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Authors: Hannon, Susan J., Gruys, Rogier C., and Schieck, Jim O.

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Susan J. Hannon, Rogier C. Gruys & Jim O. Schieck

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We assessed sex ratio, annual survival rates and patterns of seasonal mortality of female and male willow ptarmigan *Lagopus lagopus* in northwestern British Columbia. Annual sex ratio of birds on the breeding area did not statistically differ from a 1:1 ratio over eight years, although in six of the eight years males were more numerous. Over eight years, annual survival, based on return rates of banded birds, was 41-63% for males and 30-54% for females. We analysed seasonal patterns of mortality using radio-tagged birds. During four springs and summers, female survival varied from 74 to 97%. They suffered the highest mortality during late prelaying, incubation and pre-fledging brood rearing periods, and most were killed by raptors. Broodless females survived better (100%) than females accompanied by broods (77%). No radio-tagged males died during two breeding seasons. Survival for both sexes was lower in autumn/winter (40-60%) than in spring/summer (75-100%). In autumn, the highest mortality for both sexes occurred during the late brood rearing and winter moult periods, coinciding with the autumn raptor migration. Both sexes had similar mortality rates over winter, despite separating by habitat. Another peak in male mortality occurred in late winter/early spring during the period of transient territoriality, whereas no females were killed during this time. From 1.4 to 3 times as many males as females were killed by hunters. Higher mortality of males during the hunting season and in late winter may balance the higher mortality of females during the breeding season, resulting in a breeding sex ratio that is close to unity.

Key words: breeding, Lagopus lagopus, mortality, sex, survival, willow ptarmigan

Susan J. Hannon, Rogier C. Gruys & Jim O. Schieck**, Department of Biological Sciences, University of Alberta, Edmonton, Alberta, Canada T6G 2E9 - e-mail addresses: sue.hannon@ualberta.ca (Susan J. Hannon); rgruys@uvic.ca (Rogier C. Gruys); jims@arc.ab.ca (Jim O. Schieck)*

Present addresses:
**U Vic Communications, University of Victoria, P.O. Box 1700 Stn Csc, Victoria, British Columbia, Canada V8W 2Y2*
*** Forest Resources, Alberta Research Council, Bag 4000, Vegreville Alberta, Canada T9C 1T4*

Corresponding author: Susan J. Hannon

Male biased breeding sex ratios are common in monogamous birds (Breitwisch 1989) and may be caused by differential mortality of the sexes at the juvenile or adult stage. There are six main differences between the sexes that could contribute to differential mortality in adults:

1) Differential parental investment: females tend to invest more in reproduction and thus may have higher energetic stress or risk of predation than males (Trivers 1972).
2) Differential breeding philopatry: females tend to switch territories more than males on return to breeding areas (Greenwood & Harvey 1982). Switching to an unfamiliar territory may lead to an increase in predation risk.
3) Differential migration: females tend to migrate further than males in autumn and thus may incur higher mortality (Gauthreaux 1978).
4) Differences in body size: males are usually larger than females, hence females may suffer higher mortality during stringent winter conditions (e.g. Schluter & Smith 1986).
5) Differences in dominance status over winter: for birds spending the winter in flocks, males are often dominant to females and have higher access to resources (e.g. Desrochers, Hannon & Nordin 1988).
6) Differences in susceptibility to hunting: depending on the mating system and differential movements of males and females to wintering areas, one sex may incur higher hunting mortality (e.g. Zwickel 1982).

Willow ptarmigan *Lagopus lagopus* are a predominantly monogamous grouse species (Hannon 1984). Both sexes are territorial during the breeding season, but males are more conspicuous during territorial defence, advertisement and mate guarding (Bergerud & Mossop 1984). Male willow ptarmigan contribute more parental investment than other grouse species, remaining with the female throughout prelaying, laying and incubation and defending the brood. Only females incubate. Although breeding philopatry is high, females switch territories more than males, but females that switch have similar mortality to non-switchers (Schieck & Hannon 1989). Both sexes remain in the vicinity of the breeding areas until the snow becomes too deep for foraging, after which most females migrate into boreal forest and males to sheltered areas in subalpine tundra close to breeding areas (Mossop 1988, Gruys 1993). Adult males are larger than females in winter (550 g vs 475 g), but there do not appear to be dominance interactions in winter flocks (Mossop 1988). Finally, since the sexes separate in winter, males may incur higher hunting mortality because they remain in areas more accessible to hunters. Overall then, hypotheses 1, 3, 4 and 6 appear to be relevant to willow ptarmigan, and we test these indirectly by documenting seasonal and annual mortality patterns of males and females.

Methods

Study area

We conducted this study during 1979-1982 and 1984-1989 at the Chilkat Pass in northwestern British Columbia, Canada (59° 50'N, 136° 35'W). In this area, willow ptarmigan breed in subalpine tundra dominated by willow *Salix* spp. shrubs and winter either in boreal forest (females) or areas of higher cover in the subalpine (males). The topography, vegetation and climate of the area are described in more detail elsewhere (Weeden 1960, Hannon 1984, Gruys 1993).

Capture, banding and radio-tagging

Ptarmigan were captured in nets or with nooses (Hannon 1983) on a 4.5 km^2 study area and marked with a unique combination of an aluminium and three plastic colour bands. Sexes were distinguished on the basis of differences in plumage and voice (Hannon & Roland 1984), and ages were determined by comparing pigmentation on the eighth and ninth primaries (Bergerud, Peters & McGrath 1963). In July 1987 and 1988, 15-21g radio transmitters (either Austec, Canada or Biotrack, UK) were placed on 32 males and 35 females and tracked until the next spring. In early May of 1986-1989, a total of 174 resident females were radio-tagged, and in May 1988 and 1989, 47 territorial males were radio-tagged and followed until July. All collars were attached with a necklace made of harness wire or soft cord. During the breeding season birds were located visually 2-5 times per week. In autumn and winter we tried to locate each bird visually at least once a week, but once the ptarmigan had left the breeding area this was often not possible because many were inaccessible.

Annual survival and sex ratio of leg-banded birds

During the springs of 1979-1982 and 1984-1989 we banded over 95% of birds that lived and bred on the study area and plotted their territories (Hannon 1983). The areas were searched thoroughly, and based on band combinations and unique plumage features, we knew the identities of all resident birds. We searched the study areas for marked birds each spring, and the percentage of birds returning to their territories was calculated. Breeding philopatry is high for this species (Schieck & Hannon 1989), so we assumed that birds that were not sighted on the study area had died. Spring sex ratio was calculated by counting all territorial males and females and non-territorial males (we observed no non-territorial females). Only non-territorial males that were banded and seen on the study area at least twice were included in this tally to exclude transient birds moving through the area. Numbers of non-territorial males were likely underestimated as they are secretive and difficult to census.

Survival of radio-tagged birds

The breeding season was defined as the time from permanent settling on territories in spring to the time chicks fledged. However, because birds were not radio-tagged immediately upon settling on their territories, we only calculated mortality for the following six periods of approximately 10 days each, based on stages of the breeding cycle:

1) early pre-laying: 20 days before the date of first egg (DFE) until 11 days before DFE;
2) late pre-laying: 10 days before DFE until one day before DFE;
3) laying: DFE until incubation started;
4) early incubation: first 11 days of incubation;
5) late incubation: last 10 days of incubation;
6) pre-fledging: hatch until 10-days post hatch.

Nests were found for all radio-tagged females so DFE and hatch dates were known (Hannon, Martin & Schieck 1988). When females lost their nests to predation and did not renest, their transmitters were removed. Therefore, after laying started, we only included females that hatched young, or were killed during nesting, in the analyses.

We divided each autumn and winter into six time periods based on changes in behaviour and movement patterns (Gruys 1993):

1) post-fledging brood rearing: from 1 August to onset of winter moult (23 September);
2) winter moult: moult from summer to winter plumage (24 September-23 October);
3) fall territoriality: majority of males on territory (24 October-10 December);
4) early winter: from the time ptarmigan left the breeding grounds until 31 January;
5) late winter: from 1 February until ptarmigan returned to their territories in spring;
6) transient spring territoriality: from the time ptarmigan first returned to their territories in spring until they settled permanently.

During the study no radio-tagged males but five females were lost (neither bird nor transmitter was recovered) during winter. We assumed that these birds had died because if their transmitters had failed and they were still alive, they should have returned to the study area to breed the following spring. We excluded all birds that died within 10 days of capture from the analysis to remove mortality that might have been caused by handling stress. Birds that were killed by hunters (three males, one female) were not used in the calculation of natural survival rates.

We calculated Kaplan-Meier survival estimates and standard errors (Pollock, Winterstein, Bunck & Curtis 1989) separately for each sex and time period. This method allows birds to be added or removed ('censored') from the sample during the study. We used a generalized Kruskal-Wallis H-Test (Lee 1980) to determine if survival curves were significantly different among years or between sexes. When a test was not significant in two or more years, but data in each of the years showed a trend in the same direction, we combined the probabilities (Sokal & Rohlf 1981). We considered differences significant when $P \leq 0.05$.

Determining date and causes of mortality

Whenever possible, dead radio-tagged ptarmigan were collected and the remains, along with any sign of predators, were described. During the periods in which ptarmigan were on or near their territories (April-September), the date of predation was usually known within five days. However, the mortality date of birds that were depredated during winter in inaccessible areas had to be estimated from the freshness of the kill and depth of snow on the remains (Hannon & Gruys 1987). We classified predators as either mammals (mostly red foxes *Vulpes vulpes*), raptors, or unidentified predators. To determine the identity of the predator, we compared the remains to those killed by known predators and to descriptions in the literature (Einarsen 1956, Jenkins, Watson & Miller 1964, Hannon & Gruys 1987, Thirgood, Redpath, Hudson & Donnelly 1998). However, it was not always possible to establish the cause of death, because in some cases few or no remains could be found. Moreover, ptarmigan may have been depredated after they were weakened by parasitism or food shortage or wounded by hunters. Thus, we were measuring proximate mortality only.

Effects of radio-tagging

To determine whether radio-tagging in autumn and winter affected survival, we compared overwinter survival of radio-tagged birds with that of individuals with leg bands only. Survival of leg-banded males was defined as the percentage of males counted in spring that returned in a subsequent spring. Females that lost their nest were often very secretive, and as a result were easily overlooked. Therefore we used only leg-banded and radio-tagged females that successfully hatched chicks in comparing female overwinter survival. We excluded birds that were killed by hunters. To determine whether radio-tagging during the breeding season influenced mortality, we compared return rates of radio-tagged and leg-banded females (no radio-tagged males were killed during the breeding season) in the subsequent spring. We only used data for birds marked in 1986 and returning in 1987 as that was the only year in which we had sufficient females that were not radio-tagged.

Predator community

The common predators of adult ptarmigan on the subalpine breeding area at the Chilkat Pass are red foxes and gyrfalcons *Falco rusticolus*, which are present throughout the year (Mossop 1988), and northern harriers *Circus cyaneus* (Hik, Hannon & Martin 1986) and golden eagles *Aquila chryseatos* during the summer (Mossop 1988). Bald eagles *Haliaeetus leucocephalus*, peregrine falcons *F. peregrinus* and goshawks *Accipiter gentilis* migrate through the Chilkat Pass during spring and autumn (Weeden 1960). The Chilkat Pass is one of only three passes which connect the Yukon Territory to the Pacific Ocean. Hence, it acts as a funnel for migrating raptors. Some ptarmigan spend the winter in the boreal forest north of the Chilkat Pass (Gruys 1993) where goshawks, great horned owls *Bubo virginianus*, coyotes *Canis latrans* and lynx *Lynx lynx* are found throughout the year (Doyle & Smith 2001, O'Donoghue, Boutin, Murray, Krebs, Hofer, Breitenmoser, Breitenmoser-Wüersten, Zuleta, Doyle & Nams 2001). Red foxes use forested areas to a lesser extent (O'Donoghue, Boutin, Hofer & Boonstra 2001).

While in the field, all sightings of predators and the time afield were recorded. Foxes were difficult to observe in summer, thus we only used sightings for foxes when snow covered the ground. We did not quantify numbers of predators in boreal forest as sightings were obscured by trees, and we spent too little time in the forest.

Hunting mortality

The hunting season extended from 15 August to 28 February each year. During the 1987/88, 1988/89 and 1989/90 hunting seasons we set up a hunter check station at the Pleasant Camp Canada Customs station 55 km south of the Chilkat Pass on the only road access to the area for hunters from the south (the majority of hunters). All hunters were asked to give one wing and any bands from each bird shot. Sex was determined using the length of the eighth primary and wing chord in a discriminant analysis (Gruys & Hannon 1993).

Table 1. Sex ratio of willow ptarmigan in spring in the Chilkat Pass, northwestern British Columbia. N = total number of birds observed, and G-test compares observed sex ratio to a 1:1 sex ratio.

Year	Sex ratio	N	G	P
1980	1.04	51	0.009	0.92
1981	1.23	78	0.31	0.57
1984	1.14	75	0.16	0.68
1985	1.29	204	1.65	0.19
1986	1.14	223	0.50	0.48
1987	0.96	153	0.03	0.86
1988	0.99	135	0.004	0.95
1989	1.04	116	0.017	0.89

Results

Spring sex ratios of ptarmigan

Sex ratios of willow ptarmigan in spring did not differ statistically from 1:1 in any year (Table 1), however they were slightly male biased in six of eight years. Numbers of males present may have been underestimated as some proportion of males were non-territorial each year and thus were difficult to census.

Annual survival of leg-banded ptarmigan

Return rates of males and females to the study area in spring were not significantly different for any year except 1986; however, when P-values for each year were combined, the return rates of adult females were significantly lower than those of adult males (Table 2). Annual survival rates of males and females were not correlated ($r_s = 0.02$, $P = 0.95$)

Survival of radio-tagged ptarmigan

Mortality during the breeding season

Mortality of females during the breeding season varied significantly among years from five to 26% (χ^2 =

Table 2. Percentage of leg-banded adult willow ptarmigan observed in one spring returning to the breeding grounds the next spring at the Chilkat Pass, northwestern British Columbia. N = total number of birds banded the previous spring, and the G-test was used to test for difference in return rates between males and females.

	Males		Females			
Year	% Return	N	% Return	N	G	P
1980[1]	41	29	53.7	54	1.13	0.29
1981	48.1	27	42.5	73	0.25	0.62
1982	41.5	41	30.4	23	0.75	0.39
1985	50	36	42	50	0.53	0.47
1986	61	118	38.9	113	11.28	<0.001
1987	57.9	121	52.2	134	0.81	0.37
1988	63.4	82	50.9	102	2.85	0.09
1989	57.3	75	42.7	82	3.34	0.07
Combined probabilities during 1980-1989					32.76[2]	<0.01

[1] Return from spring 1979 to spring 1980.

[2] $-2\sum(\ln P)$ for 1980-1989; P value result of χ^2-test, df = 16 (Sokal & Rohlf 1981).

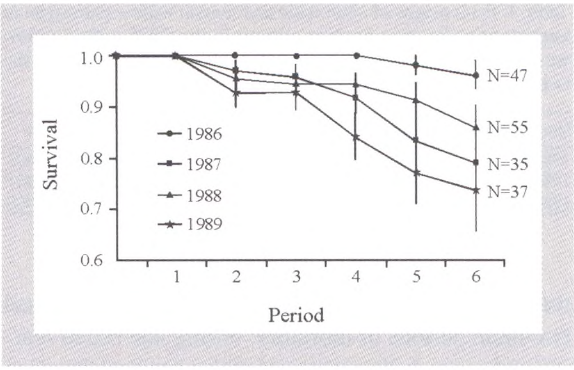

Figure 1. Kaplan-Meier survival estimates (±SE) of radio-tagged female willow ptarmigan during the six periods of the breeding seasons of 1986-1989 in the Chilkat Pass, northwestern British Columbia. The periods are: 1) early prelaying, 2) late prelaying, 3) laying, 4) early incubation, 5) late incubation and 6) prefledging.

24.0, df = 3, $P < 0.001$). In three of four years, periods of highest mortality occurred during the late prelaying, incubation and pre-fledging brood rearing periods (Fig. 1). Females that accompanied broods had higher mortality than broodless females: six of 23 females with broods died, whereas none of nine broodless females died ($G = 4.02$, $P = 0.04$; calculated for females from hatch until 15 September 1987 and 1988 combined). In both years all radio-tagged males survived the breeding season (1988: $N = 17$; 1989: $N = 27$).

During the breeding season the majority of identified kills of females were made by raptors (Table 3), although many predators were unidentified. The highest number of raptors sighted during the breeding season was in the early and late prelaying periods (Fig. 2). Mammal predation (primarily foxes) was lower but fairly consistent through the breeding season (see Table 3).

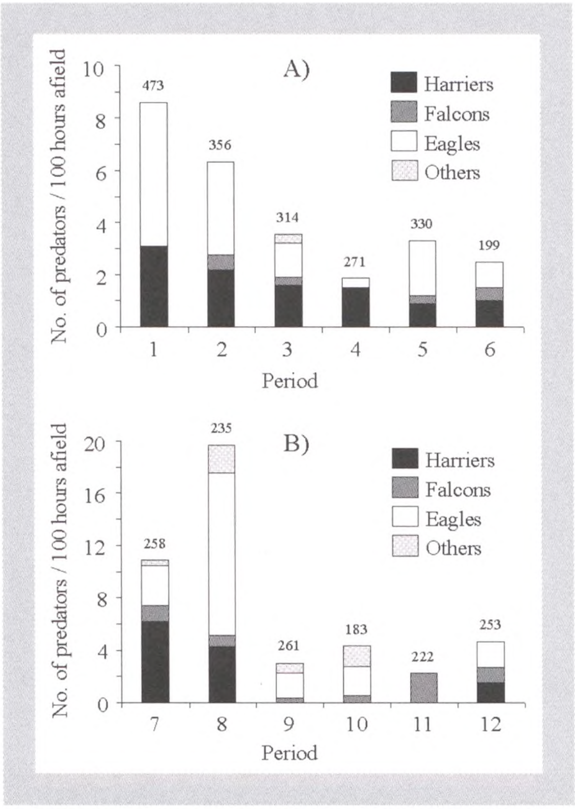

Figure 2. Numbers of raptors sighted per 100 hours afield during A) the six periods of the 1987 and 1988 breeding seasons and B) the six periods of the 1987-1989 non-breeding seasons in subalpine habitat in the Chilkat Pass, northwestern British Columbia. Numbers above bars denote hours of observation for each period. In A), the periods are the same as in Figure 1, and in B), the periods are: 7) brood rearing, 8) winter moult, 9) fall territoriality, 10) early winter, 11) late winter, 12) transient spring territoriality. Falcons include gyrfalcons and peregrine falcons, eagles include golden and bald eagles, others include goshawks, short-eared owls and unidentified raptors.

Table 3. Identity of predators of radio-tagged female and male willow ptarmigan during the breeding (1986-1989) and non-breeding (1987-1989) seasons in the Chilkat Pass, northwestern British Columbia.

	Females			Males		
Period	Mammal	Raptor	Unidentified	Mammal	Raptor	Unidentified
Early pre-laying	0	0	0	0	0	0
Late pre-laying	2	4	4	0	0	0
Laying	1	0	1	0	0	0
Early incubation	2	2	4	0	0	0
Late incubation	2	4	5	0	0	0
Brood rearing-pre-fledge	1	3	2	0	0	0
Total during breeding	*8*	*13*	*16*	*0*	*0*	*0*
Brood rearing post-fledge	0	6	1	1	3	0
Winter moult	0	0	1	0	1	0
Fall territoriality	0	0	1	0	0	0
Early winter	0	1	0	0	0	2
Late winter	0	2	2	1	0	1
Transient spring territoriality	0	0	0	1	2	1
Total during non-breeding	*0*	*9*	*5*	*3*	*6*	*4*
Grand total	8	22	21	3	6	4

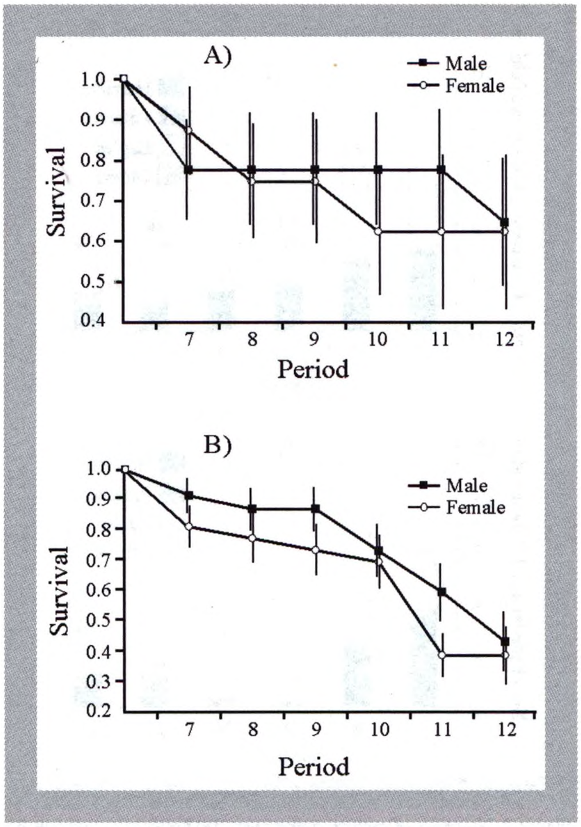

Figure 3. Kaplan-Meier survival estimates (±SE) of radio-tagged male and female willow ptarmigan during fall and winter periods of A) 1987/88 and B) 1988/89 in the Chilkat Pass, northwestern British Columbia. The periods are the same as those given in Figure 2B. For males N = 9 and 22 and for females N = 8 and 26 for 1987/88 and 1988/89, respectively.

Table 4. Percentages of adult male and female willow ptarmigan in hunting bags for three hunting seasons in the Chilkat Pass, northwestern British Columbia. N = total number of birds shot, and the G-test compares to a 1:1 sex ratio.

Hunting season	Males	Females	Unknown	N	G	P
1987/88	71.8	23.6	4.5	600	78.9	<0.001
1988/89	66.5	20.8	5.9	529	69.0	<0.001
1989/90	55.4	39.6	2.2	506	6.7	0.009

Mortality in autumn and winter

Total mortality of males and females during the autumn and winter did not differ in either year of the study (1987/88: $\chi^2 = 1.05$, df = 1, P = 0.29; 1988/89: $\chi^2 = 1.10$, df = 1, P = 0.27; Fig. 3), nor was there a significant difference in mortality rates between years (females: $\chi^2 = 0.66$, df = 1, P = 0.51; males: $\chi^2 = 0.63$, df = 1, P = 0.53). Overall, survival was lower in autumn/winter (40-60%) than in spring/summer (75-100%). In 1987/88 males had two main periods of mortality: during late brood rearing and again during transient spring territoriality (see Fig. 3). In 1988/89 mortality was highest through winter and early spring territoriality. All males killed during transient territoriality were off their territories.

For females in both years, mortality was high during the late brood rearing and winter moult periods (see Fig. 3), coinciding with the autumn raptor migration through the pass (see Fig. 2). Most of the ptarmigan that were killed during this period were killed by raptors (see Table 3). The second peak in mortality for females occurred on their wintering grounds, in early winter in 1987/88 and late winter in 1988/89 (see Fig. 3). Survival of females that moved to the boreal forest was not significantly different from that of females remaining in subalpine habitat (forest: survival = 0.50, SE = 0.11, N = 14; subalpine: survival = 0.71, SE = 0.13; N = 21; $\chi^2 = 0.70$, P = 0.48). Resident gyrfalcons were observed sporadically in subalpine areas throughout the winter (see Fig. 2). Tracks of foxes, wolves *Canis lupus*, weasels *Mustela* spp. and wolverines *Gulo gulo* were seen each winter, but mammals were sighted only sporadically. In the boreal forest, goshawks, great horned owls, coyotes and lynx were observed (R. Gruys, unpubl. data). No females were killed during the spring transient territoriality period (see Fig. 3).

Hunting mortality

More males than females were killed by hunters in all three hunting seasons from 1987 through 1990 (Table 4).

Table 5. Overwinter survival of radio-tagged and leg-banded willow ptarmigan during the winters of 1987/88 and 1988/89 at the Chilkat Pass, northwestern British Columbia. Only females with successful nests were included. N = total number of birds banded or radio-tagged, and the G-test was used to compare survival of leg-banded and radio-tagged birds.

	Females				Males			
Winter	Survival	N	G	P	Survival	N	G	P
1987/88								
Radio-tagged	0.50	6	0.49	0.48	0.65	9	0.20	0.66
Leg banded	0.67	21			0.59	95		
1988/89								
Radio-tagged	0.32	19	0.73	0.39	0.43	22	0.29	0.59
Leg banded	0.44	32			0.48	48		

Effect of radio transmitters on mortality

Overwinter survival of radio-tagged ptarmigan was not significantly different from the return rates of leg-banded birds to the study area (Table 5). In 1986, females that had been radio-tagged during the summer had a similar return rate the next spring as females that had been leg-banded only (radio-tagged: 34 of 54 returned; leg-banded: 30 of 55 returned; G = 0.79, P = 0.38).

Discussion

Mortality during the breeding season

Differential mortality between the sexes during the breeding season is usually attributed to differences in parental investment between the sexes (Trivers 1972). Male willow ptarmigan have higher amounts of investment than males of other grouse species, beginning in spring with defence of the territory and continuing until broods disperse (Wittenberger 1978). Despite this, male willow ptarmigan appeared to be invulnerable to predation once they had settled permanently on their territories. Females on the other hand incurred significant mortality during the breeding season, primarily from raptors. Males spend more time alert than females while on their territories (Bergerud & Mossop 1984), which may decrease their vulnerability to predation. In addition, by the late prelaying period, males are moulting rapidly into cryptic summer plumage and their territorial behaviour declines (Hannon & Wingfield 1990), rendering them inconspicuous. Although males accompany the brood and defend the chicks, they are less defensive than females (Pedersen & Steen 1985, Sandercock 1991). Interestingly, males and females of the conspecific red grouse *L.l. scoticus* in Scotland (Redpath & Thirgood 1997) and willow grouse *L.l. lagopus* in Sweden (Smith & Willebrand 1999) had similar survival over the breeding season.

Patterns of breeding season mortality in white-tailed ptarmigan *L. leucurus* were similar to those of willow ptarmigan in the Chilkat Pass: males had lower mortality than females (Braun, Martin & Robb 1993). Male white-tailed ptarmigan initiated molt into alternate plumage in spring prior to females, making them more cryptic. In rock ptarmigan *L. mutus*, however, spring predation of males is generally higher than for females (Gardarsson 1971, Nielsen & Cade 1990, Cotter, Boag & Shank 1992), occurring after males have established their territories. The difference between the three ptarmigan species may be related to availability of cover on the territories in spring or the conspicuousness of the male rock ptarmigan's white plumage when snow has melted (Montgomerie, Lyon & Holder 2001). Neither white-tailed nor rock ptarmigan males accompany or defend their broods.

Higher mortality for females than for males during breeding has been reported for other grouse species (e.g. Watson 1965, Braun & Rogers 1971, Angelstam 1984) and is likely related to the higher parental investment by females. Most of the mortality of female willow ptarmigan occurred during late prelaying, incubation and brood rearing. During the late prelaying period females are actively foraging (Hannon & Martin 1992), and their gonads are developing rapidly (Hannon & Wingfield 1990). Foraging in open tundra environments may put female ptarmigan at a high risk of predation (Wittenberger 1978, Bergerud 1988a). During incubation, females rely on cryptic plumage and behaviour to avoid predation, but females on nests often do not flush until a potential predator is very close, particularly during late incubation (S. Hannon, pers. obs.). Finally, prior to chicks' fledging, females stay closer to and defend the brood more aggressively and have lost a higher percentage of body mass due to incubation than males (Hannon & Roland 1984, Sandercock 1991). In concert, these may place females at a higher risk to predators than males. The rigours of chick rearing for females are also reflected by higher mortality of females with broods vs broodless females, a situation also documented for spruce grouse *Dendragapus canadensis* (Herzog 1979) and blue grouse *D. obscurus* (Sopuck 1979).

Mortality in autumn and winter

Differential mortality of the sexes in autumn and winter could be caused by the sexes wintering in habitats with different amounts of cover, different predation intensity and hunting pressure or by differences in body size and hence resistance to severe winter conditions. In willow ptarmigan, mortality was high for both sexes in autumn, when they were still on the breeding areas and this coincided with the autumn raptor migration and moult into winter plumage, a period of energetic stress (West 1968). Although females lost a higher percentage of body mass than males during incubation and early brood rearing (Hannon & Roland 1984), mortality of males and females was similar during this period. In addition, even though female body mass was lower than that of males, body mass of ptarmigan increases throughout the winter, suggesting that food is not limiting winter survival (Mossop 1988). Red grouse and willow grouse also had similar mortality between the sexes over winter in Scotland (Redpath & Thirgood 1997) and Sweden (Smith & Willebrand 1999), respectively. In these subspecies, males and females share wintering areas.

Ketterson & Nolan (1982) suggested that male birds, although they do not migrate as far as females, face more rigorous winter conditions, and hence mortality balances out between the sexes. Despite differences in distances travelled (60% of males moved up to 10 km and 60% of females moved up to 25 km from their territories), and differences in habitat, weather and predators (Gruys 1993), mortality of ptarmigan that moved to the boreal forest was not higher than that of birds in subalpine habitat, nor was natural mortality over winter different between the sexes. However, during the period of our study, numbers of snowshoe hares *Lepus americanus* in the boreal forest were increasing (Boutin, Krebs, Boonstra, Dale, Hannon, Martin, Sinclair, Smith, Turkington, Blower, Byrom, Doyle, Doyle, Hik, Hofer, Hubbs, Karels, Murray, Nams, O'Donoghue, Rohner & Schweiger 1995), and thus predators may have concentrated on the more numerous hares, reducing predation on female ptarmigan. Winter mortality of females may increase when numbers of hares decline and predators switch to ptarmigan wintering in the boreal forest (e.g. Hörnfeldt 1978, Angelstam, Lindström & Widén 1984, Keith & Rusch 1986). Interestingly, the three years with the lowest female return rates (1982, 1985 and 1986) were years of declining and low snowshoe hare numbers in the boreal forest north of our study area (Boutin et al. 1995).

Although natural mortality of males and females was similar over autumn and winter, males were more likely to be killed by hunters than were females. Most males remain in subalpine areas throughout autumn and winter and most of the hunting takes place in this area (Gruys 1991). Once females leave the breeding areas in early winter they experience little hunting pressure. Males predominate in the harvest of several grouse species (reviewed in Bergerud 1988b). The reverse situation occurs for blue grouse, where males migrate uphill in early autumn leaving females with broods more susceptible to hunting mortality at lower elevations (Zwickel 1982).

Males have a final period of increased mortality in early spring when they move from their wintering areas back to their territories in the more open breeding areas. During periods of bad weather they moved off their territories to more protected locations nearby (Gruys 1991). All males were killed in the latter areas, or in transit. Unfamiliarity with these protected areas may have resulted in higher predation risk to males at a time when spring raptor migration was occurring. In spring most females remained in their wintering areas longer than males, and did not settle on their territories until up to two weeks after males, when more snow had melted and cover was much greater on the breeding grounds (Gruys 1993).

Annual mortality and spring sex ratios

We have documented that natural mortality of the sexes in autumn and winter is similar, but that females have higher mortality during the breeding season, presumably owing to a higher risk of predation due to their higher parental investment. Annual mortality rates of leg-banded birds indicated that overall, males survived better than females, and although spring sex ratios were not statistically different from unity, there was a trend in most years for males to be more abundant. Spring sex ratios may be close to unity because of mortality that the males suffer during the hunting season or because we underestimated male abundance by missing non-territorial males.

Effect of radio transmitters on risk of predation

In order for our results to be valid, mortality could not be affected by radio transmitters. Except for a small number of birds that died soon after having transmitters affixed, survival did not appear to be influenced by transmitters. Both overwinter and annual survival of radio-tagged and leg-banded ptarmigan was similar. Average transmitter weight was below the maximum 5% of body weight recommended by Cochran (1980), and the radio was usually preened under the neck feathers with only the aerial visible. Thirgood, Redpath, Hudson, Hurley & Aebischer (1995) also found no effect of neck-mounted radio tags on red grouse survival. Thus we conclude that our data represent natural mortality rates for the population studied.

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