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UNIVERSITY OF ALBERTA

POPULATION ATTRIBUTES AND REPRODUCTIVE BIOLOGY OF ROCK PTARMIGAN IN THE CENTRAL CANADIAN ARCTIC

BY

RICHARD CLEMENT COTTER

A thesis submitted to the Faculty of Graduate Studies and Research in partial fulfillment of the requirements for the degree of MASTER OF SCIENCE.

DEPARTMENT OF ZOOLOGY

EDMONTON, ALBERTA

FALL 1991

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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 POPULATION ATTRIBUTES AND REPRODUCTIVE BIOLOGY OF ROCK PTARMIGAN IN THE CENTRAL CANADIAN ARCTIC submitted by RICHARD CLEMENT COTTER in partial fulfillment of the requirements for the degree of MASTER OF SCIENCE.

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ABSTRACT

This study examined the reproductive biology and population dynamics of rock ptarmigan (*Lagopus mutus*) in the central Canadian Arctic. Rock ptarmigan from two locations near Windy Lake, N.W.T., were banded and fitted with radio transmitters in 1988 and 1989. These two locations differed principally in the density of nesting raptors, one high (SWL study site) and one low (NWL study site). Radio-marked birds were followed from onset of incubation through to fledging in both years. Breeding populations of rock ptarmigan at Windy Lake fluctuated in size from year to year. Data from this study and previous work at Windy Lake, although inconclusive, appear to indicate a 10-year cycle in population size, which is what has been observed in other populations. Mean clutch size of completed first nests was 8.7 eggs, which produced for that part of the female population that completed a first clutch an average of 4.3 offspring, giving a reproductive efficiency of nearly 50%. Clutch size was significantly larger among adult than yearling hens. However, there was no difference between the two age groups in fledging or breeding success, mean brood size at fledging, nor survival of breeding females to the next year (true in male rock ptarmigan as well). Renesting was observed, but was restricted mostly to hens that lost their nest during laying. The only significant difference in demography between ptarmigan from the two locations was observed in 1988 when ptarmigan from SWL experienced significantly higher nest loss than ptarmigan from NWL. Predation was the major identified cause of nest loss at both sites, with predation of the hen accounting for approximately 25% of all losses and predation of the clutch most of the remainder. Falcons (principally *Falco rusticolus*, but also *F. peregrinus*) were responsible for 95% of all depredations on adult rock ptarmigan, with no sex or age bias observed among ptarmigan in susceptibility to predation. The major nest predators probably included gulls (*Larus* spp.), foxes (either *Alopex lagopus* or *Vulpes vulpes*), and ermine (*Mustela erminea*). Nest loss was highest in 1988, which coincided with a crash in microtine numbers. Yearling hens suffered proportionally higher nest loss than adults that year, suggesting an increased susceptibility to nest predation during years of low microtine numbers, particularly among yearling ptarmigan.

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TABLE OF CONTENTS

LIST OF TABLES

Table | Page

Table Page

LIST OF FIGURES

Figure Page

I. GENERAL INTRODUCTION

The rock ptarmigan (*Lagopus mutus*) is the most northerly distributed and best arctic-adapted of all grouse (subfamily Tetraoninae), breeding in the rocky, desert-like habitat of the high arctic (Godfrey 1986). It has one of the widest distributions of any grouse species (Johnsgard 1983), and yet has been one of the least studied. Because of its holarctic distribution, the specific regions inhabited by rock ptarmigan may differ in several aspects, such as topography, climate, food resources, and predation pressures. In light of these inherent differences between regions, it is useful to have comparative data on all aspects of the biology and ecology of the rock ptarmigan throughout its range in order to understand the extent of adaptive plasticity in the species.

Unfortunately, arctic research has been greatly limited in the past, because of the expense and the logistical difficulties of working in an isolated and a harsh environment. Recent advances in research techniques such as the increased accessibility of radio telemetry, as well as an increased interest in northern ecosystems and wildlife problems by universities and governments have made more and better research possible.

Some aspects of the biology of rock ptarmigan, such as breeding behaviour (MacDonald 1970, Watson 1972), moult patterns (Salomonsen 1939, Hewson 1973, Watson 1973), and diet and foraging behaviour (Weeden 1969, Pullianinen 1970, Bernard-Laurent 1983, Thomas 1984) have been well documented. Most research into the reproductive biology (Weeden 1965, Steen and Unander 1985, Brodsky 1986, Olpinsky 1986) and population dynamics (Gudmundsson 1960, Watson 1965, McGowan 1972, Weeden and Theberge 1972, Desmet 1988, Gardarsson 1988) of this species, however, is incomplete because of difficulties in obtaining sufficient sample sizes, difficulties in locating and following birds throughout the entire breeding season, and difficulties in determining the fate of individuals. With the advent of radiotelemetry, problems such as these have been overcome to some extent and a more complete picture of both reproductive biology and population attributes of such species as the rock ptarmigan may be obtained.

The first objective of my study was to describe and document population attributes of rock ptarmigan in the central Canadian Arctic. Timing of breeding events, dispersion, breeding philopatry, recruitment, population structure, natality and mortality (principally predation) of rock ptarmigan over the course of the breeding season were studied and are discussed in Chapter II.

The second objective of this study was to describe the reproductive biology of rock ptarmigan and to examine the patterns of attrition in fecundity. Information on the breeding chronology, reproductive parameters (clutch size, number hatched, number fledged), reproductive success (hatching and fledging success), reproductive loss (predation of eggs, chicks, and breeding adults), and population productivity is presented in Chapter III.

Such information as presented in Chapter II and Chapter III on rock ptarmigan, compared with studies from regions with different selective forces, provides insight into mechanisms affecting survival, densities, population dynamics, and fecundity. In Chapter IV I discuss the results presented on population attributes and reproductive biology, and in particular I consider the role of observed mortality levels and breeding success on yearly changes in the size of spring breeding populations.

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II. POPULATION ATTRIBUTES OF ROCK PTARMIGAN IN THE CENTRAL CANADIAN ARCTIC

INTRODUCTION

The rock ptarmigan (*Lagopus mutus*) has one of the widest distributions of any grouse species (Johnsgard 1983), yet has been one of the least studied. Data on population dynamics have been collected in various parts of its range by a number of researchers (Williams 1954, Gudmundsson 1960, Weeden 1963, Weeden 1964, Watson 1965, Jenkins and Watson 1970, MacDonald 1970, McGowan 1972, Weeden and Theberge 1972, Steen and Unander 1985, Nielsen 1986, Brodsky 1986, Olpinsky 1986, Poole 1987, Desmet 1988, Gardarsson 1988). Most of this information had been collected through counts or observations of unmarked birds. Information on causes and rates of mortality has also been collected (Gudmundsson 1960, Weeden 1962, 1963, Watson 1965, Weeden and Theberge 1972, Unander and Steen 1985, Nielsen 1986, Poole 1987, and Gardarsson 1988), although on fewer populations than considered in studies of population dynamics. Most of these studies relied on finding unmarked birds that were killed on a study area, or by analyzing prey remains of predators (eg. Nielsen 1986, Poole 1987).

While these studies have provided much information on various attributes of populations of rock ptarmigan, they have raised further questions which need to be addressed. Generally, these are more specific questions. Are there age or sex biases in predation, philopatry, settlement patterns, and territory size? Are ptarmigan more susceptible to predation at certain times of the year and within the breeding season? Do age and sex ratios vary with phases of a population cycle? Are there differences in seasonal movements either within a sex or between sexes? To examine these questions requires specific techniques: banding birds to enable field identification and radio-marking birds to enable tracking of individuals over a required period of time. The latter enables a researcher to locate birds on the study area at will, as well as to ascertain their fate (*i.e.* alive/dead), to locate their nests readily, to follow the fate of the clutch and brood, and to study movements and territorial activities. If a bird had been depredated, telemetry makes it possible to locate its remains and possibly determine the date of death and identity of the predator. Few studies have attempted to address any of these aspects of rock ptarmigan biology using radio-telemetry, and none from the Canadian arctic, which encompasses a major portion of the rock ptarmigan's range.

The primary objective of this study was to describe the population attributes of rock ptarmigan in the central Canadian arctic. Specific objectives were to document the timing of spring arrival on the breeding grounds, patterns of dispersion, breeding philopatry, and demography of a breeding population of rock ptarmigan. The secondary objective was to examine the nature and effect of predation on rock ptarmigan survival, population structure and dynamics. To achieve these objectives, data were compared between an area with a high density of predators (primarily raptors) and one with a low density. Throughout this study the densities and location of raptor eyries was known for the Kilgavik region (determined by the Department of Renewable Resources of the Government of the Northwest Territories). Raptors, and in particular gyrfalcons (*Falco rusticolus*), are major predators of rock ptarmigan during the breeding season (Jenkins *et al.* 1964, Bergerud and Mossop 1984, Nielsen 1986, Poole 1987, Poole and Bromley 1988). A specific objective was to determine which predators were involved and their relative impact, as sources of mortality, on a population of rock ptarmigan. Other objectives were to determine whether an age or sex bias existed in vulnerability to predation in rock ptarmigan, the timing of predation relative to the annual cycle of ptarmigan, and whether temporal and spatial differences existed in mortality patterns. The extent to which differences were related to seasonal and annual variables, and to spatial differences (high and low predator densities) was examined.

STUDY AREA AND METHODS

Study Site

The study area, located at Windy Lake, is approximately 4 km inland from Hope Bay in the Northwest Territories (approximately 68° 5' N and 106° 40' W). Windy Lake lies almost in the centre of the Kilgavik study area used by Poole (1987) in his study of gyrfalcons (*Falco rusticolus*). The closest settlement was Cambridge Bay, N.W.T., 140 km to the northeast across Dease Strait.

Topographically the area consists of gently rolling tundra punctuated by small rock outcrops. The main geological features of the area are granitic intrusions, and diabase dykes and sills (Fraser 1964). The diabase formations (lines of cliffs or circular blocks of rock rising above the surrounding terrain) provide nesting ledges for gyrfalcons, peregrine falcons (*Falco peregrinus*), golden eagles (*Aquila chrysaetos*), rough-legged hawks (*Buteo lagopus*), and ravens (*Corvus corax*). These are the major predators of ptarmigan (Cramp and Simmons 1980, Bergerud and Mossop 1984, Nielsen 1986, Poole 1987).

The flora consists of wide-ranging, low-arctic tundra species (Porsild and Cody 1980). The dominant vascular plants are willow (*Salix* spp.), birch (*Betula* spp.), crowberry (*Empetrum* spp.), Labrador tea (*Ledum palustre*), and bell heather (*Cassiope tetragona*).

The climate of the region is dry and cold. Precipitation varies from 100 to 150 mm annually, and the January and July mean daily maximum temperatures are -30 and 10° C (Poole 1987). Snow covers the land approximately 260 days of the year, with snow-melt usually beginning from mid-May to early June. For a further description on the flora, fauna, and climate of the region refer to Poole and Bromley (1988).

Two populations of rock ptarmigan were studied at Windy Lake: one was located near its north end (NWL population, Fig. II-1,A), the other near its south end (SWL population, Fig. II-1,B). The two populations were 5.5 km apart at their closest point, and covered areas similar in size (ca. 8.5 km^2 each) (Fig. II-1). In 1989, the northern boundary of NWL was modified slightly to remove the northernmost section (see Fig. II-1). Nevertheless, the area used in 1989 overlapped 91% the area used in 1988. Density of male and female rock ptarmigan were calculated as *n* per 100 ha by dividing number of resident, breeding birds in the two populations by total area inhabited by each population (see Fig. II-1).

Although the topography and vegetation of the two areas was similar, the relative nesting density of raptors in the vicinity of each site (<10 km) differed (Fig. II-1), as a consequence of availability of suitable nesting sites within each area (Poole 1987). From 1984 to 1986 inclusive, rock ptarmigan comprised 73.2% of the total prey biomass in the diet of resident gyrfalcons during the breeding season at Kilgavik (Poole 1987). An assumption of this study was that predation pressure on rock ptarmigan would be a function of

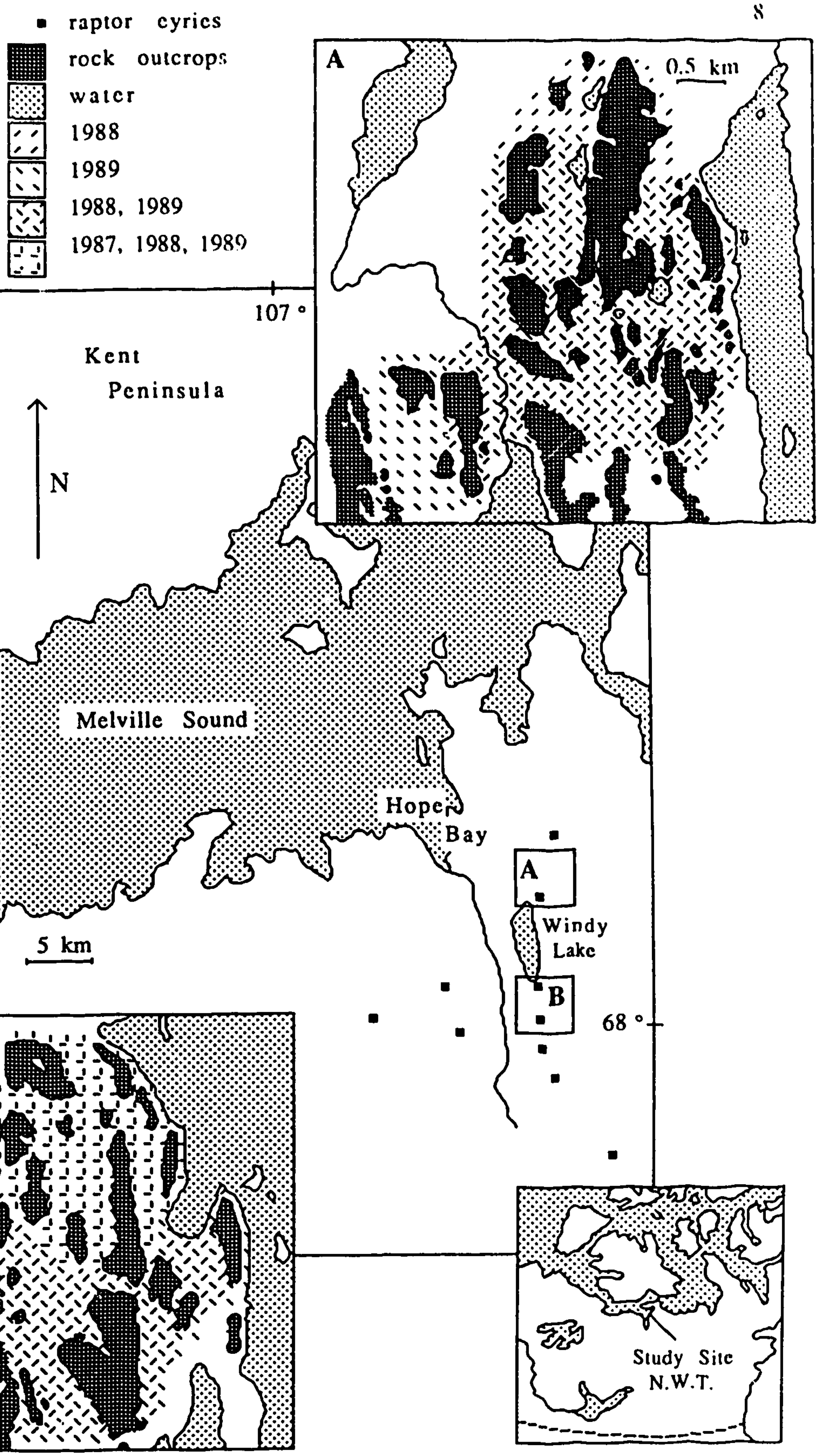

Figure II-1: Map of North Windy Lake (NWL) (A) and South Windy Lake (SWL) (B) study sites at Windy Lake, N.W.T., and location of raptor eyries within 10 km in 1988 and 1989.

the number and proximity of occupied territories of raptor species during the breeding season. Locations of all active eyries in 1988 and 1989 within 10 km of the two populations are shown in Fig. II-1.

Methods

Nearly all (96%) resident rock ptarmigan at the NWL and SWL sites were captured at the onset of the breeding season (early June) in 1987, 1988, and 1989 using a noose pole or ground nets (Hannon 1983). Sex, age, weight, and wing chord (flattened) were recorded for all individuals. Birds were classed as either adult (≥ 1 year old) or yearling (< 1 year old) based on the pigmentation of the eighth and ninth primaries (Weeden and Watson 1967, Parker *et al.* 1985). In 1988 and 1989, if the captured bird had been banded previously at Windy Lake (*i.e.* in either 1987 or 1988), it was defined as being "philopatric". If the bird had not been banded previously, it was defined as a "recruit", and was fitted with four colour-coded bands: one numbered aluminum and three numbered plastic (National Tag Co., U.S.A.).

From these data, "breeding return rate" was defined as the percent of rock ptarmigan resident (only those known to be alive) at the end of the breeding season (date when chicks were ca. 21 days old) in year one that returned to breed the following spring. "Annual return rate" was calculated as the percent of rock ptarmigan resident at the onset of the breeding season in year one that returned to breed in year two. "Site fidelity", defined as the tendency of a philopatric male or female to occupy the same territory each year, was estimated from overlaying sighting locations during the territorial and nesting period of each year. The "recruitment rate" of rock ptarmigan to Windy Lake to breed was calculated as the percent of resident birds attempting to breed that did not breed at Windy Lake the previous year. "New" or "recruit" birds were those that in 1988 or 1989 were known not to have bred on the study site the previous year(s), whereas "old" birds were philopatric individuals. In this study, a "territorial" rock ptarmigan is defined as either a male or female that was resident over the breeding season.

Arrival dates of rock ptarmigan and all other migrants to Windy Lake were noted, as well as indices of spring phenology (eg. the date snow cover declined below 50%, date of flowering of herbaceous plants, daily minimum and maximum temperature). Microtines were counted on six plots (10m x 40m), all located within the SWL study area. These plots were set up in 1984 and have been censused every year from mid June to mid July. Census techniques are provided by Poole (1987).

Rock ptarmigan were also counted on six plots (1 km x 2 km) distributed randomly in the Kilgavik region. These plots were established in 1983 to census male rock ptarmigan in late May-early June, which coincides with pair bonding, and have been censused every spring from 1983 to 1989. Census technique and description of the plots are provided by Poole (1987).

Natality and Mortality

In 1988 and 1989, at the time of capture, all female rock ptarmigan were fitted with a 12 g "necklace" radio transmitter (Biotrack, U.K.). Only half of the males were fitted with a radio transmitter: in 1988 with an 18 g "backpack" radio transmitter (Telemetry Systems, U.S.A.), and in 1989 with a 12 g "necklace" transmitter. Half of the marked males were not fitted with a transmitter; they served as a control group for possible effects of the transmitter on survival (Appendix 1). Following release of the ptarmigan, the status (territorial/non-territorial, paired/unpaired), identity of mate(s), and territory location were determined for each bird.

The fate of adult males and females was documented through regular surveys (every 3-4 days) of the respective territories, conducted through to the end of the breeding season. If an individual rock ptarmigan was not visible, it was located by radio telemetry, or in the case of males not radio-marked then by intensive searches of its territory. In the case of nesting females, upon initial discovery of the nest (during egg-laying or early in incubation), the hen was flushed and the eggs were counted. In order to determine hatching success (Chapter III), nests (of half the females) were visited on a regular basis at which time the female was again flushed and the eggs counted.

In this study, survival of rock ptarmigan chicks were determined at the end of July , by which time most chicks were 3-4 weeks old. However, chicks are considered "fledged" if they survived to 10 days post-hatch, at which time they gain the ability of flight. A hen (and her mate) was "successful" if one or more chicks fledged. Productivity was defined as the average number of chicks fledged per hen that hatched young, and population productivity, the average number of chicks fledged per hen that initiated nesting.

When a rock ptarmigan had been depredated, I attempted to identify the type of predator from the remains and location. Consequently all birds with transmitters that were lost to predators were found and documented. The fate of males without transmitters could not be ascertained for all individuals, and the recorded number of males preyed upon during the breeding season is, therefore, a minimum value. Predation rate was calculated as the percent of resident males or females at the onset of the breeding season which were documented as having been depredated.

Survival rates of banded rock ptarmigan were calculated using the Kaplan-Meier (K-M) product limit method, as modified by Pollock *et al.* (1989) for staggered entry of animals. Survival rates were calculated on a weekly basis. The K-M method calculates a survival function (S[*t*]) which is "the probability of an arbitrary animal in a population surviving *t* units of time from the beginning of the study" (Pollock *et al.* 1989). Ptarmigan whose fate was known only up to a certain date were eliminated from analysis from that date on (*ie*. right censored). Such a situation may occur if: (1) not all the birds are radio-marked, (2) a bird had a transmitter which failed during the study, (3) a bird emigrated out of the study area, or (4) a bird survived past the end of the study period (White and Garrot 1990). When dates of last observation and documented death or censorship spanned several days, the median date was used. Statistical differences in the survival function between age groups, years, and areas were carried out using the most conservative of the three "approximate chi-square" tests presented by Pollock *et al.* (1989). For detailed reviews of this method, and others, refer to Kurzejeski *et al.* (1987), Pollock *et al.* (1989), and White and Garrot (1990).

In order to identify the species of predator for each rock ptarmigan killed, all remains (if found) were collected. Where the identity of the predator was not obvious at the kill site, a description of the location, the date, and the type and condition of the remains was recorded. These records and remains were analyzed in the lab using published literature for identifying the predator species involved (Einarsen 1956, Jenkins *et al.* 1964, Nielsen 1986). In some cases of gyrfalcon predation, the identity of gyrfalcon as the predator was confirmed by the presence of the appropriate leg band(s) at a nearby gyrfalcon eyrie or plucking post.

All 2x2 contingency analyses used the *G*-test of independence with Williams Correction to test for relationship between the observed frequencies recorded for the two classes (Sokal and Rohlf 1981). The significance level was set at $P<0.05$ for all tests.

RESULTS

Timing of spring arrival

Male rock ptarmigan were observed at Windy Lake in early May in each year of this study. At this time of year they were found primarily in flocks (tens to hundreds). Most established territories during the second week of May. Females arrived on the study area 2-3 weeks later than males, generally during the second and third week of May, a time when winter conditions still persisted at Windy Lake, with snow cover exceeding 80% and minimum daily temperatures below 0° C. As was observed in Iceland (Gardarsson 1988), male rock ptarmigan at Windy Lake concentrated their activities within large home ranges until females arrived on the breeding grounds. Although males displayed territorial behaviour before females arrived, few aggressive boundary disputes were observed. Although territory size was not determined in this study, it was evident from observations that territories were not contiguous in either NWL or SWL study sites. During cold spells and storms, males would regroup into small flocks of generally less than 20 individuals. Once females arrived, the intensity of territorial defense and courtship displays by males increased. On June 2, 1988 and June 4, 1989, snow cover had receded to less than 50% of ground cover. These dates followed 1 or 2 warm (daily minimum temperature > 0°C), calm days during which a major snow melt occurred. Laying began shortly thereafter (ca. 1-5 days) in both years.

Dispersion

A total of 112 rock ptarmigan were banded at Windy Lake between 1987 and 1989: 52 at SWL, 45 at NWL, and 15 outside these two areas (Table II-1). At time of banding, females weighed significantly more than males, whereas the wing chord of males were significantly longer than that of females (Appendix 2). In 1988 and 1989, a total of 61 males and 49 females bred or attempted to breed at Windy Lake. The density (number per 100 ha) of breeding birds at Windy Lake averaged 5.8 in 1987 (SWL only), 3.4 in 1988, and 2.5 in 1989, a decline of 21.1% among males and 32.5% among females from 1988 to 1989. Within the larger Kilgavik region, the spring density of breeding males declined each year from 1985 to 1989, after three consecutive years of increases (Appendix 3). The density of breeding hens in 1988 and 1989 was lower than that of territorial males as not all males were successful in attracting a mate. Excluding males for which the mated status was not

Table II-1: Total number of resident rock ptarmigan at the onset (June 1) and end (July 31) of the breeding season in areas of relatively high (SWL) and low (NWL) densities of nesting raptors at Windy Lake, N.W.T.. Unless otherwise indicated, a difference in number of males and females indicates unpaired individuals. Enclosed in paranthesis are percentage yearlings.

Year	Study Site	Size of Study Site (ha)	Onset of Breeding No. Males	Onset of Breeding No. Females	End of Breeding No. Males[†]	End of Breeding No. Females	End of Breeding No. Juveniles
1987	SWL	310	9	9	-	-	-
			(33.3)	(66.7)	-	-	-
1988	SWL	830	16[a]	14	11	8	24
	NWL	890	15[b]	13	9	9	50
	OFF[††]	-	2	1	0	1	0
			(43.3)	(46.4)	(45.0)	(33.3)	-
1989	SWL	830	12	7	4	7	46
	NWL	865	12	11[c]	6	8	35
	OFF[††]	-	4[d]	3	1	2	16
			(7.4)	(70.0)	(9.1)	(70.6)	-

[†] minimal number since the fate of several males without transmitters unknown.

[††] OFF = outside either SWL or NWL.

[a] includes one unbanded.

[b] includes two unbanded and two for which the mated status was unknown.

[c] includes one unbanded and one case of bigamy.

[d] includes one unbanded and one for which the mated status was unknown.

determined, the percentage of unmated territorial males at Windy Lake ranged from 10% (3/31) in 1988 to 26% (7/27) in 1989 (*G*=2.58, df=1, *P*=0.11).

The density of rock ptarmigan at the end of the breeding season (late July) at Windy Lake in 1988 rose to 6.5 birds per 100 ha and in 1989 to 6.3 birds in response to the addition of juveniles to the population (Table II-1). At this time of year, juveniles comprised 66.7% of the population in 1988, and 76.4% in 1989 on the two main study sites (NWL and SWL). From late July 1988 to early June 1989, the number of rock ptarmigan at NWL and SWL decreased by 62.2%. Loss of juveniles accounted for most of the decline. The number of juveniles at NWL and SWL declined from August 1988 to the next spring by 82.1%, whereas the number of adults declined by only 24.3%. The density of juveniles on the two study sites was 11.1% higher in 1989 than in 1988.

Recruitment and breeding return rate

Based on the number of birds that returned in 1989 which had been resident at Windy Lake at the end of the breeding season in 1988, significantly more males (75%, 15/20) returned than females (11.1%, 2/18) (*G*=16.54, df=1, *P*<0.01). Combining spring records of 1988 and 1989, a total of 19 males and 3 females returned to breed a second year at Windy Lake. Annual return rate of banded birds for 1988 and 1989 combined was lower than breeding return rate, averaging 48.7% in males and 8.1% in females. Although territories were not accurately mapped, site fidelity was evident in all philopatric individuals. Age did not influence the probability of male rock ptarmigan returning to breed the following season (adults: 0.65, 11/17; yearlings: 0.67, 8/12; *G*=0.01, df=1, *P*=0.92). Breeding success of a male in one year did not affect the probability of that male returning (0.21, 4/19) or not returning (0.30, 3/10) to the same area to breed in the following year (*G*=0.26, df=1, *P*=0.61). Of the three females that were philopatric in 1988 or 1989, one paired with the same mate in both years.

Analysis of birds returning more than one year at Windy Lake is limited to birds banded in 1987 at SWL. One of the nine males banded that year was known to have been depredated that summer. Of the remaining eight (whose fate was not followed that summer), four (50%) returned in 1988, and of those two returned (50%) again in 1989. There were no females banded in 1987 that returned in both 1988 and 1989, nor any that may have nested elsewhere in 1988 and then returned to Windy Lake in 1989.

The percentage of new rock ptarmigan recruited into the breeding population at Windy Lake in 1989, within the common area studied in both 1988 and 1989 (Fig. II-1), was 30% (6/20) for males and 87% (13/15) for females (Fig. II-2). Of the males recruited to the area, all but one were adults, and only twowere successful in attracting a mate. Recruited females, on the other hand, were comprised mostly of yearlings (only three were adults). Since all females in 1988 and 1989 initiated nesting, irrespective of age, it is probable that the three adult females had nested elsewhere in 1988. Pooling data from 1988 and 1989, 22.2% of males and 19.1% of females were adults breeding for the first time at SWL and NWL. As well, in both years the proportion of recruits in the breeding population was significantly higher among females (0.86, 18/21) than males (0.33, 9/27) (G=13.75, df=1, P<0.01).

Sex and age ratios

The sex ratio of rock ptarmigan breeding at Windy Lake showed a preponderance of males (1:0.83) (Table II-1), although, based on the sample size, the ratio was not significantly different from a 1:1 ratio (X^2=1.13, df=1, P=0.29). Furthermore, sex ratio did not differ between sites (SWL, 1 male : 0.75 females; NWL, 1:0.89; G=0.18, df=1, P=0.67). The ratio of adult to yearling rock ptarmigan breeding at Windy Lake varied considerably between years for both males and females. The ratio of adult to yearling males was 1:0.76 in 1988 and 1:0.08 in 1989, yet among females an opposite ratio trend was observed: 1:0.87 in 1988 and 1:2.33 in 1989 (Table II-1). Pooling the 2 years, among males adults exceeded yearling (1:0.36), but among females adults were fewer than yearlings (1:1.29). Thus, yearlings constituted only 11% of territorial males but 56.3% of breeding females.

Natality

Of hens that settled at Windy Lake to breed in 1988 and 1989, 96% (47/49) initiated nesting, the other 4% (n=2) died after pairing but before laying, and were not replaced. All but one of the 49 hens were caught, banded, and fitted with a radio transmitter. Of the hens that initiated nesting, 28 were successful in fledging chicks; giving a reproductive success rate of 60% for the population. For the 28 hens that successfully fledged young (11 from SWL, 15 from NWL, and 2 from OFF), the productivity was 6.7 chicks per hen, or a total of 188 chicks. Hen productivity was similar at NWL (6.3) and at SWL (7.0) (t=0.70, df=24, P=0.49).

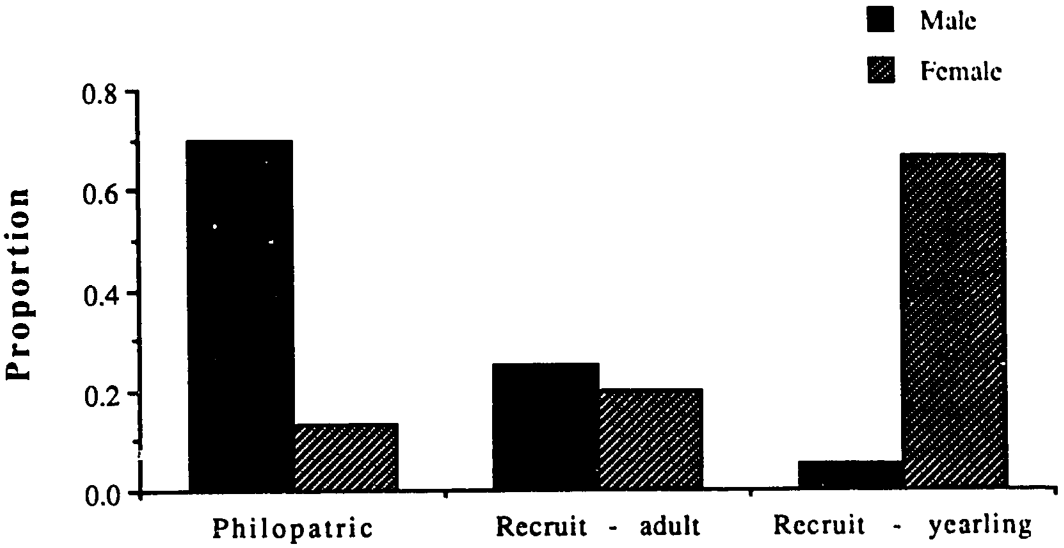

Figure II-2: Proportion of rock ptarmigan that were either philopatric or recruited adults and yearlings at Windy Lake, N.W.T., in 1989.

The population productivity, based on all 49 hens that settled, was 3.8 chicks per hen, with no difference between SWL (3.7 chicks per hen) and NWL (4.0 chicks per hen) (t=-0.26, df=43, P=0.80). Likewise, there was no difference in the mean number of chicks produced by adult (3.8) and yearling (4.0) hens (t=-0.17, df=46, P=0.86). There was also no significant difference in the population productivity between 1989 (5.0 chicks per hen) and 1988 (3.0 chicks per hen) (t=-1.92, df=47, P=0.06). Productivity remained nearly constant between years at NWL (t=0.39, df=22, P=0.70), whereas it was 3.5 times greater at SWL in 1989 (t=-3.38, df=19, P=0.003) (Fig. II-3). Of the 49 hens that initiated nesting, only two (4.1%) nested in both 1988 and 1989, and though they accounted for 8.2% of total nesting attempts in the two years, they contributed 14% of the population productivity. In late summer of 1988, there were 1.9 juveniles per adult, whereas in 1989 there were 3.5 juveniles per adult.

Survival and Mortality

Survival

The survival rate (S[t]) of rock ptarmigan over the breeding seasons (May 30 - July 31) of 1988 and 1989 was 0.82 at Windy Lake. Rock ptarmigan survived no better at NWL than at SWL (0.86 vs. 0.78, Fig. II-4, A), despite the density of nesting raptors being considerably less within 10 km of NWL (Table II-2). The survival function for females (0.87) and males (0.78) did not differ (Fig. II-4, B). Adult rock ptarmigan did not survive better than yearlings (0.81 vs. 0.84: X^2=0.04, df=1, P=0.84). The difference in survival rates between adults and yearlings were not statistically significant for either males (0.80 vs. 0.77: X^2=0.22, df=1, P=0.64) or females (0.84 vs. 0.87: X^2=0.13, df=1, P=0.72). There was no significant difference in survival between males and females at either SWL or NWL, nor in survival of males and females between SWL and NWL (Table II-3).

Mortality

During the 26 months from June 1987 to July 1989, a total of 128 rock ptarmigan was marked and released. Of these, 23 rock ptarmigan which were resident at Windy Lake in ≥1 years were found dead, producing a minimum mortality rate of 18%. This rate is minimal because the fate (*ie*. alive/ dead/ emigrated) could not be determined for all birds at the end of the breeding season. Additional ptarmigan may have actually died, forcing the mortality rate higher. Assuming that all rock ptarmigan of unknown fate at the end of a breeding season were dead, and those that did not return the following year

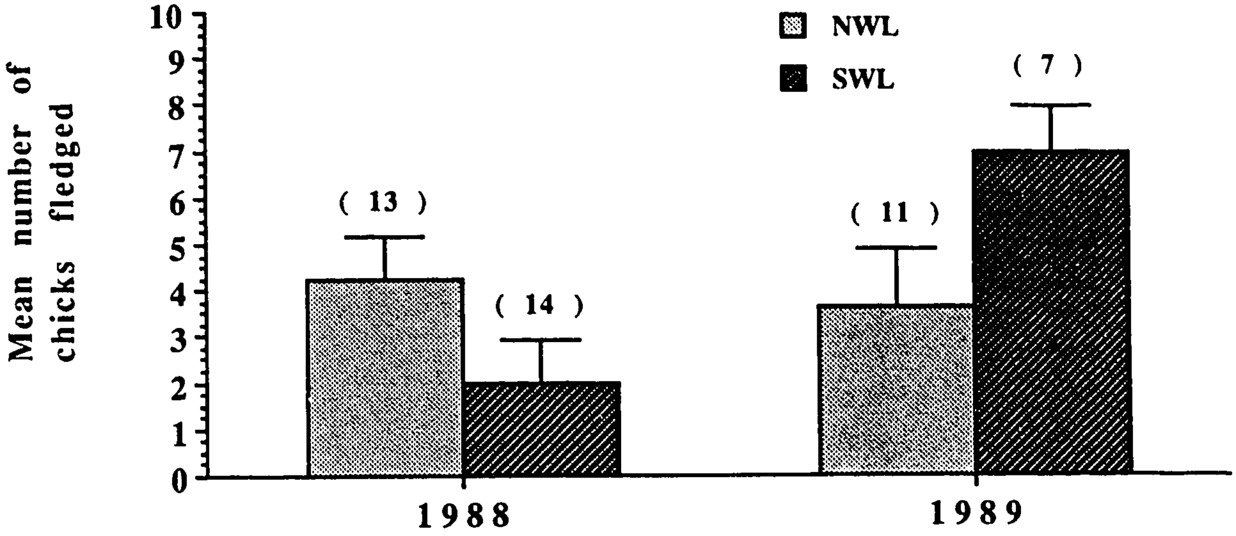

Figure II-3: Productivity (with standard error bars and sample size in parantheses) of all female rock ptarmigan that settled to breed in areas of relatively high (SWL) and low (NWL) densities of nesting raptors at Windy Lake, N.W.T., in 1988 and 1989.

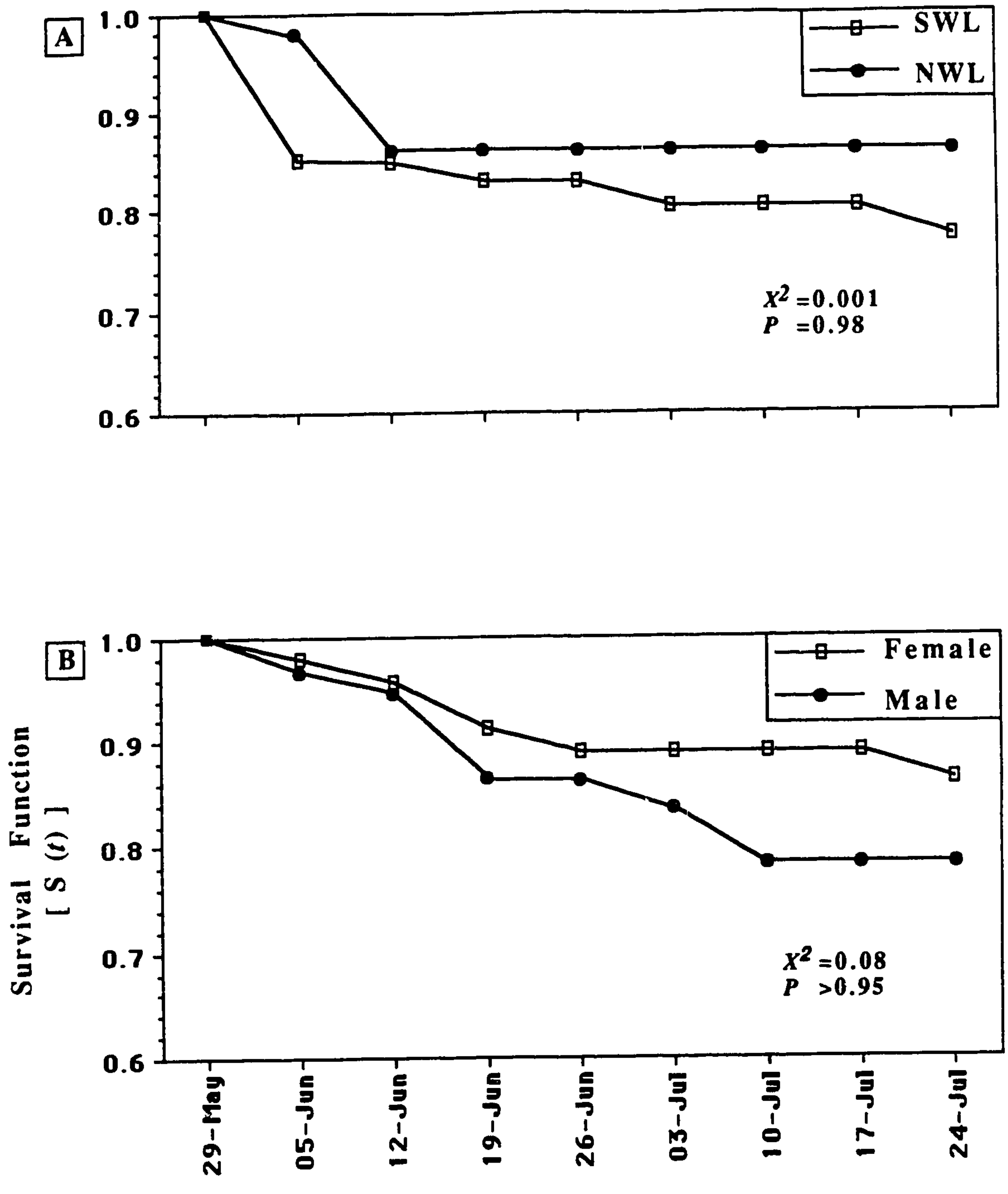

Figure II-4: The Kaplan-Meier survival function (modified for staggered entry of animals) for rock ptarmigan: A) from areas of relatively high (SWL) and low (NWL) densities of nesting raptors, and B) for males and females at Windy Lake, N.W.T. in 1988 and 1989.

Table II-2: Number of nesting raptors within 10 km of South Windy Lake (SWL) and North Windy Lake (NWL) populations of rock ptarmigan at Windy Lake, N.W.T., in 1988 and 1989.

Raptor species	1988		1989	
	SWL	NWL	SWL	NWL
Gyrfalcon	4	1	1	1
Peregrine falcon	3	2	2	1
Golden eagle	1	0	0	0
Raven [a]	1	1	1	0
Total	9	4	4	2

[a] considered as a "functional raptor" (White and Cade 1971).

Table II-3: Survival function (S[*t*]) of male and female rock ptarmigan during the breeding season (May 30 - July 31, 1988 and 1989), in areas of high (SWL) and low (NWL) densities of nesting raptors at Windy Lake, N.W.T..

Study Area	Female	Male	χ^2 [a]	*P*
SWL	0.8357	0.7500	0.23	0.63
NWL	0.8696	0.7600	0.62	0.43
χ^2 [a]	0.01	0.28		
P	0.92	0.60		

[a] an approximate chi-square test (Pollock *et al.* 1989).

had perished, then the maximum annual mortality rate would be 57%. For females this rate is higher (61%) than for males (50%). The mortality rate during the breeding season alone (1988 and 1989) was not significantly different between males (16.4%, 10/61) and females (16.3%, 8/49) (G=0.00, df=1, P>0.95).

Predation was the cause of death for virtually all (91.3%, 21/23) rock ptarmigan found dead at Windy Lake over the three summers. Only two rock ptarmigan (one female, one male) deaths were not attributed to predation; both were found within their respective territory, and neither bird was marked or damaged in any manner; the female was very emaciated.

Species of predators

In 1988 and 1989 there were more than twice as many raptors nesting within 10 km of the SWL population of rock ptarmigan, as within 10 km of NWL (Fig. II-1 and Table II-2). Other potential avian predators during the summer months included Thayer's (*Larus thayeri*) and glaucous gulls (*L. hyperboreus*), jaegers (*Stercorarius pomarinus, S. parasiticus, S. longicaudus*), rough-legged hawk (*Buteo lagopus*), snowy owl (*Nyctea scandiaca*) and the short-eared owl (*Asio flammeus*) (Poole and Bromley 1988). The two gull species nested on islands (> 20 km from Windy Lake) in the Elu Inlet (Fig. II-1), and a few gulls were observed occasionally flying over either SWL or NWL. It is doubtful, however, that gulls were important predators on adult rock ptarmigan (Martin 1985), although it is possible that these opportunistic predators (Terres 1982) may have preyed on eggs and chicks. There is very limited evidence that jaegers prey on birds as large as adult rock ptarmigan (Terres 1982, Martin 1985), although, like gulls, they may have preyed on eggs and chicks. All three species of jaegers found at Windy Lake are rare (Poole 1987), and very few (<5) were observed during three summers. Both species of owls are classified as "occasional" in the Windy Lake region (Poole 1987). Snowy owls are known to prey on adult rock ptarmigan (Steen and Unander 1985), and remains of willow ptarmigan have been found in short-eared owl nests at Anderson River, N.W.T. (Hannon and Barry 1986). However, through most of their range both species prey principally on microtines and not on ptarmigan (Terres 1982). Rough-legged hawks, as well, prey primarily on microtines (Terres 1982) but will kill chicks of woodland grouse (Sonerud 1985), and probably prey on rock ptarmigan chicks. In 1988 and 1989 there were no rough-legged hawks nesting within 30 km of either NWL or SWL, and none was observed in the Windy Lake region during incubation or brood rearing. Mammalian predators of rock ptarmigan are generally rare at Windy Lake; the only species classified as "common" was the arctic ground squirrel (*Spermophilus parryii*) and "fairly common", the red fox (*Vulpes vulpes*) (Poole 1987). All others are "occasional" or "rare" in the region; these include the grizzly bear (*Ursus arctos*), gray wolf (*Canis lupus*), arctic fox (*Alopex lagopus*), ermine (*Mustela erminea*), and the wolverine (*Gulo gulo*) (Poole 1987). Personal observations of these species in the Windy Lake during May - August from 1987 to 1989 was as follows: arctic ground squirrels were abundant in 1987 and 1988 but rare in 1989; one individual was observed of each canid species; one grizzly bear was observed in both 1988 and 1989; on three occasions in 1989 ermines were observed; and during the month of May tracks of wolverine were seen on two occasions. I have no evidence or reason to believe that any of these mammals hunted or favored one site (*i.e.* SWL or NWL) over the other. Thus one would expect predation pressure from these predators to have been fairly uniform through both sites.

Ravens, gulls, rough-legged hawks, arctic ground squirrels, and ermines are egg and chick predators, whereas all other species could be considered either adult and/or egg and chick predators.

Level of predation

Of the 21 kills recorded, 17 (81%) occurred during the breeding season, one during fall, and three sometime between mid-summer and winter (Appendix 4). The predation rate during the breeding season (June 1-July 31) for all 3 years combined was 14%. Of the breeding population at Windy Lake (Table II-1), 5.6% were found depredated in 1987, 14.8% in 1988, and 14.3% in 1989, rates that were not significantly different (*G*=0.61, df=2, *P*=0.74).

Major predators

The predator was identified for all of the 21 kills found on the study area during the summers of 1987, 1988 and 1989 (Appendix 4). Of these depredated rock ptarmigan, all but one were killed by falcons; seven by gyrfalcons, one by a peregrine falcon, and 12 by either peregrines or gyrfalcons (Table II-4). Only one rock ptarmigan, a female, was preyed upon by a mammalian predator; either a red or an arctic fox. Pooling the 3 years, falcons killed equal numbers of males (10) and females (10). The number of falcon kills in 1988 and 1989 at SWL (n=7) was the same as at NWL; whereas the one fox kill was at SWL. Mammalian predation on breeding rock ptarmigan at Windy Lake was

Table II-4: Number of known depredations by predators on male and female rock ptarmigan in areas of relatively high (SWL) and low (NWL) densities of nesting raptors at Windy Lake, N.W.T., in 1987, 1988 and 1989.

Year	Study Site	Sex	Predator Species			
			Gyrfalcon	Peregrine Falcon	Falcon spp. †	Fox spp. ††
1987	SWL	Male	1	0	0	0
		Female	2	0	1	0
1988	SWL	Male	1	1	0	0
		Female	1	0	2	1
	NWL	Male	0	0	2	0
		Female	0	0	2	0
1989	SWL	Male	3	0	0	0
		Female	0	0	0	0
	NWL	Male	0	0	2	0
		Female	0	0	1	0

† killed by either a gyrfalcon or a peregrine falcon.

†† killed by either a red or an arctic fox.

minor, accounting for only one (5%) of the depredations found at Windy Lake from June 1987 to July 1989

Proximity of nesting raptors

In 1988, when the difference between NWL and SWL in the number of raptors nesting within 10 km was pronounced, there was no significant difference (*G*=0.06, df=1, *P*=0.81) in the predation rates on rock ptarmigan in the two areas, 14.3% (4/28) and 16.7% (5/30), respectively. In 1989 the predation rates were again very similar on the two areas, 13.0% (3/23) at NWL and 15.6% (3/19) at SWL (*G*=0.06, df=1, *P*=0.81). Combining the 2 years together further emphasized a lack of difference in the predation rates between NWL (13.7%, 7/51) and SWL (16.3%, 8/49) (*G*=0.13, df=1, *P*=0.72). Analyzing the sexes separately and pooling the 2 years showed no significant difference between the proportion of males killed at NWL (14.8%, 4/27) and SWL (17.9%, 5/28) (*G*=0.09, df=1, *P*=0.76), nor for females between the two areas (NWL: 12.5%, 3/24; SWL: 14.3%, 3/21) (*G*=0.03, df=1, *P*=0.86).

Sex, age and temporal variation in predation

Pooling all cases of depredations in 1988 and 1989 which were known to occur during the breeding season revealed no significant difference in the percentage of males (15%, 9/61) and females (14%, 7/49) killed (*G*=0.01, df=1, *P*=0.92). Of the rock ptarmigan that were depredated during the breeding season in 1988 (n=9), four were males (12.1%, n=33) and five were females (17.9%, n=28). In 1989, however, the predation rate was more skewed with five males (17.9%, n=28) taken against only two females (9.5%, n=21). This difference in the proportion of males and females killed was not significant in either 1988 (*G*=0.37, df=1, *P*=0.54) or in 1989 (*G*=0.66, df=1, *P*=0.42). The proportion of females killed in 1988 was almost twice that for 1989; however, the difference was not significant (*G*=0.66, df=1, *P*=0.42). There was also no significant difference in the predation rates on males between years (*G*=0.37, df=1, *P*=0.54).

The percentage of adult (14%, 9/63) and yearling (14%, 6/42) rock ptarmigan depredated during the breeding season at Windy Lake (1988 and 1989) was not significantly different (*G*=0.00, df=1, *P*>0.95), and this was true for both males (*G*=0.24, df=1, *P*=0.62) and females (*G*=0.10, df=1, *P*=0.75). There was little difference in the predation rates on yearling and adult males, 20.0% (n=15) versus 14.3% (n=42), and the same was true for females, 11.1% (n=27) versus 14.3% (n=21). Combining the sexes, adults and yearlings had the same predation rate, 14.3% (n=110). Furthermore, there was no difference (P>0.5) in the proportion of adults and yearlings killed of either sex in 1988 or in 1989. It was possible to ascertain the exact age (1, 2, or ≥ 3 years old) of 35 rock ptarmigan, and therefore analyze predation rates in these three age classes. Of these rock ptarmigan, six were depredated, of which three were yearlings (15%, 3/20), two were 2-years old (33.3%, 2/6), and one was ≥ 3 years old (11.1%, 1/9), a non-significant difference among classes (G=1.08, df=1, P=0.30).

In 1988 and 1989, there were significantly more rock ptarmigan killed in June (n=14) than in July (n=2) (G=10.35, df=1, P<0.01) (Fig. II-5). The difference, however, was significant in males (G=11.13, df=1, P<0.01) but not in females (G=1.03, df=1, P=0.31). There was no difference between the proportion of males or females killed in either June (G=0.50, df=1, P=0.48) or July (G=2.46, df=1, P=0.12).

DISCUSSION

Spring arrival and dispersion of rock ptarmigan

In each spring from 1987 to 1989, female rock ptarmigan arrived on the study area 1 or 2 weeks after most males had arrived. Later arrival by females has been documented in other populations of rock ptarmigan, such as in Iceland (2-3 weeks; Gardarsson 1988), northern Quebec (1 week; Olpinsky 1986), and Melville Peninsula, N.W.T. (1-2 weeks; Brodsky 1988). In the Kilgavik region surrounding Windy Lake, Poole (1987) noted that rock ptarmigan migrated into the area generally from the southwest during early May, but the nature of winter and spring movements of rock ptarmigan is still largely unknown. Rock ptarmigan have been observed in the Kilgavik region throughout winter, generally in small flocks (D. Stern, pers. comm.). Poole (1987), however, found very little evidence of rock ptarmigan (two birds and 25 sets of tracks) during 800 km of snowmobile travel throughout the region in late March and early April in 1986. Populations of rock ptarmigan in Alaska and Iceland have been observed to migrate from the breeding grounds during autumn to overwintering areas where the sexes then segregate (Weeden 1964, Gardarsson 1988). In Alaska, rock ptarmigan migrate from alpine breeding areas to wintering ranges below timberline (Weeden 1964), but on the Island of Hrisey, off the northern coast of Iceland, many old males remain close to their breeding grounds throughout the winter

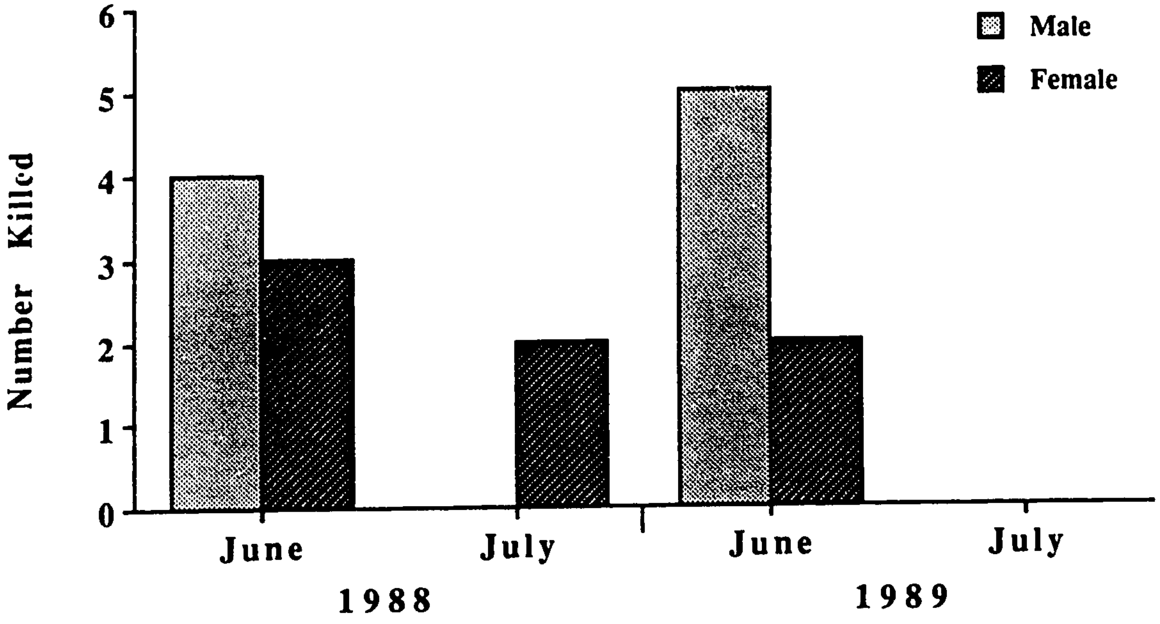

Figure II-5: Number of male and female rock ptarmigan killed during June and July in 1988 and 1989 at Windy Lake, N.W.T..

(Gardarsson 1988). It is possible that a situation similar to that observed on Hrisey may occur at Windy Lake. Therefore, on the basis of the observations of rock ptarmigan movements in Alaska and Iceland, the majority, if not all, rock ptarmigan at Windy Lake may move off their breeding territories in autumn, and while some may overwinter on the tundra, some may migrate south, perhaps as far south as the taiga.

The density of the spring breeding population of rock ptarmigan at Windy Lake declined in each successive year of this study, a decline that can be traced back to 1986, after three consecutive years of increase (Appendix 3). Although census data from Windy Lake exists for only 7 years, the pattern of year to year changes observed is similar to that documented in Greenland (Braestrup 1941), Iceland (Gudmundsson 1960), and Alaska (Buckley 1954) where rock ptarmigan fluctuate over an approximate 10 year cycle (Weeden and Theberge 1972). Furthermore, recent population studies of rock ptarmigan, though too short in duration to confirm a nonrandom fluctuation pattern, have documented population fluctuations similar in magnitude and rate of change to that observed at Windy Lake over a 7-year period (Watson 1965, Weeden and Theberge 1972, Nielsen 1986, Gardarsson 1988). In each of these populations, the magnitude of the difference in the size of the population between low and peak year was less than five fold: Windy Lake, 3.7 (this study); Hrisey Island, 4.9 (Gardarsson 1988); NE Iceland, 2.4 (Nielsen 1986); Scotland, 3.0 (Watson 1965); Alaska, 2.6 (Weeden and Theberge 1972). A similar magnitude in population fluctuations have been observed in the one other tundra-nesting grouse species (and a close relative of the rock ptarmigan), the willow ptarmigan (*L. lagopus*). At Anderson River, approximately 900 km west of Windy Lake, willow ptarmigan populations fluctuated 3.5 fold over a 28 year period (1958-1985) (Hannon and Barry 1986).

Within a species, cyclic fluctuations occur relatively synchronously over large geographical areas in several northern animals, such as the snowshoe hare (*Lepus americanus*) (Keith and Windberg 1978) and the willow ptarmigan (Hannon and Barry 1986). Data from population studies of rock ptarmigan are inconclusive with respect to the degree of geographic synchrony in the fluctuations of this species. From 1960 to 1969, populations of rock ptarmigan in central Alaska reached their highest numbers in 1962 and their lowest in 1965. During this same time period in Iceland, however, populations reached their peak in 1966, 1 year after they reached their low in

Alaska. However, from 1983 to 1985 the density of territorial male rock ptarmigan increased each successive year in both Iceland (Nielsen 1986) and the central Canadian arctic (Poole 1987). Although densities recorded in Iceland were actually more than double those at Windy Lake, the rate of increase was similar; the density increased at Windy Lake (18%) and in Iceland (13%) from 1983 to 1985. As well, density of rock ptarmigan increased from 1982 to 1983 in both northern Quebec (14%; Olpinsky 1986) and in Iceland (43%; Nielsen 1986). Despite the limited nature of this data set, it suggests that synchrony in annual changes in the breeding populations may occur over a wide geographic area.

Recruitment and breeding philopatry

Male and female rock ptarmigan showed a significant difference in the proportion recruited and rate of return to the breeding population at Windy Lake. Most males in both years had previous breeding experience at Windy Lake, but very few females, at least since 1987, had any previous experience at Windy Lake. The sexes also differed in the age composition of the birds recruited. Although there were few males recruited into the breeding population in any given year, most were adults, whereas most of the females recruited were yearlings. There is no evidence that rock ptarmigan cannot breed in their first year (Johnsgard 1983), therefore, the presence of adult birds amongst recruits suggests interyear movements between breeding areas. In many populations, there is a surplus of males that do not attract a mate, as was observed at Windy Lake.

Less commonly observed, though, were males that were not only non-breeding, but also non-territorial. Such groups of males, often referred to as "floaters", have been observed in Svalbard (Steen and Unander 1985). At Windy Lake, some males were either never seen again or seen for only 1 or 2 days after they had been caught and banded. One such male, fitted with a radio transmitter at time of capture, remained in the same vicinity for 2 days, and then was never observed again (neither visually nor via a radio-signal). It is not known if these "transients", most of which were yearlings, were simply on transit to other breeding areas, or trying to establish a territory at Windy Lake but failing moved on to try elsewhere. It is possible, therefore, that adult male recruits were "floaters" from the previous year, or they provided evidence of breeding dispersal in males of this species.

Whereas it was common to observe apparently unmated territorial males in this population, unmated males without a territory have not been documented. In a discussion of dispersal, Greenwood (1980) postulated that for a territorial species, the sex that defends the resources should be expected to show higher philopatry. In rock ptarmigan, males are territorial whereas females are generally considered less territorial (MacDonald 1970, Olpinsky 1986), and the observations on philopatry and breeding dispersal in both sexes of rock ptarmigan from Windy Lake support Greenwood's (1980) hypothesis.

It is unclear why, at Windy Lake, there were a few females that not only were philopatric but also showed very high site fidelity between years, while other females either dispersed or suffered overwinter mortality. Possibly there were differences in prior breeding success or age of the females. The two females that were philopatric in 1989 had successfully fledged chicks in 1988. However, there were 11 other females at Windy Lake that fledged chicks in 1988 but did not return in 1989 (fate unknown). Breeding success did not appear to influence subsequent rate of return in males at Windy Lake, nor was it an important factor for either sex in northern Quebec (Olpinsky 1986), nor in willow ptarmigan in northern British Columbia (Schieck and Hannon 1989).

It is possible that there is "limited" breeding dispersal among females from year to year, such that the probability of finding them on the study area in subsequent years becomes a function of the distance normally dispersed. Such observations have been made in northern Quebec by Olpinsky (1986); he collected banded females on his study area during the breeding season of 1984 that had nested there in 1982, but not in the intervening year.

The low productivity in 1988 was followed by a sharp decline in the size of the breeding population the following spring. In many populations of rock ptarmigan, as well as willow ptarmigan and red grouse (*L. l. scoticus*), breeding success (as measured by the number of juveniles per adult in autumn of year one) correlated positively with proportional changes in breeding numbers from year one to year two (Bergerud *et al.* 1985, Watson and Moss 1987). Though this correlation has been observed in several regions, there is no consensus among researchers about the causal mechanisms. Bergerud *et al.* (1985) argue that breeding success in one year causes changes (positive correlation) in breeding numbers the next, whereas Watson and Moss (1980, 1987) argue that, although such correlations have been observed in some populations (not in all populations of ptarmigan and unusually in tetraonids as a whole), winter loss and changes in spring territorial spacing cause the changes in spring numbers. Bergerud *et al.* (1985) plotted the breeding success (measured as number juveniles per adult in year 1) versus proportional change in breeding numbers (year 1 to year 2) for rock ptarmigan populations from Alaska (Weeden and Theberge 1972), Scotland (Watson 1965), and Iceland (Gardarsson 1971). Correlations were positive and fairly strong (minimum r=0.689) for all three populations. What differed, though, between the three populations was the minimum number of juveniles per adult in autumn required to reflect a positive change (*i.e.* increase) in breeding numbers the following spring. This minimum number was *ca.* 2.0 in Alaska, 0.75 in Scotland, and 3.5 in Iceland. This figure is not known precisely for rock ptarmigan in the central Canadian arctic, but from the one datum available from late July 1988 to June 1989 the number was 1.9. Since the size of the breeding population decreased the following year, the minimum ratio needed for the population to increase must be greater than 1.9. In 1989 the number of juveniles per adult in late July was 3.5. Unfortunately, it is not known what the size of the breeding population on the Windy Lake study sites was in 1990, after a near doubling of chick production the previous year. However, in the region surrounding Windy Lake the number observed on helicopter censuses of territorial males (taken during mid-June each year from 1987 to 1990) increased by 46% in 1990 from 1989 (C. Shank, pers. comm.). If the breeding population on the Windy Lake study area increased similarly in 1990, then the autumn juvenile:adult ratio required for the population to increase is probably between 1.9:1 and 3.5:1.

Demography

In both 1988 and 1989, there was an excess of territorial males relative to females attempting to breed. An excess of territorial males has also been observed in Scotland (Watson 1965), Japan (Soikiro *et al.* 1969), and Svalbard (Unander and Steen 1985), but not in Iceland (Gardarsson 1988). Rock ptarmigan in Scotland and Japan inhabit montane regions, whereas in Iceland, Svalbard, and northern Canada they inhabit arctic tundra. Gardarsson (1988) postulated that the reason for an excess of territorial males in the more southern montane regions but not in Iceland reflected a different predator community in those regions, in particular the absence of gyrfalcons.

This may also apply as well to Svalbard where gyrfalcons do not breed (Cramp and Simmons 1980). However, this does not explain the excess at Windy Lake as the region harbours one of the highest nesting densities of gyrfalcons in the world (Poole 1987). Since females at Windy Lake do not suffer higher mortality than males during summer, perhaps females incur higher overwinter mortality than males which could explain the surplus of males on the breeding grounds.

Data from Windy Lake and elsewhere suggest that a correlation may exist between sex ratio and annual changes in size of breeding population. In Scotland, the population of breeding rock ptarmigan declined each successive year from 1951 to 1957 (Watson 1965). During that period, the sex ratio in spring was highly skewed in favour of males (range: 1.4-2.0 males per female). The population reached its lowest level in 1957, after which the spring density of breeding birds increased each year until the end of the study in 1964. During the increase phase, the sex ratio was almost equal (range: 0.9-1.1 males per female) (Watson 1965). At Windy Lake, there was a sharp decline in the population of breeding birds in 1989 from 1988. This decrease coincided with an increase in the ratio of males to females. Although the ratio was skewed in favor of males in 1988, the ratio was more highly skewed in 1989. An excess of males in years of population decline and an equal or skewed ratio in favor of females in years of population increase may be a consequence of differential annual mortality during increase and decrease phase of population fluctuations. In 1989 the population of breeding birds declined sharply from 1988 levels, and the decrease in density of breeding birds was higher among females than males.

On Svalbard, Unander and Steen (1985) observed nonterritorial, unmated male rock ptarmigan (*i.e.* floaters) on their study area throughout the breeding season. The age structure of these floaters was not determined, but in the American redstart (*Setophaga ruticilla*), in which floaters persist, most were yearlings (Ficken and Ficken 1967). Thus, if yearlings attempt but are unsuccessful in attaining a territory, they may join a flock of floaters. Such a flock may or may not be observed if one is studying only a finite area and they happen to reside outside that area. If this were the case at Windy Lake during the summers of this study, it could explain the very low number of territorial yearling males recorded on the study area. If there were no yearling floaters outside the Windy Lake study areas, then the observed adult bias in the age ratio could have been the result of differential mortality. There was no age bias in male mortality during the breeding season, therefore, if it occurs it must be during fall or winter. Nielsen (1986) and Poole (1987) each observed an increase in the proportion of rock ptarmigan in the diet of gyrfalcons following increased mobility of rock ptarmigan chicks, usually in August, a time that also coincided with the fledging of gyrfalcons.

In the population of breeding females at Windy Lake, no non-mated individuals were recorded, nor has there been documentation of female floaters in other populations of rock ptarmigan. Therefore, the higher percentage of yearlings in the population of females at Windy Lake is likely the result of higher mortality among adult females than adult males. Differential mortality between sexes was not recorded during two breeding seasons at Windy Lake, therefore, if it occurs it must be during autumn or winter. Female rock ptarmigan appear to migrate farther than males and overwinter in different locations (Weeden 1964). As such, mortality may be higher on females at this time. A similar age ratio was recorded among willow ptarmigan breeding at Anderson River, N.W.T., and a similar explanation was postulated for it (Hannon and Barry 1986).

A positive correlation between fluctuations in densities in spring and the proportion of yearlings in a population have been recorded in some populations of rock ptarmigan. Weeden and Theberge (1972) observed that the number of yearlings fluctuated in parallel with spring densities (1961-1969) in Alaska ($r=0.59$, $P=0.07$).

Mortality - losses resulting from predation

Over the course of the breeding seasons of 1988 and 1989, no sex bias was observed in the mortality of rock ptarmigan at Windy Lake. This was true of loss of adults through predation either by month (June and July) or by stage (laying, incubation and brood rearing; Chapter III). This lack of differential loss concurs with the similar proportions of each sex found among prey remains at gyrfalcon eyries at Kilgavik (Poole 1987). Poole collected prey remains from May to early August each year from 1984 to 1987, observing no sex bias among the ptarmigan remains collected either during May-June or during July-August. In the Kilgavik region July 1 coincides roughly with the post-nuptial moult of male rock ptarmigan (last week of June) and the hatching of the eggs (first week of July). Before this date, females have been cryptic (both in plumage and behaviour) for a period of 3 to 4 weeks, whereas males have been cryptic for generally less than a week (MacDonald 1970, pers. obs.). It has been suggested that variation in mortality rates over the year, observed in male and female rock ptarmigan (Gardarsson 1971, Weeden and Theberge 1972), are a consequence of differences in conspicuousness (behaviour and plumage) of the sexes during the incubation phase of the breeding season (Bergerud and Mossop 1984). Nielsen (1986) reported a strong male bias in rock ptarmigan remains collected during April-June at gyrfalcon eyries in Iceland, whereas in July he observed a significant female bias. He compared the number of kills found for each sex with an assumed 1:1 spring sex ratio. This assumption is, however, questionable since, in many years, the spring sex ratio is skewed in favour of males (this study, Watson 1965). Consequently, Nielsen's (1986) conclusions must be accepted with caution.

Although there was no sex bias in predation, there was an observed temporal bias in predation over the course of the breeding season. Rock ptarmigan, both adults and yearlings of both sexes, incurred most loss to predation in the month of June. There is little empirical data from other studies on relative levels of predation during the breeding season; nevertheless, Nielsen (1986) and Poole (1987) both reported seasonal variations in the vulnerability of rock ptarmigan to gyrfalcon predation. Nielsen (1986) observed two seasonal peaks in vulnerability, the first during the territorial stage in the early part of the breeding season, and the second commencing after the territorial system has collapsed and ptarmigan chicks are capable of sustained flight in late summer and lasting on into early winter. Poole (1987) reported a similar seasonal variation in rock ptarmigan vulnerability at Kilgavik. He also observed an inverse correlation between the percentage of ptarmigan in the gyrfalcon's diet and the availability of juvenile arctic ground squirrels. At Windy Lake, juvenile ground squirrels emerge in July (Poole 1987), and their emergence coincided with a sudden drop in the percentage of ptarmigan in the collected prey remains. Thus, the level of predation pressure on ptarmigan may reflect the relative vulnerability of other potential prey species.

Adult and yearling rock ptarmigan were preyed upon in proportions equal to their availability. Adult males and females, some of which had previous breeding experience at Windy Lake, incurred losses similar to those of yearling males and females breeding for the first time.

The importance of rock ptarmigan as a prey species within the arctic community is evident, particularly to gyrfalcons which overlap to a large extent their holarctic distribution, and which have a high percentage of ptarmigan in their diet (Bergerud and Mossop 1984). At Kilgavik, adult rock ptarmigan are known to be preyed upon by gyrfalcons, peregrine falcons and golden eagles, and their remains have also been found in raven nests (Poole and Bromley 1988). Although ravens may occasionally kill adult rock ptarmigan (Nielsen 1986), they have also been observed scavenging rock ptarmigan from gyrfalcon caches (Poole and Bromley 1988). There is no evidence that rough-legged hawks kill adult rock ptarmigan at Kilgavik (Poole and Bromley 1988), and the scarcity of the two owl species, in addition to the fact they, and rough-legged hawks as well, prey principally on microtines (Cramp and Simmons 1980), likely renders them of minor importance as ptarmigan predators. The lack of confirmed predation by golden eagles is likely because of the scarcity of eagle nests close to the Windy Lake study area in any of the 3 years of this study (C. Shank, pers. comm.), and the fact that they rely more on arctic hares, ducks and ground squirrels than on rock ptarmigan during the summer (Poole and Bromley 1988). Although a report of herring gulls killing adult willow ptarmigan and of jaegers attacking them exists (Martin 1985), there was no evidence of such predation on adult rock ptarmigan at Windy Lake.

In the Kilgavik region, the two falcon species comprised over half the population of nesting raptors within 10 km of the Windy Lake study sites. It is, therefore, not surprising that these two falcons accounted for the majority of rock ptarmigan killed by avian predators during the breeding season of 1988 and 1989. It was often impossible to determine which falcon had made the kill simply from the remains found since both species handle prey in a similar fashion (Jenkins *et al.* 1964, Cramp and Simmons 1980). Fortunately, it was possible to visit, at the end of the breeding season, the closest eyrie (one gyrfalcon and two peregrines) to collect evidence, such as numbered bands, of marked rock ptarmigan taken from the Windy Lake study sites. From 1987 to 1989, such evidence was found at the gyrfalcon eyrie, confirming the identity of the predator for three ptarmigan. Even though more than half of the falcon kills found could not be classified to species of falcon responsible, all but one kill of those for which the species was known were killed by gyrfalcons. If one considers the relative importance of rock ptarmigan in the diet of tundra gyrfalcons (major; Poole and Bromley 1988) and peregrines (minor; Bradley and Oliphant 1991), it is probably safe to assume that most of the falcon kills were, in fact, gyrfalcon kills. Even without ascribing more of the kills to them, gyrfalcons accounted for more than two-thirds of the kills for which predator identity was determined. In the central Canadian arctic, therefore, gyrfalcons would seem to be the most important predator of rock ptarmigan during the breeding season, as suggested by Bergerud and Mossop (1984), Nielsen (1986), Poole (1987), and Gardarsson (1988).

The density of nesting raptors in the vicinity of NWL and SWL differed, yet the levels and timing of predation on rock ptarmigan in the two areas was not different. Very little information on the hunting range and habits of gyrfalcons has been collected, as such using the criteria of number of eyries within 10km of the study areas may not accurately reflect hunting pressure at each site as gyrfalcons nesting further than 10km may in fact hunt there. As a result, it is possible that the predation pressure from these falcons was equal at both study sites, and consequently kill rates would be expected to be similar.

Mammalian predation on rock ptarmigan at Windy Lake during the breeding season was minor. Both species of fox found in the Windy Lake region have been reported to prey on rock and willow ptarmigan (Gudmundsson 1960, Hannon and Gruys 1987). Throughout the year red foxes were found to be just as important a predator as raptors on willow ptarmigan in northern British Columbia (Hannon and Gruys 1987). At Windy Lake, red foxes are at the northern edge of their range (Banfield 1974), and therefore, they are probably present only in low numbers. Gudmundsson (1960) reported that arctic foxes prey on adult rock ptarmigan in Iceland, but provided no data on levels or timing of their depredations. However, depending on the region, arctic foxes may be an important egg predator, while killing few adults. On Svalbard (Steen and Unander 1985) and in the eastern Canadian arctic (Brodsky 1988), arctic foxes destroyed numerous clutches but killed no adults. It is perhaps not surprising, therefore, that few, if any, adult rock ptarmigan were killed by foxes at Windy Lake.

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III. THE REPRODUCTIVE BIOLOGY OF ROCK PTARMIGAN IN THE CENTRAL CANADIAN ARCTIC

INTRODUCTION

The reproductive biology of rock ptarmigan (*Lagopus mutus*) has been documented in a number of locations throughout its range. Most information has come from populations in Alaska (Weeden 1962, Weeden 1963, Weeden and Theberge 1972, McGowan 1972), Scotland (Watson 1965), Iceland Gardarsson (1971, 1988), and Svalbard (Steen and Unander 1985). In Canada, breeding behaviour has been described (MacDonald 1970), as have territoriality (Olpinsky 1986) [illegible] mating tactics (Brodsky 1988a, b). These studies, however, provided little empirical data on breeding success and patterns of attrition from egg to fledged young.

To date, the most in-depth study of the reproductive biology of rock ptarmigan was conducted by Steen and Unander (1985) on Svalbard. Their study was the first to follow the fate of marked hens from the onset of the breeding season through to the end of fledging. However, despite data on many aspects of the reproductive biology, little was reported on attrition rates during the major stages of either nesting or brood rearing. Such information is necessary to understand the role of fecundity in the life history traits of a species (Martin *et al.* 1989). Only recently has this type of information been collected on grouse species, with only one study of ptarmigan (*Lagopus lagopus*) (Martin *et al.* 1989). Furthermore, although levels of nest loss in rock ptarmigan have been documented in various parts of its range by several researchers (Watson 1965, Weeden 1965, Weeden and Theberge 1972, Steen and Unander 1985, Brodsky 1988a, Gardarsson 1988), little has been reported on the timing and cause of clutch or brood losses. Nor have any of the studies attempted to examine breeding success and patterns of attrition with respect to abundance of predators. These aspects must be investigated in order to provide a comprehensive picture of overall reproductive success for any population.

The objective of this study was to describe as completely as possible the reproductive biology of a population of rock ptarmigan from the central Canadian Arctic. Specifically, data were collected on fecundity and rates of attrition from egg through to independent offspring. Attrition was analyzed at both the egg and clutch level. The timing, rate, and source of predation on hens, clutch, and broods were recorded as well. The reproductive variables measured were examined for effects of year, female age, and abundance of predators ([illegible] measured by number of nesting raptors near two populations).

STUDY AREA AND METHODS

The study area, located at Windy Lake, is approximately 4 km inland from Hope Bay on the southeast side of Melville Sound and Elu Inlet in central Northwest Territories (approximately 68° 5' N and 106° 40' W). Topographically, the area is primarily gently rolling tundra punctuated by small rock outcrops. The flora is dominated by low-arctic tundra species. Further description of the vegetation, climate and geology of the area is reported in Chapter II.

Two local populations of rock ptarmigan were studied: one located near the north end of Windy Lake (NWL population), the other near the south end of Windy Lake (SWL population). The two populations were approximately 5.5 km apart, and covered areas similar in size (ca. 8.5 km^2). Topography and vegetation of the two areas were similar, but the relative nesting density of raptors in the vicinity (<10 km) was different, one high (SWL) and one low (NWL) (Chapter II). Data were analyzed initially for area effects, and where there were none, data from the two sites were pooled for subsequent analyses.

Nearly all rock ptarmigan that settled at NWL and SWL to breed in 1988 and 1989 were captured at the onset of the breeding season (early June) with a noose pole and ground nets (Hannon 1983). As well, a small number of birds were captured outside these two areas (OFF). For field identification, all individuals were fitted with four colour-coded leg bands: one numbered aluminum and three numbered, plastic, coloured bands. Body weight, wing chord (flattened), sex and age were recorded for all individuals. Birds were classed as either adult (≥ 1 year old) or yearling (< 1 year old), based on the pigmentation of the eighth and ninth primaries (Weeden and Watson 1967, Parker *et al.* 1985). Young of the year were termed "juveniles". All females were fitted with a 12 g 'necklace' radio transmitter (Biotrack, U.K.), and half of the males with either a 'necklace' transmitter or an 18 g 'backpack' radio transmitter (Telemetry Systems, U.S.A.). Following release, the status (territorial/non-territorial, paired/unpaired), identity of mate(s), territory and nest location were determined for each ptarmigan pair. Territory, nest, and brood locations were mapped onto a cover map of the study area (drawn from a 1:50,000 scale topographic map), and UTM (Universal Transverse Mercator) coordinates were recorded.

The fate of banded rock ptarmigan, as well as of nests and broods, was documented to the end of the breeding season (end of July) through regular surveys (every 3-4 days) of the respective territories. Upon each nest visit, the hen was flushed and an egg count taken. This provided data on timing of egg or clutch loss, as well as hatching date. To control for possible effects of visitation on mortality rates and nesting success, half of the nests were randomly chosen to serve as a control group. Nests in this group, with the exception of the initial disturbance when the nest was found and the clutch counted, were not disturbed during the remainder of incubation (Appendix 1). Similarly, half of the broods were randomly chosen as a control and were visited less frequently (Appendix 1).

Nests (first and renests) were located by following radio-marked hens, and all nests were found during laying or early in incubation. Clutch size was recorded at the time of the first visit. If the nest was first found during laying, and was designated as a 'disturbed' nest, then the total clutch laid was determined during subsequent visits. If the nest was designated an 'undisturbed' nest, total clutch laid could only be determined by visiting the nest at hatching (or as close to as possible) to count the number of eggs, egg shells, or chicks. Length of incubation in rock ptarmigan is 21 days (Godfrey 1986), and from nests that were visited regularly (disturbed), it was possible to predict date of hatching for most nests within 48 hrs. All nests were checked at hatch to ascertain hatching success. Rock ptarmigan chicks are precocial and leave the nest accompanied by the hen within 24 hrs of hatching. At each brood visit, a brood count was taken. Broods were visited through the end of July by which time all were at least 16 days old, and most were 21-24 days old.

The locations of nests and broods were marked in the field with a geological surveyor stake placed 100 m away, and from which a compass bearing to the nest or brood was recorded.

Juveniles began to fly at 8-10 days of age, and in this study were considered fledged at 10 days post-hatch, even though survival of most chicks was determined to 21-24 days of age.

A hen and her mate were successful breeders if they fledged one or more chicks. Reproductive (or "state") variables described in this study include clutch initiation date, total clutch laid (TCL), clutch size at hatch (CSH), number of chicks that leave the nest (CLN), and brood size at fledging (BSF). These terms are described in further detail by Martin *et al.* (1989). Three transition probabilities connect these four variables: egg survival (P1=CSH/TCL) - reflects partial clutch loss during incubation; hatching success (P2=CLN/CSH) - reflects eggs that did not hatch and chicks that were abandoned at the nest; and fledging success (P3=BSF/CLN) - reflects partial brood loss during brood rearing (Martin *et al.* 1989). For all analyses, these variables are always > 0. Three additional probabilities account for those individuals that failed to hatch or fledge any chicks: total nest failure (TNF) - all eggs were depredated or abandoned before any hatched; total hatching failure (THF) - all eggs incubated to full term but failed to hatch, or, if eggs hatched, no chicks left the nest; total brood failure (TBF) - none of the chicks that left the nest fledged (Martin *et al.* 1989). Two variables describe overall reproductive performance: reproductive success (BSF/TCL; only hens with BSF >0) - reflects partial loss during the breeding season; and reproductive efficiency (%) (BSF/TCL; only for hens that laid a complete clutch) - reflects loss during the breeding season for the whole breeding population (Martin *et al.* 1989). The probability of renesting was also calculated (PRN) - the proportion of hens which suffered total nesting failure and renested (excluding hens that were depredated).

To examine if any of the variables described above varied over the 2 years, or differed between the two study sites or between the two age groups of hens, each variable was tested in a factorial analyses of variance (ANOVA) examining for any effects of these three factors (year, area, and age) as well as any interaction effects. Where no statistical differences were found in a category, data were pooled for subsequent analyses.

Survival rates of clutches from initiation of laying through to fledging, and of broods from hatch to fledging, were calculated using the Kaplan-Meier (K-M) product limit method, as modified by Pollock *et al.* (1989) for staggered entry of animals (nests or broods). Survival rates were calculated on a daily basis. The K-M product limit method, which calculates a survival function [$S(t)$], is described in detail in Chapter II. Statistical differences in the survival function between age groups, years, and areas were carried out using the most conservative of the three "approximate chi-square" tests presented by Pollock *et al.* (1989).

All *t*-values were two-tailed, and, unless otherwise noted, unpaired comparisons. All 2x2 contingency analyses used the *G*-test of independence with Williams Correction to test for relationship between the observed frequencies recorded for the two classes (Sokal and Rohlf 1981). For all analyses of variances, variables that violated assumptions of normality or homogeneity of variances were ranked and then tested. The significance level was set at $P<0.05$ for all tests.

RESULTS

Mating System

The mating system of rock ptarmigan at Windy Lake was almost exclusively monogamous; out of a total of 48 males (1988 and 1989 combined) which attracted a mate, only one was bigamous. Not all territorial males (17.2% (10/58) in 1988 and 1989) were successful in attaining a mate. On the other hand, all female residents on the study area were paired.

Laying and incubation

The first egg was laid on June 7 in 1988 and on June 5 in 1989. For first nests, the mean date of clutch initiation in 1988 was June 9, and in 1989 it was 1 day later , June 10. The mean date of initiation of renests (years combined) was 12 days later than for first nests (Table III-1). In 1988, yearling hens initiated laying approximately 1 day earlier than adult hens (Table III-2), but in 1989 they initiated more than 4 days later than adult hens (Table III-2). There were no year, study area, and female age effects nor interaction effects on clutch initiation date in a three-factor ANOVA (Table III-3). In both years, a second clutch was laid by some females that lost their first clutch. The mean date of clutch initiation of renests was 11 days later than the mean date for first nests (Table III-1). Combining both years, 85.3% (29/34) of all hens initiated their first clutch between June 7 and June 11 (Fig. III-1, A). Such a high degree of synchrony in initiation was observed among both adult (86.7%) and yearling hens (84.2%) in that time period (Fig. III-1, B). Unlike first nests,

Table III-1: Descriptive statistics of first nests and renests of rock ptarmigan at Windy Lake, N.W.T. (data pooled for 1988 and 1989).

	First Nest			Renest		
Reproductive Variable	Mean [a]	S.E.	*n*	Mean [a]	S.E.	*n*
Clutch initiation date (June)	9.24	0.45	34	20.67	2.08	6
Total clutch laid	8.74	0.15	38	5.00	0.52	6
Total nest failure	0.45	0.07	47	0.33	0.21	6
Egg survival	0.97	0.03	26	1.00	0.00	4
Clutch size at hatch	8.50	0.35	26	5.00	0.71	4
Total hatching failure	0.00	0.00	26	0.00	0.00	4
Hatching success	0.99	0.72	26	0.95	0.05	4
Chicks leaving the nest	8.38	0.35	26	4.75	0.75	4
Total brood failure	0.00	0.00	26	0.50	0.29	4
Fledging success	0.83	0.04	26	0.66	0.09	2
Brood size at fledging	6.96	0.43	26	3.50	0.50	2
Reproductive success	0.79	0.04	26	0.66	0.09	2
Reproductive efficiency (%)	53.92	6.75	38	22.02	14.12	6
Probability of renesting	0.38	0.13	16			

[a] calculation of means excluded data of values equaling 0.

Table III-2: Reproductive variables of first nests for adult and yearling rock ptarmigan hens in 1988 and 1989 at Windy Lake, N.W.T..

	Adult hens			Yearling hens		
Reproductive Variable	Mean †	S.E.	*n*	Mean †	S.E.	*n*
1988						
Clutch initiation date (June)	9.33	0.75	12	8.00	0.50	8
Total clutch laid	8.67	0.26	12	8.22	0.28	9
Total nesting failure	0.47	0.13	15	0.69	0.13	13
Egg survival	0.89	0.11	8	1.00	0.00	4
Clutch size at hatch	7.63	0.98	8	8.50	0.50	4
Total hatching failure	0.00	0.00	8	0.00	0.00	4
Hatching success	0.99	1.39	8	1.00	0.00	4
Chicks leaving the nest	7.50	0.96	8	8.50	0.50	4
Total brood failure	0.00	0.00	8	0.00	0.00	4
Fledging success	0.88	0.04	8	0.80	0.05	4
Brood size at fledging	6.50	0.87	8	6.75	0.48	4
Reproductive success	0.76	0.10	8	0.80	0.05	4
Reproductive efficiency (%)	50.66	12.51	12	35.45	14.16	9
Probability of renesting	0.50	0.29	4	0.38	0.18	8
1989						
Clutch initiation date (June)	7.33	1.20	3	10.55	0.90	11
Total clutch laid	9.80	0.37	5	8.75	0.25	12
Total nesting failure	0.40	0.24	5	0.21	0.11	14
Egg survival	1.00	0.00	3	1.00	0.00	11
Clutch size at hatch	9.67	0.67	3	8.82	0.26	11
Total hatching failure	0.00	0.00	3	0.00	0.00	11
Hatching success	1.00	0.00	3	0.98	1.38	11
Chicks leaving the nest	9.67	0.67	3	8.64	0.28	11
Total brood failure	0.00	0.00	3	0.00	0.00	11
Fledging success	0.82	0.14	3	0.81	0.08	11
Brood size at fledging	8.00	1.53	3	7.09	0.73	11
Reproductive success	0.82	0.14	3	0.80	0.08	11
Reproductive efficiency (%)	49.29	21.45	5	72.96	9.60	12
Probability of renesting	0.00	0.00	2	0.50	0.50	2

† calculation of means excluded data of values equaling 0.

Table III-3: Three-factor ANOVA of rock ptarmigan reproductive variables for completed, first nests. The analyses examine the single factor and interaction effects of female age, year, and study area on the dependent variables. The transition probabilities variables were angularly transformed before analysis.

Dependent Variables	Overall Model df	 F	 P	Significant Sources of Variation	 F [†]	 P
Clutch initiation date (June)	7	0.70	0.67	- [††]	-	-
Total clutch laid	7	1.56	0.19	female age	6.11	0.02
Egg survival	7	0.27	0.96	-	-	-
Clutch size at hatching	7	0.61	0.74	-	-	-
Hatching success	7	0.63	0.73	-	-	-
Chicks leaving the nest	7	0.88	0.54	-	-	-
Fledging success	7	0.63	0.72	-	-	-
Brood size at fledging	7	0.49	0.83	-	-	-
Reproductive success	7	0.67	0.69	-	-	-
Reproductive efficiency	7	0.84	0.56	-	-	-

[†] F - value based on Type III Sum of Squares.

[††] "-" indicates there were no single factor nor interaction effect, and consequently no F nor P value.

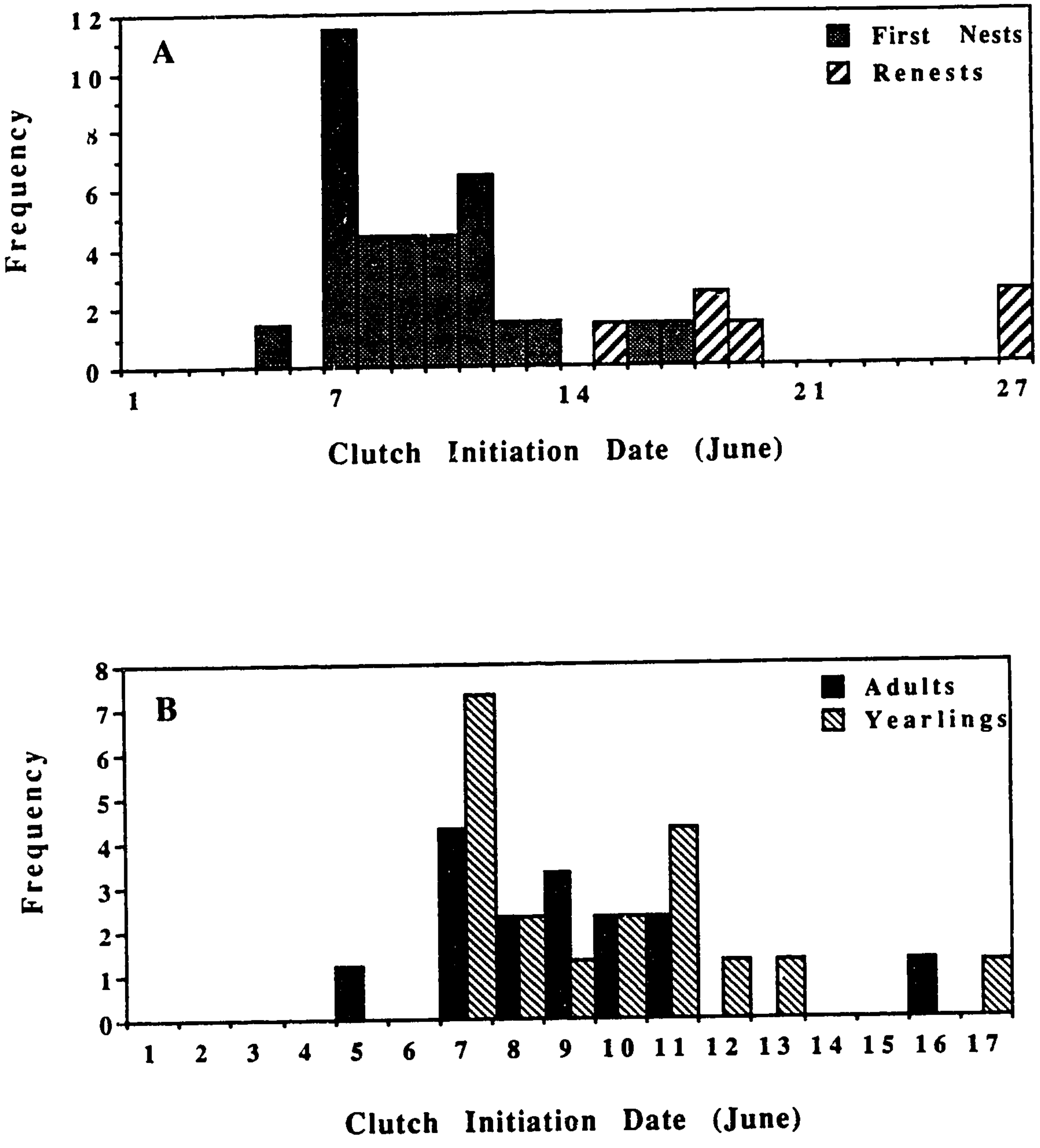

Figure III-1: Frequency of clutch initiation dates of: A) first nests and renests, and B) of adult and yearling hens (first nests only), in a population of rock ptarmigan at Windy Lake, N.W.T. (1988 and 1989 pooled).

there was no similar degree of synchrony in initiation of renests. Of the hens that laid a second clutch, there are data from only two on date of loss of the first nest and the date of initiation of the second clutch. One of these two hens had laid a complete first clutch of eight eggs, which she lost early in incubation: she initiated her second clutch 3 to 7 days after she lost her first clutch. The other hen lost her first clutch during laying (she had laid between one and four eggs), and she initiated her second clutch 2 to 5 days after she lost her first clutch.

The mean total clutch laid (TCL) for first nests was 8.74, significantly higher than in renests (t=8.57, df=42, P=0.00) (Table III-1). For first nests, adult hens laid significantly larger clutches than yearlings in 1989 (t=2.30, df=15, P=0.04), but not in 1988 (t=1.17, df=19, P=0.26) (Table III-2, Fig. III-2). Although there was not a significant year effect on TCL (F=3.12, P=0.09), adult hens laid significantly larger clutches in 1989 than in 1988 (t=-2.44, df=15, P=0.03). There was no difference in TCL for yearlings between 1988 and 1989 (t=-1.40, df=19, P=0.18). Pooling the two age groups, the mean TCL was smaller in 1988 (8.5) than in 1989 (9.1). The third factor analyzed for effects on TCL, study area (*i.e.* NWL and SWL), did not have a significant effect, nor were there any interaction effects (Table III-3).

Even though adult hens laid larger clutches than yearlings in one of the years of this study, there were no differences in the mean TCL of pairs in which both birds were adults, both were yearlings, or one was an adult and one a yearling (F=1.09, P=0.37). Of 34 pairs in which both birds were marked and of known age, 35% were both adults, 15% were both yearlings, 9% were composed of an adult female and yearling male, and 41% were composed of an yearling female and adult male. There was also no difference in the mean date of clutch initiation between the four groups (F=0.97, P=0.42).

The date of clutch initiation and the total clutch laid by a hen were related neither to her body weight nor her body size (using wing chord as an index) during laying (at time of capture). Neither initiation of laying nor total clutch laid were correlated to body weight (clutch initiation date: r^2=0.02, n=23, P=0.57; TCL: r^2=0.05, n=26, P=0.30) nor wing chord length (clutch initiation date: r^2=0.05, n=33, P=0.22; TCL: r^2=0.03, n=37, P=0.30). As well, total clutch laid (first nests only) was not correlated with date of clutch initiation (r^2=0.06, n=34, P=0.17).

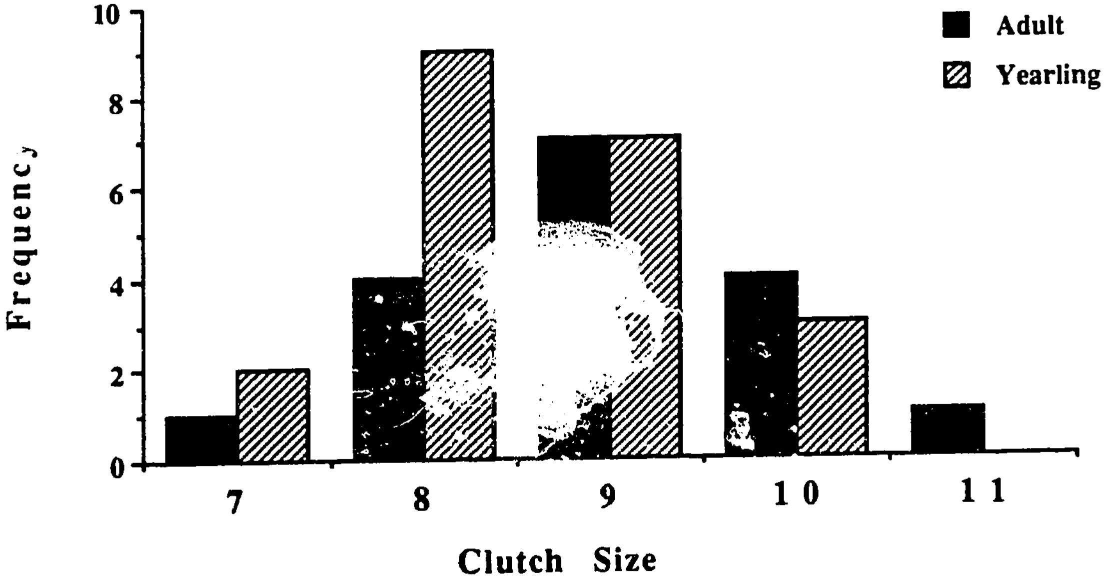

Figure III-2: Frequency of clutch sizes (TCL) of complete, first nests of adult and yearling rock ptarmigan hens at Windy Lake, N.W.T. (1988 and 1989 pooled).

Clutch survival and hatching success

Of the hens surviving to initiate clutches (47/49), 83% (39) successfully completed first nests (Table III-4). Apparently all hens that attempted renests were successful in completing the clutch. Of completed first nests, 66.7% (26/39) successfully hatched (Table III-4). Of renests, the same success rate was recorded (66.7%, 4/6) as for first nests. Among first nests, there were, proportionally, half as many nests lost during laying (0.17) as during incubation (0.33); the difference, however, was not significant (Table III-5). Most nest failures occurred during the first 2 weeks of incubation (Fig. III-3).

Of all hens that initiated nesting, 63.8% (30/47) successfully hatched a clutch, whether from a first or a second nesting attempt. However, because only 55.3% (26/47) had their first clutch survive to hatching, there was a total nesting failure (TNF) of 44.7%. A significant difference was observed in 1988 in the proportion of first nests from SWL or NWL that hatched, but in 1989 there was no difference (Table III-5). The proportion of first nests at NWL that hatched was similar in both years (G=0.02, df=1, P=0.89), whereas the proportion of nests that hatched at SWL was significantly higher in 1989 than in 1988 (G=7.73, df=1, P=0.01).

There was no difference between adult and yearling females in the proportion of clutches that hatched (Table III-5). Among adult hens, there was no difference between 1988 and 1989 in the proportion of first clutches that hatched (G=0.06, df=1, P=0.81); however, yearling hens were more successful in 1989 than in 1988 (G=6.15, df=1, P=0.01) (Table III-5).

Of those hens with first nests that failed, 28.6% (6/21) renested. The probability of renesting was 0.38 (6/16), with no difference in the proportion of adult (0.33, 2/6) and yearling hens (0.40, 4/10) that renested (G=0.06, df=1, P=0.81) but the proportion of hens renesting from SWL (0.60, 6/10) was greater than at NWL (0.0, 0/6) (G=6.94, df=1, P=0.01). There was no difference in the probability of renesting in 1988 (0.42, 5/12) and in 1989 (0.25, 1/4) (G=0.32, df=1, P=0.57). Pooling data from the two summers, the probability that a female renested (excluding hens that were depredated) was significantly greater if she lost her first clutch during laying (0.71, 5/7) than during incubation (0.11, 1/9) (G=5.90, df=1, P=0.02).

The mean clutch size at hatch (CSH) for first nests was 8.5 eggs (Table III-1). There were no single factor nor interaction effects in a three-factor ANOVA with year, study area, and female age as factors (Table III-3).

Table III-4: Number of rock ptarmigan hens that died before laying, number of first nests initiated, lost, successfully fledging ≥ 1 chick, and percent successful by female age and area (SWL: high density of nesting raptors; NWL: low density of nesting raptors) at Windy Lake, N.W.T., 1988 and 1989. Figures in parantheses are corresponding values for renests.

Year	Category	Hens died before laying	Nests Initiated	Periods of Loss			Fledged	% Successful
				Laying	Incubation	Brood		
1988	Total	0 (0)	28 (5)	6 (0)	10 (2)	0 (2)	12 (1)	42.9 (20.0)
	Female age							
	Adult	0 (0)	15 (2)	2 (0)	5 (1)	0 (0)	8 (1)	53.3 (50.0)
	Yearling	0 (0)	13 (3)	4 (0)	5 (1)	0 (2)	4 (0)	30.8 (0.0)
	Area							
	SWL	0 (0)	14 (5)	4 (0)	7 (2)	0 (2)	3 (1)	21.4 (20.0)
	NWL	0 (0)	13 (0)	2 (0)	2 (0)	0 (0)	9 (0)	69.2 (-)
	OFF	0 (0)	1 (0)	0 (0)	1 (0)	0 (0)	0 (0)	0.0 (-)
1989	Total	2 (0) [a]	19 (1)	2 (0)	3 (0)	0 (0)	14 (1)	73.7 (100)
	Female age							
	Adult	1 (0)	5 (0)	0 (0)	2 (0)	0 (0)	3 (0)	60.0 (-)
	Yearling	0 (0)	14 (1)	2 (0)	1 (0)	0 (0)	11 (1)	78.6 (100)
	Area							
	SWL	0 (0)	7 (1)	1 (0)	0 (0)	0 (0)	6 (1)	85.7 (100)
	NWL	2 (0) [a]	9 (0)	0 (0)	3 (0)	0 (0)	6 (0)	66.7 (-)
	OFF	0 (0)	3 (0)	1 (0)	0 (0)	0 (0)	2 (0)	66.7 (-)

[a] includes one unbanded of unknown age.

Table III-5: Number of nests (complete first nests only) that were successful and unsuccessful in hatching and fledging in a population of rock ptarmigan at Windy Lake [a], N.W.T, in 1988 and 1989.

Year	Hatching / Fledging [b]	Study Site		Female Age		Stage [c]	
		SWL	NWL	Adult	Yearling	Laying	Incubation
1988	Successful	3	9	8	4	22	12
	Unsuccessful	11	4	7	9	6	10
	G	6.15		1.39		3.16	
	P	0.01		0.24		0.08	
1989	Successful	6	6	3	11	17	14
	Unsuccessful	1	3	2	3	2	3
	G	0.70		0.54		0.35	
	P	0.40		0.46		0.55	
Total	Successful	9	15	11	15	39	26
	Unsuccessful	12	7	9	12	8	13
	G	2.73		0.001		3.00	
	P	0.10		0.98		0.08	

[a] all birds from NWL, SWL, and OFF, unless otherwise indicated.

[b] among first nests all that hatched also succeeded in fledging chicks.

[c] number of nests that were successful and unsuccessful through laying and incubation periods.

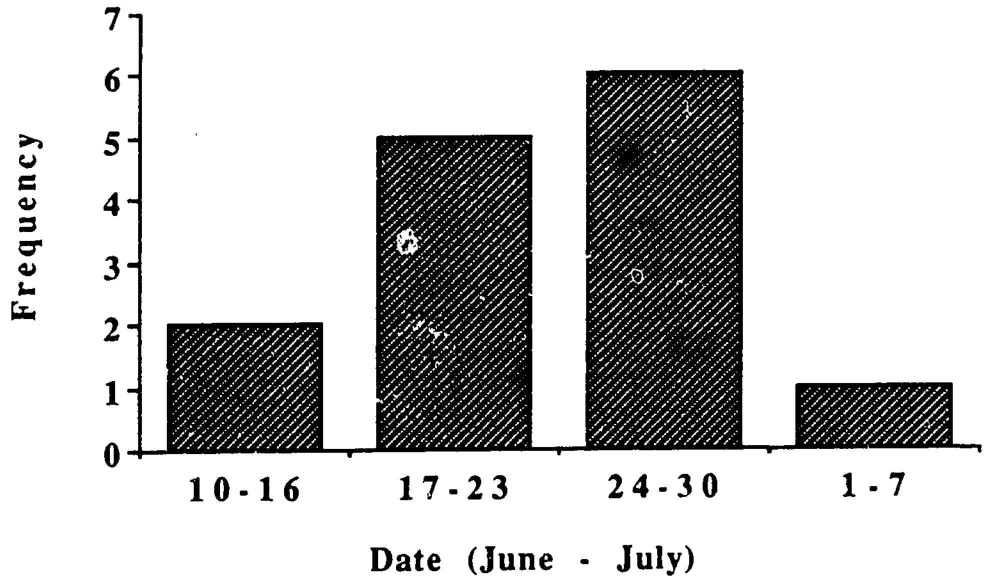

Figure III-3: Frequency of nest loss dates for first nests of rock ptarmigan at Windy Lake, N.W.T. (1988 and 1989 pooled). The mean date of initiation of incubation was June 17.

Egg survival (P1) in nests which hatched at least one egg was very high, approximately 97% (221/228) for first nests and 100% for renests (Table III-1). Hatching success (P2) was also very high, almost 99% of eggs from first nests and 95% of eggs from renests hatched and had the chicks leave the nest (Table III-1). There were no factors nor interaction effects in a three-factor ANOVA (year, study area, and female age) affecting either egg survival or hatching success (Table III-3).

Fledging and reproductive success

In 1988 and 1989, a total of 53 nests were initiated: 47 first nests and 6 renests. Of these, 52.8% (28/53) were successful in fledging a brood. The percentage of hens that settled at Windy Lake to breed in 1988 and 1989 that fledged a brood was 57% (28/49), resulting in an average of 3.8 chicks fledging per hen (see Chapter II).

Of all nesting attempts (first and renests) that failed, only 8% (2/25) failed during brood rearing, and both of these were renests (2/4). As a result of no total brood failures (TBF) among first nests, therefore, the proportion of hens that initiated nesting and bred successfully (*i.e.* fledged a brood) equals the proportion of hens that successfully hatched a clutch (presented earlier).

Fledging success (P3) of chicks hatched from first nests (0.83) was higher than from renests (0.66) (Table III-1). There were no factors nor interaction effects in a three-factor ANOVA (year, study area, and female age) that affected fledging success (Table III-3).

There were significantly more chicks leaving the nest (CLN) from first than from renests (Table III-1). As with CSH, there were no factors nor interaction effects on CLN in a three-factor ANOVA (year, study area, and female age) (Table III-3).

Overall survival (K-M survival function) of all clutches from initiation of laying through to day 21 post-hatch (day 1 to day 51) was 62.5%, and for first nests only it was 65.0% (Fig. III-4). The rate of loss of nests was relatively linear until day 22 post clutch initiation, at a mean daily rate of 1.6%. This date coincided roughly with beginning of week 3 of incubation. Survival after this date levelled off and did not decrease further. There were no significant differences in the survival (K-M survival function) between nests of adult or yearling hens, nor between nests from NWL or SWL study areas (Table III-6).

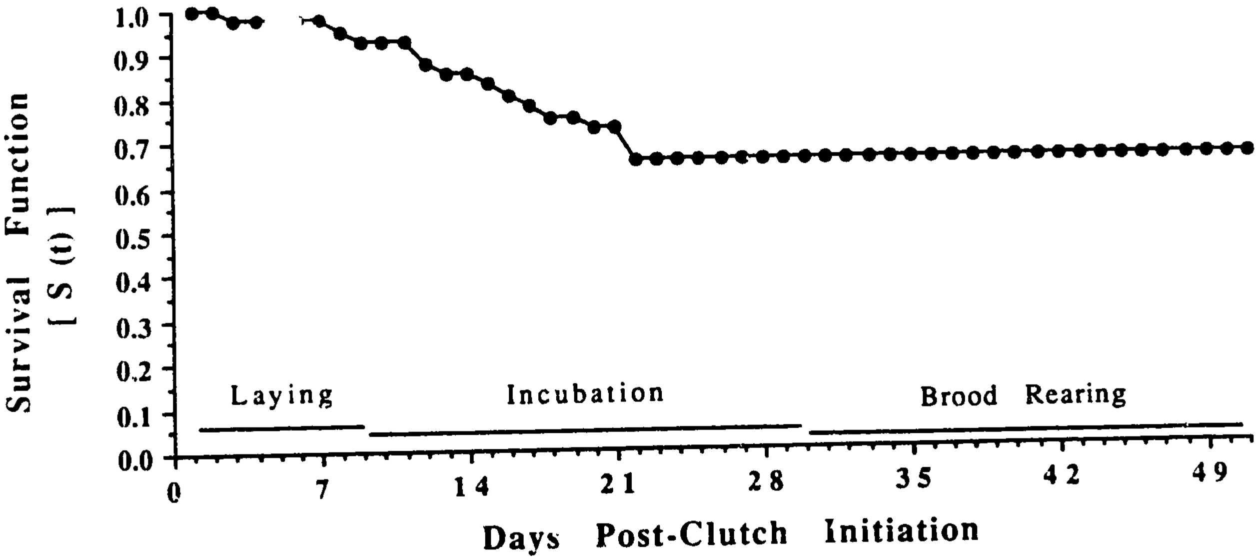

Figure III-4: The Kaplan-Meier survival function of rock ptarmigan clutches (first nests only) at Windy Lake, N.W.T. (1988 and 1989 pooled) from clutch initiation through to chicks being 3 weeks of age. Day 20 post-clutch initiation equals July 1.

Table III-6: Survival function (S[*t*]) of rock ptarmigan clutches from Windy Lake, N.W.T., at day 51 post clutch initiation (*i.e.* chicks 3 weeks old).

Category	Survival Function	X^2	P [a]
Study Area [b]			
NWL	0.750	1.15	0.28
SWL	0.563		
Female Age [c]			
Adult	0.619	0.12	0.73
Yearling	0.684		
Year [b]			
1988	0.486	4.83	0.03
1989	0.833		

[a] testing for statistically significant differences between the two groups of the category; *P* based upon an approximate chi-square test (Pollock *et. al.* 198[illegible]

[b] includes only first nests.

[c] includes first nests and renests.

However, in 1989 the survival function among first nests was significantly greater than it was in 1988 (Table III-6).

The mean brood size at fledging was higher at SWL than at NWL in both 1988 and 1989 (Fig. III-5), but not significantly in either year (1988: t=1.48, df=10, P=0.17; 1989: t=0.65, df=10, P=0.53). There were no year, female age, area, and interaction effects on BSF (Table III-3). There was no difference in mean BSF (complete first nests only) among the four sex-age groups, and this was the case whether unsuccessful hens were included (F=0.28, P=0.84) or excluded (F=0.22, P=0.88) from the analyses (1-way ANOVA). Furthermore, there was no difference between any of the four sex-age groups in the proportion of hens that successfully fledged $\geq$ 1 chick(s) (G=0.49, df=3, P=0.92).

Brood survival (K-M survival function) was high during brood rearing, 75% at day 21 post-hatching (Fig. III-6, A). Chicks are capable of flying short distances at about 10 days of age (Weeden 1963), and there was no difference in the survival of chicks before (from hatch to day 10 post hatch) or after (from day 11 to day 21 post hatch) they are able to fly (Fig.III-6, B). There were no significant differences in the survival function of broods between adult and yearling hens, between broods from NWL or SWL, or between broods from 1988 or 1989 (Table III-7).

First nests, as compared to renests, contributed most to the overall productivity of the population of rock ptarmigan at Windy Lake. Of all chicks at Windy Lake in 1988 and 1989 that that survived to 3 weeks of age, 97.1% (166/171) were from a first nesting attempt, whereas only 2.9% (5/171) were from a renesting attempt.

The reproductive success of first nests and renests was similar (Table III-1). The percent of total eggs laid that fledged (*i.e.* reproductive efficiency) was 49.6% (S.E.=6.31, n=44). Among completed first nests, there were no differences in either reproductive success or reproductive efficiency between 1988 and 1989, between adult and yearling hens, nor between SWL and NWL populations (Tables III-2, 3). Reproductive efficiency of completed, first nests was 22% higher in 1989 than in 1988, however the difference was not significant (Table III-2, 3). Pooling years and area, RE was similar between adults (mean=50.3 S.E.=10.5, n=17) and yearlings (mean=56.9%, S.E.=9.0, n=21) (t-value=-0.48, df=36, P=0.63). The increase in 1989

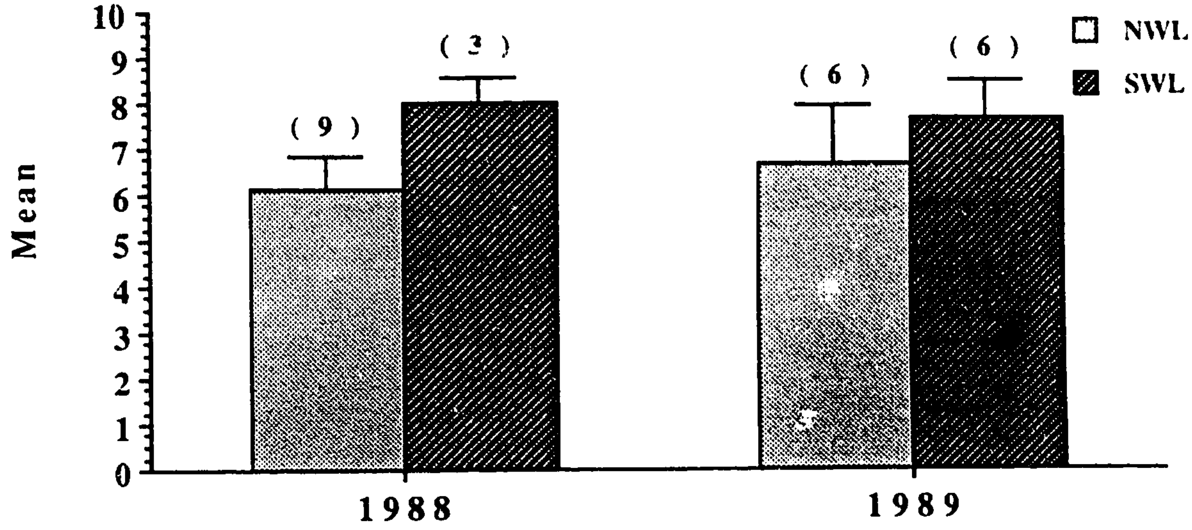

Figure III-5: Mean number of chicks fledged (BSF) per successful hen (with standard error bars and sample size in parantheses) in areas of relatively high (SWL) and low (NWL) densities of nesting raptors at Windy Lake, N.W.T., in 1988 and 1989.

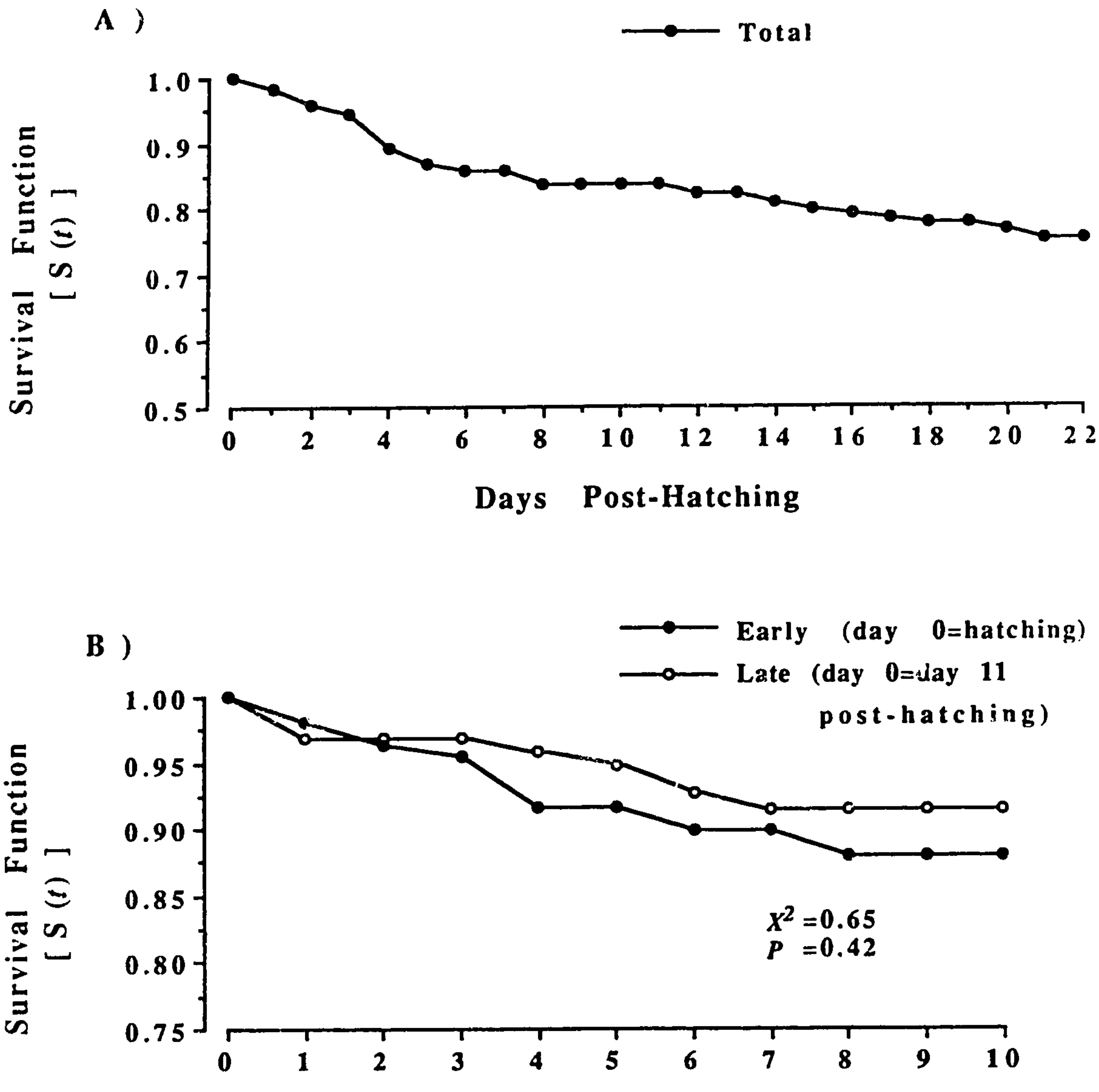

Figure III-6: Kaplan-Meier survival function of rock ptarmigan chicks (first nests only) at Windy Lake, N.W.T. (years pooled): A) chicks from hatch to day 22 post hatch, B) chicks during early stage of brood rearing (preflight) and late stage of brood rearing (capable of flight). The K-M survival curves in B) were tested for differences with an approximate chi-square test (Pollock *et al.* 1989).

Table III-7: Survival function (S[t]) of rock ptarmigan broods from Windy Lake, N.W.T., at day 21 post-hatching.

Category	Survival Function	X^2	P [a]
Study Area			
NWL	0.699	1.29	0.26
SWL	0.769		
Female Age			
Adult	0.805	2.80	0.94
Yearling	0.687		
Year			
1988	0.702	0.01	0.92
1989	0.664		

[a] testing for statistically significant differences between the two groups of the category; P based upon an approximate chi-square test (Pollock *et. al.* 1989).

is reflected in the population productivity which was 67% higher in 1989 than in 1988 (see Chapter II). In both 1988 and 1989, the difference in RE between NWL and SWL was not significant. In 1989, RE declined slightly at NWL, though not significantly (*t*=0.58, df=18, *P*=0.57). At SWL, however, the RE was significantly higher in 1989 than in 1988 (*t*-value=-3.19, df=10.6, *P*=0.01).

The greatest decline in the means between state variables, for both adult and yearling hens, was between CLN and BSF (Fig. III-7).

Of completed first clutches, the most frequent size was 9, and nests with this clutch size most frequently successfully fledged a brood (Fig. III-8, A). The most productive clutch size (*i.e.* mean BSF per clutch size), however, was 11 (Fig. III-8, B). The least productive clutch size was eight, with increasingly larger clutches fledging more chicks (Fig. III-8, B).

Breeding success was not related to date of initiation of laying nor to clutch size. Successful hens did not initiate a clutch earlier or later than unsuccessful hens (*t*=0.75, df=32, *P*=0.46), nor did the hens have significantly larger or smaller clutch sizes (TCL) (*t*=0.31, df=36, *P*=0.76). Breeding success was also not related to the hen's weight during the period of laying. Since body weight of hens begins to decrease rapidly during laying, an analysis of covariance was used with date of weighing as a covariate to compare body weights with breeding success. There was no difference in the mean body weight of successful hens and unsuccessful hens (*F*=0.62, *P*=0.44). Furthermore, body weight of hens was not correlated with reproductive success (complete first nests only), and this held true if unsuccessful hens were included (r^2=0.00, n=26, *P*=0.77) or excluded (r^2=0.05, n=19, *P*=0.36).

Sources of Reproductive Failure

Of the females that settled at Windy Lake to breed in 1988 and 1989, eight females (16.3% of total female breeding population, see Chapter II) died during the breeding season. Thus, for those rock ptarmigan pairs complete nesting failure resulted. Predation was the cause of all but one mortality; further details are presented in Chapter II.

Hatching failure was very low as only 1.2% (3/242) of all eggs that were present in the nest at hatching failed to hatch. Total nesting failure among all hens that initiated laying was significantly greater in 1988 (57%, 16/28) than in 1989 (26%, 5/19) (*G*=4.33, df=1, *P*=0.04).

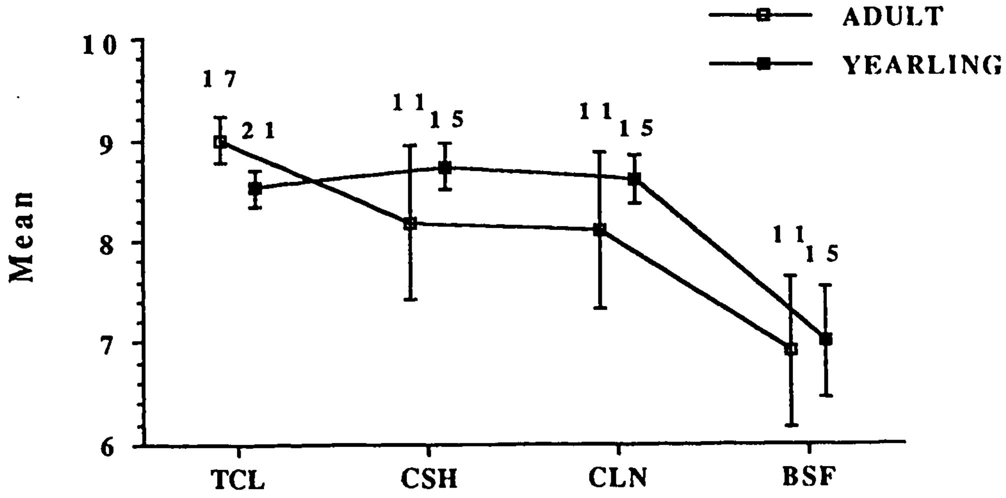

Figure III-7: Mean (with standard error bars and sample size) total clutch laid (TCL), clutch size at hatching (CSH), chicks leaving the nest (CLN), and brood size at fledging (BSF) from completed first nests of adult and yearling hen rock ptarmigan at Windy Lake, N.W.T., in 1988 and 1989.

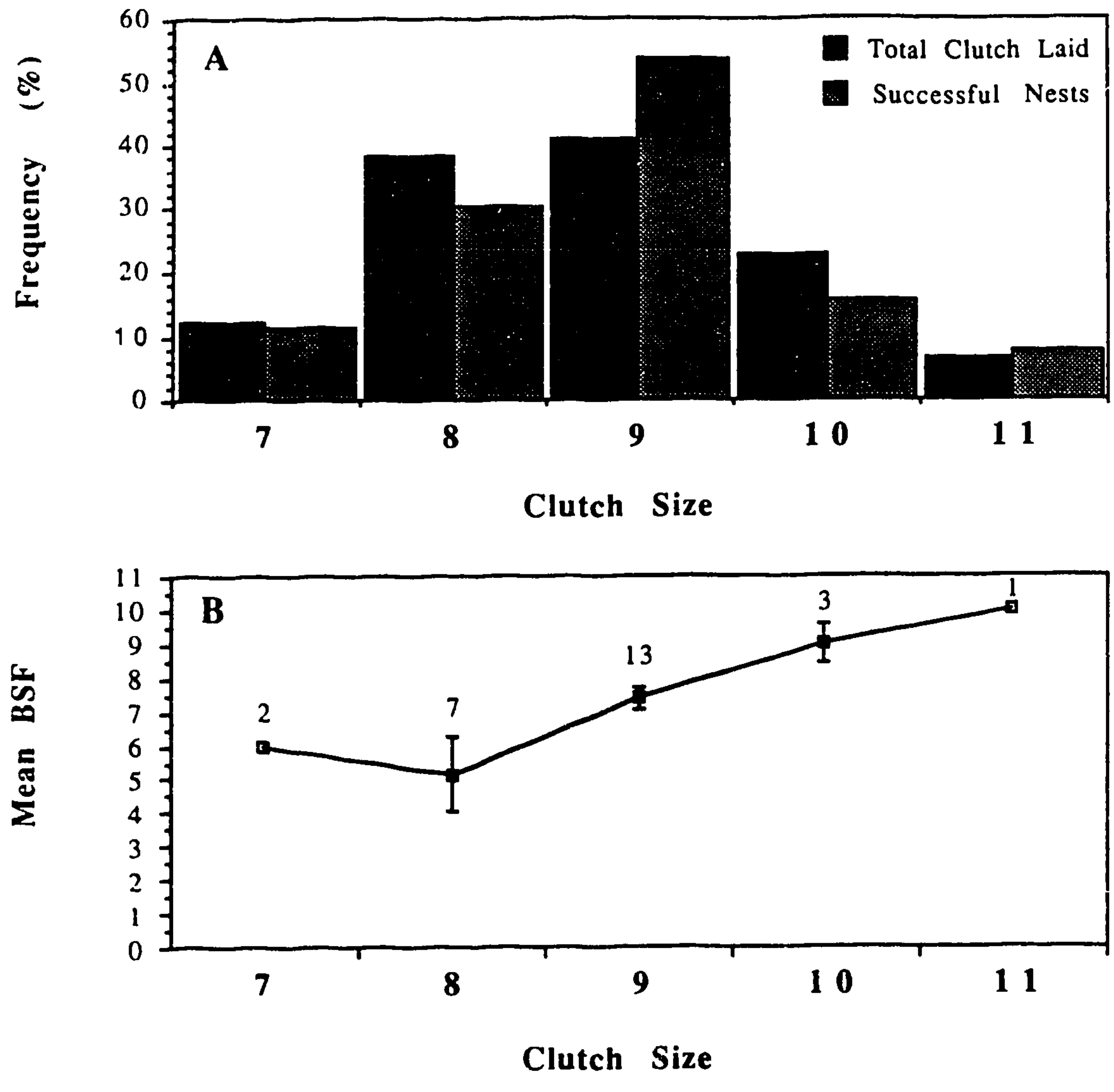

Figure III-8: Frequency of clutch sizes (TCL) and of nests that fledged ≥ 1 chick(s) relative to initial TCL (A), and mean number of chicks fledged (BSF) (with standard error bars and sample size) relative to TCL (B), of rock ptarmigan at Windy Lake, N.W.T. (1988 and 1989 pooled).

Predation

Adults

There was one hen killed prior to laying, one during laying, four during incubation, and one during brood rearing. The observed frequencies of depredations during the stages of the breeding cycle were not statistically different from an expected equal number of depredations during each stage (X^2=2.00, df=1, P=0.37). As well, the difference in the proportion of hens that were killed before or after hatching was not different (G=3.34, df=1, P=0.07).

Predation of hens caused the failure of 11.3% (6/53) of all nesting attempts. This rate was three times higher in 1988 (0.15, 5/33) than in 1989 (0.05, 1/20); however, the difference was not significant (G=1.30, df=1, P=0.25). There were more than twice as many females killed during the breeding season in 1988 (five) than in 1989 (two); however, the proportion of the total breeding population that was depredated was not significantly different between years (see Chapter II).

With respect to total nesting failures, predation of hens was responsible for 24% (6/25). There was no difference in the proportion of nests lost because of depredation of hens between NWL (0.29, 2/7) and SWL (0.19, 3/16) (G=0.24, df=1, P=0.62), nor between 1988 (0.25, 5/25) and 1989 (0.20, 1/5) (G=0.00, df=1, P>0.95).

There was no difference in the proportion of females killed between the two study areas (Chapter II), and this was true in 1988 (NWL: 0.15, 2/13; SWL: 0.21, 3/14; G=0.15, df=1, P=0.70) and 1989 (NWL: 0.09, 1/11; SWL: 0.00, 0/7; G=0.67, df=1, P=0.41). Analyzing for year differences for each site separately shows that proportion of hens killed at either NWL (G=0.19, df=1, P=0.66) or SWL (G=2.23, df=1, P=0.14) did not differ between 1988 and 1989.

In 1988, depredation of the hen caused 15% (5/33) of all nesting attempts to fail, whereas in 1989 this rate was only 5% (1/20), a non-significant decrease (G=1.30, df=1, P=0.25).

Nests

The mean egg survival of all nests was 97% (221/228) (Table III-1). All the egg loss that occurred was from one clutch, which had 87.5% (7/8) of its clutch depredated. In spite of such heavy egg predation, the hen did not abandon and the one remaining egg hatched. Although direct evidence was not obtained, an ermine (*Mustela erminea*) was observed on two occasions in the vicinity (within 20m) of that nest.

Pooling the data from 1988 and 1989, 47% (25/53) of all nests failed to hatch. Predation of the hen was responsible for 24% of these nest failures. It is not known what caused the other nests to fail, but the three nests that failed in 1989 during incubation were found to be empty of eggs or of any remains, suggesting predation. Renests had a higher success rate in hatching, than first nests, but as well the cause of failure is not known. In 1988, 45% (15/33) of all nests were depredated, as compared to only 20% (4/20) in 1989, a difference that approached significance (*G*=3.56, df=1, *P*=0.06).

Broods

There were only two total brood failures (TBF) out of 30 nests that hatched young, for a fledging rate of 93.3% for nests. One of the two TBF was a result of the hen being killed, when the brood was less than a week old. The other hen had a clutch of 5 eggs, 4 of which hatched, and all the chicks perished before they were 9 days old. Both of these total brood failures were from SWL in 1988, and were from renests. No observations were made on cause of chick mortality, however, several avian and mammalian predators were present in the area during the summer that likely preyed on rock ptarmigan chicks (see Chapter II).

DISCUSSION

Mating System

Rock ptarmigan are typically classified as having a monogamous mating system (Weeden 1963, Bergerud and Mossop 1984), and indeed the mating system of rock ptarmigan breeding at Windy Lake, N.W.T., in 1988 and 1989 was almost exclusively monogamous

Several hypotheses have been presented to explain the evolution of monogamy in grouse (Wittenberger 1978, Wittenberger and Tilson 1980), and factors which limit polygyny in ptarmigan have been examined by Bergerud and Mossop (1984) and Hannon (1984). Bergerud and Mossop (1984), in their review of the pair bond in ptarmigan, concluded that monogamy is the mating system of tundra ptarmigan because males are needed for vigilance in the open habitat, continuous daylight, and the presence of effective avian predators. Predators at Windy Lake killed 14% of the total population of hens during the breeding seasons of 1988 and 1989. Of all the hens that attempted to breed in those two summers, 43% failed to fledge any chicks; the failures were caused principally by loss through predation of the hen, clutch, or brood (see Chapter II). Predation at Windy Lake may, in fact, be sufficiently high each breeding season for monogamy to have evolved primarily to counter high predation pressures.

As pointed out initially by Wittenberger and Tilson (1980) and reiterated by Hannon (1984), a monogamous system in a species or population cannot be explained by a single hypothesis. Many other factors may come into play, such as the short length of the breeding season, and territory size and/or quality of the resources. As well, these and/or other factors may influence the level of polygyny in a population, which, though in most rock ptarmigan populations studied to date is low (this study, Unander and Steen 1985, Watson 1965), but can be higher (70%, Olpinsky 1986). It is evident that much further work is needed to examine factors influencing the level of polygyny in any given population.

Laying and incubation

In both 1988 and 1989, laying began during the first week of June, shortly after 1 or 2 days of significant snow melt when ground snow cover declined below 50%. As observed in other populations of rock ptarmigan (MacDonald 1970, Weeden and Theberge 1972, Olpinsky 1986), initiation of laying of first nests was highly synchronous at Windy Lake. Unlike on Svalbard (Steen and Unander 1985), however, initiation of laying was not found to be correlated with preincubation body weight. It is possible at Windy Lake there was insufficient variation in body weight between hens (Appendix 2) to demonstrate such a correlation.

The mean clutch size of first nests of rock ptarmigan at Windy Lake was 8.7 eggs, which falls within the range reported from other populations: 6.9-8.2 in central Alaska (Weeden 1965), 6.6 in Scotland (Watson 1965), 10.4-11.0 in Iceland (Gardarsson 1988), 8.4 for adult hens in Svalbard (Steen and Unander 1985), 8.3 on Bathurst Island, N.W.T. (MacDonald 1970), and 8.8 on Melville Peninsula, N.W.T. (Brodsky 1988a). Clutch sizes from these locations suggest that they are larger in populations of rock ptarmigan from tundra regions (Iceland, Svalbard, Windy Lake, Melville Peninsula, N.W.T., and Bathurst Island, N.W.T.) relative to populations from more southern montane regions (Alaska, Scotland). Westerskov (1956) reported a trend for larger clutch sizes in rock ptarmigan populations with an increase in latitude, a trend which has been observed in many avian species (Ricklefs 1980). However, a similar relationship does not appear to exist for willow ptarmigan in either Euarasia (Martin *et al.* 1989) or North America (Hannon and Barry 1986).

The mean clutch size of renests at Windy Lake was five eggs, significantly smaller than first nests. Although no other studies of rock ptarmigan have reported clutch size of renests, in several populations of willow ptarmigan it has been reported that clutch size of renests was smaller than that of first nests (Parker 1981, Erikstad *et al.* 1985, Martin *et al.* 1989).

Year, female age, and study site differences

Clutch initiation of first nests at Windy Lake was highly synchronous both within and between years, between adult and yearling hens, and between SWL and NWL study sites. On Svalbard, Steen and Unander (1985) found that yearling rock ptarmigan hens initiated egg-laying later than adult hens. They also reported, however, that yearling hens weighed significantly less than adults. Consequently, Steen and Unander (1985) surmised that the later initiation by yearlings was more a function of the condition of the hen, as expressed in body mass, than age and breeding experience. A similar relationship was observed for willow ptarmigan from northwestern British Columbia where Hannon *et al.* (1988) noted that hens which laid early were significantly heavier that those that laid in middle or later periods. Hannon *e al.* (1988) also observed that although heavier hens laid earlier, they were not larger (as measured by wing length), and so they concluded that "the condition of females, rather than their size, is relevant to the timing of reproduction". At Windy Lake, and as was observed in northern Quebec (Olpinsky 1985), there was no correlation between date of clutch initiation and body weight, nor was there any difference in the mean date of clutch initiation between the two age groups of hens. At Windy Lake there was no difference in the preincubation body weight of adult and yearling hens; therefore, it is probable that yearling hens at Windy Lake were able to procure sufficient food through the winter and spring for vitellogenesis.

There are several other factors which have been shown to cause variations in timing of breeding within or between years, or between geographical areas within a grouse species. These include ambient temperature, snow cover, yearly differences in phenology, photoperiod, behavioural interactions, rainfall, local habitat, and the brevity of the breeding season (Watson 1965, Lack 1968, Immelman 1972, Weeden and

T[illegible]ge 1972, Keppie and Towers 1990). Snow melt and the date that snow cover receded below 50% was very close in 1988 and 1989, thus it is perhaps not surprising that such a high degree of synchrony in initiation of laying was observed in those 2 years.

Clutch size in many populations of rock ptarmigan has been recorded to vary from year to year, and at Windy Lake the difference was close to being significant between 1988 and 1989. In ptarmigan, variations in mean clutch size between years and among locations have been shown to be related to several factors, including density, proportion of yearlings in the population, body mass of females in spring, date of clutch initiation, episodes of bad weather, and parasite loads (Martin *et al.* 1989). Weeden (1965) observed an inverse relationship between density and clutch size (r=-0.82, P<0.05) in rock ptarmigan from central Alaska. Such a correlation could not be tested for rock ptarmigan at Windy Lake because clutch size was recorded for only 2 years. On Svalbard, Steen and Unander (1985) observed that the heavier a hen the earlier she initiated her clutch, and they also recorded a positive correlation between body weight and clutch size, which would suggest a correlation between clutch initiation date and total clutch laid. It was also observed on Svalbard that preincubation weight of yearling hens was less than that of adults, and total clutch laid of yearlings was considerably smaller than that of adult hens (yearlings: mean=5.8, adults: mean=8.4) (Steen and Unander 1985). It would appear that a direct correlation exists with body condition (preincubation weight) and clutch size for Svalbard rock ptarmigan. At Windy Lake, however, it appears that this relationship does not exist. No correlation was found between clutch size and either body weight or clutch initiation date. There was also no difference in body weight between adult and yearling hens, although in 1 year of the study there was a significant difference in mean clutch size of adult and yearling hens. Overall, the majority of adult females laid clutches of nine eggs or more, whereas most yearlings laid clutches of eight eggs or less. Larger clutch sizes in older, experienced hens have been observed in blue grouse (*Dendragapus obscurus*) (Zwickel 1975). Possible explanations for an age effect include experience in finding food, and differences in physiological maturity between the age classes (Lack 1954, Zwickel 1975). Lack (1954) favored the former explanation, whereas Zwickel (1975) on the basis of data collected on blue grouse argued for the latter explanation. Zwickel (1975) based his argument primarily on the fact that while adult blue grouse laid significantly larger clutches than yearlings, nesting success did not differ between the two age classes. A difference would be expected if yearlings were less capable of procuring enough food for a normal size of clutch laid, then this inadequacy should also affect hatchability and fertility of eggs, and consequently overall nesting success (Zwickel 1975). Several researchers (Boag 1965, Zwickel *et al.* 1966) have documented that yearling female blue grouse weigh less than adults, which Zwickel (1975) argues is in turn related to physiological maturity and consequently clutch size. This explanation may also apply to Svalbard rock ptarmigan, the yearlings of which also weighed less and laid smaller clutches. It appears, on Svalbard at least, hens that cannot attain optimal body weight initiate breeding later and lay smaller clutches than hens which are, at the onset of breeding, in better condition.

Little data exist for rock ptarmigan on the effect of age and prior breeding experience on the reproductive success of either the cock or the hen. Rock ptarmigan can only be categorized initially as either 1 year old or as ≥2 years old. Obviously, a 1-year-old has no prior breeding experience, and since natal philopatry is very low in most ptarmigan populations (Olpinsky 1986, Martin and Hannon 1987), yearlings would probably have no previous experience with the breeding area. Nevertheless, clutch size did not vary with the age of the pair in rock ptarmigan at Windy Lake, similar to the situation in willow ptarmigan at Chilkat Pass, B.C. (Hannon and Smith 1984).

There was a trend only for hens that initiated laying earlier to lay more eggs than those laying later. In willow ptarmigan, Erikstad *et al.* (1985) noted an inverse correlation between clutch size and date of clutch initiation. Myrberget (1967) observed a similar seasonal trend, and he reported that a delay of 4 days corresponded with a mean reduction in clutch size of one egg. At Windy Lake, clutch size for nests initiated on June 11 (n=6) was only 0.6 of an egg smaller than clutches initiated 4 days earlier on June 7 (n=11).

There was no difference in the probability of renesting for adult and yearling hens. There was, however, a significantly greater probability of renesting if the first nest was lost during laying than during incubation. This is likely related to the brevity of the breeding season, and amount of investment already put into the first nesting attempt. Hens that lost their clutches during laying had a shorter interval before they began their second clutch. This has also been observed by Brodsky (1988a) who observed that those that lost a clutch during laying initiated a second clutch within 1 day, and those that lost a clutch during incubation would renest within 2 to 4 days. At Windy Lake, available data on the interval were limited, but it seemed to be longer than that observed by Brodsky (1988a).

Nesting success and sources of reproductive failure

Of the hens that successfully laid a complete first clutch, two-thirds successfully hatched their clutch. For those hens that were not successful, the major cause appeared to be predation. Since males do not incubate, predation of the hen necessarily resulted in the failure of the clutch. Of the nests that failed during incubation, predation of the hen was responsible for approximately one-third. Falcons (either *Falco rusticolus* or *F. peregrinus*) were responsible for all but one of the predations, with a fox (either *Alopex lagopus* or *Vulpes vulpes*) responsible for the other. In many populations, foxes and ermines are major egg predators (Weeden and Theberge 1972, Steen and Unander 1985, Brodsky 1988a). Although direct observations were not obtained, an ermine (one of only three observed during the two summers at Windy Lake) was observed on two occasions in the vicinity (within 20m) of the only nest suffering partial clutch loss (7 out of 8 eggs). Data on nests that suffered predation were only available for 1989, and during that summer all depredated nests were found within 3 days of being depredated. All these nests were found empty, with no egg shell remains or other sign of the predator. Both avian and mammalian nest predators often remove eggs from nests of grouse and waterfowl, leaving no trace of their identity (Myrberget 1985, Trevor 1989). At Windy Lake foxes (of either species) and ermines were the most likely predators involved.

Most nest loss at Windy Lake occurred early in incubation, during the first 2 weeks, which coincided with the last 2 weeks of June. Clutch loss was linear during laying and up to start of the third week of incubation, at which point the mean survival rate plateaued at 65% without further decrease. Although the timing of emergence and abundance of juvenile ground squirrels (*Spermophilus parryii*) were not documented in the 2 years of this study, in previous years at Windy Lake (1984-1986) they emerged around July 1 (Poole 1987). The significance of the timing of the emergence of juvenile ground squirrels was shown by Poole (1987), who observed that ptarmigan made up the bulk (>90% biomass) of the gyrfalcons' diet in June, whereas in

July it dropped considerably (~70% biomass) with juvenile ground squirrels assuming an important part of the diet.

Year, female age, and study site differences

The proportions of first nests that hatched at SWL and NWL were similar in 1989 but not in 1988; hatching success at SWL was lower than at NWL in 1988 and lower than at SWL in 1989. This difference resulted from a significantly higher nest loss at SWL during incubation in 1988 than in 1989. There were more than twice as many raptors (major predators of adult ptarmigan, Chapter II) nesting within 10 km of SWL than within the same distance of NWL, yet the higher number of predators nesting at SWL did not result in higher predation rate on the SWL population. This fact may indicate that predation pressure was similar at both sites possibly a consequence of gyrfalcons that nested further than 10km of either site hunting in those areas (Chapter II). From visual observations of potential egg predators (foxes, ermines, ravens, gulls, and jaegers), there appeared to be no difference in their abundance between years or locations, although it should be noted quantitative data on abundance of these predators were not collected. Hence the reasons for greater losses at SWL in 1988 remain unclear.

Nesting success varied considerably between years, from less than 50% in 1988 to almost 75% in 1989. Both loss of the female and of the eggs to predators were considerably higher in 1988 than in 1989. Thus the cause of the failures appeared to be nest predation and not desertion. Reproductive success was very similar for adult and yearling hens. This success, approximately a rate of 70-75%, was not only similar between the age groups within each of the 2 years of the study, but between years as well, with a maximum difference of only 5%. Unlike reproductive success, which is a measure of attrition from total clutch laid to brood size at fledging (successful hens), reproductive efficiency which is also the same measure of attrition, but for all hens in the breeding population, did vary between years and between age groups. Reproductive efficiency was consistent among adult hens; however, it more than doubled in 1989 among yearling hens. Since reproductive efficiency incorporates total nesting failures, this higher rate in 1989 reflects the higher breeding success in 1989 for the population as a whole and in particular among yearling hens. Consequently, breeding success was higher in 1989 primarily because yearlings fared better that year relative to the previous year.

Although quantitative data on abundance of nest predators were not collected, it is possible that numbers of predators were considerably higher in 1988 than in 1989, which would explain higher nest loss that year. Even if number of predators did not vary between years, it is possible that predation pressure on eggs and chicks may have been higher in 1988. Although in most studies of ground nesting birds the identity of egg or chick predators has not been collected, indirect correlations have been documented between egg loss and microtine numbers in several species (Myrberget 1985, Sutherland 1988). In peak years of microtine numbers, generalist predators have an abundance of easily accessible food (Myrberget 1970). However, when microtine numbers decline, these same predators switch to other prey, including grouse eggs and chicks (Myrberget 1970), which in turn experience a decrease in survival rates (Lindström *et al.* 1987). Microtines at Windy Lake appear to undergo regular fluctuations in population size in an approximate 3-year cycle (Appendix 5). Similar fluctuations in microtines have been documented in Scandinavia, where it was observed that egg predation in willow ptarmigan was especially heavy following each crash in the microtine population (Myrberget 1972). Microtines at Windy Lake peaked in 1984 and 1987 (Appendix 5), and numbers were again very high in 1990 (C. Shank, pers. comm.). Microtine density and nest loss in the 2 years of this study followed this pattern: in 1988 very low density of microtines and very high ptarmigan nest loss, whereas in 1989 microtine numbers were higher and ptarmigan nest loss was considerably lower.

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IV. CONCLUDING DISCUSSION

Long term studies on rock ptarmigan (*Lagopus mutus*) in Greenland (Braestrup 1941), Iceland (Gudmundsson 1960), and Alaska (Buckley 1954) have documented regular fluctuations in spring breeding populations over an approximate 10-year period. Breeding populations of rock ptarmigan at Windy Lake, N.W.T., fluctuate in size from year to year; however, data were insufficient to conclude that these fluctuations were either regular or, if so, at what interval. Nor can it be concluded what causes the annual changes.

In 1988 and 1989, all hens which settled to breed at Windy Lake were successful in pairing with a male. However, not all territorial males were successful in obtaining a mate. This was not the consequence of polygyny as most males were monogamous, but resulted from a male-biased sex ratio at the onset of the breeding season.

Hens at Windy Lake were highly synchronous in initiation of laying both between and within each year of the study. Laying began shortly after ground snow cover receded below 50%, which in 1988 and 1989 occurred during the first week of June. The majority of hens which deserted or had their first clutch depredated during the laying stage renested. Hens which lost their first nest after incubation had commenced rarely renested. The majority of nest loss occurred during incubation; consequently, the probability of renesting for all hens was low and the contribution of renests to overall fecundity was minor.

Four reproductive state variables were measured in this study, each corresponding with a nesting stage. These variables were: total clutch laid, clutch size at hatching, number of chicks leaving the nest, and brood size at fledging. These variables did not differ for ptarmigan breeding at the NWL or SWL study sites, nor did they differ for ptarmigan breeding in 1988 or 1989. Of these four variables, only total clutch laid was affected by female age. Although the range in clutch sizes overlapped between adult and yearling hens, adults tended to lay larger clutches (9 or more) than yearlings (8 or less). Data from other regions do not show a consistent relationship between clutch size and age. In central Alaska, mean clutch size over a 5-year period never varied more than 0.9 eggs between adult and yearling hens (Weeden and Theberge 1972), whereas on Svalbard the mean clutch size of adults was 2.6 eggs larger than yearlings (Steen and Unander 1985). It is not known which age-related factors may influence clutch size, but explanations postulated for other avian species include differences in ability in finding food (Lack 1954) and differences in physiological maturity between the age classes (Zwickel 1975). Both adult and yearling hens laid somewhat larger clutches in 1989 than in 1988. It is not known why clutch sizes at Windy Lake were larger in 1989 as compared to 1988; however, studies of tetraonids have shown several factors to cause variations in clutch size between years or between locations. Some of these factors include breeding density, body mass of females in spring, date of clutch initiation, climatic conditions, and parasite loads (Martin *et al.* 1989).

The reproductive state variables are joined by transition probabilities: egg survival, hatching success, and fledging success. All three probabilities were very high, the first two were close to 100%, and the last one approximately 75%. These probabilities did not differ between years, study sites, or between age classes of hens. As a result, differences in the latter three state variables all flow from initial differences in the total clutch laid.

Of all hens that settled to breed at Windy Lake in 1988 and 1989, 57% were successful in fledging a brood (one or more chicks). The major cause of nest failure was predation, of which clutch predation was responsible for almost three-quarters, hen predation approximately one-fourth, and total brood loss less than 5%. Identity of nest predators were not ascertained in this study, although probable important predators, based on observations from other studies and their occurrence at Windy Lake, include foxes (*Alopex lagopus* or *Vulpes vulpes*), ermines (*Mustela erminea*), ravens (*Corvus corax*), and gulls (*Larus* spp.). Even though nearly half of all hens failed to produce any offspring, overall productivity for the population in the 1988 and 1989 was high, 3.5 chicks per pair. Breeding success (measured as number of juveniles per adult; Bergerud *et al.* 1985) in those 2 years was slightly lower than productivity at 2.6 juveniles per adult rock ptarmigan. In many populations of rock ptarmigan, breeding success correlates positively with proportional changes in breeding numbers from 1 year to the next. From the limited data at Windy Lake (2 years), the minimum autumn ratio above which breeding populations the following spring would increase and below which it would decrease probably lies between 2.0 and 3.5 juveniles per adult. If a correlation exists at Windy Lake between breeding success in year one and size of breeding population in year two, those factors which directly affect productivity would in turn affect annual changes in breeding populations. At Windy Lake, predation must be considered an important factor as hen and clutch predation were the main causes of nesting failures.

Nest loss at Windy Lake may have been related to abundance of microtines. Microtines at Windy Lake undergo regular population fluctuations in an approximate 3-year cycle: peaking in 1987, crashing in 1988, and recovering in 1989. Nest losses were considerably higher in the microtine 'crash' year than the following year when microtine numbers had begun to recover. When microtine numbers crash, their predators must switch to alternative prey, such as ptarmigan clutches. Such a scenario may have occurred at Windy Lake.

Breeding populations of rock ptarmigan at Windy Lake have declined each successive year from 1985 through to 19[illegible]. The high juvenile-to-adult ratio recorded in 1989, and the higher count in June of 1990 over 1989 at Kilgavik suggest that the population decline may have bottomed out in 1989 (4 years after peak in 1985), and may increase each successive year. If the population cycles in an approximate 10-year period as populations do elsewhere, it would continue to increase until levels peak in 1995.

Approximately 15% of the breeding population (both male and female rock ptarmigan) were depredated each summer at Windy Lake. Identity of adult predators was determined in this study, and gyrfalcons (*Falco rusticolus*), peregrine falcons (*F. peregrinus*) and foxes were responsible for all kills. The two falcons species were responsible for over 95% of all kills. Unfortunately, it was not possible to determine which falcon species was responsible, but among those kills where it was possible, nearly 90% were by gyrfalcons. Food habit studies on tundra populations of these two falcons have shown [illegible] to be a major component in the diet of gyrfalcons (Poole and [illegible] 1988), and of minor importance in the diet of peregrine falcons ([illegible] and Oliphant 1991). In light of the fact that within the Kilgavik region surrounding Windy Lake densities of breeding gyrfalcons are among the highest recorded for this species, it is perhaps not surprising that gyrfalcons are the major predators of rock ptarmigan at Windy Lake. The relative density of all species of nesting raptors at NWL and SWL did not affect predation levels or timing of predation on rock ptarmigan in those two areas.

Just as there were no differences in predation rates between areas, there also was no age nor sex bias observed in predation over the breeding season at Windy Lake in 1988 and 1989. The lack of a male bias in predation, especially during the incubation phase, is contrary to what has been reported elsewhere where it had been explained that the male bias is a consequence of a difference in plumage and behaviour during this time period (Bergerud and Mossop 1984). There was no difference in the proportion of males and females killed in June or in July. There was a significant difference, however, in the proportion of both sexes killed during June as compared to July. All but one of the depredations occurred during incubation in the month of June. Ptarmigan may be less vulnerable in July than June, especially males as they have moulted into their brown cryptic summer plumage by this time. As a result of behavioural and plumage changes that occur at the time of hatch, as well as increased vegetative cover when shrubs attain their leaves, predators may find it increasingly difficult to locate ptarmigan. This may also coincide with a sudden increase in the availability of alternate prey. At Windy Lake Poole (1987) observed that a sharp drop in the proportion of ptarmigan in the diet of gyrfalcons occurred when juvenile arctic ground squirrels (*Spermophilus parryii*) became available upon emergence above ground.

Fall and winter winter movements are not known for the population of rock ptarmigan breeding at Windy Lake, nor are losses during this period. In central Alaska, male and female rock ptarmigan segregate during the winter, with females migrating further from their breeding grounds than males (Weeden 1964). If a similar situation occurs for rock ptarmigan breeding at Windy Lake, the observed male bias in the sex ratio at the onset of the breeding season and the return rate observed in both 1988 and 1989 may result from a higher overwinter mortality of females. If the sexes overwinter in different areas, the predator community may also be different in each area; such a difference may cause differential mortality between the sexes (Gruys 1991).

Survival of individual rock ptarmigan was apparently adversely affected when they were fitted with radio transmitters. Two types of transmitters were used, an 18-g backpack and a 12-g necklace transmitter, but predation rates on males did not differ with type. These results support the conclusions of some studies (such as Marks and Marks 1987) but not those of other studies (Erikstad 1979, 1986). The potential consequence of these results are that the observed predation levels may be abnormally elevated. The other potentially adverse researcher effect, that is visiting nests and broods, did not influence predation rates on adults or clutches, at least at the level of disturbance registered in this study. Clearly, further research on the subject of the effect of the researcher and techniques used is required.

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V. Appendix 1: IMPACT OF RESEARCHER ON SURVIVAL AND BREEDING SUCCESS IN ROCK PTARMIGAN

INTRODUCTION

There is currently much debate over the effect of researchers on an animal's behaviour and survival. One area of concern is the effect of fitting an animal with a radio transmitter. Radio telemetry has gained popularity in recent years as it enables biologists to collect data on a variety of behavioural and life history attributes that otherwise would not be possible (Chabaylo 1990). However, the fitting of a transmitter to a bird must have some effect on its energetics (American Ornithologists' Union 1988), which may in turn affect its survival, behaviour, and/or reproductive success. Several avian studies designed specifically to examine effects of radio transmitters have documented adverse effects (Boag 1972, Boag *et al.* 1973, Gilmer *et al.* 1974, Lance and Watson 1977, Erikstad 1979, Herzog 1979, Perry 1981, Warner and Etter 1983, Hines and Zwickel 1985, Massey *et al.* 1988, Wanless *et al.* 1988, Chabaylo 1990). The documented effects from most of these studies, which varied from a small to a large effect, are summarized by Chabaylo (1990).

The effects of marking and visiting nest have also been examined (Evans and Wolfe 1967, Willis 1973, Picozzi 1975, Robert and Ralph 1975, Bart 1978, Lenington 1979, Ollason and Dunnet 1980, Götmark and Åhlund 1984, Nichols *et al.* 1984, Westmoreland and Best 1985, Galbraith 1987). The effect of nest markers on clutch survival has been inconclusive. Picozzi (1975) found the placement of nest markers increased clutch predation in well-concealed artificial ground nests (chicken eggs), whereas Galbraith (1987) observed no effect on clutch survival in lapwings (*Vanellus vanellus*). Visiting nests have been documented to decrease reproductive success (Willis 1973, Howe 1979, Lenington 1979, Westmoreland and Best 1985) and increase desertion and predation of eggs and chicks in some species (Dwernychuk and Boag 1972, MacInnes and Misra 1972, Picozzi 1975, Reed 1975, Ellison and Cleary 1978, Anderson and Keith 1980, Steen and Unander 1985). However, other studies have documented little or no effect on reproductive success or predation resulting from visiting nests (Sugden 1978, Livezey 1980, Galbraith 1987).

In light of the above observations, research incorporating radio telemetry and/or regular nest visits should attempt to minimize potentially adverse effects, and try to determine the nature of effects (if any) and interpret how they may have affected the data which the study set out to collect.

In a study of population dynamics, predation, and reproductive biology of rock ptarmigan (*Lagopus mutus*) in the central Canadian Arctic (Chapters II, III), I investigated for potential effects of outfitting the birds with radio transmitters on survival of males. Furthermore, effects of regular nest and brood visits were examined.

METHODS

In 1988 and 1989, a population of rock ptarmigan were studied at Windy Lake, N.W.T. (68° 5' N, 106° 40' W). Nearly all resident rock ptarmigan were captured at the onset of the breeding season (early June) in both years, at which time all birds were fitted were four colour-coded leg bands to enable field identification. Furthermore, all female rock ptarmigan were fitted with a 12-g 'necklace' radio transmitter (Biotrack, U.K.), and half of the males were fitted with a radio transmitter, either an 18-g 'backpack' (Telemetry Systems, U.S.A.) (1988) or a 12-g 'necklace' (1989). Males not fitted with a radio transmitter served as a control group for testing effects of transmitters on survival.

Nests were initially discovered by radio-tracking a female to her nest during laying or early in incubation. Upon initial discovery of the nest, the hen was flushed and the eggs were counted. To examine any possible adverse effects of visitation on mortality rates (on adults, eggs, chicks), nests were divided into pairs, with each nest of the pair located on a neighbouring territory. One set of nests (one randomly chosen from each pair) was visited as described above and was defined as being 'disturbed'. The other set of nests was not visited during the remainder of incubation. Instead, the hen's approximate location and status (on or off the nest, dead or alive) were determined by telemetric triangulation, maintaining a distance of 50 to 100 m from the hen. These nests were defined as being 'undisturbed'. Similarly, pairs of broods were divided randomly into two groups: those visited 'frequently' (every 3-4 days) and, as a control, those which were visited 'infrequently' (every 6-9 days).

RESULTS

Effect of radio transmitters on male rock ptarmigan

In each of 1988 and 1989, the proportion of radio-marked males killed exceeded that of unmarked males (Table V-1). Combining the two years, the proportion of radio-marked males killed was significantly greater than unmarked males when birds of unknown fate were excluded (*G*=6.38, df=1, *P*=0.01). Adding birds of unknown fate to the alive group increased the difference between radio-marked and unmarked groups (*G*=9.32, df=1, *P*<0.01), whereas if birds of unknown fate were, in fact, killed by predators and not found, the difference between the two groups is no longer significant (*G*=0.39, df=1, *P*=0.53). Analyzing only radio-marked males, there was no significant difference in predation rate between males (excluding unknowns) fitted with a backpack transmitter (4/11) (in 1988) or with a necklace transmitter (4/9) (in 1989) (*G*=0.13, df=1, *P*=0.72).

Effect of researcher visiting nests

Visiting nests on a regular basis (every 2-3 days) versus on an irregular basis (once during incubation) did not significantly affect susceptibility to predation of either hens or clutches. The proportion of hens depredated was similar at 'disturbed' nests (0.08, 2/24) and 'undisturbed' nests (0.10, 2/20) (*G*=0.03, df=1, *P*=0.86) (Table V-2). As well, the proportion of nests which hatched successfully was similar at 'disturbed' (0.63, 15/24) and 'undisturbed' (0.55, 11/20) nests, the difference being non-significant (*G*=0.25, df=1, *P*=0.62). Pooling data from 1988 and 1989, there was no difference in the total clutch laid by hens that were 'disturbed' (mean=8.00, S.E.=0.43, n=19) and 'undisturbed' (mean=8.58, S.E.=0.28,n=19) (paired *t*=-1.13, df=18, *P*=0.28). Furthermore, there was no difference in the mean clutch size at hatch (CSH) (excluding hens with total nest failure) between the two groups ('disturbed': mean=8.11, S.E.=0.66, n=9; 'undisturbed': mean=8.00, S.E.=0.90, n=9; paired *t*=0.09, df=8, *P*=0.93).

Table V-1: The fate of radio-marked and unmarked male rock ptarmigan at the end of the breeding season in 1988 and 1989 at Windy Lake, N.W.T. (numbers either killed, unknown, or alive).

Year	Radio-marked			Unmarked		
	Killed	Alive	Unknown	Killed	Alive	Unknown
1988	4	7	3	0	13	6
1989	4	5	3	1	6	9

Table V-2: Fate of female rock ptarmigan with nests that were either 'disturbed' or 'undisturbed' and/or broods that were visited either 'frequently' or 'infrequently' during the breeding season at Windy Lake, N.W.T., in 1988 and 1989.

Stage	Status	1988		1989	
		Killed	Alive	Killed	Alive
Nest	Disturbed	2	12	0	8
	Undisturbed	2	10	0	8
Brood	Frequent	0	7	0	7
	Infrequent	1	7	0	8

Effect of researcher visiting broods

Only one female from those visited 'infrequently' was depredated during brood rearing (Table V-2). Moreover, all 'frequently' visited hens fledged chicks, but only 87.5% of 'infrequently' visited hens did so.

Pooling data from 1988 and 1989, there was no difference in the mean brood size at fledging between broods that were visited 'frequently' (mean=5.71, S.E.=0.64, n=14) and 'infrequently' (mean=5.86, S.E.=0.76, n=14) (paired *t*=-0.14, df=13, *P*=0.89). There was also no difference in fledging success (angularly transformed before analysis) between the two groups of hens ('frequent': mean=0.72, S.E.=0.07, n=14; 'infrequent': mean=0.65, S.E.=0.08, n=14; paired *t*=-0.22, df=11, *P*=0.83). Furthermore, there was no difference in the proportion of hens that fledged ≥1 chick(s) which were visited 'frequently' (1.00, 14/14) and 'infrequently' (0.88, 14/16) (*G*=2.11, df=1, *P*=0.15), nor was there a difference in the proportion of hens in each group that was depredated ('frequent': 0.00, 0/14; 'infrequent': 0.06, 1/16; *G*=0.86, df=1, *P*=0.35). There was also no difference in the proportion of chicks which left the nest that fledged ('frequent': 0.73, 80/110; 'infrequent': 0.72, 91/127; *G*=0.03, df=1, *P*=0.86).

DISCUSSION

Impact of radio telemetry

Much of the current concern with respect to radio telemetry is centred on the direct effects on the survival of birds outfitted with a radio transmitter. In this study on rock ptarmigan at Windy Lake, there were significantly more confirmed kills of radio-collared males than males without transmitters. A significant effect is contrary to what has been reported with respect to survival in willow ptarmigan (Schieck 1988, Gruys 1991), nesting success in rock (Theberge and West 1973, Brodsky 1986) and willow ptarmigan (Lance and Watson 1977, Erikstad 1979), and on behaviour in rock ptarmigan (Brodsky 1986). However, Marks and Marks (1987) reported that predators selectively preyed on radio-marked sharp-tailed grouse, and in mallards (*Anas platyrhnchos*) Chabaylo (1990) observed that nest desertion was higher for radio-marked than unmarked birds and that female post-hatch behaviour and weight gain were altered by radio-marking. Since this study of ptarmigan was not designed to address the effect of transmitters on survival and behaviour, the statistical and biological significance of my findings on survival are difficult to guage. This was because the fate of more than one third of the males not fitted with a transmitter was unknown at the end of the breeding season. Assuming all were alive, then the difference in survival of unmarked and radio-marked individuals was statistically significant. It should be noted, however, in 1989 leg bands were found at nearby gyrfalcon eyries for two of the four radio-marked males killed and none for any of the nine unmarked birds whose fate was unknown. If all males of unknown fate were assumed to have been killed, then the statistical difference disappears. If being outfitted with a radio transmitter increased vulnerability and probability of predation in males, the level of predation observed among females may have been abnormally high, since all females in this study were radio-marked.

Clearly, the effect of radio telemetry requires further attention and study. Until more critical studies can be undertaken, the implications of this study should be considered carefully. Future studies using radio telemetry should consider the possible effects of the harness and transmitter type on the birds, and should test for it in some manner.

Effect of researcher visiting nests and broods

Under the conditions of this study, regular visits to nests or broods did not affect survival of either eggs and chicks, nor of hens, clutches, or broods. Nests and broods that were visited regularly were as successful as those nests and broods that were visited infrequently. None of the variables measured, whether state or transition variables (Chapter III), or proportion of hens that were killed or suffered total nesting failure varied between the two groups. These results contrast sharply with those of Steen and Unander (1985) who studied the breeding biology of Svalbard rock ptarmigan. In one of the years of their study, they reported a nest depredation rate of 56 percent, all by arctic foxes, with no renesting attempts. The authors noted that human interference in their study may have contributed to the high level of nest depredation (*i.e.* suggesting that regular visits to the nests may have provided cues for arctic foxes to locate nests). At Windy Lake, the effect of visiting nests and flushing the incubating hens could have been two-fold: 1) a scent trail to the nest left by the researcher, could have been used by mammalian predators such as foxes or ermines to find the nest; 2) flushing the hen from the nest may have either made the hen more easily detected by a perched or flying avian predator, or the disturbance of the vegetation by the researcher approaching and at the nest may have provided visual cues for such avian predators to locate the nest (Dwernychuk and Boag 1972). It was the first effect that Steen and Unander (1985) concluded was the principle cause of the unnaturally high nest predations they observed on Svalbard. In this study, care was taken not to mark nests or brood locations so as to avoid such visible cues to predators (Picozzi 1975). In an area such as Windy Lake, where little cover was more than 1 m in height, and foxes were present, albeit at very low densities during this study, either effect was possible. However, there was no difference in adult or nest survival between either the 'disturbed' or 'undisturbed' group during incubation, nor between frequently and infrequently disturbed groups during brood rearing. Foxes were the most likely mammalian predator to use a scent trail left by regular visits to a nest. On the other hand, ravens and gulls were the most likely to use nest markers as cues. It is possible that since there are fewer predator species on the tundra (Bergerud and Mossop 1984), that such disturbance might have less impact than in a region with more predators and predator species. It is also possible that a threshold had been surpassed, even at the 'undisturbed' or 'infrequent' levels, above which ground predators would not take more prey, whether adults, clutches, or chicks, of a particular species.

In this study care was taken to leave as little sign as possible to mark a nest or brood, and as well to minimize time at the nest or brood while disturbance was taking place. Such activities, while requiring some forethought and planning, did not lessen the amount of information that needed to be collected for this study, and may have lessened the impact on survival and overall reproductive success of those disturbed.

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VI. Appendix 2: MORPHOLOGY OF ROCK PTARMIGAN

Table VI-1: Body weight and wing chord length of the two sex-age classes of rock ptarmigan in early June at Windy Lake, N.W.T., in 1987, 1988, and 1989.

Sex	Age	1987	1988	1989	Years Pooled
Body Weight (g)		Mean ± S.E., n	Mean ± S.E., n	Mean ± S.E., n	Mean ± S.E., n
Female	Adult	553.3 ± 26.0, 3	512.5 ± 6.1, 13	512.5 ± 14.9, 4	518.7 ± 6.6, 20
	Yearling	551.0 ± 18.2, 5	514.0 ± 15.8, 9	527.2 ± 17.7, 9	527.2 ± 10.1, 23
Male	Adult	490.0 ± 9.1, 4	494.6 ± 3.9, 15	519.0 ± 8.0, 10	502.4 ± 4.2, 29
	Yearling	475.0 ± 5.0, 2	493.4 ± 2.2, 12	503.3 ± 13.0, 3	493.0 ± 3.1, 17
Female		551.9 ± 13.8, 8	513.1 ± 7.2, 22	522.7 ± 12.9, 13	523.2 ± 6.2, 43
Male		485.0 ± 6.7, 6	494.1 ± 2.4, 27	515.4 ± 6.9, 13	498.9 ± 2.9, 46
Wing Chord (cm)					
Female	Adult	-	18.4 ± 0.1, 15	18.5 ± 0.2, 6	18.4 ± 0.1, 21
	Yearling	-	18.2 ± 0.2, 12	18.2 ± 0.1, 14	18.2 ± 0.1, 26
Male	Adult	-	19.4 ± 0.1, 18	19.3 ± 0.2, 12	19.3 ± 0.1, 30
	Yearling	-	18.9 ± 0.1, 13	19.3 ± 0.2, 5	19.0 ± 0.1, 18
Female		-	18.3 ± 0.1, 27	18.3 ± 0.1, 20	18.3 ± 0.1, 47
Male		-	19.2 ± 0.1, 31	19.3 ± 0.1, 17	19.2 ± 0.1, 48

Table VI-2: Three-factor ANCOVA of year, sex, and age effects on body weight and wing chord length in a population of rock ptarmigan at Windy Lake, N.W.T.. Date of weighing was used as the covariate in the analysis.

Trait	Source of variation	df	Mean square	*F*	*P*
Body weight	year	2	1546.97	1.65	0.20
	sex	1	15331.45	16.31	<0.01
	year*sex	2	3991.43	4.25	0.02
	age	1	121.96	0.13	0.72
	year*age	2	108.97	0.12	0.89
	sex*age	1	869.60	0.93	0.34
	year*sex*age	2	361.50	0.38	0.68
Wing chord	year	1	0.31	0.18	0.67
	sex	1	17.03	64.68	<0.01
	year*sex	1	0.04	0.14	0.71
	age	1	1.10	3.91	0.05
	year*age	1	0.21	0.82	0.37
	sex*age	1	0.01	0.02	0.88
	year*sex*age	1	0.28	0.96	0.33

VII. Appendix 3: SPRING CENSUS OF TERRITORIAL MALE ROCK PTARMIGAN

Table VII-1: Numbers of territorial male rock ptarmigan counted on census plots at Windy Lake, N.W.T., from 1983 to 1989.

	Mean number of male ptarmigan counted (number of counts) †						
Plot	1983	1984	1985	1986	1987	1988	1989
A	4.5 (2)	-	7 (1)	5 (1)	3 (1)	-	2 (1)
B	7 (1)	8 (5)	8 (2)	10.5 (2)	5 (1)	4 (1)	2 (1)
C	3 (2)	-	5 (1)	6 (1)	-	-	0 (1)
D	2.5 (2)	-	4 (2)	1 (1)	6 (1)	4 (1)	1 (1)
E	5 (1)	-	-	6 (1)	-	-	2 (1)
F	-	1.2 (5)	2 (2)	3 (1)	4 (1)	2 (1)	1 (1)

† Data from 1983 to 1986 are from Poole (1987).

VII. Appendix 3: SPRING CENSUS OF TERRITORIAL MALE ROCK PTARMIGAN

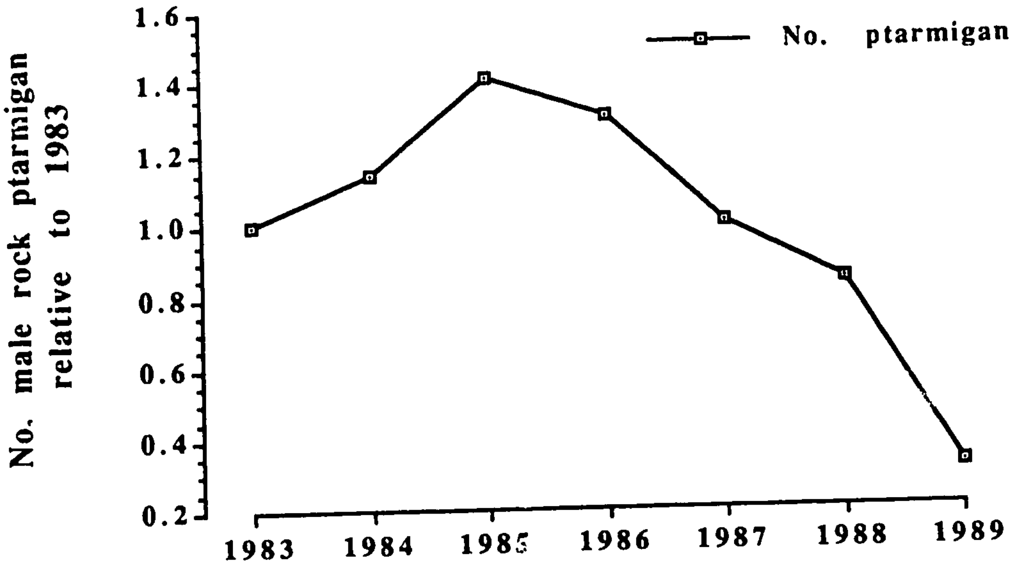

Figure VII-1: Index of number of male rock ptarmigan breeding at Windy Lake, N.W.T., 1983 to 1989. Data for 1983 to 1986 are from Poole (1987).

VIII. Appendix 4: PREDATION ON ADULT ROCK PTARMIGAN

Table VIII-1: Sex and band number of rock ptarmigan depredated, as well as the year, period predation occurred, predator species, and the location where the remains were found for all banded rock ptarmigan known depredated in 1987, 1988, and 1989 at Windy Lake, N.W.T..

Year	Sex	Band # [a]	Period Predation Occurred [b]	Predator [c]	Remains Found
1987	Male	214 [s]	incubation	gyrfalcon	gyrfalcon eyrie
	Female	205 [s]	≥ incubation	gyrfalcon	gyrfalcon plucking post
		211 [s]	≥ incubation	falcon	on ground; study area [d]
		219 [s]	≥ incubation	falcon	on ground; study area [d]
1988	Male	230 [s]	laying - early incubation	falcon	side of steep cliff
		239 [n]	incubation	peregrine falcon	on ground; territory
		252 [s]	laying - early incubation	gyrfalcon	side of steep cliff
		259 [n]	incubation	falcon	on ground; territory
	Female	209 [s]	incubation	falcon	head, viscera on ground; territory
		225 [s]	brood	gyrfalcon	head, viscera on ground; territory
		228 [s]	≥ fledging	falcon	on ground; territory

Table VIII-1: continued

Year	Sex	Band # [a]	Period Predation Occurred [b]	Predator [c]	Remains Found
1989	Male	240 n	incubation	falcon	on ground; territory
		256 n	incubation	falcon	on ground; territory
		269 s	late incubation	fox	on ground; territory
		212 s	< laying	gyrfalcon	on ground; territory
		268 s	laying	gyrfalcon	gyrfalcon plucking post
		270 n	early incubation	falcon	on ground; territory
		284 s	laying	gyrfalcon	gyrfalcon plucking post
		304 n	incubation	gyrfalcon	head, viscera on ground; territory
	Female	298 s	laying	falcon	head, viscera on ground; territory
		unbanded	< laying	falcon	on ground; territory

[a] s = ptarmigan is from South Windy Lake study site, and n = ptarmigan is from North Windy Lake study site.

[b] "≥" indicates during or after; "<" indicates before.

[c] species: gyrfalcon (*F. rusticolus*), peregrine falcon (*F. peregrinus*), falcon (either *Falco rusticolus* or *F. peregrinus*), fox (either *Alopex lagopus* or *Vulpes vulpes*).

[d] remains, primarily skeleton and leg bands, were discovered on study area the following breeding season.

IX. Appendix 5. INDEX OF MICROTINE POPULATION SIZE

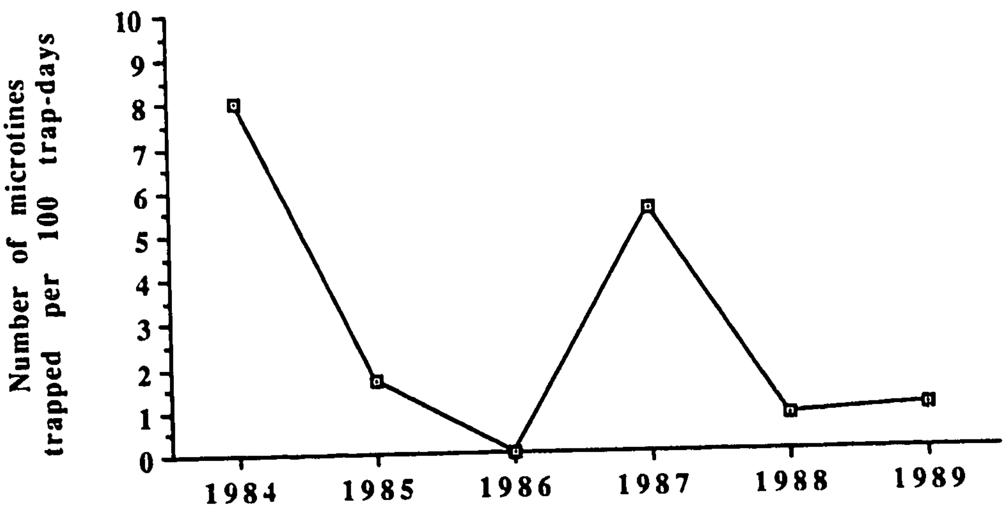

Figure IX-1: Index of microtine population size at Windy Lake, N.W.T., 1984 to 1989. Data for 1984 to 1986 are from Poole (1987).