National Library of Canada
Bibliothèque nationale du Canada

Canadian Theses Service
Service des thèses canadiennes

Ottawa, Canada
K1A 0N4

NOTICE

The quality of this microform is heavily dependent upon the quality of the original thesis submitted for microfilming. Every effort has been made to ensure the highest quality of reproduction possible.

If pages are missing, contact the university which granted the degree.

Some pages may have indistinct print especially if the original pages were typed with a poor typewriter ribbon or if the university sent us an inferior photocopy.

Previously copyrighted materials (journal articles, published tests, etc.) are not filmed.

Reproduction in full or in part of this microform is governed by the Canadian Copyright Act, R.S.C. 1970, c. C-30.

AVIS

La qualité de cette microforme dépend grandement de la qualité de la thèse soumise au microfilmage. Nous avons tout fait pour assurer une qualité supérieure de reproduction.

S'il manque des pages, veuillez communiquer avec l'université qui a conféré le grade.

La qualité d'impression de certaines pages peut laisser à désirer, surtout si les pages originales ont été dactylographiées à l'aide d'un ruban usé ou si l'université nous a fait parvenir une photocopie de qualité inférieure.

Les documents qui font déjà l'objet d'un droit d'auteur (articles de revue, tests publiés, etc.) ne sont pas microfilmés.

La reproduction, même partielle, de cette microforme est soumise à la Loi canadienne sur le droit d'auteur, SRC 1970, c. C-30.

NL-339 (r. 88/04)

Canada

THE UNIVERSITY OF ALBERTA

TERRITORY SELECTION AND SITE FIDELITY IN WILLOW PTARMIGAN: THE IMPORTANCE OF QUALITY AND FAMILIARITY WITH TERRITORY AND PARTNER

by

JIM SCHIECK

A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH
IN PARTIAL FULFILMENT OF THE REQUIREMENTS FOR THE DEGREE
OF DOCTOR OF PHILOSOPHY

DEPARTMENT OF ZOOLOGY

EDMONTON, ALBERTA

FALL 1988

ISBN 0-315-45447-4

THE UNIVERSITY OF ALBERTA

RELEASE FORM

NAME OF AUTHOR JIM SCHIECK

TITLE OF THESIS TERRITORY SELECTION AND SITE FIDELITY IN WILLOW PTARMIGAN: THE IMPORTANCE OF QUALITY AND FAMILIARITY WITH TERRITORY AND PARTNER

DEGREE FOR WHICH THESIS WAS PRESENTED DOCTOR OF PHILOSOPHY

YEAR THIS DEGREE GRANTED FALL 1988

Permission is hereby granted to THE UNIVERSITY OF ALBERTA LIBRARY to reproduce single copies of this thesis and to lend or sell such copies for private, scholarly or scientific research purposes only.

The author reserves other publication rights, and neither the thesis nor extensive extracts from it may be printed or otherwise reproduced without the author's written permission.

(SIGNED) Jim Schieck

PERMANENT ADDRESS:

770 Cardiff
Sarnia Ontario
N3B 4N8

DATED Oct 14 1988

THE UNIVERSITY OF ALBERTA

FACULTY OF GRADUATE STUDIES AND RESEARCH

The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research, for acceptance, a thesis entitled TERRITORY SELECTION AND SITE FIDELITY IN WILLOW PTARMIGAN: THE IMPORTANCE OF QUALITY AND FAMILIARITY WITH TERRITORY AND PARTNER submitted by JIM SCHIECK in partial fulfilment of the requirements for the degree of DOCTOR OF PHILOSOPHY.

Supervisor

John R Spence

Jan O. Murie

External Examiner

Date Sept 26, 1988

ABSTRACT

I evaluated some factors that may influence settlement and site fidelity to breeding territories of willow ptarmigan. Yearling males did not settle on territories of older males that returned. They, however, had opportunities to get territories of similar quality to those obtained by older males. Yearling females settled at times similar to older females with non-returning partners but later than older females with partners that returned. The first yearling females to settle did not survive better or, have higher reproductive success than those settling later. In addition, choice of territory and partner by yearling females were not consistent among sets of females having the same suite of territories to choose from.

Males that had bred in previous years almost always returned to their previous territory. If a female's previous partner returned she usually settled on her previous territory; if her previous partner did not return she usually paired with a previous neighbor. Those patterns may have been maintained through reproductive advantages of breeding with familiar partners; individuals breeding with a familiar partner had higher reproductive success and produced higher quality chicks than individuals breeding with an unfamiliar partner. Breeding on familiar areas did not appear to influence reproductive success. Although males and females switched territories following low reproductive success, they did not have higher reproductive success or produce higher quality chicks after than before they moved or than the pairs on their former territories.

After controlling for differences among years, age classes and individuals pairing with familiar partners, an individual's reproductive success one year was not related to its previous reproductive success. Some territories, however, consistently had pairs with earlier dates of first egg and relatively larger clutches. This difference among territories may not have been detectable at the time willow ptarmigan settled. In this population familiarity with partners appeared to

influence choice of breeding situation more than differences among quality of breeding situations.

ACKNOWLEDGEMENTS

I thank Val Loewen, Rob Florkiewicz, Tracy Sorochan, Rogier Gruys, Pat O'Reilly, Don McKinnon, Pam Johnston, Jon Swenson, Don Schieck, Bruce McKay and Jeannette Schieck for their the assistance with the data collection. I am especially indebted to the Gila Dog for finding the birds that I could not. Susan Hannon and Kathy Martin allowed me to use information they collected on willow ptarmigan on and near the study area. Dave Mossop provided logistical support and a place to stay while I was in Whitehorse. The research was supported by grants from NSERC, the Boreal Institute of North America, the Arctic Institute of North America and University of Alberta Equipment Grants.

My supervisor Susan Hannon and colleague Kathy Martin spent many hours discussing and reviewing the ideas I dreamed up during the past four years. My advisors Jan Murie, David Boag and John Spence provided valuable comments on these ideas after they had become a bit more refined. Susan Hannon, Kathy Martin, Jan Murie and Peter Dunn reviewed earlier drafts of the thesis.

Finally I thank the students, faculty and staff of the Department of Zoology for providing an enjoyable atmosphere in which to study ecology.

Table of Contents

LIST OF TABLES

LIST OF TABLES cont.

LIST OF TABLES cont.

LIST OF FIGURES

I. GENERAL INTRODUCTION

Most species of north-temperate and arctic birds are migratory. Each spring individuals must establish or re-establish if they bred in previous years, a breeding territory. Orians (1969) and Fretwell and Lucas (1970) proposed that individuals choose among potential areas and settle in a manner that maximizes their survival and reproductive success. This is an intuitively appealing hypothesis and, with support from studies on mating systems (Garson et al. 1981) and settlement patterns (Searcy and Yasukawa 1981, Wittenberger 1981, Greenwood and Harvey 1982, Blancher and Robertson 1985, Gottlander 1987), has become widely accepted. However, settlement may be more complex than suggested by Fretwell and Lucas (1970). First-time breeders may be excluded from the best areas and/or partners by previous breeders (Korpimaki 1988) although they should settle in a manner that maximizes their reproductive success under the constraints imposed. In populations where all areas and partners are of similar quality, individuals may not be able to make effective choices; here they may settle randomly or simply return to previous areas (Eliason 1986, Wootton et al. 1986, Freed 1987, Lightbody and Weatherhead 1987, Leonard and Picman 1988). Time of arrival and spacing behavior may greatly influence settlement in such populations.

If characteristics of the breeding situation (e.g. territory and mate; Wittenberger 1976) influence seasonal reproductive success (hereafter called reproductive success), individuals should attempt to choose good situations. Dates on which territories are occupied or density of pairs in an area are correlated with characteristics of the habitat and partner in some studies (Andersson 1982, Siegel-Causey and Hunt 1986, Belles-Isles and Picman 1986, Eliason 1986, Nagata 1986, Yasukawa and Searcy 1986, Clark and Weatherhead 1987, Gottlander 1987, Leonard and Picman 1987, Powers 1987, Probst and Hayes 1987) but not in others (Weatherhead and Robertson 1977, Bedard and LaPointe 1984, Searcy et al.

1985, Bowman and Bird 1986, Wootton et al. 1986, Freed 1987, Gauthier 1987, Lightbody and Weatherhead 1987). The influence of characteristics of habitat and partner may have been overlooked in these latter studies; many variables may influence the quality of breeding situations and it is impossible to investigate them all.

Assuming that differences exist among breeding situations, indirect methods may be used to evaluate whether individuals choose situations that maximize their reproductive success. The first individuals to settle should choose the best situations and have higher reproductive success than individuals settling later. In addition, if individuals are breeding in relatively poor situations they should switch to better situations before breeding again. Results consistent with both these predictions have been found. Garson et al. (1981), Alatalo et al. (1984), and Siegel-Causey and Hunt (1986) found that the first individuals to arrive at the breeding area chose territories where subsequent reproductive success was the greatest. Age effects may have confounded these analyses (Korpimaki 1988) because previous breeders often arrived earlier than first-time breeders (Eliason 1986, Frances and Cooke 1986). Consistent with the second prediction, individuals with relatively low reproductive success had a higher probability of switching territories between breeding seasons, than individuals with relatively high reproductive success (MacDonald 1977, Freer 1979, Hilden 1979, Lawn 1982, Redmond and Jenni 1982, Oring and Lank 1982, Dow and Fredga 1983, Oring et al. 1983, Skeel 1983, Harvey et al. 1984b, Shields 1984, Gratto et al. 1985, Eliason 1986, Weatherhead and Boak 1986, Gavin and Bollinger 1988). Whether they moved to better areas, however, usually was not evaluated.

In some populations individuals may have opted to return to areas where they were known to their neighbors, regardless of their previous reproductive success, because territory acquisition was less costly in those areas (Yasukawa 1979, Lawn 1982, Eliason 1986, Robinson 1986, Picman 1987, Stamps 1987). For example, in blue grouse (Dendragapus obscurus; Lewis and Zwickel 1981) and painted buntings (Passerina ciris; Lanyon and Thompson 1986) males usually returned to their previous territories even though territories where expected reproductive success was higher were vacant and being settled by first-time breeders. The lower cost of returning to a familiar territory may have increased survival and more than compensated for the reproductive benefits lost by not moving.

Familiarity with area and/or partner also may increase the relative value of a breeding situation. Individuals familiar with their breeding area may spend less time searching for resources and refuges and have more time and energy to produce offspring than if they were on unfamiliar areas (Greenwood and Harvey 1982). Individuals that paired together previously may spend less time courting and thus have more time and energy to produce offspring (Rowley 1983, Gratto et al. 1985, but see Cooke et al. 1981, Cuthbert 1985). Familiarity between partners often will be confounded by familiarity with territories because breeding site fidelity is high in many species of birds (Greenwood and Harvey 1982). These relationships may be further complicated if reproductive success is related to age since first-time breeders (young individuals) cannot return to previous partners or breeding territories whereas older individuals can.

The overall aim of my research was to evaluate the factors that influenced settlement and site fidelity in a population of willow ptarmigan (Lagopus lagopus alexandrae) at Chilkat Pass, northwestern British Columbia. I analyzed settlement for each age-sex group separately because the relative importance of these factors may have differed between the sexes and between first-time and previous breeders. This population was well suited for a study on settlement patterns: boundaries of a territory could be determined accurately in a few hours, information could be obtained for 60 to 80 pairs each year, all individuals could be caught and marked, reproductive success could be determined, and information was available from previous years for many individuals.

In Chapter II I evaluated settlement of first-time breeders (yearling individuals). Settlement should not have been affected by familiarity with area, partner or neighbors for these individuals because all chicks moved from their natal territory (Martin and Hannon 1987). Consequently, they should have chosen territories based on values of the breeding situations, although they may have been constrained by individuals that settled earlier. I assessed whether yearling individuals were excluded from some territories or partners by older individuals. In addition, I assessed whether the females that settled early acquired better situations (had better survival or higher reproductive success) than those that settled later. Lastly, I allowed two sets of yearling females to settle on the same suite of territories and determined whether breeding situations were chosen in a consistent manner. In Chapter III I documented the patterns of site fidelity and territory switching for individuals that had bred previously and evaluated whether these patterns resulted in individuals selecting territories and partners that maximized their survival and reproductive success. Results from Chapters II and III indicated that individuals were either not choosing territories and partners that maximized their reproductive success, or t there were no differences among territories and partners. In Chapter IV I examined the latter alternative by determining the amount of the variance in reproductive success that was due to differences among males, females and territories.

A. NATURAL HISTORY

As background information I have presented a short summary of territory occupancy by willow ptarmigan at Chilkat Pass. Additional information on willow ptarmigan in this area can be found in Hannon (1982) and Mossop (1988).

Willow ptarmigan breed in the subalpine zone of Chilkat Pass (northwestern British Columbia, Canada; 59° 50' N, 136° 35' W; elevation 890 m). This zone is approximately 25 km long and from 2 to 8 km wide, with numerous small creeks, ponds and wet meadows scattered throughout. During the winter, between one and three meters of snow accumulates on the valley floor. Snow-pack usually melts by late May and the valley floor usually remains free of snow until mid October. The dominant shrubs, willow (Salix spp.) and dwarf birch (Betula glandulosa) are between one and four meters tall.

Although, a few willow ptarmigan were present on, or near, the study area throughout the winter; most individuals moved to areas with taller and denser vegetation (Mossop 1988, Hannon and Gruys in press). Flocks, composed predominately of males, returned to the breeding area in late March and early April. These flocks broke up on calm days and lone or small groups of males roosted throughout the breeding area. During 1986 and 1987 the study area was searched regularly for willow ptarmigan prior to males becoming territorial. In those years males started defending territories near the end of April and 139 of 142 males began defending territories, with stable boundaries, within one day of each other. Thus, either males established territories within a day or they established them prior to actively defending them. During the month prior to males defending territories 128 of 142 males were observed on their eventual territory at least once, and one male was observed on his eventual territory on 14 occasions. Thus, some males spent considerable time on their territory before actively defending them.

Although approximately 10% of the willow ptarmigan present on the study area during March and early April were females, most females did not return from their wintering areas until late April. At this time hens, alone or in small groups, moved from territory to territory. Approximately 75% of the females settled by mid May and all settled by mid June in 1986 and 1987, the years when settlement was recorded accurately. Between 1979 and 1987, 259 of 356 males (73%) had one female settle on their territory, 32 males (9%) had two females settle, 1 male (0.3%) had three females settle and 65 males (18%) had no females settle on their territory. After settling, females interacted aggressively with other females intruding on their territory.

Egg laying started in late May. If the clutch was preyed upon during laying or incubation a second clutch was sometimes laid and 2 of 17 females that lost their second clutch to predators laid a third clutch. One hundred and fifty-two of 170 pairs had their first nests on their territory, the other 18 nests were 5 to 40 m inside neighboring territories. Clutches were incubated by females, and males roosted approximately 40 m (range 5 to 180 m) away. Most broods hatched in late June or early July but some broods from replacement clutches hatched in late July (Hannon et al. 1988). Usually, the male and female remained with their brood until flocks formed in late August.

Overall, males established territories two or three weeks earlier than females. Both males and females restricted their activities to their territory for the two or three weeks prior to laying, during laying and during incubation. Unpaired males often left their territory once hens started laying on other territories. Pairs that lost their clutches and did not produce a second clutch, remained on their territory for two to three weeks after losing their clutches.

Some broods left their territory within hours of the last chick hatching and more than 25% of the broods moved off their natal territory during the first week after hatch. The probability of broods being found on their natal territory decreased and the mean distance from their territory increased with time since hatching. Some flocks (young plus adults from two or more broods) remained on the breeding area until approximately one meter of snow accumulated on the ground (Mossop 1988). After that most individuals moved 2 to 20 km to areas with taller and denser vegetation for the winter (Mossop 1988).

Intrasexual aggression by willow ptarmigan at Chilkat Pass was most common during the prelaying and laying periods. Territories probably influenced reproductive success and/or survival for both sexes; both males and females actively defended territories (Hannon 1983). The most probable functions of territories for willow ptarmigan are to secure food (Lance 1978b, Miller and Watson 1978 but see Steen et al. 1985), secure mates (Miller and Watson 1978, Pedersen 1984) or decrease predation by increasing inter-individual spacing (Hannon 1983).

II. TERRITORY AND MATE SELECTION BY YEARLING WILLOW PTARMIGAN: ARE DIFFERENCES AMONG BREEDING SITUATIONS IMPORTANT ?

A. INTRODUCTION

A fundamental assumption of habitat selection models is that individuals choose breeding situations (territories and mates, Wittenberger 1976) that maximize their survival and/or and reproductive success (Orians 1969, Fretwell and Lucas 1970). Pleszczynska and Hansell (1980) found female lark buntings (Calamospiza melanocorys) to chose sites that maximize their reproductive success and Siegel-Causey and Hunt (1986) found that the first double-crested cormorants (Phalacrocorax auritus) to arrive on the breeding area chose sites where reproductive success was the highest. For most species, however, evidence for the assumption was weak and indirect; individuals that switched territories between years had lower reproductive success prior to switching than individuals that did not switch territories (Dow and Fredga 1983, Oring et al. 1983, Skeel 1983, Harvey et al. 1984b, Shields 1984, Gratto et al. 1985, Gavin and Bollinger 1988, but see Bedard and LaPointe 1984), although in these studies not all individuals switched territories following low reproductive success. Bowman and Bird (1986) and Lanyon and Thompson (1986) found that the first individuals to settle did not have the highest reproductive success; factors other than expected reproductive success may influence settlement in these populations. Knowledge of refuges may increase survival (Greenwood and Harvey 1982) and familiarity with neighbors may decrease the cost of acquiring a territory (Yasukawa 1979). The resulting benefits from those factors may more than offset any increase in annual reproductive success that would occur if the individual move to a better breeding situation.

For species in which individuals are migratory and have low natal philopatry, most first-time breeders are not familiar with any territory, partner or neighbors. Consequently, familiarity will not influence settlement for most first-time breeders and they should attempt to choose the best breeding situations that are available. Some territories may be occupied by older individuals because they return and establish territories before first-time breeders (Lack 1968, Bedard and LaPointe 1984, Eliason 1986, Frances and Cooke 1986). In addition, previous breeders may be dominant and exclude yearlings from choice areas (Lanyon and Thompson 1986, Walton and Nolan 1986). If previous breeders chose breeding situations with the highest potential for reproduction (Yasukawa and Searcy 1986, Gavin and Bollinger 1988), only relatively poor situations may be available for first-time breeders (Rippin and Boag 1974, but see Lewis and Zwickel 1981). Those yearlings that arrive first may settle in the best breeding situations and those arriving later may have only marginal habitat available (Fretwell and Lucas 1970, Siegel-Causey and Hunt 1986). Thus, some reproductively mature yearlings may forgo breeding until relatively good situations become available (Lewis and Zwickel 1981, Jamieson and Zwickel 1983) or they are able to evict a territory owner (Arcese 1987, Eckert and Weatherhead 1987b).

In this Chapter I determined whether older willow ptarmigan settled earlier and/or evicted yearlings. I predicted that if yearlings were not excluded from the best areas they would have 1) had territories of similar size, 2) survived as well, 3) had similar reproductive success and 4) produced chicks of similar quality to older individuals. Differences between yearling and older individuals may be due to yearlings being excluded from the best territories, although they could also be due to older individuals being more efficient at producing offspring. I also predicted that the first yearlings to settle would have chosen the best breeding situations and thus potentially have survived better, have had higher reproductive success or produced chicks of higher quality than those yearlings settling later. Yearlings that settled relatively late may have had poorer success simply because they had less time to acquire the resources needed for survival or reproduction. However, if these relationships were not present then the first yearlings to settle were not choosing better breeding situations than those settling later. Lastly, I manipulated settlement so two sets of yearling females settled on the same suite of territories. If some breeding situations were better than others, I expected territories to have been chosen in the same order by both sets of yearlings.

B. METHODS

Between 1985 and 1987 all willow ptarmigan on a 3 km^2 area were captured using either noosing poles (Zwickel and Bendell 1967) or nets (Hannon 1983). Unique combinations of a numbered aluminum and three colored plastic leg bands were attached to all individuals when first captured. Sex was determined using wing length, height of comb and plumage coloration (Hannon and Roland 1984) and age was classified as yearling or older based on the amount of pigmentation on the eighth and ninth primaries (Bergerud et al. 1963). Each time an individual was seen, its location was recorded in relation to permanent grid markers, spaced 100 m apart, placed throughout the study area.

Many individuals that bred on or near the study area between 1979 and 1984 were marked as part of a previous study (Hannon 1983, 1984, Hannon and Roland 1984, Hannon and Smith 1984). In addition, willow ptarmigan near the study area were marked and followed as part of two other concurrent studies between 1985 and 1987. Where applicable, I have used information from those studies to supplement the information I collected.

Territorial boundaries were determined between mid April and late May using sightings of birds, boundary disputes and territorial calls (after Hannon 1984). Most territories were contiguous and males often displayed, fought and called at the boundaries. A few boundaries changed position by up to 20 m from day to day (these shifts changed territory size by less than 10%). In those cases, the boundary was assumed to be the middle of the zone of overlap. Territories bordering two large meadows, on which willow ptarmigan were seldom observed, were assumed to extend 50 m into the meadow. If a territorial male died or disappeared during spring the boundaries of surrounding territories were re-determined.

In 1986 and 1987 territories were searched at least once every fourth day, usually every second day, between the arrival of females and the start of incubation. Patterns of molt were used to identify unbanded individuals. Females were classified as settled if they were present on the territory for three days and were assumed to have settled mid-way between the searches when they were not seen and first seen. Dates of female settlement were not determined during 1985 because territories were not searched as frequently that year. Nine females (5%) moved after being classified as settled, and their settlement date was taken as the time they settled on the territory on which they nested. Subsequent to settling, hens were captured and equipped with a radio-transmitter. Disturbance and radio-telemetry may have slightly increased predation on clutches (Appendix 1), but this should not bias my conclusions because I evaluated differences between groups of individuals and most of the females in all groups had transmitters.

Mating status of each male (paired versus unpaired) was determined. Nests were found using radio-telemetry, with the aid of pointing dogs, or by searching around roosts of males. Reproductive success was higher for first than for subsequent nesting attempts in the same year (Martin et al. in press.). To have data that were comparable among pairs, measures from first nesting attempts were compared. Clutch size at the start of incubation and number of chicks that left the nest were determined by flushing the female from her nest at the start of incubation and counting hatched eggs, respectively. Brood sizes and post-hatch locations of broods were determined at least once every fourth day, until mid

September, during 1985. Due to problems with capturing females after their chicks could fly, transmitters were removed from females on the day their brood hatched in 1986 and 1987. In those years broods were located subsequently by searching with the help of pointing dogs. Number of chicks that fledged (number of flying chicks alive 15 to 25 days post hatch) was determined. Fledge counts were used only if they were consistent or were obtained in an area where chicks could be observed easily.

Sample size was larger for the clutch size analyses than for analyses involving number of chicks that hatched or fledged because of clutch loss. In addition, differences among groups in the number of chicks that hatched and the number of chicks that fledged reflected the differences in clutch sizes. Throughout the thesis I have presented data on clutch size for first nests. For completeness, the comparisons involving clutch size at hatch, number of chicks hatching and number of chicks fledging were given in Appendix 2. Recruitment of chicks to the breeding population was not analyzed because natal philopatry was low (all chicks moved from their natal territory, Martin and Hannon 1987); young that disappeared may have dispersed and recruited elsewhere. Two measures of seasonal reproductive success were analyzed: 1) whether or not the individual had any chicks hatch during the season and 2) the number of fledged chicks that an individual produced during the season.

The probability of chicks surviving to reproductive maturity and acquiring a breeding territory may differ among broods. Chicks produced earlier may have a higher probability of recruiting (Dhondt and Huble 1968, Arcese 1987, Martin and Hannon 1987). In addition, heavier chicks may become dominant as adults (Roskaft 1983, Murphy 1985) and/or survive better (Moss et al. 1981, but see Martin and Hannon 1987), especially, during adverse weather conditions (Middleton 1982). I analysed two potential measures of chick quality: 1) date of first egg (date the first egg of the clutch was laid) and 2) chick weight (mean body mass at hatch for chicks from the brood).

Date of first egg was calculated by back-dating from the date the clutch or brood was found using parameters estimated from this population (Appendix 3). Hens with nests found prior to incubation were assumed to have laid one egg every 1.1 days. Dates of first egg for clutches found between the first and twelfth day of incubation were estimated as the date the clutch was found minus the number of days it had been incubated minus the clutch size. Up to day twelve of incubation, the number of days a clutch had been incubated could be determined by floating the eggs in water (Westerkov 1956). If a nest was found after the twelfth day of incubation, date of first egg was estimated as date of hatch minus 22 days minus clutch size. Finally, if a nest was not found but chicks from a brood were caught before they were ten days old, date of first egg was estimated as the date the chicks were caught minus the age of the chicks minus 29 days. Age of chicks could be determined for up to nine days after hatch using wing length (Hannon, unpublished data).

Breeding individuals were defined as surviving if they were observed in a subsequent year. This measure was confounded by dispersal, but of the breeding individuals known to have moved, only 8% (Chapter III, Figure III-1) moved more than one territory between years and an area, at least one territory wide, around the study area was searched each spring. In addition the identities of birds in flocks near the study area were recorded each spring.

Territory size, date on which female settled, survival of adults, mating status, reproductive success and quality of chicks produced differed among years (Appendix 4, Hannon et al. 1988). Therefore, I standardized data for variation among years (grand mean minus yearly mean was added to all values for a year; Perrins and Jones 1974). It was not possible to standardize categorical variables for year effects and sample sizes were not large enough to include year effects in the contingency analyses. As a consequence of data being combined among years interactions between year effects and other factors could not be analysed.

Clutch size was related to date of first egg and chick weight was related to both clutch size and date of first egg. Thus, analyses of covariance (ANCOVA) were used to evaluate differences in clutch sizes over and above that due to date of first egg (date of first egg was the covariate) and for differences in chick weights over and above that due to clutch size and date of first egg (clutch size and date of first egg were covariates). These variables have been renamed, relative clutch size and relative chick weight, to reflect the relative nature of these analyses. There were no interactions between the factors and covariate(s) in any of the analyses.

I included males and females as separate factors when evaluating whether older individuals fared better than yearlings. Unique sums of squares (Norusis 1986) were used because these ANCOVAs and ANOVAs were not balanced. For categorical variables 3-way contingency analyses were used. Individuals with familiar partners were not included in these analyses because familiarity with partner may have confounded the differences among age classes (Chapter III). Sample size constraints precluded excluding pairs on familiar territories; that should not confound the comparisons because pairs on familiar and unfamiliar territories had similar success (Chapter III).

In analyses in which the independent variable was continuous (date of first egg or territory size) slightly different analytical techniques were used. Date female settled, seasonal fledging success, and date of first egg were analysed using simple linear regression. Relative clutch size and relative chick weight were analysed using residual analyses (Atchley et al. 1976). Age of partner, female survival, total clutch loss and the probability of producing chicks in the season were analysed using logistic regression (Dixon 1983).

I chose to test for significance only when sample sizes of the groups were greater than five for the ANOVAs and ANCOVAs and the lowest row or column total was greater than five for contingency analyses. Means were presented ± one standard deviation. I judged relationships as significant if the probability of occurrence by chance was less than 0.05. Sample sizes differed among tests because some data were missing.

Manipulation Of Settlement For Yearling Females

During 1987 yearling females were allowed to settle on a group of 30 territories where females that had bred there previously had been removed (captured and held in cages or shot) when first sighted. Starting 23 April territories were searched systematically to determine when yearling females settled. In this experiment a female was classified as "settled" if her mate followed her around, it was difficult to chase her from the territory and she returned shortly after being chased away. Mid-way through the period when females were settling on other areas (3 May), all yearling females that had settled on the experimental area were removed. Another set of yearling females allowed to settle 4 May to 12 May. This created two periods where the same suite of territories and males were available for yearling females.

C. RESULTS

Are Yearlings Being Excluded From The Best Areas ?

Males - Both yearling and older males were present on the breeding area prior to territories being defended. Thirty-three of 36 yearling males became territorial at the same time as older males, but three established territories approximately two weeks later. Breeding site fidelity was high for returning males (Chapter III), so yearlings were restricted usually to the area previously occupied by males that died; 32 yearling males settled on territories of non-returning males and 4 yearling males inserted between the territories of returning males. Territories may have been selected prior to the active defense of them (some territorial vocalizations were heard in late fall and early spring) and older males may have had an advantage at this time.

Yearling males had a lower probability of acquiring a partner than older males ($\underline{X}^2=47.1$, $\underline{df}=1$, $\underline{P}<.01$; 64% of 143 yearling and 93% of 208 older males were paired). None of the yearling males that established a territory by inserting between the territories of returning males acquired a partner. Yearling males that acquired partners had similar survival, similar reproductive success and produced chicks of similar quality to older males (Table II-1A and II-1B). Thus, the only difference between the success of older and yearling males was that many yearlings did not acquire a partner.

Size of territory was positively related to the number of females settling on it (oneway ANOVA $\underline{F}=18.7$, $\underline{P}<.01$; unpaired, monogamous and bigamous males had territories of 3.8±2.0, $\underline{N}=43$, 4.6±2.3, $\underline{N}=181$ and 6.2±2.0, $\underline{N}=25$ ha, respectively). Survival, reproductive success and quality of chicks produced were not related to territory size (Table II-2; polygamous females were assumed to divide their male's territory equally). Possibly, if females had settled on very small territories, the ones not selected, they would have had lower survival, lower reproductive success or produced lower quality chicks. An alternative explanation for there being a relationship between a male's mating status and his territory size, was that a male's quality was reflected in both. However, males that did and did not acquire partners had similar survival between years ($\underline{X}^2=1.8$, $\underline{df}=1$, $\underline{P}=.18$; 170 of 284 males (60%) that acquired a partner and 31 of 59 males (53%) that did not acquire a partner survived to the next year) and all unpaired males acquired partners the following year. Therefore, if unpaired males or their territories were of relatively low quality their quality increased between

Table II-1A. Date female settled, survival, reproductive success, and quality of chicks produced for pair-age categories of willow ptarmigan. Means (standardized for year effects) ± SD are presented for continuous variables, percentages are presented for categorical variables. Sample sizes are in parentheses.

	Pair-age Categories [a]			
males: females:	yrl yrl	old yrl	yrl old	old old
Date Female Settled (May)	7.3±9.3 (21)	8.6±12.0 (35)	9.9±5.9 (41)	7.8±18.0 (19)
Male Survival (%)	59 (56)	56 (57)	64 (14)	48 (23)
Female Survival (%)	55 (86)	48 (87)	47 (36)	43 (37)
Reproductive Success				
Relative Clutch Size	7.7±1.1 (60)	8.0±1.2 (71)	8.5±1.0 (17)	8.2±1.1 (43)
Total Clutch Loss (%)	52 (60)	48 (79)	52 (21)	49 (49)
Produce Chicks In Season (%)	80 (95)	76 (114)	90 (40)	73 (56)
Season Fledging Success	4.6±1.8 (34)	4.5±2.1 (51)	5.1±2.3 (12)	4.5±2.5 (18)
Chick Quality				
Date Of First Egg (June)	3.6±3.5 (99)	3.8±4.1 (112)	3.1±2.9 (38)	3.9±4.2 (103)
Relative Chick Weight	14.4±0.9 (19)	14.6±1.0 (35)	14.8±0.6 (9)	14.6±1.0 (27)

a - yrl=yearling, old=older

Table II-1B. Tests of differences between pair age categories of willow ptarmigan for date female settled, survival, reproductive success, and quality of chicks produced. Two factors were used in the analyses; male age and female age.

	Effect Of Male Age On		Effect Of Female Age On		Interaction Between Male Age And Female Age [a]	
	F/X^2 [b]	P	F/X^2	P	F/X^2	P
Date Female Settled	0.2	.64	0.0	.99	0.7	.41
Male Survival	0.2 [c]	.68	0.2	.67	0.0	.84
Female Survival	0.8	.37	0.8	.37	0.1	.81
Reproductive Success						
Relative Clutch Size [d]	0.5	.47	7.7	.01	1.7	.20
Total Clutch Loss	0.2	.63	0.0	.96	0.2	.70
Produce Chicks In Season	0.9	.33	0.2	.66	0.2	.65
Season Fledging Success	0.0	.95	0.7	.41	0.0	.99
Chick Quality						
Date Of First Egg	0.2	.64	0.0	.98	0.0	.97
Relative Chick Weight [e]	0.0	.88	1.2	.28	0.8	.37

a - for contingency analyses the test for the three-way interaction is reported
b - F is reported for ANOVAs or ANCOVASs, X^2 is reported for contingency analyses
c - unpaired territorial males are included in this analysis
d - date of first egg is used as a covariate in this analysis
e - two covariates are used in this analysis: date of first egg and clutch size

Table II-2. Date female settled, survival, reproductive success and quality of chicks produced in relation to size of territory for female willow ptarmigan. Continuous and categorical variables were analysed using least suares and logistic regression analyses, respectively.

	Relationship With Territory Size		Regression Coefficient	Sample Size
	F/X² [a]	P		
Date Female Settled	0.0	.91	0.07	84
Female Survival	0.0	.92	NA	158
Reproductive Success				
Relative Clutch Size [b]	3.8	.05	0.07	140
Total Clutch Loss	0.1	.78	NA	194
Produce Chicks In Season	0.7	.40	NA	222
Season Fledging Success	0.8	.38	0.10	74
Chick Quality				
Date Of First Egg	1.2	.28	0.17	181
Relative Chick Weight [c]	2.0	.16	-0.76	71

NA - not applicable

a - F is reported for least squares regressions, X² is reported for logistic regressions

b - date of first egg was used as a covariate in this analysis

c - two covariates were used in this analysis: date of first egg and clutch size

years. Possibly, males fared better because the size of their territory increased between years (Chapter III).

Females - When they first arrived in the spring, females foraged, roosted and were courted by males on many different territories. The date that females settled was similar for yearling and older females (Table II-1A and II-1B). There was no evidence of females being evicted after they had settled by later arriving females; the nine females that moved subsequent to settling did so at least two days before another female settled on that territory. Thus yearling females had the potential to get breeding situations that were as good as those obtained by older females with non-returning partners. Females that paired with their previous partner, however, settled earlier than other females (Chapter III) and always returned to their previous territory.

Yearling females settled on territories of similar size, survived as well, had similar reproductive success and produced chicks of similar quality to older females, except that older females had clutches with 0.5 more eggs (Table II-1A and II-1B). The larger clutches of older females translated into 0.4 more chicks and 1.1 more fledglings (Appendix 2). Yearling females had potential to get breeding situations of similar quality to those obtained by older females. Possibly, however, they were less able to discriminate among qualities of breeding situations than older females and thus made poorer choices or alternatively, older females were more efficient at producing offspring.

Choice Of Breeding Situation By Yearling Females

These analyses were done for females only because I was not able to document the order of settlement for males; most males started defending their territories on the same day. Yearling females settled between 26 April and 7 June. Age of partner, female survival, reproductive success and quality of chicks produced were not related to the date yearling females settled (Table II-3). Thus, yearling females that settled early did not acquire better breeding situations than those settling later.

Eleven older males, 10 yearling males and 9 males of unknown age had territories on the experimental area in 1987. Males of unknown age probably were yearlings because all the males on this area during 1986 were banded and males seldom switched territories (Chapter III). Fifteen females that bred on the area during 1986 returned during late April 1987 and were removed. Twenty-two yearling females were on the experimental area and were removed at the end of the first period. Fifteen of these 22 females were classified as settled. The other 7 were not included in the analyses but were removed because they may have selected a territory even though they were not acting territorially. This would have biased the order territories were selected during the second period. Fourteen yearling females settled during the second period.

Approximately half of the territories on which females settled during the first period were chosen again during the second period (Table II-4, Figure II-1). This was not different than that expected if a maximum of one female settled on a territory and females chose territories at random ($X^2=0.0$, $df=1$, $P=1.0$). The rank order that territories were chosen was not correlated between the two periods ($T=-.33$, $N=7$, $P=.38$; Kendall's rank correlation).

Females did not settle with older males preferentially to yearling males (first period $X^2=0.1$, $df=1$, $P=.82$; second period $X^2=1.2$, $df=1$, $P=.27$) or territories on the edge of the study area preferentially to central territories (first period $X^2=0.6$, $df=1$, $P=.35$; second period $X^2=0.1$, $df=1$, $P=.80$). In addition, they did not choose large territories first (first period $T=0.28$, $N=15$, $P=.19$, second period $T=-0.08$, $N=15$, $P=.75$; Kendall's rank correlation between territory size and rank order females settled for that period). Only territories with accurate boundaries were included in this analysis.

Table II-3. Age of partner, survival of female, reproductive success [illegible] quality of chicks produced in relation to the date yearling female willow ptarmigan settled. Continuous and categorical variables were analysed using least squares and logistic regression analyses, respectively.

	Relationship With Settling Date		Regression Coefficient	Sample Size
	F/X^2 [a]	P		
Age Of Partner	0.2	.64	NA	56
Female Survival	0.1	.78	NA	40
Reproductive Success				
Relative Clutch Size [b]	0.0	.33	0.01	48
Total Clutch Loss	0.2	.70	NA	55
Produce Chicks In Season	0.0	.87	NA	55
Season Fledging Success	0.3	.62	0.04	14
Chick Quality				
Date Of First Egg	0.8	.37	0.04	55
Relative Chick Weight [c]	0.0	.87	0.03	27

NA - not applicable

a - F is reported for least squares regressions, X^2 is reported for logistic regressions

b - date of first egg was used as a covariate in this analysis

c - two covariates were used in this analysis: date of first egg and clutch size

Table II-4. The number of territories on which yearling female willow ptarmigan settled during the first and/or second period of the experiment, 1987. The number expected for each category, if a maximum of one female settled on each territory and females were choosing territories randomly, is given in parentheses.

		First Period	
		A Female Settled	A Female Did Not Settle
Second Period	A Female Settled	7 (7)	7 (7)
	A Female Did Not Settle	8 (8)	8 (8)

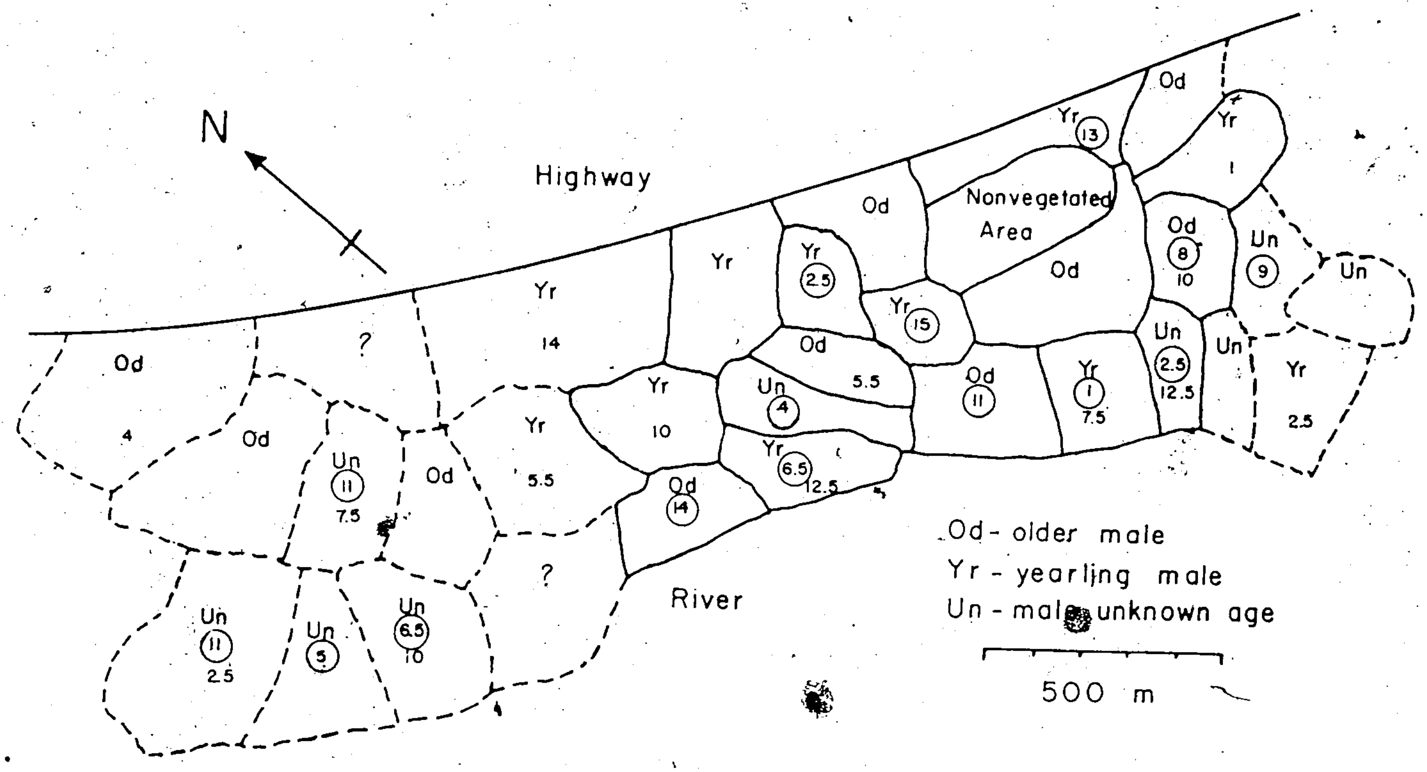

Figure II-1. The order yearling female willow ptarmigan settled during the first (ranks are circled) and second (ranks are not circled) periods of the experiment in 1987. Females settling on the same day are assigned tied rankings. Solid and dashed lines represent known and approximate territorial boundaries, respectively. ? are in areas where the mating status of the territorial male is not known.

D. DISCUSSION

Are Yearlings Excluded From The Best Areas ?

Males - In both this and other populations of L. lagopus (Watson 1970, Watson and Miller 1971, Miller and Watson 1978, Hannon 1983, Pedersen 1984), males on larger territories were more likely to acquire a partner than males on smaller territories. At Chilkat Pass older males had a higher probability of acquiring a partner than yearling males possibly because females tended to return to their previous partner between years (Chapter III).

Yearling males usually were restricted to areas that were vacant due to overwinter mortality of the previous owners. Some yearling males may have had the choice of establishing a small territory or not having a territory. By acquiring a small territory they may have gained the foot-hold that was necessary to breed in future years. Similar to red-winged blackbirds (Agelaius phoeniceus; Picman 1987), returning male willow ptarmigan increased the size of their territories between years ($F=11.3$, $P<.00$, $df=1, 70$; repeated measures ANOVA) and all unpaired males acquired a partner the following year. However, yearling males that did not establish a territory but remained on the area throughout the summer, also may have been able to establish a territory in the future as observed in other species (Yasukawa 1979, Jamieson and Zwickel 1983, DeVos 1983, Arcese 1987). The costs and benefits of establishing a small territory have not been determined, although Watson and Jenkins (1968) and Watson (1985) suggested that male red grouse (L. lagopus) without territories had low survival.

Male L. lagopus on larger territories had a higher probability of acquiring a partner (Watson 1970, Watson and Miller 1971, Miller and Watson 1978, Hannon 1983, Pedersen 1984, this study). These results were surprising since a female's reproductive success was not related to the size of her territory (Watson and Miller 1971, Miller and Watson 1978, Erikstad et al. 1985, this study) and there was no relationship between size of territory and the order in which territories were selected by yearling females in the natural situation or the experiment. Possibly females settled without regard to the boundaries of a male's territory. If this were true, larger territories, by virtue of covering more area than small territories, would have a higher probability of females settling. Alternatively, females may have settled with a particular male, but required a minimum amount of space. In this case, females that encountered relatively small territories may have opted to move to larger territories.

Inter-female spacing has been suggested to reduce predation on adults and clutches (Herzog and Boag 1978, Krebs and Davies 1978, Picman 1988), and this may be the reason females require a minimum amount of space. However, I found no relationship between territory size and survival of female or clutch loss and O'Reilly and Hannon (in press) found that clutch loss was not related to spacing of artificial nests.

Territory establishment by yearling males at Chilkat Pass differed from that found in red grouse (Watson and Jenkins 1968, Lance 1978a, Watson 1985). In red grouse some older breeders were evicted during the fall by young males. Young males that acquired territories and breeders that retained territories at that time, constituted the breeding population the next spring, although a few males died and were replaced by non-territorial males during the winter. At Chilkat Pass yearling males probably did not force previous breeders to abandon their territories in the fall; intra-male aggression was rare and males often formed flocks during the fall and winter (Mossop 1988, pers. obs.). In addition, yearling males did not evict previous breeders when territories were established in the spring (pers. obs.). At Chilkat Pass, mortality and site fidelity of previous breeders greatly influenced the settlement of yearling males. Settlement may have differed between willow ptarmigan and red grouse because willow ptarmigan were migratory and red grouse were sedentary. A similar dichotomy has been found for other species that were migratory (Picman 1988) and those that were sedentary (DeVos 1983, Arcese 1987, Freed 1987, but see Herzog and Boag 1978).

Females. With the exceptions of territories where both members of a pair returned, yearling female willow ptarmigan settled at similar times to older females, and older females did not evict yearling females after the yearlings had settled. Thus, yearlings had the potential to acquire breeding situations that were as good as those obtained by some older females and had as much time to gather resources needed for reproduction as these older females. Yearlings, however, produced smaller clutches and consequently fledged fewer chicks than older females.

Neither Martin (1985) nor Myrberget (1986) found differences in reproductive success between yearling and older females in other populations of willow ptarmigan. However, Hannon et al. (1988) found that at Chilkat Pass older females pairing with older males started laying earlier, and Hannon and Smith (1984) found those pairs produced more chicks. It was difficult to evalua[illegible] differences among studies because data were analyzed differently. In addition, the analyses may have been confounded by pairing with familiar partners because I found familiarity with partner influenced an individual's reproductive success (Chapter III). Possibly, experience or age were important only under certain environmental conditions (e.g. those at Chilkat Pass) since age was related to reproductive success only at this location.

Older females may have been able to discriminate among breeding situations more accurately than yearlings and thus acquired better territories. Older females had knowledge from previous breeding seasons whereas, since natal philopatry was low (Martin and Hannon 1987), yearling females probably relied on features that were present at the time they settled. Approximately one meter of snow pack was present at this time (Hannon et. al 1988). An alternative explanation for older females producing larger clutches than yearlings, is that older females were more efficient at converting resources into eggs. This was not evaluated in this study.

Choice Of Breeding Situation By Yearling Females

There appeared to be large differences in physical relief and vegetation composition among territories (pers. obs.) and one may have expected females to have chosen based on those differences, especially since reproductive success and quality of chicks produced on some territories was consistently better than on others (Chapter IV). Yearling female willow ptarmigan at Chilkat Pass did not settle in the manner predicted by Fretwell and Lucas (1970); yearling females that settled early did not fare any better than those settling later and choice of breeding situation was not consistent among females in the experiment. Possibly, the relative values of breeding situations differed among females and each chose the territory or male that was best for her (Nur 1986). Females that switched territories between years provided an indirect test of this hypothesis; they should have moved to a better territory or partner and if their ability was similar among years their reproductive success should have been higher after switching. Contrary to the prediction females did not fare better after moving than before (Chapter III), nor did they fare better than the female on their previous territory (Chapter III).

A second potential explanation for the apparent lack of selection by yearling females was that if the probability of finding a suitable territory was low or if production of offspring was related to time of settling, it may not have been to the female's advantage to search further once a suitable breeding situation was found (Alatalo et al. 1988, Slagsvold et al. 1988, but see Korpimaki 1988). Suitable breeding situations probably were not difficult to find for female willow ptarmigan because 1) they did not settle on the first territory they encountered, 2) after all females had settled some territorial males did not have partners, although these tended to be males on small territories, and 3) females settled as secondary partners on large territories, although this may not have been possible on small territories (Hannon 1983). In addition, timing of reproduction was not related to date of settling for willow ptarmigan. Thus it was doubtful that females were choosing the first available situation.

A third potential explanation for the apparent lack of choice by yearling females was that values of breeding situations did not differ greatly and females would have gained little attempting to rank them (Wootton et al. 1986). Quality of all breeding situations may have been similar if habitat was homogenous and partners were all of similar quality (Searcy 1979, Wootton et al. 1986, Lightbody and Weatherhead 1987), habitat was heterogenous but males adjusted territory size so that territories were larger in poorer habitats (Seastedt and MacLean 1979, Miller and Watson 1978, Watson et al. 1984a). A fourth potential explanation for ~~the~~ apparent lack of choice by yearling females was that although quality of territories and males influenced reproductive success, yearling females were unable to assess differences among breeding situations and did not choose good situations (Searcy 1979).

At Chilkat Pass all males may have been of similar quality to first-time breeding females; there were no apparent advantages to females pairing with older males (Chapter III) and differences among males did not appear to influence reproductive success (Chapter IV). Some territories, however, consistently had earlier dates of first egg and larger clutches that others (Chapter IV) and it would have been beneficial for yearlings to choose those territories. Differences in territory quality may have been too small for yearling females to assess (Wootton et al. 1986) or the important habitat characteristics may have been buried under the snow when the females settled. Thus, as suggested for marsh wrens (Cistothorus palustris; Leonard and Picman 1988), female willow ptarmigan may have been unable to make effective choices, even though differences were present.

In other species (savannah sparrows (Passerculus sandwichensis), Bedard and LaPointe 1984; painted buntings (Passerina ciris), Eliason 1986; bobolinks (Dolichonyx oryzivorus), Wootton et al. 1986; tropical house wrens (Troglodytes aedon), Freed 1987; yellow-headed blackbirds (Xanthocephalus xanthocephalus), Lightbody and Weatherhead 1987) females did not appear to settle based on the Fretwell and Lucas (1970) model. Those, and the present study, were in areas with relatively high population density and consequently all territories may have been equally suitable (Searcy 1979, Wootton et al. 1986). Habitats may have been selected on a larger scale with individuals settling in good before marginal habitats, but choosing randomly within the good habitat (Weatherhead and Boak 1986, Wootton et al. 1986, but see Gavin and Bollinger 1988).

III. BREEDING SITE FIDELITY IN WILLOW PTARMIGAN: THE INFLUENCE OF PREVIOUS REPRODUCTIVE SUCCESS AND FAMILIARITY WITH PARTNER AND TERRITORY

A. INTRODUCTION

In many species of birds, individuals breed on areas they used in previous years (Greenwood and Harvey 1982). High site fidelity may act to promote pairing with familiar partners or breeding on familiar territories, both of which may increase reproductive success. Individuals pairing with familiar partners may breed earlier than individuals with unfamiliar partners (Rowley 1983, Gratto et al. 1985, but see Cooke et al. 1981, Cuthbert 1985, Freed 1987). Those individuals also may forage more efficiently or be better able to avoid predators on areas where they are familiar with the resources and refuges (Greenwood and Harvey 1982). Site fidelity could reduce the costs of acquiring and holding territories because neighbors often recognize each other (Brooks and Falls 1975, Falls and McNichol 1979, Falls 1982) and are less aggressive towards known individuals than towards unfamiliar individuals (Yasukawa 1979, Robinson 1986, Stamps 1987, Ydenberg et al. 1988).

Site fidelity, however, is not always beneficial. If characteristics of territories (Fretwell and Lucas 1970, Garson et al. 1981, Alatalo et al. 1986, Stacey and Ligon 1987) and partners (Weatherhead and Robertson 1979, Harvey et al. 1984b, Coulson and Thomas 1985, Nol and Smith 1987) influence an individual's reproductive success, individuals in relatively poor breeding situations (having poor territories or partners, Wittenberger 1976) may choose to switch territories before breeding again (e.g. Darley et al. 1977, Dow and Fredga 1983, Oring and Lank 1982, Harvey et al. 1984b, Shields 1984).

The relative influence on site fidelity of familiarity with area, partner and neighbors, and differences in quality among breeding situations, may differ among populations (Wootton et al. 1986). Most authors have addressed only whether individuals switched territories as a result of low reproductive success (e.g. Skeel 1983, Harvey et al. 1984b, Shields 1984, Gavin and Bollinger 1988) or whether they chose territories based on characteristics that influenced their reproductive success (e.g. Garson et al. 1981, Blancher and Robertson 1985, Siegel-Causey and Hunt 1985). Relatively little emphasis has been placed on the the importance of familiarity with area, partners or neighbors (see Picman 1981, Wootton et al. 1986, Lanyon and Thompson 1986 for exceptions) even though most individuals that bred previously attempt to settle on familiar areas, with familiar partners and with familiar neighbors (Greenwood and Harvey 1982).

In this Chapter I documented the frequency of individuals returning to their previous territory and its association with past reproductive success to determine 1) whether individuals chose familiar partners or territories and 2) whether individuals switched from breeding situations with relatively low survival and reproductive success. Then, I tested whether an individual's survival, reproductive success and quality of chicks produced was related to 1) whether it returned to its previous territory or 2) whether it paired with its previous partner. In addition, since females that switched territories usually moved to territories of older males, I determined whether a female's survival, reproductive success and quality of chicks produced was related to the age of her partner. Lastly, for individuals that switched territories between years I evaluated whether reproductive success or chick quality was higher after switching than before they moved, or was higher than that of the pair on their previous territory.

B. METHODS

General field methods and analytical techniques were described in Chapter II. To avoid confusing switching territories with expansion of territories an individual was classified as switching territories between years only if its new territory and its previous territory overlapped by less than 25%.

C. RESULTS

Site Fidelity, Territory Switching And Their Relationship To Previous Reproductive Success

Males - Breeding site fidelity was high for males; only 15 of 167 (9%) switched territories between years (Figure III-1). Nine males that switched (60%) moved to an adjacent territory but one male moved 11 territories away from his initial territory. Yearling and older males had similar probabilities of switching territories between years (Figure III-2; $X^2=2.9$, $df=1$, $P=.09$).

Unpaired males were more likely to switch territories before the next breeding season than paired males (Figure III-2; $X^2=12.1$, $df=1$, $P<.01$, monogamous and polygamous males were combined in the analyses). The probability of males switching territories was not associated with survival of their previous partners ($X^2=2.8$, $df=1$, $P=.10$; 2 of 65 (3%) and 5 of 46 (11%) switched territories when their partners did and did not return, respectively). The probability of switching territories between year x and year x+1 was not related to whether they produced chicks in year x ($X^2=2.1$, $df=1$, $P=.10$; 7 of 88 (8%) and 7 of 43 (16%) switched following producing and not producing chicks, respectively). Males with earlier dates of first egg in year x were more likely to switch than males with later dates of first egg ($X^2=7.2$, $df=1$, $P=.01$, logistic

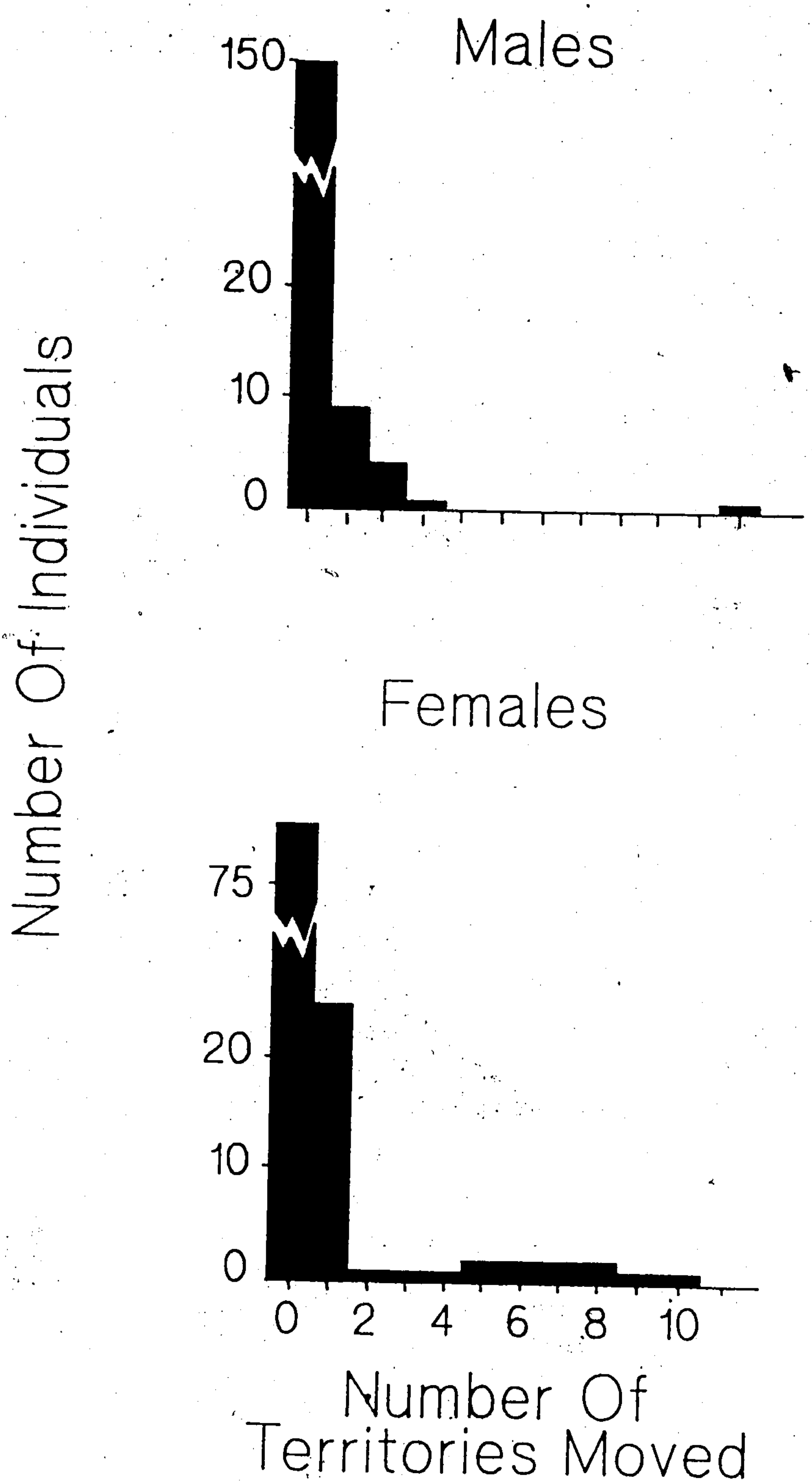

Figure III-1. Between year breeding dispersal of willow ptarmigan.

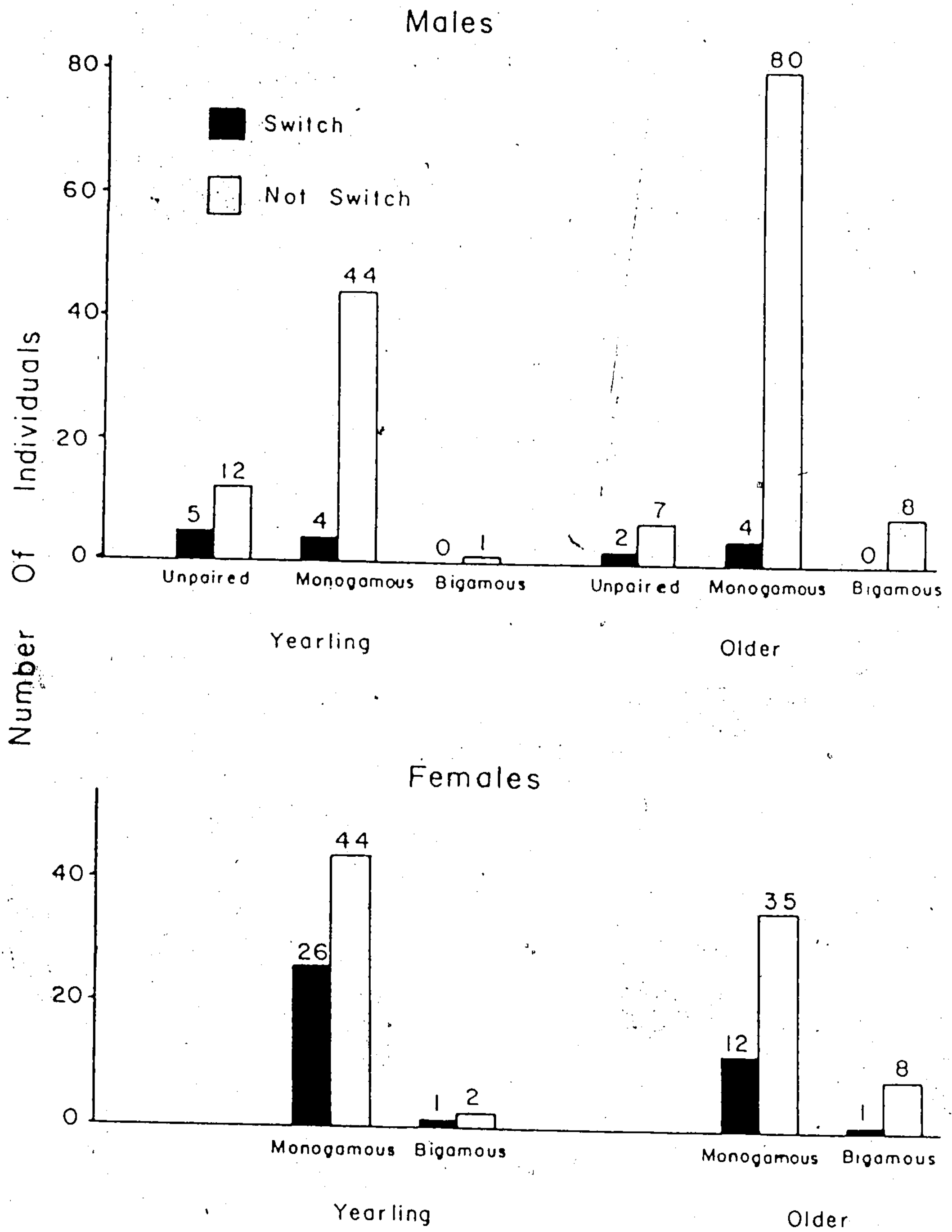

Figure III-2. Number of willow ptarmigan that switched and did not switch territories between breeding years categorized by age and pairing status of the individual prior to moving. Numbers above bars denote sample size.

regression; mean date of first egg was 1.4 June ±4.1 days, N=7 for switchers and 4.8 June ±3.3 days, N=84 for non-switchers). This relationship was opposite that predicted since males moved from relatively good territories; chicks produced early had a relatively high probability of recruiting (Martin and Hannon 1987). The relatively early date of first egg for males that switched territories resulted in them switching following producing 0.5 more eggs, 1.2 more chicks and 1.4 more fledglings than than males that did not switch. The sample size, however, was very small for males not switching territories (N= 3, 2, 1 for clutch size, number hatching and number fledging respectively) and consequently the results may not be robust.

Females - Forty of 129 returning females (31%) switched territories between years and 25 of these (63%) moved to an adjacent territory (Figure III-1). Females had a higher probability of switching territories between years than did males (X^2=23.3, df=1, P<.01; Figure III-1). Yearling and older females had similar probabilities of switching territories between years (Figure III-2; X^2=2.8, df=1, P=.09).

On 80 occasions both members of a pair present in year x returned and bred in year x+1. Fifty-six of these pairs (70%) returned to their previous territory and paired with their previous partner (Table III-1). In 3 cases both members of a pair present in year x had different partners in year x+1 and returned again in year x+2. In one of these 3 cases, partners paired with each other again in year x+2. Females had a higher probability of switching territories if their previous partner disappeared than if he returned (X^2=7.2, df=1, P=.01; Table III-1). Thirty-five of 40 females moved to the territories of older males, whereas only 3 and 2 moved to the territories of yearling and unknown aged males, respectively. Those females that moved settled with older males more often than expected at random (X^2=16.7, df=1, P=.01), based on the age ratio of 1

Table III-1. Number of female willow ptarmigan switching territories between breeding seasons categorized by survival of their previous partner and fate of their previous territory.

	Male Survived		Male Did Not Survive And Female's Previous Territory Occupied By	
	Male Returned To Previous Territory	Male Switched Territories	Previous Neighbor	Non-neighbor [a]
Female Switched Territories	19	1	7	13
Female Returned To Previous Territory	56	4 [b]	13	9

a - 20 of these males were yearlings, the age of the other two males was unknown

b - these 4 males re-claimed 30-70% of their previous terrotory but the female paired with a previous neighbor that owned the rest yearling to 1.47 older territorial males.

Monogamous and bigamous females had a similar probabilities of switching territories between years (Figure III-2, $\underline{X}^2=1.3$, $\underline{df}=1$, $\underline{P}=.29$). Females that did not produce chicks during year x had a higher probability of switching territories between years x and x+1 than did females that produced chicks during year x (Table III-2). This analysis was confounded by whether or not the female's previous partner returned. If he returned, the probability of switching was associated with the probability of her producing chicks in the previous year ($\underline{X}^2=13.7$, $\underline{df}=1$, $\underline{P}<.01$; 5 of 7 switched subsequent to producing no chicks whereas 7 of 55 switched subsequent to producing chicks). If he did not return, probability of switching was independent of the probability of producing chicks ($\underline{X}^2=0.8$, $\underline{df}=1$, $\underline{P}=.37$; 4 of 6 switched subsequent to producing no chicks whereas 13 of 28 switched territories subsequent to producing chicks). Switching territories by females was not related to other measures of reproductive success or quality of chicks produced (Table III-2).

Potential Causes Of Territory Switching And Site Fidelity

The high degree of breeding site fidelity observed in this population would be expected if familiarity with area, partner or neighbors increased an individual's survival and/or reproductive success. Therefore, I evaluated the consequences of settling on familiar versus unfamiliar areas and with familiar versus unfamiliar partners. In addition, since females usually moved to the territories of older males, I evaluated whether age of mate was related to a female's survival and reproductive success. Finally, since males were more likely to switch territories following low mating success, and females following low reproductive success, I evaluated whether they moved to areas that resulted in them being more successful.

Table III-2. Reproductive success and quality of chicks produced for female willow ptarmigan that switched and those that did not switch territories between year x and year x+1. Analyses involve variables measured during year x. Continuous and categorical variables were analyzed using logistic regression analyses and contingency analyses, respectively. Means (standardized for year effects) ± SD are presented for continuous variables, percentages are presented for categorical variables. Sample sizes are in parentheses.

	Switch	Not Switch	$\underline{X}^2$	P
Reproductive Success				
Relative Clutch Size [a]	7.9±1.1 (24)	7.7±1.2 (35)	0.4	.49
Total Clutch Loss (%)	42 (24)	43 (49)	0.0	.92
Produce Chicks In Season (%)	69 (29)	94 (69)	11.3	<.01
Season Fledging Success	4.2±2.3 (10)	4.7±1.8 (33)	0.5	.84
Chick Quality				
Date Of First Egg (June)	4.4±4.3 (29)	3.7±4.1 (58)	0.5	.49
Relative Chick Weight [b]	14.9±0.6 (14)	14.4±1.2 (29)	1.0	.32

a - date of first egg was used as a covariate in this analysis

b - two covariates were used in this analysis: date of first egg and clutch size

Familiarity With Area - All individuals on familiar territories were older and some were with familiar partners whereas many individuals on unfamiliar territories were yearlings and none were with familiar partners. I have not included individuals that were pairing with their previous partner in these analyses. Sample size was very small if only older individuals were included in the analyses, so I included both yearling and older individuals. Only the clutch size comparison for females was confounded by age effects because other measures of reproductive success, quality of chicks produced and survival were not related to pair-age (Chapter II, Tables II-1A and II-1B).

Probability of males acquiring a partner in year x+1 was similar for males that did or did not switch territories (i.e. were on familiar versus unfamiliar territories, Table III-3). In addition, survival, reproductive success and quality of chicks produced in year x+1 was similar for males and females that did or did not switch territories (Tables III-3 and III-4). Thus familiarity with territories appeared to be of little value to either males or females.

Familiarity With Partner - Only data from older males paired with older females were used in these analyses to eliminate the potentially confounding age effects. Individuals pairing with familiar partners never switched territories whereas 8 of 34 males (24%) and 28 of 36 females (78%) paired with unfamiliar partners switched territories. However, familiarity with area should not have confounded the analyses because there were no apparent advantages to being on familiar territories (see above).

Individuals that paired with their previous partner laid their first egg earlier and produced relatively heavier chicks than pairs composed of unfamiliar partners (Table III-5). Starting to lay two days early translated into 0.3 more eggs, 0.3 more chicks and 0.3 more fledglings (Appendix 2). Although, individuals that paired with their previous partner settled earlier than pairs composed of

Table III-3. Survival, pairing status, reproductive success and quality of chicks produced for male willow ptarmigan that did and did not switch territories between year x and year x+1. Analyses involve variables mesasured during year x+1. Means (standardized for year effects) ± SD are presented for continuous variables, percentages are presented for categorical variables. Sample sizes are in parenheses.

	Switch	Not Switch	$\underline{F}/\underline{X}^2$ [a]	$\underline{P}$
Survival (%)	50 (8)	55 (49)	0.1	.79
Acquired A Partner (%)	100 (10)	93 (76)	0.7	.40
Reproductive Success				
Relative Clutch Size [b]	9.9±4.8 (9)	8.6±2.2 (48)	1.0	.31
Total Clutch Loss (%)	44 (9)	42 (59)	0.0	.91
Produce Chicks In Season (%)	80 (10)	71 (68)	0.4	.54
Season Fledging Success	5.9±1.6 (4)	4.6±2.3 (25)	1.3	.27
Chick Quality				
Date Of First Egg (June)	4.5±2.2 (10)	6.3±5.0 (63)	1.2	.28
Relative Chick Weight [c]	14.6±1.0 (6)	14.7±1.0 (34)	0.0	.84

[a] $\underline{F}$ is reported for ANOVAs or ANCOVASs, $\underline{X}^2$ is reported for contingency anlyses

[b] Date of first egg was used as a covariate in this analysis

[c] Two covariates were used in this analysis: date of first egg and clutch size

Table III-4. Survival, reproductive success and quality of chicks produced for female willow ptarmigan that did and did not switch territories between year x and year x+1. Analyses involve variables measured during year x+1. Means (standardized for year effects) ± SD are presented for continuous variables, percentages are presented for categorical variables. Sample sizes are in parentheses.

	Switch	Not Switch	F/X^2 [a]	P
Survival (%)	29 (14)	40 (10)	0.3	.56
Reproductive Success				
Relative Clutch Size [b]	7.9±1.3 (24)	8.5±0.7 (13)	0.8	.38
Total Clutch Loss (%)	62 (29)	60 (15)	0.0	.89
Produce Chicks In Season (%)	57 (30)	73 (15)	1.2	.28
Season Fledging Success	5.6±2.7 (7)	4.2±2.5 (7)	0.9	.37
Chick Quality				
Date Of First Egg (June)	4.2±5.0 (30)	2.9±3.6 (14)	0.7	.41
Relative Chick Weight [c]	14.2±1.1 (10)	14.7±0.8 (6)	0.6	.45

a - F is reported for ANOVAs or ANCOVASs, X^2 is reported for contingency anlyses
b - date of first egg was used as a covariate in this analysis
c - two covariates were used in this analysis: date of first egg and clutch size

Table III-5. Date female settled, female survival, reproductive success and quality of chicks produced for willow ptarmigan that paired with their previous partners and those pairing with unfamiliar partners. Means (standardized for year effects) ± SD are presented for the continuous variables, percentages are presented for categorical variables. Sample sizes are in parentheses.

	Previous Partner	Unfamiliar Partner	$\underline{F}/\underline{X}^2$ [a]	$\underline{P}$
Date Female Settled	Apr. 24.7±8.2 (20)	May 7.8±18.0 (19)	8.1	.01
Female Survival (%)	34 (29)	43 (37)	0.5	.47
Reproductive Success				
Relative Clutch Size [b]	8.6±1.2 (29)	8.3±1.1 (43)	0.0	.97
Total Clutch Loss (%)	55 (33)	49 (49)	0.2	.62
Produce Chicks In Season (%)	70 (46)	75 (56)	0.2	.68
Season Fledging Success	5.9±1.7 (14)	4.5±2.5 (18)	3.3	.08
Chick Quality				
Date Of First Egg (June)	2.0±3.0 (43)	3.9±4.2 (55)	5.8	.02
Relative Chick Weight [c]	15.2±0.9 (14)	14.6±1.0 (19)	4.7	.04

a - $\underline{F}$ is reported for ANOVAs or ANCOVAs, $\underline{X}^2$ is reported for contingency anlyses
b - date of first egg was used as a covariate in this analysis
c - two covariates were used in this analysis: date of first egg and clutch size

unfamiliar partners (Table III-5) this probably was not the cause of laying relatively early because date of first egg was not related to date female settled for individuals not pairing with familiar partners (Chapter II). Other measures of reproductive success, chick quality and survival were similar for individuals that paired with their previous partner and those paired with an unfamiliar partner (Table III-5).

Age Of Male - To avoid the confounding influence of pairing with familiar partners, only females not pairing with their previous partner were included when evaluating the influence of age of males. Familiarity with territories should not have confounded the analyses because there were no advantages to being on familiar territories (see above). Survival, reproductive success and quality of chicks produced did not differ between females paired with yearling versus older males (Chapter II, Tables II-1A and II-1B). Thus, females that switched apparently did not gain by pairing with older males.

Did Individuals Move To Better Breeding Situations Between Years ? - Repeated measures ANOVAs and ANCOVAs (before-after switching was the repeated measure in Table III-8; previous-present territory was the repeated measure in Table. III-9) were used to control for variation among individuals and among territories. Sample size was insufficient to use repeated measures analyses for males. Familiarity with partners and territories did not confound these analyses because individuals that switched territories never bred with familiar partners or on familiar territories. The analyses could be confounded by age effects; individuals were younger during the breeding season before they switched territories than during the season after. Age effects were present for the probability of males acquiring partners and relative clutch size, and thus those were the only analyses that were confounded.

Males appeared to gain by switching territories; they had a lower probability of acquiring a partner before than after switching territories (Table III-6). This tendency was similar for yearling and older males ($\underline{X}^2$=0.9, $\underline{df}$=1, $\underline{P}$=.34; 3-way contingency analyses using the factors male age, mating status and before-after switching). However, all unpaired males that did not switch territories ($\underline{N}$=15) also acquired a partner in the following year. The increased probability of acquiring a partner after switching territories was not due to an increased territory size; territory size was similar before and after switching (Table III-6). Although sample size was small, males that were paired had similar reproductive success and produced chicks of similar quality before and after switching territories (Table III-6). In addition, new pairs (year x+1) on the territories that the males had occupied prior to switching (year x) had similar success to the males that moved (Table III-7, again sample sizes were small). Thus, males probably did not gain or lose by switching territories.

Opposite to the predictions, females were more likely to lose their first clutch and produced relatively light chicks after switching territories than they did in the season prior to switching (Table III-8). Other measures of reproductive success and chick quality were similar before and after switching territories (Table III-8). New pairs (year x+1) on territories that females had occupied prior to switching (year x) were as successful as the females that moved (Table III-9). Thus, it appeared that females also did not gain, and possibly lost, by switching territories.

D. DISCUSSION

Breeding site fidelity of willow ptarmigan at Chilkat Pass was high even though overwinter mortality resulted in about 50% of the territories being available each spring. High breeding site fidelity is common for many species of birds (Greenwood and Harvey 1982, Lawn 1982, Eliason 1986, Lanyon and Thompson

Table III-6. Territory size, mating status, reproductive success and quality of chicks produced for male willow ptarmigan before and after they switched territories. Means (standardized for year effects) ± SD are presented for continuous variables and percentages are presented for categorical variables. Sample sizes are in parentheses. Tests were not performed when sample size was less than five for either group.

	Before Switching	After Switching	F/X^2 [a]	P
Territory Size	4.4±1.4 (9)	4.8±1.7 (9)	0.3 [b]	.62
Acquired A Partner (%)	36 (11)	100 (11)	10.3	<.01
Reproductive Success				
Relative Clutch Size	9.1±1.4 (3)	9.9±4.9 (9)		
Total Clutch Loss (%)	33 (3)	44 (9)		
Produce Chicks In Season (%)	20 (10)	70 (10)	5.1	.03
Season Fledging Success	5.4±1.2 (3)	5.9±1.6 (4)		
Chick Quality				
Date Of First Egg (June)	1.4±4.1 (7)	4.6±2.2 (10)	4.1	.06
Relative Chick Weight	13.5 (1)	15.0±1.0 (6)		

a - *F* is reported for ANOVAs, X^2 is reported for the contingency analyses
b - this analyses was done using repeated measures ANOVA (before-after being the repeated measure)

Table II-7. Territory size, mating status, reproductive success and quality of chicks produced for male willow ptarmigan on new territories following switching compared with pairs on the male's former territory. Means (standardized for year effects) ± SD are presented for continuous variables and percentages are presented for categorical variables. Sample sizes are in parentheses. Tests were not performed when sample size was less than five for either group.

	Previous Territory	Present Territory	*F*/*X*² [a]	*P*
Territory Size	3.9±1.1 (5)	4.5±2.0 (7)	0.3	.59
Acquired A Partner (%)	83 (6)	100 (7)	1.3	.29
Reproductive Success				
Relative Clutch Size	7.1±0.3 (4)	10.5±5.4 (7)		
Total Clutch Loss (%)	50 (4)	57 (7)		
Produce Chicks In Season (%)	50 (6)	71 (7)	0.6	.43
Season Fledging Success	1.5±2.9 (6)	2.8±4.2 (7)	0.4	.54
Chick Quality				
Date Of First Egg (June)	3.4±0.6 (5)	4.3±2.5 (7)	0.5	.48
Relative Chick Weight	14.7±1.8 (2)	14.2±1.1 (3)		

a - *F* is reported for ANOVAs, *X*² is reported for the contingency analyses

Table III-8. Reproductive success and quality of chicks produced for female willow ptarmigan before and after they switched territories. Means (standardized for year effects) ± SD are presented for continuous variables and percentages are presented for categorical variables. Sample sizes are in parentheses.

	Before Switching	After Switching	$\underline{F}/\underline{X}^2$ [a]	$\underline{P}$
Reproductive Success				
Relative Clutch Size [c]	7.8±1.1 (18)	8.1±1.4 (18)	0.1	.74
Total Clutch Loss (%)	33 (21)	66 (21)	4.7	.03
Produce Chicks In Season (%)	71 (24)	58 (24)	0.8	.35
Season Fledging Success	4.2±2.3 (10)	5.5±2.5 (10)	1.4 [b]	.30
Chick Quality				
Date Of First Egg (June)	4.6±4.5 (25)	4.1±5.3 (25)	0.2	.66
Relative Chick Weight [d]	14.8±0.6 (14)	14.0±1.1 (9)	4.9 [b]	.04

a - $\underline{F}$ is reported for ANOVAs or ANCOVASs, $\underline{X}^2$ is reported for the contingency analyses

b - these analyses were done using ANOVA or ANCOVA because sample sizes were not great enough for the repeated measures analyses

c - date of first egg was used as a covariate in this analysis

d - two covariates were used in this analysis: date of first egg and clutch size

Table III-9. Reproductive success and quality of chicks produced for female willow ptarmigan on new territories following switching compared with the pairs on the female's former territory. Means (standardized for year effects) ± SD are presented for continuous variables and percentages are presented for categor[illegible] variables. Sample sizes are in parentheses.

	Previous Territory	Present Territory	F/X^2 [a]	P
Reproductive Success				
Relative Clutch Size [c]	8.1±0.7 (13)	7.9±1.4 (13)	0.0	.98
Total Clutch Loss (%)	43 (14)	[illegible] (14)	1.3	.24
Produce Chicks In Season (%)	76 (17)	59 (17)	1.2	.27
Season Fledging Success	2.9±1.7 (6)	2.4±1.6 (6)	0.4	.40
Chick Quality				
Date Of First Egg (June)	4.1±4.4 (15)	4.5±5.6 (15)	0.0	.84
Relative Chick Weight [d]	14.7±0.7 (10)	14.4±1.1 (7)	0.0 [b]	.85

a - F is reported for ANOVAs or ANCOVASs, X^2 is reported for the contingency analyses

b - this analysis was done using ANCOVA because sample sizes were not great enough for the repeated measures analyses

c - date of first egg was used as a covariate in this analysis

d - two covariates were used in this analysis: date of first egg and clutch size

1986, but see Hilden 1979, Korpimaki 1988) including tetraonid species (sage grouse (Centrocercus urophasianus), Berry and Eng 1985; blue grouse (Dendragopus obscurus), Lewis 1986; ruffed grouse (Bonasa umbellus), Boag 1976; spruce grouse (D. canadensis), Herzog and Boag 1978; willow ptarmigan, Pedersen et al. 1983, Martin 1985; rock ptarmigan (L. mutus), Unander and Steen 1985; and white-tailed ptarmigan (L. [illegible]curus), Choate 1963). Breeding site fidelity may be beneficial if it results in individuals knowing the locations [illegible] resources and refuges on their territory (Harvey and Greenwood [illegible], pairing with familiar partners (Rowley 1983) or being familiar with their neighbors ([illegible]kawa 1979, Picman 1987).

Familiarity With Area - The high degree of site fidelity found in willow ptarmigan probably was not maintained by benefits of being on familiar territories. I found no advantages to individuals breeding on familiar versus unfamiliar territories. These results were not due to an increase in territory quality that compensated for lack of familiarity, because individuals breeding on territories that switchers had occupied previously fared as well as the switchers.

Although Gratto et al. (1985) and Wegge and Larsen (1987) suggested that familiarity with breeding territories was beneficial and may have caused the high degree of site fidelity they observed, they did not test this prediction. Metzgar (1967) found that white-footed mice (Peromyscus leucopus) had a lower probability of being preyed upon if they were familiar with an area. Korpimaki (1988) found that Tengmalm's owls (Aegolius funereus) started laying earlier and laid more eggs on familiar than on unfamiliar areas, although this did not translate into increased fledging success. In addition, his analyses were confounded by age of individuals and quality of the areas; individuals breeding on familiar areas were older and on the best areas. More studies are needed before the general applicability of being familiar with territories can be evaluated adequately.

Familiarity With Partner - Individuals that pair with their previous partner may establish a territory and breed early, thus increasing their reproductive success (Rowley 1983). Those benefits may increase as the number of seasons the pair has been together increases and thus be most noticeable in species where individuals are long-lived (Coulson 1966, Ollason and Dunnet 1978). However, even in species where individuals breed for only two or three years, pairing with a previous partner may be beneficial (Bryant 1979, Newton 1986, but see Nol et al. 1984, Gratto et al. 1985, Freed 1987).

The high degree of site fidelity for willow ptarmigan may have been due to the benefits of pairing with a familiar partner. About 30% of the willow ptarmigan at Chilkat Pass had their partner return and of those, seventy percent paired with their previous partner. Individuals pairing with their previous partner had earlier dates of first egg than those pairing with an unfamiliar partner and that had carry-over effects of larger clutches, more chicks hatching and more chicks fledging. Martin (1985) also found that if a willow ptarmigan's partner returned, most paired with their previous partner. Neither Martin (1985) nor Hannon et al. (1988), however, found that individuals pairing with their previous partner fared better than those pairing with an unfamiliar partner. Possibly relationships were overlooked in those studies because the variables I found significant were not analysed and sample sizes in their analyses were smaller.

Females that could have paired with their previous partner, but did not, usually did not produce chicks the previous season. However, if their previous partner did not return, switching by female willow ptarmigan was not related to the probability of producing chicks. These two patterns were consistent with the hypothesis that reproductive success was influenced by male quality (and not territory quality) and females switched to avoid poor partners. However, the probability of producing chicks during the season did not appear to be influenced by differences among males (Chapter IV). Possibly, the analyses in Chapter IV were not powerful enough to detect differences among males.

In many species of migratory birds males return and establish territories before females (Lack 1968, Frances and Cooke 1986) and are less likely to switch territories than females (Greenwood 1980). Greenwood suggested that this pattern was due to familiarity with neighbors being more important for males than for females because males interact with neighbors to acquire territories whereas females simply settle on a male's territory. Although Greenwood's hypothesis is consistent with the differences in site fidelity between male and female birds, I propose another hypothesis, which is also not exclusive, but is equally well supported.

In many species of birds some males do not get partners (Emlen and Oring 1977). The higher degree of intrasexual competition among males than among females may result in males arriving before females to compete for territories on which females will settle. Once a male has established a territory he may be able to exclude other males from it (Krebs 1982 but see Ydenberg et al. 1988). If there are reproductive benefits to pairing with familiar partners, most males may reclaim their previous territories to facilitate this pairing because they cannot assess whether their previous partner will return. Females, on the other hand, arrive after males have settled and may return to their previous territories if their previous partner is present but have a lower degree of site fidelity if their previous partner is not present. Thus, on average, site fidelity for females will be lower than that for males.

In Greenwood's (1980) hypothesis, advantages to having familiar neighbors result in males having a higher degree of site fidelity than females. I suggest that advantages to pairing with familiar partners result in males having a higher degree of site fidelity than females. If Greenwood's hypothesis is correct unpaired and paired males should have similar site fidelity, whereas in my hypothesis unpaired males should have lower site fidelity than paired males. There is a complicating factor in that unpaired males may be on poor territories originally and thus are more likely to switch than paired males (e.g. Gavin and Bollinger 1988).

I found that male willow ptarmigan did not move to better territories between years. Consequently, breeding site fidelity of unpaired males can be used to evaluate Greenwood's (1980) and my hypothesis. The level of site fidelity for unpaired males 19 of 26 (72%) was intermediate between that for paired males 133 of 141 (94%) and that for females with partners that did not return 22 of 42 (52%), although, not significantly different than females with partners that did not return ($\underline{X}^2=2.9$, $\underline{p}=.08$). These data can best be interpreted as partial support for both hypotheses. Familiarity with neighbors may cause higher site fidelity for unpaired males than for females with partners that did not return, but inability to pair with previous partner causes lower site fidelity for unpaired than for paired males. It would be informative to know whether the patterns found in willow ptarmigan are present in other species.

<u>Age Of Partner</u> - It would have been advantageous for males to pair with older females since older females had higher reproductive success than yearlings (Chapter II). However, in monogamous and polygynous species females usually are the limiting sex (Emlen and Oring 1977, Murray 1984) and thus males may be constrained to accept any female. This probably applies to willow ptarmigan since every year some males remain unpaired.

Age of male is positively related to number of young produced in many species with altricial young (Ralph and Pearson 1971, Harvey et al. 1979a, 1984a, 1985; Searcy and Yasukawa 1981, Labedz 1984, Reese and Kadlec 1985, Newton 1986, Nol and Smith 1987, but see Freed 1987), possibly because they are better foragers (Carl 1987, Maccarone 1987, van Riper 1987, Enoksson 1988, Sullivan 1988). In species with precocial young, male parental care may be less important

(Hannon 1983, Oring et al. 1983, Martin and Cooke 1987), although males may still reduce the amount of harassment their partners receive, act as sentinels, or help care for their broods (Hannon and Smith 1984).

Female willow ptarmigan that switched territories between years, almost always moved to the territories of older males. There were no apparent advantages to females pairing with an older male if he was not her previous partner. In addition, yearling females did not choose older males preferentially to yearling males (Chapter II). Hannon et al. (1988) found that older females paired with older males started laying sooner and Hannon and Smith (1984) found those pairs fledged more chicks than if either partner was a yearling. However, their analyses were confounded by individuals pairing with familiar partners and I found the same benefits for individuals pairing with familiar partners.

Females that switched territories between years may have been attempting to pair with familiar partners. Most females whose previous partner did not return switched territories and usually they moved to a territory owned by a previous neighbor. In addition, seven females that switched moved onto territories where they had been sighted with the male late the previous summer (this was a minimum estimate because little effort was directed towards observing the association between males and females during the summer and fall).

Familiarity With Neighbors - In many species of birds, antagonistic interactions among territorial individuals are common during territory establishment and the early part of the breeding season (Lack 1968). Site fidelity may lower these costs (Yasukawa 1979, Greenwood 1980, Brooks and Falls 1985, Lawn 1982, Lanyon and Thompson 1986, Robinson 1986, Picman 1987, Stamps 1987) because neighbors are less aggressive towards each other than towards unfamiliar individuals (Falls and McNichol 1979, Falls 1982, Whitfield 1986). Thus, unless the qualities of the new areas are much greater than the ones they are leaving, individuals may not gain by moving to new areas with new unfamiliar neighbors. This has been recognized as a possible influence on site fidelity for some time (Yasukawa 1979) yet often has been ignored (see Robinson 1986, Freed 1987, Picman 1987, Stamps 1987 for exceptions).

Although not tested in this study, familiarity with neighbors has potential to be important for willow ptarmigan. Males rarely switch territories, males that switch usually move to an adjacent territory, territory boundaries are contested vigorously each spring and approximately 50% of the males survive between years. Male blue grouse were less aggressive towards neighboring males than towards unfamiliar males (Falls and McNichol 1979) and this also may be true for willow ptarmigan. The amount of aggression displayed towards familiar and unfamiliar neighbors during territory establishment and the consequence of this aggression on territory size is needed to evaluate the importance of having familiar neighbors.

Familiarity with neighbors may be less important for females than for males. Inter-female aggression is less common than inter-male aggression (pers. obs.). In addition, females appear to have breeding opportunities each year since there are always some unpaired territorial males, although these tend to be males on small territories, and females may settle polygamously on large territories, although inter-female aggression may limit that opportunity on small territories (Hannon 1983).

<u>Did Individuals Move To Better Breeding Situations Between Years ?</u> - In this and other studies (e.g. Lewis and Zwickel 1981, Gratto et al. 1985, Eliason 1986, Lanyon and Thompson 1986, Yasukawa and Searcy 1986, Freed 1987, Parmelee and Pietz 1987, Wegge and Larsen 1987), most individuals did not switch territories between years. Individuals that switched territories between years

usually were those that produced relatively few offspring (Smith 1978, Lawn 1982, Redmond and Jenni 1982, Oring and Lank 1982, Dow and Fredga 1983, Oring et al. 1983, Skeel 1983, Shields 1984, Gavin and Bollinger 1988, this study). In other studies it has been assumed that individuals moved to breeding situations that increased their reproductive success. This assumption, however, rarely has been evaluated. In two lekking species, sharp-tailed grouse (Tympanuchus phasianellus) and black grouse (Tetrao tetrix), males initially settled on the periphery of a lek and had low copulatory success, but moved towards the center between years and increased their success (Rippin and Boag 1974, DeVos 1983). Thus, these individuals probably moved to better territories between years.

In willow ptarmigan individuals did not appear to move to better breeding situations between years. Males had a higher probability of switching territories if they were unpaired than if they had a partner and had a higher probability of acquiring a partner after than before switching. However, unpaired males that did not switch also had a higher probability of acquiring a partner the following year. In addition, males that switched fared no better than males that settled on the previous territories of the switching males. Female willow ptarmigan tended to switch territories if they did not produce chicks. They did not, however, appear to move to better breeding situations since after switching they did not have a higher probability of producing chicks than before moving, nor did they have a higher probability of producing chicks than the females that settled on the previous territories of the switching females.

Some territories were better than others (Chapter IV) and individuals that moved could have moved to those territories. If the differences among territories were small, however, individuals may have made incorrect choices (Searcy 1979, Eliason 1986, Wootton et al. 1986, Lightbody and Weatherhead 1987). In addition, predation of clutches and young may have been unpredictable and obscured benefits of choosing good territories. However, if predators live in an area for a number of years or have long term memories (Sonerud 1985) simply changing territories may be beneficial.

Both unpaired males and females with partners that did not return had relatively high levels of switching territories. Similar results have been found in other studies (Harvey et al. 1984a, Gratto et al. 1985, Martin 1985). Those individuals could not pair with their previous partners and thus may have had lower costs to switching territories than individuals with partners that returned. Possibly I overlooked benefits to switching territories for those individuals; for example, if the individual's previous territory was being defended by a new breeder and there were undefended territories of similar quality present, it may have been beneficial for the individual to move. Advantages of breeding with a familiar partner may have made an individual's previous territory more valuable than other territories and thus individuals that potentially could pair with familiar partners may have been less likely to switch.

Unlike Gavin and Bollinger (1988) I feel that the influence of territory and mate quality have been over-emphasized because they are consistent with accepted models of settlement (e.g. Orians 1969, Fretwell and Lucas 1970). I think the relative influence of differences among breeding situations the influence of being with familiar partners, on familiar territories and having familiar neighbors need to be evaluated more thoroughly before general conclusions can be made. In addition, the relative influence of each factor may differ among age-sex categories and thus should be analyzed separately for each.

IV. INDIVIDUAL AND TERRITORIAL VARIABILITY IN RELATION TO TIME OF SETTLING AND REPRODUCTIVE SUCCESS IN WILLOW PTARMIGAN

A. INTRODUCTION

An individual's reproductive success may [illegible] influenced by several factors. Reproductive success is correlated with the bio[illegible]position and the physical structure of the territory (Pleszczynska and Hansell 1980, Wittenberger 1981, Skeel 1983, Blancher and Robertson 1985, Conner et al. 1986, Lanyon and Thompson 1986, Siegel-Causey and Hunt 1986, Boag 1987, Leonard and Picman 1988, but see Bedard and LaPointe 1984, Greenlaw and Post 1985, Wootton et al. 1986). In addition, an individual's genotype and/or nutrition during early life, may affect its subsequent behaviour and morphology and thus influence its reproductive success (Dhondt and Huble 1968, Watson and Miller 1971, Moss et al. 1981, Moss and Watson 1982, Arcese and Smith 1985, Brook 1986, Clutton-Brock et al. 1986, Thouless and Guinness 1986). Furthermore, the genotype of an individual may influence the number of grand offspring produced by influencing survival and reproductive success of its offspring (Weatherhead and Robertson 1979, Bradbury and Gibson 1983).

The most straight-forward approach to evaluate whether the quality of males, females or territories influence the production of offspring, is to look for correlations between specific characteristics and reproductive success. If the important characteristics are obvious this technique works well; for example vegetation structure at the nest (Pleszczynska and Hansell 1980) and nest-placement within the colony and physical structure of the nest site (Siegel-Causey and Hunt 1986) influenced reproductive success. However, analysing specific characteristics may be fruitless if there are no obvious relationships between characteristics of territories and reproductive success; many potentially important characteristics must be analysed and unless a relationship is found, it can be argued that the wrong characteristics were studied. If most of the variance in reproductive success is due to stochastic processes (e.g. Eliason 1986, Wootton et al. 1986, Lightbody and Weatherhead 1987) analysing specific characteristics may be fruitless.

A second major difficulty with calculating correlations between specific habitat and morphological characteristics and reproductive success, is that cause and effect cannot be determined. If the most dominant individuals live in the best areas (Orians 1969, Searcy and Yasukawa 1981, Yasukawa 1981, Alatalo et al. 1986, Eckert and Weatherhead 1987a) and have the best partners (Newton 1986, Korpimaki 1988) one cannot use correlations to separate the influence of territories from the influence of individuals. However, to evaluate the relative importance of the "polygyny threshold hypothesis" (Orians 1969) and the "sexy son hypothesis" (Weatherhead and Robertson 1979), for example, one must determine whether variation in reproductive success is due to variation among habitats or variation among males (Searcy and Yasukawa 1981, Wittenberger 1981). Indirect techniques may be more appropriate in these circumstances. If the reproductive success of an individual is influenced by its physical characteristics or by characteristics of its territory, and if characteristics of territories and individuals are similar between years, then the reproductive success of a specific pair on a specific territory should be similar among years.

The relative influence of males, independent of the influence of females and territories, can be determined from the repeatability of reproductive success between years for males that change partners and territories (Newton and Marquiss 1984). In natural systems, few males may switch territories or partners. In these situations the relative influence of males independent of that for femal and territories can be determined by calculating whether between year variance in reproductive success is greater for the set of territories where the males differ between years than for the set of territories with the same males present both years (modified from Hogstedt (1980) to include a term for males). The influence of females and territories on reproductive success can be determined using similar techniques.

In this Chapter I determined whether survival and reproductive success of individuals and on territories were repeatable between years. In addition, I determined whether the dates individuals and territories were chosen by females were repeatable between years. If reproductive success or survival were repeatable I expected the order in which males or territories were chosen by females to be consistent between years.

B. METHODS

General field methods and a description of the variables were presented in Chapter II. Only those territories ($\underline{N}$=181) that were in the same location and of similar size between years (greater than 75% of the larger territory overlapped the smaller territory) were included in the following analyses.

Yearly differences in the values of territories or the abilities of individuals lowers the repeatability of reproductive success and consequently the influence of pairs plus territories on reproductive success would be underestimated by inter-year correlations. At Chilkat Pass reproductive success and quality of chicks produced by willow ptarmigan differed among years (Appendix 4), reproductive success of older females was higher than that for yearlings (Chapter II) and individuals that paired with their previous partner had higher reproductive success than individuals that paired with an unfamiliar partner (Chapter III). Data were adjusted (grand mean minus group mean was added to all values for that group, Perrins and Jones 1974) for those effects prior to partitioning the variance in reproductive success.

Total variance in reproductive success (V_{Tot}) was divided into components due to variation among males (V_m), variation among females (V_f), variation among territories (V_t) and unexplained variation (V_u) such that

$$V_{Tot} = V_m + V_f + V_t + V_u.$$

By pairing observations between year x and year x+1 eight independent sets of data were obtained (Table IV-1, e.g. set F included females that switched territories and partners between years, females were the same but males and territories were different between years). The contribution of unexplained variance should have been similar for each set. Unexplained variance included measurement error, stochastic processes and other effects not included in the model.

Variance between years was estimated for each set (Appendix 5). Variance within males, females and territories between years (set A) was estimated using cases where both members of a pair returned to their previous territory between years. Variance within females plus territories between years (set B) and within males plus territories between years (set C) were estimated using cases where females and males, respectively, returned to their previous territories between years and paired with a new partner. It was not possible to estimate variance within pairs between years (set D) because pairs never switched territories. Variance within territories between years (set E) was estimated using territories where both members of the previous pair disappeared. Variance within females between years (set F) and within males between years (set G) were estimated using cases where females and males, respectively, switched territories between years. Variance between all the factors (set H) was estimated for each year and the weighted mean (weighted according to sample size) used. Ninety-five percent confidence intervals were calculated for each estimate of variance using the boot-strap method and 1000 iterations (Sokal and Rohlf 1981, Lanyon 1987).

If levels of a factor differed in their ability at producing offspring and these differences were repeatable between years (e.g. if abilities of females differed and were repeatable between years), then the estimate of between year variance in reproductive success for the set where levels of a factor were the same between years would have been lower than if levels of that factor also

Table IV-1. Composition of the sets for which variance in probability of females settling, date females settled, survival of adults, reproductive success and quality of chicks produced was estimated for willow ptarmigan at Chilkat Pass. The cases included in each set are outlined in the Methods.

Set	Factors For WhichLevels Were The Same Between Years	Factors For Which Levels Were Different Between Years	Components Included In The Variance Estimate
A	males + females + territories	---	V_u
B	females + territories	males	$V_m + V_u$
C	males + territories	females	$V_f + V_u$
D	males + females	territories	$V_t + V_u$
E	territories	males + females	$V_m + V_f + V_u$
F	females	males + territories	$V_m + V_t + V_u$
G	males	females + territories	$V_f + V_t + V_u$
H	---	males + females + territories	$V_m + V_f + V_t + V_u$

Male Effects = E - C i.e. $(V_m+V_f+V_u)-(V_f+V_u)$

Female Effects = C - A i.e. $(V_f+V_u)-(V_u)$

Territory Effects = H - E i.e. $(V_m+V_f+V_t+V_u)-(V_m+V_f+V_u)$

Unexplained Variance = A i.e. V_u

V_m - variance due to differences among males
V_f - variance due to differences among females
V_t - variance due to differences among territories
V_u - unexplained variance

varied (e.g. in set F the same females were used between years and the estimate of variance was lower than V_{Tot} by the amount V_f; $V_F = V_m + V_t + V_u$).

By subtracting the appropriate sets, variance attributed to a particular factor was determined (Table IV-1; e.g. variance attributed to females (V_f) was equal to set C ($V_f + V_u$) minus set A (V_u)). If there was more than one way to estimate variance attributed to a factor I used the sets with the largest sample sizes. Variance attributed to each factor was estimated 1000 times (subtracting the 1000 estimates for each set) and the 95% confidence interval determined from these estimates. If the confidence interval of the variance attributed to a factor included zero, then that factor did not influence the variable significantly (i.e. differences between the levels (individuals or territories) of that factor did not increase the variance in reproductive success significantly).

Categorical variables (whether or not a female settled, adult survival, total clutch loss and whether or not chicks were produced during the season) were analyzed using contingency analyses. For example, if some males consistently acquired partners and others consistently were unpaired, the probability of males acquiring a partner one year would have been associated positively with whether they acquired partners in the previous year.

Whether some females consistently fared better than others was estimated from set F (the same females between years but with different partners and territories) and whether some territories consistently were better than others from set E (the same territories between years but with different pairs). Sample size in set G was not sufficient to evaluate whether some males consistently fared better than others. Differences among territories, however, did not influence the categorical variables (see Results). Thus, whether some males consistently fared better than others was estimated from the combined sets G (the same males between years but with different partners and territories) plus B (the same males and territories between years but with different females).

The contingency analyses provided minimum estimates of whether differences among males, females and territories influenced survival of adults, probability of males acquiring a partner and probability of producing chicks. Repeatabilities for males were lowered by the amount that differences among females and territories influenced the variables because males that switched partners and territories were used in these analyses. Similarly, repeatabilities for females and territories were lowered by the amounts that differences among males and territories and males and females, respectively, influenced the variables. Yearly differences also may have reduced the strength of the relationships; some individuals or territories may have appeared inconsistent simply because the proportion of individuals or territories that were successful or unsuccessful varied among years.

C. RESULTS

The date females settled, reproductive success and quality of chicks produced did not differ among males (Table IV-2, the confidence intervals for the variance attributed to differences among males included zero). In addition, whether a male acquired a partner, survival of his partner, and whether he produced chicks from his first clutch or during the season were not positively associated between years (Table IV-3). The probability of a male having chicks hatch from his first clutch was negatively associated with whether or not he had chicks hatch from his first clutch the previous year (Table IV-3); a result opposite from that expected if some males were consistently better than others. The cause of this relationship was not obvious. Although, the nests of some males may have been found by predators more easily than the nests of others (e.g. the amount of time spent near their nest and the tendency to lead predators away from their nest may have differed among males) there was no reason for these tendencies to have switched between years. Possibly males moved to poorer territories or had poorer partners in one year than in the other.

Table IV-2. Variance in date female settled, reproductive success and quality of chicks produced for willow ptarmigan attributed to differences among males, females or territories. Lower and upper limits for the 95% confidence intervals are presented below the estimates.

	Variance Attributed To Differences Among			Unexplained Variance	Total Variance
	Males	Females	Territories		
Date Female Settled	77 -142 , 467	-41 -230 , 100	-72 -459 , 114	126 54 , 321	111 83 , 145
Reproductive Success					
Relative Clutch Size [a]	-0.3 -0.7 , 0.2	0.2 -0.4 , 0.5	0.8 [b] 0.5 , 1.1	0.4 0.2 , 0.6	1.0 0.8 , 1.2
Season Fledging Success	1.8 -2.1 , 5.3	-0.8 -5.2 , 2.9	-1.6 -4.7 , 1.2	6.0 3.0 , 10.0	5.6 4.3 , 6.9
Chick Quality					
Date Of First Egg	-3.9 -11.8 , 2.7	0.7 -8.3 , 9.8	8.4 [b] 3.4 , 14.5	10.8 4.4 , 17.8	15.5 11.5 , 20.6

a - date of first egg was used as a covariate in this analysis
b - the effect is significantly different from zero

Table IV-3. Frequency of female survival, males acquiring a partner, loss of first clutch and production of chicks during the season for males that changed partners and/or territories between year x and year x+1. Expected values are below the observed frequencies.

		Female Survival		Acquired A Partner		Loss Of First Clutch		Produce Chicks During Season	
		Year x		Year x		Year x		Year x	
		Yes	No	Yes	No	Yes	No	Yes	No
Year x+1	Yes	2	12	49	9	3	9	12	20
		3.0	11.0	49.0	9.0	6.0	6.0	14.7	17.3
	No	4	10	0	0	10	4	10	6
		3.0	11.0	0.0	0.0	7.0	6.0	7.3	8.7
$\underline{X}^2$		0.8		0.0		5.6		2.7	
$\underline{P}$		.36		1.0		.02		.10	

The date females settled, reproductive success and quality of chicks produced did not differ among females (Table IV-2). In addition survival of a female's partner, and whether she produced chicks from her first clutch or during the season were not positively associated between years (Table IV-4). Thus, differences among females did not appear to influence survival of their partners, their reproductive success or the quality of chicks they produced.

Date of first egg and relative clutch size differed in a consistent manner among territories (Table IV-2). Fifty-four percent of the variance in date of first egg and 80% of the variance in relative clutch size were attributed to differences among territories. Although sample sizes were not sufficient to test whether variance in number of chicks hatching and number of chicks fledging from first clutches were due to differences among territories, these two variables were related to clutch size ($\underline{r}=.59$, $\underline{df}=130$, $\underline{P}<.01$; $\underline{r}=.36$, $\underline{df}=65$, $\underline{P}<.01$, respectively). Thus the number of young produced from first clutches may have varied in a repeatable manner among territories although loss of clutches and chicks to predators may have been stochastic and resulted in hatching or fledging success not being repeatable between years. The date females settled and number of chicks fledging in the season, did not differ among territories (Table IV-2). In addition, whether a female settled on a territory, survival of adults on the territory, and whether chicks hatched from first clutches or during the season on the territory were not positively associated between years (Table IV-5).

The power of the tests involving categorical variables was low (see Methods), but trends should have been present if differences in quality among individuals and territories influenced the variables. However, trends towards a positive association between years were present in only 3 of 12 contingency analyses (Tables IV-3, IV-4, IV-5). Thus, differences in quality among individuals and territories probably did not influence the probability of females settling, survival of adults or the probability of producing chicks.

Table IV-4. Frequency of male survival, loss of first clutch and production of chicks during the season for females that changed partners and territories between year x and year x+1. Expected values are below the observed frequencies.

		Male Survival		Loss Of First Clutch		Produce Chicks During Season	
		Year x		Year x		Year x	
		Yes	No	Yes	No	Yes	No
Year x+1	Yes	6	1	4	10	11	4
		4.7	2.3	4.7	9.3	11.0	4.0
	No	2	3	3	4	8	3
		3.3	1.7	2.3	4.7	8.0	3.0
X^2		2.7		0.4		0.0	
P		.10		.51		.97	

Table IV-5. Fequency of adult survival, female settlement, loss of first clutch and production of chicks during the season for territories that were used by different pairs between year x and year x+1. Expected values are below the observed frequencies.

		Male Survival		Fe[illegible] Sur[illegible]		Female [illegible]ttlement		Loss Of First Clutch		Produce Chicks During Season	
		Year x		Year [illegible]		Year x		Year x		Year x	
		Yes	No	Yes	No	Yes	No	Yes	No	Yes	No
Year x+1	Yes	6	13	3	8	44	7	7	4	15	9
		6.3	12.7	3.8	7.2	42.9	8.1	6.9	4.1	13.8	10.2
	No	6	11	5	7	4	2	5	3	8	8
		5.7	11.3	4.2	7.8	5.1	0.9	5.1	2.9	9.2	6.8
X^2		0.6		0.5		1.6		0.0		0.6	
P		.81		.47		.21		.96		.43	

D. DISCUSSION

Using repeatability analyses to evaluate the influence of males, females and territories is based on the assumption that the relative qualities of individuals and territories are similar between years. If the relative qualities of individuals or territories vary, repeatability analyses will underestimate the influence of individuals and territories and overestimate the influence of stochastic processes. I removed variation in reproductive success among years, between age classes and due to individuals pairing with familiar partners, prior to performing the analyses. However, the ability of individuals still may differ between years if individuals that reproduced successfully one year use all their energy reserves (Clutton-Brook et al. 1986). Furthermore, characteristics of the habitat may vary among years if environmental conditions vary.

In willow ptarmigan (Martin and Cooke 1987, Schieck unpublished data) and other species (Lewis and Zwickel 1981, Smith 1981, Murie and Dobson 1987, Korpimaki 1988) previous production of young or number of young produced previously did not adversely affect current reproductive success. Thus the relative qualities of willow ptarmigan probably were similar among years.

Whether the relative values of territories were similar among years was more difficult to assess; structure of vegetation, vegetative growth, number of predators and population density may vary among years and these have been shown to affect reproductive success of <u>L. lagopus</u> (Miller et al. 1966, Watson et al. 1984b). In mid and late successional stages, species composition of the vegetation and vegetative structure are similar among years, particularly in northern areas where growth is slow (Babb 1977). Other environmental factors, however, may vary greatly between years. These environmental factors, however, should be similar for all territories I studied because the study area was only 4 km^2. Thus the relative values of territories should be similar among years.

Survival of partner, reproductive success and quality of chicks produced by willow ptarmigan at Chilkat Pass did not vary in a repeatable manner between years for either males or females. Thus quality of individual, over and above that due to age and familiarity with partner, appeared to have little influence on survival and reproduction in willow ptarmigan. More than half of the variation in date of first egg and relative clutch size were attributed to differences among territories. Possibly the amount and quality of food present on territories during laying differed among territories. Production of chicks was related to vegetative features on the territory in other populations of L. lagopus (Miller et al. 1966, Moss 1969, Watson et al. 1984b). In studies where vegetative characteristics did not appear to be related to production of chicks (Miller and Watson 1978, Erikstad et al. 1985, Steen et al. 1985) the important characteristics may not have been analysed and the influence of differences among territories overlooked. Alternatively, differences among territories may not have influenced reproduction in some populations if resources were superabundant (e.g. Steen et al. 1985), if individuals in poorer habitats defended larger territories than individuals in good habitats (Watson 1964, 1970, Lance 1978b, Miller and Watson 1978) or if individuals on poor territories foraged outside their territory (Steen et al. 1985).

Between year repeatability of reproductive success for female L. lagopus has been analysed on three other occasions. Hannon et al. (1988) found that at Chilkat Pass, but not in northern Manitoba, some female willow ptarmigan consistently bred earlier than others. Date of first egg was positively related to clutch size (Hannon et al. 1988) and recruitment (Martin and Hannon 1987) for willow ptarmigan at Chilkat Pass. Hannon et al. (1988), however, did not evaluate whether the repeatability of reproductive success they found was due to inherent differences among females, or due to differences among territories and breeding philopatry. Moss and Watson (1982) argued that size of eggs greatly influenced survival and recruitment of red grouse chicks, and found that some females consistently laid larger eggs than others, both in the wild and in captivity. They concluded that most of the differences in egg sizes found between females were due to differences among females' inherent abilities, not due to differences among territories. Erikstad et al. (1985) used an analysis similar to the one I used (only they did not consider the influence of males, did not provide information regarding placement of territories between years and did not provide confidence intervals for their estimates) and found clutch size of female willow grouse was repeatable between years. They concluded that differences among females' abilities were more important than differences among qualities of territories. I had larger sample sizes and evaluated more variables than either Moss and Watson (1982) or Erikstad et al. (1985), yet did not find consistent differences in reproductive success among females.

Reproductive success was repeatable between years for individuals in other species (Kliuijver 1951, Perrins and Jones 1974, Searcy 1979, Findlay and Cook 1980, Smith 1981, van Noordwijk et al. 1981, Newton and Marquis 1984, Nol et al. 1984, Coulson and Thomas 1985, Harvey et al. 1985, Clutton-Brook et al. 1986, Thouless and Guinness 1986). In addition, reproductive success on a territory was repeatable between years for other species (Krebs 1970, Hogstedt 1980, Askenmo 1984, Newton and Marquiss 1984, Blancher and Robertson 1985, Coulson and Thomas 1985, Siegel-Causey and Hunt 1985, Lanyon and Thompson 1986, Newton et al. 1986, Nilsson 1987, Stacey and Ligon 1987, Korpimaki 1988). In most of these studies, however, breeding site fidelity was high and the observed repeatability of reproductive success may have been due to consistent differences among the qualities of territories, individuals or both territories and individuals. Furthermore, in many of these studies reproductive success may not have been repeatable simply because territories were not plotted and may not have been of similar size or shape between years.

The influence of qualities of individuals and territories on reproductive success have been separated for relatively few species (black-billed magpies (Pica pica), Hogstedt 1980; Eurasian sparrowhawks (Accipiter nisus), Newton and Marquiss 1984; kittiwake gulls (Risa tridactyla), Coulson and Thomas 1985; song sparrows (Melospiza melodia), Hochachka et al. in press; and willow ptarmigan, Erikstad et al. 1985, this study). In black-billed magpies, song sparrows and willow ptarmigan at Chilkat Pass differences among qualities of territories had greater influences on reproductive success than differences among qualities of individuals, whereas the opposite was true for willow ptarmigan in Norway, Eurasian sparrowhawks and kittiwake gulls. Thus, the relative influence of qualities of individuals and territories differed among species and even among populations within a species. More studies are needed before general patterns can be evaluated.

The influence of stochastic events on reproductive success and survival is even less well understood. In willow ptarmigan at Chilkat Pass, about half of the variance in date of first egg and relative clutch size was unexplained by differences among territories and individuals. In addition, other measures of reproductive success, quality of chicks produced and survival of adults were not repeatable between years for individuals or territories. Thus, at Chilkat Pass quality of individual and territory may have had much less influence on survival of adults and production of offspring than stochastic processes.

Although differences in quality among territories at Chilkat Pass resulted in some individuals starting to lay before others and having larger clutches than others, these differences were not great; 69% of the females laid their first egg within 4 days of the median date of first egg and 72% of the first clutches were 7, 8, or 9 eggs. Differences in quality among individuals and territories may have had little influence on reproductive success at Chilkat Pass because all territories may have been in good habitat and resources abundant on all territories.

Subsequent to initial differences in reproductive success, stochastic process may have greatly affected production of offspring in willow ptarmigan at Chilkat Pass. Loss to predation may be stochastic and between 30 and 70% of first clutches were destroyed by predators each year (Martin et al. in press) In addition,approximately 30% of the chicks disappeared before fledging. In other species stochastic ~~processes~~ also appeared to greatly influence reproductive success; between year repeatability of reproductive success for individuals and territories ranged from 0.00 to 0.63 (Smith 1981, Findlay and Cooke 1980, Newton and Marquis 1984, Blancher and Robertson 1985, see Lessells and Boag 1987 for corrections of some of these estimates). Thus between 37 and 100% of the variation in reproductive success may have been due to stochastic processes. The relative importance of stochastic process on reproductive success may have been under-emphasized in the past due to difficulties with estimating them.

At Chilkat Pass some territories repeatedly had earlier dates of first egg and larger clutches than others. The relative dates territories were selected, however, were not repeatable between years. In addition, the first yearling females to settle did not have higher survival or reproductive success than yearlings that settled later (Chapter II) nor was choice of breeding situations consistent among the sets of yearling females in the settling experiment (Chapter II). Furthermore, returning breeders that switched territories did not have higher survival or reproductive success after than before switching (Chapter III). Thus, even though there were differences in qualities of territories that potentially affected reproductive success, individuals did not choose territories based on those differences.

If the important characteristics of territories were not detectable when individuals were settling, individuals may not have been able to choose the best available territory (Searcy 1979, Wootton et al. 1986). Rather they may have simply chosen the appropriate habitat type (Weatherhead and Boak 1986) and settled at random within this habitat (Wootton et al. 1986, Lightbody and Weatherhead 1987). The date on which meadows became free of snow may have influenced timing of production of eggs for willow ptarmigan at Chilkat Pass (Hannon et al. 1988) yet that may not have been discernable at the time of settling since willow ptarmigan settled up to a month before snow-melt (pers. obs.). Individuals that bred previously, however, should have known the position of good habitat, yet individuals switching territories between years did not move to better territories. Possibly, predation of clutches and young was stochastic and masked benefits of being on good territories; even though clutch size differed among territories in a repeatable manner, production of young may not have been repeatable. If this was correct, choice of territory may have been of little consequence as long as the territory w[illegible]od habitat.

Partitioning the variance in reproductive success into components due to differences among qualities of individuals and territories provides a powerful tool for studying territory and mate choice; if differences among qualities of individuals or territories influence reproductive success, good breeding situations should be chosen before poorer ones (Fretwell and Lucas 1970). Polygyny or polyandry may occur, if some breeding situations are better than others, even after one partner has settled (Orians 1969). If, however, there are differences among qualities of breeding situations that influence reproductive success, yet good breeding situations are not chosen before poorer situations, then factors other than expected reproductive success probably influence territory choice and conventional settlement models may not be applicable.

V. THESIS DISCUSSION

Theoretical models of settlement provide an appealing evolutionary framework for studying patterns and process. Orians' (1969) "polygyny threshold model" and Fretwell and Lucas' (1970) "habitat selection model" have become well known and many studies have been designed to test predictions arising from these. In many species of birds, individuals choose where to settle based on the characteristics of territories and partners (e.g. Ralph and Pearson 1971, Stacey and Ligon 1987) with more individuals settling in good habitats (e.g. Pleszczynska and Hansell 1980) or with good partners (e.g. Weatherhead and Robertson 1977). However, these patterns are not universal and the generality of Orians' (1969) and Fretwell and Lucas' (1970) models needs to be evaluated.

Searcy (1979) and Wootton et al. (1986) argue that where differences among breeding situations are slight, individuals may not be able to evaluate the differences and use other criteria when settling. Even when values of breeding situations differ, familiarity with area, partner or neighbors may more than compensate an individual for not moving to a better breeding situation between breeding attempts (Smith 1978, Lewis and Zwickel 1981, Lanyon and Thompson 1986). Individuals on familiar territories may survive better and have a higher reproductive success if resources and refuges are difficult to find but located similarly between years (Greenwood and Harvey 1982). Individuals with familiar partners may breed earlier in species where breeding activities are complex and must be synchronized (Rowley 1983). Being familiar with neighbors may reduce the cost of acquiring a breeding territory when competition for territories is great (Yasukawa 1979, Picman 1987).

The biology of willow ptarmigan and structure of their habitat makes it difficult to predict a priori whether familiarity with area, partner or neighbors will influence reproductive success and consequently have potential to influence choice of breeding situation. Familiarity with area may be important at Chilkat

Pass since the habitat appeared complex; many ponds, streams and wet meadows are scattered throughout the area and the species composition and density of vegetation varies among territories. Food and refuges, however, may not be difficult to find because willow ptarmigan are herbivorous (Johnsgard 1983, and references therein) and roost and nest near or under many types of shrubs (pers. obs.). Synchronizing breeding activities may be a problem because pairs do not spend the winter together (Mossop 1988 pers. obs.). Partners, however, appear to become synchronized quickly (the few females that settled relatively late, began laying within a week of settling) and most individuals pair two or three weeks before nesting sites become free of snow. Familiarity with neighbors may be important because intrasexual competition for breeding territories appears to be intense and population density on the study area is greater than most other areas in the Yukon (D. Mossop pers. comm.). During this study, though possibly not at higher population densities (Hannon 1983), most, possibly all, males and females acquired a breeding territory. Thus, prior to documenting settlement patterns and analysing the differences between individuals with familiar versus unfamiliar partners and on familiar versus unfamiliar territories I was unable to predict which factors would influence territory choice.

Choice of breeding situation by willow ptarmigan that had bred previously appeared to be more influenced by familiarity with partners and neighbors than by differences in quality among territories or partners (Chapter III). That was true even though 1) differences among territories influenced date of first egg and clutch size, 2) individuals had little opportunity to breed with familiar partners (overwinter mortality of adults was about 50%) and 3) about half the neighbors were unfamiliar each year. Choice of breeding situation by first-time breeders did not appear to be influenced by differences in quality of territories or partners (Chapter II). The factors influencing settlement for those individuals was not known although mortality of previous breeders and spacing behavior may have been important.

To compare settlement in willow ptarmigan with settlement in other species I compiled a list of studies in which the influence of characteristics of the habitat and partner and familiarity with area, partner and neighbors had been evaluated. No distinction was made between first-time and previous breeders in these studies, thus I have not evaluated these groups separately. In many different types of habitat individuals chose territories based on habitat characteristics (Tables V-1 and V-2). Possibly habitats were more complex in these other studies than for willow ptarmigan at Chilkat Pass resulting in differences among territories that were discernible at the time individuals were choosing territories (Searcy 1979, Wootton et al. 1986). However, Orians (1969) suggested that marsh habitats were more complex than most other types and three of six studies in which choice of territory was not related to habitat characteristics, were in marsh habitats (Table V-1). Thus complexity of habitat may be only one of many factors that influences whether individuals choose territories based on habitat characteristics.

In Orians' (1969) settlement model polygamy occurs because some territories or partners are better than others; more than one individual settles on the best territories or with the best partners. Thus, in polygamous species variation in quality among territories or partners should be greater than in monogamous species, and the influence on settlement of characteristics of the territory or partner should be more noticeable. This trend was not apparent; characteristics of the territory or partner influenced settlement in 21 of 24 polygamous populations and 17 of 18 monogamous populations (Tables V-1 and V-2). In two populations, both of which were polygamous, neither characteristics of territories nor characteristics of partners appeared to influence settlement (Table V-1). Thus, a polygyny threshold may not occur in many populations. Rather polygyny may be due to site fidelity of previous breeders (Eliason 1986, Searcy and Yasukawa

Table V-1. Factors influencing territory selection in male birds. Habitats were classified as tundra (Tund), grassland (Grass), marshland (Marsh), scrub woodland (Scrub), decidious woodland (WoodD), coniferous woodland (WoodC), mixed woodland (WoodM), residential (Town) and in laboratory (Lab). Mating systems were classified as monogamous (Mon), polygamous (Pol) or Promiscus (Pro). All classifications were taken from the articles that are cited.

Species	Habitat	Mating System	Characteristics Of		Familiarity With			Author
			Habitat	Partner	Area	Partner	Neighbors	
Willow Warbler (Phylloscopus trochilus)	Scrub	Pol	-	-	Y?	-	Y?	Lawn 1982
Blackpoll Warbler (Dendroica striata)	WoodC	Pol	Y	-	-	-	-	Eliason 1986
Song Sparrow (Melospiza melodia)	Scrub	Mon	Y	-	N	-	N	Arcese and Smith 1985
Field Sparrow (Spizella pusilla)	Scrub	Pol	N	-	-	-	-	Best 1977
Rufous-collared Sparrow (Zonotrichia capensis)	Town	Mon	Y?	-	-	Y?	-	Smith 1978
White-crowned Sparrow (Zonotrichia leucophrys)	Grass	Mon	Y	Y	-	-	-	Ralph and Pearson 1971
Painted Bunting (Passerina ciris)	Scrub	Pol	Y	-	Y?	Y?	-	Lanyon and Thompson 1986
Blackbird (Turdus merula)	-	Mon	-	-	Y?	-	-	Greenwood and Harvey 1982
Eastern Kingbird (Tyranus tyranus)	Scrub	Mon	Y?	-	-	-	-	Blancher and Robertson 1985
Red-winged Blackbird (Aegetiaus phoeniceus)	Marsh	Pol	-	-	-	-	Y	Yasukawa 1979
"	Marsh	Pol	-	-	N	-	Y	Picman 1987
Pinyon Jay (Gymnorhinus cyanocephalus)		Mon	-	Y	-	-	-	Marzluff and Balda 1987
Barn Swallow (Hirundo rustica)	Marsh	Mon	-	-	-	-	Y?	Shields 1984
Acorn Woodpecker (Melanerpes formicivorus)	WoodM	Pro	Y	-	-	-	-	Stacey and Lingon 1987
Tropical House Wren (Troglodytes aedon)	Scrub	Mon	-	-	-	N	Y?	Freed 1987
Marsh Wren (Cistothorus palustris)	Marsh	Pol	Y	-	-	-	-	Leonard and Picman 1987

Table V-1. cont.

Species	Habitat	Mating System	Characteristics Of		Familiarity With			Author
			Habitat	Partner	Area	Partner	Neighbors	
Spotted Sandpiper (Actitis macularia)	Grass	Pol	-	Y	-	-	-	Oring et al. 1983
Temminck's Stint (Calidris temminckii)	Grass	Pro	-	-	Y?	-	-	Hilden 1979
Semipalmated Sandpiper (Calidris pusilla)	Marsh	Mon	-	-	Y?	N	-	Gratto et al. 1985
Ruffed Grouse (Bonasa umbellus)	WoodM	Pro	Y	-	-	-	-	Boag 1976
Willow Ptarmigan (Lagopus lagopus)	Scrub	Pol	-	-	-	-	Y?	Lance 1978b
"	Scrub	Pol	-	-	Y?	-	-	Hannon and Roland 1984
"	Scrub	Pol	N	N	N	Y	Y?	this study
Blue Grouse (Dendragapus obscurus)	WoodC	Pro	Y?	-	-	[illegible]	-	Lewis and Zwickel 1981
"	"	"	-	-	-	-	Y?	Lewis 1986
"	"	"	Y?	-	Y?	-	Y?	Jamieson and Zwickel 1983
Black Grouse (Tetrao tetrix)	Scrub	Pro	Y	-	Y?	-	Y?	DeVos 1983
Sharp-tailed Grouse (Pedioecetes phasianellus)	Grass	Pro	-	-	-	-	Y?	Moyles and Boag 1981
Common Capercaillie (Tetrao urogallus)	WoodC	Pro	-	-	Y?	-	-	Wegge and Larsen 1987
Tengmalm's Owl (Aegolius funereus)	WoodM	Mon	Y	-	Y?	-	-	Korpimaki 1987, 1988
Kittiwake Gull (Rissa tridactyla)	Town	Mon	Y	-	-	-	Y	Coulson and Thomas 1985
Luaghing Gull (Larus atricilla)	Marsh	Mon	Y	-	-	-	-	Montevecchi 1978
Caspian Terns (Sterna caspia)	Grass	Mon	Y?	-	-	N?	-	Cuthbert 1985
Double-crested Cormorant (Phalacrocrax auritus)	Beach	Mon	Y	-	-	-	-	Siegel-Causey and Hunt 1986

Y = yes, N = no and - = unknown
? - suggested but not measured

Table V-2. Factors influencing territory selection in female birds. Habitats were classified as tundra (Tund), grassland (Grass), marshland (Marsh), scrub woodland (Scrub), decidious woodland (WoodD), coniferous woodland (WoodC), mixed woodland (WoodM), residential (Town) and in laboratory (Lab). Mating systems were classified as monogamous (Mon), polygamous (Pol) or Promiscus (Pro). All classifications were taken from the articles that are cited.

Species	Habitat	Mating System	Characteristics Of		Familiarity With			Author
			Habitat	Partner	Area	Partner	Neighbors	
Middendorff's Grasshopper-warbler (Locustella ochotensis)	Scrub	Mon	Y	N	-	-	-	Nagata 1986
Blackpoll Warbler (Dendroica striata)	WoodC	Pol	N	Y	-	-	-	Eliason 1986
Song Sparrow (Melospiza melodia)	Scrub	Mon	Y	-	N	-	N	Arcese and Smith 1985
Field Sparrow (Spizella pusilla)	Scrub	Pol	Y	N	-	-	-	Best 1977
Savannah Sparrow (Passerculus sandwichensis)	Marsh	Mon	N	-	-	-	-	Bedard and Lapointe 1984
Rufous-collared Sparrow (Zonotrichia capensis)	Town	Mon	Y?	-	-	N?	-	Smith 1978
Dickcissel (Spiza americana)	Grass	Pol	Y	-	-	-	-	Zimmerman 1966
Lark Bunting (Calamospiza melanocorys)	Grass	Pol	Y	-	-	-	-	Plszczynska and Hansell 1980
Eastern Kingbird (Tyranus tyranus)	Scrub	Mon	Y?	-	-	-	-	Blancher and Robertson 1985
Bobolink (Dolichonyx oryzivorus)	Grass	Pol	N	N	-	-	-	Wootton et al. 1986
"	"	"	Y	-	-	-	-	Wittenberger 1980
Pied Flycatcher (Ficedula hypoleuca)	WoodD	Mon	Y?	N?	-	-	-	Alatalo et al. 1984
"	WoodD	Mon	Y?	Y	-	-	-	Gottlander 1987
Red-winged Blackbird (Agelaius phoeniceus)	Marsh	Pol	-	-	Y?	Y?	Y?	Picman 1981
"	"	"	Y	Y	-	-	-	Yasukawa 1981

Table V-2. cont.

Species	Habitat	Mating System	Characteristics Of		Familiarity With			Author
			Habitat	Partner	Area	Partner	Neighbors	
Red-winged Blackbirds (Agelaius phoeniceus)	"	"	Y	-	-	-	-	Lenington 1980
"	"	"	N	Y	-	-	-	Weatherhead and Robertson 1977
"	"	"	Y	-	-	-	-	Holm 1973
Yellow-headed Blackbird (Xanthocephalus xanthocephalus)	Marsh	Pol	N	N	-	-	-	Lightbody and Weatherhead 1987
Pinyon Jay (Gymnorhinus cyanocephalus)	-	Mon	-	Y	-	-	-	Marzluff and Balda 1988
Yellow-rumped Caciques (Cacicus cela)	WoodM	Pol	Y	-	-	-	Y	Robinson 1986
Village Weaverbird (Ploceus cucullatus)	Lab	Pol	Y?	-	-	-	-	Collias and Victoria 1978
Acorn Woodpecker (Melanerpes formicivorus)	WoodM	Pro	Y	-	-	-	-	Stacey and Ligon 1987
Tropical House Wren (Troglodytes aedon)	Scrub	Mon	-	-	-	N	Y?	Freed 1987
European Wren (Troglodytes troglodytes)	Scrub	Pol	Y?	Y?	-	-	-	Garson 1980
Long-billed Marsh Wren (Telmatodytes palustris)	Marsh	Pol	Y	-	-	-	-	Verner and Engelsen 1970
Marsh Wren (Cistothorus palustris)	Marsh	Pol	Y	-	-	-	-	Leonard and Picman 1987
Barn Swallow (Hirundo rustica)	Marsh	Mon	-	-	-	-	Y?	Shields 1984
Tengmalm's Owl (Aegolius funereus)	WoodM	Mon	Y	Y	Y?	-	-	Korpimaki 1987, 1988
Spotted Sandpiper (Actitis macularia)	Grass	Pol	-	Y	-	-	-	Oring et al. 1983
Semipalmated Sandpiper (Calidris pusilla)	Marsh	Mon	-	-	Y?	N	-	Gratto et al. 1985
Temminck's Stint (Calidris temminckii)	Grass	Pro	-	-	N?	-	-	Hilden 1979
Whimbrel (Numenius phaeopus)	Tund	Mon	Y	-	-	-	-	Skeel 1983
Long-billed Curlew (Numenius americanus)	Grass	Mon	-	-	-	Y?	-	Redmond and Jenni 1982

Table V-2. cont.

Species	Habitat	Mating System	Characteristics Of		Familiarity With			Author
			Habitat	Partner	Area	Partner	Neighbors	
Willow Ptarmigan (Lagopus lagopus)	Scrub	Pol	N	Y	N	Y	N?	this study
Luaghing Gull (Larus atricilla)	Marsh	Mon	Y	-	-	-	-	Montevecchi 1978
Kittiwake Gull (Rissa tridactyla)	Town	Mon	Y	-	-	-	Y	Coulson and Thomas 1985
Caspian Terns (Sterna caspia)	Grass	Mon	Y?	-	-	N?	-	Cuthbert 1985
Double-crested Cormorant (Phalacrocrax auritus)	Beach	Mon	Y	-	-	-	-	Siegel-Causey and Hunt 1986
Goldeneye (Brucephala clangula)	Marsh	Mon	[illegible]	-	Y	-	-	Dow and Fredga 1983

Y = yes, N = no and - = unknown
? - suggested but not measured