Diet quality and food limitation in herbivores: the case of the snowshoe hare

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Arguments concerning the regulation of animal populations through food shortage are hampered by the difficulty of measuring available food. This is avoided by considering how animals respond to declining food supplies. Three alternatives exist: (*a*) maintain a constant rate of food intake by including more poor food, (*b*) increase the quantity eaten to compensate for poor quality, or (*c*) eat only high-quality foods and thus decrease the quantity eaten. Experiments with snowshoe hares (*Lepus americanus*) fed ad libitum food of different crude protein values, show hares maintain a relatively constant intake rate as quality falls. This result allows us to use mean diet quality to predict whether animals can maintain body weight under natural conditions. The threshold diet quality below which weight loss occurred was 11% crude protein in the laboratory. There is a strong correlation between diet crude protein and faecal crude protein. By collecting faecal pellets in the field, one can monitor the diet of the population. If faecal crude protein falls below 7.5%, animals lose weight as a result of insufficient good food. Field data for 1977–1980 show faecal protein for some animals dropping below this level in late winter of 1979 when the hare population was near its peak density.

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L'étude du contrôle des populations animales par insuffisance de nourriture est compliqué par la difficulté de mesurer la nourriture disponible. Cette difficulté est contournée en étudiant comment les animaux réagissent à une diminution des sources de nourriture. Il existe trois alternatives: (*a*) maintenir un taux constant d'ingestion de nourriture en ajoutant des aliments peu nutritifs, (*b*) augmenter la quantité de nourriture ingérée de façon à en compenser la mauvaise qualité et (*c*) ingérer seulement des aliments très nutritifs et diminuer par le fait même la quantité ingérée. Des lièvres *Lepus americanus* nourris ad libitum d'aliments de contenus protéiniques variés maintiennent un taux relativement constant d'ingestion de nourriture à mesure que diminue la qualité de la nourriture. Ces données nous permettent d'utiliser une qualité alimentaire moyenne pour prédire si les animaux sont capables de maintenir leur poids corporel dans des conditions naturelles. En laboratoire, le seuil de qualité alimentaire, valeur sous laquelle il y a perte de poids, a été établi à 11% de protéines brutes. Il y a une forte corrélation entre les protéines brutes de la diète et les protéines brutes des fèces. En recueillant les boulettes fécales en nature, il est possible d'évaluer la diète de la population. Si les protéines brutes des fèces sont inférieures à 7,5%, les animaux perdent du poids par insuffisance de nourriture de qualité. Des données recueillies en nature de 1977 à 1980 ont démontré que les protéines fécales de certains animaux ont atteint des valeurs inférieures à 7,5% à la fin de l'hiver 1979 au moment où la population de lièvres atteignait presque sa densité maximale.
[Traduit par le journal]

Optimal foraging theory predicts that animals, when faced with an abundant supply of food types varying in nutritional value, will select only the better types of food and will ignore the others, even if these are very abundant (Pyke et al. 1977; Krebs 1978). The converse is that, as the best foods become scarce, more lower quality food types are incorporated into the diet. A few experimental studies (e.g., Werner and Hall (1974) on sunfish; Krebs et al. (1977) on birds) support this, together with even fewer quantitative field studies. Goss-Custard's (1977) study of shore birds showed that large polychaete worms were eaten in proportion to their density, but small worms were eaten only when large worms were at low density. Thus, the birds became less selective as food supply declined. Similarly, large mammal grazers, such as wildebeest and African buffalo, showed strong selectivity for high protein grass leaves when these were abundant, but low-quality stems were eaten as leaf biomass declined; there was a clear decline in selectivity (Sinclair 1975, 1977).

This decline in selectivity as absolute food abundance declines has important implications for population dynamics. If an animal maximizes its net rate of intake of critical nutrients (either protein, energy, or minerals), then as food abundance falls, the incorporation of low quality food types will lower the average quality of the diet below the point where the animal can maintain it's body weight. The animal will eat low-quality items provided it can obtain some nutritional return above the cost of searching and digesting. This means that

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virtually all edible material that is not poisonous or inaccessible must be considered as food, even if in the long run the animal may starve on such a diet. This creates a formidable problem in measuring available food.

A consequence of this is that one should not try to measure the available quantity of food to determine whether the food supply is in excess or insufficient for the population. Instead, one should measure the mean food quality eaten by individuals and compare this with the quality at which they can maintain body weight. If they cannot maintain weight, then those animals are by definition food limited (Sinclair 1975, 1977).

We have used this approach in a study of snowshoe hares (*Lepus americanus*). Hares show a regular cycle of high and low numbers of about 10 years periodicity. Keith (1974) proposed that such fluctuations are produced by hares eating out their food supplies and then dying, either of starvation or by predation. To investigate this hypothesis, one must determine whether there is insufficient food at the peak of the cycle. Pease et al. (1979) offered branches of edible shrubs to captive hares and measured how much was eaten. A rough estimate of intake was 300 g of fresh browse per day selected from 3000 g offered. Using this estimate of 10% edible fraction, they calculated available food and concluded it was insufficient at peak hare numbers.

The main problem with this technique is that the experimenter decides what is food by selecting the plant species and parts. If the food is not what the animal feels like eating at the time (unpalatability, insufficient variety, and disturbed conditions are possible reasons), the animal will eat less than it would normally do in the wild. This would lead to an underestimate of available food. None of the hares tested by Pease et al. (1979) were able to maintain weight, which suggests that the 10% edible fraction they use is in fact an underestimate.

Because of the difficulty of estimating how a hare feeds and how much it eats, we have approached the problem in a different way, by letting the hare do the choosing in the wild, and then monitoring the mean diet quality. This paper describes the rationale and the experimental evidence for it.

Mean diet quality and food shortage

As the available good food declines, the mean quality at intake also declines because of the incorporation of poor-quality food items (Fig. 1, line A). At some point, this mean diet quality falls below the threshold of body weight maintenance. Below this threshold, it pays the animal to eat very low quality items because it can still obtain some benefit from them, and thereby reduce the rate of weight loss. If the animal continued to search for the few good-quality items without eating poorer foods, it would lose weight even faster, which in turn would reduce the time an animal can withstand nutritional stress before dying.

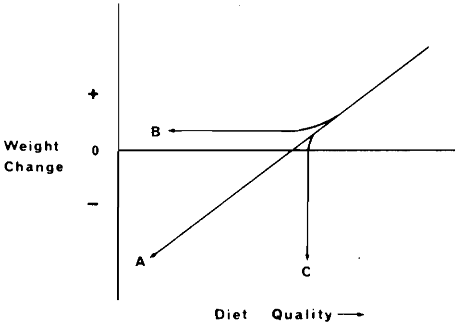

FIG. 1. Hypothetical effects on body weight produced by three feeding strategies when the supply of high-quality food declines: A is produced by including low-quality food but keeping the amount of food eaten per day constant; B by including low-quality food but increasing the daily food consumption; C by eating only high-quality food while allowing daily food consumption to fall.

If this reasoning is correct, it should be possible to identify a mean diet quality below which an animal cannot maintain body weight. Once this threshold quality is known, it can be used to determine operationally whether food supply is limited for a wild population; *if animals are found with mean diet quality below the threshold, this is the critical evidence that food is limited.* This approach avoids the problem of identifying and measuring the available food.

The use of mean diet quality as an index of food abundance may be misleading in two different circumstances. Firstly, an animal may be able to maintain body weight on a low-quality diet if it can compensate for low quality by eating a larger quantity. In Fig. 1 this would produce line B, mean diet quality declines, but the threshold of body weight maintenance is not crossed. This can be examined by measuring how much is eaten at different diet qualities. If hypothesis B is correct, the quantity eaten should increase as quality falls.

Secondly, an animal could adopt the opposite strategy of limiting its diet to high-quality foods only, and when these are in short supply, simply allow the amount eaten to fall. In Fig. 1, this would produce line C, the quality remains high but the animal loses weight rapidly because there is not enough high-quality food. Ruminants, such as white- and black-tailed deer (*Odocoileus virginianus*, *O. hemionus*) and caribou (*Rangifer tarandus*) adapt to winter conditions by voluntarily reducing their intake rate and metabolism to counteract the stress of low temperatures (Ozaga and Verme 1970; McEwan and Whitehead 1970; Moen 1978). The effect of low temperatures can be examined by measuring the amount eaten at different temperatures. The prediction for hypothesis C is that intake should decline as temperature declines.

Finally, natural foods contain secondary compounds such as resins and phenols. These compounds may interfere with digestion, causing an increase in faecal protein (Bryant and Kuropat 1980; Mould and Robbins 1981). If this occurs, it could increase the threshold value of protein for body weight maintenance. We therefore conducted some preliminary experiments to examine whether digestion in hares is affected by these chemicals.

Methods

Ten hares of both sexes were kept singly in rooms or environment chambers under constant temperature conditions and with a 7-h light period (0900–1600) at the Small Mammal Research Facility of the University of British Columbia. All experiments were performed during the winters of 1979 and 1980, between December and March (when the animals were reproductively inactive).

The food offered was either standard rabbit pellets (Purina or Buckerfields) for high quality, or pellets were made locally for low-quality food by crushing standard pellets, mixing either with cellulose powder or crushed maize cob material (Sanicel) and repelleting the mixture. In all trials, food and water (or snow) were offered ad libitum.

At intervals of 1–3 days, the animals were captured and weighed, together with the food and faecal pellets. Snowshoe hares are nervous, timid animals. They suffer some stress when captured in live traps and handled, and such stress may affect their weight: to avoid this problem, we provided the hares with aluminium boxes (46 × 21 × 21 cm) that had a sliding front trap door. The animals soon learned to hide in the boxes, and weights were obtained (to nearest 1 g) at the same time of day by the difference in occupied and unoccupied box weights on a platform scale. In this way we avoided handling the animals.

Each treatment of diet quality or temperature was matched with a control. We also tried to present each animal with the full range of treatments so that the animal could act as its own control.

When animals on a high-quality diet were presented with a lower quality diet, their first response was to stop eating (or eat only a small amount) a response we termed a "hunger strike" (see Fig. 2). Depending on the animal and how poor the food was, the hunger strike lasted 1–4 days, during which time the animal lost weight. Eventually the animal resumed eating and measurements of weight loss were considered only after intake returned to a steady amount.

Food quality was measured in terms of crude protein as a percentage of dry matter. Since in most parts of plants, protein and energy are correlated (Armstrong et al. 1964), protein can be used as an index of the nutritional content of the food. Protein content of the food pellets and the faeces were calculated from measurements of total nitrogen by the rapid microkjeldahl method of digestion (Anonymous 1975; Concon and Soltess 1973), followed by analysis of ammonia in an autoanalyser. Results were checked with a hay standard of known value and by comparison of subsamples analysed for us by the Faculty of Agriculture, University of British Columbia.

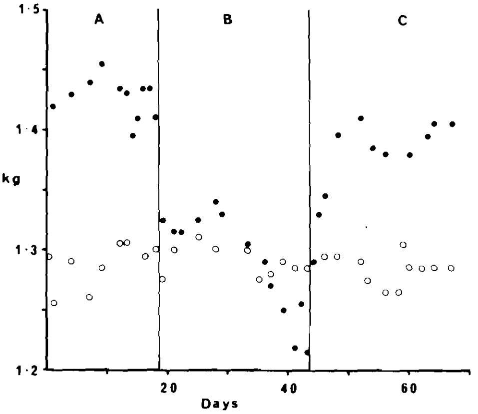

FIG. 2. Weight changes in an experimental (closed circle) and control hare (open circle). The experimental individual received 20% crude protein rabbit chow ad libitum in time periods A and C, and 9% crude protein during B. The control received 20% crude protein throughout. The lower mean weight of the control is not unusual; it is within the normal range of the field population.

The effects of resin and phenol on food digestibility were measured using rabbit chow impregnated with these chemicals. Resin was extracted from terminal twigs of young white spruce (*Picea glauca*) using ether. The extract solution was poured over 20% protein chow and the ether evaporated either at 55°C or at room temperature (about 20°C). The resin concentration in the chow was approximately 10% of dry weight, similar to that in natural food. Phenols were extracted from twigs of soapberry (*Sheperdia canadensis*) with methanol, and added to the chow in the same way as was resin. Phenol concentration was approximately 25% of that found in the plant.

Three hares were given the resin chow, and three were given the phenol chow, each for about 10 days. Food eaten and faecal output were measured daily. Faecal samples were also analysed for nitrogen as above. Measurements were made after 5 days to avoid contamination from the previous diet. Following the impregnated chow, the same animals were given normal chow treated with ether or methanol alone to obtain control values for digestibility and faecal protein after 5 more days.

Results

Mean diet quality and weight loss threshold

All hares were started at below normal body weight when they were given the different protein quality diets. On a high protein diet, a hare that was below normal weight gained weight initially and then maintained a steady weight. At lower quality diets, the initial weight gain was slower and at the threshold quality the hare was unable to regain weight; it merely maintained the under-

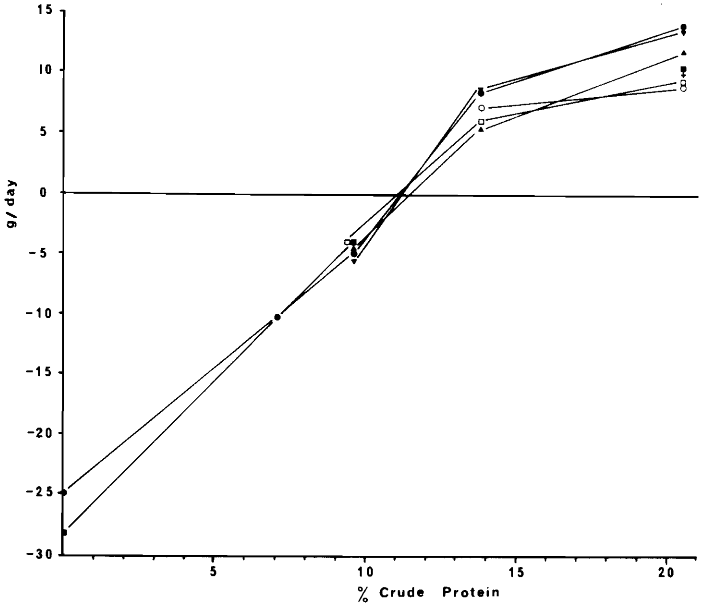

FIG. 3. The relationship of weight change to diet crude protein. Symbols refer to different individuals. Threshold of zero weight gain is estimated to occur at a diet of 11.3% crude protein.

weight condition. With below-threshold food quality, weight loss continued.

Figure 2 illustrates the weight changes of two hares. One was fed good-quality food, then poor-quality food, then returned to the high nutritional plane. The other (control) animal was maintained on the same high-quality diet throughout. The sharp initial weight loss when poor-quality food was offered (9% crude protein) was due to a hunger strike. After 4 days, the animal ate normally but was unable to regain, or even maintain weight. It regained its original weight in 10 days, when offered good food (20% crude protein).

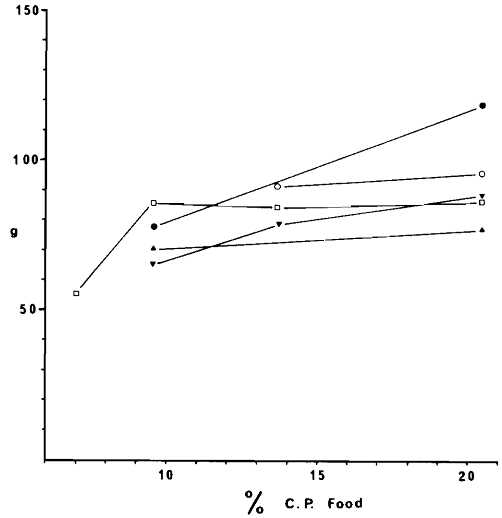

FIG. 4. The daily amount eaten in relation to the crude protein (C.P.) quality of the food. Temperature constant at 10°C. Symbols refer to different individuals.

Figure 3 shows average weight change plotted against food quality. Weight gains were measured during the 10 days following a period of weight loss from poor-quality food. At the higher quality diets, weight gains approached the physiological maximum. At the low 9% protein level, rate of weight loss was remarkably consistent in the three males and two females tested. One male and one female were offered the completely indigestible ground maize cob (Sanicel) for short periods, and both showed similar maximal rates of weight loss of 25–30 g/day. Pease et al. (1979) found that animals on starvation diet in outdoor pens in winter could lose up to 55 g/day. The threshold quality food for zero weight change was similar for the four animals tested and averaged 11% crude protein.

Consumption rate at different food qualities

If animals compensated for low mean diet quality by eating more, then intake rate should increase as quality declines (Fig. 1, line B). Figure 4 shows the quality eaten per day as a function of quality when temperature was constant at 10°C. Although there was some variability between animals, none ate more food as quality declined. Either the intake rate remained more or less constant or it decreased as quality declined. There is some evidence that this relationship also holds for natural foods; Bookhout (1965) found that hares ate less of the low-quality, unpalatable plants than the high-quality species. Hence, we reject hypothesis B of Fig. 1.

These results are in agreement with the ruminant literature (Chalmers 1961; Sinclair 1977). Hares, like ruminants, are pure herbivores and have similar nutritional physiology. The low intake rate at low-quality diets was possibly due to the longer time the food must remain in the gut for digestion to occur. Snowshoe hares perform coprophagy (eating soft pellets direct from the anus to pass the food through the gut a second time before producing the final hard pellets). Even this presumed adaptation to high-fibre diets has its limitations. Figure 5 shows the faecal output over periods of 1–4 days plotted against food consumed in the same time period. The slope of the regression lines for different food qualities is a measure of dry matter digestibility. For 20% crude protein food, apparent dry matter digestibility ((food − faeces)/food) averages 67%, and this declines to 45% for 9% crude protein food, values similar to those found for snowshoe hares by Holter et al. (1974). Apparent protein digestibility calculated from the amount of protein in the food and faeces was higher than the dry matter digestibility. For the two food types above, protein digestibility averaged 77 and 58% respectively.

Consumption rate and environmental stress

If animals responded to adverse environmental conditions, such as cold stress, by reducing their intake rate, they could consume a high-quality diet but still lose weight. Figure 6 shows that intake rate of 20% crude protein food increased as temperature declined. These results show that as body demands for maintenance increase at low temperatures, hares respond by increasing their consumption rate. Minimum temperatures in the environment chambers reached −25°C, but under natural conditions, Yukon hares may experience temperatures of −40°C for 2–3 weeks at a time. At −25°, hares eat 30–50 g (33–45%) more per day than they do at 10°C. In Alberta, Pease et al. (1979) found a similar increase in consumption rate of hares as temperature dropped.

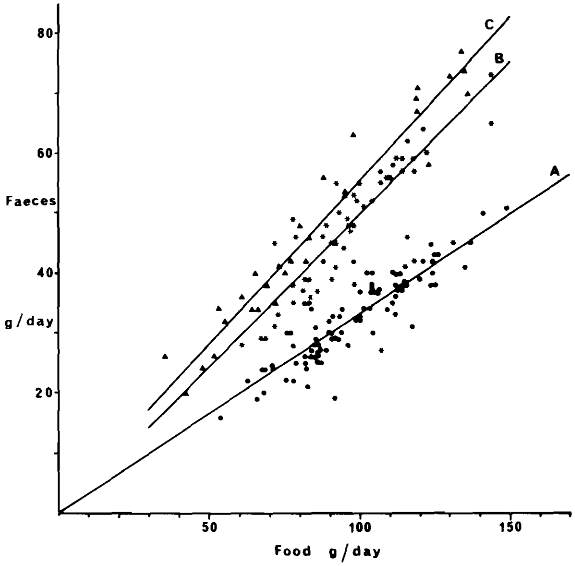

FIG. 5. The relationship of daily faecal output to food intake at three diet qualities: (A) for 20% crude protein produces an apparent dry matter digestibility of 67%; (B) for 13% crude protein produces 49% digestibility; (C) for 9% crude protein produces 45% digestibility. A, ●; B, *; C, ▲.

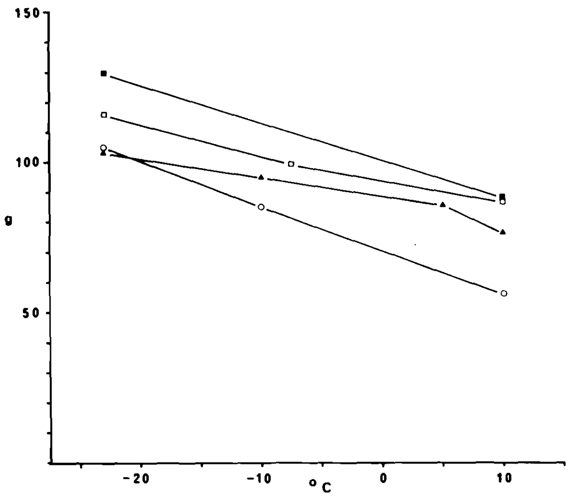

FIG. 6. The daily food intake increases as temperature declines. Food quality constant at 20% crude protein. Symbols refer to different individuals.

Monitoring diet quality under natural conditions

Direct monitoring of diet quality in live animals in the field is difficult. Therefore, we have developed an indirect method of measuring diet quality. Figure 7 shows the relationship between diet quality and the crude protein content of the faeces; there is a clear positive correlation between the two ($r = 0.96$, $n = 66$), a result similar to that found for ruminants (Bredon et al. 1963; Sinclair 1977; Mould and Robbins 1981). Over the range of 9–20% crude protein in the food, an increase of 5% crude protein results in an increase of approximately 3% crude protein in the faeces. This curve should be concave at high food values because of greater protein digestibility at those levels (Holter et al. 1974). At very low food values, the curve should turn down to meet the x-axis at approximately 2.7% crude protein, this being the value for the excretion of metabolic protein calculated by Holter et al. (1974). For our purposes, these extrapolations do not concern us

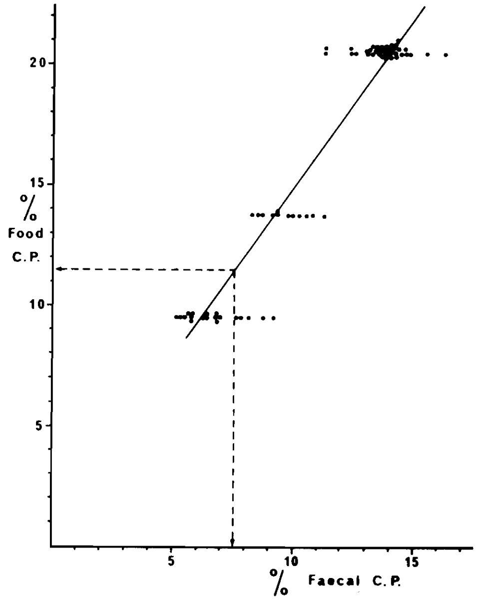

FIG. 7. The relationship of faecal crude protein (x) to food crude protein (C.P.) (y). Diet threshold for zero weight gain of 11.3% crude protein gives a faecal value of 7.5% crude protein. $y = 0.8667 + 1.409x$.

because we do not get animals in the field at these two extremes. Figure 7 shows the faecal crude protein (7.5% crude protein) equivalent to the threshold diet quality (11% crude protein) for zero weight gain.

As an example of how this method can be used, we present some field measurements in Fig. 8 collected in 1977–1980 near Kluane Lake and Dezadeash Lake, Yukon. Hares were livetrapped overnight and fresh faeces were collected from beneath the trap. Only hard, second-passage pellets were collected. Figure 8 illustrates the decline in the mean faecal quality as food changes from herbs in summer to woody stems in winter. The lowest quality occurred, as one might expect, in late winter, and a rapid increase followed in spring. In the winter of 1979–1980, mean faecal quality in some animals crossed the 7.5% crude protein threshold, suggesting that high-quality food was in short supply at that time.

The effect of secondary compounds on digestibility and faecal protein

Dry matter digestibility and faecal protein values of hares fed impregnated and control chow are given in Table 1, together with their 95% confidence limits. Phenol chow significantly lowered ($P < 0.001$) dry matter digestibility and raised the faecal protein content compared with the methanol-treated control chow. The amount of food eaten did not differ between phenol-treated and control chow. Protein digestibility of phenol chow was half that of control chow, and approached the level of 30% reported for natural foods (J. P. Bryant, personal communication). Consequently, the daily amount of protein digested was half that from control chow.

Resin-treated chow, on the other hand, had no detectable effect on either digestibility or faecal protein content. Unless our method of extraction somehow changed the resin, this extract did not appear to affect the nutrition of hares. The marked effect of phenols on the faecal protein suggests that, for natural foods, the weight maintenance threshold of faecal protein may be higher than the 7.5% of our experiments. This requires further investigation.

Discussion

Why should an animal continue to eat food which will cause weight loss? Provided it can obtain at least a small benefit from this food, it will help to reduce the rate of weight loss and the individual thus buys time. The slower this rate of weight loss, the longer the animal can withstand the adverse conditions of food shortage.

Although some animals die after losing as much as 40% of body weight, many die when 25% of their weight is lost (Pease et al. 1979), and we have found that some (e.g., juveniles) will die under the stresses of natural conditions after losing only 15% of their weight. Figure 9 illustrates how a hare of 1200 g, which we assume will die after losing 200 g, might buy time by eating low-quality food, rather than none at all. A diet of 9% crude protein allows the hare to survive a month, but a 5% crude protein diet allows survival for only 2 weeks. Bookhout (1965) showed that hares fed high-quality natural browse survived the length of his experiment (3–5 weeks) while those fed low-quality, unpalatable species, survived only 2–4 days.

The concept of a lower diet quality threshold is well known for ruminants. Cows needs a diet of at least 5% crude protein for their rumen microorganisms to function efficiently (Chalmers 1961). Sheep feeding on low-quality range grasses have a low consumption rate and microbial activity compared with those whose diet was supplemented with urea (Oh et al. 1969). For snowshoe hares, the threshold estimate of an 11% crude protein diet and the resulting estimates of survival time are highly conservative. They were calculated under optimum conditions for the animal; mild temperatures (+10°C), no competition or stress from other animals, no requirement to search for their food, and the food did not contain any inhibitory secondary plant compounds. All of these factors, together with the stresses of reproduction (males start reproductive chases in February) and parasite loads, will raise the threshold diet quality above the estimated 11% crude protein.

In the Kluane region, the main foods of hares are

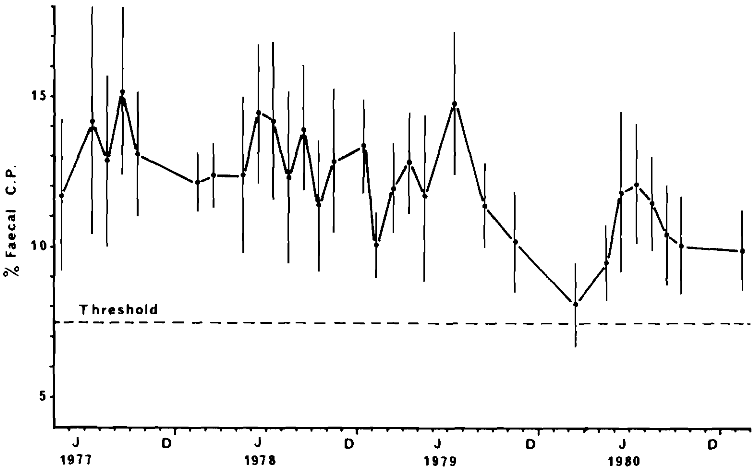

FIG. 8. Mean faecal crude protein (C.P.) from snowshoe hares in natural populations near Kluane and Dezadeash Lakes, Yukon. Vertical lines show one standard deviation.

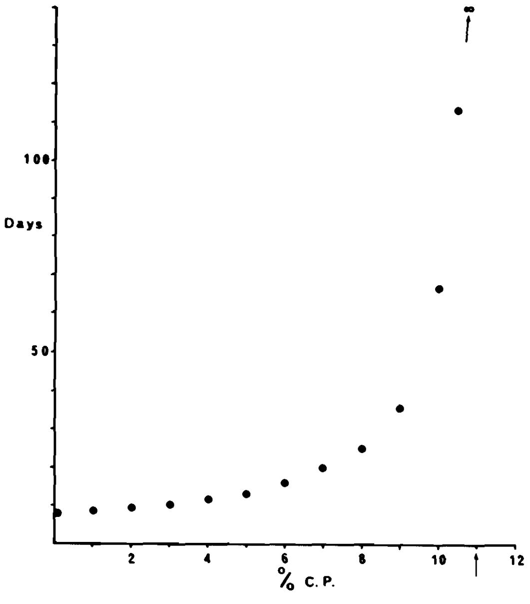

FIG. 9. Estimated time for a hare to lose 200 g body weight at different mean diet qualities below the threshold level (arrow). C.P., crude protein.

small twigs (< 5 mm diameter) of white spruce, dwarf birch (*Betula glandulosa*), and various willow (*Salix*) species. Average crude protein content of these twigs is about 6.5%, a value similar to those found in Alberta, Alaska, and Scandinavia (Klein 1977; Oldemeyer 1974; Oldemeyer et al. 1977; Lindlof et al. 1974; Pease et al. 1979). This raises the dilemma of how hares can survive on natural food, when the estimated average quality required in our laboratory studies is 11% protein.

We suggest three possible explanations for this paradox. First, average values of clipped twigs may underestimate the quality of food chosen by hares. Some of the shrubs eaten by hares (e.g., silverberry, *Eleagnus commutata*) contain at least 9% protein. Also, bark, small twigs (< 2 mm diameter) and buds of some species have protein values much above 6.5%; in dwarf birch, small twigs have 13% protein (personal observation); aspen (*Populus tremuloides*) bark has 12.7% protein (Oldemeyer 1974); soapberry bark is 20% protein, and it is this part of the shrub that hares select (personal observation). At the other extreme, the wood of most twigs is only about 5% protein. If 60% of hares' diet was 5% protein wood, and the remaining 40% was bark of 20% protein, their mean diet would contain 11% protein. In short, average values of twigs clipped at 5 mm diameter do not necessarily represent the diet that hares select.

Second, hares may be able to survive better on natural food than on our pelleted food, so that our threshold value of 11% protein is artificially high. This is clearly an area for further investigation, though there are technical problems because secondary compounds in natural food may interfere with protein digestibility. Indeed, we used pelleted food in our experiments to avoid this difficulty. Our data on faecal protein from the field suggest that hares cannot live on a natural diet of 6.5% protein.

It is important to consider the protein requirements of hares on an absolute rather than a percentage basis. Let us consider some hypothetical calculations to illustrate how input–output requirements could be met. In our experiments, hares maintain body weight at an intake value of 7 g crude protein/day. If in the wild, an animal needs this 7 g to maintain weight and produces faeces at the threshold value of 7.5% protein, we can estimate the

TABLE 1. Digestibility and faecal protein for three hares fed rabbit chow treated with phenols (experiment A) and resins (experiment B); 95% confidence limits in parentheses

	% dry matter digestibility	% faecal protein	% protein digestibility	Protein eaten (g/day)
Experiment A				
Phenol chow	43.7 (3.3)	24.15 (0.85)	32	5.1
Control chow	60.0 (2.6)	16.53 (1.08)	67	10.7
Experiment B				
Resin chow	68.3 (3.4)	15.17 (0.70)	76	15.20
Control chow	63.8 (2.3)	15.37 (1.77)	72	14.44

food quality that is required. We assume they eat natural food at 150 g dry matter per day (Bookhout 1965; Pease et al. 1979) at 30% dry matter digestibility (J. P. Bryant, personal communication). The total protein required by the animal is 7 g digested and 7.9 g in the faeces, which is, therefore, 14.9 g obtained from 150 g of food. Thus, the mean protein content of the food would be 9.9%.

However, if the diet averaged 6.5% protein (the average field value of clipped twigs), then faecal protein would only be 2.6%, a value lower than anything so far found in the field (cf., Fig. 8). It therefore seems that wild hares must select a diet higher than 6.5% protein, and that they could survive on a natural diet of 10% protein.

Third, we might have done our chemical analyses improperly. We can dismiss this possibility because we have done replicate samples to check our nitrogen values. We have also exchanged a set of 12 samples with J. P. Bryant at the University of Alaska and found good agreement ($r = 0.94$, $b = 1.03$ for regression through the origin).

We conclude that the most plausible explanation for the discrepancy between high protein requirement found in the laboratory and the low average protein content of plants in the field is that hares are highly selective in feeding on twigs of above-average protein content.

The method we offer can err in concluding food is not in short supply when in fact it is. Our approach was designed primarily to test the hypothesis that food limitation in snowshoe hares operates through protein deficiency. But food may be in short supply because of the effects of social status on feeding behaviour or because of the effects of secondary plant compounds on digestibility (Bryant 1981). Further work is needed on both these factors.

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