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Research article

Twig selection on mountain birch *Betula pubescens* by winter-feeding willow grouse *Lagopus lagopus* in a subarctic forest

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In a subarctic forest at Kvaløya, northern Norway, willow grouse *Lagopus lagopus* fed at snow level by clipping bits of twigs from mountain birch *Betula pubescens* during winter. Birch has two types of twigs ending in a terminal bud: long twigs with a smooth bark, and short twigs with rings of thicker bark. The grouse selected ringed twigs above smooth twigs despite a surplus of smooth twigs in the forest. Ringed twigs had more bark cm⁻¹ of twig length and a higher relative bark/wood ratio than smooth twigs. Smooth twigs had growth nodes that increased in diameter inwards from the tip. Because of the non-linear relation between the area and the circumference of a circle, the bark/wood ratio decreased for each node. Although being able to clip much thicker twigs, 90% of smooth twigs clipped by grouse were ≤ 2 mm in diameter. It is concluded that willow grouse fed optimally on birch in winter by selecting twigs to minimize fibrous wood intake.

Keywords: bark/wood ratio, Fennoscandian birch forest, twig diameter, twig type, winter ecology

Introduction

Willow grouse *Lagopus lagopus* has a wide circumpolar distribution, wider than any other grouse species (Johnsgard 1983). The northern forest regions of both continents are its main environment. This species of grouse lives on shrubby tundra and in open woodlands with heaths, moors and peatbogs; and sometimes above the tree line (Johnsgard 1983). In winter, many of the Eurasian populations move into more wooded cover. Forests, mostly with mountain birch *Betula pubescens*, is the typical winter habitat in Fennoscandia (Höglund 1981, Pulliainen and Iivanainen 1981, Brittas 1988, Pedersen and Karlsen 2007).

The Fennoscandia forests have challenging winter climates with low temperatures, short days and snow cover for long periods. Willow grouse are physiologically adapted to consume bulky winter food by overall increased intestinal length (Moss 1974, 1997). They mostly feed at ground level, and low-ground *Vaccinium*/*Empetrum* shrubs are important food throughout the year as long as they are available (Brittas 1988,



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Moe and Bjune 2009), but snow cover reduces the accessibility to this food in winter. During winter, they primarily feed on twigs, catkins and buds from shrubs and bushes of tree species, mainly willow (*Salix* spp.) and birch (*Betula* spp). In Ontario, Canada, Thomas (1984) found that willow stems and buds made up nearly 70% of the diet in winter. In three wintering areas in Labrador, Canada, willow was also the most prominent food item (Elson et al. 2007). Related results were reported from Alaska, USA, where over 90% of the winter food was from willows (Weeden 1969, Moss 1991). From eastern Siberia, Andreev (1991) found that a daily ration of 60 g dry weight of mostly willow buds and twigs was needed to meet the energy demands in cold winters. From Yakutia in Siberia, Isaev and Borisov (2016) reported a preference for willow towards the north and the mountains. For most of its vast distribution area, therefore, willow bark and buds are the most important winter food for willow grouse. Willow is also the dominant food north of the polar tree line in Norway (Ehrich et al. 2012) but, in the subarctic Fennoscandian birch forest, several studies have found that twigs from mountain birch are the main winter food (Rajala 1966, Myrberget 1979, Uotila et al. 1980, Helle 1981, Pulliainen and Iivanainen 1981). In a six-year study in western central Sweden, Brittas (1988) also found that willows were preferred if available, but they were covered by snow in most winters and mountain birch was the main food, always making up > 70% of the crop contents.

Mountain birch (*B. pubescens* var. *pubescens*) is the dominant deciduous tree in the northernmost forests of Fennoscandia (see taxonomic and ecological treatment by Ashburner and McAllister 2016). Willows and rowan (*Sorbus aucuparia*) also occur, as do aspen (*Populus tremula*) and alder (*Alnus incana*) in some areas, but birch dominates these forests. Scots pine (*Pinus sylvestris*) is found inland and in some coastal valleys, and Norway spruce (*Picea abies*) is common south of the birch forest. In the northernmost Norway, Sweden and Finland, birch woodland without conifers is the main forest type. Birch grows from sea level to the alpine tree line except for the eastern part of Finnmark county where it sets the polar tree line against the tundra. Further east, from the Russian Kola Peninsula, the Siberian taiga takes over as the dominant forest type, and mixed coniferous forests are also typical in North America. The subarctic birch forest without conifers is therefore unique for Fennoscandia, and it gives the landscape a distinctive character found nowhere else (Ashburner and McAllister 2016).

Within the subarctic birch forest, analysis of crop contents shows that birch twigs are the main food for willow grouse during extended periods of the winter (Myrberget 1979). These forests have a mixture of higher trees, bushes and low-ground shrubs. Because the heights of the shrub and bushes vary from below one to several meters, willow grouse find food irrespective of the snow depth. They dig into the snow for cover (Höglund 1981, Steen 1989, Moss 1997, Pedersen and Karlsen 2007) but usually not for food, although they can take dwarf shrubs and berries if the snow cover is low (Brittas 1988, Pedersen and Karlsen 2007). They may sit in trees in

winter to roost or eat catkins (Myrberget 1979, Pulliainen and Iivanainen 1981), but most often they avoid sitting high up (Brittas 1988), possibly because this exposes them to predation (Pedersen and Karlsen 2007). Their feathered feet may explain observations that they appear clumsy when sitting in trees (Höglund 1981). Höglund (1981), Pulliainen and Iivanainen (1981) and Brittas (1988) observed that catkins are made available at snow level when heavy snow loads bend down the top branches or when snow depth increases the ground level access to upper branches. Catkins are high in protein and digestibility (Brittas 1988), are preferred by grouse (Pulliainen and Iivanainen 1981, Pedersen 1991) and are consumed all winter at some sites (Pulliainen and Iivanainen 1981, Brittas 1988). However, annual and seasonal availability of catkins varies (Brittas 1988, Ranta et al. 2008) and catkins may be a less predictable winter food source than twigs. For example, access to catkins may be limited in northern coastal forests where strong winds frequently remove snow off the trees, preventing bending of branches that grouse can reach. This was the case in the present study area on Kvaløya even with the heavy snowfall in the winter of 2019–2020. Grouse are observed to fly between patches of bushes and then walk on the snow, often for long distances, to find twigs to browse (Steen 1989). When found, they use their beaks to take twigs up to the highest level they can reach. The area of foraging occurs within about a half meter above the snow surface and therefore varies along the height of the bushes as the snow level fluctuates during winter.

Willow grouse have the largest beak of the *Lagopus* species (Weeden 1969) and can clip birch twigs up to 4–5 mm thick. Up to 1 cm bits are cut from the twigs (Steen 1989, Pedersen and Karlsen 2007), stored in the crop and debarked in the gizzard (Höglund 1981) before being further digested. As digesta leaves the small intestine, the liquid fraction enters two long caeca where microbial breakdown takes place (Johnsgard 1983, Gudmundsson 2015). The fibrous fraction is rapidly voided through the colon (McBee and West 1969, Moss 1997). Pure cellulose can be digested by microbial communities in the grouse intestines, but lignin binds to structural cellulose and makes it less digestible (Chesson 1983) and lignin itself is indigestible (Steen 1989). They continue to process food while asleep at night (Moss 1997) and many characteristic, slightly curved faecal droppings are left in the overnight snow digs when the grouse leaves in the morning (Steen 1989, Pedersen and Karlsen 2007). Höglund (1981) did a meticulous analysis of the contents of such droppings collected in a birch forest area in Sweden. They were about 27 × 7 mm and contained high numbers of woody pieces of twig about 6 mm long. They had been effectively debarked and no remnants of bark were found among them in the faeces, only wood. This study shows that the wood of the consumed birch twigs had passed for a large part undigested through the gut system while the bark had been digested. The same is noted by Steen (1989) and Pedersen and Karlsen (2007).

Birch has two distinct types of approximately cylindrical twigs (see a detailed morphological description in Ashburner and McAllister 2016). The first type has long annual shoots

with a smooth and thin bark. Smooth twigs have several growth nodes that are separated by buds and get progressively thinner towards the outer (first) node and the terminal bud (Fig. 1). The second type are short perennial twigs with tightly packed, 1–2 mm wide rings of thick bark (Fig. 1). Ringed twigs vary little in thickness and have no growth nodes separated by buds, just a terminal bud (Fig. 1). Some birch branches have more smooth twigs, some have more ringed twigs and some have an even mixture. Because of the thick bark, ringed twigs are predicted to have a higher bark/wood ratio than twigs with smooth bark. In smooth twigs, the bark/wood volume ratio varies non-linearly with the diameter of the twig because of the relation between the circumference, $2\pi r$ and the area, πr^2 , of a circle. As an example, given bark 0.2 mm thick, a twig 1.5 mm thick would have about 5 times more bark in relation to wood than a twig 4.5 mm thick. Willow grouse forage on both types of birch twigs (Myrberger 1979). Brittas (1988) found that the ringed and smooth twig types (short and long shoots, respectively, in his terminology) had the same level of protein but that smooth twigs had more fat and fibre than ringed twigs. For browsers that feed on birch in winter, wood fibre imposes a handling cost in terms of a large proportion of indigestible material in the gut system (Palo et al. 1992). Assuming bark is more digestible than wood (Höglund 1981), and because the relative amounts of bark and wood vary with twig type and twig diameter, we hypothesized that willow grouse would select twigs with as much bark as possible and as little wood as possible when feeding on birch during winter. This hypothesis was tested by assessing two predictions. As ringed twigs have thicker bark than smooth twigs, the first prediction is that willow grouse will select more ringed twigs than smooth

twigs from the birch bushes. Based on the non-linear decrease in the bark/wood ratio with increasing twig diameters, the second prediction is that willow grouse feeding on smooth twigs will select a smaller diameter than they are able to clip from the birch bushes.

Study area and methods

The study was done in a birch forest on the island of Kvaløya in Tromsø, northern Norway, in the winter of 2019–2020. This was a long winter with continuous snow cover from October to June and snow depths up to nearly 2 m in April. Observations and sampling were done in two areas. The first area, Langeidet, is located at 69°41'N, 18°46'E (midpoint UTM 34WDC140328) near the suburbs Oladalen and Storelva. It is a wide, relatively flat area with low hills of birch woodland interspersed with small bogs and ponds, stretching for about 1 km in all directions at 20–30 m a.s.l. The second area, which we termed Djupelva, is located about 1.5 km farther east, at 69°41'N, 18°50'E (midpoint UTM 34WDC159329), uphill from Strand and Kvaløysletta. It is an area of continuous birch woodland about 1.5 km long and 600 m wide on the hillside of the mountain Finnlandsfjellet. The section of this area where most of the field work was done is partly flat and partly gentle slope at 70–100 m a.s.l. on both sides of the stream Djupelva. Birch bushes were very abundant in both areas and a few shrubs of rowan and willow were also present. The treeline is at 200–300 m elevation. Small groups of willow grouse, numbering from 1–2 up to 7–8 birds, stayed in both areas throughout the winter.

The field work was done from February to May 2020, and four methods were applied: 1) estimating the proportions of ringed and smooth twigs on unbrowsed birch bushes, 2) counting and measuring diameters and lengths of twigs on unbrowsed bushes, 3) measuring diameters of twigs browsed by grouse and 4) weighing bark and wood from twigs on unbrowsed bushes. The location and sampling of material of browsed bushes was done in both areas to obtain as large an amount of material as possible. Unbrowsed bushes were always available in excess in both areas, but for practical reasons location and sampling of material of these bushes was done only in the Djupelva area.

On three dates in March 2020, the proportions of the two types of twigs were estimated in two ways: by taking random walks (method 1) on skis to estimate the occurrence of the twig types on individual bushes and by direct counts (method 2) of twig types on branches from different bushes. In a random walk, three types of bushes were recorded: those dominated (defined as 60% or more) by ringed twigs; those dominated by smooth twigs; and those with relatively equal proportions of twig types. Each bush was selected from a distance (50–100 m) to avoid seeing the proportions of twig type on it beforehand. Assigning the bush type was then done by walking up and estimating the occurrence of twig types. A random walk was stopped at 30 bushes and 11 walks gave a total of 330 bushes. Numbering all twigs of both kinds were

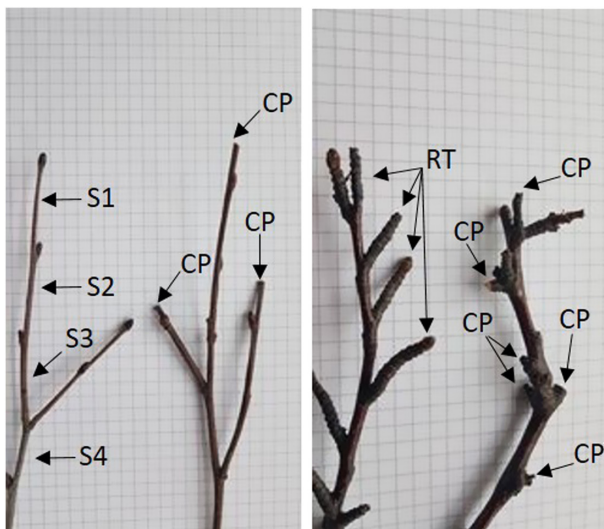


Figure 1. The willow grouse fed by clipping bits from smooth (left panel) and ringed (right panel) twigs of mountain birch at Kvaløya in winter 2020. Each panel shows unclipped (intact) twigs (left side, with S1–S4 indicating smooth twig nodes and RT indicating ringed twigs) and twigs clipped by grouse (right side, with CP indicating clipping points). The background squares are 5 × 5 mm. Photo: Sidsel Grønvik.

done in the lab on 20 branches that had been cut from randomly selected unbrowsed bushes; these were chosen from a distance to avoid bias. Another set of unbrowsed bushes was chosen in the same way, and randomly selected branches were taken to the lab where lengths and midpoint diameters of 150 ringed twigs and 150 of each of the four outer growth nodes of smooth twigs were measured with callipers to 0.1 mm accuracy (see typical examples in Fig. 1).

Bushes that had been fed on by grouse were found by following tracks on the snow (method 3). When found, the height above the snow of the highest twig that had been clipped was noted. All branches with clipped twigs were cut off and brought in for measuring. As loose twig bits were never found on the snow, the twigs had been completely eaten from the tip and inward to the clipping point. However, similar to other studies (Myrberger 1979, Steen 1989), we often found that buds from the twigs that had been clipped by grouse were discarded on the snow and not consumed. Bushes from seven localities, three in area Langeidet and four in area Djupelva, were sampled between late February and late March 2020. In the lab, the diameters of twigs that had been clipped by grouse were measured with callipers at the clipped point. All twigs of both types that had been clipped were measured on each branch. The bits that grouse clipped from smooth twigs became thicker inwards along the twig length. The diameter at the clipping point, therefore, shows how thick the twig is when a grouse stops browsing and selects a new twig.

Material from 15 samples of ringed twigs, and 15 samples of each of the four growth nodes of smooth twigs, were cut from branches taken in May 2020 (method 4) when there was still snow on the ground. As the leaf buds were unfolded, the twigs had not started to grow. The bark and wood were dry and hard, similar to what was observed in mid-winter, but the bark sleeves were easy to slit off with a fine-pointed scalpel at this time. Each sample had 10 lengths of twigs that were measured with callipers for diameters and lengths. The bark thicknesses of 15 sleeves from ringed twigs, and 15 sleeves from the thinnest node (1) and the thickest node (4) of smooth twigs were measured before the material was frozen at -18°C in clip-sealed polythene bags. The bark and wood in each sample were later weighed on a Salter micro-scale with an accuracy of 0.1 mg. The bark/wood ratios were calculated from these weights, and the weights of bark and wood per cm^{-1} of twig length were calculated by dividing the sample weight by the sum of the twig lengths in the sample.

Chi-square tests (χ^2) were used to test for differences in the frequency of twig types (ringed versus smooth twigs) in the random walks, and for comparing their numbers in unclipped bushes and in bushes browsed by grouse. We used the nonparametric Mann–Whitney U-test for differences in mean numbers of twig types on branches of unbrowsed birch bushes, and for differences in mean numbers of twig types on bushes that were clipped by grouse. To investigate the differences in twig diameters between clipped and unclipped twigs for the two twig types, and to compare diameters and lengths between the different nodes of smooth twigs, we used the parametric t-test as the data were normally distributed

around the mean. Additionally, the parametric t-test was used to test for differences in the weight of bark and wood for the two twig types and the different nodes of smooth twigs. We first checked the data for homogeneity in variance between groups using a Levene's test ($F=1.3274$, $p=0.27$), which showed no evidence of the assumption of homogeneity being validated. Consequently, we used analysis of variance (ANOVA) and the Tukey multiple pairwise-comparison test (Tukey HD) to compare the differences in bark/wood ratios between twig types and the different nodes of smooth twigs.

Results

Random walks detected a significant surplus of bushes with a dominance of smooth twigs in the forest (χ^2 -test, $p < 0.05$) with 128 of the 330 bushes dominated by smooth twigs, 94 dominated by ringed twigs and 108 with equal proportions of twig types. The total numbers of 396 smooth and 335 ringed twigs on 20 different branches also showed a higher proportion of smooth twigs than ringed twigs on the bushes (χ^2 -test, $p < 0.05$). However, numbers were highly variable with 1–41 smooth and 1–52 ringed twigs per branch, and the respective mean numbers of 19.8 and 16.8 twigs per branch were not significantly different (Mann–Whitney U-test, $p > 0.05$).

Branches with twigs that grouse had clipped were detected on 28 birch bushes in seven different localities in the two areas together (Table 1). Twigs were eaten up to 55 cm above the snow level and a total of 470 clipped twigs was detected. Of these, 122 were smooth twigs and 348 were ringed twigs, resulting in a highly significant dominance (74%) of clipped ringed twigs compared to smooth (χ^2 -test, $p < 0.01$). The numbers of clipped twigs per bush were dominated by ringed twigs compared to smooth twigs (Mann–Whitney U-test, $p < 0.05$) and varied as 1–56 for smooth twigs and 10–121 for ringed twigs among the seven localities (Table 1).

The diameters at the clipping point of the 348 ringed twigs varied between 2.0 and 4.7 mm with a mean clipped diameter of 3.2 mm (Table 2) and only 28 ringed twigs (8%) had diameters greater than 4.0 mm (Fig. 2). The diameters at the clipping point of the 122 smooth twigs varied between 1.0 and 3.2 mm with a mean clipped diameter of 1.7 mm (Table 2), and only 6 smooth twigs (5%) had diameters thicker than 2.2 mm (Fig. 2). Cumulatively, 90% of the smooth twigs were 2.0 mm or thinner at the clipping point, 50% were clipped at ≤ 1.7 mm and 25% were clipped at ≤ 1.4 mm (Fig. 3).

Unclipped ringed twigs were 6–14 mm long ($n=150$) and had a mean length of 9.0 mm (Table 2). There was no visible variation in diameter along these ringed twigs, which

Table 1. Numbers of smooth and ringed twigs clipped by willow grouse from bushes of mountain birch on Kvaløya in winter 2020.

Location	1	2	3	4	5	6	7	Total
Smooth twigs	7	2	17	5	56	1	34	122
Ringed twigs	27	16	72	10	46	56	121	348

Table 2. Diameters at clipping point of twigs clipped by willow grouse, and diameters and lengths of unclipped twigs, on bushes of mountain birch at Kvaløya in winter 2020.

	n	Diameter, mm		Length, mm	
		Range	Mean	Range	Mean
Ringed twigs					
Clipped	348	2.0–4.7	3.1		
Unclipped	150	2.0–3.9	3.0	6–14	9.0
Smooth twigs					
Clipped	122	1.0–3.2	1.7		
Unclipped node 1	150	0.9–1.8	1.3	6–21	10.8
Unclipped node 2	150	1.0–1.9	1.5	6–25	16.5
Unclipped node 3	150	1.2–2.2	1.7	9–32	18.2
Unclipped node 4	150	1.4–2.9	1.9	7–31	17.4

were 2.0–3.9 mm thick and had a mean diameter of 3.0 mm (Fig. 4, Table 2). The mean diameters of ringed twigs clipped by grouse and diameters of collected ringed twigs that were unclipped were not significantly different (t-test, $p > 0.01$). Unclipped smooth twigs were much longer than unclipped ringed twigs with a mean length of 62.9 mm for the four nodes together and mean lengths of 10.8, 16.5, 18.2 and 17.4 mm for growth nodes 1–4, respectively (Table 2). Node 1 was shorter (t-test, $p < 0.01$) than the three inner nodes, which did not differ significantly in length (t-tests, $p > 0.01$). The mean diameters of smooth twigs significantly increased from 1.3 mm in node 1 to 1.9 mm (range for all nodes, 0.9–2.9 mm) in node 4 (Fig. 4, Table 2, t-tests, $p < 0.01$).

The bark of ringed twigs had a mean thickness of 0.83 mm with variation from 0.7 to 1.1 mm. The ringed twigs had significantly thicker bark than the thickest node

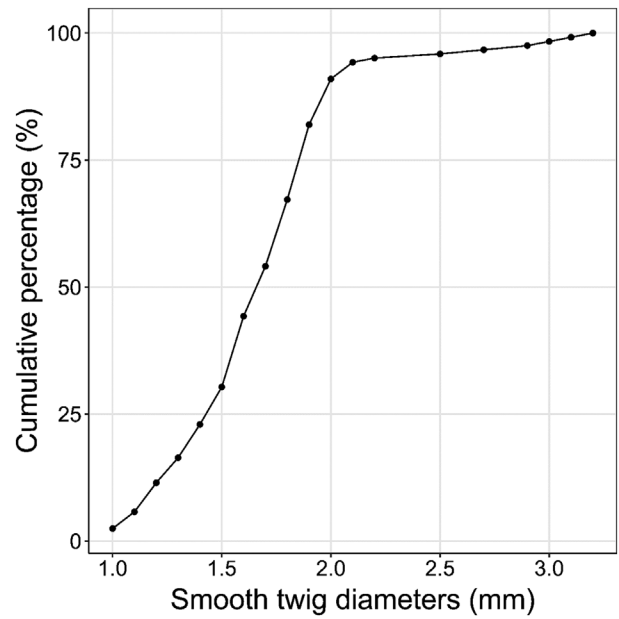


Figure 3. The cumulative percentages of diameters of smooth twigs at the point clipped by grouse.

(4) of smooth twigs (0.28 mm, range 0.25–0.35 mm), which had significantly thicker bark than the thinnest node (1) (0.17 mm, range 0.1–0.23 mm, $n = 15$, t-tests, $p < 0.01$). The mean ratio of bark weight in relation to wood weight was 5.7 in ringed twigs (Fig. 5a), which was significantly higher than in smooth twigs (4.6 in node 1 and 2.4 in node 4, Fig. 5a) (Tykey-HD, $p\text{-adj.} < 0.01$). The mean bark weight of 56.0 mg cm⁻¹ of twig length in ringed twigs was much higher than in smooth twigs, which increased inwards and was about two times higher in node 4 (21.8 mg cm⁻¹) than

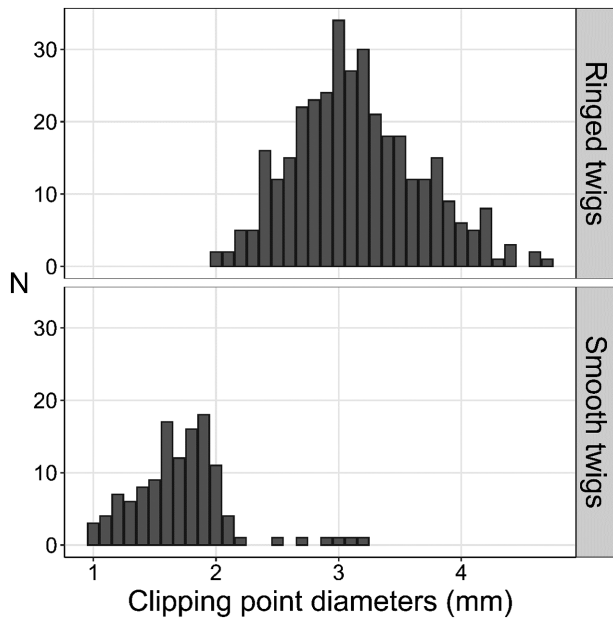


Figure 2. Diameters at the point clipped by grouse for ringed (top) and smooth (bottom) twigs.

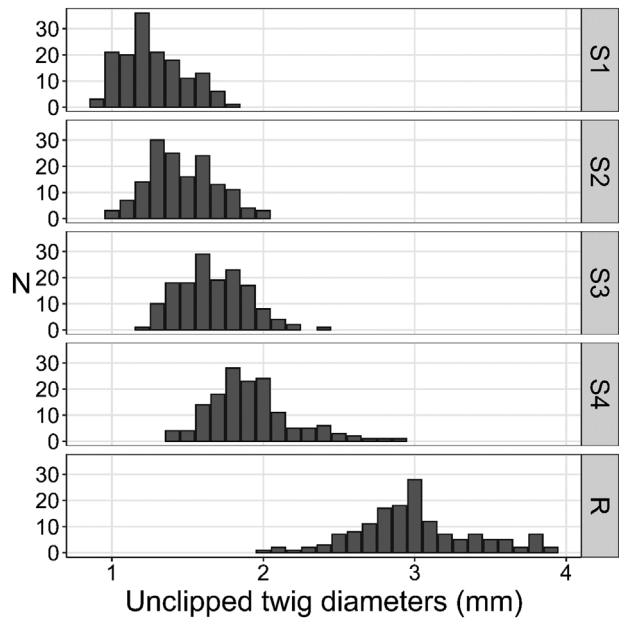


Figure 4. Diameters of unclipped (intact) smooth (top four panels, nodes 1–4; Fig. 1) and ringed (bottom panel) twigs.

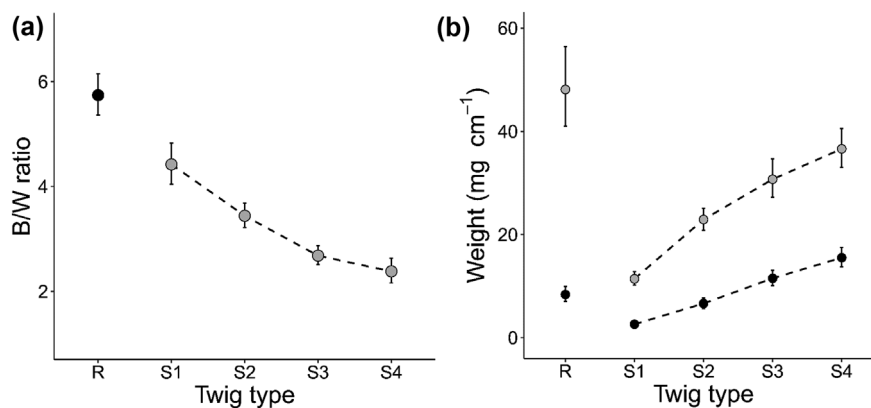


Figure 5. (a) Bark/wood (B/W) ratios of ringed (R, black dot) and node 1–4 of smooth (S1–S4, grey dots) twigs with 95% confidence intervals. (b) Weights of bark (grey dots) and wood (black dots) per cm twig length for ringed (R) and node 1–4 of smooth (S1–S4) twigs with 95% confidence intervals.

in node 1 (10.7 mg cm⁻¹) (Fig. 5b). The mean wood weights per cm twig length increased more dramatically than bark weights and were 3.7 times higher in node 4 than in node 1 (8.9 and 2.4 mg cm⁻¹, respectively). As a consequence, the bark/weight ratios decreased from node 1 to node 4 (Fig. 5a). All weight differences for bark and wood between nodes were significant (all $n = 15$, t -tests, $p < 0.01$).

Discussion

The random walks and the counts of twigs showed that smooth twigs were more available than ringed twigs on the birch bushes. Despite higher availability of smooth twigs, grouse clipped much more (74%) ringed twigs than smooth twigs. Ringed twigs were most likely selected because they had a thicker bark (mean 0.83 mm) than smooth twigs (mean 0.28 mm in the thickest node), and therefore higher bark/wood weight ratios than smooth twigs (Fig. 5a and b). Ringed twigs offer concentrated biomass per clipped twig bit because they are shorter and thicker and have the same diameter along the whole length. The whole twig can be eaten in one or two bits. The preference of ringed twigs supports the hypothesis that willow grouse should select twigs with higher bark relative to wood when feeding on birch in winter, thereby maximizing the intake of more digestible bark from the bushes.

However, grouse did consume the more abundant food type of smooth twigs, which were much longer and had a much thinner bark than ringed twigs. Diameters (Table 2) and bark thicknesses, and therefore bark weights per cm of twig length, increased inwards for each growth node but wood weights per cm twig length increased even more for each node. This gave a non-linear decrease of bark/wood ratios with increasing twig thickness. When feeding on smooth twigs, grouse may encounter a trade-off between an increase in absolute bark weight per twig length and a simultaneous decrease in the bark/wood ratio with increasing twig diameter. The results from clipped ringed twigs showed

that grouse are capable of clipping twigs as thick as 4.7 mm (Fig. 2). On smooth twigs, however, the thickest diameter they took was 3.2 mm, and 90% of the clipping points were 2 mm or less (Fig. 3). So, when feeding on smooth twigs, most clipping (95%) occurred only from the outer and thinner twig segments. Moreover, eating thicker and woody smooth twigs may require taking shorter bits and using more force and more biting and tearing per twig bit to prevent swallowing twig lengths that may be problematic to store in the crop and may require more energy to grind in the gizzard. In comparison, ringed twigs, which are all thick (Table 2), are much easier to clip because their thickness stems from bark, not wood (Fig. 5b). As predicted, results support the hypothesis that willow grouse should select ringed twigs and smaller diameters of smooth twigs with higher bark/wood ratios when feeding on birch in winter.

The present study at Kvaløya confirmed earlier studies that mountain birch is the main winter food in the subarctic Fennoscandian birch forests (Myrberget 1979, Uotila et al. 1980, Pulliainen and Iivanainen 1981). While catkins of birch can be an important dietary component for grouse (willow grouse, Pulliainen and Iivanainen 1981, Brittas 1988; black grouse, Pedersen 1991), Myrberget and Aabakken (1987) found that catkins were not important, with an annual variation of < 1, 1, 13 and 21% in their crop analyses from Senja. We focused on twigs on birch because they provide a more temporally and spatially consistent food resource for willow grouse (Hakkarainen et al. 2007). Despite consistent access to birch twigs, the proportion of ringed and smooth twigs consumed by willow grouse may be influenced by variation in relative yield of twigs and nutritional quality among twigs. By weighing crop contents from winter grouse, Brittas (1988) found that the relative proportions of long shoots (corresponding to smooth twigs) and short shoots (corresponding to ringed twigs) of mountain birch varied among years. He showed that the proportions of long shoots varied with annual yield of shoots. These results are interesting for our study at Kvaløya because we recorded the numbers and diameters of twigs that were clipped from the bushes but

could not compare this to crop contents. The relatively high proportions of smooth twigs in the crops that [Brittas \(1988\)](#) found could also be expected at Kvaløya because more birch bushes and branches on individual bushes were dominated by smooth twigs than by ringed twigs in the forest. Since smooth twigs are long and the diameters at the clipping points indicated that several bits were taken from each of them, the grouse eat a higher number of bits per twig from smooth twigs than from the shorter ringed twigs. However, instead of working with crop contents, we investigated another aspect of food quality – bark/wood ratios as a proxy for fibre – and found that, regardless of twig type, grouse selected twigs with more bark per cm twig length and higher ratios of bark relative to wood.

[Brittas \(1988\)](#) found that long shoots (equivalent to our smooth twigs) had equal protein contents, but higher fat, digestibility and fibre compared to short shoots (equivalent to our ringed twigs). Results showing ringed twigs are less digestible than smooth twigs ([Brittas 1988](#)) may be taken to be inconsistent with our assumption that bark is more digestible than wood and inconsistent with our findings that ringed twigs with a higher bark/wood ratio were clipped from bushes more often than smooth twigs that were more available ([Table 1](#)). The two shoot types were, however, treated differently in the nutritional analyses of [Brittas \(1988\)](#) because leaf buds were included with the long shoots but not with the short shoots. Since the resin in birch buds consists of a relatively high proportion of crude fat ([Bryant and Kuropat 1980](#)), including the buds may explain the higher fat content in the long shoots. In addition, the *in vitro* digestion was done in sheep rumen fluid on shoots taken directly from grouse crops, without being ground and debarked in the gizzards, as occurs in grouse. The digestibility was, therefore, measured with the bark intact on the shoots, not disintegrated as would normally occur in grouse digestion. Since ringed shoots have much thicker bark than smooth shoots, this may have negatively influenced the digestibility of ringed shoots. These results are nevertheless important because they showed that both types of twigs were fully digested, albeit with long shoots having slightly higher digestibility than short shoots. Our study adds to the [Brittas \(1988\)](#) study by indicating that bark/wood ratios and predicted higher digestibility of bark may be factors that also influence foraging by grouse. However, without knowledge of the nutritional quality of available twigs, which can vary annually ([Brittas 1988](#)), we cannot know the exact mechanism driving bush and twig selection.

Like grouse, northern mammals select plant parts that satisfy their demand for nutrients and energy in winter. [Palo et al. \(1992\)](#) studied the implications of nutritional factors important for moose *Alces alces* and mountain hare *Lepus timidus* in relation to diameters of birch twigs. They found that chemical defences (mainly phenols) and digestibility decreased, and that fibre content increased with larger twig diameters. This suggested that the browsers may trade off between nutrients and defence related to the increasing bark/wood ratios with increasing diameters. Chemical

defences in food plants are important determinants for browsing mammals ([Bryant and Kuropat 1980](#), [Iason and Palo 1991](#), [Bryant et al. 1992](#)) and there is considerable evidence that mammals learn to avoid chemical defences by ‘sampling’ (sic) the plants ([Iason and Villalba 2006](#)). Here, ‘sampling’ implies using the sense of smell that mammals have and then the sense of taste when the food is chewed before swallowing. Sampling may occur in grouse species which do select plants based on both volatile (e.g. smell) and bitter (e.g. taste) chemicals ([Guglielmo et al. 1996](#), [Frye et al. 2013](#)) and there are observations of willow grouse discarding buds of twigs consumed ([Myrberget 1979](#), [Brittas 1988](#)), possibly because the resin in the buds is unpalatable ([Steen 1989](#)). Accordingly, crop analyses ([Pulliainen and Iivanainen 1981](#), [Myrberget and Aabakken 1987](#)) show that buds constitute low amounts of food for willow grouse. Although the sense of smell by grouse is expected to be limited ([Steen 1989](#)), there is increasing evidence of reliance on olfaction and taste by birds ([Whittaker 2022](#)) including grouse ([Guglielmo et al. 1996](#), [Frye et al. 2013](#)). For willow grouse, the decreasing bark/wood ratios with increasing twig diameters in smooth twigs suggests that fibre is also an important parameter influencing foraging. Results do not exclude the potential that in addition to fibre, fat, protein and chemical defences also influence foraging of grouse. Many studies show that willow grouse are selective relative to accessibility (e.g. high yield, [Brittas 1988](#)) and nutritional quality (this study, [Moss and Hanssen 1980](#), [Brittas 1988](#), [Moss 1997](#)). This behavioural selection, coupled with low protein and energy demand in winter ([Moss 1997](#)) and behavioural adaptations to take cover and dig into snow to prevent heat loss and save energy ([Steen 1989](#), [Andreev 1991](#)), may partially explain high survival rates and physical condition during winter beyond what can be attributed to predation ([Myrberget and Aabakken 1987](#), [Smith and Willebrand 1999](#), [Sandercock et al. 2011](#)).

Birch twigs are not the food with the highest concentration of nutrients ([Moss 1974](#), [Moss and Hanssen 1980](#), [Myrberget and Aabakken 1987](#)), but it is always available in excess at snow level in the subarctic Fennoscandian winter forests. Although several other birds and mammals may eat birch in the subarctic winter (i.e. ptarmigan *Lagopus muta*, [Pedersen and Karlsen 2007](#); black grouse *Lyrurus tetrrix*, [Pedersen 1991](#); moose *Alces alces*, [Pedersen and Pedersen 2021](#); and mountain hares *Lepus timidus*, [Pedersen and Pedersen 2021](#)), none use this abundant resource as extensively as willow grouse. In his classic book on Norwegian *Lagopus* grouse, [Steen \(1989\)](#) writes that winter-feeding willow grouse walk between birch bushes and clip twigs here and there without eating them completely, and he regrets that we do not have analyses of what they take and what they reject. The present results show that willow grouse select twigs that maximize the intake of bark and at the same time minimize the intake of wood. This selective feeding mode appears as an optimal use of the highly abundant bark resource of mountain birch twigs, which may aid in survival of willow grouse in the subarctic winter forests of Fennoscandia.

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Author contributions

Anders Klemetsen: Conceptualization (lead); Data curation (supporting); Formal analysis (supporting); Investigation (lead); Methodology (lead); Validation (equal); Visualization (supporting); Writing – original draft (lead); Writing – review and editing (equal). **Aslak Smalås:** Conceptualization (supporting); Data curation (lead); Formal analysis (lead); Investigation (supporting); Methodology (supporting); Validation (equal); Visualization (lead); Writing – original draft (supporting); Writing – review and editing (equal).

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Data availability statement

Data are available from the Zenodo Digital Repository: <https://zenodo.org/record/7524312#.Y8IRRXbP1ro> (Klemetsen and Smalås 2023).

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