

# SOCIAL ORGANIZATION OF WILLOW PTARMIGAN ON THEIR BREEDING GROUNDS IN INTERIOR ALASKA

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An exploratory study of social organization in Willow Ptarmigan (*Lagopus lagopus alascensis* Swarth) in interior Alaska was carried out in spring 1970. The main aim was to examine possible roles of territorial behavior in the population dynamics of this migratory population. Some notes on food utilization and interactions between Willow and Rock Ptarmigan (*Lagopus mutus*) also were made.

The function of territorial behavior in the population processes of the conspecific but sedentary Red Grouse (*Lagopus lagopus scoticus* Lath.) in northeast Scotland is well understood (Jenkins and Watson 1970; Watson and Moss, in press). Territories are taken up in autumn and maintained throughout winter and spring until after the hens have laid. Most birds which fail to get territories in autumn die over winter from a variety of proximate causes, but a few survive and breed if opportunity arises to take over the territory of a deceased owner. In other words, territorial behavior is the cause of most overwinter mortality and limits the breeding population.

However, migratory ptarmigan do not appear to take up territories in autumn. They form flocks in winter and take up territories in spring only when they return to their breeding grounds (Weeden 1959). There is no suggestion in the literature that a noticeable proportion of nonterritorial birds exists in spring. Winter mortality cannot therefore be directly attributed to territorial behavior and limitation of the breeding stock presumably occurs by some other mechanism. What role, then, does territorial behavior play?

## STUDY AREA

The study was done in Porcupine Creek, some 10 km west of Eagle Summit in interior Alaska, from 17 April–22 May 1970.

The study area (fig. 1) consisted partly of a valley bottom with two parallel ridges of tailings derived from gold-mining operations, and part of the adjacent hillsides. The tailing ridges ran approximately east-west along the bed of Porcupine Creek, and were about 1 km

long, 50–75 m apart and 5–10 m high. Between them and abutting on the north tailing ridge were 10 roughly equidistant conical piles of tailings of about the same height as the ridge.

When I arrived on 17 April, the area was covered in variable amounts of snow up to 2 m deep and the creek was frozen. As the thaw progressed, the major part of the creek began to run between the conical tailing piles and the south ridge, with a smaller stream to the north of the north ridge.

At first, little vegetation was exposed above the snow on either hillside, but as the thaw progressed more *Salix pulchra* became available, and then ground vegetation including *Empetrum* sp., *Vaccinium vitis-idaea*, and *Vaccinium uliginosum* appeared. The thaw was most rapid on the north (south-facing) hillside.

*Salix* was the birds' main food, and Willow Ptarmigan occurred only where *Salix* was present. Its detailed distribution was therefore important; the main point is that there was much more *Salix* on the creek bed than on the hillside.

Between the ridges, sparse *S. pulchra* projected up to a meter or so above the snow which covered the creek bed. The ridges supported a good growth of mostly *Salix alaxensis* projecting up to 3 m above the snow, with some *S. pulchra*. The conical tailing piles were essentially bare of vegetation. Most of the two low-lying, ditch-like depressions where the hillsides joined the ridges supported a good growth of *Salix* in a belt a few meters wide. The belt next to the south ridge was mostly *S. pulchra*, but included some *S. alaxensis*, and was broadest (5–10 m) at the west end, in the territory of SY (fig. 1), progressively narrowing toward the east, where BS had his territory. One good patch of *S. alaxensis* occurred in this belt just to the south of the west gap in the south ridge, in the territory of WF. The belt adjacent to the north ridge was *S. pulchra* at the east and west ends but became a broad (10–15 m), lush mixture of *S. alaxensis* and *S. pulchra* for a distance of about 150 m adjacent to the gap in the north ridge, where the territory of WF adjoined that of WS.

Scattered, low *S. pulchra* occurred on the north hillside, being most common to the east and lower down in the territories of WS and T, and disappearing higher up. There was very little *S. pulchra* on the south hillside. Both hillsides were dominated by *Betula*

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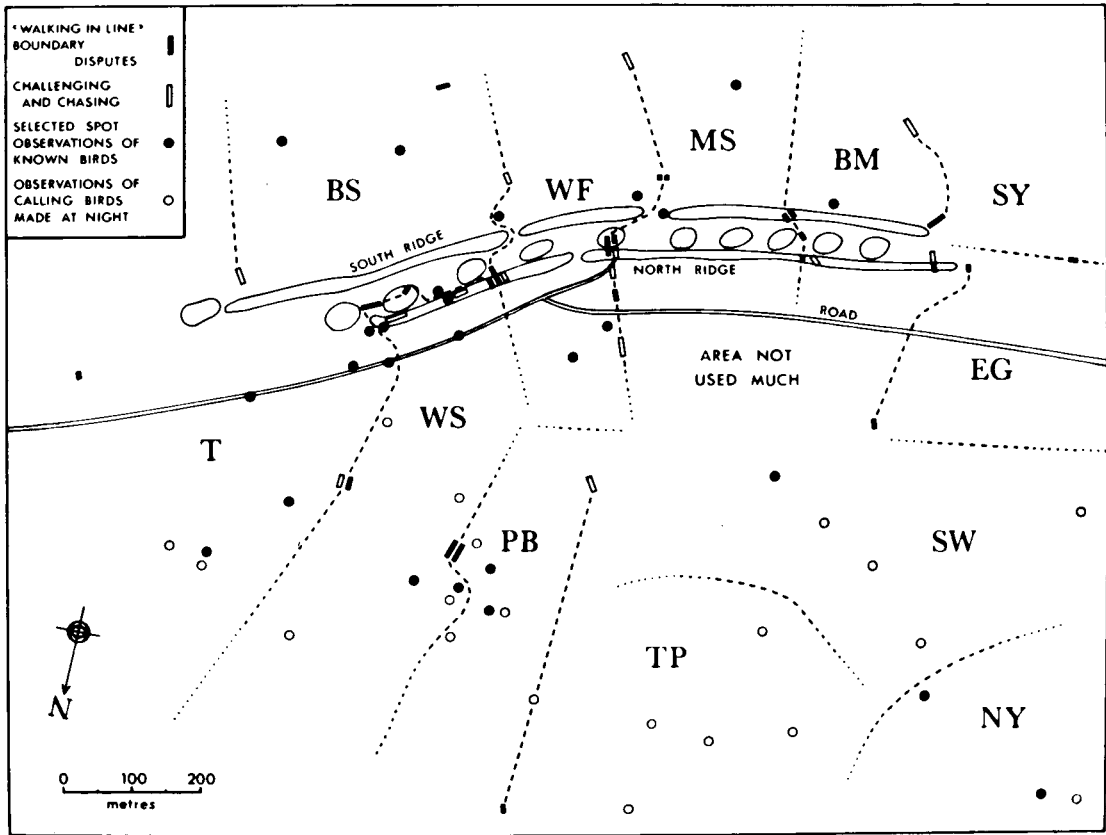


FIGURE 1. Willow Ptarmigan territories in Porcupine Creek, spring 1970.

*glandulosa*, which grew most lushly on the north. Small spruce (*Picea* sp.) occurred on the north hillside in scattered clumps of a few trees to the east and west of the area. A few larger specimens 10–15 m high occurred low down to the east in T's territory.

**METHODS**

Cocks which had territories in the creek bed were seen often; these were T, BS, WS, WF, BM, MS, EG, and SY. They were individually recognized by differences in plumage. Changes in plumage as the cocks molted were recorded by making field drawings and using binoculars and telescope. I spent less time on the north hillside and recognized cocks PB, TP, SW, and NY there as much by their positions as by their plumage. The initials denoting each cock were shortened versions of nicknames describing plumage or behavior e.g., WF was "white-face." Some hens were recognized for periods of a few days by transient features of molt.

Except for EG, cocks with territories in the creek bed were quite tame and took little notice of me, continuing their activities if I was more than 20 m or so away. Birds which had territories entirely on the hill were less tame (table 1).

It was not possible to keep all the study area in view at any one time. I had no set routine but went out at times when and to places where some activity was occurring or which seemed appropriate to solving a particular problem. A total of 149 hours in 34 days was spent in field observations.

Woody (i.e., noncaecal) droppings were collected from known birds and epidermal fragments of known plant species in samples of the droppings were counted using a slight modification of the method of Baumgartner and Martin (1939). This included 11 samples from birds feeding on the north hillside and 25 from birds feeding in the creek bed, from 29 April–22 May. No attempt was made to relate counts of food items in the droppings to proportions in the diet.

Many droppings had a white cap of urates at one end. The amount of urates in each dropping was visually rated on a scale of 1 (absent) to 4 (much).

**RESULTS AND DISCUSSION**

**MAINTENANCE OF TERRITORIES**

I did not describe postures and calls in detail. This has already been done for Red Grouse (Watson and Jenkins 1964) and I noticed

TABLE 1. Usual reactions of known Willow Ptarmigan to my presence.

Would not flush but walked away at approx.:	2 m	BS
	3–4 m	BM, MS, WF, SY, T
	7–10 m	EG, WS
Walked away at 50 + m and flushed at approx.:	5–15 m	PB, TP, SW
	30+ m	NY

little difference between the two subspecies. A difference in habits was that Willow Ptarmigan spent much time in the willow trees and adjacent territory holders often challenged each other by calling from the tree tops. Red Grouse seldom perch in trees.

Willow Ptarmigan held territories in much the same way as Red Grouse. I concluded that they were territorial because certain individual cocks were seen almost daily in the same restricted areas, where they were dominant over all other cocks and where they sang and called vigorously. No overlapping of territories was observed at any one time, but boundaries did change with time, after disputes between neighbors and as the total area utilized increased with the snow melt.

"Walking-in-line" disputes occurred at the same place on different days in five cases (fig. 1). On 13 occasions neighbors challenged each other by calling from a distance of a few meters at places where similar challenges, "walking-in-line" disputes, or other observations had already shown a boundary to exist. When I chased them on foot, three different pairs doubled back at places which I later confirmed as territorial boundaries by seeing neighbors disputing. It was a daily occurrence to see two neighbors sitting within sight of each other on either side of what was known from other observations to be their mutual boundary.

During the resurgence of territorial behavior in May (below), two disputes (WS vs. BS and BM vs. EG) were seen where boundaries that had been established in April changed. I inferred that this had happened in two further cases (MS vs. BM and one case off the study area).

The only occasions when one neighbor tolerated the intrusion of another were during three chases of nonterritorial cocks by neighboring cocks. This is also common in Red Grouse (A. Watson, pers. comm.). A typical example was on 13 May when BS spent 2 hours chasing an intruder. The usual sequence of events was that the intruder either landed in the open or dived into cover. BS had difficulty in finding the bird if it was in cover, as long as it remained still. As soon as it moved, or immediately if it had landed in the open. BS pursued it on the ground, usually silently, until they both took off again. The two cocks frequently landed on the neighboring territories of WF and WS, who were watching but did not interfere as long as the intruder was in sight. However, twice the intruder hid while BS landed in the open. BS was immediately chased off by WS.

#### ESTABLISHMENT OF TERRITORIES

In late March, I flew over Porcupine Creek in a light plane, seeing no sign of any ptarmigan in the study area and only one Willow Ptarmigan in the rest of the creek. On 17 April, there were numerous Willow and Rock Ptarmigan. This tended to confirm that the population was migratory, which is also well known locally (Weeden 1964).

The map of territories (fig. 1) indicates the final distribution of territory owners which evolved during the course of the study and had not yet stabilized when I first arrived. During the period 17–21 April, most of the creek bed was already being claimed by territory owners. There was no sign of any territorial behavior on the north hillside and the territories on the north hillside later claimed by PB, TP, SW, and NY had not yet been established.

BS, MS, BM, WF, and T were seen engaged in "walking-in-line" disputes at places which were later confirmed to be territorial boundaries, and all except T were seen in the company of hens and behaving as though paired. EG was present on his territory and was seen chasing another male off it, but I spent little time at the west end of the creek during this period, and could not say whether SY was present or not. WS was present but not behaving as though territorial, and a further nine observations were made of nonterritorial males which could have been explained by the presence of a minimum of three individuals. Patches of ground not covered by snow were visible on both north and south hillsides and were utilized by WF and MS, both with hens, and EG, as well as a minimum of one other unidentified cock.

On 23–24 April, 10 cm of snow fell, covering all the ground vegetation on both hillsides and leaving only trees and shrubs projecting. During a brief lull in the snowfall on 24 April, MS was seen to chase an unidentified cock some 200–300 m up the north hillside, where further "kohwa," "kohway," and "kohwayo" calls were heard, indicating either a chase or a boundary dispute. This was the first indication of any territorial behavior on the north hillside.

It was bright and clear on 25 April, the snow had stopped falling, and territorial behavior was briefly relaxed. This day and the next were the only days during the study when I saw groups of more than one cock, which possibly formed because of the fresh snowfall. Three recognized territorial cocks, including T and two of his neighbors who lived off the study area, were feeding with two hens in a

clump of *S. pulchra*. All three cocks had been singing on territory earlier that morning. Similarly, five cocks and one hen were seen in a loosely knit group feeding in *S. alaxensis* on the territory of MS. Both groups broke up when one cock started to attack the others. Meanwhile, WS was showing territorial behavior for the first time. I suspect that he was just establishing his territory.

By 26 April, all the birds which had territories that included part of the creek bed had established themselves, but some final details of boundaries had not yet been sorted out. On 25 and 26 April, territorial cocks were interacting on the north hillside, though I had no idea where the boundaries might be, nor how many birds were involved. From 26–29 April, boundary disputes involving BM, EG, MS, WF, and WS were seen.

On 29 April, areas on both hillsides were again snow-free and WF and WS extended their known mutual boundaries to some 50 m above the road on the north hillside, by flying up parallel to each other and calling. WF was also seen with a hen feeding on a newly snow-free patch of ground on the south hillside. Other observations indicated that all the creek territory owners extended their ranges as the snow melted during the next few days.

On 1 May, I observed the last boundary dispute (T vs. OC, who lived east of the study area), involving "walking-in-line" displays that I was to see for the next 10 days. In these 10 days, there was generally much less activity than before or after. Territorial boundaries were more or less settled and four cocks had established territories entirely on the north hillside. None of these four birds was very active during the day, so I spent the nights from 7–12 May plotting calling cocks on the north hillside. By the end of this period, it was light enough to see quite well all night and I observed that the calling males were accompanying females, which were feeding largely on shoots of *S. pulchra*. The male would occasionally sing spontaneously and sometimes fly off some distance, presumably to a territorial boundary, to answer the call of a neighbor, then return to the female, call and resume feeding. As it became lighter, the birds stopped feeding and settled down to roost. On at least three mornings, calling continued later and more vigorously from the creek than from the hillside.

On 13 May, activity again increased markedly and boundary disputes involving WS, WF, MS, EG, SW, and SY were seen. From 13–20 May, I saw 12 disputes, in which PB and TP also took part. However, by 20 May,

activity had decreased and on 21 May only six spontaneous ground songs were heard and on 22 May, only two. During these last few days BS, T, MS, WF, and BM were noted sitting quietly in the same places throughout the period of observation, and the females were not present. They were assumed to be sitting on nests.

The initial activity in April was associated with the settling of territorial boundaries. The period of little activity in the first half of May was when territories were established and enough snow had thawed for birds to live on the hillside without trespassing into the creek. The final period of activity occurred when the hens were thought to be laying, and I assume that its function was to ensure that each cock mated his own hen.

#### TRESPASSERS

There were two main classes of birds which trespassed on another's territory: (1) territorial birds from the north hillside which came down to the creek to feed; and (2) birds without known territories.

For example, PB and his mate were seen feeding on *S. pulchra* in the territory of WF on 1 and 3 May, and in the territory of BM on 5 May. On each occasion they were well out of sight of the territory owner. On 28 April, within a few minutes of each other, two unidentified cocks flew down from the north hillside to the north ridge. Here they had "walking-in-line" disputes with WF (twice) and WS, even though they were well inside the territories of the latter birds. One intruder returned noiselessly a few minutes after he had already been evicted twice and began to feed hurriedly on shoots of *S. pulchra*. When WF spotted the intruder, he gave chase on the ground. The intruder retreated but still continued to snatch mouthfuls of *S. pulchra* for a minute or so until finally evicted.

WS, PB, TP, SW, and NY had not yet set up territories on 17–21 April and so were temporarily nonterritorial. WS and at least three other nonterritorial birds were seen behaving quite boldly during this period, e.g., standing in full view, combs up, and calling. After 25 April all these cocks' territories were fairly well established and a class of cocks behaving in a fashion which had been noted only once earlier appeared. These birds were quiet, often lowered their combs, attempted to hide or froze when the territory owner appeared, and were ejected if found, sometimes being pursued for long distances. Activities of these nonterritorial individuals were observed on six different occasions—they were feeding five

times and roosting once. These observations could have been accounted for by a minimum of two birds and a maximum of four. Their behavior was very similar to that of nonterritorial Red Grouse (Watson and Jenkins 1964).

On 21 May, a known cock with a territory to the east of the study area chased another cock well over to the west of the study area, at a height of about 70 m and for a distance of at least 2 km. He returned to his territory alone. I presumed that the chased cock had no territory, partly because of the distance covered by the chase. At the same time another nonterritorial bird that was being chased by BS and neighbors was in view, so that at least two nonterritorial cocks were present at this time, when the hens were sitting.

#### HENS

Hens were more difficult to see than cocks because they were better camouflaged and their behavior made them less obvious.

Single hens were seen on four occasions in April. These could well have found mates. However, a strange hen was seen on the territory of WF on 13 May, in the presence of both WF and his mate. WF courted the new hen a few minutes after copulating with his mate. The strange hen took fright and flew off. WF pursued her onto the territories of MS and T successively. He returned alone. All the territorial cocks on the study area were mated and most hens were probably laying by this time, so it seems possible that the strange hen did not breed.

Hens were not seen disputing with each other on territorial boundaries, although on five occasions they watched the cocks' boundary disputes from close by, with every appearance of interest. Nor did they sing very often. I heard hens singing less than 10 times. Such songs were high-pitched versions of the cocks' song and presumably aggressive in function, as in Red Grouse (Watson and Jenkins 1964).

Every territorial cock in the study area was paired by the end of the study. One cock off the study area appeared to have two mates. Although every cock in the creek bed except T had been seen in the company of a hen by the end of April, they were frequently seen without hens up to about 10 May. From this time onward, cocks and hens were always in close proximity until the hens suddenly disappeared about 18–20 May, when I assumed they were sitting.

On 4 May, I watched T obtaining a mate. He was on watch at one of his usual lookouts when a hen landed on his territory some 200 m away. T flew over singing, landed near her,

ran a little closer, and began to court. After a minute or so, she flew again and landed, still on his territory; he followed and courted her again. I then lost sight of them, but T was always in the company of a hen, presumably the same bird, thereafter.

The banding data of Weeden (1959), from Chilkat Pass in British Columbia, showed that in 1958 some hens returned with the same cocks to the territories they had occupied in 1957.

#### INTERACTIONS BETWEEN ROCK AND WILLOW PTARMIGAN

There were many territorial Rock Ptarmigan on both hillsides and Willow Ptarmigan displayed on, and took grit from, the tailing piles and ridges, though they seldom fed there. Thus Willow and Rock Ptarmigan occupied territories on the same ground. Despite this, interactions were not very frequent between the two species and they usually ignored one another.

However, interactions between cocks of the two species did occur, varying from replying to a call to one violent physical combat. On each of the nine occasions where it was possible to decide, the Willow Ptarmigan dominated the Rock Ptarmigan, although four times the Rock initiated the dispute.

On five occasions Rock Ptarmigan cocks attempted to court Willow Ptarmigan hens and three times Willow Ptarmigan cocks attempted to court Rock Ptarmigan hens. In every case the hen flew off, in five cases joining a cock of her own species. No hen showed interest in cocks of the other species. It seems that hens are largely responsible for keeping the species separate, though interspecific aggression between cocks may also help. The hens' task is made relatively easy by the fact that the dark hood of cock Willow Ptarmigan looks completely different from the black eye-stripe of cock Rock Ptarmigan. The hens, on the other hand, are very similar. This situation in ptarmigan parallels that in sticklebacks, where the females are also responsible for choosing a mate of the correct species (Wilz 1970).

#### MOLT

In mid-April, the cocks still retained some white feathers covering the dark plumage on head and neck. By mid-May no white feathers were left on the hood and extensive dark patches had appeared on the mantle.

The hens were entirely white in mid-April, were molting around the neck at the end of April, and had completed their molt on head,

neck, and back by mid-May. Willow Ptarmigan were about a week to 10 days ahead of Rock Ptarmigan in molt and also in breeding condition (Ron Modafferi, pers. comm.). This is not usual because, according to R. B. Weeden (pers. comm.), breeding in the two species is generally synchronous at nearby Eagle Creek. Molt was synchronized to within 2 or 3 days in hen Willow Ptarmigan, with one notable exception. This was SY's mate whose head and neck were mostly brown but whose back was still 80% white on 22 May, when other hens were sitting. She was some 10-14 days behind the other hens in molt.

I noticed that hens kept closely to snow patches in mid-May while they were still largely white, stayed on brown, snow-free ground when they themselves had turned brown, and kept near the margins of melting snow patches when partly molted. This was especially noticeable on the north hillside, where there was considerably more bare ground than snow. The females were still largely white around 5-10 May.

#### PREDATORS

Goshawks (*Astur atricapillus*), Gyrfalcons (*Falco rusticolus*), Marsh Hawks (*Circus hudsonius*), Bald Eagles (*Haliaeetus leucocephalus*), Golden Eagles (*Aquila chrysaetos*), and a Short-eared Owl (*Asio flammeus*) were seen in the study area; red fox (*Vulpes fulva*) tracks were frequent; and a lynx (*Felis lynx*) was heard once. None of the territorial cocks was taken by predators during the study and no other Willow Ptarmigan kills were found, though one Spruce Grouse (*Canachites canadensis*) kill occurred in the study area. Spruce Grouse lived further down the creek only and signs indicated that this bird was chased up from below.

On three occasions, I was watching Willow Ptarmigan when they suddenly flew, once as far as 200 m, into thick cover, under bushes of *S. pulchra*. Each time I looked up to see a Goshawk. This was quite an effective defense, to judge by one occasion when a Goshawk came upon MS and WF in the middle of a boundary dispute. They dived into cover and the Goshawk fluttered ineffectually over the bush, unable to fly at them and apparently unwilling to approach on the ground. For about 10 min, he fluttered and perched nearby alternately, until I approached and he flew off.

Such thick cover was abundant in the creek bed but rare on the north hillside. This is an additional reason to those noted below for regarding the hillside as a habitat inferior to the creek bed for Willow Ptarmigan.

On the one occasion when I was watching a Rock Ptarmigan and a hunting Goshawk passed close by, its reaction was quite different. The bird froze and, when the Goshawk had moved on a little, slowly sidled further into the shelter of a rock and froze once more. This is the same method of defense described by White and Weeden (1966), who do not, however, distinguish between methods used by Rock and Willow Ptarmigan.

#### FOOD

In April, several birds were seen feeding on *S. alaxensis* catkins each day. By the first few days of May, this food was almost completely exhausted; the only catkins which remained were at the ends of long twigs which the birds were unable to reach. In May, most observations were of birds feeding on *S. pulchra*. They also took some birch and fed on the ground, taking the previous autumn's berries of *Empetrum* and *V. vitis-idaea*. This indicated that the Willow Ptarmigan preferred *S. alaxensis* to *S. pulchra*, which agrees with the conclusions of West and Meng (1966).

There was much less *S. pulchra* on the north hillside than in the creek bed. Furthermore, the amount of food available was especially affected by snow cover on the hillside, where the *Salix* was shorter and more easily covered than in the creek. I anticipated that birds feeding on the hillside should have a greater proportion of *B. glandulosa* in their droppings than birds feeding in the creek. In fact, there was no obvious difference in the proportions of epidermal fragments of *Salix*, *Betula*, and berries in droppings of the two classes of birds collected between 29 April and 22 May, nor was there any obvious difference between the sexes. However there was a significant ( $\chi^2 = 10.3$ ,  $P < 0.02$ , two-tailed test) difference in the amount of urates in the droppings of birds feeding in the two different areas. This would have occurred if the larger quantity of *Salix* in the creek bed had allowed the birds feeding there to be more selective of protein-rich parts of the plants.

#### CONCLUSIONS ON DOMINANCE IN RELATION TO PTARMIGAN DISPERSION AND FOOD

Territories were established in the creek, where all the preferred *S. alaxensis* and also most of the *S. pulchra* occurred, before they were established on the hill. Birds were seen being chased out of the creek on to the hillside on nine occasions but were never seen being chased off the hill into the creek. The four birds which had territories entirely on the

hillside were more nervous of my presence than those which owned some part of the creek (table 1). They also stopped singing and calling earlier in the morning than the creek birds, at least in the period 7–10 May. Ron Modafferi frequently reported seeing Willow Ptarmigan on hillsides both on and off the study area in 1970. He had not seen any Willow Ptarmigan in this habitat in 1969, when he had been doing exactly the same tasks.

At least one hill pair habitually trespassed into the creek in early May in order to feed, and of the six observations of subdominant, nonterritorial birds in the creek bed, five were seen feeding and two continued to feed even while being chased by the owners. Droppings collected from birds feeding on the hill contained less urates than those from birds feeding in the creek.

I interpret these observations to mean that the birds which established territories in the creek bed were more dominant than those which had territories entirely on the hill; that the hillside was poorer habitat than the creek, being occupied only when the population was larger than in 1969; and that birds which lived entirely on the hillsides had a poorer quality diet than those in the creek. Especially during early May, before the main thaw, there may have been a shortage of food on the hillside which caused the hill birds and nonterritorial birds to trespass into the creek.

According to present ideas (Watson and Moss, in press), nutrition of laying Red Grouse affects the survival and behavior of the young, and subsequent population processes. The preliminary observations in this paper indicate that the first preferred food was overgrazed by Willow Ptarmigan at high density, that less dominant birds may have been short of even the second preferred food at one time, and in any case had a lower protein diet than the more dominant birds. It seems likely that the plane of nutrition of the breeding population in 1970 was depressed by comparison with 1969. By analogy with present hypotheses about Red Grouse, this should have resulted in poorer breeding (not checked), the production of more aggressive young, higher overwinter mortality, and a subsequent decline in breeding densities in 1971. These ideas could form a basis for further study.

My observations do not allow precise assessment of the number of nonterritorial birds present but indicate that a small proportion of the population did not have territories. Only further work will indicate whether the

situation in Porcupine Creek in 1970 was typical of Willow Ptarmigan in other areas and at different densities. In this case, however, territorial behavior served two functions. It allowed the most dominant birds to utilize the territories which provided the best protection against avian predators and which contained the most food and the preferred food. Territorial behavior probably also excluded a small proportion of the population from breeding. This second point was not fully demonstrated since it was not shown that the nonterritorial birds were physiologically capable of breeding, but this seems likely by analogy with the fact that nonterritorial Red Grouse are capable of breeding if territory owners are removed (Watson and Jenkins 1968). The earlier occupation of the better habitat by the more dominant birds parallels the inference made by Kluyver and Tinbergen (1953) that Great Tits (*Parus major*) occupy the preferred deciduous forests before presumably less dominant birds colonize the poorer habitat of coniferous forests. Krebs (1971) also concluded that less dominant Great Tits occupied a poorer habitat. It seems intuitively obvious that one selective advantage of aggression is that it enables more dominant birds to occupy the better habitat. However, the present preliminary study is the first observation of such dispersal actually in progress.

#### SUMMARY

An exploratory study was made of social organization in a migratory population of Willow Ptarmigan on their breeding grounds.

A creek bed supporting a good growth of *Salix alaxensis* and *Salix pulchra* was occupied by territorial cocks before the adjacent hillside, where there was no *S. alaxensis* and less *S. pulchra* than in the creek bed.

*S. alaxensis* was the preferred food, but was completely exhausted by early May when the birds turned more to *S. pulchra*. The droppings of birds feeding on the hill contained less urates than those of birds feeding in the creek and it was inferred that their diet was poorer. Birds from the hillside trespassed into the creek in order to feed and were ejected when discovered by the territory owners.

From this and other circumstantial evidence, it was inferred that the hill cocks were less dominant than the creek birds and had been forced into the poorer hillside habitat by territorial competition. This habitat had not been occupied in 1969, when numbers in the area as a whole were inferred to have been lower.

A few nonterritorial cocks and possibly one unmated hen were present. These birds probably did not breed.

Rock and Willow Ptarmigan occupied territories on the same ground. On the few occasions when cocks of the two species interacted, the Willow Ptarmigan were dominant. Cocks of both species attempted to court hens of the other species, who usually flew off.

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