THE "SNOWSHOE EFFECT" OF THE FEATHERING ON PTARMIGAN FEET

E. O. HÖHN

As long ago as 1833, J. A. Naumann (Naturgeschichte der Vögel Deutschlands. Ed. by J. F. Naumann. E. Fleischer, Leipzig. 6:391) suggested that the dense feathering on the feet of ptarmigan in winter serves to reduce sinking of the feet in snow and to provide them with thermal insulation. In Willow Ptarmigan (*Lagopus lagopus*) I found that the feathers on the sole of the foot have long, branched downy barbs, as illustrated in Figure 206 of Lucas and Stettenheim (Avian anatomy. Integument. U.S. Dept. Agr., Agr. Hdbk. 362, 1972). Those on the dorsum of the foot are long semiplumes, as illustrated in Figure 188 of the same work, while broader semiplumes grow on the tarsometatarsus. These modified feathers enlarge the area of the foot as do the fringing scales on the sides of the toes of grouse in winter, but they are entirely different structures from the latter.

Neither of the functions attributed to foot feathering in ptarmigan has been tested. Moreover, they were regarded as "children's book errors" in a recent book review (E. S. Austin, Auk 98:871, 1974). In correspondence, Austin informed me that the adaptive value of foot feathering in ptarmigan had been suggested in a book for children by E. Thompson Seton, published in the early nineteen-hundreds. In view of these circumstances, I decided to test the snowshoe effect of winter ptarmigan foot feathering. I have not investigated the equally plausible thermal insulation function of these feathers.

FIGURE 1. Ventral aspect of a winter (left) and early summer (right) foot of a Willow Ptarmigan.

I have compiled (Table 1) some published data on the area of the supporting surface of the foot in ptarmigan and other gallinaceous birds that are less able to walk on snow. With them, I present my measurements of the surface of the intact and plucked winter feet of the three species of ptarmigan. The

TABLE 1. Bearing area and load per unit surface of foot in ptarmigan and some related species.

Species, Locale, Date[a]	Body weight (g)	Surface area of foot (cm²)		Load (g/cm²)		Source, if not author's data
		Feathered	Plucked	Feathered	Plucked	
Willow Ptarmigan (*Lagopus lagopus*)						
Russia and Siberia, winter	675	23–25	—	14–15	—	Formozov
N Alberta, November	600	12.2	3.9	25	77	
N Alberta, early December	600	14.9	3.2	21	94	
N Saskatchewan, early April	510	13.0	—	19.6	—	Westerskov
Rock Ptarmigan (*Lagopus mutus*)						
N.W. Territory, early June	525	6.1	1.5	43	175	
White-tailed Ptarmigan (*Lagopus leucurus*)						
Colorado, early May	330	7.9	2.2	41.8	150	
Ruffed Grouse (*Bonasa umbellus*)[b]						
Alberta, November	582	8.3	—	35	—	Westerskov
Alberta, November	665	7.6	6.5	87.5	120.3	
Gray Partridge (*Perdix perdix*)						
Alberta, November	390	4.1	—	47.6	—	Westerskov
Russia, winter	460	4.5–5	—	40–41	—	Formozov

[a] Dates indicate when the specimen was taken.
[b] In Ruffed Grouse, "feathered" means the intact foot and "plucked" the foot after removal of the toe bristles.
References: Formozov, S. N., citation in text. Westerskov, K. 1965. Winter ecology of the partridge in the Canadian prairie. Proc. N.Z. Ecol. Soc. 12:23–30.

FIGURE 2. Dorsal view of a Willow Ptarmigan foot in winter condition.

FIGURE 3. Ventral view of a Willow Ptarmigan foot in winter condition.

enlargement of the foot area by the feathering is evident. Furthermore, a unit area bears much less weight in a feathered ptarmigan foot than in a plucked foot or one merely widened by fringes of papillae on the toes as in the Ruffed Grouse (*Bonasa umbellus*) or one without any adaptation to snow as in the Gray Partridge (*Perdix perdix*).

The area of the ptarmigan foot in winter is enlarged not only by feathers but also by longer claws. In Willow Ptarmigan the average length of the claw of the middle toe is reported to be 17 mm in winter but only 9 mm in summer [S.N. Formozov, Snow cover as an integral factor of the environment and its importance in the ecology of birds and mammals. 1946. (Eng. transl., 1963, Boreal Inst., Univ. Alberta, Edmonton, Canada, Occas. Publ. No. 1:48–49)]. My measurements of this claw in several Willow Ptarmigan show less seasonal difference. In birds collected January to March the average length was 16.3 mm (8 males) and 18.2 mm (12 females), while in those collected July and August it was 12.7 mm (4 males) and 11.7 mm (4 females). The claws are still long in June because they are shed in early July. Formozov's low summer measurement appears to have been based on birds that had just shed the old claws. My measurements indicate that claws are about 30% longer in winter than during most of the summer. Even allowing that the claws of all three forward-pointing toes are involved, increases in claw length appear to make only a modest contribution to enlargement of the foot surface in winter.

TABLE 2. Depth of footprints of the feathered and plucked foot of individual ptarmigan and of the intact and debristled foot of a Ruffed Grouse.[a]

Species Date of collection	Load	Depth of footprint below surface, mm		Remarks
		feathered	plucked (or debristled)	
Willow Ptarmigan				
early December	322[b]	3–4	6–7	
	611[c]	20	30	In snow
	611[c]	0 (did not break surface)	18	from same fall 20 h. apart
Rock Ptarmigan				
early June	250[b]	14	22	
White-tailed Ptarmigan				
early May	185[c]	6	10	
	361[c]	15	24	
Ruffed Grouse				
late November	621[c]	12	28	

[a] Ruffed Grouse, though similar to Willow Ptarmigan in body weight, have longer toes; distance from tip of mid-toe claw to that of hind toe 7 and 5.8 cm, and the spread between tips of claws of lateral toes 6.2 and 5.2 cm, respectively.
[b] Foot loads close to half the bird's body weight.
[c] Foot loads close to the bird's full body weight.

I realized how efficiently ptarmigan can walk on soft snow during an attempt to capture some Willow Ptarmigan near Lake Athabasca in March. The birds, walking quite leisurely and leaving tracks only about 15 mm deep, easily kept ahead of my companion and me. Wearing only boots, I sank in the snow to mid-thigh, while he, wearing my snowshoes (small for his size), fared little better.

To find the degree to which foot feathering reduces sinking in snow, I placed on snow an intact and a plucked foot of each of the three species of ptarmigan. Some of the feet were first softened by immersion in water so that the toes could be flexed perpendicular to the tarsometatarsus and then dried in this position. A (weighed) "wall" of modelling clay between the dorsum of the middle toe and the front of the tarsometatarsus supported a (weighed) piece of cardboard placed horizontally and slotted to admit the tarsometatarsus. Weights were placed on the cardboard and the depth that the foot sank in the snow was measured (Table 2). As the tests were spread over a period of time, the consistency of the snow probably varied on different occasions; only comparisons between a feathered and an unfeathered foot under the same load are valid. The comparisons of feathered and unfeathered feet do not allow for the (probably small) contribution to the snowshoe effect of the longer winter claws, for claw lengths were identical in the feathered and plucked feet.

The data show that sinking in snow is reduced to about one-half by foot feathering with loads up to about half the bird's body weight i.e., the load carried when standing on both feet. The values for Willow Ptarmigan suggest that the effect may be even greater in snow of a certain density when, as in mid-stride, one foot carries the bird's full weight.

Foot feathering clearly increases the bearing surface of the foot by about four times and reduces sinking of the foot in snow by about half. The demonstrated snowshoe function of the foot feathering surely is adaptive, for it must inevitably reduce the energy required for all leg movements on snow.

Department of Physiology, University of Alberta, Edmonton, Alberta, Canada T6G 2H7. Accepted for publication 5 July 1976.

SNOW COVER AND THE USE OF TREES BY SPRUCE GROUSE IN AUTUMN

DANIEL M. KEPPIE

Spruce Grouse (*Canachites canadensis*) in autumn shift from a summer diet of foods taken mostly from the forest floor to a winter diet of conifer browse. Zwickel et al. (Condor 76:212–214, 1974) reviewed the data on this changeover and concluded that it occurs long before snow cover makes herbaceous food unavailable. These authors suggested four reasons for the early change in diet: (1) the shift must be gradual; (2) alternative foods decline in quality or quantity; (3) there is a change in preference; or (4) some behavioral change occurs, unrelated to food, which results in birds spending more time in trees than on the ground.

Relevant to this last possibility, I investigated whether snow in autumn affects the tendency of Spruce Grouse (*C. c. franklinii*) to spend more time in trees. Previous work on dietary change used only crop analyses and did not document snow conditions. This report augments data of earlier workers by documenting snow conditions and site selection (tree or ground) over the period that dietary change occurs.

METHODS

Data presented are proportions of Spruce Grouse found in trees from 1 August until the start of winter, 1970–72. I use the percentage of birds found in trees as an index of time spent in trees. The work was conducted in Lodgepole Pine (*Pinus contorta*) forest, about 1,750 m altitude, 27 km W of Turner Valley, Alberta. Pointing dogs were used to locate most grouse; I saw no evidence that they did not find birds in proportion to where the birds were, i.e. in the trees or on the ground. Data are omitted if the original site of the bird was in question. All sex and age categories of grouse sighted are combined. The amount of snow cover was recorded at each site a bird was found. Differences between numbers of birds in trees and on the ground were tested for statistical significance with 2×2 contingency tables (G test where appropriate). Significant differences are at least at the 0.05 level.

RESULTS AND DISCUSSION

The earliest dates of complete and lasting snow cover were 10 November, and 17 and 1 December, 1970–72 respectively. But Spruce Grouse were making increased use of trees as early as September (Fig. 1). With two exceptions (August to September, and October to November 1970), changes in birds in trees between successive months were significantly different. Temporary snow cover occurred periodically each autumn. In 1970, 23 cm of snow fell on nine separate days and covered the ground for ten days; in 1971, 88 cm of snow fell on 20 separate days and covered the ground for 47 days; in 1972, 74 cm of snow fell on 16 separate days and covered the ground for 42 days.

Data were analyzed to determine if the increased frequencies of birds in trees in early autumn, over low frequencies in late summer, were related to the beginning of snowfall. Proportions of birds in trees in August versus those in trees in September before the first snowfall (11, 20 and 7 September 1970–72 respectively) were:

	1970	1971	1972
August	6%	5%	5%
September	3%	3%	6%
χ^2	1.64	0.20	0.68
	$P > 0.05$	$P > 0.05$	$P > 0.05$

Hence, the significant increases of birds in trees from August to September in 1971 and 1972 occurred only after the first snowfall. The difference between August and September (whole months) for birds in trees was smallest in 1970, when the fewest days of snow cover in September occurred (9%; 25–26% in 1971 and 1972).

I then examined whether birds were in trees more frequently on days when snow covered more of the ground. The extent of snow was categorized daily