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Source: *Annual Review of Ecology and Systematics*, Vol. 11 (1980), pp. 261-285

Published by: Annual Reviews

Stable URL: <http://www.jstor.org/stable/2096909>

Accessed: 29/04/2010 11:17

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SELECTION OF WINTER FORAGE BY SUBARCTIC BROWSING VERTEBRATES: The Role of Plant Chemistry

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INTRODUCTION

Plant palatability frequently moderates vertebrate herbivore forage selection patterns (e.g. 72, 73, 103, 104, 111, 137, 179, 195). There is, however, considerable debate as to which plant chemical characteristics control palatability (e.g. 9, 42, 110, 118, 120, 216). On the one hand, forage proximal nutritional quality is believed to be of primary importance (e.g. 18, 51, 103, 114, 130, 133, 137, 161, 173, 215). On the other, there is increasing speculation that forage selection patterns are largely the result of avoidance of plant secondary constituents that are antagonistic to vertebrate herbivore fitness (e.g. 1, 2, 9, 12, 25, 49, 112, 116, 120, 141, 153, 165, 199, 200). In this paper we examine these alternatives for a specific system.

We consider the interface between subarctic browsing vertebrates and woody browse plants during winter and attempt to answer the following questions: During winter do subarctic browsing vertebrates (*a*) feed preferentially upon plant tissues that contain relatively high concentrations of proximal nutrients or energy, or (*b*) consistently avoid plant tissues that

contain relatively high concentrations of plant secondary constituents with known or potential antiherbivore activity?

Subarctic forests during winter offer an advantageous system in which to study the vertebrate herbivore-vegetation interaction. To date, they are minimally disturbed by humans. Consequently, the probability of encountering recently altered vertebrate herbivore foraging behavior during food-habits studies is low.

Vertebrate herbivores feed upon a wide variety of plant species whose tissues vary in proximal nutrient and secondary constituent content (e.g. 49, 102-104, 165, 195, 215, 216). Taxonomic phytochemical variation is enhanced by (a) seasonal and diurnal fluctuations in plant chemistry (e.g. 32, 43, 61, 77, 97, 102, 103, 120, 131, 132, 169), (b) effects of soil fertility upon plant chemistry (e.g. 27, 62, 63, 95, 127, 218), (c) production of phytoalexins in response to pathogen attack (e.g. 35, 112), (d) changes in plant chemistry resulting from physiological stress or aging (e.g. 74, 106, 168, 217), and (e) effects of herbivory upon plant chemistry (e.g. 25, 74-76, 168). Moreover, the effect of a plant's chemistry upon a vertebrate herbivore's foraging behavior may depend on the plant's relative frequency (29, 49, 215) and spatial relationship to other plants (10, 128) in the herbivore's habitat. Any analysis of vertebrate herbivore-vegetation interaction must deal with this potential phytochemical complexity (94). Obviously choice of a phytochemically simple system for study greatly facilitates analysis.

Subarctic forests are taxonomically monotonous (57), and woody plants tend to employ relatively nondiverse digestion-inhibiting defenses (45, 168, 169). Consequently, the potential for phytochemical diversity in subarctic forests is low. Restriction to winter minimizes temporal phytochemical chemical variation (42, 61, 208), and winter cold reduces immediate effects of plant pathogens and insect herbivores on forage chemical characteristics. Furthermore, winter is the period when vertebrate browsing pressure on subarctic plants is most intense (e.g. 2, 4, 15, 17, 28, 38, 109, 151). Consequently, winter should be the period when results of the coevolution of vertebrate browsing animals and plant chemistry should be most apparent.

Definitions

In this paper the ether-extractable fraction of woody browse is referred to as resin. The term resin is used rather than crude fat because the ether extracts of woody browse species discussed in this paper are composed, to a large extent, of terpene and phenolic resins rather than fatty acids [e.g. (12, 107, 148, 149, 164, 166, 172, 193, 194, 208, 219, 220); J. P. Bryant, unpublished information].

FORAGING BEHAVIOR AND BROWSE CHEMISTRY

Willow Ptarmigan (*Lagopus lagopus*), *Rock Ptarmigan* (*L. mutus*), and *White-tailed Ptarmigan* (*L. leucurus*)

Dominant ptarmigan tend to have diets of higher palatability, digestibility, and nutritive quality than subdominant ptarmigan (137, 139, 210). Consequently, the observation that Alaskan willow ptarmigan are dominant to Alaskan rock ptarmigan (134) suggests that the winter diet of the former should be of higher palatability, digestibility, and nutritive quality than that of the latter. The gut morphologies of the sympatric Alaskan ptarmigan suggest the following ranking of the expected digestibility and nutritive quality of their midwinter diets: willow ptarmigan diet > rock ptarmigan diet > white-tailed ptarmigan diet (136). Evidence for this hypothesis is the fact that the digestibility of Alaskan willow ptarmigan winter diet is greater than that of the winter diets of Alaskan rock ptarmigan and Alaskan white-tailed ptarmigan (135). On the other hand, when the three ptarmigan species are not in close proximity, their diets should be similar and of the highest palatability, digestibility, and nutritive quality possible (136, 137, 212).

During winter, Alaskan willow ptarmigan feed preferentially upon willow. Feltleaf willow, *Salix alaxensis*, makes up 80% of the willow ptarmigan's diet during most winters. Several other willow species (i.e. *S. glauca*, *S. arbusculoides*, *S. pulchra*, and *S. richardsonii*) are also important foods, but deep snow often limits their availability. The remainder of the diet is made up of dwarf birch catkins (*Betula nana* ssp. *exilis* and *B. glandulosa*) and a few dwarf birch foliar buds. The resinous internodes of Alaskan dwarf birches (40, 46, 87) and all green alder (*Alnus crispa*) tissues are not eaten, even though they are readily available to Alaskan willow ptarmigan during winter (90, 135, 136, 212, 214).

Alaskan rock ptarmigan feed primarily upon dwarf birch staminate catkins and, when catkins are depleted, upon foliar buds. Willow buds and internodes and a trace of green alder staminate catkins make up the dietary remainder. Dwarf birch internodes, alder internodes, and alder foliar buds are not eaten (135, 136, 212).

Alaskan white-tailed ptarmigan feed primarily upon green alder staminate catkins. This staple is supplemented with willow internodes and buds and the staminate catkins, foliar buds, and internodes of dwarf birch. Foliar buds and internodes of green alder are not eaten, even though they are among the most abundant potential foods in the Alaskan white-tailed ptarmigan's habitat (135, 136, 212).

Willow and rock ptarmigan are also sympatric during winter in Fennoscandia. There, as in Alaska, willow ptarmigan feed preferentially upon willow when it is available. They feed on birch when willow is not available and do not eat alder (137, 163, 180, 181).

Fennoscandian rock ptarmigan feed primarily upon birch staminate catkins and, to a lesser extent, foliar buds and internodes. When available, willow is a preferred food (161). Alder, while readily available, is absent from their winter diet. Thus, with the exception of birch internode use by Fennoscandian birds and the avoidance of birch internodes by Alaskan birds (136), winter diets of rock ptarmigan in these regions are similar. Interestingly, Fennoscandian birches utilized by ptarmigan (*B. nana* ssp. *nana*, *B. pubescens*, and *B. tortuosa*) have nonresinous internodes (12, 46, 87, 161).

Allopatric rock ptarmigan in Iceland feed preferentially upon willow in winter. After willow is buried by snow they feed on birch staminate catkins, and, after catkins are depleted, on birch foliar buds and internodes. Alder does not grow in Iceland and is not a potential winter food (51, 136, 137). Interestingly, internodes of Icelandic birches (*B. nana* ssp. *nana* and *B. pubescens*) also are not resinous (46, 51, 87). Allopatric white-tailed ptarmigan in Colorado and Canada feed preferentially upon willow during winter. When willow is no longer available they feed on both birch and alder staminate catkins (122, 211). Thus the forage preferences of allopatric rock and white-tailed ptarmigan are similar to those of willow ptarmigan. Willow is the preferred and predominant winter food.

Spring breeding behavior results in increased separation of Alaskan ptarmigan and, consequently, reduced interspecific competition (212). During spring all Alaskan ptarmigan species feed almost exclusively upon willow (211, 212).

These observations suggest that for ptarmigan, the palatability, digestibility, and nutritive quality of willow buds and internodes > dwarf birch staminate catkins > dwarf birch foliar buds > nonresinous dwarf birch internodes > alder staminate catkins > resinous dwarf birch internodes > alder foliar buds and internodes.

Relative forage preferences of ptarmigan in Alaska (Spearman $r_s = -0.800$, 11df, $P = 0.005$) and Fennoscandia ($r_s = -0.939$, 10df, $P < 0.001$) are negatively correlated with gross energy content of their browse. This relationship is the consequence of the 20% higher gross energy content of birch and alder tissues as compared to willow tissues (135, 173, 212, 214).

The largely alder diet of Alaskan white-tailed ptarmigan contains more metabolizable energy (2.7 kcal/g dw, 11.3 kJ/g dw) than the birch diet of Alaskan rock ptarmigan (2.3 kcal/g dw, 9.63 kJ/g dw) and the willow diet of Alaskan willow ptarmigan (2.3 kcal/g dw, 9.63 kJ/g dw) (135). Conse-

quently, the relative forage preferences of Alaskan ptarmigan are uncorrelated with the metabolizable energy content of their browse. Values for the existence metabolisms of Alaskan ptarmigan are: willow ptarmigan 117 kcal/day (5.67 W) (213), rock ptarmigan 100 kcal/day (4.85 W), and white-tailed ptarmigan 105 kcal/day (5.09 W) (135). The daily metabolizable energy intakes of Alaskan ptarmigan are: willow ptarmigan 150 kcal/day/bird (7.27 W/bird), rock ptarmigan 100 kcal/day/bird (4.85 W/bird), and white-tailed ptarmigan 105 kcal/day/bird (5.09 W/bird). Consequently, Alaskan willow ptarmigan must pay a 20% higher energetic price (135) to forage preferentially upon willows, which contain less gross and metabolizable energy than alder.

Ptarmigan forage preferences are not correlated with the proximal nutrient content of their winter browse (Table 1). This is because of low proximal nutritional quality of willow as compared to birch or alder (e.g. 2, 51, 61, 104, 114, 146, 147, 161, 173). The fiber content of ptarmigan winter browse is not correlated with ptarmigan winter forage preferences (51, 135, 161). On the other hand, digestibility of ptarmigan browse is positively correlated with ptarmigan winter forage preferences. The digestibility of willow by ptarmigan is approximately 45%, that of birch is approximately 27%, and the mixed alder-willow-birch diet of the white-tailed ptarmigan is approximately 30% digestible (135).

These values suggest that neither browse gross energy content, browse metabolizable energy content, browse proximal nutrient content, nor browse fiber content controls either the palatability, digestibility, or nutritive quality of ptarmigan winter browse. Instead these may be controlled by browse secondary constituent content. The following results are evidence for this hypothesis.

Multiple regression of browse gross energy content upon browse resin and carbohydrate fractions suggests that browse resins are more closely correlated with browse gross energy content than carbohydrates—i.e. the partial correlation with resin ($r = 0.927$, 11df, $P < 0.001$) is greater than that for carbohydrate ($r = 0.730$, 11df, $P = 0.003$). Moreover, resins and carbohydrate account for most of the variance in the regression, $r^2 = 0.875$. Consequently, the low correlation between browse carbohydrate content and ptarmigan winter forage preferences ($r_s = 0.600$, 11df, $P > 0.05$) implies that the negative correlation between ptarmigan winter forage preferences and browse gross energy content is a consequence of resin avoidance.

Willow buds are less resinous than either birch or alder foliar buds (12, 51, 135, 136, 161, 173). In Alaska, for example, feltleaf willow buds are considerably less resinous than dwarf birch foliar buds ($t = 56.944$, 4df, $P < 0.001$) and dwarf birch foliar buds are considerably less resinous than

Table 1 Simple linear and Spearman rank correlation coefficients between relative forage preferences and browse nitrogen and resin^e fractions

Species	N	Resin	Reference
Willow ptarmigan Alaska	$r_s = 0.291^a$ df = 11 $P = 0.414$	$r_s = -0.909$ df = 11 $P < 0.001$	136, 212, 214 ^{c,d}
Rock ptarmigan Alaska	$r_s = -0.500$ df = 7 $P = 0.285$	$r_s = -0.821$ df = 7 $P < 0.05$	136, 212 ^c
White-tailed ptarmigan Alaska	$r_s = -0.543$ df = 6 $P > 0.500$	$r_s = -0.857$ df = 7 $P < 0.05$	136, 211 ^{c,d}
Rock ptarmigan Iceland	$r = 0.382^b$ df = 8 $P > 0.200$	$r = -0.849$ df = 8 $P < 0.010$	51
Rock ptarmigan Fennoscandia	$r_s = 0.286$ df = 7 $P > 0.500$	$r_s = -1.000$ df = 7 $P \approx 0.005$	161, 173
Ruffed grouse Alaska	$r_s = -0.777$ df = 9 $P < 0.02$	$r_s = -0.963$ df = 9 $P < 0.001$	125 ^c
Snowshoe hare Alaska	$r = -0.325$ df = 16 $P > 0.200$	$r = -0.901$ df = 16 $P < 0.001$	104 ^c
Mountain hare Fennoscandia	$r_s = 0.274$ df = 14 $P > 0.500$	$r_s = -0.915$ df = 10 $P < 0.001$	2, 12, 113, 114, 161, 173
Moose Alaska, N.W. Canada	$r = 0.057$ df = 14 $P > 0.500$	$r = -0.868$ df = 14 $P < .001$	104, 129, 146, 147, 152, 209 ^c
Moose Fennoscandia	$r = -0.123$ df = 72 $P > 0.200$	$r = -0.908$ df = 72 $P < 0.001$	2, 114, 117, 119

^a r_s = Spearman Rank Correlation Coefficient.^b r = Correlation Coefficient.^cJ.P. Bryant, unpublished information.^dG.C. West, unpublished information.^eResin values transformed logarithmically.

green alder foliar buds ($t = 63.212$, 4df, $P < 0.001$) (J. P. Bryant, unpublished information). Staminate catkins are less resinous than foliar buds [(51, 161, 173); G. West, unpublished information]. Alaskan dwarf birch staminate catkins are considerably less resinous than Alaskan dwarf birch foliar buds ($t = 24.117$, 4df, $P < 0.001$) and Alaskan green alder staminate catkins are less resinous than Alaskan green alder foliar buds ($t = 34.821$, 4df, $P < 0.001$) (J. P. Bryant, unpublished information). Thus ptarmigan

forage preferences are negatively correlated with the resin content of their browse (Table 1).

Moss (135) suggests that resins hinder ptarmigan cecal function. Since resins of birch may hinder moose rumen function [(12); J. L. Oldemeyer, unpublished information], and resins of alder are highly toxic to deer rumen microbes (166), resins may also be inhibitory to ptarmigan cecal microbes. Moss (136) further suggests that these resins may inhibit protein digestion the way tannins do. Gohl & Thomke (56) have shown that protein assimilation by galliforms is negatively correlated with tannin-like substances ($r = -0.980$, 4df, $P < 0.001$), and Rhoades & Cates (169) have shown that some plant resins are tannin-like in their ability to complex with protein. Pulliainen's (161) data strongly suggest that resins inhibit protein assimilation by ptarmigan; the correlation between forage protein digestibility and forage resin content is negative ($r = -0.985$, 4df, $P < 0.001$). Alder resins contain several flavonoid aglycones (220), which are potential protein complexing substances (D. F. Rhoades, personal communication).

Ruffed Grouse (*Bonasa umbellus*)

In the northeastern United States ruffed grouse feed preferentially upon the overwintering staminate buds of aspens and cottonwoods (*Populus*) (e.g. 26, 58, 65–68, 105, 197). Quaking aspen (*Populus tremuloides*) is preferred over bigtooth aspen (*P. grandidentata*) ($P < 0.05$). Balsam poplar (*P. balsamifera*) staminate buds are used only in late winter after their resinous bud scales have been shed (197). In Alberta (39) and Alaska (125), the palatability of willow buds to the ruffed grouse is equal to or greater than that of the staminate buds of quaking aspen. In all three areas paper birch (*B. papyrifera*) is used much less frequently than *Populus* (39, 125, 197). For example, paper birch staminate catkins, the only part used by ruffed grouse, are considerably less palatable than quaking aspen staminate buds ($P < 0.01$) (197). Alder and conifers are not used as winter food by ruffed grouse (39, 65–68, 69, 105, 121, 125, 197), even though they are readily available (121).

Ruffed grouse preferentially feed in male aspen clones of the 30–50 year age class, mean age 34.5 years ($P < 0.01$) (39, 197). Trees of this age are more susceptible to pathogen and insect attack than juvenile aspen (13, 196, 197). Because preferred clones are often overmature and diseased, injured, or otherwise physiologically stressed, Gullion (65, 66) has suggested that ruffed grouse preferentially feed on decadent male aspen clones. That ruffed grouse feed preferentially in the upper crown of preferred aspen trees (39, 197) and that the upper crown tissues of a mature tree are more senescent and physiologically stressed than lower crown tissues (106, 174–176, 223),

suggest that the ruffed grouse feeds preferentially on physiologically stressed tissues in physiologically stressed trees.

In order of gross energy content, the preferred winter browse of Alaskan ruffed grouse is feltleaf willow buds < quaking aspen staminate buds < birch staminate catkins (214). Conifers, alder, and the resinous stage of balsam poplar buds all contain large quantities of energy rich resins. Thus winter forage preferences of Alaskan ruffed grouse are negatively correlated with gross energy content of their winter browse ($r_s = -0.943$, 6df, $P < 0.001$).

Staminate buds produced by preferred quaking aspen clones contain slightly more nitrogen than staminate buds produced by rejected clones ($P < 0.05$) (39, 68). Ruffed grouse do not, however, selectively feed upon nitrogen-rich staminate buds within a quaking aspen clone ($P > 0.05$), nor do they differentiate between willow and quaking aspen on the basis of tissue nitrogen content ($F_{2,24} = 2.244$, $P = 0.149$). Moreover, there is no consistent relationship between the forage preferences of ruffed grouse and the phosphorous, micronutrient, soluble carbohydrate, or fiber content of either willow or quaking aspen (39).

These results imply that ruffed grouse do not select winter browse because of browse gross energy or proximal nutrient content. We suggest that ruffed grouse avoid browse resins. Evidence for this hypothesis is provided as follows.

The winter forage preferences of Alaskan ruffed grouse are negatively correlated with resin content of winter browse (Table 1). Alberta ruffed grouse also avoid browse resins. In Alberta, willow buds are less resinous than quaking aspen staminate buds ($F_{3,14} = 13.515$, $P < 0.001$). Staminate buds collected from preferred quaking aspen clones in Alberta are less resinous than those collected from rejected clones ($P < 0.05$). Furthermore, quaking aspen staminate buds collected from crops of Alberta ruffed grouse are less resinous than those collected at random from preferred quaking aspen clones ($P < 0.05$). Consequently, the overall avoidance of resinous quaking aspen staminate buds by Alberta ruffed grouse is highly significant ($F_{4,24} = 26.105$, $P < 0.0001$) (39). Quaking aspen foliar buds are not eaten by ruffed grouse, and in Alaska the foliar buds of quaking aspen are more resinous than staminate buds of quaking aspen ($t = 9.662$, 4df, $P < 0.001$) (J. P. Bryant, unpublished information). Paper birch staminate catkins are more resinous than quaking aspen staminate buds (J. P. Bryant, unpublished information). Ruffed grouse only eat balsam poplar staminate buds after their resinous bud scales have been shed (197). Alder buds and conifer needles are very resinous [(208); J. P. Bryant, unpublished information] and are not eaten at all. Ruffed grouse prefer physiologically stressed tissues and such tissues are often poorly defended by resins and tannins (106, 168).

Resins avoided by ruffed grouse may lower its fitness. Resins of *Populus* contain several methylated flavonols (219) that may inhibit protein digestion (D. F. Rhoades, personal communication). Cottonwood resins are toxic to insect herbivores (31), and balsam poplar produces the greatest quantity of bud resins of any of the cottonwoods (J. D. Curtis, personal communication). Paper birch resins may hinder moose rumen function (J. L. Oldemeyer, unpublished information), and alder (166) and conifer (116, 141, 148, 149, 164–167) resins have antimicrobial activity. These resins may be toxic to ruffed grouse cecal microbes.

Spruce Grouse (*Canachites canadensis*), *Blue Grouse* (*Dendragapus obscurus*), and *Capercaillie* (*Tetrao urogallus*)

Conifer needles comprise the winter diet of these tetraonids. Tamarack (*Larix laricina*) needles are the preferred food of spruce grouse (98) and blue grouse (20) in western North America. Larch (*L. occidentalis*) needles are preferred by spruce grouse in eastern North America (30). After *Larix* shed their needles in early winter, pine (*Pinus*) becomes the preferred food of both spruce grouse and blue grouse. Blue grouse (20) and spruce grouse (98, 154–156) feed preferentially upon lodgepole pine (*P. contorta*) in western North America, and in eastern North America spruce grouse feed preferentially upon the jack pine (*P. banksiana*) (30, 69). The capercaillie feeds preferentially upon *Larix* (R. Moss, personal communication) and Scots pine (*P. sylvestris*) (115, 162, 182). Fir (*Abies*) is less palatable to spruce grouse than pine (98, 154, 192). Spruce (*Picea*) is the least palatable conifer to all three species during midwinter (20, 30, 98, 115, 154, 182). In North America white spruce (*P. glauca*) is considerably more palatable to spruce grouse than black spruce (*P. mariana*) (41, 42). During spring, however, expanding foliar buds of spruce are the preferred and predominant food of spruce grouse (80).

These birds repeatedly feed in certain trees in a population. Spruce grouse prefer older jack pine ($P < 0.01$) (69). Lodgepole pine (21) and white spruce (42) saplings less than approximately 14 years old are totally avoided by spruce grouse. Scots pine trees preferred by the capercaillie (115) and jack pine (69) and white spruce (J. P. Bryant, personal observation) trees preferred by spruce grouse are often fire scarred or otherwise injured. This suggests a preference for carbon-stressed tissue, as does the tendency of the capercaillie (115), blue grouse (82), and spruce grouse (69) to feed in the upper sun crown of host trees.

Palatability is not consistently correlated with forage gross energy content (41, 42, 155–156) or metabolizable energy content (155, 156). The poor correlation with forage gross energy content appears to reflect an avoidance of energy-rich resins (42).

Forage preferences of this group are also not consistently correlated with forage proximal nutritional quality. While spruce grouse in the Lake States Region appear to feed on jack pine needles that contain more nitrogen than rejected needles ($F_{1,9} = 13.75$, $P < 0.01$) (69), spruce grouse in Alberta do not feed preferentially upon nitrogen-rich jack pine needles (155). Alaskan spruce grouse do not select white spruce needles on the basis of any nutrient ($P > 0.05$) (41, 42). Hoffmann (82) found that blue grouse preferred nitrogen-rich needles of the white fir (*Abies concolor*) ($t = 8.43$, 12df, $P < 0.001$). Conversely, Boag & Kiceniuk (21) found no significant difference between nitrogen content of lodgepole pine needles selected and rejected by blue grouse. Pulliainen (162) has reported selection of nitrogen-rich needles by the capercaillie.

Conversely, there is a consistent negative correlation between forage preferences of this group and forage resin content. In the Lake States Region spruce grouse prefer low-resin jack pine needles ($P < 0.05$) (69). In Alaska, white spruce needles contain less resin than black spruce needles ($P < 0.01$) (42) and white spruce contains more resin in its juvenile-stage tissues than in its mature-stage crown tissues ($t = 22.869$, 4df, $P < 0.001$) (J. P. Bryant, unpublished information). Moreover, physiologically stressed conifers produce less total resin and phenolic substances than healthy trees (106).

Ellison (42) has suggested that conifer resins are avoided because of their antimicrobial activity. The antimicrobial activity of conifer resins is largely determined by the oxygenated monoterpene fraction of resin (e.g. 116, 141, 148, 149, 164, 165). That the oxygenated monoterpene fraction of Siberian conifer needle resins (larch 6.9%, pine 26.15%, fir 34.9%, spruce 43.2%) (194) is negatively correlated with forage preferences of conifer-feeding tetraonids suggests that these species avoid oxygenated monoterpenes. Capercaillie feed preferentially upon young needles within individual Scots pine (162), and young conifer needles contain lower concentrations of essential oils (149, 208) and are less inhibitory to deer rumen function than old conifer needles (149). The rapidly expanding foliar buds of conifers, for example spruce, which are preferred by these species (80), are carbon-stressed (106) and contain almost no antimicrobial essential oils (149, 208).

Rhoades & Cates (169) suggest that acidic conifer resins may also inhibit protein digestion. Data of Pendergast & Boag (155) may support this suggestion: Spruce grouse when suddenly placed on a pine needle diet go into a negative nitrogen balance at the rate of one gram protein lost per day. However, because both resins and protein are voided in the cecal droppings it is not clear whether this protein is microbial protein, body protein used in the detoxification of resins, or forage protein complexed with resin.

Snowshoe Hare (*Lepus americanus*) and *Mountain Hare* (*L. timidus*)

Forage preferences of snowshoe hares and mountain hares are willow > aspen > larch > dwarf birch > tree birch > pine (jack pine = lodgepole pine = scots pine > white pine > red pine) > fir > spruce (white spruce > black spruce) > alder (e.g. 3, 12, 22, 25, 28, 36, 38, 48, 104, 113, 114, 183, 184, 201). Cafeteria style feeding experiments have validated this preference ranking for both snowshoe (22, 25, 104) and mountain hares [(12); A. Pehrson, personal communication].

Snowshoe hares feed preferentially on certain genotypes in a plant species population. Using Douglas fir as experimental stock Dimock et al (37) demonstrated that both captive and free-ranging snowshoe hares, as well as deer, preferentially feed upon certain genotypes. They further demonstrated that the relative palatability of Douglas fir genotypes is a strongly inherited, additive, and mathematically predictable trait (186).

The juvenile-growth-form twigs of trees and shrubs are extremely unpalatable to snowshoe (25, 104) and mountain hares (153) as compared to twigs collected from mature-growth-form trees and shrubs.

Hares strongly prefer conifer terminal shoots over conifer lateral branches [(4, 6, 22, 28, 37, 38, 109); J. P. Bryant, personal observation]. Mountain hares eat the woody internodes of the mountain birch (*B. pubescens*) (12) and the aspen (*P. tremula*) (A. Pehrson, personal communication), but reject the foliar buds [(12); A. Pehrson, personal communication]. Similarly, snowshoe hares in Alaska eat the woody internodes but reject the foliar buds of the Alaska paper birch (*B. papyrifera* ssp. *humilis*), the green alder, and the balsam poplar (25).

The gross energy content of highly palatable browse species (e.g. willow and aspen) is considerably lower than that of less palatable browse species (e.g. birch, alder and conifers). The gross energy content of foliar buds is consistently higher than that of internodes (173, 214). The highly unpalatable juvenile-growth-form twigs of several important browse species of Alaskan snowshoe hares contain much greater concentrations of energy-rich resins than the much more palatable mature-growth-form twigs of these species (25). Thus hare forage preferences are negatively correlated with the gross energy content of their browse ($r_s = -0.983$, 10df, $P > 0.0001$). Willow and aspen contain lower concentrations of soluble carbohydrate in their above-ground tissues than birch and alder (114). Internodes contain lower concentrations of soluble carbohydrate than foliar buds—e.g. Alaska paper birch ($t = 13.324$, 4df, $P < 0.001$) and green alder ($t = 12.377$, 4df, $P < 0.001$) (J. P. Bryant, unpublished information). Consequently, hare forage preferences are negatively correlated with highly digestible sources of energy—i.e. soluble carbohydrate ($r_s = -1.000$, 8df, $P < 0.001$).

Willow and aspen contain lower concentrations of proximal nutrients than birch and alder (e.g. 2, 61, 104, 114, 146, 147). Small-diameter twigs from the crown of mature-growth-form angiosperm browse species contain lower concentrations of proximal nutrients than small-diameter twigs from juvenile-growth-form plants of the same species—e.g. with respect to nitrogen, bebb willow (*S. bebbiana*) ($t = 7.965$, 4df, $P = 0.002$), aspen ($t = 10.413$, 4df, $P < 0.001$), Alaska paper birch ($t = 8.384$, 4df, $P < 0.005$) (25, 104). Foliar buds of angiosperm browse species contain higher concentrations of proximal nutrients than do internodes (51, 162, 173)—e.g. with respect to nitrogen, Alaska paper birch ($t = 23.017$, 4df, $P < 0.001$) and green alder ($t = 21.907$, 4df, $P < 0.001$) (J. P. Bryant, unpublished information). Consequently, hare forage preferences are not consistently positively correlated with browse proximal nutrient content (Table 1).

These results suggest that hare forage preferences are not controlled by tissue energy or proximal nutrient content. Several lines of evidence suggest, however, that tissue secondary constituent content controls hare forage preferences.

Willow and aspen are less resinous than birch, alder, and conifers [(2, 12, 114); J. P. Bryant, unpublished information]. For example, when twig diameter is held constant, juvenile feltleaf willow is less resinous than juvenile Alaska paper birch ($t = 158.537$, 4df, $P < 0.0001$), juvenile green alder ($t = 138.222$, 4df, $P < 0.0001$), or juvenile black spruce ($t = 42.116$, 4df, $P < 0.0001$) [(25); J. P. Bryant, unpublished information]. Mountain hares prefer the mountain birch (*B. pubescens*) over *B. verrucosa*, and *B. pubescens* twigs are less resinous than *B. verrucosa* twigs [A. Pehrson, personal communication]. The oxygenated monoterpene content of Siberian conifer twigs [larch 1.2% < pine 1.3% < fir 10.7% < spruce 12.3% (194)] is negatively correlated with the palatability of these conifers to hares. Low-palatability Douglas fir genotypes bred by Dimock et al (37) contain higher concentrations of total resin, oxygenated monoterpenes, and phenolic substances in their tissues than high-palatability genotypes (164, 165, 167). Juvenile-stage twigs of several important Alaskan browse species are more resinous than similar-diameter mature-stage twigs—e.g. aspen ($t = 22.735$, 4df, $P < 0.001$), Alaska paper birch ($t = 50.731$, 4df, $P < 0.0001$), green alder ($t = 25.953$, 4df, $P < 0.0001$), balsam poplar ($t = 36.895$, 4df, $P < 0.0001$), and white spruce ($t = 22.869$, 4df, $P < 0.0001$) (25). Compared to lateral branches, conifer terminal shoots contain lower concentrations of oxygenated monoterpenes (148, 149, 172, 208) and produce extracts that are less inhibitory to deer rumen microbes (149). Foliar buds of *B. pubescens* contain six times the resin concentration of internodes (12). The resin concentration of foliar buds of mature-growth-form plants of several important Alaskan angiosperm browse species is higher than that of their internodes—e.g. Alaska paper birch ($t = 980.022$, 4df, $P < 0.0001$),

green alder ($t = 120.595$, 4df, $P < 0.0001$), and balsam poplar ($t = 45.648$, 4df, $P < 0.0001$) (J. P. Bryant, unpublished data). Consequently, hare forage preferences are negatively correlated with resin content of their winter browse (Table 1).

Barikmo (12) has demonstrated experimentally that *B. pubescens* foliar bud resin is repellent to mountain hares. Bryant [(25); unpublished information] has demonstrated experimentally that resins of quaking aspen, Alaska paper birch, green alder, balsam poplar, white spruce, and black spruce are quantitatively repellent to Alaskan snowshoe hares. Moreover, resins from low-palatability browse species and growth stages are more repellent at the same concentration than those from high-palatability browse species and growth stages. The quantitative effect of each resin thus appears to explain intraplant variability in tissue palatability while the qualitative variation in resin potency partially explains interspecific variation in browse palatability.

Feeding trials demonstrate that hare forage preferences are a reliable predictor of the nutritive value of their browse. Bookhout's (22) data show that both forage intake per unit time ($r = 0.847$, 12df, $P < 0.001$) and survival time ($r_s = 0.960$, 20df, $P < 0.0001$) of hares are positively correlated with palatability of food available to them. Other data (J. P. Bryant, unpublished information) also suggest that hare forage intake per unit time is positively correlated with browse palatability ($r = 0.992$, 8df, $P < 0.001$). Because palatability of several of the more important browse species of snowshoe hares appears to be controlled by their tissue resin content (Table 1), we suggest that these resins reduce hare fitness.

Bryant (unpublished information) has provided circumstantial evidence in support of this hypothesis. Captive snowshoe hares in Alaska can survive and gain weight on a diet of small-diameter (≤ 4 mm) twigs from the crown of mature Alaska paper birch. On this diet they eat internodes but reject foliar buds and staminate catkins. When fed juvenile-growth-stage birch twigs (diameter ≤ 4 mm), however, daily browse consumption declines by half. Snowshoe hares lose weight rapidly and will eventually die if held on a diet of the resinous, juvenile-growth-stage twigs of the Alaska paper birch (25), even though these twigs contain higher concentrations of proximal nutrients and less lignin than the nonresinous mature-growth-stage twigs of the Alaska paper birch (25, 104). Pehrson (153) has shown that mountain hares also lose weight on a diet of juvenile-growth-stage mountain birch.

The antimicrobial activity of some woody plant resins (e.g. 116, 140–144, 148, 149, 164, 166) may inhibit hare cecal microbe production. If such inhibition occurs, hare nitrogen assimilation could be lowered by as much as 50%, volatile fatty acid production could be seriously retarded or stopped, and B vitamin production could be inhibited (123). Possible inhibition of protein digestion is suggested by the potential protein complexing

capability of phenolic substances isolated from *Populus* (219) and *Alnus* resins (220) and acidic conifer resins [(169); D. F. Rhoades, personal communication]. Moreover, unpalatable genotypes of Douglas fir contain greater concentrations of water-soluble phenolics than palatable genotypes (164).

Moose (*Alces alces*)

The similarity of moose and hare forage preferences is well-documented (38, 48, 202). Willow is the preferred and predominant forage of most moose populations. The remainder of the diet, listed in a descending order of preference, is largely comprised of aspen > birch > pine > fir > alder = spruce (e.g. 1, 2, 16, 24, 85, 86, 100, 108, 117, 119, 129, 152, 209).

Moose, like hares, feed preferentially upon the crown twigs of mature (felled) trees and tall shrubs [(1, 2); J. L. Oldemeyer, W. L. Reglin, personal communication]. Moose break the stems of moderately large saplings and tall shrubs to feed upon crown twigs (54, 159, 203), even though younger plants of the same species are more available (J. P. Bryant, personal observation). Moose also prefer the terminal leaders of conifers over lateral branches (2, 17). Because of chemical characteristics of browse outlined in previous sections moose forage preferences are not well correlated with the gross proximal nutrient content of browse but are strongly negatively correlated with its resin content (Table 1). We suggest that both winter forage preferences of moose and digestibility of browse by moose during winter are controlled by plant secondary constituents. This hypothesis is supported by several lines of evidence.

Oldemeyer et al (147) have shown that in vitro digestibilities of willow and aspen in moose rumen fluid are greater than those of either Alaska paper birch or green alder. The resinous, current annual growth twigs of juvenile Alaska paper birch are less digestible in moose rumen fluid than the nonresinous, current annual growth twigs of mature-growth-form plants of this species ($t = 6.503$, 4df, $P = 0.003$) (J. L. Oldemeyer, personal communication). Indigestibility of juvenile birch is also suggested by the fact that moose on the Kenai National Moose Range in southcentral Alaska frequently die of starvation even though their rumens are full of current annual growth twigs of juvenile Alaska paper birch (147). Because a reduction in rumen microbe numbers leads to an increase in rumen turnover time (88) this observation suggests that birch resins, like those of alder (166), may be toxic to rumen microbes.

Beaver (*Castor*)

Willow and aspen are preferred and predominant foods of beaver (e.g. 5, 8, 33, 47, 55, 70, 145, 150, 183, 184, 187, 188, 191). When willow and aspen are not available, birch is preferred (96). Alder, which is infrequently cut

even when readily available (8), occurs in beaver winter food rafts as a structural material rather than a food (33, 34, 64, 78, 91, 92, 145, 188). Conifers are rarely eaten by beavers (33, 145).

The leaves, twigs, and bark of alder collected from beaver winter food rafts contain higher concentrations of nitrogen and energy than those of willow collected from the same rafts (8). This suggests that browse proximal chemistry does not control beaver forage preferences. Consequently, we suggest that browse secondary chemistry controls beaver forage preferences. Evidence for this hypothesis is provided by browse chemical characteristics outlined in previous sections of this paper.

CONCLUSIONS

Evidence reviewed in this paper strongly suggests that subarctic browsing vertebrates avoid feeding upon plant tissues that contain high concentrations of secondary chemical constituents; they do not select their winter forage on the basis of its proximal nutrient content.

The preferred forages of these herbivores are the mature-growth-form twigs of fire-adapted trees found on nutrient-rich sites, for example willow and aspen (e.g. 48, 59, 79, 108, 205, 206). A consequence of adaptation to disturbances such as forest fire is the storage of large reserves of nutrients and carbon in below-ground parts. These reserves enable disturbance-adapted woody plants to regenerate above-ground parts destroyed by disturbance (52, 62, 63). In short, subarctic browsing vertebrates prefer the mature-growth-form twigs of competitive deciduous trees and shrubs that can regenerate parts destroyed by browsing (2, 7, 52, 221).

Low-preference browse species (e.g. black spruce) are adapted to nutrient-deficient sites (189, 206). A consequence of this adaptation is the retention of large nutrient reserves in above-ground parts because of slow leaf and twig turnover rates [(62, 63, 189); Chapin, this volume]. Because they retain expensive nutrient capital in above-ground parts during winter, these species should experience severe fitness loss if they are browsed even moderately [(2, 52, 62, 63); Chapin, this volume]. In fact, subarctic evergreens are severely damaged by moderate real or simulated winter browsing (e.g. 4, 7, 17, 84, 109). Thus it should be selectively advantageous for these stress-tolerant species to make relatively large allocations of carbon to defense of their nutrient capital [(2, 62, 63, 95); Chapin, this volume]. In fact, plants associated with nutritional stress in both northern coniferous forests [(25); J. P. Bryant, unpublished information] and tropical rain forests (127) appear to make such a commitment.

Integration of a plant's defensive strategy with its primary adaptive strategy is particularly important during the juvenile growth stage. Browsing during this growth stage results in a greatly increased mortality or a greatly

reduced competitive potential because browsing retards growth into the canopy (17, 73, 84).

Under intense selection pressure to gain dominance of the canopy, competitive plants should use their extreme phenotypic plasticity with respect to carbon allocation (62, 63) to deploy carbon during juvenility in a manner that increases their probability of rapidly reaching the canopy and, upon reaching maturity, in a manner that maximizes their leaf surface area within the canopy. Thus juvenile competitive browse species should allocate a relatively large quantity of carbon to vertical growth and defense at the expense of lateral development of the crown; mature competitive browse species should allocate a relatively large quantity of carbon to lateral development of the crown at the expense of vertical growth and defense. Competitive subarctic trees such as quaking aspen (e.g. 60, 71, 158, 177, 178, 196), paper birch (e.g. 60, 71, 89), and balsam poplar (e.g. 71, 177) have extremely rapid vertical growth rates during juvenility and broad, well-developed, deliquescent crowns when mature (71). They are heavily defended by resins when juvenile and are relatively undefended when mature (25).

Stress-tolerant plants are under no great selection pressure to compete for canopy dominance. In fact, increasing evidence shows that characteristics such as a rapid growth rate and phenotypic plasticity with respect to the deployment of photosynthate become selectively disadvantageous under conditions of extreme environmental stress (62, 63). Consequently, in comparison to competitive plants, stress-tolerant plants should allocate relatively uniform quantities of carbon to defense throughout life. Evidence for this hypothesis is the small difference in resin content and thus palatability between juvenile and adult stages of stress-tolerant trees (e.g. black spruce and green alder) as compared to competitive plants (e.g. aspen, Alaska paper birch, and balsam poplar) (25, 104).

Within plant allocation of resins by subarctic browse species supports the hypothesis that plants allocate (*a*) nutrients to plant parts in direct proportion to their functional value and (*b*) defensive substances to plant parts in direct proportion to both their functional value and their value as a reservoir of expensive nutrient capital (126, 168). Foliar buds of subarctic angiosperm browse species contain approximately the same concentrations of nitrogen and phosphorous as staminate catkins and two times the concentration of resin as staminate catkins [(12, 51, 161, 173); J. P. Bryant, unpublished information.] Consequently, functionally valuable foliar buds (73) are more heavily defended than less valuable floral buds.

The reliance of both subarctic angiosperm and gymnosperm browse species upon antimicrobial resins as a winter defense suggests that resins are a particularly effective form of defense against vertebrate herbivores. A basis for this hypothesis is provided by the digestive physiology of subarctic browsing animals—i.e. cecal function versus rumen function.

Because the cecal digestive system rapidly passes browse structural carbohydrates (19, 93, 123, 190), neither lignin nor tannin-lignin complexes are effective defenses against it. However, antimicrobial resins enter the small browsing vertebrate's cecum (135, 136, 155). Because digestion in the cecum is dependent upon microbial fermentation of plant material (14, 53, 123, 124), ingestion of antimicrobial resins could be detrimental to the cecal digester. Such resins may reduce production of microbial protein, vitamins, and volatile fatty acids in the cecum; they may also be toxic and may inhibit protein digestion. They may thus be effective defenses against cecal digestors.

Resins reduce rumen microbe numbers and thus cellulose and hemicellulose fermentation rates (e.g. 116, 141–144, 148, 149, 164–166). Their ingestion should thus increase rumen turnover time, speed rumen fill, and reduce a ruminant's forage ingestion rate (88, 204). They should thus reduce ruminant predation pressure on browse plants that contain antimicrobial resins. In short, because resins render cellulose and hemicellulose indigestible and therefore functionally equivalent to lignin they are also an effective defense against ruminants. Their potential effectiveness against ruminants is increased because they may inhibit (*a*) production of microbial protein and volatile fatty acids in the rumen and (*b*) protein assimilation. They may also reduce cellulose and hemicellulose fermentation in the ruminant hindgut. That energy produced from fiber fermentation in the ruminant hindgut may provide most of the energy utilized during sodium absorption by ruminants (83) suggests that resins offer an effective defense against sodium-limited ruminants such as moose (18).

That tetraonid birds often subsist for several months on a monospecific diet of resin- or phenol-rich tissues (42, 65, 69, 136, 154, 211, 212) suggests, however, that vertebrate herbivores can facultatively counter plant chemical defenses. In fact, excretion of ornithuric acid from the cecum by red grouse (*Lagopus lagopus scoticus*) is probably the result of detoxification of prolinin and other polyphenols (138). Circumstantial evidence also suggests that resins are detoxified in the tetraonid cecum.

Data of Moss (135) and Pendergast & Boag (155) strongly suggest that browse plant resins concentrate in tetraonid ceca and are voided in cecal droppings; the extremely high caloric content of these droppings can only be explained as a result of resin concentration in the cecum. Rock and white-tailed ptarmigan (211, 212), ruffed grouse (65, 197), and spruce grouse (41, 69, 154) all gradually increase their intake of resinous forage well before they must rely upon it during the midwinter period. In rock and white-tailed ptarmigan (136) and spruce grouse (157), this gradual shift in feeding behavior is concurrent with an increase in cecal size. However, if a gradual acclimation period is not allowed before rock ptarmigan (G. C. West, personal communication), ruffed grouse (81), or spruce grouse (155,

156) are placed on their normal midwinter diet, they exhibit a negative nitrogen balance, rapidly lose weight, and may eventually die. Such results suggest that these tetraonids rely heavily upon a facultative increase in cecal detoxification capability to subsist upon a moderately resinous diet.

On the other hand, Alaskan willow ptarmigan have relatively short ceca throughout the year (136). Furthermore, the cecal size of the Alaskan rock ptarmigan, the Alaskan white-tailed ptarmigan (136), and the spruce grouse (157) decreases during the period when they feed heavily upon willow or other nonresinous foods. We suggest that a nonresinous diet does not require a large cecum for detoxification. It also does not force birds to pay the energetic and nutritional costs of detoxification (49) or the maintenance costs of enlarged ceca (135, 136). Thus while these birds can acclimate to a moderately toxic diet, their behavior suggests that such acclimation is more costly than avoidance of heavily defended tissues.

The evidence reviewed in this paper strongly suggests that the commitment of carbon to defense by subarctic woody plants is a consequence of their primary physiological adaptations to disturbance and nutritional stress. It does not suggest that predictability (168, 169) or apparency (44, 45) at either the species or tissue level is well correlated with the commitment of carbon to defense by these species. This is because (a) palatable, poorly defended, mature-growth-form tissues of fire-adapted woody plants (e.g. willows) are abundant and apparent in space and ecological time because large areas of boreal and taiga forest frequently burn (e.g. 48, 50, 79, 171, 198, 205, 222) and (b) most subarctic browsing vertebrates reside in and are adapted to early successional habitats created by these fires (e.g. 48, 59, 108). It would therefore be valuable to determine the relative roles of predictability, apparency, and primary physiological adaptations in further studies of chemical coevolution.

ACKNOWLEDGMENTS

We wish to thank Arnold Bloom, F. Stuart Chapin III, Paul Feeny, John Fox, J. P. Grime, Dan Janzen, David Klein, David Murray, David Rhoades, Robert Weeden, and Robert G. White for their constructive criticisms of the various drafts of this manuscript. Discussions with Robert Moss, Robert Weeden, and George West greatly aided our interpretation of both published and unpublished information on the feeding behavior of the tetraonid birds discussed in this paper. Discussions with Robert G. White, Ake Pehrson, and Ivar Sperber greatly facilitated our understanding of rumen and cecal function. We wish to thank J. D. Curtis, John Oldemeyer, Ake Pehrson, and George West for access to their unpublished

data. Any errors in the interpretation of data are ours. This work was made possible by grants NSF DPP7718384, NSF DEB 7823919, and Los Alamos Lab. ERDA contract N28-9758F-1.

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