (1980 and 1981).
Number of mates

Number of mates

0  3  6  9

all  2/3  1

9
Reproduction of polygynous and monogamous females

Clutch size

I compared the clutch sizes of polygynous and monogamous females for the 3 years combined and found no difference (U=138.5, N=7,40, p=0.5). Mean clutch size for polygynous females was 7.3 ± 0.56SE and for monogamous females 7.3 ± 0.20.

Hatch date and hatching success

The distributions of hatch dates of nests of polygynous and monogamous females were not significantly different (Fig. 10, Kolmogorov-Smirnov Two sample test, $\chi^2=3.09, N=30,65, p<0.15$) and thus by extrapolation, neither were the dates of laying first egg. Within polygynous groups, nests usually hatched within 2 days of one another (Fig. 11), the exceptions being one 5 days, one 13, and another 15 days after the date of hatch of the first female. The latter two females hatched their eggs much later than other females in the population and were possibly renesters.

In 1979 and 1980 most females were seen with broods (75% (N=28) and 85% (N=48) respectively), and the proportion of females with broods did not differ significantly between the two years ($\chi^2=0.68, p<0.3$). However, in 1981 fewer females appeared with broods (60%, N=46), and this proportion was significantly lower than in 1979 and 1980 ($\chi^2=5.33, p<0.025$). Nest predation was low in 1979 (10%, N=10) and 1980 (0%, N=21) and higher in
Figure 10. Distribution of dates of hatch for monogamous and polygynous females for 1980, and 1981 (hatch dates in different years and on different areas were combined by matching modal dates of hatch for monogamous females).
Figure 11. Number of days between the hatch dates of primary and secondary females within a polygynous group.
No. of days between hatch dates

No. of females

1 3 5 7 9 11 13 15
1981 (26%, N=19) (Fisher exact test, p=0.024 when 1981 was compared to 1979 and 1980 combined). Of the 50 nests found in the 3 years of the study, only one clutch was deserted, and that was by a female that had renested and had incubated for over 29 days (normal incubation is about 21 days) on infertile eggs. Therefore, if females do not produce a brood, it is likely that their nests have been destroyed by predators.

I predicted that predation should occur more frequently on nests of polygynous females since they shared male vigilance. In 1979 and 1980 both polygynous and monogamous hens were seen with broods at the same rate (Table XII). However, in 1981, the year of high nest predation, polygynous females were seen less often with broods than monogamous females (Table XII). Polygynous hens in 1981 were seen less often with brood than those polygynous females in 1979 and 1980 combined ($\chi^2=7.66$, p<0.005), whereas monogamous females in 1981 were seen with brood to the same extent as those in 1979 and 1980 ($\chi^2=0.01$, p<0.4). These analyses indicate that in a year of high nest predation, polygynous females may be more vulnerable to having their nests located and destroyed by predators. When nests were destroyed, the entire contents usually disappeared between checks on the nest (within one or two days). The main predators are likely the coloured fox, *Vulpes vulpes*, and weasels, *Mustela erminea*. Only one egg was found with a hole in it, which suggests that predation was by corvids.
Number of chicks fledged

Of females seen with broods, secondary females fledged the same number of chicks as primary females or monogamously mated females on the male removal area (Table XIII). Mean brood sizes of lone females were similar to those of paired females, when all birds on the study area were included (Table XIII). In general, it appears that secondary females (lone females), if they hatch their nests, can fledge as many chicks as females accompanied by males. I could not compare survival to breeding age of chicks raised by polygynous or monogamous parents because return rate of tagged juveniles to the study area was very low.

Predation on females in the prelaying period

In the 3 years of the study, only one predator kill of a territorial female (polygynously paired) was found during the pre-incubation period. Therefore, I have no direct evidence with which to compare predation on polygynous and monogamous females. Once laying begins, females are rarely seen by observers routinely censusing the plots until chicks hatch. If females are seen with broods, then they have obviously survived the prelaying and laying periods. But if females are not seen during the brood season they may be dead, they may have had their nest destroyed and then left the area, or they may have left the area with their brood prior to being censused. Nests of six territorial females, not resighted during the brood period, were destroyed by predators. However the disappearance
Table XIII. Mean brood counts of primary, secondary and monogamously mated females on male removal plots and lone and accompanied hens on other areas (T values for t-test and level of significance).

<table>
<thead>
<tr>
<th>Females on male removal plots</th>
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<tbody>
<tr>
<td></td>
<td>Secondary</td>
<td>Primary</td>
<td>Monogamous</td>
</tr>
<tr>
<td>Mean</td>
<td>4.9</td>
<td>4.0</td>
<td>4.7</td>
</tr>
<tr>
<td>SE</td>
<td>0.48</td>
<td>0.50</td>
<td>0.60</td>
</tr>
<tr>
<td>N</td>
<td>9</td>
<td>11</td>
<td>12</td>
</tr>
<tr>
<td>t</td>
<td>1.25 (p&lt;0.2)</td>
<td>0.28 (p&lt;0.45)</td>
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<th>Females on whole study area</th>
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<tr>
<td></td>
<td>Lone</td>
<td>With male</td>
</tr>
<tr>
<td>Mean</td>
<td>4.8</td>
<td>4.7</td>
</tr>
<tr>
<td>SE</td>
<td>0.28</td>
<td>0.22</td>
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<tr>
<td>N</td>
<td>36</td>
<td>98</td>
</tr>
<tr>
<td>t</td>
<td>0.24 (p&lt;0.45)</td>
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of the remaining females is unaccounted for. If females not
seen during the brood season were killed by predators during the
prelaying period, I would have expected them to disappear from
the plots earlier than females who were seen with broods. Dates
when females were last seen before laying began were similar for
both groups of females (Fig. 12) (1980 and 1981 only) (U=206,
N=26,18, p=0.25). Unsuccessful polygynous females did not
disappear earlier than unsuccessful monogamous hens
(U=31.0,N=5,13, p>0.05). Unless hens are more likely to be
killed by predators during laying and incubation, I conclude
that hens not seen during the brood season were not killed by
predators, but lost their nests, or left the area prior to being
censused.

Breeding success of polygynous and monogamous males

I cannot directly compare the success of polygynous and
monogamous males because brood counts were not obtained for all
females in each polygynous group. However, I can estimate the
success of males by using mean brood counts for polygynous and
monogamous females. In a year with no nest predation, a
bigamous male could produce a mean of 8.8 chicks (mean brood
count of polygynous hens=4.4, SE=0.36, N=20) and a monogamous
male a mean of 4.7 chicks. In the year of high nest predation
(1981), 46% of polygynous hens hatched eggs, thus bigamous males
had a probability of producing a mean of 8.8 \times 0.46= 4.0 chicks.
Seventy-seven percent of monogamous females hatched young. Thus
monogamous males had a probability of producing a mean of 3.6
Figure 12. Date of census in which females that were A) seen during the brood season, and B) not seen during the brood season, were last located on the plots before laying began.
A.

Date of census

Number of birds

B.

Date of census

May
chicks. Thus, polygynous males fledged many more chicks on the study area than monogamous males in a good year, and about the same number as monogamous males in a poor year.

Survival to the next breeding season

Perhaps the rigors of associating with 2 females (for the male), or raising a brood alone (for the female) could reduce survival to the next breeding season. I compared survival to the next spring of polygynous and monogamous females and males present during the brood season, and found no statistically significant differences (Table XIV).
Table XIV. Survival to the next breeding season of polygynous and monogamous females and males (data from 1979 and 1980 combined).

<table>
<thead>
<tr>
<th>Age</th>
<th>Mating status</th>
<th>No. surviving</th>
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<th>p*</th>
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<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>FEMALES</strong></td>
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* Fisher exact test
DISCUSSION

Importance of unshared male vigilance

Unshared male vigilance (Wittenberger and Tilson 1980, hypothesis 1) is clearly not essential to reproductive success and survival of female willow ptarmigan. Polygynous and monogamous females survived equally well, produced similar clutch sizes, laid eggs at the same time, and produced broods of similar size. The only difference in reproductive performance appeared to occur during incubation, when polygynous females suffered a higher loss of nests in a year when nest predation was high. These results indicate that the most important contribution of the male may be at the nest, and not during the prelaying and laying periods as suggested by Wittenberger (1978). In years of high nest predation, such as occur during cyclic declines of grouse (Weeden and Theberge 1972, Myrberget 1972), the role of the male as sentinel at the nest may become more important to female reproductive success.

These results differ from those of Miller and Watson (1978), who found that secondary females in red grouse produced smaller broods. Bigamous male red grouse did not have significantly larger territories than monogamous males, and the authors suggested that the territories did not have sufficient resources for two hens. However, it is also possible that females that share resources on smaller territories may require more male vigilance to succeed, since food availability per female is lower.
If a polygynous female can raise young successfully by herself, why then are unmanipulated populations of willow ptarmigan not polygynous? Polygyny is clearly an advantage to males. Males are opportunistically polygynous and polygynous males produce more young than monogamous males in years of low nest predation, and just as many in years of higher nest predation. Some mated males court intruding females, and attempt to separate females engaged in aggressive encounters (Chapter One). However, in order for polygyny to become the prevalent mating system, it must be advantageous for females as well (Orians 1969).

Wittenberger and Tilson (1980) proposed that ptarmigan are monogamous because territories of males do not differ enough in quality to exceed the polygyny threshold. Thus there is no advantage to a female to become a second mate of an already mated male, if unmated males on good quality territories are available. This hypothesis predicts that polygyny occurred on the male removal plot because male territory size expanded, producing a polygyny threshold where none had existed before. In the absence of data on the quality of territories in willow ptarmigan populations I cannot reject or support the polygyny threshold hypothesis. However, unmated males defend small territories (Chapter One), and in the conspecific red grouse, these territories contain half the weight of green shoots of heather as did those of monogamous males. Territories of monogamous and bigamous males appear to produce a similar yield of heather (Miller and Watson 1978). This suggests that for red
grouse at least, territory quality is variable, though whether a significant proportion of them could support two females is unclear. I know of no studies that have attempted to measure whether a polygyny threshold exists on territories of a monogamous species, and therefore Wittenberger and Tilson's hypothesis 2 remains untested, and could explain why willow ptarmigan are monogamous.

**Female aggression and the maintenance of monogamy**

There is an alternative explanation of the natural and experimentally induced polygyny on large male territories (Chapter One). Female willow ptarmigan chase and attack females that intrude on their territories, thus preventing unmated females from settling, at least on small to medium sized territories (Chapter One). However, the upper limit of female territory size is lower than that of males (Fig. 7), and defence by females of large territories may become too costly energetically. Thus, when males were removed, and the territory sizes of the remaining males increased (Fig. 5), females could no longer defend the entire area.

Wittenberger and Tilson (1980) dismissed the hypothesis that female aggression prevents polygyny in birds, because females must expend large amounts of energy in egg laying and incubation, and repelling additional females would cost more than to tolerate them. However the cost to females to repel potential second females depends on a number of factors not considered by Wittenberger and Tilson and which differ in
different habitats. I propose that polygyny results when a female is unable to defend economically the whole of her mate's territory against other females. The following factors may influence a female's ability to defend her territory and hence the incidence of polygyny, if a polygyny threshold exists.

**Length of the breeding season**

As a female's reproductive cycle progresses, the amount of area she is able to defend decreases markedly. For example, the territories of resident female spruce grouse decrease in size from early spring to late spring as eggs develop and laying begins (Herzog and Boag 1978). During incubation the area defended decreases further. If climatic or other environmental conditions permit a long breeding season, then a second female will be able to settle and breed while the first is laying or incubating. Nero (1956) noted that female redwings *Agelaius phoeniceus* attempted to defend a large portion of the male's territory in spring but when nesting began they defended less area. Aggression by females in polygynous species may delay settling of secondary females and hence reduce potential harem size (Holm 1973, Crawford 1977, but see Yasukawa and Searcy 1981). In blue grouse, few yearlings settle until after adults have begun to lay eggs, and this has been attributed to social inhibition through interactions with adults (Hannon et al. 1982).

Monogamous ptarmigan species live in areas with short breeding seasons and the hatch of nests is highly synchronous.
(e.g. Weeden 1963, Giesen et al. 1980). Nests of willow ptarmigan in the Chilkat Pass all hatched within a 26-day period, and 88% of the hatch occurred during the first two weeks. If a female has not settled by a certain date, she may have insufficient time to build up reserves for egg-laying, lay her eggs, incubate, and successfully raise a brood. In the continuous female removal experiment, replacement of removed females was rapid until hens in the unmanipulated population began to lay eggs. After this point few hens attempted to settle, suggesting that it was too late in the season to breed successfully (Chapter One). Synchrony of nest initiation because of the brevity of the breeding season may be a factor which maintains monogamy in other tundra-breeding species (Weatherhead 1979).

**Male:female territory size ratio**

If a male is capable of defending a very large territory, he may be able to accommodate two females. Obviously the benefits to a male to attract more than one mate are substantial. He will be able to produce many more offspring than a monogamous male. McLaren (1972) has in fact suggested that the adaptive function of territoriality in males is to attract a second female. However, in some situations, it may be physically impossible for a male to defend a territory much larger than the female's. Factors which could decrease male:female territory size ratio are high male intruder pressure, low female intruder pressure, low size dimorphism.
(male equal to or smaller than the female) or a combination of these. Environmental factors, such as severe weather conditions or scarcity of food, could counteract sexual selection for larger body size in males, making them equal in size to females and less able to defend a larger territory.

Male to female territory size ratio in willow ptarmigan is 0.99 (means for birds on HR 1981: males: 2.79± 0.372, N=23; females: 2.82± 0.197SE, N=18). Males had a higher upper limit to territory size than did females, although the most frequently chosen territory size was the same for both sexes. Male and female territories are probably similar in size because first, male willow ptarmigan are only slightly larger than females (Wiley 1974), and second, because of high energetic costs to the male to defend a territory larger than the female's. When competitors were removed during the male removal experiment, the size of the remaining males' territories increased dramatically (Chapter One) indicating that high intruder pressure probably increases the energetic costs of defending a territory and keeps territories small. High intrusion pressure reduces territory size in other species (Myers et al. 1979, Ewald et al. 1980).

To summarize, female willow ptarmigan may prevent polygyny from occurring by aggressively attacking potential secondary females. Although this behaviour may be energetically expensive, a female benefits by having access to unshared male vigilance, which may be particularly important during years of high predation. Two factors enable female willow ptarmigan in unmanipulated populations to defend territories against
potential secondary females: 1) breeding seasons are short so that once a female begins to incubate and cannot defend the territory, it is too late for other females to settle; and 2) territories of males are rarely larger than those of females, so females can defend the entire area and prevent a second female from settling early in the season.

Tests of the Female Aggressiveness Hypothesis

To test whether female aggression enforces monogamy for a particular species, one must first determine whether a potential for polygyny exists on territories of monogamous males. This could be done by reducing the aggressiveness of the first female to allow a second female to settle, and then assessing whether both females could produce young. Alternatively, an artificial polygyny threshold could be maintained by supplementing particular territories with food or nest sites. If more females attempt to settle on these territories than on Controls, and if they are prevented from doing so by the behaviour of the resident females, the female aggressiveness hypothesis would be supported.

As Wittenberger and Tilson (1980) pointed out, a single hypothesis is not sufficient to explain monogamy in all situations. Aggression by females may enforce monogamy only under a limited set of environmental conditions. If the costs to a female of defending a territory outweigh the benefits of exclusive access to resources and male vigilance or parental care, then a female would not be expected to engage in this
behaviour. Thus, in habitats where breeding seasons are long or where males can economically defend much larger territories than females, primary females would not be expected to react aggressively to secondary females, unless this behaviour delays settlement of the secondary female and ensures more male parental investment in the young of the first female.

**Mating systems in grouse**

In the above discussion, I took as given that territories of males and females overlap and that ptarmigan have a long-term pair bond, and then asked why are they not polygynous? Most grouse species are promiscuous, males and females associate only during copulation, and territories or home ranges of males and females do not overlap extensively (Hjorth 1970, Wiley 1974). What ecological factors have selected for a pair bond and overlapping territories in monogamous grouse?

Wittenberger (1978) suggested that monogamous grouse species inhabit areas where food is scarce in spring so that females benefit by associating with males and relying on male vigilance during foraging. Promiscuous species apparently live in areas with abundant food, females do not need to forage on territories of males, and avoid them because of increased conspicuousness to predators. Thus food abundance, he suggests, leads to a promiscuous mating system. To support this hypothesis, Wittenberger compared spring diets of monogamous and promiscuous species and concluded that monogamous species generally have a polytypic diet, and promiscuous species a
monotypic diet. He equated a monoculture of food resources to a superabundance of food.

I suggest that there are no data to support this hypothesis. First of all, spring diets of most monogamous species are monotypic (Peters 1958, West and Meng 1966, Moss 1969, Weeden 1969). For ptarmigan species, it is not until the snow melts and hens have begun to lay that the diet becomes more diverse. Secondly, it is not the diversity of the diet that should be compared among species, but the abundance and dispersion of food plants in the habitat. A knowledge of the nutritional value of each plant species and plant part would be required since grouse and ptarmigan are selective feeders (Moss et al. 1973). Thirdly, if food is scarce in the habitat of willow ptarmigan, then females that share male vigilance should have lower breeding success than those that do not. I found no differences in survival, clutch size, or date of initiation of laying between females that shared male vigilance and those that did not.

Bradbury (1981) suggested that a key factor in the development of a particular mating system type is the ratio of female to male home range size. If females have very large home ranges, then males would be unable to defend them, and a strategy of self-advertisement rather than resource defence would be favoured for males. This hypothesis may explain the evolution of leks in certain promiscuous species, since females of these species may occupy extensive home ranges in spring (Robel et al. 1970, Wallestad 1975). However, the disparity
between size of home ranges of females and males of other promiscuous species (those in which males are dispersed over the breeding range), appears to be much less marked, and is in some cases close to zero (e.g. spruce grouse: Herzog and Boag 1978; ruffed grouse: Maxson 1978; blue grouse: Hannon et al. 1982). More detailed studies of the dispersion and home range sizes of females in spring are required for most tetraonid species, however, based on the information cited above, Bradbury's hypothesis does not appear to explain why non-lekking promiscuous species are promiscuous.

Females of both monogamous and promiscuous species with dispersed males, appear to be intolerant of other females during spring (Watson and Jenkins 1964, Stirling 1968, MacDonald 1970, Herzog and Boag 1977, Hannon 1980, Chapter One), and some have been described as territorial (Herzog and Boag 1978, Chapter One). If the territory of the male covers the same ground as that of the female, then he is probably restricted to breeding with one female, whereas if he has a separate territory, he may have access to several females with abutting home ranges. Obviously the latter situation would be favourable to males unless some feature of the environment makes at least some vigilance or parental investment by the male necessary to the female's reproductive success. In habitats of monogamous grouse this may be high predation pressure in open environments, or scarcity of food as Wittenberger (1978) suggested, or both. Clearly what is needed is more information on the availability of preferred food and predation pressure in the habitats of
grouse species of different mating system types.

By removing males from a monogamous population of willow ptarmigan I tested whether unshared male vigilance or parental care was essential to female reproductive success and survival. I found that vigilance by males at nests may be important, but otherwise females that share male vigilance do as well as those that do not. However, each female received some assistance from her mate, and thus the experiment did not test whether totally unaided females could survive and produce young. To test fully whether emancipation of the male from vigilance and parental care is possible in habitats of monogamous grouse species, one must remove all but a very few males, so that male investment in each female approaches zero.
CHAPTER FOUR: CONCLUDING REMARKS

All bird species show some form of spacing behaviour. Whether this behaviour can limit population size has been a question that has generated much controversy. Lack (1968) hypothesized that most bird populations are limited through density-dependent mortality of young in the nonbreeding season, primarily through starvation. In this view, territorial behaviour simply serves to space out the the remaining individuals on the breeding area. The opposing view is that, although the final cause of death of juveniles may be starvation, predation, or disease; this mortality is socially induced (Watson and Moss 1970).

There are two ways to distinguish between these hypotheses: 1) Remove territorial birds to determine whether there is a surplus of individuals that have been prevented from breeding; and 2) Add food in winter to increase overwinter survival of juveniles. If extrinsic factors limit population size, then the predicted results of these two experiments are: 1) little or no replacement of removed birds; and 2) an increase in the breeding density. In Chapter Two I listed a number of species in which surplus birds had been identified. These results reject the first prediction. Food has been added in winter to habitats of several passerine populations, with little or no increase in the subsequent breeding density (Krebs 1971, YomTov 1974, Samson and Lewis 1979, Smith et al. 1980). These results are not startling, considering that most population studies are conducted in good habitat, where resources are abundant.
Extrinsic factors may be more important in marginal habitats or at the edge of a species' range. An intermediate view is that changes in extrinsic factors may be sufficient but not necessary, to cause fluctuations in population size and that intrinsic mechanisms operate when extrinsic factors have not reduced juvenile mortality sufficiently (Boag et al. 1979, Watson and Moss 1979).

Most previous studies have not considered the influence of female spacing behaviour on population regulation. They have assumed that numbers of both sexes are regulated in the same way and have emphasized the role of the male. However, since the sexes must invest differentially in the production of young, males and females are expected to have very different mating strategies, and may be affected by the environment in different ways. For males, females may be a limiting resource, and changes in the spacing behaviour of males may be related to the availability of mates. Females, on the other hand, may be more finely attuned to changes in resources, and may alter their home range sizes or density in response to variations in a resource faster than males do (Fordham 1971, Watson and Moss 1980, Taitt 1981). Crowded conditions may also have more immediate and detrimental effects on the reproductive physiology of females (Christian 1971, Myers et al. 1971), which could lower production, or, via maternal effects, cause subsequent variations in spacing behaviour of the young (Watson and Moss 1972). Thus changes in the spacing behaviour of females, and the factors which cause them, may be of more importance in
regulating population size than those in males.

The main contribution of this thesis has been to challenge the existing view that spacing behaviour of males determines numbers of both males and females in a monogamous species. In willow ptarmigan, the number of breeding females may not be limited by the density of males: females can settle and breed successfully at high density despite a substantial reduction in the number of males. The territorial behaviour of females prevents some potential female recruits from settling and breeding, and this may constrain the population to a monogamous mating system. Females may also influence the settlement patterns and density of males by inciting disputes among cocks and altering their territorial boundaries.

Can my results be generalized to other species, or are they specific to monogamous territorial birds? Aggressiveness can affect population size by deferring maturity of juveniles, reducing reproduction in mature animals, increasing juvenile or adult mortality, and increasing dispersal (King 1973). Many studies on promiscuous and polygynous species have indicated that interfemale agonistic behaviour has obvious effects on numbers in the population. For example, aggressive interactions among females in harems or small social groups has increased the mortality of juveniles of low ranking females (e.g. seals: Christian and LeBoeuf 1978, Reiter et al. 1981, McCann 1982; and monkeys: Wilson et al. 1978). Reproduction by subordinate females has been reduced or inhibited completely in birds (Carrick 1963, Crawford 1977), small mammals (Christian 1971,
Myers et al. 1971, Rood 1980), and primate species (Dunbar and Dunbar 1977, Wilson et al. 1978). In microtine rodents, high densities of females have been related to delayed sexual maturation and reduced survival of juveniles (Bujalska 1973, Boonstra 1978, Redfield et al. 1978, Saitoh 1981). Increased mortality of adults denied access to breeding sites has been documented in squirrels (Carl 1971).

On the weight of this accumulating evidence of the importance of interfemale agonistic behaviour in affecting population density, future studies on population regulation should consider female behaviour as an important factor. More work is required to clarify the physiological and environmental factors affecting spacing behaviour in females and to manipulate this behaviour to test hypotheses about its role in determining population density, and its related effects on the development of particular mating system types.
LITERATURE CITED


