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Autumn and Winter Movements and Sexual Segregation of Willow Ptarmigan

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ABSTRACT. Willow ptarmigan (*Lagopus lagopus alexandrae*) in northern British Columbia leave their breeding areas during autumn and winter. The movements differ between males and females. In this study I examine the causes and extent of these differences. Ptarmigan did not leave their breeding grounds immediately after the breeding season, but remained on or near their territories until December. After chicks fledged, part of the population moved uphill from their territories. Coincident with moult into winter plumage, ptarmigan moved farther from their territories. Both movements were probably to areas with better protection against predators. After moulting, all tagged males and half of the tagged females returned to their territories, and males resumed territorial display. Ptarmigan remained on their territories until increasing snow cover depleted cover, forcing them to leave. Males left the breeding grounds later than females and returned earlier in spring. In winter females moved farther than males, supporting the reproductive strategy hypothesis, but segregation was not complete. Sexual segregation may not be related to migration alone, but could occur at any time ptarmigan are in flocks.

Key words: willow ptarmigan (*Lagopus lagopus alexandrae*), autumn territoriality, winter movements, sexual segregation, northern British Columbia

RÉSUMÉ. Le lagopède des saules (*Lagopus lagopus alexandrae*) de la Colombie-Britannique septentrionale quitte son aire de nidification durant l'automne et l'hiver. Les déplacements du mâle diffèrent de ceux de la femelle. Ces recherches portent sur le degré et les causes de cette différence. On a trouvé que le lagopède ne quitte pas son aire de nidification immédiatement après la saison nidificatrice. Il reste sur son territoire ou à proximité jusqu'au mois de décembre. Après que les jeunes se sont emplumés, une partie de la population migre vers un territoire plus élevé. En même temps qu'il revêt son plumage d'hiver, le lagopède s'éloigne de son territoire. Ces deux mouvements se font probablement en direction d'aires offrant une meilleure protection contre les prédateurs. Après la mue, tous les mâles marqués et la moitié des femelles marquées reviennent sur leur territoire et les mâles reprennent leur comportement territorial. Le lagopède reste sur son territoire jusqu'à ce que l'accumulation de neige cache le couvert, ce qui le force à partir. Le mâle quitte son aire de reproduction après la femelle et y revient avant elle au printemps. En hiver, la femelle s'éloigne plus loin que le mâle, ce qui appuie l'hypothèse de la stratégie reproductive, mais la ségrégation n'est pas totale. Il se peut que la ségrégation sexuelle ne soit pas reliée uniquement à la migration, mais qu'elle ait lieu chaque fois que le lagopède se retrouve dans une volée.

Mots clés : lagopède des saules (*Lagopus lagopus alexandrae*), territorialité d'automne, déplacements hivernaux, ségrégation sexuelle, Colombie-Britannique septentrionale

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INTRODUCTION

Segregation of the sexes in the non-breeding season is common among both mammals (Clutton-Brock *et al.*, 1982; Main and Coblentz, 1990) and birds (Myers, 1981). In North America male willow ptarmigan remain with their mates and chicks throughout brood rearing (Wittenberger, 1978), but after brood break-up in September the sex and age classes segregate (Mossop, 1988). Most adult males remain in subalpine habitat, whereas females and the majority of juveniles move to the boreal forest (Weeden, 1964; Irving *et al.*, 1967; Höhn, 1984). While they are segregated, males and females may be exposed to different predators, weather conditions, or food availability. As a result the sexes may suffer differential overwinter mortality. Moreover, both ptarmigan and snowshoe hare (*Lepus americanus*) numbers in boreal regions of North America fluctuate with a period of 8-11 years (Bergerud, 1970; Hannon and Barry, 1986; Krebs *et al.*, 1986; Mossop, 1988). It has been suggested that when numbers of snowshoe hares in the forest decline, generalist predators switch to tetraonids (Rusch and Keith, 1971). Such differences in environmental conditions or mortality could result in a shortage of members of one sex, as has been observed in populations of willow ptarmigan (Martin, 1985; Hannon and Barry, 1986) as well as other species of grouse (e.g., Zwickel *et al.*, 1983; Angelstam, 1984). However, Mossop (1988) observed that in years with little snow most female willow ptarmigan at Chilkat Pass, British Columbia, remained near the breeding grounds. Hence, the extent of migration and segregation of the sexes may vary annually, which in turn affects differences in overwinter mortality risk between the sexes. Thus, differential winter movements play an important role in ptarmigan winter ecology.

Bergerud and Gratson (1988) reviewed segregation of the sexes in northern grouse species. They argued that females select habitat most suitable for raising offspring, whereas males attempt to maximize breeding opportunities (hereafter referred to as "reproductive strategy" hypothesis). During winter survival is important to both sexes, and females will select areas offering the greatest protection against predators. For males, however, it is hypothesized that competition for breeding sites outweighs the risk of predation. Consequently, males will remain closer to their breeding grounds than females (Bergerud and Gratson, 1988). Main and Coblentz (1990) concluded that segregation of the sexes in ungulates was also caused by different reproductive strategies of males and females.

To date, studies that documented movements of ptarmigan outside the breeding season used either counts of wintering

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ptarmigan or band recoveries from hunters (Weeden, 1964; Myrberget, 1976; Gardarsson, 1988; Mossop, 1988). These methods can provide an estimate of direction and distance of ptarmigan movements, but as ptarmigan move farther from their breeding grounds, the chance of finding marked birds becomes smaller, resulting in a bias towards short-distance movements (Greenwood and Harvey, 1982). Moreover, it is difficult to examine the timing and causes of winter movements with these methods. I equipped adult willow ptarmigan at Chilkat Pass with radio transmitters and followed them throughout the autumn and winter to document: 1) the timing and extent of movements by ptarmigan over two seasons; 2) the factors influencing movements of ptarmigan during autumn and winter; and 3) the degree of segregation of male and female ptarmigan at Chilkat Pass. I will discuss the results in light of the reproductive strategy hypothesis.

METHODS

Study Area

Chilkat Pass is located in northwestern British Columbia (59°50′N, 136°35′W; Fig. 1). Ptarmigan breed in subalpine habitat dominated by willow (*Salix* spp.) and dwarf birch (*Betula glandulosa*) reaching a height of 1.5 m (Weeden, 1960). On the Pacific side the pass descends abruptly into a narrow valley covered by coastal forest, with a dense cover of willow and alder at higher elevations (Weeden, 1959). To the north, the pass descends into an open canopy white spruce (*Picea glauca*) forest, interspersed with willow and birch. The ground is usually snow covered between October and May. During most winters snow depth reaches approximately 1-1.5 m. Willow ptarmigan at Chilkat Pass have been studied since 1979 on a 4.5 km² site (Hannon, 1983; Fig. 1; "intensive study area"). Weeden (1959) and Mossop (1988) carried out earlier studies of willow ptarmigan at nearby sites.

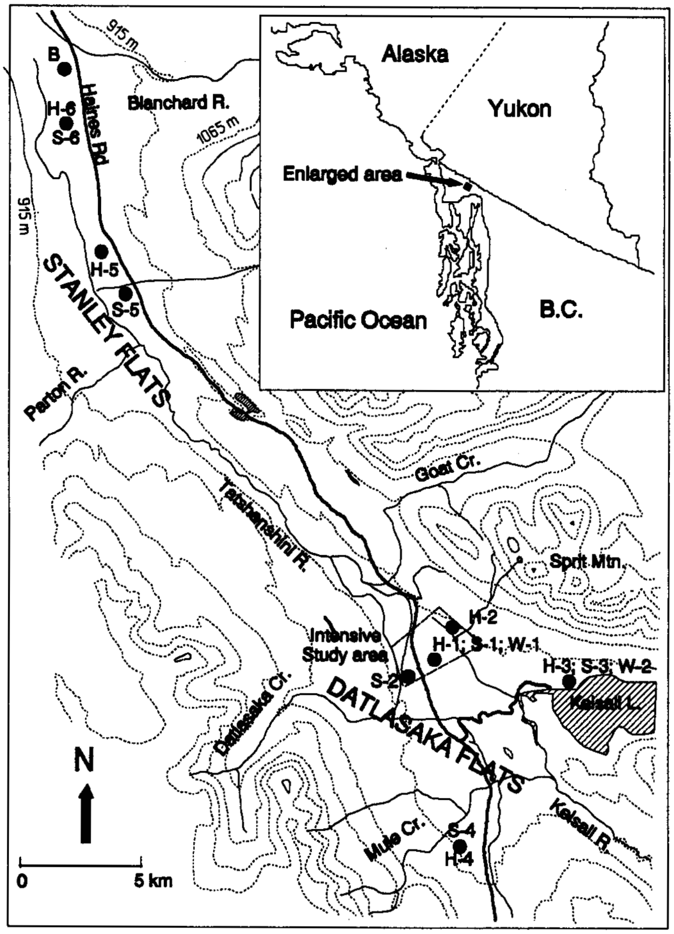

FIG. 1. Map of study area at Chilkat Pass, B.C. H=habitat measurement sites, S=snow measurement sites, W=windrun measurement sites, B=barometric pressure measurement site. Ptarmigan were radio tagged in the intensive study area (surrounded by a dashed line).

Capture, Marking, and Radiotelemetry

Methods for capture and marking of ptarmigan were described by Hannon (1983). Sexes were distinguished on the basis of differences in plumage and voice, and age was estimated by comparing pigmentation on the eighth and ninth primary (Bergerud *et al.*, 1963). The age of many marked birds was known exactly, as they had been marked as yearlings for earlier studies.

From July to November 1987, I tracked nine territorial males and nine resident females equipped with radio transmitters (Austec, Edmonton, Alberta). From July 1988 to April 1989 I followed 23 territorial males and 26 resident females fitted with transmitters (Biotrack, Wareham, Dorset, U.K.). Transmitters were attached with a necklace of harness wire (Schieck, 1988) or soft cord (Kenward, 1987). Their weight ranged between 15 and 21 g. Additional data were available from 1985, when J.O. Schieck followed movements of 16 radio-tagged females from April until 1 September (Schieck, 1988).

If possible, radio-collared birds were located visually once per week, using hand-held Yagi antennas. I recorded their location and the average height of the vegetation (in dm above the snow) within a 10 m radius of each bird. In 1988-89 I also located radio-tagged ptarmigan by triangulation using a truck-mounted removable null-dipole antenna, modified after Hallberg *et al.* (1974). I tried to triangulate each tagged bird once a week, and more often if time and weather permitted. During spring territoriality birds were located daily. In addition I conducted four aerial surveys between January and March 1989. The surveys covered all valleys within a 50-100 km radius to the south, east, northwest, and north of Datlasaka Flats.

I defined the territory of ptarmigan as the area they used between 5 May and 20 June. During this period both males and females defended territories. Their locations were determined through near-daily observations. In autumn I considered a bird on its territory if it was sighted within 100 m of its spring territory.

In both years several birds were killed through predation and hunting (Gruys, 1991) or were lost. I included these birds in the analyses until the time they were either killed or lost.

Winter Moult

To determine if autumn movements coincided with moult into winter plumage, I calculated a moult score in 1988 by estimating the percentage of white feathers for the head, neck, and back separately to the closest 10% (0 unmoulted [brown] and 100 completely white) (see Hannon and Wingfield, 1990). I added the three numbers to obtain a total moult score. I defined the location to which birds moved in late September as their moulting area.

Autumn and Winter Periods

I divided autumn and winter into six time periods of approximately 60 days each (except winter moult, which was 30 days). I based the periods on changes in migratory behaviour. When I could not determine exactly when a bird changed its behaviour (e.g., on what date it moved from its brood rearing area to its winter moulting area) I used the average date of all collared birds. The periods were defined as follows, with average dates for all birds in brackets: brood rearing, from 1 August (start of the study) until the onset of winter moult (23 September); winter moult, moult into winter plumage (24 September–23 October); autumn territoriality, from the time ptarmigan returned to their territories in October-November until they left in November-December (24 October–10 December); early winter movements, from the time ptarmigan left the breeding grounds (males: 5 December, females: 20 November) until 31 January; late winter movements, from 1 February until ptarmigan returned to their territories in spring (males: 21 March, females: 6 April); and transient spring territoriality, from the time ptarmigan first returned to their territories in spring until they settled permanently (1 May).

I defined the areas to which ptarmigan moved when they left the breeding grounds in November-December as their wintering grounds. Because many birds did not spend the entire winter in one location, I used the location in which each bird spent more than 50% of the winter as its winter location. The distance travelled to and from the wintering grounds was measured on a map along the most likely route taken, i.e., through the valleys rather than across mountain ranges.

Comparison of Habitat between Breeding and Wintering Areas

To compare habitat characteristics between the breeding and wintering areas, I set up six permanent grids in September 1988 on which I measured change in vegetation cover and height over the winter (H 1-6 on Fig. 1). Two sites were located on the intensive study area (H-1 and H-2), three sites were placed in nearby areas where males were found throughout winter 1987-88 (H-3, H-4, and H-5), and one site was located in an open spruce forest near the edge of subalpine habitat (H-6).

Each habitat grid consisted of 4 parallel lines of 5 transects, each 10 m long, spaced 200 m apart. I measured cover according to the line intercept method (Canfield, 1941) along a 10 m measuring tape on each transect. I expressed cover as percentage of the line covered by vegetation. Because height of vegetation varied on the transect, I defined the average height of vegetation for each transect as the height (rounded to the nearest 50 cm) above which horizontal density was less than 10%. To measure density I divided a 2 m × 0.5 m board into 10 × 10 cm squares. The board was placed upright at the stake marking each transect, and percentage of the squares covered by vegetation was counted from 10 m away at the end of the transect line (Nudds, 1977).

Snow and Weather

During the first season I recorded snow depth at permanent stakes on the breeding grounds (S-1 on Fig. 1), at a subalpine area where males wintered (S-5), and at the edge of the boreal forest (S-6). During the second season I added one site on the breeding grounds (S-2) and two subalpine sites (S-3 and S-4). At each of the six locations I randomly placed three stakes in shrubs and three in the open. I took snow depth measurements once every two weeks throughout each winter.

I compared wind speed between the breeding area and male wintering grounds (Kelsall Lake) with wind-run metres, which measured total accumulated wind in km at 2.5 m above the ground/snow surface (Fig. 1; W-1, W-2). I obtained an average wind speed by dividing the accumulated wind by the number of seconds between two readings.

I observed that both in autumn and spring ptarmigan left their territories during snow storms and moved to protected areas (see below). Other authors have suggested that birds can predict bad weather through their sensitivity to changes in atmospheric pressure (Kreithen and Keeton, 1974; Gill, 1989). In 1988-89 I recorded atmospheric pressure at Blanchard River, 20 km north of the study area (Fig. 1, B), with a high precision barometer/altimeter (Thommen TX-21, accuracy ± 1 mbar). I calculated the intensity of low or high pressure condition by subtracting the relative atmospheric pressure for that altitude (913 mbar) from the absolute pressure. I compared the change in barometric pressure throughout the autumn and spring territorial periods with the change in the percentage of birds on their territories during those same periods using a cross correlation function (Wilkinson, 1988).

Statistical Analysis

When variables were distributed normally, I employed parametric statistics; otherwise I used appropriate non-parametric statistics (Siegel, 1956; Sokal and Rohlf, 1981). I used a Nonparametric Multiple Comparison by Simultaneous Test Procedure (STP-Test; Sokal and Rohlf, 1981) to test if differences were significant among multiple individual groups tested by non-parametric methods. Critical values for the STP-Test were corrected for ties (Sokal and Rohlf, 1981). In the analysis of two-way tables I used a G-Test or a G-Randomization Test with 1000 iterations when one or more of the cells contained a value of less than 5 (Sokal and Rohlf, 1981). I considered differences significant when P values were less than 0.05.

RESULTS

Timing and Extent of Movements on Breeding Grounds

Brood Rearing: In 1988 all males and all but one female were on their territories in the middle of July. Starting in late July/early August 1988 the percentage of males and females remaining on their territories decreased gradually, until less than 30% remained by the end of brood rearing (Fig. 2). In 1987 the number of males (n=5) and females (n=4) known to be on their territories had dropped from 5 and 4 respectively on 18 July to 4 and 0 respectively by 15 September. In 1985 the percentage of males (n=6) and females (n=8) on their territories dropped from 100% on 20 July to 67% and 50% respectively on 28 August. In both 1987 and 1988 all radio-tagged ptarmigan that left their territories moved uphill but remained within 6 km of their territories during brood rearing (Table 1). The direction of movement depended on the location of the territory: those birds with territories closer to the west side of the valley moved to the western slopes, whereas those with territories on the east side moved uphill on the eastern slopes. In 1988, both males and females were found in small family groups during brood rearing, but males on their territories were found in significantly smaller groups than birds off their territories (Table 4).

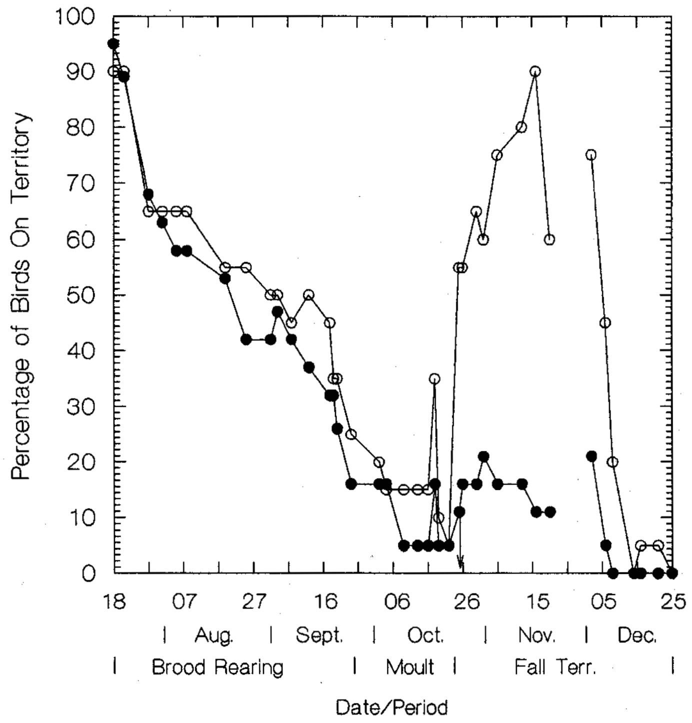

FIG. 2. Percentage of radio-tagged male (○; n=20) and female (●; n=19) ptarmigan on their territories, July-December 1988. Only birds that were tracked throughout the entire period were included. I made no observations between 21 and 30 November. First snowfall is indicated by an arrow.

Neither sex nor reproductive success determined if a ptarmigan left its territory during brood rearing. Males did not remain on their territories more often than females (males on territory, 1985 and 1988 combined: 64.5% of 31; females: 50% of 32; G=1.3; P=0.25). Eight of 19 females and 7 of 18 males with broods left their territories during the brood rearing period, whereas 3 of 8 females and 3 of 11 males without broods left their territories (females: $G_{rand.}=5.0$; P=0.12; males: $G_{rand.}=1.2$; P=0.53). Departure of males from their territories in August appeared to be influenced by territory location. Significantly more males that occupied territories in the central, flat part of the study area left in August (9 of 14) than birds that occupied territories along a nearby creek or on the hillside (4 of 19; $G_{rand.}=6.4$; P=0.01). More females from the flat portion of the study area left their territories (8 of 10) than from the hill (9 of 19), but the difference was not significant ($G_{rand.}=2.2$; P=0.15). Cover on the permanent habitat site on the central flat area (H-1) in September was significantly less (Table 2) and average height of vegetation in September was significantly lower (Table 3) than on the nearby hillside (H-2). Thus, especially among males, only birds occupying areas with less cover and lower vegetation may have left their territories.

Winter Moult: Starting in mid-September 1988, 76% of 17 males and 59% of 17 females moved farther from their territories than they did during the brood rearing period. Both males and females were significantly farther from their territories during moult than during the brood rearing period (Table 1). Most birds remained within Datlasaka Flats, but 35% of 20 males and 44% of 16 females moved to nearby side valleys (Datlasaka Creek and Goat Creek; Fig. 1). Moreover, 4 males and 1 female that I lost between mid-September and mid-October may have left Datlasaka Flats. In 1987, 1 of 5 males had left their territories by 22 September,

TABLE 1. Mean distance (km) radio-collared willow ptarmigan were found from their spring territories during autumn and winter

	Females				Males			
Period[1]	x̄	SE	Range	N	x̄	SE	Range	N
1987								
Brood rearing	1.98[2]	0.556	0.2- 3.4	5	1.09[2]	0.537	0.0- 3.5	7
Winter molt	4.05[2]	1.101	1.1- 6.7	4	2.28[2]	0.753	0.0- 5.2	5
Autumn terr.	7.20[2]	2.790	3.3-11.1	2	0.08[2]	0.017	0.0- 0.1	4
1988								
Brood rearing	1.18[3]	0.278	0.0- 4.6	23	0.88[3]	0.293	0.0- 5.7	22
Winter molt	3.07[3]	0.515	0.0- 6.5	18	2.57[3]	0.469	0.0- 6.2	21
Autumn terr.	0.89[3]	0.242	0.0- 2.8	16	0.19[3]	0.024	0.0- 0.4	20
Early winter move	25.80[3]	6.860	4.3-88.0	12	13.67[3]	4.214	2.0-55.0	18
Late winter move	30.17[3]	6.165	3.9-88.0	14	20.78[3]	6.385	0.3-90.0	16
Trans. spring terr.	1.03[3]	0.299	0.0- 2.1	8	0.23[3]	0.183	0.0- 2.4	12

[1] See text for definition of time periods. No data for winter 1987-88.
[2] Values in column are significantly different at P<0.01 (Kruskal-Wallis Test).
[3] Values in column are significantly different at P<0.001 (Kruskal-Wallis Test).

TABLE 2. Average cover (%) on the breeding area and in wintering areas, autumn and winter 1988-89 (n=20 for each site)[1]

	September		December		March	
	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE
Haines Rd.[2]	23.4^{abcde}	4.2	1.4^{abcd}	0.4	1.2^{abc}	0.5
Sprit Mtn.[2]	61.5^{a}	6.2	3.3^{efg}	0.9	4.3^{d}	1.0
Kelsall L.	66.1^{b}	5.4	13.0^{bf}	2.4	11.4^{bf}	2.2
Mule Cr.	64.3^{c}	5.0	15.6^{ae}	2.0	14.1^{ade}	1.8
Stanley Fl.	61.9^{d}	6.3	7.7^{c}	1.3	2.6^{ef}	0.9
Forest edge	60.6^{e}	4.8	13.5^{dg}	2.9	9.6^{c}	2.7

[1] Within each column values with identical superscripts are significantly different at P=0.05 (STP-Test).
[2] Breeding grounds.

TABLE 3. Average height of vegetation (dm) on the breeding area and in wintering areas, autumn and winter 1988-89 (n=20 for each site)[1]

	September		December		March	
	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE
Haines Rd.[2]	12.3^{abcd}	1.3	1.8^{abc}	0.7	0.5^{abc}	0.3
Sprit Mtn.[2]	18.5^{a}	1.4	2.0^{def}	1.0	1.8^{d}	0.5
Kelsall L.	18.3^{b}	1.0	6.8^{ad}	1.0	4.5^{ae}	0.9
Mule Cr.	18.0^{c}	1.0	7.8^{be}	1.0	7.3^{bdf}	0.8
Stanley Fl.	16.8	1.3	5.5	1.4	2.0^{ef}	0.8
Forest edge	35.0^{d}	5.6	22.0^{cf}	5.5	10.5^{c}	3.2

[1] Within each column values with identical superscripts are significantly different at P=0.05 (STP-Test).
[2] Breeding grounds.

2 by 30 September, and 4 by 7 October. Only 1 male did not leave its territory. The first all-white birds were seen on 15 October of that year, nine days before permanent snow cover. In both years movements were uphill from the brood rearing areas, and many birds moved well above the limit of vegetation into boulder fields. In 1988 both males and females joined flocks during the moulting period (Table 4).

The timing of these movements preceded the onset of winter moult (Fig. 3). Salomonsen (1939) found that ptarmigan start to moult into winter plumage when the average temperature is 3-8 °C and stop when temperatures are 9-11° lower. Temperatures at Chilkat Pass were approximately +5 °C at the onset of the 1988 winter moult and -5 °C at its termination.

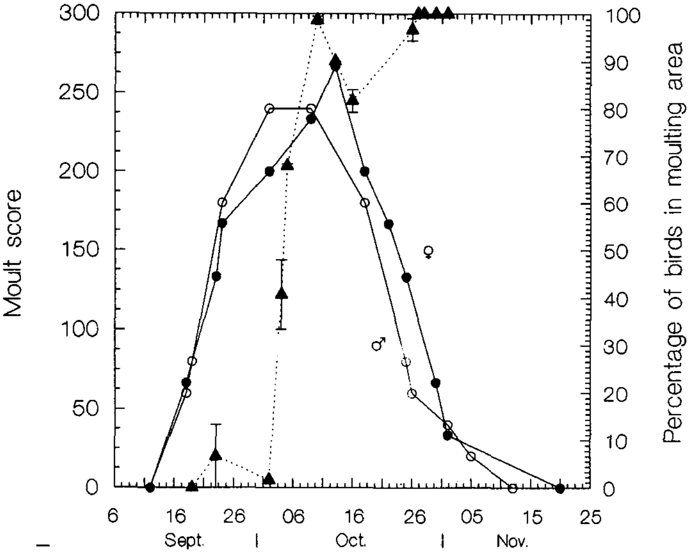

FIG. 3. Percentage of radio-tagged adult male (○; n=17) and female (●; n=17) ptarmigan in winter moult area and average moult score ± SE (Δ) of observed ptarmigan, autumn 1988. I defined winter moult area as the area to which birds moved after the middle of September. Birds that did not leave their territory were not considered to be in a moulting area.

Autumn Territoriality: In 1988, 55% of 20 radio-tagged males and 16% of 19 radio-tagged females returned to their spring territories on 26 October (Fig. 2). All males had returned by 5 November, although at no time were all males on their territories simultaneously, as some birds left their territories for short periods (see below) (Fig. 2). In 1987, all radio-tagged males had returned to their territories by 8 November, but the exact date was not measured. Of 19 females 53% returned to their territories in 1988, but they stayed a shorter period than males, and no more than 21% of females were on their territories simultaneously (Fig. 2). However, in 1988 females were significantly closer to their territories during autumn territoriality than during the moulting period (Table 1b; STP-Test on birds seen in all three periods, females on and off territory combined; U=138.0; P<0.05). In autumn 1987 neither of the 2 radio-tagged

TABLE 4. Flock size of radio-tagged male and female ptarmigan on and off their territories at Chilkat Pass during winter 1988-89

	Females				Males			
Period[1]	$\bar{x}$	SE	Range	N	$\bar{x}$	SE	Range	N
On territory								
Brood rearing	2.2^{a}[2]	0.28	1- 8	32	1.4^{ad}	0.17	1- 6	38
Autumn terr.	2.9	0.77	1- 10	11	3.4^{e}	0.65	1- 30	55
Trans. spring terr.	2.0^{bc}	0.11	1- 3	30	1.6^{bf}	0.09	1- 4	66
Off territory								
Brood rearing	3.0	0.43	1- 8	21	3.4^{d}	0.89	1- 20	21
Winter molt	47.2	20.34	3-200	12	49.3	27.61	13-200	6
Autumn terr.	21.6	8.89	1- 70	7	11.8^{e}	4.57	1- 50	10
Early winter move	88.0	23.04	1-150	7	78.1	16.04	1-200	18
Late winter move	43.0	35.12	1-200	5	67.3	12.84	6-200	18
Trans. spring terr.	11.9^{c}	3.12	1- 30	14	12.4^{f}	3.52	1- 30	14

[1] See text for definition of time periods.
[2] Values with identical superscripts are significantly different at P<0.05 (Mann-Whitney U-Test).

females returned to their territories, but 2 banded females were seen on their territories in November. During both years, all of the females whose exact location was known remained within 11 km of their territories (Table 1).

Both males and females that returned to their territories in 1988 left the flocks they had joined during the moulting period. When off their territories, however, they remained in flocks (Table 4). Group size of males on their territories was significantly different among periods (Kruskal Wallis Test; $H=14.1$; $df=3$; $P=0.001$), but not so for females.

In both years, supra-orbital combs became prominent on males during autumn territoriality, although they appeared to be smaller than in spring. Male territorial calls were heard at dawn and dusk, and on several occasions males were engaged in border disputes or chased others from their territories. Occasionally, a female territorial call was heard. I could not quantify these observations, however. In both years I observed many unbanded males along with banded males on territories on the study area, where during the breeding season the entire breeding population was banded. I assumed that most unbanded birds were juveniles.

In 1988 the return of ptarmigan to their territories appeared to coincide with the first snowfall on the breeding grounds (Fig. 2). The first radio-tagged birds returned to their territories on 18 October, when the lower limit of snow was approximately 100 m above most territories. Nearly all birds left again on 19 October, prior to a large storm. By 24 October all territories were covered with 1-5 cm of snow. Birds returned to their territories between 23 and 26 October (Fig. 2).

Between 16 and 20 November 1988 several birds of both sexes left their territories, but half the males and two of the females that left had returned by 2 December (Fig. 2). Some of the temporary departures from territory in October and November coincided with decreasing atmospheric pressure intensity. However, there was no significant correlation between changes in the percentage of birds on territory and changes in barometric pressure in the preceding 24 hours (males: corr.$=-0.27$; $SE=0.26$; $P>0.05$. Females: corr.$=-0.08$; $SE=0.25$; $P>0.05$). Moreover, not all storms were preceded by a sharp decrease in pressure. Nor did all declines in pressure forewarn a storm. Therefore, movements by ptarmigan off their territories were not influenced solely by changes in barometric pressure.

Movements to Wintering Grounds: In 1988 males moved to their wintering grounds significantly later than females (females: $\bar{x}=$ 20 November; $sd=10.6$ days; $n=14$; males: $\bar{x}=5$ December; $sd=7.02$ days; $n=20$; $t=4.3$; $P<0.001$). Ptarmigan wintering farther from the breeding grounds could be expected to leave their territories earlier than those wintering nearby. However, the departure date from the breeding grounds was not correlated with the distance ptarmigan of either sex moved to their wintering grounds (Spearman rank correlation; females: $r_s=0.08$; $n=13$; $P>0.05$; males: $r_s=-0.10$; $n=20$; $P>0.05$). By 14 December 1988 all radio-tagged ptarmigan had left their territories and started moving towards their wintering grounds, although two males returned to their territories in the third week of December (Fig. 2). In 1987 all ptarmigan also left their territories in the second week of December. After they left the breeding grounds, both males and females joined large flocks (Table 4).

In late December 1988, cover and height of vegetation above the snow were significantly heterogeneous among permanent habitat sites ($H=46.0$; $df=5$; $P<0.001$). Average cover and height of vegetation were significantly less on the breeding grounds (H-1 and H-2) than in alpine wintering areas (H-3, H-4, and H-5) or at the edge of the boreal forest (H-6) (Tables 2, 3). In September vegetation cover and average height of vegetation at H-1 were significantly lower than at any of the other sites (Tables 2, 3), but cover and height of vegetation at H-2 were not. Hence, cover and height of vegetation were decreasing faster at H-2 than in the wintering areas.

Despite the difference in cover and height of vegetation among habitat sites in December, snow depth in that month was not significantly different among sites in either year (Tables 5, 6; Kruskal Wallis Test; 1987: open: $H=4.73$; $P=0.09$; $df=2$; shrubs: $H=4.24$; $P=0.12$; $df=2$; 1988: open: $H=9.69$; $P=0.08$; $df=5$; shrubs: $H=6.96$; $P=0.22$; $df=5$). The great difference in snow depth between shrubs and open areas at H-1 in December 1988 was related to high winds at that site: wind speed at W-1 was much higher than at W-2 throughout autumn and winter 1988-89 (W-1: $\bar{x}=3.81$ m/s; W-2: $\bar{x}=0.52$ m/s; t-Test after Box-Cox transformation; $\lambda=(1/3)$; $t=10.6$; $df=1$; $P<0.001$). Wind speeds at H-4 appeared similar to those at W-2. Thus the difference in vegetation cover and height between breeding and wintering grounds was at least partly caused by differences in wind speed.

One female moved to her wintering grounds 50 km north of the breeding area in eight days or less, but many ptarmigan did not move directly to the areas where they spent the

TABLE 5. Mean snow depth (cm) at breeding and wintering grounds of willow ptarmigan, December 1987 and March 1988

	December				March			
	open		shrubs		open		shrubs	
Site	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE
Haines Rd.[1]	72.7	6.0	93.0	12.8	131.7	8.6	130.3	4.2
Stanley Fl.	105.3	6.0	97.7	8.9	162.3	7.5	148.3	5.1
Forest edge	94.3	7.7	60.3	9.0	122.3	2.6	76.7	10.0

[1] Breeding grounds.

TABLE 6. Mean snow depth (cm) at breeding and wintering grounds of willow ptarmigan, December 1988 and March 1989

	December				March			
	open		shrubs		open		shrubs	
Site	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE
Haines Rd.[1]	34.7	14.5	79.3	8.9	58.0	3.8	74.0	8.5
W. Haines Rd.[1]	69.0	7.1	77.3	4.9	74.3	3.9	72.7	9.1
Kelsall L.	55.7	1.5	76.7	6.3	74.7	5.2	78.7	5.4
Mule Cr.	66.0	6.2	70.7	3.3	77.0	4.6	65.0	4.0
Stanley Fl.	62.3	3.3	78.7	8.5	89.7	3.4	90.7	8.8
Forest edge	83.7	5.3	50.3	5.5	93.0	7.4	80.3	8.2

[1] Breeding grounds.

majority of the winter. Eight of 20 males were known to have changed location during the course of the winter, as did 4 of 15 females. Birds that remained in subalpine habitat moved between Mule Creek and Kelsall Lake (10 km) or from Datlasaka Flats to Stanley Flats (15 km). Those that left the breeding grounds moved to lower elevations later in winter (Gruys, 1991). Neither males nor females were significantly farther from their territories in late winter than in early winter (Table 1; Mann-Whitney U test; females: U=57.0; P=0.82; males: U=85.5; P=0.57). When data from early and late winter periods were combined, males moved significantly shorter distances than females (Table 7; Kolmogorov-Smirnov test; D=0.47; P=0.04). All birds that left Datlasaka Flats moved in a northerly or northeasterly direction (Gruys, 1991). In those directions the edge of the boreal forest lies at approximately 20 km from the breeding grounds. Thus, in 1988-89, 20% of the males and 67% of females moved past the edge of the boreal forest during the winter. However, several males moved as far as females, and the longest recorded movement (90 km) was made by a male.

Return to the Breeding Grounds: In spring 1989, radio-tagged males returned to their territories significantly earlier than females (males: $\bar{x}$=21 March; sd=6.0 days; n=8; females: $\bar{x}$=6 April; sd=9.7 days; n=8; t=3.9; P<0.01). The two males that returned to their territories in late December returned again in the second half of January and stayed there the rest of the winter. The first of the remaining males returned to their territories on 17 March (Fig. 4). All males but one returned to their territories before the end of March. The date male ptarmigan returned to their territories was highly correlated with the distance they had to move from their wintering grounds (Spearman rank correlation; r_s=0.95; n=8; P<0.01; males on territory since January excluded).

If males try to remain as close to their territory as possible, then the question arises as to why some males moved as far as females, especially because males that moved farther returned to their territories later. Males have high breeding philopatry (Schieck and Hannon, 1989), and thus older males are more familiar with their territory and may have an advantage over younger males when defending it. As a result, older males may be able to regain their old territory even if they arrive several days later than young males (Ketterson and Nolan, 1983). There was a trend for males that moved to the forest to be older than males that stayed in the alpine (Alpine: average age = 2.4 yr; sd=1.4; n=16; Forest: average = 4.3 yr; sd=2.9; n=4; t=1.86; P<0.10). However, there was no significant correlation between the distance males moved to their wintering grounds and their age (Spearman rank correlation matrix; r_s=0.26; P>0.05).

TABLE 7. Comparison of maximum distances moved by males and females to their wintering areas, 1988

	Males (n=20)		Females (n=15)	
Distance from territory (km)	%	Cum. %	%	Cum. %
0- 5[1]	25.0	25.0	6.7	6.7
5-10	35.0	60.0	26.7	33.3
10-15	10.0	70.0	0.0	33.3
15-20	10.0	80.0	0.0	33.3
20-25	0.0	80.0	26.7	59.9
40-45	5.0	85.0	20.0	79.9
50-55	5.0	90.0	6.7	86.6
55-60	5.0	95.0	6.7	93.3
85-90	5.0	100.0	6.7	100.0

[1] 0.001-5.000 km.

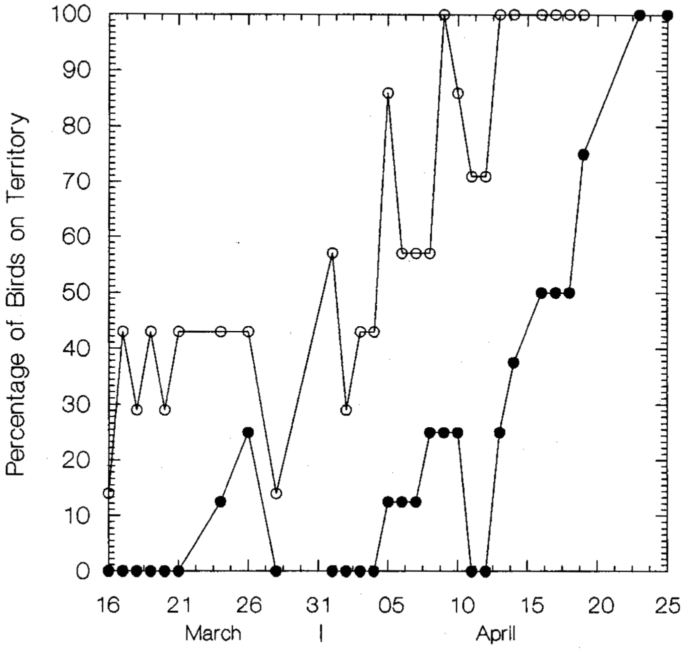

FIG. 4. Percentage of radio-tagged male (o; n=7) and female (●; n=8) ptarmigan on their territories, March-April 1989. Birds depredated during spring territoriality excluded.

In 1988 the first males were sighted on their territories in the same week (21 March) as in 1989. Yet, when male ptarmigan returned to their territories in March 1988, snow depth on the breeding grounds was nearly twice as great as when they returned in March 1989 (Tables 5, 6).

In March 1989 cover and average height of vegetation were heterogeneous among habitat sites (Tables 2, 3; cover: H=45.6; P<0.001; df=5; height: H=34.2; P<0.001; df=5). Cover at H-1 was still significantly less than at the wintering grounds, and cover on H-2 was significantly less than at H-3 and H-4. Height of vegetation at H-1 was significantly lower than at the wintering grounds, and height of vegetation at H-2 was significantly lower than at H-4. Hence, when males returned, the breeding grounds had less cover and lower vegetation than the wintering grounds.

In March 1988, snow depth in shrubs was significantly heterogeneous among sites (Table 5; H=6.9; df=2; P=0.03) but not in open areas (H=4.5; df=2; P=0.11). When males returned in March 1989, snow depth was not significantly different among sites in either shrubs or in open areas (Table 6; open: H=10.4; df=5; P=0.07; shrubs: H=4.4; df=1; P=0.50). Thus, the difference in cover and height of vegetation among sites was not caused by differences in snow depth.

In 1989, the first two females returned to their territories in late March but left again after several days (Fig. 4). Most females did not arrive until the second week of April. The two females that returned early spent the winter nearby at Kelsall Lake. The other two females that wintered at Kelsall Lake also moved closer to the breeding grounds in late March but were not seen on their territories. The date females returned to their territories was correlated with the distance they had to move from their wintering grounds ($r_s=0.77$; $n=8$; $P<0.05$). The age of females wintering near the breeding grounds was similar to that of females wintering farther away (Alpine: average age = 1.8 yr; sd=1.0; n=4; Forest: average = 2.0 yr; sd=0.8; n=10; $t=0.43$; $P>0.5$).

After their return to the breeding grounds, all females and all males but one left their territories at least once before settling permanently (Fig. 4). As in autumn, some of these departures from territory coincided with decreasing atmospheric pressure intensity. However, similar to the situation in autumn, there was no significant correlation between the percentage of birds on their territories and barometric pressure in the preceding 24 hours (males: corr.=0.15; SE=0.19; $P>0.05$; females: corr.=0.08; SE=0.19; $P>0.05$). Therefore, changes in pressure did not accurately explain all movements of ptarmigan from their territories.

In spring 1989 both males and females off their territories were in significantly larger groups than birds on their territories (Table 4). Group size of birds off their territories in spring was similar to group size of birds off their territories in autumn. Males on their territories were in significantly smaller groups than females on their territories (Table 4).

Height of Vegetation near Ptarmigan

In most periods of 1988-89 average height of vegetation near both sexes of ptarmigan was greater than 1 m (Table 8). Height of vegetation near female ptarmigan off their territories was similar throughout autumn and winter (Table 8; Kruskal Wallis Test; $H=7.8$; $df=5$; $P=0.17$). Vegetation height near males off their territories, however, varied significantly among periods ($H=28.8$; $df=5$; $P<0.001$) and was lowest in late winter and spring. During all three periods male ptarmigan on and off their territories were found in areas with similar height of vegetation. During transient spring territoriality, however, females on their territories were found in significantly lower vegetation than females off their territories (Table 8).

TABLE 8. Vegetation height (dm) within 10 m of radio-tagged male and female ptarmigan on and off their territories at Chilkat Pass during winter 1988-89

	Females				Males			
Period[1]	$\bar{x}$	SE	Range	N	$\bar{x}$	SE	Range	N
On territory								
Brood rearing	14.1[a]	0.59	0-20	32	12.4[a]	0.59	0-22	38
Autumn terr.	12.2	1.14	1-16	11	12.7	0.36	8-20	55
Trans. spring terr.	7.5[b]	0.55	0-14	22	6.7	0.38	0-15	56
Off territory								
Brood rearing	11.9	0.94	0-18	24	13.5	1.06	5-25	19
Winter molt	10.0	1.43	0-15	12	13.0	1.67	8-20	6
Autumn terr.	11.6	1.44	6-17	7	12.3	0.90	9-17	10
Early winter move	17.9	2.44	10-30	7	13.6	0.78	6-20	18
Late winter move	23.0	7.15	0-50	6	8.9	0.85	6-17	18
Trans. spring terr.	13.8[bc]	1.91	3-20	13	6.6[c]	0.96	4-18	13

[1] See text for definition of time periods.

Height of vegetation near both sexes on their territories was heterogeneous among periods (Table 8; males: $H=73.6$; $df=2$; $P<0.001$; females: $H=34.7$; $df=2$; $P<0.001$). Ptarmigan were found in tallest vegetation during brood rearing and lowest vegetation during spring territoriality. During brood rearing males were found in significantly lower vegetation than females (Table 8).

DISCUSSION

Timing and Extent of Movements on Breeding Grounds

Brood Rearing: After chicks hatched, willow ptarmigan occupying territories in areas with less cover and lower vegetation left their territories and moved uphill. This is consistent with patterns found in other populations and species of ptarmigan (Gelting, 1937; Gardarsson and Moss, 1970; Bossert, 1980; Andersen *et al.*, 1986). Gelting (1937), Braun (1971), and Andersen *et al.* (1986) suggested that ptarmigan moved to higher elevations after the breeding season because snow melted late there, delaying plant phenology. Since the nutritive value of plants decreases with age (van Soest, 1983), they concluded that food quality at higher elevations was better. Moreover, snow patches found at higher elevations offer camouflage to white-tailed ptarmigan (*L. leucurus*), which moult into winter plumage at that time (Braun, 1971; see below). Variation in the extent of uphill movements and the proportion of the population that moves uphill is caused by variation in timing of snow melt (Andersen *et al.*, 1986) and quality of the territories (see Mercer, 1967). Bergerud and Gratson (1988) suggested that in the first two weeks after hatch female grouse with broods select open, insect-rich habitats, but once chicks mature, females move to denser cover to avoid detection by predators. I found ptarmigan both off and on their territories in dense cover during brood rearing. Mortality of adult ptarmigan was high during raptor migration in early September (Gruys, 1991). Hence, ptarmigan may attempt to reduce risk of predation by selecting areas with dense cover. At Chilkat Pass, variation in movements among ptarmigan may depend on food availability or quality on the territories as well as on availability of cover. As a result, only ptarmigan from territories lacking those components would move uphill.

Winter Moult: Movements by willow ptarmigan farther uphill in September preceded moult into winter plumage. Salomonsen (1939) and Hewson (1973) observed that initiation of winter moult coincided with a decrease in temperature. On the other hand, Host (1942) argued that moult in willow ptarmigan is regulated by day length. The change in temperature from above to below freezing is a cue to predict arrival of snow, but its timing can vary widely among years, whereas the change in day length is constant. So change in temperature is probably a less reliable cue than change in day length.

During winter moult many birds moved well above the limit of vegetation onto boulder fields, where patches of snow were already present. Other populations and species of ptarmigan also move to areas with snow during winter moult and remain above the snow line (Kristoffersen, in Myrberget, 1976); Gudmundsson, 1960; Braun, 1971). Thus, during the period in which ptarmigan moult into their winter plumage they may select areas that offer protection from predators. Formation of large flocks during this period provides additional protection against predators (Bergerud and Gratson, 1988). Movements during the winter moulting period, therefore, are probably primarily related to predator avoidance.

Autumn Territoriality: In autumn all males and about half of the females returned to their territories between late October and early December. During that time there was a resurgence of territorial defence, especially by males. Males appeared to leave flocks and return to their territories directly after the breeding area was snow covered. Although I could not quantify territorial behaviour as such, the fact that many calls were heard and ptarmigan were alone on their territory, especially in the mornings, suggests that ptarmigan indeed defended their territories. The larger group sizes during autumn territoriality were probably due to the timing of sightings. Most spring sightings were made shortly after dawn, whereas in autumn many were made towards the middle of the day. By this time most territorial behaviour had ceased, and territorial males would allow other birds on their territories (Jenkins *et al.*, 1963).

A similar resurgence in territorial activity has been observed in other willow (e.g., Bergerud and Mercer, 1966; Voronin, 1978; Pedersen *et al.*, 1983) and rock ptarmigan (*L. mutus*) (Watson, 1965; Bossert, 1980) populations. The timing and extent of autumn territoriality, however, varies with local conditions. Harper (1953) and Bossert (1980) noted an increase in territorial calling of willow and rock ptarmigan respectively after first snowfall. On the other hand, autumn territoriality in willow ptarmigan in Newfoundland and Norway (Mercer, 1967; Pedersen *et al.*, 1983) and Scottish red grouse (*L. l. scoticus*) (Jenkins *et al.*, 1963) resumes as early as September, well before permanent snow cover.

In both years of this study, ptarmigan left their territories in December, when cover diminished. In the absence of snow or under mild winter conditions ptarmigan will defend their territories throughout the winter (e.g., Jenkins *et al.*, 1963; Watson, 1965), but most populations of ptarmigan are forced to leave their territories when cover becomes unavailable. As a result, territorial activity in autumn will be more pronounced among populations with sufficient cover, such as among red grouse, and less obvious or absent when breeding grounds are snow covered early in autumn, as among white-tailed ptarmigan. Bergerud and Gratson (1988) suggested that late sexual maturity as a result of local conditions may also keep juveniles in some populations of ptarmigan from displaying in fall. Thus, willow ptarmigan appear to display in autumn whenever local conditions permit them to do so.

Movements to Wintering Grounds

Timing and Extent of Movements: Most ptarmigan stayed in vegetation of, on average, 1 m or taller throughout autumn and early winter. Hence, ptarmigan may have left their territories because height of vegetation decreased below 1 m as snow depth increased. Mossop (1988) reached similar conclusions. He roughly estimated food availability and found that food was not a limiting factor in determining movements of ptarmigan from the breeding grounds. I did not measure food availability, as it was very difficult to obtain accurate estimates.

In both winters of this study, ptarmigan left the breeding grounds in mid-December. There was less snow in open areas in December 1988 than at the same time in 1987, but in 1988 strong winds redistributed the snow into the shrubs. Furthermore, in 1988 heavy, wet snow bent most shrubs, which further decreased height of vegetation. Therefore, in this population departure of ptarmigan from their breeding grounds is ultimately caused by lack of cover, which in turn is caused by a combination of snow depth, snow density, and wind speed. The gradual movements of ptarmigan and changing of wintering grounds during winter, as Mossop (1988) also observed, probably reflect changes in local conditions over the winter.

The difference in wind speed between the breeding area and the subalpine wintering grounds explains why in both years large numbers of ptarmigan were seen in the protected parts of Datlasaka Flats, and not closer to the breeding area, 5-10 km away. High winds increase convective heat loss of animals (Marchand, 1987). Wind also compacts the snow, making it more difficult for ptarmigan to dig snow burrows, which protect them from heat loss and predation. Moreover, the high winds on the breeding grounds redistributed much of the snow into the vegetation, leaving little exposed, and caused blowing snow to abrade any exposed vegetation (Formozov, 1963). The latter effect partly explains the difference in height of vegetation between the H-1 habitat site, which was situated in a high wind area (Gruys, 1991), and other sites. The S-2 snow site is slightly more protected from the high winds because it lies behind a moraine.

Weather conditions also control winter movements of other grouse species. During mild winters rock and white-tailed ptarmigan, as well as sharp-tailed grouse (*Tympanuchus phasianellus*) and sage grouse (*Centrocercus urophasianus*), moved shorter distances than during more severe winters (Beck, 1977; Hoffman and Braun, 1977; Bossert, 1980; Herzog, 1980; Dunn, 1984; Swenson, 1985). The plasticity in the timing and extent of winter movements by grouse is accounted for by differences in local conditions (Herzog, 1980). Thus, variation in snow cover between years will influence winter movement patterns.

Timing of Return to Breeding Grounds: In 1989 males returned to their territories 2-3 weeks earlier than females. Similarly, males returned earlier to their territories in populations of rock ptarmigan (Weeden, 1964; Gardarsson, 1988), blue grouse (*Dendragapus obscurus*) (Anthony, 1903; Bendell and Elliott, 1967), and migrating spruce grouse (*D. canadensis*) (Herzog and Keppie, 1980). There was a strong relationship between the time males returned to their territories and the distance they had to move from their wintering grounds. Moreover, the first males returned to their territories at approximately the same date both years, regardless of snow depth at the breeding grounds. Thus, timing of return by males is probably controlled by an external factor, such as photoperiod. In contrast, females may, in addition to photoperiod, adjust the timing of return to the breeding grounds to weather and snow conditions, as has been documented for other migrants (Lewis and Farner, 1973). This accounts for the poorer correlation between the timing of female return and the distance females moved from the breeding grounds. Thus, there appears to be no advantage for females to winter nearby (assuming individuals arriving earlier would have a better chance of obtaining a territory). Mortality of females that moved to the boreal forest was not significantly higher than of females that remained in alpine habitat, but sample sizes were small (Gruys, 1991). However, there may be other advantages to wintering nearby, such as lower movement-related energy expenditure.

Nearly all ptarmigan left their territories for short periods in both autumn and spring. These departures appeared to be related to periods of bad weather. Similar movements have been recorded in other populations and species of ptarmigan (Jenkins *et al.*, 1963; Braun *et al.*, 1976; Bossert, 1980; Pedersen *et al.*, 1983; Thingstad, 1984), as well as in song sparrows (*Melospiza melodia*) and white-crowned sparrows (*Zonotrichia leucophrys*) (Wingfield *et al.*, 1983; Wingfield, 1985). Clearly, availability of cover and absence of high winds outweigh the benefit of territory occupation.

Snowfall and high winds can rapidly hinder feeding and eliminate shelter. Moreover, snowfall from one storm could bury most vegetation, and searching for better cover during a storm would be energetically expensive. Therefore, it is advantageous for ptarmigan to be able to predict when storms occur, so they can leave their territories and reach suitable cover (see Buttemer, 1985). Changes in feeding behaviour prior to storms have been observed in other species of birds (Buttemer, 1985). Storms are usually preceded by a drop in atmospheric pressure (Battan, 1984). As homing pigeons (*Columba livia*) are sensitive to very small changes in pressure (Kreithen and Keeton, 1974), they, as well as other species, may use such changes to predict storms. Although pressure intensity was often low when ptarmigan at Chilkat Pass left their territories, ptarmigan did not leave during all decreases in pressure. Nor were all storms preceded by declining pressure. Therefore, ptarmigan probably use additional cues to predict the arrival of storms.

Vegetation Height near Ptarmigan

Ptarmigan generally sought vegetation greater than 1 m, but during transient spring territoriality tall vegetation was probably not available on the breeding grounds. The fact that females were found in taller vegetation than males on their territories during brood rearing and off their territories during transient spring territoriality supports the reproductive strategy hypothesis at least for those periods. On the wintering grounds, however, females were not found in significantly taller vegetation than males. This was probably due to small sample size and inaccessibility of females in the boreal forest, where vegetation was most likely to be taller.

Segregation of the Sexes

During winter 1988-89 most males remained in alpine areas within 20 km of their territories, whereas most females moved farther into the boreal forest. Aside from wintering closer to the breeding grounds, males left their territories later and returned earlier than females. These findings support the reproductive strategy hypothesis. However, the fact that segregation was incomplete suggests that there may be additional factors influencing movements of ptarmigan outside the breeding season. Differences in movements among ptarmigan of different age or social status could play a role.

During winter male and female ptarmigan segregate spatially through differential migration, but others have observed segregation of tetraonins within the same area as well (Koskimies, 1957; Seiskari, 1962; Schmidt, 1969; Braun and Schmidt, 1971; Mossop, 1988). In this study, some segregation of male and females appeared to take place during winter moult, but I could not quantify it. Hence, in grouse segregation might not be related to migration alone but might occur at any time birds are in flocks off their territories. Beck (1977) suggested that differential cover requirements could play a role, but I found no evidence for that except during spring transient territoriality. More intensive study of movements and habitat use during periods in which grouse are off their territories but in the same area may provide important cues to the causes of segregation in these species (Weeden, 1964).

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