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POPULATION BIOLOGY OF SNOWSHOE HARES. III. NUTRITION, PLANT SECONDARY COMPOUNDS AND FOOD LIMITATION

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SUMMARY

(1) We studied the population dynamics and protein nutrition of snowshoe hares (*Lepus americanus*) in the Kluane Lake region, Yukon from 1977 to 1986. Plant secondary compounds in winter food plants were monitored from ether (resin) and methanol (phenolic) extracts.

(2) Extracts of phenols and resins in concentrations normally found in natural food decreased protein digestibility of processed rabbit food by 40–80% in laboratory experiments. Extracts at half normal concentration did not affect digestibility of protein compared to controls.

(3) Digestibility of dry matter of winter food plants was 40% in the more preferred species and 20% in less preferred species.

(4) Faecal protein from wild hares was used as an index of mean food quality consumed by hares. Faecal protein was lower in winter than summer. In the winters of peak numbers (1978–82), some animals obtained food of a quality lower than necessary to maintain body weight, indicating food limitation.

(5) On the food-supplemented experimental areas, protein indicated there was adequate food in all years except 1980. Since the hare population declined in these areas in 1982 in the presence of adequate food, we conclude that food limitation was not a necessary cause of the decline on the scale of these experiments.

(6) Plant secondary compounds declined through the increase, peak and decline phases of the hare cycle. Phenols increased 2 years after hare numbers dropped due to new growth of juvenile shoots. These results are contrary to the hypothesis that fluctuations in secondary compounds cause the hare cycle.

(7) The proportion of juvenile twigs in the available food, containing high amounts of secondary compounds, remained low during the decline and first year of low hare density. This is contrary to the plant structure hypothesis which predicts that juvenile twigs should be predominant in the decline and first 2–3 years of the low phase.

(8) We suggest that predation is a necessary cause of the hare cycle and in some circumstances, it may be the only cause. The hare cycle is constant in period but variable in amplitude. Food limitation may occur as a consequence of high amplitude rather than a cause of it.

(9) It remains to be tested whether predation can act alone or synergistically with food limitation on a larger scale.

INTRODUCTION

General hypotheses

Long-term research on the dynamics of snowshoe hare (*Lepus americanus* Erxleben) populations in southern Yukon, Canada, has been testing hypotheses on causes of the 10-year cycles in numbers. One current idea (Keith 1974, 1983) is that lack of food causes peak populations to decline through starvation. This had been supported by measurements of vegetation and calculated food requirements (Pease, Vowles & Keith 1979), and by measurements of body fat (Keith *et al.* 1984). Predators contribute to the decline in hare numbers and subsequently keep hares scarce while the vegetation regrows during the low phase of the cycle. Eventually the high reproductive rate of hares allows them to escape predator regulation and increase in numbers to a new peak. In this hypothesis, predators do not cause the initial decline, but act as the second factor of a two-stage process.

An alternative proposal (Bryant & Kuropat 1980; Bryant 1981; Fox & Bryant 1984) suggests that hare browsing induces cyclical variations in plant secondary compounds, e.g. resin, which then result in cyclical mortality and reproduction of the hares.

We tested these hypotheses by a feeding experiment in which some populations of wild hares had access to additional good quality processed food in winter (17% crude protein), and we monitored the population response to this treatment (Krebs *et al.* 1986). In addition, we monitored the winter food supply (Smith *et al.* 1988) and plant secondary compounds. We identify five hypotheses to explain the hare cycle. These and the predictions they make are given in Table 1. Evidence concerning the first prediction (1a) of the food limitation hypothesis has already been presented by Krebs *et al.* (1986). They found that the decline in numbers was not prevented, and that the delay in the decline was 6 months and 18 months in the replicates. In the replicate with a 6-month delay, the addition of food has little effect on timing of the cycle, and the effect was only moderate in the second replicate. However, we could not reject the food hypothesis using demographic data alone because: (i) it was possible we had not provided enough feeding sites for all animals to have access to the extra food (Graf 1985; Sinclair 1986), so they may still have been food limited; (ii) they had severely browsed the natural food on these sites (Smith *et al.* 1988); and (iii) in the critical winter of 1982–83 moose (*Alces alces*) discovered the feeders, ate much of the processed rabbit food, and may not have left enough for the hares. In this paper, we examine whether the food-supplemented and control populations of hares had adequate food (predictions 1, 1b) by monitoring their levels of faecal protein (Sinclair, Krebs & Smith 1982).

Vegetation available to the hares and the natural food that they ate was measured through one cycle (Smith *et al.* 1988). These measurements showed, as in earlier studies, that hares at peak numbers ate a large fraction of their food supply. The two most preferred plant foods in our experimental area are grey willow (*Salix glauca* L.) and bog birch (*Betula glandulosa* Michx.). However, hares did not eat all of the available food and there may have been sufficient food remaining to support the population. It is not possible to estimate the food required by hares from that available (Sinclair, Krebs & Smith 1982), a limitation that also applies to the earlier studies of Pease, Vowles & Keith (1979). Faecal protein, however, does provide a test of whether natural food was limiting the hare populations on our control areas.

The secondary compound hypothesis predicts (2) an increase of these chemicals in foods plants during the peak and decline phases, and a decrease in the low phase of the

TABLE 1. Hypotheses for the cause of the snowshoe hare cycle.

	Hypothesis		Prediction
(1)	Simple food limitation.	(1a)	Addition of food holds a population constant at peak numbers.
		(1b)	Control populations show evidence of undernutrition.
(2)	Fluctuating secondary compound content.	(2)	Increase of these chemicals in food plants during the peak and decline phase of cycle, and decrease in low phase after 2–3 year lag.
(3)	Plant structure.	(3a)	The proportion of unpalatable juvenile twigs in available food increases during the peak and decline phases.
		(3b)	This proportion decreases in the low phase after a time lag of 2–3 years.
(4)	Food shortage followed by increased predation.	(4a)	Addition of food stops the cycle at peak numbers.
		(4b)	Control populations show evidence of undernutrition and higher predation mortality.
(5)	Simple predation.	(5a)	Hare numbers decline after the peak in the presence of supplemental food.
		(5b)	There is no evidence that hares are starving in control populations.

hare cycle after a lag of 2–3 years (Bryant 1981). Therefore, we monitored the resinous and phenolic constituents of the two most commonly eaten winter foods, grey willow and bog birch.

A variation of the secondary compound hypothesis (Fox & Bryant 1984) is that chemical content remains constant in mature twigs but that the relative proportions of juvenile and mature twigs available to hares changes. Since juvenile shoots have more secondary compounds than mature shoots (Bryant & Kuropat 1980; Sinclair & Smith 1984a), changes in their proportions available to hares influences the amount of these chemicals that hares eat. This plant structure hypothesis predicts (3a, 3b) that the proportion of juvenile twigs in the available food is higher in the peak and decline phase and for 2–3 years in the subsequent low phase, than in the increase phase. We measured the abundance of juvenile and mature twigs on sample bushes of grey willows in control and food-supplemented areas.

Causes of hare mortality at Kluane were monitored through the peak and decline phases using radiotelemetry (Boutin *et al.* 1986; Trostel *et al.* 1987). Predation was the main cause of mortality during the winter. However, this technique could not determine whether the predators were catching starving or healthy prey, and hence whether predation acted alone or synergistically with food shortage. Measures of faecal protein during the winter can also help to resolve this problem by distinguishing between predictions 4b and 5b.

Faecal protein

Experimental studies on nutrition of captive hares have shown that faecal protein content is correlated with protein in the food (Sinclair, Krebs & Smith 1982). Hares maintained body weight with 11% crude protein (CP) in the food and 7·5% CP in the faeces when they ate processed rabbit food with no secondary compounds in it. Therefore, in the field, animals producing lower values than 7·5% CP in their faeces can be regarded as starving. This is a conservative prediction because secondary compounds in the natural food could raise the faecal protein content. To estimate the effect of these chemicals on faecal protein, extracts of these compounds from natural food were added to the processed food and fed to hares. In a separate series of trials, natural food was fed to the animals to measure digestibility and faecal protein. These results are used to interpret the field data on faecal protein levels.

METHODS

Digestibility of food of captive hares

Eight hares were kept singly in cages under constant environmental conditions at the Small Mammal Facility, University of British Columbia. During winter, day length was kept at 7 hours with a temperature of 8 °C. During summer, day length was 16 hours and temperature held at 12 °C. Experimental animals in the summer were not pregnant or lactating.

In the winter trials, twigs from various species of plants normally available to hares in the Yukon winter, were brought frozen to Vancouver and offered to hares for 24-h periods. Fresh and dry weights of plants offered and remaining after 24 h were measured by drying subsamples of the plants at 80 °C for 48 hours. All faecal material was collected in a net under the cage, dried and weighed, and a sample was analysed for nitrogen content. This procedure was repeated for 3–4 days. Before and after an experimental trial the animals were supplied with rabbit feed (17% crude protein). The weight difference between dry food eaten (F) and dry faecal material (T), expressed as a percentage of food eaten, gave a measure of the apparent digestible dry matter (% ADDM).

The summer trials examined the effects of plant ether extracts (resin) and methanol extracts (phenolics) on food digestibility. Resin was extracted from mature and juvenile twigs of bog birch and white spruce (*Picea glauca* (Moench) Voss) using ether. The extract solution was poured over 17% CP feed and the ether evaporated. A control sample of feed was treated in the same way with clean ether. The resin concentration on the feed was similar to that in the natural food (15% dry weight). Feed samples with extracts at the natural concentration were termed 'normal' samples. A further set of treated feed contained half the normal resin content, and was labelled 'diluted' feed. Phenols were extracted in the same way from the same species using methanol.

The feeding protocol for treated feed was similar to that for natural foods. Before and after the treated feed was offered, methanol or ether-treated control feed was supplied to match the experimental feed. The faecal protein fraction (FPF) was measured from Kjeldahl digestion using a Tecator Kjeltec Auto 1030 Analyzer. The total faecal protein (TP) produced from 100 g dry food eaten was calculated as:

$$\mathrm{TP} = 100(1 - \mathrm{ADDM}) \times \mathrm{FPF}. \qquad (1)$$

With a known food protein weight (FP) in the 100 g eaten, the percentage apparent digestible protein (% ADP) is found by:

$$\%\mathrm{ADP} = 100(\mathrm{FP} - \mathrm{TP})/\mathrm{FP}. \qquad (2)$$

Faecal analysis for wild hares

Our experimental studies and their controls were conducted on nine areas near Kluane Lake, Yukon, the details of which are given in Krebs *et al.* (1986). Five of these (1050, Gribble's, Silver Creek, Beaver Pond, Kloo Lake) were control plots on the mainland and two (Microwave, Dezadeash) were food-supplemented areas. The vegetation and trapping procedures used on each area are described in Krebs *et al.* (1986). The first time an animal was caught during a trapping session, a sample of its faecal pellets was collected and labelled. It was dried and later analysed for nitrogen content. Care was taken to avoid pellets contaminated with urine. When pellets were dried, contaminated ones were identified by a surface layer of white powder. The crude protein fraction was estimated from the nitrogen content by multiplying by the constant 6·25. Nitrogen content was measured using the Kjeltec Analyzer or a Technicon Autoanalyzer II that analyses ammonium ions by the method of Slawyk & MacIsaac (1972).

One confounding problem was that moose disturbed our feeders, and this disturbance may have affected the ability of hares to obtain supplemental food. On food-supplemented areas, hares had access to about 15–20 feeders where there was 17% CP rabbit feed. During the winters of 1981–82 and 1982–83 moose destroyed these feeders and ate much of the feed. Barbed-wire fences and stronger feeders were built in the first of these years on Microwave, but this reduced the number of sites to about six and by the second year moose had destroyed these. In the second winter four feeders protected under fallen logs survived on Dezadeash. On Microwave, food was placed on the ground in an open sack, for about 2 months (mid-October to mid-December 1982), where most of it was eaten overnight by moose; effectively only one feeding station existed. Subsequently, five stout aluminium pole stockades were constructed; these protected five feeders for the remaining time.

Secondary compounds in winter food plants

A 'twig' is defined here as the plant material distal to a stem diameter of 5 mm. Samples of juvenile twigs from grey willow and bog birch were collected in winter, and kept frozen until analysed. We define 'resin' here as the ether-extractable product following Bryant, Chapin & Klein (1983) and Fox & Bryant (1984). Plant samples were ground in a blender and soaked in ether for 1 week. The ether was decanted into a second weighed jar and allowed to evaporate. The sample was soaked in fresh ether for a total of three washings. The accumulated resin was then weighed.

We define 'total phenols' as the methanol-extractable product. Plant samples were soaked in 50 ml of 85% methanol–15% water for 2 weeks; 1 ml of the extract solution was diluted in 200 ml water. To 1·0 ml of this diluted extract 1·0 ml of Folin-Denis reagent was mixed. After 3 mins, 1·0 ml of 2N sodium carbonate was added. The solution was left for 1 h to develop a blue colour. If a precipitate formed, the solution was centrifuged. Absorbance was measured at 725 nm in a spectrophotometer as an index of phenolic content g^{-1} dry weight (Swain & Goldstein 1964; D.F. Rhoades, personal communication).

Mature and juvenile winter twigs

Juvenile twigs are defined as one season's growth from the root stock, and they have a long, straight unbranched form. All other twigs are defined as 'mature'. Mature twigs of grey willow have a branched growth form at the top of large stems (see photograph of

TABLE 2. Digestibility and faecal protein of snowshoe hares eating 100 g rabbit feed treated with secondary compounds from juvenile bog birch and juvenile white spruce. Normal concentrations are those found in the natural plants, and dilute concentrations are half normal. n = 8 except for % faecal protein for resin spruce and phenol birch where n = 4. 95% C.I. in parentheses.

	Food	Dry matter digestibility (%)	Faecal protein (%)	Protein digestibility (%)	Faecal protein (g)
(a)	Control				
	Normal rabbit feed	66·0 (±1·0)	13·45 (±0·67)	72·9	4·61
	Control phenol solvent	69·4 (±1·6)	14·39 (±1·27)	74·1	4·40
	Control resin solvent	68·6 (±1·5)	13·96 (±1·05)	74·2	4·38
(b)	Normal extract concentrations				
	Resin birch	38·9 (±6·0)	17·18 (±2·43)	38·3	10·50
	Resin spruce	35·5 (±11·1)	15·93 (±1·96)	39·6	10·27
	Phenol birch	13·5 (±8·3)	13·74 (±0·77)	30·1	11·89
	Phenol spruce	—	—	—	—
(c)	Dilute extract concentrations				
	Resin birch	67·1 (±2·3)	13·72 (±4·95)	73·4	4·51
	Resin spruce	71·9 (±1·4)	15·80	73·9	4·48
	Phenol birch	67·5 (±3·4)	13·80	73·6	4·49
	Phenol spruce	67·0 (±12·2)	15·30 (±1·15)	70·3	5·05

Salix alaxensis, Fig. 1 in Bryant *et al.* 1985). These become available to hares during winter when snow bends them over. The number of twigs on tagged bushes was estimated by techniques described by Smith *et al.* (1988). After initial calibration using calipers, diameters of twigs were estimated by eye. A sample of clipped twigs was dried to obtain dry biomass. The same bushes were counted each year.

Juvenile twigs of bog birch were the first season's regrowth from the root stock or the main stems after these had been browsed. Mature twigs were those at the ends of unbrowsed main stems. Juvenile twigs of white spruce were the terminal 20 cm from branches of trees less than 150 cm high. Mature twigs were those from the ends of lower lateral branches of large trees (> 10 m high), these being the branches that were browsed when snow build-up allowed hares to reach them. We did not sample trees of other heights because they were out of reach of hares and were thus not browsed.

RESULTS

Plant secondary compounds and hare nutrition

The effect of plant secondary compounds on the digestion and nutrition of hares was examined by comparing the digestibilities of 17% crude protein rabbit feed with and without ether (resin) and methanol (phenolic) extracts from juvenile bog birch and juvenile white spruce. The control feed was treated with the appropriate solvent, but apparent dry matter digestibility (% ADDM) did not differ from untreated feed (Table 2a). Normal concentrations of resins from both birch and spruce (Table 2b) halved the %ADDM when compared to the controls (Table 2a). Normal concentrations of phenols from juvenile birch reduced the %ADDM of the feed to one-fifth of the control level, and hares refused to eat feed with normal phenol concentrations from spruce. We have subsequently found that his phenol extract from spruce contains high concentrations of camphor, which is a potent deterrent to feeding for hares (Sinclair, Jogia & Andersen 1988).

TABLE 3. Digestibility and faecal protein of snowshoe hares eating 100 g of each plant species. $n=8$ for all species except juvenile spruce where $n=4$. 95% C.I. in parentheses

Food	Dry matter digestibility (%)	Faecal protein (%)	Faecal protein (g)
Normal feed	66·0 (±1·0)	13·56 (±0·67)	4·61
Grey willow	39·8 (+8·1)	13·60 (±2·77)	8·19
Felt leaf willow	40·4 (±6·2)	12·35 (±1·86)	7·36
Mature white spruce	22·1 (±7·0)	13·61 (±3·59)	10·60
Juvenile white spruce	18·0 (±12·5)	12·64 (±8·15)	10·36
Balsam poplar	34·9 (±6·6)	18·57 (±2·73)	12·10
Soapberry	24·5 (±6·5)	20·75 (±1·76)	15·67

Normal resin extracts also increased the % protein in the faeces (Table 2b). All normal concentrations of extracts approximately halved the % protein digestibility. Hence, faecal protein output increased compared to that for the controls.

The dilute concentrations of extracts from both birch and spruce produced no significant effects on either dry matter or protein digestibility of rabbit feed (Table 2c) compared to controls. This result suggests that the effects of plant secondary compounds on digestibility of natural foods may be avoided if these compounds are diluted by other foods lacking the same compounds.

Digestibility of natural food species

The five plant species offered to captive hares were grey willow (*Salix glauca*), felt leaf willow (*S. alaxensis* (Anderss). Cov.), balsam poplar (*Populus balsamifera* L.), soapberry (*Shepherdia canadensis* (L.) Nutt.) and white spruce. Juvenile twigs were offered from the two willows and spruce since these are normally available in winter. Four of the eight animals refused to eat juvenile spruce, and all eight animals refused to eat juvenile balsam

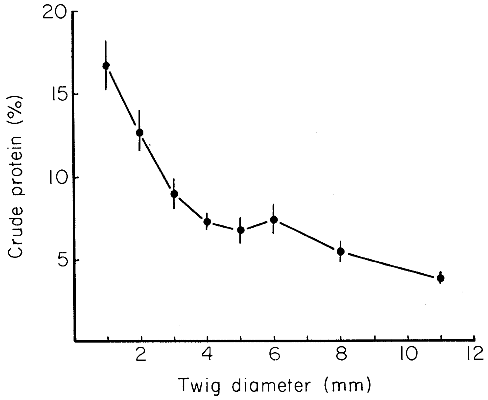

FIG. 1. Mean crude protein of twigs of bog birch distal to the clipping point at different diameters. Vertical bars are 1 S.E.

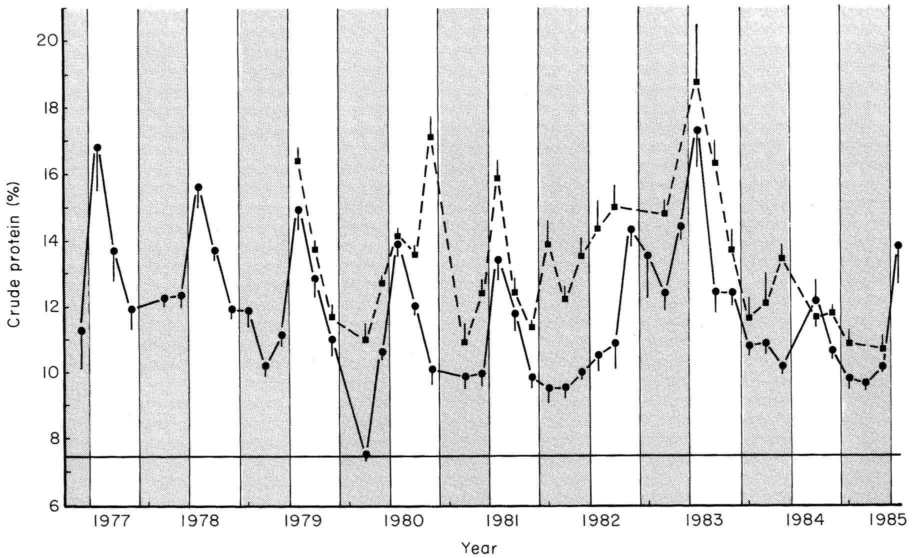

FIG. 2. Mean faecal crude protein of snowshoe hares over 2-month periods from five control grids (Silver Creek, 1050, Beaver Pond, Kloo Lake, Gribble) (——) and from two experimental food supplemented grids (Dezadeash, Microwave) (– – –) from 1977 to 1985. The horizontal line is the 7·5% CP threshold level in the faeces below which animals should lose weight from undernutrition (from Sinclair, Krebs & Smith 1982). Winter months (Dec.–May) are shaded. Vertical bars are 1 S.E.

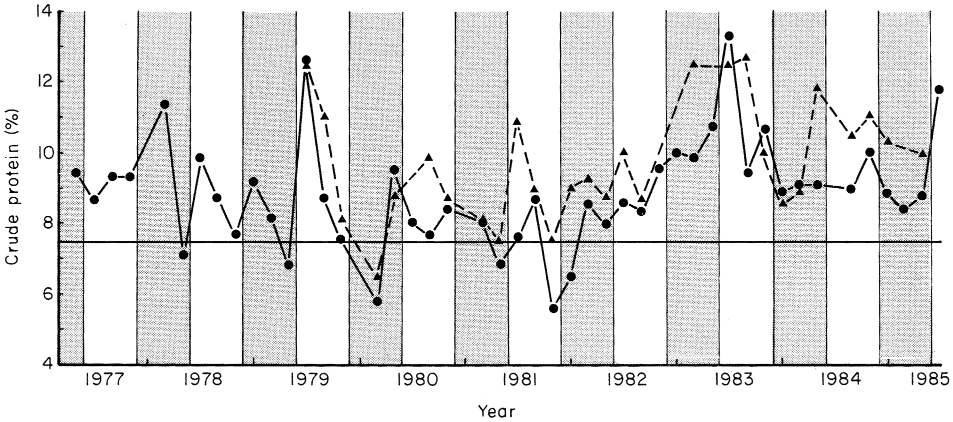

FIG. 3. The minimum faecal crude protein value recorded in a 2-month period from the five control grids (——) and two food-supplemented grids (– – –). The horizontal line is 7·5% CP threshold level in the faeces below which animals should lose weight. Winter months (Dec.–May) are shaded. See Fig. 2 for details.

poplar. Thus, mature twigs of spruce, balsam poplar and soapberry were also offered. Soapberry is a low bush which has only mature twigs available in winter.

The % ADDM for all trials was considerably lower than that for rabbit feed (Table 3). The highest values, around 40%, were for the two common willow species. The lowest

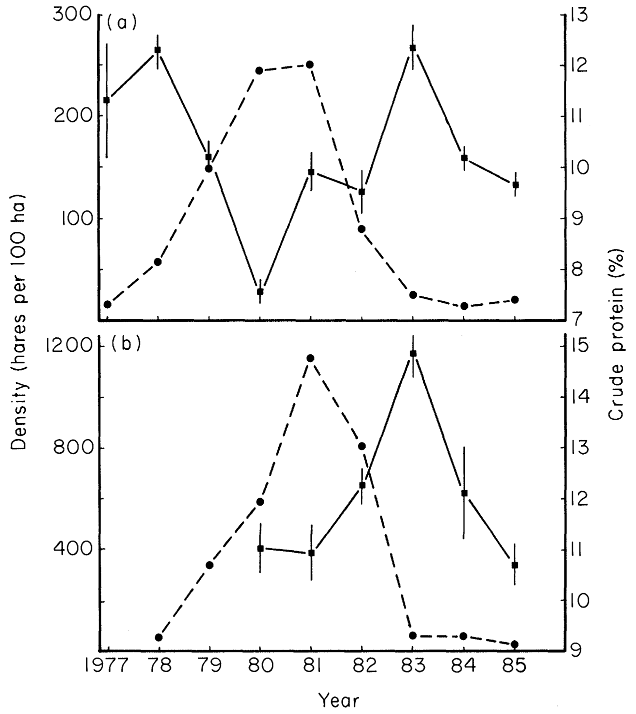

FIG. 4. (a) The lowest 2-month mean faecal crude protein value recorded each year from five control grids (——), and the mean snowshoe hare density from the same grids (see Fig. 2) (– – –). Hare densities are those of 1 April, and faecal protein values are from the preceding winter, usually the February–March period. Vertical bars are 1 S.E. (b) the same measures recorded from two food-supplemented grids.

values, about 20%, came from white spruce and soapberry. These figures are similar to the few other reported measurements (e.g. Holter, Tyler & Walski 1974).

Faecal protein content from the willows and white spruce (about 13% crude protein) was similar to that from rabbit feed, but balsam poplar and soapberry produced significantly more protein (Wilcoxon matched pairs signed ranks test, $P < 0{\cdot}05$). From % ADDM and the faecal protein content, the weights of protein defaecated from 100 g of dry grey willow or felt leaf willow eaten are calculated from eqn (1) as 8·2 g and 7·4 g, respectively (Table 3). Faecal output has been estimated to be about 50% of the protein eaten in feeding trials (Holter, Tyler, Walski 1974). Hence, if hares are to achieve nitrogen balance on a purely willow diet in the wild, they must select grey willow at 16·4% CP ($2 \times 8{\cdot}19$ g per 100 g food) and felt leaf willow at 14·7% CP.

Birch twigs were clipped at different diameters in winter, and analysed for protein as a mean for all material distal to the clipping point (Fig. 1). We found that for very small twigs (<1 mm diameter) protein values reach 16·7% CP. Thus, with the measured digestibility values and selective foraging, animals could obtain sufficient protein from at least one of the plant species, bog birch, commonly fed upon at Kluane.

Faecal protein from the wild population

There were no consistent differences in faecal crude protein from snowshoe hares on the five control areas. Thus, data from the five control areas were pooled (Fig. 2). Means are

TABLE 4. Lowest mean faecal protein over a 2-month period during winter and mean snowshoe hare densities towards the end of winter (1 April) for control and food-supplemented grids. One S.E. in parenthesis.

	Control grids		Food grids	
Winter	Faecal protein (%)	Density per 100 ha	Faecal protein (%)	Density per 100 ha
1976–77	11·28 (±1·15)	15·2	—	—
1977–78	12·27 (±0·31)	57·4	—	53·5
1978–79	10·21 (±0·29)	148·4	—	335·1
1979–80	7·56 (±0·22)	246·6	11·01 (±0·47)	786·5
1980–81	9·92 (±0·38)	251·7	10·95 (±0·56)	1155·7
1981–82	9·53 (±0·42)	88·4	12·26 (±0·33)	808·3
1982–83	12·36 (±0·47)	26·1	14·83 (±0·40)	59·8
1983–84	10·17 (±0·22)	15·0	12·08 (±0·89)	56·3
1984–85	9·66 (±0·22)	20·0	10·69 (±0·39)	22·5

computed for the 2-month periods December–January, February–March, April–May, these being the winter and spring months; and June-July, August–September, October–November as the summer and autumn period. The threshold value below which animals should lose weight through undernutrition is shown at 7·5% CP. This is a conservative value calculated by Sinclair, Krebs & Smith (1982) with no effects from secondary chemicals, which would raise the threshold. In our experiments with normal concentrations of birch compounds added to artificial feed, faecal protein increased on average by 1% (Table 2b), although the difference is not statistically significant. If this value is correct, the threshold would lie at 8·5% CP.

In general, mean faecal crude protein was lower in winter than in summer. In only one winter (1979–80) did the mean fall to the 7·5% CP threshold. Figure 3 shows the minimum

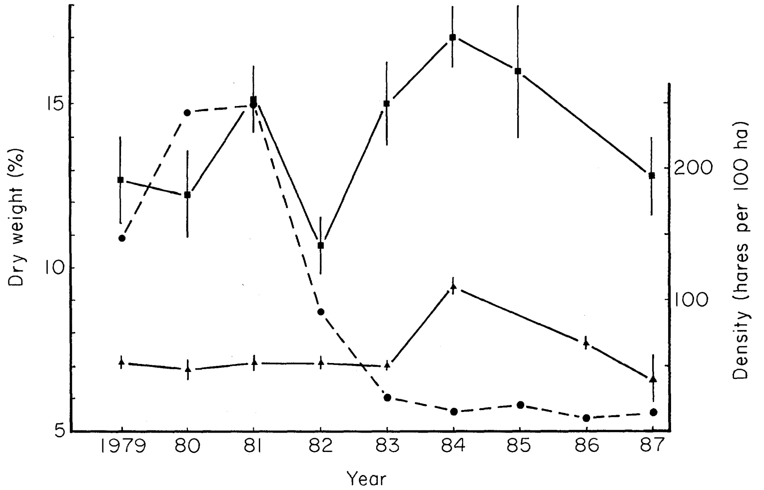

FIG. 5. The resin content of twigs from grey willow (▲) and bog birch (■) collected in winter. Hare density from five control grids (see Fig. 2) is shown by the broken line. Vertical bars are 1 S.E.

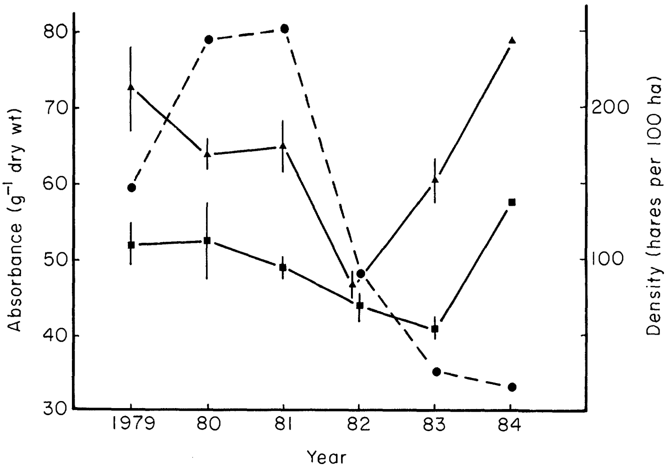

FIG. 6. The total phenolic content from grey willow (▲) and bog birch (■) collected in winter. Hare density from five control grids is shown by the broken line. Vertical bars are 1 S.E.

values recorded for each time period from the five control areas pooled, since they showed no consistent differences. In five winters (1977–78 to 1981–82) these values fell below this threshold, indicating that part of the population sampled on the control areas was underfed at these times. These were the years of increasing and peak population density (Fig. 4).

Figure 2 also shows the pooled mean and S.E. for faecal protein from two food-supplemented populations. From the time that measurements began in 1979, faecal protein from the food-supplemented animals was higher than that from the control

TABLE 5. Mature and juvenile grey willow twigs on bushes at three control sites (1050), Beaver pond, Kloo Lake) and one food-supplemented site (Microwave)

	1983	1984	1985	1986	1987
1050					
Number mature	271	366	512	1114	670
Number juvenile	18	33	122	68	138
% mature	93·8	91·7	80·8	94·2	82·9
Beaver Pond					
Number mature	550	706	909	1012	727
Number juvenile	63	64	312	204	145
% mature	89·7	91·7	75·3	83·2	83·4
Kloo Lake					
Number mature	581	709	834	—	538
Number juvenile	39	83	193	—	60
% mature	93·7	89·5	81·2	—	90·0
Microwave					
Number mature	38	15	6	29	662
Number juvenile	107	205	306	304	129
% mature	26·2	6·8	1·9	8·7	83·7

animals in every time period but one. The exception, August–September 1984, was minor and occurred when hare density was very low. Extra food was not being provided because it was summer.

The minimum faecal protein values on the food-supplemented areas remained above minimum values from the control areas in all but five time periods (Fig. 3). For the time periods when food-supplemented and control areas can be compared, minimum faecal protein values on the food-supplemented areas were significantly above those on the control (Wilcoxon test, $n=21$, $P<0{\cdot}01$). The minimum value on the food-supplemented areas fell below the 7·5% CP threshold only in the winter 1979–80, the year before the peak, and equalled the threshold in the two subsequent winters but otherwise remained above it.

The lowest mean faecal protein values for two monthly periods each year (Fig. 2) usually occurred in February–March. These lowest mean winter values are plotted in Fig. 4, together with the mean hare density for control and food-supplemented areas (measured on the following 1 April, Table 4). In both situations faecal protein was low during peak densities, but it was also low later on when hare density was low. Consequently, there is no direct correlation (using Spearman rank tests) between faecal protein and mean hare density either during the same winter or in winters before and after them. However, there is a significant negative correlation ($r_s=-0{\cdot}84$, $n=7$, $P<0{\cdot}05$) between minimum faecal protein and the annual density decline two winters later in the control areas. A similar relationship may have been present on the food-supplemented areas but the data are insufficient for a statistical test.

Plant secondary compounds in winter food

Samples of birch and juvenile grey willow twigs were collected for analysis during the winters (between November and March) from 1978–79 until 1986–87. The mean resin content is shown in Fig. 5, together with the mean density of hares on the five control areas for the same winter (the estimate of density on the following 1 April). For grey willow, resin remained constant except for a small increase 2 years after hare numbers dropped. Birch resin was much higher and more variable than that of grey willow. However, changes in birch resin did not show any consistent trends with hare density: resin content went down when hare numbers dropped, but then it increased again at low hare density. In general, resin changes neither preceded, nor predicted changes in hare density.

Figure 6 shows the values for total phenols for the same two plant species. Both showed the same general pattern: phenols showed a steady decline through the increase, peak, and decline phases of the hare cycle. When hares reached low density, phenol content increased again. There is a significant negative correlation (Spearman $r_s=-0{\cdot}83$, $P<0{\cdot}05$) between hare density and birch phenol content two winters later, and grey willow had a similar but not significant correlation. This suggests that phenol content was declining as a consequence of hare browsing, and it increased only after browsing dropped to low levels and with a lag of 2 years. Similarly, there was a positive correlation between minimum faecal protein in one year (Fig. 4) and birch resin content 1 year later ($r_s=0{\cdot}83$, $P<0{\cdot}05$). In short, plant chemical responses appeared to be following the hare cycle rather than preceding it.

Proportions of mature and juvenile twigs

In May from 1983 to 1987, mature and juvenile twigs were counted on about twenty willow bushes at each of three control sites (1050, Kloo Lake except 1986, and Beaver

Pond) and one food-supplemented site (Microwave). The numbers of twigs counted are given in Table 5. On the control areas the number of mature twigs increased by a factor of 1·43–1·89 over the 2 years 1983–85, but juvenile twigs increased even faster, by a factor of 4·95–6·78. Consequently, the proportion of mature twigs showed a significant decline on all three control areas over the 2 years. By 1986, most of the juvenile shoots had grown into the mature category again.

On the food-supplemented site (Microwave) ring-barking of the main willow stems was so severe that there were hardly any mature twigs left by the winter of 1982–83. This was the first winter of lower densities. Juvenile twigs had begun to sprout from the root stocks in summer 1982, and were counted first in May 1983. One year later, the number of mature twigs had declined (Table 5), not because of browsing, but because the few remaining large stems had died naturally; and this process continued up to 1986. Simultaneously, juvenile twigs were increasing at the same rate (by a factor of 5·19 over 1983–85) as that on the control grids. It was a further 2 years before these twigs grew enough to be classified as mature, in 1987.

In general, while hare numbers were high, juvenile grey willow shoots (which are more accessible than mature twigs) were heavily browsed and most of the vegetation was composed of mature twigs. These mature twigs remained usable as food by hares because snow loads gradually bent the stems over until they were lying flat and within reach. Only by 5 years after hare numbers dropped did plants successfully regrow twigs to the mature stage.

DISCUSSION

Food supply

Demographic analysis of the hare population by Krebs *et al.* (1986) has shown that food-supplemented populations at Kluane still declined in number, and the food treatment caused only a small delay in the decline compared with control populations. However, despite the extra food, hares may still have starved. The present data (Fig. 2) show that the food-supplemented populations had, on average, a diet well above the level where they would lose weight from undernutrition. Secondly, in only one winter (that of 1979–80) did we detect any underfed animals (Fig. 3), and this was well before the decline in density on the food-supplemented areas (Fig. 4). Thirdly, during the winter of most severe decline in hare numbers on these food-supplemented areas (1982–83), faecal protein was high and well above the starvation level. This evidence indicates that the population of these areas had access to sufficient food during the decline; and the disturbance caused by moose, mentioned earlier, did not affect the nutrition of hares. We therefore conclude that the cycle of hare numbers persisted in the presence of locally superabundant food.

On the control areas, segments of the population appeared to be underfed during five winters covering the increase, peak and decline phases (Fig. 3), with strong effects evident during the peak and decline years. In particular, the averge protein diet of the population was below body maintenance requirements in the first winter of peak numbers (Fig. 2). Smith *et al.* (1988) report that hares on the mainland control areas lost weight on average each winter from 1979 to 1982. This suggests that at high hare density some animals cannot obtain enough to eat because of the declining food supply reported by Smith *et al.* (1988). We conclude, therefore, that lack of food does occur during the hare cycle we observed (prediction 1b) but because the cycle persists with superabundant food (contrary to prediction 1a), food shortage is not a *necessary* component of the cycle. It follows that food shortage alone need not cause the cycle nor affect its periodicity.

We recognize, however, that there may be a scale effect in our results; a small patch of high hare density surrounded by low hare density towards the end of the decline phase could attract so many predators (for example) that hare numbers are driven down. In other words, the scale of our food addition experiment was small enough that its effects may have been swamped by predators from the surrounding large area where high quality hare food was scarce. It remains to be seen whether we shall obtain the same result on a larger scale, an experiment which we are now conducting. At least, we have demonstrated one case where hare numbers have declined in the presence of superabundant food.

Hare cycles have a relatively constant periodicity but a variable amplitude. In cycles with large amplitude, food shortage could be severe. In cycles with low amplitude, food may remain abundant and starvation could be largely absent. Similarly, there are areas, such as on flood plains in Alaska, where extensive ring-barking and vegetation damage occurs on a local scale at peak hare densities (Bryant *et al.* 1985), and other areas, such as Kluane, where little damage is recorded. But in both areas the cycle persists with the same periodicity. Food shortage, therefore, appears to be a (variable) consequence of the cycle, and not a cause of it.

Two aspects of the food supply have not yet been considered in detail; one is summer food. Figure 2 suggests that protein in summer food fluctuates with hare density, apparently being low when hare numbers are high. This aspect deserves further investigation because juvenile mortality in summer and autumn is correlated with the cycle (Krebs *et al.* 1986). The causes of juvenile mortality, however, are unknown. The second aspect concerns the hypothesis of Wolff (1980) which suggests that hares move into habitats with less cover and poorer food quality as numbers build up and good habitats with cover are eaten out. Thus, good habitats should show signs of heavy browsing but little mortality from predation, whereas poor habitats should show the converse low browsing effects and higher mortality by predators. The different observations of browsing effects in Alaska and Yukon may result from the habitats differing in their acceptability to hares for food and cover.

Plant responses and the hare cycle

The hypothesis that cycles in plant secondary compounds cause the hare cycle (Bryant 1981; Fox & Bryant 1984), predicts that these compounds increase during the peak and decline phases of the hare cycle, and decrease during the low phase after a 2-year lag (prediction 2). From our data, the resin in grey willow (Fig. 5) showed little change. In birch the resin component was variable; it declined while hare numbers were dropping, increased in the early low phase and declined 4 years after the drop in hare numbers. Danell & Huss-Danell (1985) also found that moose browsing lead to a decline rather than an increase in resins in *Betula pendula* Roth. and that browsing by mountain hares (*L. timidus* L.) was not affected by changes in resin content.

We found that bog birch phenols reduced the digestibility of protein by more than 50% (Table 2b). Similarly, phenols from *B. pendula* in northern Sweden reduced the digestibility of food of ruminants (Palo, Sunnerheim & Theander 1985), and phenols from various willows (*Salix* spp.) in Finland lowered the digestibility of food of mountain hares (Tahvanainen *et al.* 1985). However, phenol content of both bog birch and grey willow at Kluane decreased during the peak and decline phases and increased in the low phase of the hare cycle, again contrary to prediction 2. The secondary compound hypothesis cannot, therefore, explain declines in hare numbers as Bryant (1981) has suggested. Changes in plant chemical constituents follow the cycle in hare numbers, lagging some 2 years behind it. They cannot cause the cycle because they change in the wrong direction, going down when hare numbers are high and vice versa. Jonasson *et al.* (1986) also concluded that secondary compounds showed no clear relationship to the 4-year cycles in rodent density, and that phenols and nutrients varied more according to climatic fluctuations.

The plant structure hypothesis (Fox & Bryant 1984) predicts that the proportion of juvenile twigs (containing high amounts of unpalatable secondary compounds) in the available food should be high during the peak and decline phases and for 2–3 years in the low phase (predictions 3a, 3b). Our data on grey willow (Table 5) shows that the portion of juvenile twigs was low in the decline and first year of the low phase before increasing in 1985, contrary to prediction 3a.

The growth of juvenile shoots was a direct result of lack of browsing; their appearance was a consequence of the decline in hare numbers and not a cause of this decline. This conclusion is supported by the increase in plant growth following the hare cycle decline, reported by Smith *et al.* (1988) at Kluane and by Wolff (1978) in Alaska. We note, however, that there are few juvenile twigs on willows at Kluane at any time, in contrast to some sites in Alaska reported by Bryant (1981). Coley, Bryant & Chapin (1985) have proposed that site differences in resource availability for plants could affect the amount and type of plant defence, and recent fertilization experiments (Bryant 1987; Bryant *et al.* 1987) support this idea. This might also explain the differences in plant response recorded at Kluane and Alaska. Further, Fox & Bryant's (1984) prediction that high proportions of juvenile twigs in the low phase of the hare cycle could delay the *increase* in numbers, is partially supported by our measurements of twigs (Table 5); the increase in proportion of unpalatable juvenile twigs during the low phase of hare density may limit the availability of hare food until these twigs have matured some 3–5 years later.

Hare nutrition

Our initial conclusion that body weight maintenance could be achieved only with a mean diet of 11% crude protein (Sinclair, Krebs & Smith 1982), has been criticized on the grounds that average plant protein is far below this value and in the region of 5–7% CP (Pehrson 1984; but see Sinclair & Smith 1984b). Our measurements on the digestibility of natural food (Table 3) show that dry matter digestibility is at best 40% for the commonly eaten foods, dropping to 20% or lower for less preferred species. These measurements for hares are consistent with others in the literature (Holter, Tyler & Walski 1974; Sperber 1974; Walski & Mautz 1977; Pehrson 1981, 1983; Reichardt *et al.* 1984; Bryant *et al.* 1985). Given the protein content of the faeces (our experimental values in Table 3 were very similar to those from the wild in Fig. 2), the low digestibility means that nitrogen balance can be achieved only when food protein is at 14–16%, even higher than our original 11% CP estimate.

Figure 1 shows there are components of the winter food supply which have protein values sufficient to support hares. However, these same components, the very small twigs from the previous summer's growth, also contain the highest levels of plant secondary compounds. Reichardt *et al.* (1984) and Fox & Bryant (1984) show that these small twigs are the ones that are avoided by hares in choice tests. On the other hand, Smith *et al.* (1988) record that most of these twigs are eaten during the peak phase in numbers; and mountain hares on Swedish islands appear to choose the higher protein twigs of heather

(*Calluna vulgaris*) when few other food plant species are present (Angerbjorn & Pehrson 1987). Secondary compounds, when placed in rabbit feed at concentrations found in the wild, halved the digestive efficiency of protein. However, when dilute concentrations were used (half that in the wild), there was no effect on protein digestibility (Table 2).

We suggest three explanations for the observation that hares apparently need a diet high in protein but are unable to digest twigs containing such protein levels.

(a) Hares can detoxify small quantities of plant compounds by diluting them with other food types. If each plant species has a different secondary compound, and if the effects of these compounds are not additive, then a mixed diet could dilute the compounds from each individual species. By detoxifying small amounts of each compound, the animals could then digest the high protein (Pehrson 1981; Robbins *et al.* 1987).

(b) Our experimental results on food digestibility as well as those of Bryant *et al.* (1985) and Pease, Vowles & Keith (1979) derive from feeding trials using few plant species. It is possible that there are nutritional deficiencies (minerals, vitamins, amino-acids) in each plant species, so that a mixture of species is needed to make a complete diet. For example, sodium may be in short supply (Botkin *et al.* 1973; Belovsky & Jordan 1981; Pehrson 1983; Risenhoover & Peterson 1986), or calcium (Lindlof, Pehrson & Johansson 1978), or potassium (Lindlof, Lindstrom & Pehrson 1974), or some plants may be deficient in amino-acids.

(c) Our digestibility measurements may be wrong because of the artificial experimental situation. The most appropriate test is to measure food choice and food digestibility in free-ranging hares. Sperber's (1974) preliminary estimates of 30–40% digestibility in free-ranging mountain hares, agree with our laboratory measures but further work is needed.

Does the snowshoe hare cycle have a single cause or multiple causes?

McNamara & Houston (1987) model how starvation and predation may limit population size. In the case of snowshoe hares, strong interactions between starvation and predation could occur if hares live in habitats where they are forced to expose themselves to predators because of food shortage; i.e. there would be multiple causes of the cycle. In principle, however, predators may regulate a population even when there is superabundant food and animals are achieving their maximum rate of food intake, i.e. there may be little interaction between factors and a single cause of the cycle is possible. The appropriate test to decide which scenario applies to snowshoe hares is to compare the same population with and without predators.

Similar arguments can be produced for the interaction of social behaviour and extrinsic factors such as food supply and predation. Social behaviour could influence how animals forage or are exposed to predators; and the amount of food may alter how animals behave. Laboratory experiments on snowshoe hares (Sinclair 1986) have shown that under conditions of superabundant food, social status does not affect food acquisition, but when food is limiting social status determines who obtains the food, i.e. food supply affects the social behaviour.

The results from our experiment on snowshoe hare populations at Kluane have ruled out all but two of the five hypotheses considered (Table 1) for the cause of the cycle:

(a) a simultaneous food–predator interaction, i.e. a variation of hypothesis 4;
(b) a simple predator–prey interaction produces the regular periodicity (hypothesis 5), with weather creating a stochastic element which alters the amplitude of the cycle. Food shortage occurs during cycles of high amplitude but not during low amplitude cycles. Food shortage is, therefore, a result of the cycle, not a cause of it.

The first of the above hypotheses is supported by our observations that: (i) animals lost weight during winter in years of high densities (Smith *et al.* 1988); (ii) some hares were short of food during winter in the same years, as judged by assays of faecal protein; and (iii) hares had a major impact on the supply of winter food and may have faced relative food shortages; remaining food may have been too high in fibre or in plant secondary compounds to have allowed sufficient nutrient intake (Smith *et al.* 1988).

The second hypothesis is supported by results from our food-addition experiments which showed that the cycle persisted in the presence of sufficient food (prediction 5a). This means that under the conditions of our experiment, food shortage is not necessary and that predators can act alone to produce the cycle. Other data which support this hypothesis are reported by Keith *et al.* (1984), Boutin *et al.* (1986) and Trostel *et al.* (1987). In these studies, predation accounted for the majority of hare deaths during the peak and decline phases of the cycle. Trostel *et al.* (1987) also showed that predation acted in a delayed density-dependent way with a lag of 1 year. Similar findings for individual predator species have been reported by Keith *et al.* (1977). Simulation models of these data by Trostel *et al.* (1987) show that this lag was not sufficient by itself to produce a cycle; lags of 2–3 years were needed to produce a simple predator–prey cycle with narrow and constant values of recruitment rate towards the low end of those seen in nature, and hence the models were unrealistic. However, if the change in searching behaviour (functional response) of the predators like that recorded by Keith *et al.* (1977) and Ward & Krebs (1985) is incorporated in the model, an 8–11 year cycle appeared with hare density changes similar to those recorded in the field. Our observations on hares killed by predators did not distinguish whether predators could act alone by killing healthy hares (prediction 5b), or whether they were taking mainly starving hares, and hence acting synergistically with food supply (prediction 4b). Data from Keith *et al.* (1984), however, support the latter prediction, as do the records of hare deaths from starvation without predators given in Boutin *et al.* (1986) and Trostel *et al.* (1987).

The amplitude of hare cycles is variable. We have hypothesized that, as a consequence of this variability, food shortage occurs during cycles of high amplitude but not during low cycles. Another interpretation of this variable amplitude has been given by Schaffer (1984) and Schaffer & Kot (1986). Their analysis of lynx fur data (1821–1913) given in Elton & Nicholson (1942) shows that low and high peaks tend to alternate and, therefore, a 20-year cycle is superimposed on the 10-year cycle. They conclude that the system is deterministic but variable (i.e. displays 'chaotic' behaviour), and that three independent variables (predators, hares, and vegetation) and not two must be involved. This is consistent with the simultaneous food–predator hypothesis. However, since these conclusions are based on fur-trapping records which incorporate changes in the fur trade, economics and other confounding factors, it would be useful to analyse data more directly related to hare numbers.

CONCLUSION

Five principle hypotheses have been proposed to explain the 10-year snowshoe hare cycle: (i) a simple food hypothesis, (ii) the plant secondary compound hypothesis, (iii) the plant structure hypothesis, (iv) a two-stage hypothesis with food shortage followed by predators, and (v) a simple predator hypothesis.

Two hare populations were fed supplemental food from 1977 to 1985, and their demography and nutrition were compared to that of control populations. Nutrition was monitored by faecal protein analysis. Supplemental food raised the density of those populations, but the cycle persisted with a delay of 6–18 months. Except for a brief period in the early peak, the food-supplemented populations had superabundant food. Therefore, on the scale of our experiments, we reject the first and (in its initial form) the fourth hypothesis because food shortage was not a necessary cause of the cycle.

Changes in the secondary compound content of food species, and in the relative proportions of mature and juvenile twigs showed trends opposite to those predicted by the second and third hypotheses. Plants regenerated juvenile stems and increased their secondary compounds after hare density dropped, suggesting that changes in plant form and chemistry were following the hare cycle and not causing it.

Observations on hare mortality have shown that predators cause the majority of deaths. Evidence from faecal protein and body weights showed that some hares were starving on the control areas and this evidence could suggest a simultaneous action of predators and food supply: a modification of the fourth hypothesis. However, the food-supplement experiment shows that predators can act alone in producing the cycle at least on a local scale, supporting the fifth hypothesis. Food shortage could be a consequence of the cycle and not a cause of it; its effect could depend on the amplitude of the peak (which is variable from cycle to cycle) and may or may not act with predation. This scenario is an elaboration of the fifth hypothesis. Future work is needed to distinguish between the fourth and fifth hypotheses.

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REFERENCES

Angerbjorn, A. & Pehrson, A. (1987). Factors influencing winter food choice by mountain hares (*Lepus timidus* L.) on Swedish coastal islands. *Canadian Journal of Zoology*, **65,** 2163–2167.

Belovsky, G. E. & Jordan, P. A. (1981). Sodium dynamics and adaptations of a moose population. *Journal of Mammalogy*, **62,** 613–621.

Botkin, D. B., Jordan, P. A., Dominsky, A. S., Lowendorf, H. S. & Hutchinson, G. E. (1973). Sodium dynamics in northern ecosystems. *Proceedings of the National Academy of Sciences, U.S.A.*, **70,** 2745–2748.

Boutin, S. A., Krebs, C. J., Sinclair, A. R. E. & Smith, J. N. M. (1986). Proximate causes of losses in a snowshoe hare population. *Canadian Journal of Zoology*, **64,** 606–610.

Bryant, J. P. (1981). The regulation of snowshoe hare feeding behaviour during winter by plant anti-herbivore chemistry. *Proceedings of the World Lagomorph Conference* (Ed. by K. Myers & C. D. MacInnes), pp. 720–731. University of Guelph, Guelph, Canada.

Bryant, J. P. (1987). Feltleaf willow–showshoe hare interactions: plant carbon/nutrient balance and floodplain succession. *Ecology*, **68,** 1319–1327.

Bryant, J. P., Chapin, F. S. & Klein, D. R. (1983). Carbon/nutrient balance of boreal plants in relation to vertebrate herbivory. *Oikos*, **40,** 357–368.

Bryant, J. P., Clausen, T. P., Reichardt, P. B., McCarthy, M. C. & Werner, R. A. (1987). Effect of nitrogen fertilization upon the secondary chemistry and nutritional value of quaking aspen (*Populus tremuloides* Michx.) leaves for the large aspen tortix (*Choristoneura conflictana* (Walker)). *Oecologia*, **73,** 513–517.

Bryant, J. P. & Kuropat, P. J. (1980). Selection of winter forage by sub-arctic browsing vertebrates: the role of plant chemistry. *Annual Review of Ecology and Systematics*, **11,** 261–285.

Bryant, J. P., Wieland, G. D., Clausen, T. & Kuropat, P. (1985). Interactions of snowshoe hare and feltleaf willow in Alaska. *Ecology*, **66,** 1564–1573.

Coley, P. D., Bryant, J. P. & Chapin, F. S. (1985). Resource availability and plant antiherbivore defense. *Science*, **230,** 895–899.

Danell, K. & Huss-Danell, K. (1985). Feeding by insects and hares on birches earlier affected by moose browsing. *Oikos*, **44,** 75–81.

Elton, C. & Nicholson, M. J. (1942). The ten-year-cycle in numbers of the lynx in Canada. *Journal of Animal Ecology*, **11,** 215–244.

Fox, J. F. & Bryant, J. P. (1984). Instability of the snowshoe hare and woody plant interaction. *Oecologia*, **63,** 128–135.

Graf, R. P. (1985). Social organization of snowshoe hares. *Canadian Journal of Zoology*, **63,** 468–474.

Holter, J. B., Tyler, G. & Walski, T. (1974). Nutrition of the snowshoe hare (*Lepus americanus*). *Canadian Journal of Zoology*, **52,** 1553–1558.

Jonasson, S., Bryant, J. P., Chapin, F. S. & Andersson, M. (1986). Plant phenols and nutrients in relation to variations in climate and rodent grazing. *American Naturalist*, **128,** 394–408.

Keith, L. B. (1974). Some features of population dynamics in mammals. *Proceedings of the International Congress of Game Biologists*, **11,** 17–58.

Keith, L. B. (1983). Role of food in hare population cycles. *Oikos*, **40,** 385–395.

Keith, L. B., Cary, J. R., Rongstad, O. J. & Brittingham, M. C. (1984). Demography and ecology of a declining snowshoe hare population. *Wildlife Monographs*, **90,** 1–43.

Keith, L. B., Todd, A. W., Brand, C. J., Adamcik, R. S. & Rusch, D. H. (1977). An analysis of predation during a cyclic fluctuation of snowshoe hares. *Proceedings of the International Congress of Game Biologists*, **13,** 151–175.

Krebs, C. J., Gilbert, B. S., Boutin, S., Sinclair, A. R. E. & Smith, J. N. M. (1986). Population biology of snowshoe hares. I. Demography of food-supplemented populations in the southern Yukon, 1976–84. *Journal of Animal Ecology*, **55,** 963–982.

Lindlof, B., Lindstrom, E. & Pehrson, A. (1974). Nutrient content in relation to food preferred by mountain hare. *Journal of Wildlife Management*, **38,** 875–879.

Lindlof, B., Pehrson, A. & Johansson, A. (1978). Summer food preference by penned mountain hares in relation to nutrient content. *Journal of Wildlife Management*, **42,** 928–932.

McNamara, J. M. & Houston, A. I. (1987). Starvation and predation as factors limiting population size. *Ecology*, **68,** 1515–1519.

Palo, R. T., Sunnerheim, K. & Theander, O. (1985). Seasonal variation of phenols, crude protein and cell wall content of birch (*Betula pendula* Roth.) in relation to ruminant *in vitro* digestibility. *Oecologia*, **65,** 314–318.

Pease, J. L., Vowles, R. H. & Keith, L. B. (1979). Interaction of snowshoe hares and woody vegetation. *Journal of Wildlife Management*, **43,** 43–60.

Pehrson, A. (1981). Winter food consumption and digestibility in caged mountain hares. *Proceedings of the World Lagomorph Conference* (Ed. by K. Myers & C. D. MacInnes), pp. 732–742. University of Guelph, Guelph, Canada.

Pehrson, A. (1983). Digestibility and retention of food components in caged mountain hares, *Lepus timidus*, during the winter. *Holarctic Ecology*, **6,** 395–403.

Pehrson, A. (1984). Faecal nitrogen as an index of hare browse quality. *Canadian Journal of Zoology*, **62,** 510–513.

Reichardt, P. B., Bryant, J. P., Clausen, T. P. & Wieland, G. D. (1984). Defense of winter-dormant Alaska paper birch against snowshoe hares. *Oecologia*, **65,** 58–69.

Risenhoover, K. L. & Peterson, R. O. (1986). Mineral licks as a sodium source for Isle Royal moose. *Oecologia*, **71,** 121–126.

Robbins, C. T., Hanley, T. A., Hagerman, A. E., Hjeljord, O., Baker, D. L., Schwartz, C. C. & Mautz, W. W. (1987). Role of tannins in defending plants against ruminants: reduction in protein availability. *Ecology*, **68,** 98–107.

Schaffer, W. M. (1984). Stretching and folding in lynx fur returns: evidence for a strange attractor in nature? *American Naturalist*, **124,** 798–820.

Schaffer, W. M. & Kot, M. (1986). Chaos in ecological systems: the coals that Newcastle forgot. *Trends in Ecology and Evolution*, **1,** 58–63.

Sinclair, A. R. E. (1986). Testing multi-factor causes of population limitation: an illustration using snowshoe hares. *Oikos*, **47,** 360–364.

Sinclair, A. R. E., Jogia, M. K. & Andersen, R. J. (1988). Camphor from juvenile white spruce as an antifeedant for snowshoe hares. *Journal of Chemical Ecology*, **14,** 1505–1514.

Sinclair, A. R. E., Krebs, C. J. & Smith, J. N. M. (1982). Diet quality and food limitation in herbivores: the case of the snowshoe hare. *Canadian Journal of Zoology*, **60,** 889–897.

Sinclair, A. R. E. & Smith, J. N. M. (1984a). Do plant secondary compounds determine feeding preferences of snowshoe hares? *Oecologia*, **61,** 403–410.

Sinclair, A. R. E. & Smith, J. N. M. (1984b). Protein digestion in snowshoe hares. *Canadian Journal of Zoology*, **62,** 520–521.

Slawyk, G. & MacIsaac, J. J. (1972). Comparison of two automated ammonium methods in a region of coastal upwelling. *Deep-Sea Research*, **19,** 521–524.

Smith, J. N. M., Krebs, C. J., Sinclair, A. R. E. & Boonstra, R. (1988). Population biology of snowshoe hares. II. Interactions with winter food plants. *Journal of Animal Ecology* **57,** 269–286.

Sperber, I. (1974). Food utilization of *Lepus timidus* in the winter. *Proceedings of the International Congress of Game Biologists*, **11,** 175–177.

Swain, T. & Goldstein, J. L. (1964). The quantitative analysis of phenolic compounds. *Methods in Polyphenol Chemistry* (Ed. by J.B. Pridham), pp. 131–146. MacMillan, New York.

Tahvanainen, J., Helle, E., Julkunen-Tiitto, R. & Lavola, A. (1985). Phenolic compounds of willow bark as deterrents against feeding by mountain hare. *Oecologia*, **65,** 319–323.

Trostel, K., Sinclair, A. R. E., Walters, C. J. & Krebs, C. J. (1987). Can predation cause the 10-year hare cycle? *Oecologia*, **74,** 185–193.

Walsky, T. W. & Mautz, W. W. (1977). Nutritional evaluation of three winter browse species of snowshoe hares. *Journal of Wildlife Management*, **41,** 144–147.

Ward, R. M. P. & Krebs, C. J. (1985). Behavioural responses of lynx to declining snowshoe hare abundance. *Canadian Journal of Zoology*, **63,** 2817–2824.

Wolff, J. O. (1978). Burning and browsing effects on willow growth in interior Alaska. *Journal of Wildlife Management*, **42,** 135–140.

Wolff, J. O. (1980). The role of habitat patchiness in the population dynamics of snowshoe hares. *Ecological Monographs*, **50,** 111–130.

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