

The Herbivore-Based Trophic System

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INTRODUCTION

The tundra is well known for its conspicuous and abundant animal populations. Indeed, tundra may be better characterized by caribou, wolves, lemmings, snowy owls, ptarmigan and hordes of flies than by any other feature, at least in popular literature. The next two chapters consider the composition and organization of animal communities, and their participation in the energy and nutrient dynamics of the coastal tundra ecosystem.

Ultimately, all heterotrophic activity, animal and microbial, depends upon the energy and nutrients fixed by green plants in net primary production. The amount of net primary production (Chapter 3) sets a limit upon the abundance and production of heterotrophic organisms. Two more or less distinct trophic systems based upon this net primary production may be recognized in virtually all ecosystems—a herbivore-based system that begins with the consumption of living autotroph tissue, and a detritus-based system that begins with the consumption of dead organic matter (Figure 10-1) (Batzli 1974, Heal and MacLean 1975). The distinction corresponds broadly to an aboveground and belowground division (perhaps reflecting a paucity of information on belowground herbivory). The two trophic systems may converge to some extent, particularly at the top carnivore level, and a single animal population may function in both trophic systems; this is a categorization of trophic functions rather than animals.

Several important conceptual differences distinguish the two trophic systems. The herbivore-based system begins with the consumption of living plant tissue, and thus impacts directly upon plant production, growth, and reproduction. Thus herbivores (or, indirectly, carnivores preying upon herbivores) modify the rate of input of chemical energy

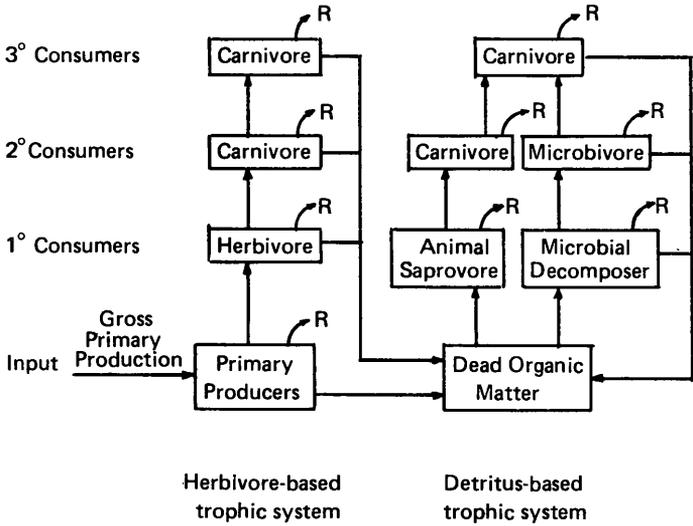


FIGURE 10-1. A generalized trophic structure for terrestrial ecosystems, showing the distinction between herbivore-based and detritus-based trophic systems. Arrows represent the flow of energy and materials; R represents respiratory loss of energy. (After Heal and MacLean 1975.)

(fixed carbon) into the ecosystem. The detritus-based system is based upon the consumption of dead organic matter. Saprovores and microorganisms influence the ecosystem through their control of the rate of decomposition and cycling of mineral nutrients. There is ample reason to believe that, in tundra, this is particularly important (Chapter 5). Other distinctions between the herbivore- and detritus-based trophic systems are discussed by Heal and MacLean (1975).

Herbivore-based food chains in arctic regions contain relatively few taxa. Whole groups of invertebrates that are common in grasslands at lower latitudes, e.g. insects and mollusks, have few representatives in the Arctic (MacLean 1975a). The most abundant herbivores are homeotherms, probably because they can maintain high rates of activity and growth at low temperatures.

Herbivorous birds, especially ptarmigan (*Lagopus* spp.) and geese (*Anser albifrons*, *Branta canadensis* and *Chen hyperborea*), use the North American tundra as a breeding ground during summer, but their occurrence and impact appear to be patchy. While avian herbivores generally migrate south in late summer, some ptarmigan do overwinter on inland tundra where they consume mostly willow buds and twigs (West and Meng 1966).

Some mammalian herbivores also occur sporadically on the tundra. Ground squirrels (*Spermophilus parryii*) may reach impressive densities along river banks and beach ridges, where substrate suitable for constructing their winter hibernacula can be found. Hares (*Lepus othus*, = *timidus*, and *L. arcticus*) rarely reach significant numbers on tundra, though summer herds of 100-150 occasionally appear (Batzli 1975a). The two remaining groups of mammalian herbivores, the microtine rodents (*Lemmus*, *Dicrostonyx* and *Microtus*) and the ungulates (*Rangifer* and *Ovibos*), frequently reach high densities over wide areas of tundra, and represent most of the biomass in the first link of the herbivore chain in tundras.

Differences in body size and mobility of the microtine rodents and ungulates lead to different tactics for dealing with the severe arctic climate (Batzli et al. 1981). The large ungulates have more insulation and can withstand lower temperatures (Scholander et al. 1950). When winter snow conditions or temperatures become intolerable, they can travel long distances to more favorable habitats. In contrast, the small microtines have poor insulation and must rely upon increased metabolism to maintain body temperature. Because they lack the ability to move long distances, they must select or create favorable microhabitats in order to survive severe winter conditions. Large body size gives ungulates the opportunity for a long life span and iterative reproduction. However, two other characteristics associated with large body size—a longer developmental period and an increased parental investment in each offspring (Pianka 1970)—reduce the ability of ungulates to respond rapidly to favorable conditions by reproducing, and populations remain relatively stable. Small microtines, by comparison, suffer greater mortality in severe environments, but their shorter developmental time and greater fecundity allow them to respond rapidly to favorable environmental conditions. The following exposition describes and compares the most important components of the herbivore-based trophic systems at Barrow, dominated by microtine rodents, and at Prudhoe Bay, dominated by ungulates.

HERBIVORY AT BARROW—LEMMINGS

Introduction

In the coastal tundra at Barrow the brown lemming (*Lemmus sibiricus*, = *trimucronatus*) is the dominant herbivore. The density of trap-pable animals (post-weanlings) may reach 225 ha⁻¹. Collared lemmings (*Dicrostonyx torquatus*, = *groenlandicus*) are usually scarce, about 0.1 per hectare, though densities on elevated ground may be higher. They

have reached substantial numbers only once in the last 20 years, 27 ha⁻¹ in 1971 (Figure 10-2). No other vertebrate herbivores regularly inhabit the Barrow peninsula, but a few caribou (*Rangifer tarandus*) and ptarmigan (*Lagopus lagopus*) visit occasionally. A discussion of herbivory can therefore center on a single species: the brown lemming.

Population Dynamics and Demography

Changes in the lemming population have been monitored for 20 summers, from 1955 to 1974. During that time densities have fluctuated between peaks of up to 225 trappable lemmings ha⁻¹ and lows of 0.02 ha⁻¹, with three to six years elapsing between peaks (Figure 10-2). Although reliable estimates of population size were not made before 1955, high densities were also observed in 1946, 1949 and 1953 (Pitelka 1957b). These fluctuations have traditionally been called cycles, largely because of their great amplitude (3 or more orders of magnitude), even though all aspects of successive cycles are not alike.

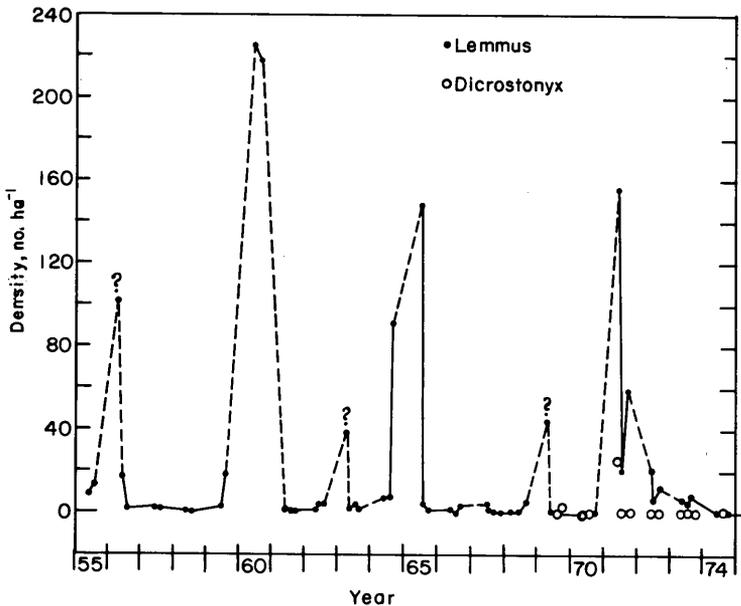


FIGURE 10-2. Estimated lemming densities averaged for all habitats in the coastal tundra at Barrow for a 20-year period. The question marks indicate numbers based upon observations other than trapping.

Mean densities for the entire tundra at Barrow are mainly useful for considering annual trends (Figure 10-2). The densities were calculated by calibrating results from extensive snap-trapping done at seven sites in five habitat types (Pitelka 1973). Local densities may depart markedly from overall densities, but the general trends from year to year were similar in all habitats.

A description of the sequence of events during a standard cycle can begin with the development of a high population. During the pre-high winter, lemmings reproduce in nests constructed out of dead grass and sedges and placed at the base of the snowpack. The population grows rapidly and reaches a peak in late spring. Breeding ceases during May, so few young are still in the nest during snowmelt, but juveniles continue to be recruited into the trappable population until early June. Before snowmelt there may be signs of stress. Many lemmings burrow to the surface and wander about, sometimes dying (Rausch 1950, Thompson 1955b). During snowmelt massive clipping of graminoids and disruption of moss and lichen carpets are revealed, and lemmings scurry everywhere. Large numbers of predators attack the exposed lemmings. Particularly prominent are pomarine jaegers (*Stercorarius pomarinus*), snowy owls (*Nyctea scandiaca*) and least weasels (*Mustela nivalis*). During the summer lemming survival declines, and the population crashes to a low level, where it remains for one to three years.

While this may be the general scenario, careful analysis of trapline data indicates that each cycle has peculiarities of its own (Pitelka 1973). In 1956, 1963 and 1969 populations increased under the snow, but declined before it was possible to measure maximum densities. In 1956, considered a peak year, an early snowmelt began in May, exposing the lemmings to avian predators. In 1963 and 1969 predation under the snow by weasels was unusually heavy (Pitelka 1973, MacLean et al. 1974), and normal peak densities of more than 100 ha⁻¹ were never reached. The highest recorded density occurred during the 1960 peak, which lasted through the summer despite heavy predation and widespread destruction of habitat. In contrast, during 1965 the population declined to less than 1% of its initial density during the course of the summer. The decline following the population peak in 1971 was not as great, and, unlike all other post-high summers, in the summer of 1972 lemmings were present in moderate numbers. The population did not reach its usual low density of less than 0.5 ha⁻¹ until 1974. During the pre-high summer of 1964 densities reached unusually high levels, but the population merely doubled during winter to produce the 1965 high. The pre-high summer of 1970 represents the other extreme: densities remained low, and the population increased by a factor of 250 during the ensuing winter. The combination of events since 1965, which has been especially peculiar compared with previous cycles, has been described in detail by Pitelka (1973).

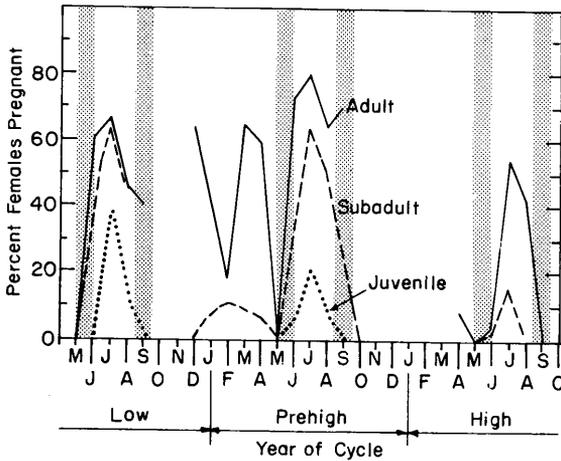


FIGURE 10-3. *The percentage of female lemmings pregnant in each age class during the course of a cycle. Sample sizes range from 10 to 746 and include all females collected by Pitelka (1973) during 1952-65. Data were collected for only one winter (1962-63). The shaded bars separate summer and winter and indicate times when mean air temperatures are near 0°C. (After Osborn 1975.)*

Demographic changes accompany these population fluctuations. Suppression of breeding, indicated by a low incidence of pregnancies, occurs in May just before snowmelt and in September during freeze-up (Figure 10-3). When lemmings do breed at these times, nests lie exposed on the surface because burrows are filled with ice or water or the snow cover is not well developed. Summer breeding appears to decline regularly in late August, although less so in pre-high years, but the resumption of breeding in early summer varies, depending upon temperature and the timing of snowmelt (Mullen 1968). During these breeding pauses the population structure shifts toward the older age classes, and density declines. Once the summer season begins, the population reproduces maximally—nearly every female is pregnant by mid-July—and the population structure shifts toward the younger age classes. If survival is high, the population increases rapidly. In general older females become pregnant more frequently than younger ones. The breeding intensity of adults varies little from summer to summer, but juveniles and subadults breed much less during the summer of a high population (Figure 10-3).

Little is known about the winter breeding season except that it lasts

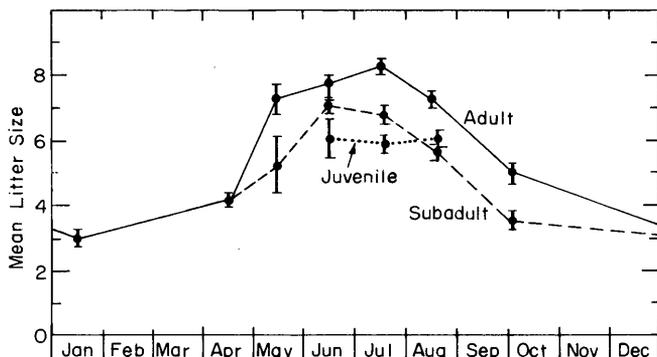


FIGURE 10-4. Mean litter sizes for different age classes of lemmings throughout the year for the period 1952-65. Vertical bars represent ± 1 SE. (After Osborn 1975; based upon data of Pitelka 1974.)

from November through April. Far fewer females are pregnant in mid-winter than in summer. Breeding intensity varies more during winter than summer, probably depending upon the snowpack, thermal conditions and the availability of food, but there is little direct evidence for this. Lack of winter nests, lack of placental scars in adult females in spring and decreases in the population indicate that during some winters little, if any, reproduction occurs (MacLean et al. 1974).

Litter sizes differed among age classes of lemmings and among seasons (Figure 10-4). Older females have larger litters during summer; the mean litter size is eight for adults, seven for subadults and six for juveniles. During midwinter mean litter size declines to three. Although statistical analysis (ANOVA, $p < 0.05$) indicated significant, but minor, differences in average litter sizes from summer to summer, they did not appear to be related to the phase of the cycle (Osborn 1975).

Dramatic changes in survival rates from summer to summer do occur, from 70% per 28 days to 10% per 28 days for adults in July, but our knowledge of survival rates throughout a cycle is scanty. Changes in sex ratio indicate that survival of males tends to be lower than survival of females during the summer and higher during the winter, possibly as a result of differential predation. Osborn (1975) developed a computer simulation model that allows survival rates and density of sucklings, which are not trappable, to be estimated by a trial and error procedure, given information on age-specific reproductive rates and on population structure. Using the reproductive rates and litter sizes discussed above, together with field observations of age structure and population size during summer, he estimated density of sucklings and survival rates for each

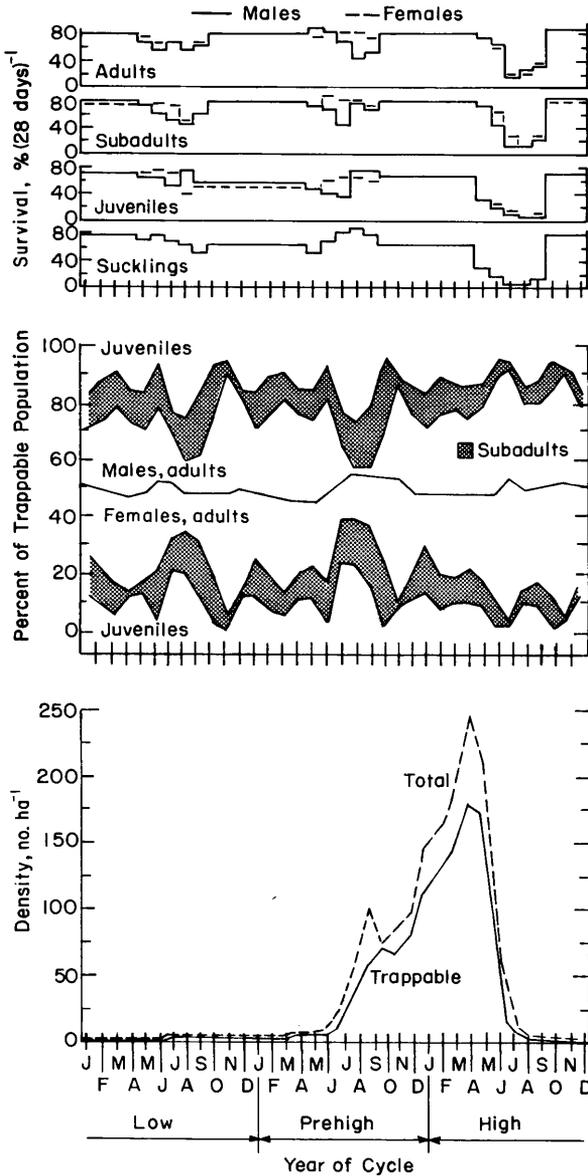


FIGURE 10-5. The density and demography of brown lemmings through a standard three-year cycle calculated by a population model. (After Osborn 1975.)

age, sex and reproductive class for a standard cycle based upon data from 1961-65 (Figure 10-5). In the model, survival rates for October through April were not varied with time and should be viewed as average values over the winter.

One of the most striking results of these simulations was the small increase in survival of lemmings required to build a peak population (Figure 10-5). Sucklings accounted for about half of the population during the pre-high summer and one-quarter of the peak population. During this time, reproductive rates were no better than the previous year, but suckling and female survival improved slightly. Even with high reproductive rates survival rates of sucklings and juveniles during the pre-high summer needed to be relatively high for the population to increase as observed in the field. During the population crash the survival rates of young animals remained very low so that at times the population became almost completely adult. Survival rates for sucklings are based only on litters whose mother also survives; when a nursing female dies her litter also dies. Thus, improvement of female survival has a double effect on population growth.

Habitat Use

Lemmings do not make equal use of various habitat types, so any analysis of herbivory must consider spatial patterns of habitat utilization. We use two scales in our analysis, mesotopographic units and microtopographic units (Figure 10-6).

Snap-trap lines run by Pitelka for 19 years in the Barrow area provided information on habitat utilization. These lines were divided into five habitat types, which can be arranged along a moisture gradient and

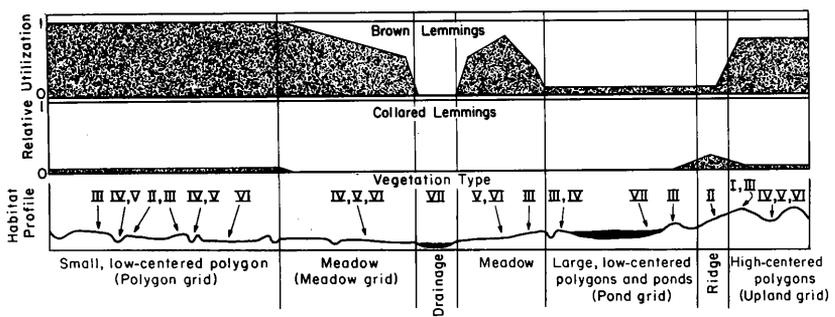


FIGURE 10-6. *The relative utilization by lemmings of habitat types on the Barrow research area. The numerals above the topographic profile indicate vegetation types (Table 1-4).*

correlated with the vegetation types given in Chapter 1 (Table 1-4):

1. Ridges: well-drained raised areas with *Salix* heath vegetation (I, II).
2. High-centered polygons: polygons with well-drained centers and with wet troughs and ponds between them (I, III, V, VI).
3. Low-centered polygons: polygons with mesic centers and with wet troughs between them (II, III, IV, V, VI).
4. Graminoid flats: wet meadow with mixed graminoid vegetation (V, VI).
5. *Carex* flats: wet meadow dominated by *Carex* (VI).

Although densities varied, the pattern of habitat use was fairly consistent from year to year. In early summer, well-drained areas dominated by high-centered polygons were the most heavily used, and twice as many lemmings were captured there as in any other habitat. By late summer the use of such areas decreased markedly, while use of areas dominated by low-centered polygons and of low-lying meadows increased. This pattern reflects the fact that low habitats are flooded in early summer but become drier as the summer progresses. The extremes of the moisture gradient, ridge and *Carex* meadow, received substantial use only when population densities were high. Collared lemmings, when present, usually were found in ridge or high-centered polygon habitats (Figure 10-6).

Density estimates and signs of activity on four 2.25-ha live-trapping grids in the immediate vicinity of the Biome research area gave a slightly different picture of habitat use. During winter nest densities were greater in high-centered polygons than other habitats, but population densities at snowmelt and winter clipping of vegetation were greater in low-centered polygons (Table 10-1). Clipping rates indicate the amount of winter foraging, while nests may reflect the intensity of reproduction. All indicators of activity support the notion that the polygon and pond habitats, which had relatively uniform vegetation heavily dominated by *Carex*, were used least by lemmings. Summer population densities and the rates of clipping indicate that the low-centered polygons and meadows were used most heavily, particularly in the summer of 1972 and the winter of 1973. At lower densities, in the summer of 1973 and the winter and summer of 1974, use of high-centered and low-centered polygons was more similar.

Use of the meadow depended upon moisture conditions. The summer of 1972 was relatively dry, so lemmings moved into the lower, wetter portions of the grid as standing water receded, and the overwintering population was similar to that on low-centered polygons (Table 10-1). The summer of 1973 had late rains, however, and much of the meadow was flooded at freeze-up. As a result, the overwintering population during 1974 was only a third of that on low-centered polygons.

TABLE 10-1 *Summary of Indicators of Brown Lemming Activity in Four Habitats at Barrow*

	1972	1973	1974
Winter nest density (no. ha ⁻¹)			
High-centered polygons	—	24.9	18.5
Low-centered polygons	—	18.2	12.9
Meadow	—	17.2	4.2
Polygons and ponds	—	2.7	0.4
Summer population density (no. ha ⁻¹)			
High-centered polygons	3.4–14.7	3.1–4.0	0.3–0.6
Low-centered polygons	12.9–46.1	3.1–4.9	0.3–0.6
Meadow	—	2.5–3.1	0.9–1.2
Polygons and ponds	1.6–7.7	0.3–1.5	0.0–0.6
Percentage of graminoid tillers clipped			
High-centered polygons	14.8	12.3	2.4
Low-centered polygons	—	25.1	6.7
Meadow	—	24.3	1.9
Polygons and ponds	—	5.4	0.3

Note: Densities are seasonal extremes. Habitat types are illustrated in Figure 10-6.

These observations support several generalizations. First, brown lemming activity, both summer and winter, tends to be concentrated in polygonal terrain, which has a mixture of relatively dry and wet habitat. Second, low, wet areas with vegetation heavily dominated by *Carex* and dry ridges with *Salix* heath are the areas least utilized by brown lemmings. Third, the use of low-lying meadows with mixed graminoids varies depending on seasonal and annual moisture conditions.

Lemming activity is neither randomly nor uniformly dispersed within the larger topographic units discussed above, and the use of local microtopographic units must also be considered. Habitats with well-developed high-centered and low-centered polygons have the greatest microtopographic relief and support the greatest winter nesting. Ninety-three percent of 139 nests examined in 1974 were located in polygon troughs. Winter clipping of vegetation is also concentrated in troughs, where the density of shoots is higher, but patches of clipping occur in all microtopographic units. In 1973 we found clipping percentages of 25 to 50% in troughs, where graminoid shoot densities were about 3000 m⁻², 15% on rims with 2000 shoots m⁻², and 5% in basins with 1000 to 1500 shoots m⁻².

Summer activity patterns have been more intensively studied than winter patterns. Using techniques of radio tracking, Banks et al. (1975) showed that individual lemmings may move over 1 km day⁻¹; however, most lemmings live in home ranges of highly variable size. Females tended

TABLE 10-2 *Home Ranges (Mean \pm 1 SE in Hectares) of Lemmings on Low-centered Polygons*

	1972	1973
Males	1.33 \pm 0.28 (12)	0.88 \pm 0.28 (13)
Females	0.68 \pm 0.37 (6)	0.41 \pm 0.31 (11)

Note: Sample sizes are given in parentheses.
Source: Banks et al. (1975).

to have smaller home ranges than males (Table 10-2), but the variability is such that differences were not statistically significant. Differences also occurred from year to year, but again variability was high. Analysis of the frequency of movements of 5 m or more indicated that males moved more than females and that more movement occurred in 1972 than in 1973 (ANOVA, $p < 0.01$).

The greater movement of males probably results from the mating system of lemmings, viz. promiscuous polygamy. Males can increase their fitness by touring the habitat in search of females, whereas females restrict their movements, usually moving between foraging sites and nesting burrows. A combination of increased energy requirements and vulnerability to predation when moving probably limits male movements. The greater movement of lemmings in 1972 than in 1973 was correlated with higher population density (Table 10-1), hence greater social interaction, and with a lower rate of predation in 1972.

Summer activity in polygonized terrain takes place primarily in the troughs. Lemming burrows are concentrated on the sides of troughs above the water line or on the sides of high-centered polygons. Summer nests are usually located in these burrows or under elevated patches of moss (*Sphagnum* spp.). Runways follow troughs, particularly the frost cracks associated with them. Foraging activity is concentrated near the burrows and along the sides of runways. About 95 to 100% of graminoid shoots in the immediate vicinity of burrows are repeatedly clipped while the burrow remains occupied. Away from the burrows, clipping is patchy, and intensity decreases as distance from the runways increases. Cheslak (pers. comm.) found only from 0 to 30% of shoots clipped at a distance of 0.5 m from runways when lemming densities were moderate, about 10 ha⁻¹. Maps of the locations of radio-tagged lemmings show patterns that match the patterns of polygon troughs (Banks, pers. comm.). In nonpolygonized terrain the association with microtopographic features is not so clear, and lemming activity appears to be located in more randomly distributed patches, but, again, clipping is concentrated near runways.

Although collared lemmings are not abundant on the coastal tundra at Barrow, they are more common than brown lemmings at many other tundra sites (Bee and Hall 1956, Krebs 1964, Fuller et al. 1975, Batzli and Jung 1980), and they present an interesting contrast. Collared lemmings generally prefer higher, drier habitats than brown lemmings, particularly areas where dicotyledonous plants are common. They excavate more elaborate burrow systems than brown lemmings and do not use runways, which are not required in habitats without dense graminoid growth.

Nutrition and Energetics

Diet

The food habits of lemmings, as of most herbivores, vary with season and habitat. In general, however, collared lemmings and brown lemmings specialize on different food types. Collared lemmings take primarily dicotyledons supplemented by graminoids, whereas brown lemmings take primarily graminoids supplemented by mosses. *Salix* appears to be the most important dietary item of collared lemmings in summer (40 to 50%) and may be even more important in winter. *Dicrostonyx* feces from winter nests contain large amounts of willow leaves. Dietary specialization reflects more than differences in habitat preference because dietary compositions remain distinct even at sites where both species occur (Batzli 1975a).

We have examined the food habits of brown lemmings in some detail. Significant seasonal changes in diet occur, from about 80% graminoids in mid-summer to 55% in mid-winter. Changes with habitat appear to be greater in summer than winter. During July graminoids may contribute only 70% of the diet in polygonal terrain but over 90% in low, wet meadows. During winter the variation of graminoid content between habitats is only $\pm 5\%$. Dicotyledonous plants make up a fairly consistent 5 to 10% of the diet, and lichens contribute less than 1%; thus, most of the shifting to and from graminoids is matched by opposite trends for mosses.

Selection among graminoid species has been examined in the laboratory by Melchior (pers. comm.). Lemmings selected the sedges *Eriophorum russeolum* and *E. scheuchzeri* in greater amounts than other species when offered a choice of graminoid species in the form of sod blocks. Naturally occurring dicotyledonous species were ignored or consumed in very small amounts. Living green leaves and leaf sheaths were consumed; dead plant parts were rejected. Inflorescences were consumed by some lemmings and rejected by others. Thompson (1951) reported similar results; *Lemmus* preferred sedges and grasses and *Dicrostonyx* preferred

Salix and herbaceous dicotyledons. Only *Eriophorum* ranked highly as a preferred item for both lemmings.

Comparison of dietary composition in the field with the vegetational composition of the habitat shows that *Lemmus* selects *Dupontia fisheri*. The percentage in the diet is about twice the percentage in available forage during midsummer (Batzli 1981). Consumption of the most abundant and widely distributed graminoid, the sedge *Carex aquatilis*, is highly correlated with availability ($r = 0.91$, $p < 0.01$), and it is taken at a level of about half of its availability. Surprisingly, *Eriophorum* (*E. angustifolium*, *E. russeolum* and *E. scheuchzeri*, taken together) shows a lower preference rating despite its higher ranking in the laboratory trials.

In winter, graminoid shoots die back to about 1 cm above the ground, and tissue below this point freezes while green and nutritious. Food preferences are less apparent then, and lemmings consume the major graminoids approximately in proportion to their availability. Because polygon troughs, the favored winter habitat, contain much *Dupontia*, this species is also an important winter food of lemmings.

Energy Requirements

The total assimilated energy required by a lemming can be estimated by summing the energy demands for maintenance, growth and reproduction and the amount of energy lost in urine. Urinary loss of energy for lemmings on natural diets equals approximately 5% of respiratory energy (Batzli and Cole 1979). Maintenance energy requirement, or respiration, can be expressed as average daily metabolic rate, which is a function of body size, ambient temperature and activity. Collier et al. (1975) have developed a model of lemming energetics. The current version of that model (Peterson et al. 1976) is

$$\text{ADMR} = (1.28W^{0.75} - 0.45T + 6.40)4.19$$

where ADMR is average daily metabolic rate in kJ day^{-1} , W is live body weight in grams and T is ambient temperature in $^{\circ}\text{C}$. Measurements of the metabolic rate of free-living *Lemmus* using doubly labeled water, D_2^{18}O , indicated that extrapolations from laboratory results probably underestimate the metabolic rates of lemmings in the field by 40% (Peterson et al. 1976). Therefore, the following calculations based upon the curve of Collier et al. (1975) give conservative estimates of energy requirements.

The above equation was based upon animals with stable weights; additional energy is required for growing animals. The amount needed is determined by the growth rate of the individual and the efficiency with

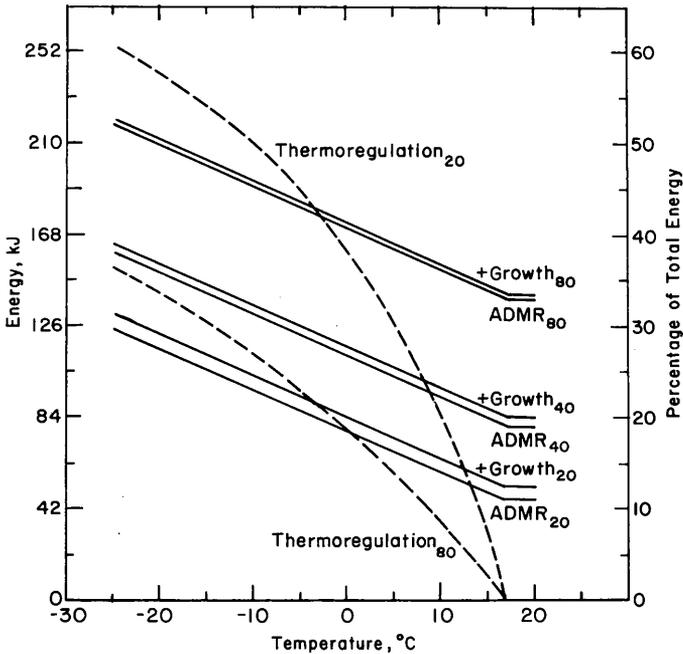


FIGURE 10-7. *The relationship of energetic requirements of non-reproducing lemmings (solid lines) and percentage of energy used for thermoregulation (dashed lines) to ambient temperatures. Subscripts give the body weight of lemmings in grams.*

which assimilated energy can be transformed into tissue. Growth rates of lemmings have been summarized by Batzli (1975a) and allow for the development of sexual dimorphism in size beginning as subadults, 30 to 60 days old. In order to calculate the total energy used for growth, 25% of the energy stored in new tissue must be added, given an efficiency of tissue growth of 0.80 (Blaxter 1967). Assuming that growth is independent of ambient temperature, growth adds a constant energy increment to the average daily metabolic rate.

Energy requirements for maintenance and growth as a function of ambient temperature differ markedly for juvenile and adult lemmings (Figure 10-7). The average daily metabolic rate increases significantly with declining ambient temperature; for the 20-g juvenile lemming it increases nearly 3-fold over the temperature range $+17^{\circ}$ to -25°C , the annual range of temperature usually encountered by a lemming.

The average daily metabolic rate equation separates the energy cost

of thermoregulation, $1.87 \text{ kJ } ^\circ\text{C}^{-1}$, from the cost of maintenance. The cost of thermoregulation expressed as percent of total energy requirements, average daily metabolic rate plus growth, is zero at $+17^\circ\text{C}$, which is the lower limit of thermoneutrality, compared with 36% of the total for the 80-g lemming at -25°C and 60% for the 20-g lemming at -25°C .

Energy required for reproduction includes that invested in growth of fetuses and production of milk for sucklings. Fetuses grow from 0 to 3.3 g over the 21-day gestation period, an average growth rate of 0.25 g day^{-1} . Given an average summer litter of seven (Figure 10-4), the reproductive female must support an average fetus growth of 1.75 g day^{-1} . Actually, the growth is concentrated in the latter phases of gestation. After a tissue growth efficiency of 0.80 is applied, the cost of pregnancy is about 75% greater than that for growth of the 20-g lemming (Figure 10-7).

The cost of suckling growth must also be supported by the breeding female. Applying a growth rate of 0.8 g day^{-1} to a litter of seven gives a value of 5.6 g of suckling growth per day. Since 1 g suckling live weight has an energy content of 4.19 kJ, this is equal to 23.5 kJ. This must be divided by 0.3, the value for efficiency of conversion of milk to suckling tissue, and by 0.7, the value for efficiency of milk production by the mother (Brody 1945, Hashizume et al. 1965). The energy requirement is therefore 113 kJ day^{-1} , equal to the average daily metabolic rate of a 40-g lemming at 5°C . Thus, lactation plays an immense role in the energetics of lemmings. Securing this additional energy requires more activity by reproducing females, which further increases energy demand. Lemmings usually are able to satisfy this demand during summer, but during winter, when the cost of thermoregulation is high and forage is sparse, litter size declines to three (Figure 10-4).

Reproduction would not be possible at all during winter without the construction of nests. The value of the nest to the lemming was explored by MacLean and Thomsen (pers. comm.) using a heat flow model. The model regards the lemming as a homeothermic body of temperature T_L and radius b , proportional to the cube root of body mass. The lemming must produce heat at a rate q that is equal to the heat flow from the warm lemming to the cold surroundings. The nest forms an insulating layer of inner radius b and outer radius a around the lemming.

The model shows that an equilibrium heat distribution is rapidly established in the inner layer of the nest around the lemming. At this time

$$q = 4\pi k(T_L - T_A)[ab/(a - b)]$$

where k is the thermal conductivity of the nest material in $\text{J s}^{-1} \text{ cm}^{-1} ^\circ\text{C}^{-1}$ and T_A is the temperature of the snow around the nest. Heat flow is determined by the temperature gradient, the radius of the lemming and

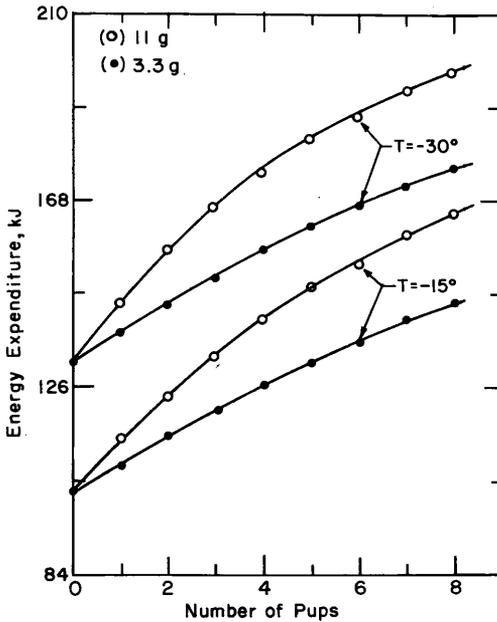


FIGURE 10-8. *The simulated daily energy expenditure by a reproducing female lemming with a winter nest in relation to litter size, weight of pups and ambient temperature T. (MacLean and Thomsen, pers. comm.)*

the radius of the nest. Under winter conditions heat flow from the nest is considerably less than the average daily metabolic requirement without a nest. For a 60-g lemming at an air temperature of -30°C the average daily metabolic rate maintained over the entire day gives 199 kJ of energy used. The time that can be spent in a nest depends upon energy reserves, which can be estimated from the stomach capacity equation discussed below. Assuming 30-minute bouts of foraging with metabolism at the average daily rate, interspersed between bouts of nest use, total energy use by a 60-g lemming with a nest of 12-cm radius is 129 kJ day^{-1} .

A large nest is crucial for winter reproduction. It reduces the energy cost to the female and prevents rapid cooling and death of the sucklings prior to the development of homeothermy at 10 to 12 days of age. The physiological processes involved in reproduction are energy-demanding, especially lactation. However, much of the heat from respiration by the female goes into the nest, and thus contributes to homeothermy. Before the sucklings develop homeothermy the major costs of reproduction come from 1) the increased radius of the nest contents, the female plus young, which leads to greater heat flow from the nest; 2) the need to re-warm cooled sucklings following a period of absence; and 3) the growth of the sucklings. The estimated energy expenditure of a lemming supporting a maximum reproductive load, six 11-g heterothermic sucklings at an ambient temperature of -30°C , is 186 kJ (Figure 10-8), or 144% of

TABLE 10-3 Comparison of Population Dynamics and Energetics of Mammalian Herbivores at Two Coastal Tundra Sites

	Barrow		Prudhoe Bay			
	<i>Lemmus sibiricus</i>	<i>Dicrostonyx torquatus</i>	<i>Lemmus sibiricus</i> *	<i>Dicrostonyx torquatus</i> *	<i>Spermophilus parryii</i> *	<i>Rangifer tarandus</i>
Density (no. ha ⁻¹)	0.02-195	0.01-25	0.01-10	0.01-10	0.05	0.001-0.01
Animal residence (days ha ⁻¹ yr ⁻¹)	71-28,380	15-3,638	15-1,455	15-1,455	6.8	0.6-1.9
Biomass dry wt (kg ha ⁻¹)	0.0003-2.6	0.0002-0.3	0.0002-0.15	0.0002-0.15	0.05	0.04-0.52
Biomass residence (kg days ha ⁻¹ yr ⁻¹)	1.0-383	0.4-40	0.4-18	0.4-18	6.8	24-27
Ingestion (MJ ha ⁻¹ yr ⁻¹)	18-7000	2.9-669	5.7-531	2.9-271	3.0	24-78
Assimilation (MJ ha ⁻¹ yr ⁻¹)	5.9-2333	1.9-435	1.9-177	1.9-176	2.1	13-43
Respiration (MJ ha ⁻¹ yr ⁻¹)	5.4-2095	1.7-394	1.7-159	1.7-159	1.9	11-37
Production (MJ ha ⁻¹ yr ⁻¹)	0.27-105	0.036-8.3	0.085-8.0	0.036-3.3	0.095	0.24-0.78
Population efficiencies						
A/I	0.33	0.65				0.55
P/I	0.015	0.012				0.010
P/A	0.045	0.019				0.018
P/R	0.050	0.021				0.021
Turnover time (yr)	0.21	0.27				9.1

*Exact densities and year-to-year variations are unknown. Populations of ground squirrels are relatively stable (Carl 1971, Batzli and Sobaski 1980).

Note: Ranges of values for extreme years are shown. Densities and biomass values are instantaneous, others are cumulative totals of average monthly values.

the energy used by a nonreproductive female with a similar nest of 12-cm outer radius. The additional energy cost of reproduction is rather low compared to earlier calculations because nonreproductive lemmings have a high rate of energy use at such low temperatures, even with a nest.

Total population energy demand for a high year (September of a pre-high year through August of a high year) has been calculated by summing energy requirements for the individuals of each category present each month. Monthly changes in density, population structure and reproductive intensity were estimated for a standard cycle in which trapable densities reached 150 ha^{-1} (Batzli 1975a). The low population was assumed to have a similar structure, but average densities for the whole year were 400 times less than for the high population (Table 10-3).

Grodziński and Wunder (1975) reported that production, the sum of all energy deposited in new tissue, averaged 2.3% of respiration for rodent populations in general, a value slightly higher than the 2% predicted by Turner (1970) for vertebrate homeotherms. When rising to a peak, production for a population of *Lemmus* at Barrow was 5% of respiration. This value is the highest known for a homeotherm and occurs despite the high energy requirements of thermoregulation. The high production results from nearly year-round reproduction and the high population turnover rate of *Lemmus*. Values calculated for *Dicrostonyx* are more similar to those for other small rodents.

Digestion and Ingestion

In order to calculate ingestion rates for the population, we must know the mean composition of the natural diet and the digestibility of natural forage as well as energetic demand. The information on the food habits of lemmings presented above has been averaged across habitats, and overall summer and winter digestibilities calculated (Figure 10-18). A mean digestive efficiency of 33% for energy is derived from these values and applied to assimilation to give an estimate of ingestion.

The digestive efficiency of *Lemmus* is strikingly low, much lower than that of *Dicrostonyx* and most other herbivorous mammals (Batzli and Cole 1979), and dramatically elevates the ingestion rate. The material within the plants may be separated into structural carbohydrate, composed of cellulose, hemicellulose and lignin, and nonstructural carbohydrate. Nonstructural carbohydrate is material contained in the cell cytoplasm and should be much more easily digested than structural carbohydrate. Total nonstructural carbohydrate (TNC) in graminoid shoots varied between 30 and 40% of the biomass for most of the growing season on moist meadows (Chapter 5, Figure 5-5). Lipid concentration found in shoots varied from 5 to 15%. Therefore, the observed 36% digestibility of graminoids can be accounted for by digestion of TNC and lipids.

Although digestibility of tundra graminoids by brown lemmings is

low compared to the 45% to 55% digestibility of temperate grasses by other microtine rodents (Batzli and Cole 1979), tundra graminoids are higher in total nonstructural carbohydrate and lipids than are temperate graminoids (Chapter 5). Thus, the higher digestibilities achieved by temperate microtines must result from the breakdown of a significant portion of the structural tissue. For lemmings, however, the rate of energy and nutrient assimilation is maximized at the expense of efficiency. Food is passed rapidly through the gut and only the most easily digested fraction assimilated. Melchior (pers. comm.), in laboratory feeding trials using graminoids as food, showed that hunger reached maximal levels after two hours of food deprivation, and we found that guts were virtually empty after three hours. Following a change of diet, fecal pellets attributable to the new diet appeared in 35 minutes.

The rapid passage of food through the gut and the high daily energy demand require that a significant amount of each day be spent foraging. During summer adult lemmings spend about 60 to 70% of their time out of the burrow (Banks et al. 1975, Peterson et al. 1976). Melchior (pers. comm.) estimated the stomach capacity of adult male lemmings by feeding animals to satiation; food consumed was approximately 10% of body weight. This gives a stomach capacity of about 125 usable joules per gram of lemming:

$$\text{Stomach capacity} = 0.1W \times 0.20 \times 18,900 \times 0.33 = 125 \text{ J g}^{-1}$$

where W is the body weight of the lemming in grams, 0.20 is the proportion dry weight in forage, 18,900 represents the average number of joules per gram dry weight of forage and 0.33 is the proportion of joules assimilated. Given this stomach capacity, and assuming that the value derived for adult males holds for all age classes, we may calculate the number of times the gut must be filled each day to satisfy the energy requirements of average daily metabolic rate plus growth. Since both stomach capacity and body weight are proportional to the volume of the animal, we assume that stomach capacity increases linearly with weight, whereas average daily metabolic rate increases with $W^{0.75}$. Gut capacity increases more rapidly with size than does metabolism, and the number of gut fillings needed to satisfy average daily metabolic rate falls. Growth rate also decreases with size, further reducing the required number of fillings per day. Small lemmings (20 g) require 22 to 52 fillings per day while large lemmings (80 g) require only 14 to 22 as temperature varies from +15 to -25 °C. The large number of fillings does not represent the number of foraging bouts, however, as lemmings may spend an hour or more out of the burrow at a time, at least during summer, and probably refill the stomach before it is empty (Peterson et al. 1976).

Perhaps the most revealing expression of energy demand for the

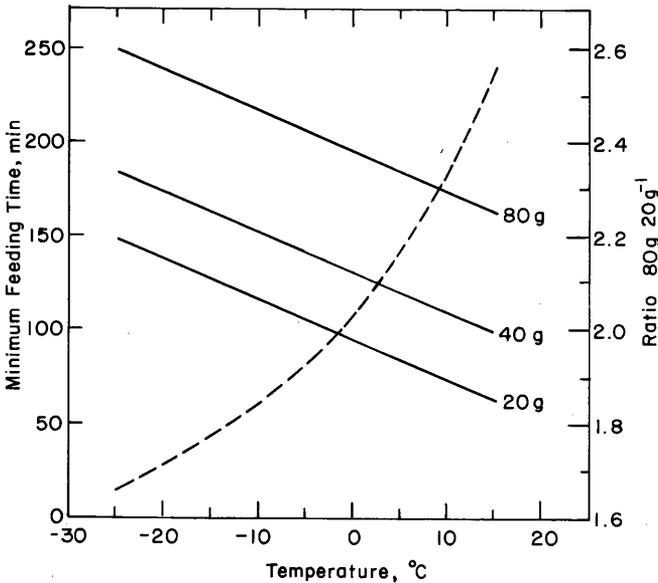


FIGURE 10-9. *The minimum feeding times required to meet the energetic demands of different-sized lemmings at several temperatures, assuming high availability of forage (no search time). Ratios of feeding times for large and small lemmings are shown by the dashed line.*

lemming is the time spent foraging. Each foraging bout requires the lemming to leave the warmth and protection of the nest or burrow and risk exposure to predators and/or lower temperatures. Melchior (pers. comm.) found that, with grasses and sedges provided *ad libitum*, mean food intake (± 1 SE) was 0.14 ± 0.02 gdw min^{-1} . At this rate, a 40-g lemming could fill its stomach in slightly less than six minutes. Since no search was involved this rate is limited only by handling time, and provides an estimate of maximum ingestion rate. Minimum daily foraging time may now be calculated as a function of body weight and ambient temperature (Figure 10-9):

$$\begin{aligned} \text{Min. feeding time} &= \text{Stomach capacity} \times \text{Max. ingestion rate}^{-1} \\ (\text{min day}^{-1}) & \quad (\text{gdw}) \quad \quad (\text{g min}^{-1}) \\ & \times \text{Required energy} \times \text{Stomach capacity}^{-1} \\ & \quad (\text{J day}^{-1}) \quad \quad (\text{J}) \end{aligned}$$

Thus, small lemmings require more separate fillings, but less time to fill the gut and less feeding time even at low temperatures. Of course,

rate of intake may increase with size, but an 80-g lemming would have to eat 66% faster than a 20-g lemming at low temperatures and 156% faster at high temperatures to spend similar amounts of time feeding. No relationship between body size and maximum feeding rate could be found in Melchior's data.

Actual foraging times would include search for and selection of food and would be much greater than minimum feeding times. Furthermore, during winter lemmings must leave the nest to forage under lower subnivean temperatures. While they are away from the nest, nest temperature falls. More time spent foraging increases energy demand, which increases the necessary foraging time. A positive feedback relationship exists and accentuates winter energy requirements.

Nutrient Relationships

One of the most intriguing aspects of lemming nutrition is its relationship to plant nutrient concentration and nutrient flux. Nutrient contents of plants vary widely with plant species, plant part, site, season and year (Chapter 5). Changes in forage quality have serious implications for lemming nutrition. For instance, the preference for *Dupontia fisheri* in midsummer may be related to the fact that it tends to grow in nutrient-rich areas. Indeed, the general propensity of lemmings to use vegetation more in troughs and wet meadows than in drier areas may be related to the higher nutrient status of graminoids in those areas.

Interest in the role of nutrients in lemming population dynamics led to examination of the nutrient dynamics of lemmings in relation to food habits and nutrient content of the forage. Of the energy ingested by the population as a whole, 1.5% is retained as production (Table 10-3):

$$P/I = A/I \times P/A = 0.33 \times 0.045.$$

The balance is lost as urine and feces, or through respiration. Since the energy and nutrients come from the same food, we may calculate the P/I value for nutrients as

$$P/I_{[N]} = 1.5(L/F_{[N]} \times 1.2^{-1}) = 1.3L/F_{[N]}$$

where $P/I_{[N]}$ is the percentage of a nutrient retained by the lemming population, 1.5 is the percentage of energy retained, $L/F_{[N]}$ is the ratio of nutrient concentration in lemmings to forage, and 1.2 is the ratio of energy concentration in lemmings to forage.

Calculated values for forage (Table 10-4) represent typical values and ignore wide variation for some nutrients, so only major trends

TABLE 10-4 *Relative Concentration of Energy (kJ gdw⁻¹) and Nutrients (mg gdw⁻¹) in Forage and Lemmings*

	Concentration in forage (F)*	Concentration in lemmings (L)†	Concentration factor (L/F)	P/I (%)
Energy	18.9	21.8	1.2	1.5
N	25	103	4.1	5.3
K	20	8	0.4	0.5
P	2	27	13.5	17.6
Mg	3	5	1.7	2.2
Ca	2	31	15.5	20.2
Na	1	5	5.0	6.5

*Data from Tieszen (unpubl.); Chapin et al. (1975).

†Data from Bunnell (unpubl.).

Note: Percentage of forage nutrients retained in lemming production given by ratio of production to ingestion (P/I) calculated from equation given on p. 356.

should be considered. Relatively large amounts of the calcium and phosphorus in forage are retained as lemming production, and these nutrients may be limiting for lemmings. If assimilation is low with high fecal loss, or if recycling within the body is inefficient with high urinary loss, the animal is in danger of entering negative nutrient balance, particularly during pregnancy and lactation when nutrient demands are high.

A simulation model of lemming nutrition was constructed to explore the nutrient balance in lemmings (Barkley et al. 1980). The model calculates the amount of nitrogen, phosphorus and calcium that a lemming could absorb from a given diet; the amount of nutrients required, given the lemming's body size, growth rate and reproductive condition; and the changes that occur in the lemming's nutrient pool. Normal nutrient pools were calculated from data of Bunnell (pers. comm.). Because little information was available on lemmings' ability to absorb nutrients or on their endogenous loss rates, which determine minimum nutrient requirements, this part of the model relied heavily upon nutritional information for the laboratory rat. In rats, and presumably in lemmings, absorption and losses are functions of ingestion, fecal output, metabolic rate and nutritional condition. Relatively high absorption rates and low loss rates were used, so the model was conservative and biased against the production of nutrient deficiencies.

The total amount of forage consumed was based upon lemmings' energetic requirements, food habits and forage digestibility. The standard model used a diet consisting of 80% graminoids and 20% mosses during midsummer and 60% graminoids and 40% mosses during mid-

winter. Continuous shifts in the diet mimicked the field situation. Nutrient concentrations in graminoids were those reported for the *Carex-Oncophorus* meadow for 1970 when nutrients were low and for 1973 when nutrients were high (Chapter 5; Chapin et al. 1975).

Early runs of the model, using a combination of starting ages, dates and nutrient concentrations, showed that only reproducing females would experience serious deficiencies—depletion of normal body pool by more than 25%. A series of runs were then conducted to compare the effects of different litter sizes, nutrient contents of forage, digestibility of forage and food habits of reproducing females. In years when there were low concentrations of nutrients in their forage, adult females (120 days old) could barely support litters of seven during midsummer, four during winter and two during late August. No offspring could be supported during late June of such years. In winter, reproduction was limited by nitrogen, calcium and phosphorus, but in early and late summer only calcium and phosphorus were limiting. During summers when there were high levels of nutrients in the vegetation, 30-day-old subadults could raise litters of eight. As expected, smaller litters and slower growth in older animals improved the nutrient status of the lemmings.

The simulation indicated that the condition of nutrient-deficient lemmings could be improved during summer by an increase in the intake of mosses or a reduction in digestive efficiency for energy and dry matter (Figure 10-10). In winter these tactics also improved calcium and phosphorus deficiencies, but they caused worse deficiencies in nitrogen. Reduced digestibility allowed the extraction of minerals from more total dry matter because the lemming had to eat more to meet energy requirements. These results help to explain some unusual aspects of lemming biology. The low digestibility of forage by lemmings, compared to temperate microtines, appears paradoxical since existence in an arctic environment increases energy requirements. However, the results of the model suggest that lemmings confront a nutritional situation where calcium and phosphorus availability are more critical than energy. Low digestive efficiency for energy requires greater food intake and thus increases nutrient availability. Adjusting the model so that energy digestibility was improved caused reproducing lemmings to become calcium- and phosphorus-deficient, even when nutrient levels in the forage were high. Calcium and phosphorus concentrations in arctic forage appear to be low compared to those in temperate forage (Table 10-5). Low digestive efficiency for energy by lemmings may have evolved to assure an adequate intake of inorganic nutrients. The lower limit of digestibility must be determined by the actual ability of lemmings to find enough food and pass it through the gut. The actual digestibilities are the result of several conflicting pressures.

The model also helps to explain the presence of relatively high

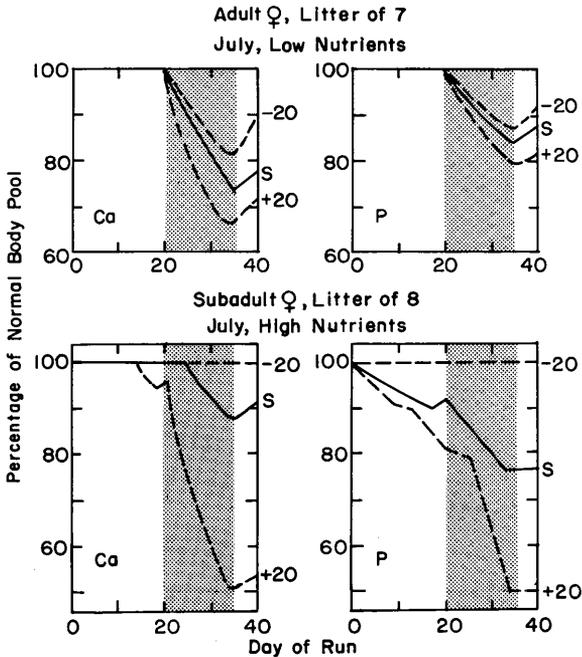


FIGURE 10-10. Simulated nutrient pools in reproductive female lemmings with normal digestibility of energy in diet (S), 20% higher digestibility (+20) and 20% lower digestibility (-20). The assumptions of the model are given in the text. The shaded area represents lactation. (After Barkley 1976.)

TABLE 10-5 Concentrations (Mean \pm 1 SE) of Nutrients in Shoots of Mature Graminoids from Four Temperate Grasslands and from Coastal Tundra at Barrow

Habitat	No. of species	Nutrient (% dry wt)			Reference
		N	Ca	P	
Great Basin	5	1.07 \pm 0.22	0.53 \pm 0.11	0.19 \pm 0.07	Harner and Harper (1973)
Northern Great Plains	16	1.43 \pm 0.34	0.28 \pm 0.08	0.14 \pm 0.05	Johnston and Bezeau (1962)
Tall Grass Prairie	4	1.13 \pm 0.39	0.39 \pm 0.26	0.19 \pm 0.08	Gerloff et al. (1964)
Mown Grasslands	6	1.47 \pm 0.38	0.42 \pm 0.06	0.29 \pm 0.08	National Academy of Sciences (1969)
Coastal Tundra	7	1.86 \pm 0.07	0.16 \pm 0.01	0.13 \pm 0.01	Chapin et al. (1975)

amounts of moss in lemming diets, up to 40% in winter, even though the digestive efficiency for energy of mosses is low. Lemmings fed only mosses reduce their intake and quickly starve. Results from the model suggest that mosses serve as nutrient supplements because they are 10 to 20% higher than graminoids in phosphorus concentration and 200 to 300% higher in calcium. The low digestive efficiency for energy of mosses requires a larger food intake, and hence assures a larger intake of nutrients. But mosses cannot be used exclusively as forage because of low digestible energy or other nutritional deficiencies.

Finally, reproduction during winter, when energy demand is already high, becomes more understandable with the hypothesis that growth and reproduction are limited by nutrient availability rather than energy availability. In fact, the high energy demand of thermoregulation may assure an adequate intake of nutrients, and conditions for reproduction may be nearly as favorable in winter as they are in late summer, if sufficient forage is available to meet energy demands.

PREDATION ON LEMMINGS

Introduction

Predators are conspicuous in the tundra at Barrow during the summer of a lemming high, and their populations have received considerable attention (Pitelka et al. 1955, Maher 1970, 1974, MacLean et al. 1974). A separation of avian and mammalian predators also distinguishes migratory predators from those remaining through the winter (Table 10-6). Their relative abundance throughout a standard lemming cycle is shown in Figure 10-11.

During the high winter, when the major increase to a high lemming population occurs, the only predators are the arctic fox and two species of weasels. Occasional snowy owls are seen in a pre-high winter, but they are so scarce as to be negligible. The immigration of snowy owls begins in late winter (April) of a high year and nesting commences in mid-May, well before snowmelt. At snowmelt they are joined by pomarine jaegers, glaucous gulls and, in some years, short-eared owls (Pitelka et al. 1955). The total intensity of predation rises dramatically and reaches its maximum at snowmelt, when lemmings are both most numerous and most exposed. A period of intense territorial activity follows, both within and between species. Nonbreeders are forced to marginal habitat, if they remain at all. The breeding population, with some attrition of unsuccessful birds, remains through the rest of the season. Migration of jaegers occurs in August, and snowy owls follow in September and early October. Following the departure of avian predators, foxes and weasels are again

TABLE 10-6 Summary of Characteristics of Predator Populations in the Coastal Tundra at Barrow

Predator	Mean adult body wt (g)	Characteristics of populations	Density (no. km ⁻²)	Prey
Snowy owl (<i>Nyctea scandiaca</i>)	♀♀: 2120 ♂♂: 1730	Territorial when lemmings high; relatively stationary, non-breeding when lemmings moderate; absent when lemmings low.	0-2	Obligate lemming predator.
Short-eared owl (<i>Asio flammeus</i>)	♀♀: 400 ♂♂: 280	Irregular nester when lemmings high; absent in other years.	0-2	Obligate lemming predator.
Pomarine jaeger (<i>Stercorarius pomarinus</i>)	♀♀: 740 ♂♂: 650	Territorial when lemmings high; strong numeric response. Absent at low densities.	0-15	Obligate lemming predator.
Parasitic jaeger (<i>S. parasiticus</i>)	♀♀: 510 ♂♂: 420	Wanderer, singly or in small groups; occasional breeder, but may be excluded by territorial pomarines when lemmings high.	Great temporal and spatial variability (~60 bird-days yr ⁻¹)	Birds; facultative lemming predator.
Long-tailed jaeger (<i>S. longicaudus</i>)	♀♀: 315 ♂♂: 280	Wanderer, often in large groups, especially in July.	Great temporal and spatial variability (~50 bird-days yr ⁻¹)	Lemmings; bird eggs and young; adult craneflies in July.
Glaucous gull (<i>Larus hyperboreus</i>)	♀♀: 1230 ♂♂: 1510	Non-breeding flocks occur regularly, mainly at dump.	May be locally dense, usually just fly over.	Facultative lemming predator.
Arctic fox (<i>Alopex lagopus</i>)	~4000	Density appears unrelated to lemmings; common in winter when moves to coast, scarce in summer; affected by fur trappers.	0-2	Scavenger—both marine and terrestrial; bird eggs and young; lemmings.
Least weasel (<i>Mustela nivalis</i>)	40-70	Strong numerical response to lemming density; recolonizes each high; non-migratory.	0-25	Primarily lemming predator; may turn to bird eggs and young when lemmings crash.
Ermine (<i>M. erminea</i>)	100-110	Moderate numerical response to lemming density; non-migratory, but wanders.	0-2	Lemmings, birds and their eggs.

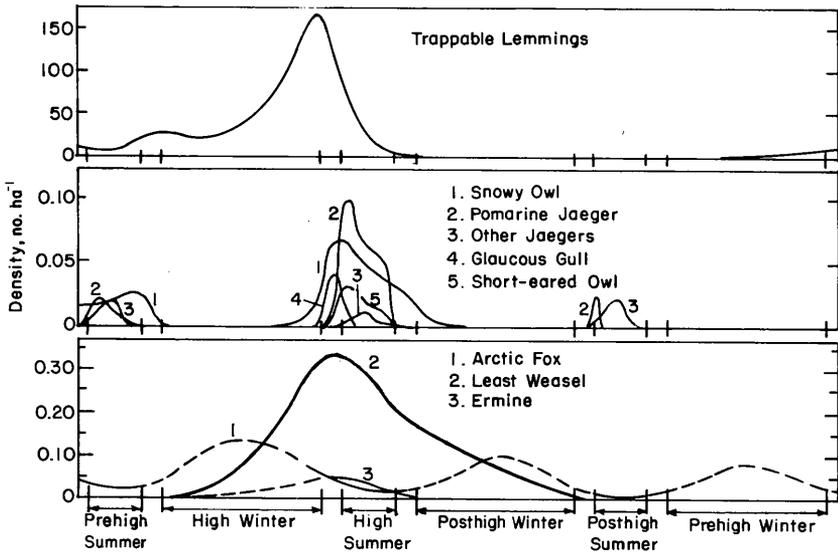


FIGURE 10-11. *The estimated densities of predators during the course of a standard lemming cycle for the coastal tundra at Barrow. Periods of snowmelt and freeze-up are indicated between summer and winter. (After Pitelka et al. 1955, and unpublished observations of authors.)*

the only predators. Presumably, these remain until the lemming population has declined to the point that it will no longer sustain predators. Foxes then switch to alternative food, especially dead waterfowl and sea mammals, but weasels may disappear from the Barrow peninsula altogether between lemming highs. Avian predators are usually scarce in the post-high summer.

Abundance of Predators—Numerical Response

The rate at which predators take lemmings is the product of the numerical response (number of predators per unit area) and the functional response (number of prey taken per predator) to prey density (Holling 1959). If lemming density is insufficient to support breeding when jaegers and owls arrive at Barrow, they quickly move on, and only nomadic individuals are seen throughout the summer. If the density of the lemmings is intermediate to high, both snowy owls and pomarine jaegers establish breeding territories, and in both species the density of the territories depends upon the abundance of lemmings. Maher (1970) concluded that pomarine jaegers did not establish territories if the density of

trappable lemmings was below about 12 ha^{-1} . At higher lemming densities the density of breeding jaegers increased and approached an asymptote of about $7.3 \text{ nesting pairs km}^{-2}$ at lemming densities above 100 ha^{-1} . The lemming density required for breeding is higher for snowy owls than it is for jaegers. Snowy owls have not bred on the Barrow peninsula in the absence of breeding jaegers, but jaegers have bred during periods of low to moderate lemming density when snowy owls did not. The density of owls during breeding is much lower than that of jaegers, and the owls' numerical response to the number of lemmings is less consistent. Pitelka et al. (1955) estimated the density of snowy owls on the Barrow peninsula to be 0.2 pair km^{-2} during the 1953 lemming high, and Pitelka (1973) estimated a density of about 1 pair km^{-2} during the 1960 high.

The difference in territory size in these two species may result from a difference in timing of nesting. Snowy owls arrive, establish territories, and begin their clutches well before snowmelt. The only exposed ground at this time is on ridges, bluffs and high-centered polygons, where the combination of wind and sublimation of snow produces small snow-free areas. Owls watch for lemmings while sitting on these vantage points. Thus, the extent of exposed ground in the spring may help to determine breeding density, along with amount of lemming movement over the snow.

Pomarine jaegers generally arrive later and establish territories around the time of snowmelt, when the tundra is rapidly becoming exposed and lemmings are maximally exposed. Jaegers search for lemmings while patrolling or hovering about 10 m above the ground. The strong numerical response in jaeger populations suggests that territory size is set by food supply. The territories are larger than necessary in June, but by July the demand for food is higher, since the young must be fed, while the lemming population has usually declined.

For the first few weeks of summer, there are often many more pomarine jaegers and snowy owls present than eventually establish territories and breed. At low to intermediate lemming densities, jaegers engage sporadically in territorial behavior. Unless mating and nesting ensue, the birds quickly abandon the territory and leave the area. In contrast, nonbreeding snowy owls may remain localized in an area for long periods of time. Even when lemming densities are high, some jaegers do not breed. Pitelka et al. (1955) estimated jaeger densities at $15 \text{ to } 25 \text{ km}^{-2}$ during early summer 1953; the breeding population later that summer was $6.9 \text{ pairs km}^{-2}$. Maher (1974) estimated the nonbreeding population as 25 to 50% of the breeding population in 1956 and less than 25% in 1960, two other peak years. Thus, in a pre-high season, the density of snowy owls may increase during the summer while jaeger density always declines after a spring peak (Figure 10-11).

The numerical response of other avian predators is less clear. Short-

eared owls bred at a density of 1.0 pair km^{-2} in the 1953 lemming high, were absent during the 1956 and 1960 highs and bred at low densities during the 1965 and 1971 highs. Parasitic and long-tailed jaegers occur primarily as nonbreeding nomads in late June and July, although a few parasitic jaegers may breed when lemming populations are high. These smaller jaegers are excluded by the aggressive behavior of the pomarine jaeger (Maher 1970, 1974).

Once breeding densities have been established, the density of avian predators during late summer depends upon breeding success. Jaegers lay no more than two eggs; clutches with one egg may occur when lemming densities are low to moderate (Maher 1970). The clutch size of snowy owls varies considerably. Nine nests in 1952–53 had a mean of 6.3 eggs per clutch and a range of 4 to 9 (Pitelka et al. 1955). Clutches as large as 14 have been observed in Lapland (Wasenius, cited by Watson 1957). Watson (1957) indicated that the clutch size of the snowy owl on Baffin Island was a function of lemming density, and this appears to be the case in the Barrow area as well.

The fledging success of both pomarine jaegers and snowy owls is highly variable and depends upon the continued availability of lemmings through the breeding season (Pitelka et al. 1955, Maher 1970). In each of the high years of 1956, 1960 and 1965 lemmings were sufficiently dense at snowmelt for jaegers to establish territories at their maximum density of about 7 pairs km^{-2} . In 1956 lemming density fell rapidly to less than 2 ha^{-1} in August, and jaeger breeding success was 4%. In 1960 lemming density remained high all summer, with an estimated density of 215 animals ha^{-1} in August, and jaeger breeding success was 55%. In 1965 lemming density fell from 150 ha^{-1} in June to less than 1 ha^{-1} in August, and almost no jaegers fledged (Maher 1970). Thus, a high lemming population in June does not guarantee that significant jaeger recruitment will occur. Indeed, Pitelka et al. (1955) found higher breeding success in the pre-high year of 1952 than in the high year of 1953. Given the tendency of the lemming population to increase during a pre-high summer and decline rapidly in the summer of a population high, breeding success of jaegers may often be better during years of moderate lemming density.

Snowy owls begin incubation with the first egg laid, resulting in an interval between hatchings of about 40 hours (Watson 1957). Hence, in a brood of eight chicks the youngest and oldest will differ in age by about 2 weeks. Since the parents tend to feed the more active and aggressive young first, the older chicks survive at the expense of the younger if lemmings become scarce. This mechanism allows a close adjustment of owl breeding success to changes in lemming density through the season. Pitelka et al. (1955) estimated fledging success of snowy owls to be less than 50% in 1952 and 1953. Even with pre-fledgling mortality of 75%, the mean clutch reported by Pitelka et al. (1955) of 6.3 eggs would produce

1.6 fledged young, well above the maximum of 1.1 fledged young per jaeger nest (2 eggs \times 55% success rate) reported by Maher (1970) for 1960.

Mammalian predators are difficult to observe, and major population changes occur in winter, so less is known about their population fluctuations. The role of the arctic fox is modified by the proximity of the ocean and by human activities. Although foxes hunt lemmings, they also have access to an abundant supply of carrion, primarily carcasses of marine mammals and eiders that are crippled and lost by hunters. Foxes are trapped commercially by man during the winter. As a result, fox density shows little correlation with lemming density (Figure 10-11), although a strong numerical response is reported elsewhere (MacPherson 1969). An adult female fox regularly hunted and caught lemmings on the Biome research area throughout the summer of 1974, but foxes are usually more abundant in winter than in summer. The main denning areas are inland, possibly because of the low density of breeding waterfowl in the coastal tundra. In some areas foxes are known to take large numbers of waterfowl eggs (Underwood 1975).

Of all predators the least weasel appears most closely tied to the lemming. Least weasels may be absent from the coastal tundra at Barrow during years when the lemming population is low, but they appear during lemming peaks. Presumably, recolonization occurs from areas to the south where the lemming cycles are of lower amplitude and where local asynchrony of fluctuations of coexisting microtine species may allow maintenance of a more stable predator population (Pitelka 1957b). Nevertheless, the strong numerical response that occurs during most high winters results from reproduction. The reproductive cycle of *Mustela nivalis* differs from that of other small mustelids in that delayed implantation does not occur. This allows the least weasel to make a rapid reproductive response to increasing or high lemming populations. Juveniles collected at Barrow on 18 May and 6 June 1963 attest to the occurrence of winter breeding. Four pregnant females collected during summers with high lemming densities contained 15, 12, 12 and 3 (\bar{x} = 10.5) embryos, compared with an average of 4.8 for temperate zone females (B. Fitzgerald, pers. comm.). Thus, a dramatic reproductive response to lemming density appears to be present.

By immigration and reproduction least weasels can increase from nearly zero to maximum densities over the course of a pre-high summer and high winter (MacLean et al. 1974). Thompson (1955b) estimated the peak density at 25 km⁻² during the 1953 lemming high, a value that Maher (1970) considered conservative. Maximum densities since 1969 have been far less than this. MacLean et al. (1974) reported 59 least weasels collected during summers following winters when lemming densities increased (1953, 1956, 1960, 1963, 1965, 1969), but only seven specimens in all other summers.

Ermine likewise show a numerical response to lemming density, although the response is less than that of the least weasel (MacLean et al. 1974). Ermine usually occur on the Barrow peninsula when lemming populations increase, but the density of ermine is probably less than 10% of the density of the least weasel.

Weasels differ from avian predators in their response to declining lemming populations. Low lemming density leads to reproductive failure and reduction of the population of adult jaegers and owls. By early fall, regardless of nesting success, all avian predators have departed. Weasels are less mobile; they remain through the summer into the post-high winter, and exert considerable predation pressure upon the declining lemming population. Eventually, by death or emigration, weasel density falls to undetectable numbers that characterize the low phase of the lemming cycle.

Nutrition and Energetics of Predators—Functional Response

Predators characteristic of the coastal tundra at Barrow are categorized as obligate or facultative lemming predators (Table 10-6). Obligate predators are those whose presence depends upon an adequate population of lemmings. Such predators show the largest numerical response and the absence of a strong functional response. Facultative predators are able to maintain a population at times of low lemming density by use of alternative food sources. Their numerical response to lemming density is small or even inverse, but they show a marked functional response. This section will consider two aspects of the functional response of predators: 1) changes in prey selection associated with changes in the density of primary and alternate prey, and 2) bioenergetic factors which determine rate of prey capture and consumption.

Clear differences in the food habits of jaegers are evident between years and between species (Maher 1974). Remains of lemmings were found in 98% of the pellets of pomarine jaegers taken in the high lemming years of 1956 and 1960, indicating the strong dependence of breeding pomarine jaegers upon lemmings. Lemmings were found in 100% of 75 pellets collected in 1959, when a few pairs of pomarine jaegers attempted breeding during a period of much lower lemming density. Even when lemming populations were low, lemmings were found in 41% of 56 stomachs of transient, nonbreeding pomarines collected in 1957 and 1958. This slight functional response was of little importance because the birds were rarely seen after mid-June

Parasitic jaegers preyed more on birds and their eggs than did the other jaegers, particularly when lemming densities were low (Maher 1974). However, during the 1956 lemming high, lemmings accounted for

75% of the food items in pellets of the parasitic jaeger. Data were available for the long-tailed jaeger only for the 1955-58 period when this species took fewer birds and many more insects than did the other jaegers. Long-tailed jaegers are most common in July, when adult craneflies (Tipulidae) are abundant on the tundra surface.

Comparable data on prey selection by snowy owls in relation to lemming density are lacking. Pitelka et al. (1955) noted that *Lemmus* makes up the bulk of the prey, but they also found owl pellets containing the remains of a variety of birds, ranging in size from the Lapland longspur to the old-squaw duck, as well as the remains of a least weasel. Examination of pellets over many years shows that the fraction of the diet consisting of lemmings is as large for snowy owls as for pomarine jaegers and may be even larger at low to moderate lemming densities.

Arctic foxes depend not only on lemmings but also on carrion during the winter and on birds and their eggs during summer. Using the lemming population dynamics model, a lemming mortality equivalent to 13.5 kg ha^{-1} was estimated during the winter (September-May) of a lemming high. These carcasses could constitute an important food source. Mullen and Pitelka (1972) investigated the disappearance of lemming carcasses by placing dead lemmings on the tundra in autumn. They found that virtually all carcasses disappeared by the following spring. In some cases other lemmings were implicated, but weasels were few, and winter observations indicated that foxes were primarily responsible for the removal of carcasses.

No data are available on the summer diet of foxes in the Barrow region, but in the Prudhoe Bay region Underwood (1975) found remains of *Lemmus* and *Dicrostonyx* in 86% of 50 fresh scats in an inland area and 75% of 24 scats in a coastal area, despite generally low densities of microtines during the 1971 summer. Birds were found in 50% of the scats from inland and 63% of the scats from the coast. Underwood (pers. comm.) reports finding as many as 30 lemming carcasses in a single fox den at other sites on the Arctic Slope. It is likely that the functional response of foxes to lemming density is much greater than their numerical response.

Data on the winter diet of both species of weasel derive from observations of remains and scats at lemming nests (MacLean et al. 1974), and thus may be biased in favor of lemmings. However, in the absence of alternative prey during winter, it seems safe to say that virtually the entire diet consists of lemmings. During summer weasels also take birds and their eggs, and a functional response to lemming density is probable.

Selective predation upon sex or age classes within the lemming population could influence the population dynamics of the lemmings. Since both jaegers and owls regurgitate pellets containing the bones of their prey, it is possible to estimate the frequency of capture of various classes

of prey. Maher (1970) analyzed the remains of lemmings in pomarine jaeger pellets collected in the high lemming years of 1956 and 1960. The proportion of prey in the smallest size class, corresponding to nestlings, was greater in 1956, when lemming density declined rapidly during the summer, than in 1960, when lemmings remained abundant throughout the summer. Osborn (1975) compared the 1960 distribution of prey in jaeger pellets with estimates of relative abundance of different age classes and sexes from snap-trapping data. Little or no difference was evident. These observations do not rule out selectivity because snap trapping probably overestimated the frequency of males in the population. Greater movement by males than females exposes males to more traps, just as it exposes them to more predation. Although more male lemmings were found in jaeger pellets in 1960, Maher's 1956 sample contained a greater proportion of females (54%). Thus, there seems to be no consistent selection of males by jaegers.

Pitelka et al. (1955) determined the sex of 76 lemmings accumulated at a single snowy owl nest in June 1953; 25 were females and 51 were males. A similar preponderance of males was found by Thompson (1955c) in snowy owl pellets. The greater vulnerability of males to owl predation seems clear.

During the winter weasels prey heavily upon lemmings and live in the nests of their victims. MacLean et al. (1974) suggested that the large nests that are subject to the greatest predation are built by breeding females and that weasel predation may be concentrated upon reproductive females. This hypothesis may be tested by comparing the sex ratio of lemming populations after winters with heavy predation with the sex ratio after winters with little predation (Table 10-7). The sex ratio significantly favored males after the winters of 1959-60 and 1964-65; a sex ratio favoring males after the 1962-63 winter is marginally significant. During all three of these winters weasel predation was heavy (MacLean et al. 1974). Breeding also occurred during these winters, so the stress of breeding might have contributed to the skewed sex ratios.

The quantity of food removed per predator can be examined by calculating the number of prey needed to meet the energy requirement or by field observation of prey capture rate. The latter approach allows for the interaction of behavior and energy requirement in a natural setting, but such data are not easy to obtain.

Gessaman (1972) studied the metabolic rate of snowy owls by measuring both the oxygen consumption and the food intake of birds confined in outdoor pens. He concluded that the daily consumption of an average adult owl was 6.6 60-g lemmings during the coldest period of the winter ($T = -29^{\circ}\text{C}$) and 4 lemmings in summer ($T > -5^{\circ}\text{C}$). Pitelka et al. (1955) observed food consumption by a captive immature snowy owl kept in an outdoor cage during summer. During the late phase of growth,

TABLE 10-7 Sex Ratios of Lemming Populations in Spring

Year	Date	♂♂	♀♀	♂♂/♀♀	χ^2
1959	1-15 June	70	97	0.72	4.37**
1960	16 May-15 June	520	278	1.87	73.39†
1961	16 May-15 June	46	49	0.94	0.09
1962	1-15 June	248	226	1.10	1.02
1963	16 May-15 June	245	204	1.20	3.74*
1964	1-15 June	104	106	0.98	0.02
1965	16 May-15 June	308	215	1.43	16.54†

* $p < 0.10$.** $p < 0.05$.† $p < 0.001$.

Source: Data from Pitelka (unpubl.).

it consumed an average of 7.5 60-g lemmings day⁻¹. After its weight stabilized, food consumption fell to 5.4 lemmings day⁻¹, a value 35% greater than Gessaman found for summer.

Maher (1970) estimated the food requirement of pomarine jaegers by direct observation of adults, which were unfettered, and chicks, which were penned in the field. Chicks near the age of fledging consumed about 3.3 60-g lemmings day⁻¹, about one lemming less than adults.

Because of the very high insulating value of the winter pelage relative to the summer coat, the maintenance energy requirement of arctic foxes does not change appreciably through the year (Underwood 1971). Deposition of fat during summer, use of fat during winter and changing activity patterns modify the annual energy budget greatly. Total assimilated energy requirements for a single fox varied more than five-fold over the year. Requirements were greatest in August, about 4609 kJ day⁻¹, equivalent to 14.7 60-g lemmings, and least in April, about 838 kJ day⁻¹ or 2.7 60-g lemmings. This remarkable difference may help to explain the greater density of foxes during winter than summer, even though food appears to be more available in summer.

The energy requirements of arctic weasel populations have not been measured. But extrapolating from Brown and Lasiewski's (1972) equations for *Mustela frenata*, MacLean et al. (1974) estimated that a 65-g least weasel living at an ambient temperature of -20°C would have a resting metabolic rate of 409 kJ day⁻¹, which would require consumption of 1.3 60-g lemmings day⁻¹. However, weasels use lemming nests in winter, and maintaining a microclimate at 0°C reduces the resting metabolic rate to 281 kJ day⁻¹, requiring only 0.9 60-g lemming day⁻¹.

Estimates of winter predation by weasels can be based upon remains

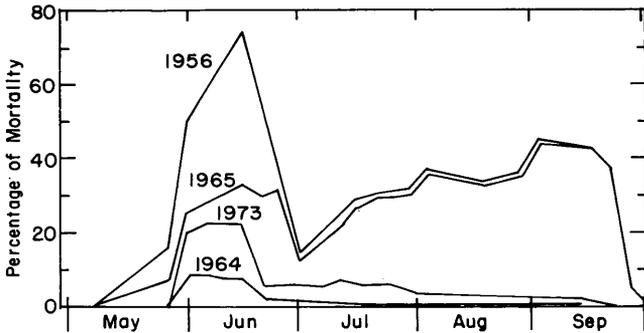


FIGURE 10-12. *The impact of avian predators on lemming populations in 4 years as indicated by the percentage of mortality accounted for by predators. Lemming densities are given in Figure 10-2. (After Osborn 1975.)*

found in winter nests. High predation rates—20% of nests on Banks Island (Maher 1967) and 35% of nests at Barrow (MacLean et al. 1974)—have been reported. The actual percentage of the population consumed was probably much higher since weasels usually consume more than one lemming per nest. But exact predation rates could not be calculated because the number of lemmings using each nest and the number of nests built by each lemming are unknown.

In order to assess the impact of avian predators on lemming populations, Osborn (1975) modeled the numerical and functional responses of snowy owls and pomarine jaegers. His model contains the information discussed above, plus growth curves of Watson (1957) for the snowy owl and Maher (1970) for the pomarine jaeger. He calculated the mortality rates for lemming populations when they were high enough to ensure breeding by the two avian predators, and expressed predation as the percentage of mortality (Figure 10-12).

In general, the model indicated that avian predation accounted for the greatest amount of mortality at snowmelt in early June when non-breeding pomarine jaegers were still present. In 1956 and 1965, when the lemming population declined rapidly from peak levels, predation became an important source of mortality again in late summer when lemming populations were low. In 1964 and 1973, when lemming populations increased in late summer, percent predation declined. The simulation for the early summer of 1972 showed the maximum impact of predation: 88% of total mortality. In 1960, when lemming densities were at their highest recorded levels, absolute predation rates were also highest (79 g ha⁻¹ day⁻¹), but avian predation accounted for only 39% of the mortality. Finally, Osborn found that in early June the amount of predation

relative to standing crop of lemmings peaked at lemming densities of 25 ha⁻¹ and dropped off rapidly at lower or higher densities.

Osborn did not simulate predation for summers when lemming populations were low, but there is some evidence suggesting that predation relative to standing crop is quite high. Pomarine jaegers do not defend territories when lemming populations in early June are less than 10 ha⁻¹. At these densities lemmings are distributed in small patches, upon which wandering predators prey. The percentage of lemmings taken may be greater than during years when lemmings are protected from other predators by pomarine jaegers.

During 1972 one of the live-trapping grids was located within an area that was defended by a nesting pair of pomarine jaegers and we observed minimum survival rates for adult lemmings of 40 to 70% per 28 days. On two other grids not defended by jaegers lemming survival rates were less than 20% per 28 days. During 1973 and 1974 no jaegers nested in the study area, and adult survival rates were less than 30% per 28 days on all grids. Wandering jaegers and owls were relatively common in all three years. Weasels were present in 1973, and in 1974 an arctic fox resided in the study area. Animals on trapping grids not defended by territorial jaegers appeared to be healthy, and all females were reproducing, so predation by other predators appeared to be the most likely cause of the high mortality.

FACTORS INFLUENCING LEMMING POPULATIONS

Abiotic Factors

One of the most dramatic features of tundra is the rapid transition between the mild summer and the severe winter. Because they neither migrate nor hibernate, lemmings must function throughout even the most extreme conditions. During the summer, temperatures near the ground are above freezing, but they are nearly always below the lower limit of thermoneutrality (17°C) of lemmings (Figure 10-7). Hence, even summer temperatures cause metabolic rate and food demand to be elevated above the minimum value, but they pose little direct threat to survival.

Habitat flooding at the time of snowmelt and again, in some years, following July and August rains may be a greater danger to lemmings. Much of the low-lying habitat, including meadows, polygon troughs and basins of low-centered polygons, becomes inundated. Since water destroys the insulation value of lemming fur, and the high specific heat of water makes it an effective heat sink, lemmings must keep dry most of the time. Slight flooding (2 to 3 cm deep) can make a habitat unsuitable except for occasional foraging. At snowmelt the subnivean habitat col-

lapses and the lemming population is concentrated into small areas of suitable habitat; when populations are dense, a period of intense social interaction may ensue. Lemmings may be forced into unfamiliar habitat where they may become more susceptible to predation. Thus, spring is a particularly traumatic period during which breeding subsides and mortality is high. In years of high rainfall much of the low-lying habitat continues to be flooded and unavailable to lemmings most of the summer. Polygon troughs and wet meadows, which are most susceptible to flooding, have the highest density of food plants and are preferred winter habitat. If these areas are flooded at freeze-up, they can remain unavailable to lemmings all winter long. The effect of late-season flooding may be greater than its spatial extent alone would suggest.

In August and early September lemmings encounter the only marked diurnal change in light intensity and temperature that they experience. The snowpack generally develops between mid-September and mid-October; delay poses two dangers for lemmings. First, if the vegetation becomes coated by freezing rains, the energy cost of foraging greatly increases. Second, in the absence of snow the ground surface is exposed to increasingly low nighttime temperatures. The reduction of breeding at this time attests to the severity of the period in the annual cycle of the lemming. Fuller (1967) has suggested that weather conditions in autumn can be a major factor influencing the population dynamics of lemmings.

The dense and shallow snow cover offers only modest protection from winter cold; very low temperatures are encountered at the ground/snow interface. In 1970-71 the temperature at the ground surface under 30 cm of snow at the *Carex-Oncophorus* meadow dropped below -20°C in early December and to -25°C in early March (Chapter 2). In March 1972 the mean temperature was -26°C under 29 cm of snow (MacLean et al. 1974). Temperatures as low as -32°C were recorded under 15 cm of snow.

Lemmings apparently take advantage of the higher temperatures that are found under deeper snow by concentrating their activity in polygon troughs. MacLean et al. (1974) found a significant correlation between nest density and amount of topographic relief ($r = 0.52, p < 0.01$), and presented evidence that winter reproduction was inhibited in years of shallow snow accumulation.

The structure of the snowpack may be just as important to lemmings as its depth. Once the snowpack accumulates, moisture is redistributed, and a strong structural profile develops (Chapter 2). The profile consists of two main layers: a fine-grained wind-packed layer of high density, and a large-grained layer of very low density (depth hoar). Where the snow is shallow the depth hoar layer may be thin or nonexistent. Although lemmings can move easily through depth hoar, dense snow may exclude them from a portion of the habitat. Freezing rains or partial thaws after

the snowpack has developed can produce ice layers in the snowpack, and these also inhibit the formation of depth hoar.

The subnivean atmosphere has been suggested as another important feature of the winter environment of lemmings. The dense, wind-packed snow offers high resistance to gaseous diffusion. Kelley et al. (1968) and Coyne and Kelley (1974) demonstrated a buildup of subnivean carbon dioxide in fall, and again in spring. On two occasions, concentrations rose rapidly to 700 and 1500 ppm. While well above normal levels of 320 ppm, these values appear to be too low to influence the physiology of lemmings. Alveolar air in mammalian lungs is normally 5×10^4 ppm CO_2 , and that level could easily be maintained by a slight change in respiratory rate (Johnson 1963).

Snow chimneys, tunnels dug by lemmings to the snow's surface, are frequent when lemming populations are high. Melchior (pers. comm.) found that they are used most during fall and spring, when release of gas under the snow is to be expected. Lemming tracks are often seen in fresh snow around the chimneys. Sometimes the tracks may be traced to the same or another chimney, indicating that the lemming returned to the subnivean environment. In other cases the tracks lead to a dead lemming or to signs of predation by foxes or owls. There are obviously risks associated with ventures above the snow. The advantages are unknown but may include escape from the toxicity of the subnivean atmosphere or dispersal to new habitat by an easier route when the depth hoar layer is poorly developed.

In summary, reproduction regularly subsides at snowmelt and during freeze-up before the snowpack develops, indicating that these are periods of stress for lemmings. Mortality rates, particularly from exposure to predators, are high at snowmelt. Circumstantial evidence suggests that a shallow snowpack and low winter temperatures inhibit winter reproduction, but we found no significant correlation between snow depth and spring population densities at Barrow over the past 25 years ($r = +0.18$; $p > 0.25$). If the depth hoar layer of the snowpack is poorly developed, winter populations decline, apparently because insufficient forage is accessible to them. Adequate snow depth and a well developed hoar layer are necessary but not sufficient to allow a population increase during winter. Unfavorable abiotic factors may contribute to the decline of high populations, but they do not appear to be necessary for the decline. Poor winter conditions can reduce populations to extremely low levels and prevent recovery of the population, thereby altering the timing of peaks. In summer, flooding may restrict the habitat available to lemmings, but reproduction and survival do not appear to be directly affected.

Predation

The general characteristics and feeding patterns of predator populations have been discussed above. In this section the impact of predation on the population dynamics of lemmings will be evaluated. Osborn's (1975) simulation indicated that in some years avian predators could account for 88% of the early summer mortality of lemmings. The major impact came at snowmelt when lemming densities were about 25 ha^{-1} , and percent predation dropped off rapidly at higher densities. Maher (1970) calculated the total impact of all predators on lemming populations during a high year. The calculations were based on the assumption that no young lemmings were weaned until mid-July and that mean litter size was six. Both assumptions are conservative (Batzli et al. 1974). He concluded that predation could not prevent population growth during the summer if lemming densities were greater than 65 ha^{-1} at snowmelt. Since lemming densities during high years are usually greater than 100 ha^{-1} at snowmelt, something in addition to predation must account for declines during the following summer. Predatory impact at high lemming densities is reduced by the protection afforded lemmings by territorial pomarine jaegers. During summers with lower population levels, when jaegers are not territorial, predation rates may be high enough to prevent population increases. Thus, predation contributes substantially to the rapid decline of lemming densities during some summers, and may even prevent population growth in others, but it is not sufficient to cause the decline of lemming densities from peaks.

During winter weasels are the most important lemming predators, and there is some evidence that winter predation rates may be sufficient to restrict the growth of lemming populations. During 1963 and 1969, lemming populations reproduced under the snow, but by snowmelt the populations had been reduced, and there was evidence of intense predation by weasels (Mullen 1968, MacLean et al. 1974). Maher (1967) reported a similar circumstance on Banks Island.

Pearson (1966) argued that the most significant effect of predators on cycling populations of microtines is the reduction of populations to extremely low levels, which delays their recovery. Maher (1970) and MacLean et al. (1974) supported this view as it applied to lemming populations. The increased mortality that adult lemmings experience during summers when populations are low lends further credence to such a role for predation. However, high populations of lemmings usually develop under the snow and not during summer, so the critical period is winter. If winter predation regulates lemming populations, intensity of predation should be negatively correlated with the change in lemming density. Our data for the winters of 1969 through 1974 do not show this trend. During

four out of five winters populations did not increase even though predation was low. We conclude that high predation rates are not a necessary condition for the maintenance of low populations.

In summary, predation contributes to population declines and may be sufficient to prevent increases at low densities, but it is not sufficient to account for summer declines following a peak. Furthermore, relaxation of winter predation will not necessarily lead to population increases.

Nutrition

Weber (1950a) observed many dead lemmings and devastated vegetation following the spring 1949 population peak; he therefore proposed that exhaustion of food supplies and subsequent starvation caused the decline. However, Thompson (1955a) noted that after the peak in 1953 vegetation grew rapidly, even though total primary production was only half that expected with no grazing. Most of the dead lemmings that Thompson found appeared to be victims of predation. He suggested that lemming populations declined because of high predation rates and low reproductive rates, which resulted from low vegetative cover and poor forage availability. Pitelka (1957a, b) supported and expanded Thompson's views to include the possibility of changes in forage quality as a factor influencing lemming reproduction. Finally, Pitelka (1964) and Schultz (1964, 1969) proposed the nutrient-recovery hypothesis to account for the cyclic nature of lemming population dynamics. According to the hypothesis the nutrient concentration in vegetation declines following a lemming high and does not increase sufficiently to support good reproduction by lemmings for two or three years. The hypothesis is complex, involving several components of the ecosystem, and it will be considered in detail. Schultz's descriptions contain a few gaps concerning the mechanisms which drive the nutrient-recovery hypothesis, so we have embellished it slightly in the following treatment and tried to make explicit all the major causal links.

The fundamental interactions and mechanisms of the nutrient-recovery hypothesis are summarized in Figure 10-13. Intensive grazing takes place during the winter buildup of the lemming population and continues until the population crashes during the summer, apparently as a result of the combined effects of habitat destruction and predation. At snowmelt soluble nutrients released into the meltwater from urine, feces and clipped vegetation are rapidly taken up by growing plants. Thus, nutrient concentrations are high in the early summer forage. Later in the summer this growth becomes standing dead material, and locks up some nutrients that would otherwise be available the following summer.

In addition to releasing nutrients the lemmings' intensive grazing re-

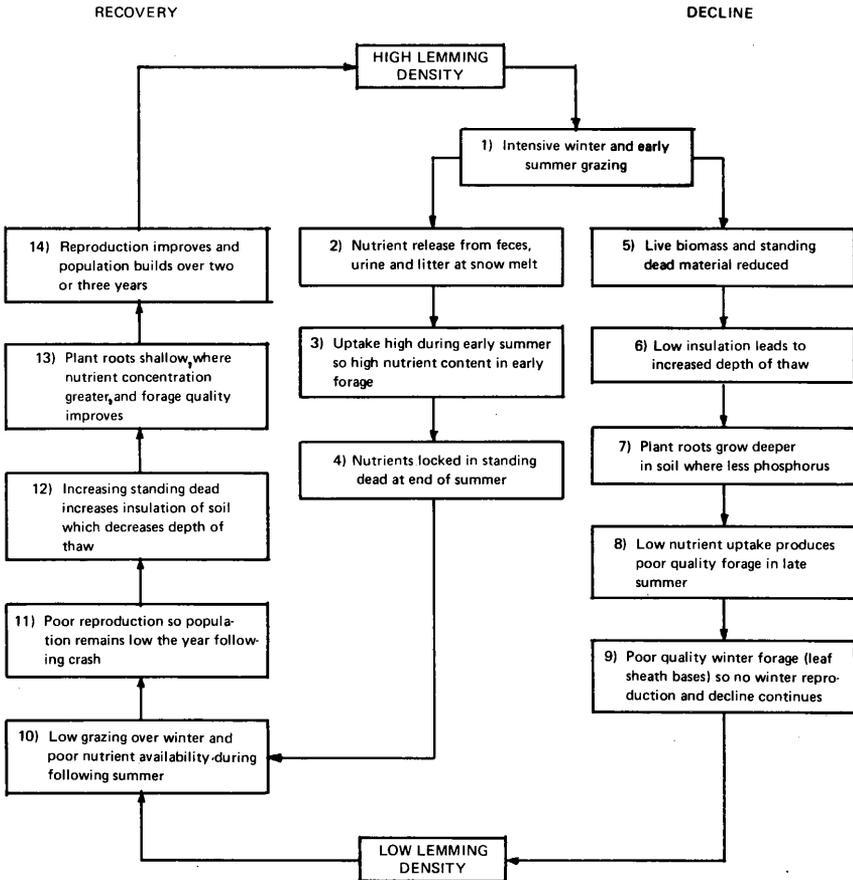


FIGURE 10-13. Summary of steps in the nutrient-recovery hypothesis. (Adapted from Schultz 1964, 1969.)

duces the amount of standing live and dead plant material during the summer of a lemming decline. This in turn reduces the albedo of the soil and its insulating cover, and the depth of thaw increases. As the depth of thaw increases, plant roots penetrate more deeply to where soil nutrient solutions (particularly phosphorus) are more dilute, and the available nutrients are distributed throughout a larger volume of soil. The low nutrient uptake of these roots leads to low nutrient concentrations in late summer growth, so that the leaf sheath bases produced then provide poor winter forage for lemmings. Because of the poor quality forage little lemming reproduction occurs during the winter, and the decline continues. There is little winter grazing, so the nutrient pulse in the spring is weak, and the nutrient quality of the vegetation stays low during that summer.

Lemming reproduction remains low during the summer and winter after a decline, and the standing dead material begins to accumulate. The increase in standing dead material and litter improves insulation over the soil and reduces the depth of thaw over the next two or three summers. As the depth of thaw decreases, plant roots are confined to soil with higher nutrient concentrations, and forage quality improves. Lemming reproduction then increases, and the population grows until a new peak is reached, usually 3 to 4 years after the last.

Our evaluation of the major premises of the nutrient-recovery hypothesis follows. Heavy grazing by lemmings can drastically reduce the standing crops of live and dead aboveground biomass (Dennis 1977) and increase feces and urine output (steps 1-3, Figure 10-13). The total consumption of graminoids by lemmings during a high year amounts to over 40 g m^{-2} , nearly 50% of the annual aboveground production and 20% of the total net production. Consumption is less than $1 \text{ g m}^{-2} \text{ yr}^{-1}$ when populations are low (Figure 10-14).

About 70% of the dry weight consumed is returned to the surface as feces and urine. Except for nitrogen, potassium and sulfur, minerals are primarily returned in feces (Wilkinson and Lowrey 1973). While the urinary minerals are readily available to plants, those in feces may not be. Most fecal phosphorus probably occurs as calcium diphosphate, a form that is soluble in a weakly acidic (pH 5) solution (Barrow 1975). The rate of nutrient loss from feces will depend upon where they are located. For instance, feces in ponded troughs or basins of low-centered polygons should lose their phosphorus more rapidly than feces on rims. Since most lemming feces are deposited in places where standing water occurs, at least during snowmelt, and since the tundra soil solution is acidic (pH 4.5 to 5.5), fecal phosphorus should be readily available to plants. Preliminary leaching experiments, using a solution that mimicked the soil solution, showed that over 80% of phosphorus was removed from feces in 24 hours (Chapin et al. 1978).

Standing dead plant material can amount to 40 g m^{-2} at snowmelt (Chapter 3), four to five times the dry weight of live material. Most of this represents the previous summer's production less those nutrients that have been removed by translocation and leaching. By felling standing dead over the winter, lemmings do add organic material to the tundra surface where it will decompose more rapidly, but its nutrient content is less than half of that from feces and urine deposited during the high winter. Disruption of mosses and lichens, which also takes place when the lemming population is at its peak, may also increase the rate of decomposition, but the amount is unknown.

The total influx of nutrients produced by lemming activity may be considerable. The average amount of soluble phosphorus in the top 5 cm of soil is 0.5 to 4 g m^{-2} , whereas the amount deposited in lemming feces

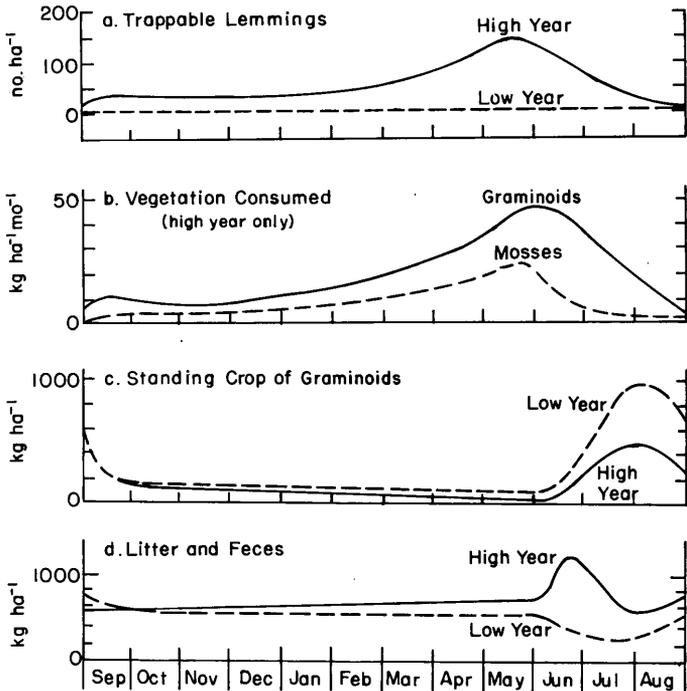


FIGURE 10-14. *Idealized comparison of lemming density, forage consumption, standing crop of forage and deposition of waste products during years with high and low populations. The calculations for lemmings are based on data presented earlier in the chapter. The density estimates include only animals usually caught in traps (> 20 days old), but consumption and waste are calculated for the entire population.*

during a year when the population is high, assuming 90% solubility, is about 90 mg m^{-2} . The phosphorus pool turns over very rapidly, and graminoids must absorb about 3 mg P g dw^{-1} of plant material produced, assuming an average of 0.3% total phosphorus. Since the peak above-ground standing crop averages 80 g m^{-2} , lemming feces would provide 35 to 40% of the required phosphorus. Most of the nutrient release from feces probably occurs during snowmelt in spring. That pulse spurs early nutrient uptake by plants and microbes since phosphorus uptake is proportional to phosphate concentration (Chapin and Bloom 1976). Hence, the first three premises of the nutrient-recovery hypothesis appear to be substantiated (Figure 10-13).

The idea that large quantities of nutrients may be tied up in organic matter during the summer following a lemming peak (step 4, Figure 10-13) is less tenable. Lemmings reduce the aboveground standing crop of vascular plants by about 50% at midsummer of a peak year (Figure 10-14) so nutrient storage in standing dead at the end of summer is also reduced. Furthermore, 75% of the phosphorus put into live biomass may be removed by translocation in late summer and by leaching the following spring (Chapin, pers. comm.). Although a few lemming carcasses may be found at snowmelt, large numbers of carcasses do not accumulate on the tundra, apparently because they are eaten by predators and scavengers (Mullen and Pitelka 1972). Nutrients from all tissues other than bones are probably returned rapidly to the soil. Phosphorus and calcium are concentrated in lemming bones, but only 10 to 20% of the total phosphorus and calcium in lemming forage is retained in bone. In a high year lemmings consume about half of the aboveground vascular plant production, so no more than 5 to 10% of the total phosphorus and calcium content of forage could be sequestered in lemming bones.

In some spots, where lemmings have grubbed for rhizomes, the standing crop of vascular plants may be reduced 90% (Schultz 1964, Dennis 1968). Thinning of the plant canopy does increase depth of thaw, although Schultz does not provide quantitative data. A simulation model suggests that complete removal of the canopy increases maximal depth of thaw by about 20% of normal, or about 5 cm, when the surface is saturated with water (Ng and Miller 1977). If the moss layer is drier, the effect on thaw is somewhat less. When lemmings are excluded from patches of tundra for long periods of time, standing dead plants continue to accumulate, and thaw depth is reduced as much as 25% (Batzli 1975b). Thus, the fifth and sixth premises are supported, although the effect on depth of thaw does not seem to be large.

Schultz (1964) presented evidence that total calcium and phosphorus decreased with depth in tundra soils; however, soluble soil nutrients do not necessarily follow the same pattern (Chapter 7), although soluble inorganic phosphorus usually does (Barèl and Barsdate 1978). The decline in nutrient absorption rates of temperate plants for 7 to 10 days after grazing, reported by Davidson and Milthorpe (1966), might also support the nutrient-recovery hypothesis. But the nutrient absorption rates of tundra graminoids increase following grazing under field conditions (Chapin 1980b). Moreover, the direct impact of grazing upon nutrient absorption rates would not last long.

Schultz's idea that roots would exploit greater soil depths does not seem likely when one considers that the plants could use the more concentrated nutrients in the upper soil horizons. In fact, all roots of *DuPontia fisheri* and the secondary absorbing roots of *Carex aquatilis*, the two most important forage plants for lemmings, are found in the upper

soil horizon, regardless of thaw depth (Chapter 5). Furthermore, when soil temperatures and thaw depth increase as a result of human disturbance, nutrient availability and plant production increase (Bliss and Wein 1972, Challinor and Gersper 1975, Chapin and Van Cleve 1978), rather than decrease as the nutrient-recovery hypothesis predicts. For these reasons, the links between depth of thaw, nutrient availability in soil and nutrient concentrations in plants that are proposed by the hypothesis (steps 7-9, Figure 10-13) do not seem tenable. A more likely explanation for the decline in plant phosphorus concentration observed by Schultz (1964) in the years following peaks in the lemming population is that intensive grazing and grubbing for rhizomes sharply decrease plant phosphorus reserves. Simulations suggest that plant nutrient reserves may be severely depleted by grazing (Chapin 1978). The involvement of other ecosystem components need not be invoked.

Nutrient levels in forage may influence both litter size and the timing of reproduction of lemmings (steps 9-14, Figure 10-13). Phosphorus, calcium and nitrogen all have been implicated by a model of nutritional physiology of lemmings (see *Nutrition and Energetics*). Apparently lemmings have adapted to low nutrient availability through high forage intake rates, low digestive efficiency of energy and selection of mosses as a calcium supplement. Even if low nutrient quality of forage sometimes prevents lemming population growth, it probably is only one of several factors which can do so. Poor snow conditions and high weasel densities may also prevent population growth during winter. Hence, forage quality may influence the rate of lemming population growth, but other factors unrelated to nutrition may be equally important.

In 1973 the depth of thaw averaged about 10% less than in 1972. Low air temperatures caused peak standing crop of aboveground *DuPontia* to be 25% lower, but concentration of phosphorus was 200% greater (Chapter 5, Table 5-4). These changes are similar to those expected during the course of a lemming cycle according to the nutrient-recovery hypothesis. Yet in 1973 the lemming density was only 5 to 10 ha⁻¹, about half that of 1972, and the population declined during the winter of 1973-74. The nutrient-recovery hypothesis predicts that it should have increased.

Our general conclusion is that the nutrient-recovery hypothesis, as developed by Schultz, should be modified. Lemming activity does not appear to control the nutrient concentration of forage by changing depth of thaw, nor do trends in lemming populations necessarily follow trends in forage quality, at least as indicated by phosphorus concentration. Nevertheless, the hypothesis has been valuable because it pointed out the importance of considering vegetational quality as well as quantity for herbivore populations.

The quality of available forage is difficult to evaluate. About 40 spe-

cific nutrients are known to be required by rodents (National Academy of Sciences 1972), but the exact requirements of lemmings are unknown. Some nutritional work has been done on lemmings and their forage, which forms the basis for our tentative conclusions regarding the role of forage quality in population dynamics.

Calculations of the energy requirements of lemmings during population buildup to a peak of 150 ha^{-1} showed that in a normal high year suitable forage would be completely utilized before snowmelt (Batzli 1975a). Some high population levels seem to reach 225 ha^{-1} or more before declining, so insufficient available energy appears to be contributing to population decline in late spring of some years. Death may occur directly by starvation since the average level of body fat in carcasses we collected before and during snowmelt was about 2%, the level at which starving lemmings die in the laboratory. The continued decline of populations through the summer can not be related to lack of available food, but there may be continuing effects of earlier undernutrition.

Reproducing females require considerably more energy than non-reproducing females. So insufficient forage relative to energy requirements may also explain why there are fewer pregnancies and smaller litters during the winter breeding season. The level of available graminoids then is one-tenth that of midsummer. Lemmings may not be able to maintain the necessary rate of forage intake on such a dispersed resource. Recent experiments show that rate of forage intake increases linearly with forage availability (Batzli et al., in press).

Although there is considerable variation from year to year and site to site, tundra graminoids are often low in calcium and phosphorus (Table 10-6). Batzli (unpubl. obs.) found that the temperate microtine *Microtus californicus* does not reproduce well when fed a diet with levels of calcium similar to the highest amounts found in tundra graminoids. Lemmings, however, perform well on such forage; and metabolic experiments have shown that nonreproductive subadults are in slight positive balance for all minerals except sodium. But when lemmings are reproducing and when the nutrients in forage are at their lowest levels, this may not be true. Laboratory animals fed natural forage ate more *ad libitum* than was required to meet their energy needs, and fat levels rose to 15 to 20% of body weight. In the field, where energy requirements are greater, fat averages only 3.5% of body weight. Apparently the ability to process large amounts of vegetation, which is related to low digestibility for energy, allows lemmings to do well on a diet that would not support temperate microtines. The simulation model of lemming nutrition (see *Nutrition and Energetics*) led to the same conclusion and indicated that reproductive success might be curtailed in years of poor forage quality.

Schultz (1969) conducted experiments in which the nutrient status of tundra vegetation was changed. By fertilizing heavily he increased the

protein, calcium and phosphorus levels in graminoids well above those in nonfertilized areas. Fertilization apparently increased winter reproduction in 1968; there were about 75 winter nests ha^{-1} in the fertilized area and none in the control areas. The effect continued through 1971, although by then it was less dramatic. Melchior (pers. comm.) reported 14 nests ha^{-1} in the fertilized areas and 2 ha^{-1} on the control plots. These results suggest that, at least during some winters, reproductive performance of lemmings can be stimulated by improving vegetation quality.

In summary, lemming populations often increase up to a limit imposed by their food supply and begin to decline when there is not enough food to meet energy demands. However, in summer primary production exceeds the lemmings' requirements, and lack of food cannot explain the continued population decline. Several lines of evidence suggest that lemmings can survive on low quality forage because of nutritional adaptations, but the lack of nutrients may still reduce winter reproduction.

Intrinsic Factors

All the factors influencing lemming populations discussed so far are extrinsic, residing outside of the population itself. Several investigators have suggested that intrinsic factors such as behavior, physiology and genetics may be equally important and that social interactions and aggression increase with increasing population density. Christian and Davis (1965) proposed a hormonal imbalance to account for a population's decline. Chitty (1967) and Krebs et al. (1973) argued that some types of lemmings emigrate more or die sooner than others, thus changing the genetic composition of the remainder of the population. Changes in genotypic frequencies within the population are held to be responsible for changing reproductive and survival rates.

Some work has been done on physiological changes in lemmings at Barrow. Mullen (1965) looked at blood glucose and formed elements of blood during four summers. There was no evidence of physiological changes associated with population density. Krebs and Myers (1974) found no evidence that physiological stress played a role in the production of microtine cycles. Andrews et al. (1975) reported changes in adrenal activity and kidney disease associated with population density and climatic factors, but often these do not appear to be consistent or statistically significant. Thus the consequences of these endocrine adjustments for population dynamics of lemmings are unclear. Using a process of elimination Krebs (1964) concluded that genetic changes influenced lemming populations at Baker Lake, Canada, but gave no direct evidence. No studies of emigration or genetics have been done on lemmings at Barrow.

Summary

Even though little can be said about the role of intrinsic factors in lemming population dynamics, it seems clear that extrinsic factors can exert a strong and overriding influence. In order for lemming populations to reproduce and grow during winter, good quality forage must be available, the snowpack must be suitable and mammalian predators must

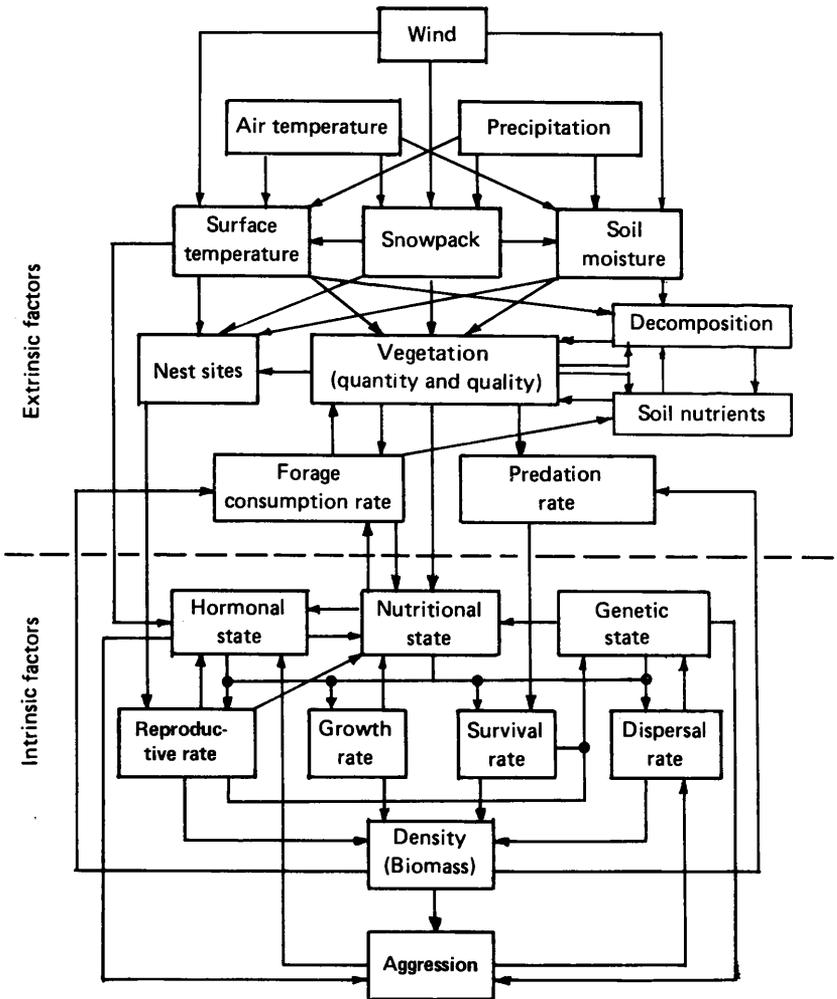


FIGURE 10-15. Diagram of relationships among factors influencing lemming population density.

be scarce. Only when all three of these conditions prevail can a high population be attained. A high population may begin to decline because of inadequate availability of forage, but only high mortality, resulting from predation or some other factor, and reduced recruitment can make the decline continue through the summer. Therefore, it does not seem that any single extrinsic or intrinsic factor can explain the population dynamics of lemmings. Rather, lemming populations respond to a number of factors that act and interact concurrently to determine the timing and amplitude of fluctuations (Figure 10-15).

Dramatic fluctuations in the lemming population occur because the high reproductive output of lemmings during a single favorable winter allows them to increase their density by 100-fold or more, and these high levels cannot be sustained. The population usually peaks every three to six years, which implies that winters meeting all the necessary conditions occur every three to six years. Why favorable winter conditions are spaced at that interval is not clear. The underlying causes of the cyclic pattern are not likely to be random. But considering the variability in cycles during the past 25 years (Figure 10-2), and the relationships between factors that influence population density (Figure 10-15), it seems clear that random factors, particularly weather, strongly influence the population dynamics of lemmings.

HERBIVORY AT PRUDHOE BAY—CARIBOU

Introduction

The herbivore community in the Prudhoe Bay region is more varied than that at Barrow. There are caribou, willow ptarmigan and ground squirrels in addition to two kinds of lemmings. Each of the three small mammals requires a different habitat (Figure 10-16). Ground squirrels prefer stream bluffs, stabilized sand dunes near rivers, and pingos, where soil conditions allow construction of deep burrows. Within their home range the density and biomass of ground squirrels is high, but overall density is low (Table 10-3) because of their patchy distribution (Figure 10-16). Collared lemmings live around pingos, on stream banks and on polygonal terrain (Feist 1975, Batzli, unpubl. obs.). Brown lemmings prefer wetter habitats, as they do at Barrow. They are usually found in polygonal terrain with high-centered polygons and well-developed troughs where the vegetation is dominated by a variety of graminoids. The range of density and biomass of lemmings in the Prudhoe Bay region is relatively low (0.01 to 10 animals ha^{-1} or 0.2 to 150 g dry wt ha^{-1}) compared with Barrow (Table 10-3). Much of the Prudhoe Bay vegetation is dominated by *Carex* and *Salix* spp., which grow on low, flat areas, often

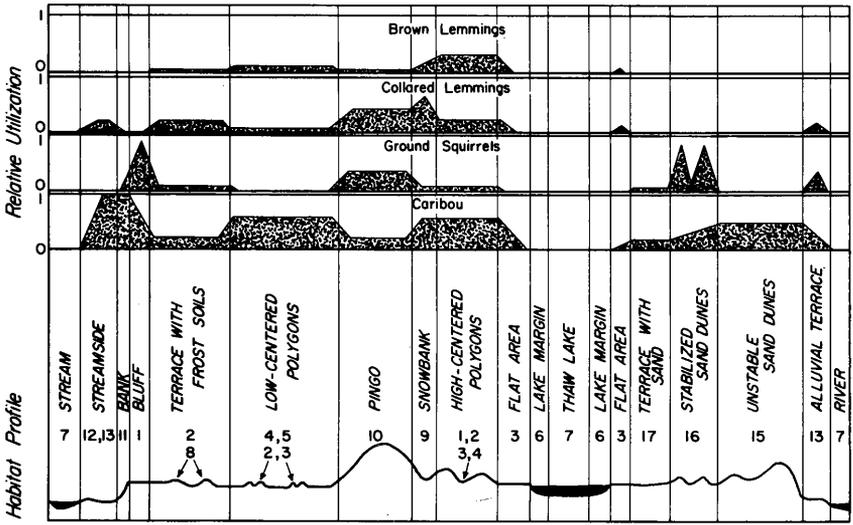


FIGURE 10-16. Relative habitat utilization by herbivores near Prudhoe Bay. The numerals above the habitats refer to vegetation types identified by Webber and Walker (1975) for the Prudhoe Bay region.

with large low-centered polygons, a habitat little used by lemmings at Barrow. Furthermore, the areas most favored by brown lemmings are also heavily utilized by caribou, whose trampling disturbs the habitat. Both factors may account for the modest lemming populations in the Prudhoe Bay region.

Caribou represent the largest biomass of herbivores in the Prudhoe Bay region (Table 10-3). Because of their mobility caribou utilize a wide variety of landforms and vegetation types, and a large study area must be considered. During 1972-73 a resident population of 200 to 500 animals inhabited the Prudhoe Bay region, a 2340-km² area of Coastal Plain bounded by the Kuparuk and Sagavanirktok Rivers in the west and east and by Prudhoe Bay on the north and the White Hills toward the south. These caribou constitute a portion of the Central Arctic caribou herd which has been identified in recent years by Cameron and Whitten (1979). During summer migratory herds of up to 3000 caribou may also pass through the region, and when they are under severe insect attack thousands may be concentrated in the coastal sand dunes associated with the river systems.

Habitat Utilization by Caribou

Migratory caribou move into the Prudhoe Bay region from herds that overwinter in Canada or south of the Brooks Range. The calving areas, located in the northern Foothills, consist of undulating terrain, frequently intersected by small streams. The first snowmelt north of the Brooks Range usually occurs in these areas (Hemming 1971). Snow is gone by the time caribou arrive for calving, and graminoids (*Eriophorum* spp.) have begun to grow, although green vegetation is very sparse. Calving commences as early as 25 May and usually ends by 20 June (Lent 1966, Skoog 1968, White et al. 1981), and the main influx of migratory caribou reaches the Prudhoe Bay region by late June. The resident caribou calve on the Coastal Plain and the Foothills (Cameron and Whitten 1979).

During the summer caribou graze either in small nursery groups of 2 to 10 cows with their calves and an occasional yearling, or in groups of 3 to 20 bulls and yearlings (White et al. 1975). Early grazing is concentrated on exposed ridges and pingos that are dominated by dicotyledons. As the snow melts, caribou begin to graze on polygonal terrain and drained lake beds whose vegetation is dominated by graminoids and dwarf willows. Some of the poorly drained centers of low-centered polygons and lake beds do not dry until late summer, and the graminoid-dominated vegetation of these areas is utilized then. For most of the summer, caribou prefer to graze on stream banks where the biomass and species diversity of the forage is high (White et al. 1975). The general summer movement pattern appears to be determined by the phenological progression of vegetation types and associated changes in their nutritional status.

As the season progresses caribou move back from the Coastal Plain to the Foothills, but daily movement patterns are less distinct due to the overriding effects of harassment by mosquitos (*Aedes* spp.) and warble flies (*Oedemagena tarandi*). During the warmest periods vegetation associated with standing water is avoided, presumably because it is prime mosquito habitat. Caribou gain some relief from mosquito harassment by grazing and walking into the prevailing wind. Or they move to the coastal sand dunes where it is cooler and windier than inland. Trail networks generally join the preferred grazing areas with those areas where they seek relief. Where several trails join at the shores of larger lakes the soil becomes deeply rutted and completely devoid of moss and vascular plants. Once the temperature drops and insect harassment abates, caribou graze slowly through the vegetation towards preferred habitat. Little use is made of the trail systems at this time (White et al. 1975).

In late October groups of caribou gather in herds of over a thou-

sand, and the animals migrate south to the wintering grounds during October through December. Groups of the Central Arctic herd overwinter on the Coastal Plain and northern Foothills. Occasionally an early snowfall in the Brooks Range prevents the migration of most of the caribou, and large herds overwinter on the Arctic Slope (Lent 1966, Hemming 1971). Some of the surviving calves and yearlings of these herds may become adjusted to overwintering on the Arctic Slope and add to the nonmigratory component of the northern caribou populations.

Population Dynamics and Demography

The number of caribou grazing on the Coastal Plain varies according to migratory patterns, the number of resident caribou and the stage of their annual reproductive cycle. The number varies seasonally and annually in the Prudhoe Bay region. The estimates in Figure 10-17 are based on the total available area, not all of which is utilized by the caribou. Estimates based on the seasonal home range can be 5 to 15 times as high and give a good indication of habitat utilization during a season or year (Gaare and Skogland 1975). But the areas visited shift from year to

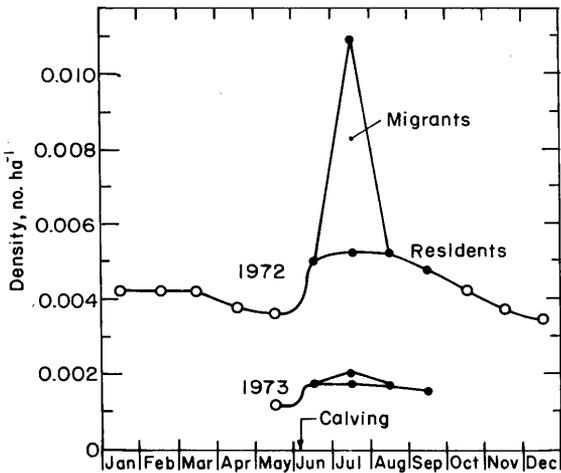


FIGURE 10-17. The density of caribou in the Prudhoe Bay region during two years. The solid dots are based on observations of White et al. (1975); the open dots were calculated assuming reproductive performance equivalent to the Porcupine herd as reported by Calef and Lortie (1973).

year and estimates based on total available area may give a better indication of the long-term population levels. The average resident caribou density in the Prudhoe Bay region was similar to recent estimates of the density of the Porcupine herd in 1972 (0.004 caribou ha⁻¹; Calef and Lortie 1973, Calef 1978), and the eastern Canadian Kaminuriak herd in 1973 (0.002 caribou ha⁻¹; Parker 1972). These densities seem small, but the biomass they represent in the region is greater than that of lemmings, particularly when large numbers of migratory caribou move into the area (Table 10-3).

In response to photoperiod, breeding activity commences with aggressive behavioral displays between adult males in mid- to late September. Peak rutting occurs in late October to early November (Kelsall 1968, Whitehead and McEwan 1973). Estrus in female caribou begins in late September, and estrus cycles recur at 10-day intervals (McEwan and Whitehead 1972). The date of peak calving varies from year to year, which suggests that secondary factors such as nutrition and climate may modify the timing of both rut and parturition. Gestation lasts about 210 days. The effects of winter nutrition on the gestation period are uncertain; however, nutrition can affect birth weights of calves and milk production in lactating females (Skjenneberg, pers. comm., White and Lulich, unpubl. obs.). Normally one calf is born; twins are rare.

The age at which caribou first breed varies (Kelsall 1968). Female calves rarely breed, and frequently females are as old as 3½ years when they breed for the first time. Under good nutritional conditions up to 30% of females will conceive as yearlings, and caribou older than 4 years have peak pregnancy rates of 78 to 90% (Kelsall 1968). Female caribou breed until they are at least 16 years of age with little decline in fertility.

Mature female caribou generally breed annually. However, when severely undernourished some females do not come into estrus, and lactation continues through January (Reimers, pers. comm.). Under these circumstances breeding in alternate years would be expected. Disease, as well as nutrition, may affect fertility. For example, brucellosis probably caused lowered pregnancy rates in the Western Arctic herd in 1961 (Lent 1966).

In the Prudhoe Bay region, when calves were 4 to 6 weeks of age, 67% of non-yearling females had calves with them in 1972 and 31% had calves in 1973. Few caribou were observed in 1973, and the estimate may not be representative (White et al. 1975). The estimated number of females with calves in the Porcupine herd to the east of Prudhoe Bay was 50% for 1972 (Calef and Lortie 1973). Caribou calves have a high mortality rate, which can be attributed to inclement weather, predation and accidents. By the end of the first year the cohort has normally been reduced 40 to 50% (Kelsall 1968, Parker 1972). Lack of data on age-specific mortality precludes the construction of life tables, but survivor-

ship curves have been compared. In reindeer herds with low early mortality, the mean expected life span may be as high as 4 years, but a value of 2.5 to 3.0 years has been reported for the Kaminuriak caribou herd west of Hudson Bay (Parker 1972, White et al. 1981).

Nutrition and Energetics

During the summer months caribou graze on both graminoids and dicotyledons while moving slowly at 0.5 to 1.2 km hr⁻¹. Bouts of grazing are interspersed with periods of rumination during which they lie down. There are four to six grazing periods daily with a high degree of synchrony within each group.

When not harassed by insects caribou spend 48 to 53% of the day grazing. Lactating females spend more time eating and less time searching and walking during a grazing period than do adult males, non-lactating females, and yearlings (White et al. 1975, Roby 1978). The activity cycle is highly modified on days of heavy insect harassment when as little as 30% of the day may be spent eating. On days of intense warble fly activity, trotting and running may take up 25% of the day. From late June through early August caribou suffer insect harassment for up to 25% of the entire period, and attacks may last for over an hour (White and Russell, unpubl. obs.). Thus, grazing periods are often interrupted, and trampling of the vegetation is increased.

Although the mouth parts of the caribou are large, grazing is selective. Rejected plant parts, particularly dead and coarse material, are expelled from the rear of the mouth and drop back to the tundra almost continuously while the caribou is eating. On summer range, rejection may be as high as 20% of all vascular plants clipped; foraging and trampling may waste considerably larger amounts of lichens (Gaare and Skogland 1975, White and Trudell 1980). When feeding on willow, caribou nip leaf parts, buds and some current year's stems, but they exclude older stems and twigs. Dead material of low nutritional value forms 15 to 20% of the diet in the Prudhoe Bay region (White et al. 1975), indicating some inefficiency in the selection and sorting processes.

Some selection of food results from selection of habitat type. Within the vegetation types there is further selection of plant species and parts. Early in the season an obvious preference is shown for the inflorescences of some dicotyledons, e.g. *Pedicularis sudetica* and *Saxifraga* spp. Because of their low availability, inflorescences do not make up a large component of the caribou diet, but selective grazing on flowers may be important because of its influence on plant populations.

Analysis of forage consumed by caribou in the Prudhoe Bay region showed that the dominant plant species in the diet were those that are

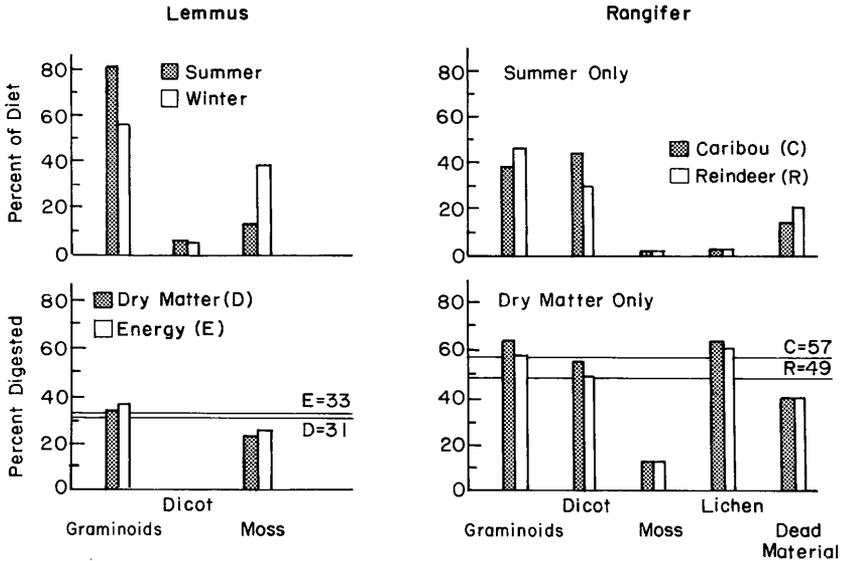


FIGURE 10-18. The composition and digestibility of diet for lemmings and caribou. The horizontal lines represent mean digestibilities for the overall diet. (After White et al. 1975, Batzli and Cole 1979.)

most available in the vegetation type. These include the graminoids *Eriophorum angustifolium*, *Carex aquatilis* and *Dupontia fisheri*, and several willows—*Salix pulchra*, *S. arctica*, *S. ovalifolia* and *S. lanata*. This generalized feeding was modified slightly by preferences for a few species of herbaceous dicotyledons and lichens (White et al. 1975). Dicotyledons made up a slightly higher percentage of the diet of caribou than did graminoids. Vascular plants contributed 92% of the diet (Figure 10-18). Mosses were eaten in such small amounts that intake may have been accidental.

Estimates of *in vitro* dry matter digestibility of hand-picked plant samples were used to calculate the mean digestibility of dietary components (Person 1975, White et al. 1975, Person et al. 1980, White and Trudell 1980). Rumen inoculum was obtained from caribou and rumen-fistulated reindeer while they were grazing on tundra. The ranges in digestibility of individual species were large for graminoids (52 to 79%) and shrubby dicotyledons (21 to 71%), but the mean ± 1 SE digestibility of graminoids ($54 \pm 3\%$ to $64 \pm 3\%$, depending on species mixture) was not significantly different from shrubs ($45 \pm 5\%$). Forb and lichen digestibility was similar to that of graminoids, but mosses had very low digestibility (Figure 10-18). Based on the relative occurrence of these dietary components mean summer estimates of digestibilities of all forage consumed were 57% for caribou and 49% for reindeer. The lower di-

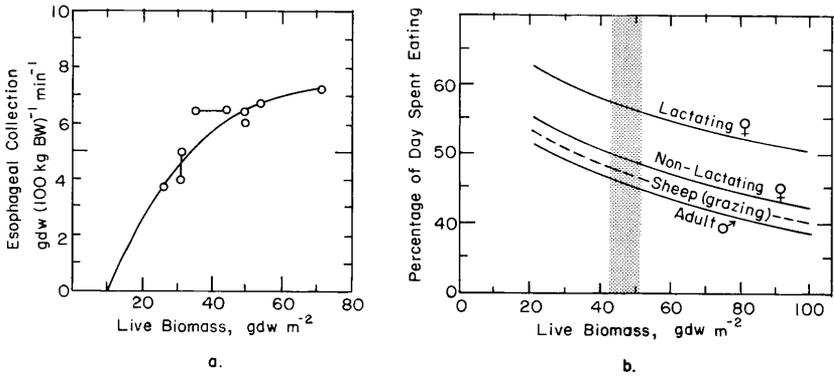


FIGURE 10-19. Consumption of forage by esophageal-fistulated reindeer (a) and the percentage of the day spent eating (b) in relation to the available green forage. The dashed line represents sheep grazing on range similar in available biomass to that of the Prudhoe Bay region. The solid lines represent the extrapolation of the relationship to caribou. The shaded column represents available biomass of vascular plants in the Prudhoe Bay region in July. (After White et al. 1975.)

gestibilities estimated for reindeer may reflect the effects of confining them to specific vegetation types.

The potential digestibility of all material from the vegetation types in the Prudhoe Bay region varies considerably, but selection of green material would provide increased digestive efficiency. By following the phenological progression in vegetational development, caribou may be able to maintain maximum digestibilities of 57 to 63% throughout the summer (Person et al. 1975, White et al. 1975, White 1979).

Whether or not caribou can select individual plants for digestibility is not known, but Klein (1970) suggested that they select for protein and minerals, particularly phosphorus. *In vitro* digestibility is inversely related to nondigestible components such as lignin (White et al. 1975, Person et al. 1975). And selection for high digestibility should also provide higher intake of cell contents that contain most of the soluble protein and phosphorus. It seems likely that caribou select vegetational types and the plant species and parts within those types that are highest in general nutritional quality, but they avoid plant species and parts that contain toxic secondary compounds (White and Trudell 1980).

Selection of vegetational types may also maximize the quantity of food eaten. Non-lactating female reindeer grazing on *Carex-Eriophorum* meadows were used by White et al. (1975) to estimate food intake. The availability of green vascular plants was an important factor controlling the rate of consumption of food (Figure 10-19a). Studies with grazing

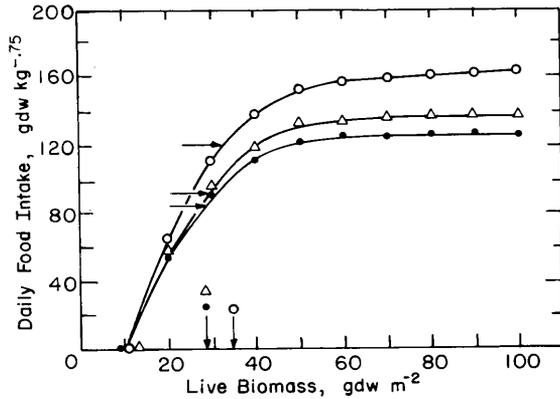


FIGURE 10-20. Theoretical relationships between daily food intake and the availability of live biomass of vascular plants for lactating females (\circ), adult males (\bullet), and non-lactating females (\triangle). The relationships were calculated as the product of the relationships shown in Figure 10-19. The arrows indicate the daily food intake required to maintain body weight and, therefore, the amount of live biomass of available plants required before the caribou would gain weight. (After White et al. 1975.)

sheep and reindeer have shown that the time spent grazing declines as available biomass increases (Alden and Whittaker 1970, Young and Corbett 1972, Trudell and White 1980). The curves for adult males and lactating females in Figure 10-19b were extrapolated from the data for non-lactating females. Presumably, curves for caribou would be similar.

The theoretical relationship between daily food intake and available plant biomass for reindeer can now be calculated (Figure 10-20, Trudell and White 1980). Food intake for lactating reindeer exceeds that for non-lactating reindeer because lactating females spend more time grazing. The theoretical relationships in Figure 10-20 are similar to actual observations of food intake in relation to plant biomass reported for domestic sheep grazing in Mediterranean grassland systems (Arnold 1964, Arnold and Dudzinski 1967).

Assuming that caribou and reindeer have similar grazing response functions, food intake of caribou in the Prudhoe Bay region during summer is directly related to seasonal changes in standing crop of green vascular plants, which peaks in midsummer (Chapter 3). In particular, food intake declines rapidly when the availability of green biomass becomes less than 40 to 50 g m⁻². Maximum food intake, when green biomass is greater than 50 g m⁻², would be expected only for the month of July and early August in *Carex-Eriophorum* meadows. By selecting vegetation

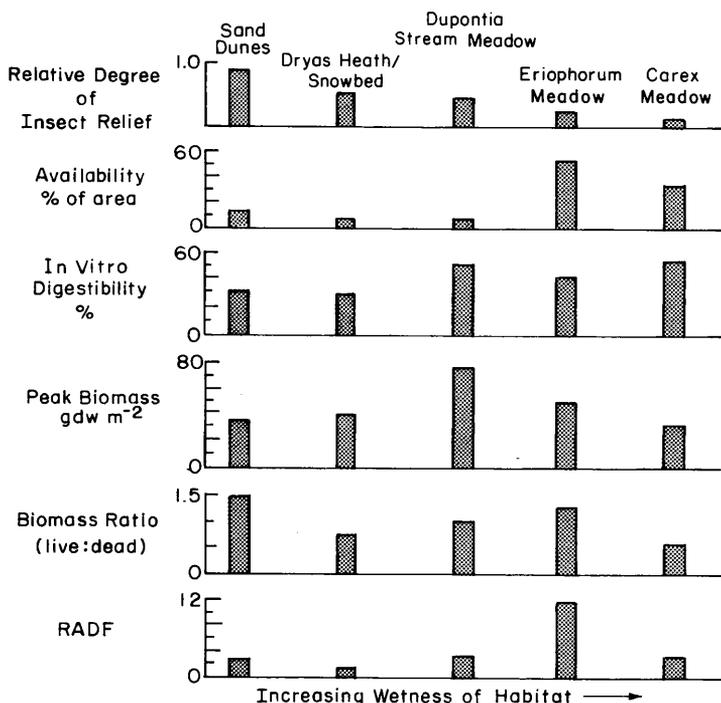


FIGURE 10-21. Characteristics of the vegetation types in the Prudhoe Bay region. The relative degree of insect relief is an index scaled to the wetness of the habitat. RADF (relative availability of digestible forage) = availability \times digestibility \times biomass \times biomass ratio. (After White et al. 1975.)

types highest in green biomass caribou could maintain a period of maximum food intake from late June to mid-August.

Each vegetational type has different attributes with respect to caribou grazing in the Prudhoe Bay region (Figure 10-21). The product of four measured parameters—availability of habitat, digestibility of forage, peak green biomass and ratio of live-to-dead material—was used as a summary index of the relative availability of digestible forage for each habitat. The relative availability of digestible forage appeared to be positively correlated with the distribution of caribou on days without insect harassment, particularly in groups of ten or fewer individuals (Figure 10-22a). Caribou group size was generally between one and ten individuals following severe harassment as herds moved from relief areas to preferred grazing areas. On days with harassment, distributions changed noticeably, and there was no relationship to the relative availability of digestible forage (Figure 10-22b).

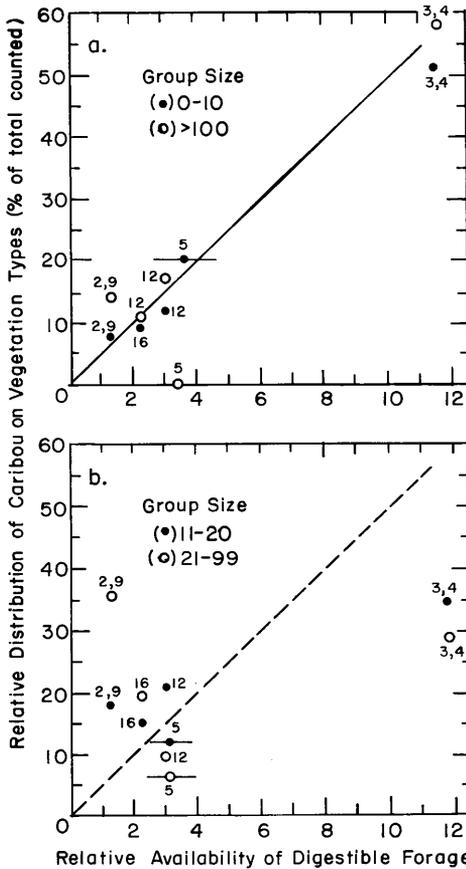


FIGURE 10-22. The relationship of the distribution of caribou among habitats to the estimated relative availability of digestible forage for those habitats when under no insect attack (a) or mild to severe attack (b). The numbers refer to habitat types given in Figure 10-16. (After White et al. 1975.)

To investigate the possible influence of food quality on factors regulating food intake a model of caribou rumen function (RUMENMET) was constructed (White et al. 1981). The model interfaced factors regulating food intake with factors responsible for digestion and outflow from the rumen. The rumination time required to reduce the particle size of unfermented material, so that it could leave the rumen, limited the amount of time available for grazing, particularly when forage digestibility was low. Thus, although the availability of green plant biomass regulates the actual eating rate, the digestibility of the food controls the amount of time the animal must ruminate and the amount of time left for grazing. Results from the model indicated that daily food intake may ultimately be regulated by the digestibility of the diet of caribou, a result well documented for domestic ruminants (Baumgardt 1970, Baile and Mayer 1970).

Seasonal changes in available plant biomass and digestibility of for-

age (White et al. 1975) were used to generate estimates of food and energy intake and rumen function parameters with RUMENMET. The number of grazing events, the time spent grazing, and the rate of ruminal volatile fatty acid production predicted by RUMENMET agreed with field observations in the Prudhoe Bay region (White et al. 1981) when the rumen capacity was expressed as:

$$\text{Rumen capacity} \cong 21 W \times 18.9 \times 0.57 = 226 \text{ kJ kg}^{-1}$$

where $21 W$ is the dry matter capacity of the rumen in relation to body weight (g kg^{-1}), 18.9 is the energy content of the forage (kJ g^{-1}) and 0.57 is the proportion of energy assimilated. This capacity is about half the daily energy requirement of an adult non-lactating caribou during summer.

At the end of summer, green biomass at Prudhoe Bay declines markedly to 10 g m^{-2} or less on all vegetational types except those on rims of low-centered polygons and pingos, where 20 g m^{-2} remains (Webber and Walker 1975, White et al. 1975). In most vegetation types a large amount of standing dead graminoid leaves is available. But this material is generally high in crude fiber and lignin, and expected digestibility would be only 30 to 40% (White et al. 1975). At this time caribou could continue to eat mostly green forage and maintain a relatively high digestibility, or they could consume larger amounts of dead material. RUMENMET was used to evaluate the effectiveness of these alternative tactics. If caribou continued to feed only on green material, then metabolizable energy intake would be about 30% of energy requirements. However, if both green and standing dead material were ingested, the model predicted that the daily metabolizable energy intake would be about 75% of energy requirements.

Even if caribou could consume almost all available food on exposed ridges and at the base of feeding craters, the Prudhoe Bay region appears to be poor winter range. In interior Alaska good winter range for caribou is characterized by shallow snow and high lichen biomass ($>100 \text{ g m}^{-2}$; Hanson et al. 1975). Supplementation with frozen green graminoids is possible (Klein 1970, Hemming 1971), and maintenance requirements can probably be met. In the Prudhoe Bay region exposed ridges and pingos contain the highest lichen biomass. However, these areas constitute only 5% of the vegetated area (White et al. 1975), and the biomass of lichens is generally less than 10 g m^{-2} (Williams et al. 1975).

Population energetics can be calculated from estimates of energy expenditure by age and sex classes within the population combined with estimates of productivity by age class. A flow chart was used to calculate energy expenditures of adult male and female caribou (Table 10-8). Average daily metabolic rate was computed using the model ACTIVE (Bunnell et al., unpubl.), which was constructed to simulate the grazing

TABLE 10-8 *Flow Chart for Calculating Energy Requirements of Adult Grazing Caribou ($\text{kJ kg}^{-0.75} \text{ day}^{-1}$)*

Standard Fasting Metabolism (FM)	$\text{FM}_S = 444$ $\text{FM}_W = 402$	McEwan (1970), caribou $S = \text{summer (1 June-31 Oct)}$ $W = \text{winter (1 Nov-31 May)}$
+		
Energy required for maintaining body function		
↓		
Resting Metabolism (RM)	$\text{RM} = 536 \text{ to } 608$	T. Hammel (unpubl.), reindeer
+		
Energy required for food ingestion and digestion (energy cost of eating and specific dynamic effect)	$\text{RM} = 565$	White and Yousef (1978), White et al. (1975), reindeer
↓		
Maintenance Energy of Sedentary Animal (MM_R)	$\text{MM}_R = 2\text{FM}_S = 888$ $= 2\text{FM}_W = 758$	Kleiber (1961), general
+		
Energy cost of locomotion and grazing activity		
↓		
Maintenance Energy of Grazing Animal (MM_G), equivalent to Average Daily Metabolic Rate (ADMR)	$\text{MM}_{F(S)} = 2.8 \text{ FM}_S$ $\text{MM}_{F(W)} = 2.2 \text{ FM}_W$ $\text{ADMR} = 884 \text{ to } 1244$	See text
+		
Energy deposited in production (P) plus the energy cost of each process (tissue growth efficiency, E_G ; efficiency of milk synthesis, E_M ; efficiency of fattening, E_F)	$E_G = 0.80$ $E_M = 0.70$ $E_F = 0.81Q_M + 3.0$ $= 0.50 \text{ to } 0.70$	Agricultural Research Council (1965), general $Q_M = \text{metabolizable energy of diet/gross energy of diet at maintenance}$
↓		
Metabolizable Energy Requirements (MER)	$\text{MER} = \text{ADMR} + P_G/E_G$ $+ P_M/E_M + P_F/E_F$	
+		
Energy loss in urine and fermentation gases		
↓		
Assimilated Energy Requirement (AER)	$\text{AER} = \text{MER}/0.82$	Blaxter (1962), domestic ruminants
+		
Energy loss in feces (energy digestibility D_F)	$D_F = 0.57 \text{ to } 0.63$	
↓		
Gross Energy Requirement (GER) or Ingestion	$\text{GER} = \text{AER}/D$ $= 1608 \text{ to } 1877$	White et al. (1975), caribou

behavior and activity patterns of caribou. The model indicated that activity significantly affected the average daily metabolic rate and that the energy spent in grazing and evading insects needed to be determined. Grazing involves almost continuous movement, so it was necessary to estimate the energy cost of walking on tundra (White and Yousef 1978). ACTIVE calculated that, compared to days with no harassment, the average daily metabolic rate increased 1.06 times during mild harassment and 1.6 times during severe harassment, and averaged 2.8 times the standard rate during summer. Energy expended on locomotion increases from 17% of the average daily metabolic rate on insect-free days to approximately 60% during severe insect harassment.

Because of their heavy insulation, thermoregulation is not a problem for caribou in winter (White 1975), but the energy required for winter activities has not been determined. The assumption was made that energy expended in digging through snow was no higher than that expended during mild insect harassment. The average daily metabolic rate was then calculated to be 2.2 times the standard fasting rate. Thus, during the year the average daily metabolic rate in non-lactating caribou varied from 884 to 1244 kJ kg^{-0.75}.

Estimates of the production efficiency of each cohort of a caribou population were made from data of Krebs and Cowan (1962) and Kelsall (1968). In calves 3.0 and 4.6% of gross energy intake were used for production by males and females, respectively. Efficiencies declined to approximately 2% in animals between two and three years old and to zero in animals older than five years. Energy secreted in milk was taken as production of calves rather than a component of female production. The main reason for the low efficiency of production is the amount of energy required to support metabolism during winter, particularly from December to June when productivity is negative, and the animals lose weight.

The metabolic requirement for milk production during the first three weeks of lactation is very high—10.5 to 12.6 MJ day⁻¹ or 40 to 50% of the average daily metabolic rate. This energy is required during May and June when primary production is negligible, and the predicted rates of energy intake would be low. Preliminary studies on reindeer grazing in shrub tundra in central Alaska indicate that the peak rate of milk secretion can vary from 0.8 to 2.2 liters day⁻¹ (5.4 to 14.7 MJ day⁻¹), depending on food intake (White, unpubl. obs.). Thus, lactation can be less than optimal, and the growth rate and survival of calves may be related to the diet. Data for grazing reindeer show that the growth rate of calves depends on milk production for at least 50 days. After 50 days milk production declines rapidly (Holleman et al. 1974), and females begin to rebuild the nutrient pools in their bodies (Cameron and Luick 1972).

The general demographic pattern and data on production and gross intake were used to calculate population energetics for caribou (Table

10-3). At a density of 0.001 to 0.01 animal ha⁻¹ annual production was 0.24 to 0.78 MJ ha⁻¹ yr⁻¹. Energy retained, or productive energy, amounted to 1% of gross energy intake, 1.8% of assimilated energy, and 2.1% of respired energy.

Although calves make up only 15% of the population, they contribute 30% of the production. Seventy percent of the production is contributed by the 0- to 3-year-old caribou, which make up only 29% of the population. Thus, disturbances which affect the younger animals, e.g. adverse weather conditions, poor range quality or constant predation and harassment, have a marked effect on the population's productivity.

Population energetics in caribou can be compared with previous calculations for elephants (*Loxodonta africanus*—Petrides and Swank 1966) and white-tailed deer (*Odocoileus virginianus*—Davis and Golley 1963). Average caribou biomass (14 MJ ha⁻¹) was much lower than that of elephants (297 MJ ha⁻¹) or white-tailed deer (54 MJ ha⁻¹). Biomass and population turnover are reflected in absolute production of 0.78, 14 and 27 MJ ha⁻¹ yr⁻¹, respectively, for the three species. However, efficiency of production with respect to energy intake, assimilation and respiration was similar for all species.

In addition to energy, caribou must receive sufficient nutrients from their forage to maintain a normal physiological state. Some insight into the relative importance of various nutrients for caribou can be gained by considering the degree to which nutrients in the diet must be retained. Similar calculations were made for lemmings.

TABLE 10-9 *Relative Concentration of Energy (kJ gdw⁻¹) and Nutrients (mg gdw⁻¹) in Vascular Plants and Caribou*

	Concentration in summer forage (F*)	Concentration in caribou (C)†	Concentration factor (C/F)	P/I** (%)
Energy	18.9	28.9	1.5	1.0
N	25	72	2.9	1.9
K	20	6	0.3	0.2
P	2	15	7.5	5.0
Mg	3	1	0.3	0.2
Ca	2	30	15.0	10.0
Na	1	5	5.0	3.3

* Data as in Table 10-4.

† Based on tissue values estimated for 100-kg domestic cattle (Agricultural Research Council 1965).

** Estimates based on equation analogous to that used for lemmings (p. 356).

Note: Retention of ingested nutrients in caribou represented by ratio of production to ingestion (P/I).

Nearly all production of caribou derives from summer range, so nutrient retention can be considered only in relation to summer forage. Retention of nutrients in the diet, the P/I ratio in Table 10-9, shows that nitrogen, phosphorus, calcium and sodium must be concentrated strongly, but not as strongly as for lemmings (Table 10-4). Nevertheless, nutrient availability could be as important for caribou as for lemmings.

No model has been constructed to explore the tactics open to caribou to maximize nutrient intake and to minimize nutrient loss by conservation and recycling processes as has been done for lemmings. However, if studies made on reindeer apply to caribou, then caribou may conserve nitrogen through urea recycling (Wales et al. 1975), and this mechanism may conserve use of energy, water and glucose as well (White 1975).

COMPARISON OF GRAZING SYSTEMS

Now that the main features of the herbivore-based food chains have been described, it should be clear that microtine rodents and ungulates represent very different approaches to herbivory. This section will compare the main features of these two grazing systems and point out their consequences for the coastal tundra ecosystem as a whole.

Population Characteristics

Perhaps the most conspicuous difference between microtines and ungulates is body size. Although that may seem to be a trivial observation, many life history characteristics of *Lemmus* and *Rangifer*, which determine characteristics of populations, appear to be a function of body size (Table 10-10).

The ratio of body size between lemmings and caribou remains nearly constant from birth through adulthood; caribou weigh about 1500 times as much as lemmings. Both species need to grow by a factor of 20 from birth to adulthood, but lemmings grow relatively faster. Thus, lemmings double their birth weight in four days and reach adult weights in 120 days whereas caribou take four times as long. The association of higher metabolic and growth rates with smaller body size is well known (Kleiber 1961). Generally, the efficiency of growth does not change. Small and large animals produce the same amount of new tissue for each unit of energy digested, but small animals produce the new tissue more rapidly.

Two other life history characteristics associated with small body size are a high reproductive rate and a short life span (Smith 1954). These relationships are dramatic in the lemming-caribou comparison.

Because lemmings have a large mean litter size (seven) and a rapid

TABLE 10-10 *Life History Characteristics of Lemmus and Rangifer*

	<i>Lemmus</i>	<i>Rangifer</i>	Ratio <i>Lemmus/Rangifer</i>
Body size			
Newborn (kg)	0.0033	5.0	0.0007
Weanling (kg)			
Individual	0.013	42	0.0003
Litter	0.091	42	0.0022
Adult (kg)	0.080	100	0.0008
Metabolic (kg ^{0.75})	0.15	32	0.0047
Growth			
Time to double birth wt (yr)	0.011	0.045	0.24
Total growth (kg)	0.077	95	0.0008
Adult/Newborn	24	20	1.2
Weanlings/Adult	1.1	0.42	2.6
Reproduction			
Litter size	7.0	1.0	7.0
Gestation (yr)	0.058	0.42	0.14
Lactation (yr)	0.041	0.44	0.094
Litters yr ⁻¹ (max.)	9.0	1.0	9.0
Age at first reproduction (yr)	0.15	2.0	0.075
Survival			
Maximum life span (yr)	1.5	20	0.075
Expected length of life (yr)	<0.1 to 0.3	2.9	0.069
Potential population growth*			
λ_{max} (yr)	1300	1.5	870

*Assume no deaths and that female lemming produces one litter per month (3.5 ♀♀ per litter), begins reproducing at two months and can produce nine months of the year. A female caribou produces one litter per year (0.5 ♀♀ litter⁻¹).

growth rate, the total weight of the litter at weaning is 1.1 times that of the mother. A weanling caribou weighs only 0.4 as much as its mother. The relative investment of a female lemming in each litter must therefore be much greater than that of a female caribou. The same would be true during a life span because the number of litters produced is similar. Surviving to maximum age and reproducing at a maximum rate, a lemming could produce 14 litters and a caribou 18. During a normal life span both species might be expected to produce one or two litters. A longer life appears to compensate somewhat for slower development and lower reproductive rates in caribou so that the total production of litters is similar. It is the number of individuals per litter, resulting in the large biomass of the litter relative to the mother, that produces a greater investment in offspring per female lemming. These results are consistent with those of Millar (1977), who concluded that litter size is the most important factor affecting the reproductive efforts of mammals in general.

Just as the ratio of body size remains similar for lemmings and caribou at any stage in their life cycle, two important measures of survival,

the maximum and the mean expected lifetime, are about 14 times greater in caribou than in lemmings. Remarkably, the usual ages at first reproduction bear a similar relationship, which again suggests compensation between length of life and speed of development. Of course, the expected life span varies with any changes in the life table, so seasonal and annual differences will make its ratio between lemmings and caribou much more variable than that for maximum length of life.

The consequences of life history differences can be immense when considered at the population level. For instance, if we assume that survival is 100%, the potential population increase for lemmings during one year (λ_{max}) is a factor of 1300 while that for caribou is only 1.5 (Table 10-10). High reproductive potential allows lemmings to respond quickly to temporarily favorable conditions, but such high local densities are reached that they cannot be maintained. Thus, population densities fluctuate wildly. Caribou cannot respond quickly to short-term changes in the environmental conditions, and their population densities change slowly in response to long-term changes in environment.

Because of the great discrepancy in size of the major grazers, density figures (Table 10-3) do not give a good comparison of the two grazing regimes. The extreme changes in density of lemmings are modified somewhat if the time of residence is included (line 2), but the best comparative figure of the amount of grazers present is probably biomass residence (line 4), which compensates for both body size and time of residence. Even this measurement shows that the annual grazing population on the coastal tundra at Barrow is much more variable than that in the Prudhoe Bay region. The annual biomass residence at Barrow may vary between twenty times less and five times more than at Prudhoe Bay.

Energy flow through biomass is disproportionately large in lemmings compared with caribou because of the small body of the lemming. Maximum annual respiratory rates of lemming populations at Barrow are 50 times those of caribou in the Prudhoe Bay region, and relative production rates are even higher. Lemmings do not produce young any more efficiently than caribou, but in relation to their size they produce more. Among lemmings, *Lemmus* produces more than *Dicrostonyx* because litters are slightly larger and breeding seasons are longer (Batzli 1975a). The result of these relationships is that even in the Prudhoe Bay region, where caribou account for most of the biomass of grazers, the respiration and production of lemmings is often greater than that of caribou. Population efficiency and turnover time reflect the same relationships; lemming production efficiencies are greater than those of caribou, and turnover times are about 40 times shorter (Table 10-3).

Food Consumption and Foraging Patterns

The grazing regime imposed by these populations depends not only on their biomass but also on their rate of food consumption and on the composition of their diet. Rates of food consumption must allow at least sufficient assimilation to supply energy requirements. Because of their high energy requirements small mammals often put more grazing pressure on tundra vegetation, even in the Prudhoe Bay region, than do caribou. Although *Dicrostonyx* and *Rangifer* have similar assimilation efficiencies (~ 0.55 to 0.65) *Lemmus* has much lower efficiency (0.33), which further increases ingestion.

The gut capacity of *Lemmus* for digestible nutrients is 60% that of *Rangifer* in relation to body weight (Table 10-11), hence lemmings must fill their stomachs more often. However, for their size lemmings eat much faster, and the net result is that they need to spend only 20% as much time eating as caribou when forage is easily available. Interestingly, although the absolute turnover time of gut contents for lemmings is much less than for caribou, when corrected for metabolic weight (proportional to $W^{-0.25}$ according to Kleiber 1961), the relative turnover times are almost equal.

The distribution of grazing differs in its timing as well as in its intensity. Grazing by *Lemmus* becomes most intense during winter and at snowmelt when the vegetation lies dormant. Caribou migrate, and most of them leave the Prudhoe Bay region during winter, so the grazing pressure from caribou is highest during summer when plants are growing.

The species and parts of plants taken by the grazers also vary. *Lemmus* takes primarily graminoids with a supplement of mosses. During

TABLE 10-11 *Nutritional Characteristics of Mature Lemmus and Rangifer, Assuming Body Weights of 80 g and 100 kg, Respectively*

	<i>Lemmus</i>	<i>Rangifer</i>	Ratio <i>Lemmus/Rangifer</i>
Stomach or rumen capacity (J g ⁻¹ body wt)	125	226	0.56
Fillings (no. day ⁻¹)	14	2.2	6.4
Turnover time (hr) (hr kg ^{-0.25})	1.7 3.2	11 3.5	0.15 0.91
Maximum eating rate (g min ⁻¹) (g kg ^{-0.75} min ⁻¹)	0.14 0.93	6.0 0.19	0.023 4.9
Foraging time (min day ⁻¹)	160	740	0.22

Note: Energetic calculations are for summer (15°C).

summer caribou take equal amounts of the aboveground parts of dicotyledons and graminoids, about 15 to 20% of which may be dead material. During winter caribou in the Prudhoe Bay region probably take mostly dead plant material. *Dicrostonyx* specialize on dicotyledons, mostly *Salix* spp., throughout the year, but graminoids form a supplement of about 10 to 20% of their diet (Batzli 1975a). Ground squirrels eat primarily vegetative and reproductive parts of dicotyledons (Batzli and Sobaski 1980). The combined effects of these diets are that graminoids are most heavily grazed on the coastal tundra at Barrow, while dicotyledons usually receive equal, if not more, grazing pressure than graminoids in the Prudhoe Bay region.

Impact on Habitat

Five major characteristics of the grazing systems in the coastal tundras at Barrow and Prudhoe Bay can be compared (Table 10-12). Because small mammals at Barrow have been more intensively studied during the International Biological Program and because the literature on

TABLE 10-12 Comparison of Mammalian Grazing Systems in the Coastal Tundras at Barrow and Prudhoe Bay

Characteristic	Barrow	Prudhoe Bay
1. Diversity of grazers	Two species One family One order	Four species Three families Two orders
2. Dominant grazer		
a. Biomass	Lemmings (<i>Lemmus</i>)	Caribou (<i>Rangifer</i>)
b. Consumption	Lemmings (<i>Lemmus</i>)	Lemmings (<i>Dicrostonyx</i> and <i>Lemmus</i>) and caribou
3. Grazing pressure		
a. Annual	Light to heavy (cyclic)	Light to moderate (stable)
b. Seasonal	Winter > summer	Winter \cong summer
4. Forage taken	Graminoids and mosses	Graminoids and dicotyledons
5. Major impacts of grazers		
a. Microtopography	Burrows, runways and hummock formation.	Trampling, trails and burrows.
b. Vegetation	Favor graminoids and increase productivity.	Undocumented.
c. Soil	Speed nutrient cycling, increase depth of thaw and change dispersion patterns of nutrients.	Undocumented.

them is more extensive (see Batzli 1975a for review), ideas regarding their impact on tundra are more complete. The impacts can be considered in relation to three interacting components of the ecosystem, viz. microtopography, vegetation and soils. While some inferences can be drawn regarding the Prudhoe Bay region, they are largely speculative.

Lemmings at Barrow construct their burrows on elevated sites, e.g. centers of high-centered polygons or rims of low-centered polygons, which have favorable drainage. As a result, much of the drier tundra is riddled with burrows, and barren areas are formed at burrow entrances by deposition of soil. Runways connect the burrows, and hummocks often develop between runways owing to erosion of fine materials that are not stabilized by vegetation. In areas denuded by frost heaving, there seems to be progressively greater hummock development associated with increasing vegetation growth and lemming activity. Unfortunately, this sequence has not been documented by long-term observations in one area.

In the Prudhoe Bay region, where lemmings are less abundant, their impact is not as clear, although burrows and runways may be conspicuous in some areas. Ground squirrel diggings on river banks, sand dunes and pingos do create dramatic series of holes and mounds, but ground squirrels occupy only a small portion of the tundra. Caribou generally spread out as they graze, so compaction of soil caused by their trampling is not obvious except for systems of trails leading to sand dunes where they seek refuge from insect attack. Of course, the effects of grazers on microtopography presumably are reflected in the soil characteristics, such as soil temperature and depth of thaw.

Exclosure studies at Barrow, originally started in 1950, indicate that the elimination of lemming grazing causes several changes in vegetation (Batzli 1975b). At well-drained sites, carpets of mosses and lichens develop and graminoids become sparse. In low, wet sites graminoids continue to dominate, but standing dead material accumulates and productivity declines. Apparently, heavy lemming grazing disrupts mosses and lichens, which recover slowly. Graminoids, however, have their meristematic tissue under the moss layer and can replace shoots rapidly by drawing upon reserves in underground rhizomes. Chronic grazing by caribou during summer may have less effect on vegetation than the intensive grazing during winter and spring when lemming populations are high.

Grazers can affect vegetation indirectly as well as directly (Batzli 1975b). The bulbet saxifrage, *Saxifraga cernua*, appears to be concentrated around old lemming burrows and trails as does an acrocarpous moss, *Funaria polaris* (B. Murray, pers. comm.). *Saxifraga* is probably there because lemmings disperse their sticky bulbets, while *Funaria* may simply specialize on lemming feces as a substrate. Herds of caribou may have significant local effects owing to trampling and deposition of man-

ure (Bee and Hall 1956, Steere, pers. comm.), but this impact has not been measured nor have long-term patterns been studied. The moss *Voitia hyperborea* is associated with musk ox and caribou dung (Steere 1974). Heavy mats of the grasses *Arctagrostis*, *Alopecurus* and *Calamagrostis* cover tops of sand dunes and pingos occupied by ground squirrels, apparently in response to disturbance and manuring. Caribou and ground squirrels also may influence the reproductive success of some dicotyledons, particularly *Pedicularis* and *Saxifraga*, since they seem to be especially fond of their flowering heads.

A particularly interesting interaction between lemmings, soil and vegetation may be occurring in areas with low-centered polygons. Microtopography produces large differences in soil moisture within a few meters. The deepest portions of polygon troughs may contain water all summer long, whereas the basins of low-centered polygons contain water only in early summer, and their rims are never submerged. Soil organic matter is greatest in the basins (bulk density $< 0.5 \text{ g cm}^{-3}$) and least in the troughs (bulk density $> 1 \text{ g cm}^{-3}$). Exchangeable phosphorus is greatest ($240 \mu\text{g g}^{-1}$) in the troughs and least ($90 \mu\text{g g}^{-1}$) in the basins (Barèl and Barsdate 1978). Differences in soil conditions produce different vegetational communities. Graminoid shoots are most robust and dense ($\sim 3000 \text{ m}^{-2}$) in troughs and least robust and dense in basins ($1000 \text{ to } 1500 \text{ m}^{-2}$). Phosphorus concentration in plant tissues and plant production are both highest in troughs. Decomposition and, therefore, nutrient cycling appear to be most rapid in troughs because that is where production of organic matter is greatest and accumulation is least. The highest activity rates of bacteria and the highest standing crops of soil invertebrates also occur in troughs, thus accounting for high rates of decomposition. Lemmings also concentrate their activities in troughs, apparently because the most palatable and nutritious food is concentrated there.

All these observations are consistent with one another, and they allow the microtopographic units to be ranked in order of decreasing biological activity: troughs, rims and basins. The one factor that seems most likely to account for the differences in biological activity is soil phosphorus. Higher levels of phosphorus allow greater production of more nutritious vegetation, which stimulates both decomposition and herbivory. Moisture conditions may also influence decomposition, and the troughs maintain greater soil moisture during the warmest part of the summer. But why should phosphorus be concentrated in the troughs?

One explanation might be that phosphorus is leached from the rims of low-centered polygons to the troughs. But if this were the only factor, phosphorus would accumulate on both sides of the rims, in the basins as well as the troughs. Then the basins and troughs would be expected to show similar levels of available phosphorus, which is not the case. A second possibility is called the nutrient-transport hypothesis: that lemmings

transport nutrients from both basins and rims to troughs.

Polygons form in drained lake basins, which have relatively uniform topography and sediments and, therefore, an even distribution of soil nutrients before polygon formation begins. The nutrient-transport hypothesis provides an explanation for the development of the current patterns of biological activity as polygonal ground develops. The sequence of events can be hypothesized as follows.

Troughs develop over ice wedges, and the wedges continue to expand to produce the rims that surround the basins (Figure 1-10). Drainage is impeded in the central basins and the deepest parts of the troughs. Although the basins of low-centered polygons hold water during early summer, they are higher and relatively drier than the troughs by midsummer. Snow cover is deeper in the troughs during winter. Lemmings place their winter nests in troughs where deeper snow improves the microhabitat. Foraging lemmings move out from the troughs under the snow, but most feces and urine are deposited in the troughs near the nests. Nutrients accumulate in the troughs as a result of lemming activities. Nutrients are depleted in the basins where lemmings remove forage but deposit few wastes. Summer (June through September) burrows and nests are located on the relatively dry rims. The rims attain an intermediate nutrient status because they are the site of summer nests and near the winter nests. Accumulation of nutrients is associated with higher primary production and higher concentration of nutrients in the trough vegetation (Barèl and Barsdate 1978, Tieszen, pers. comm.). Improved forage reinforces the preference of lemmings for troughs. Nutrient depletion has the opposite effect in the basins. Increased activity of decomposers and soil invertebrates occurs in response to higher quality of litter and concentration of soil nutrients in troughs (see Chapter 11 for details). Accumulation of organic matter in the soil is slowed, and rates of nutrient cycling increase. Again, the opposite trends occur in the basins.

Although these events have been presented sequentially to emphasize causal relationships, all occur simultaneously. The result is a slow transition from relatively homogeneous distribution of soil properties and biological activity in drained lake basins to the marked spatial heterogeneity seen in polygonal terrain. According to the nutrient-transport hypothesis, spatial differences in biological activity are largely a result of different availability of nutrients. The pattern of nutrient availability is imposed by activities of lemmings.

Unfortunately, we do not have sufficient data to test the nutrient-transport hypothesis. The trends in soil properties and biological activity associated with polygonal terrain have been used to construct the hypothesis and cannot be used to test it. Ultimately, the causal links will need to be tested by field observations and experiments. In the absence of

TABLE 10-13 *Nutrients (kg ha⁻¹) Accumulated During a Standard Lemming Cycle (3 Years) as Calculated by a Simulation Model of Nutrient Transport by Lemmings*

	Habitats same			Habitats different		
	N	P	Ca	N	P	Ca
High plant nutrients						
Troughs	0.25	0.05	-0.07	-0.17	-0.33	-0.58
Rims	-1.03	-0.24	-0.28	-0.51	0.07	0.11
Basins	-0.32	-0.07	-0.08	-0.39	0.05	0.04
Carcasses	1.40	0.34	0.54	1.40	0.34	0.54
Low plant nutrients						
Troughs	-0.32	-0.08	-0.04	-0.31	-0.22	-0.61
Rims	-0.58	-0.13	-0.17	-0.43	-0.02	0.14
Basins	-0.16	-0.04	-0.05	-0.32	-0.02	0.04
Carcasses	1.40	0.34	0.54	1.40	0.34	0.54

Note: Four cases were run: with nutrient levels in forage high or low and with nutrient levels in forage the same or different in the three microhabitats at the beginning of the run.

such data, we have tried to determine the feasibility of the hypothesis by using computer models of lemming population dynamics and nutrition to calculate deposition of urinary and fecal nutrients in the various microtopographic units. The activity of lemmings in the various microtopographic units was distributed according to time spent in nests and percentage of shoots clipped in each unit. We assumed that excreta are formed and deposited continually. Thus, if lemmings spend 50% of their time in their nests, 50% of their excretions would be deposited in troughs, and the remaining amount would be distributed according to the amount of time spent foraging in each microenvironment. If the figures are adjusted for the relative area of each unit, the removal and deposition of nutrients can be put on an areal basis.

The results of these simulations indicate that net transportation of phosphorus from rims and basins to troughs only occurred when plant nutrient concentrations were high and the same in all habitats at the beginning of the run (Table 10-13). This would be the situation as polygonal development began in a recently drained lake basin.

In all cases the concentration of nutrients in lemming carcasses was sufficient to alter the results, depending on where those carcasses were deposited. Most carcasses found on tundra are in the troughs, near or in

winter nests. This would increase nutrient deposition in troughs. Many, perhaps most, carcasses are taken by predators. Weasels deposit their scats near the winter nests of lemmings, but avian predators regurgitate pellets on higher ground, the rims of low-centered polygons and the centers of high-centered polygons. Deposition of pellets would therefore add nutrients to rims, and this would counteract the trend of greater nutrient removal from rims than from basins (Table 10-13).

The total movement of phosphorus to troughs, assuming half of the carcasses decayed in troughs, would be 0.2 kg ha^{-1} (20 mg m^{-2}) over a three-year period, five times the average amount of soluble phosphorus found there at present. While this simulation does not prove that consumers move nutrients to polygon troughs, it does show that the nutrient-transport hypothesis is feasible.

We do not know how effective predators are as nutrient-transport systems, but snowy owls spend long periods of time on favorite centers of high-centered polygons (owl mounds). Extremely high levels of phosphorus accumulate in the soils of these mounds, and grasses such as *Arctagrostis*, *Calamagrostis* and *Poa* dominate the vegetation there as nowhere else at Barrow. Jaegers deposit their pellets on lower mounds, such as the rims of low-centered polygons, as well. The deposition of these pellets affects the foraging patterns of shorebirds. MacLean (1974b) has shown that female shorebirds must consume lemming bones when laying eggs to obtain enough calcium for their eggshells. Shorebirds, which normally forage in lower areas, search on mounds for lemming bones. Thus, nutrient transport by consumers can affect other consumers as well as producers and decomposers.

More observations, calculations and experiments are required to determine the effectiveness of consumers as nutrient-transport systems in tundra. If confirmed, these systems will be an important example of the major impact consumers can have on ecosystem structure and dynamics, much greater than that predicted by simple measurement of their biomass.

Consideration of changes in tundra vegetation and soils after removal of lemming grazing provides additional insight into the effects of grazers on coastal tundra. Batzli (1975b) sampled exclosures near Barrow that had been in place for 15 years (Schultz 1964) and 25 years (Thompson 1955c). Vegetation had changed little in low, wet sites that had standing water most of the summer. In mesic and dry sites, however, the net production of graminoid stems and leaves was almost twice as high in grazed areas as in the exclosures. Standing dead material and detritus were greater within the exclosures, suggesting that nutrient cycling had diminished in the absence of grazing. Reduced phosphorus in the soil solution under exclosed areas corroborates the hypothesis of decreased nutrient availability in the absence of grazing (Barèl, pers. comm.).

Batzli (1978) reviewed evidence for similar effects of herbivores in other ecosystems. Although the effects may not be as dramatic, herbivory in grasslands and forests may also increase the rate of nutrient cycling and change the distribution of nutrients.

SUMMARY

A single species, the brown lemming (*Lemmus sibericus*), dominates the herbivore community at Barrow. The number of trappable animals per hectare increases to a peak of 150 to 250 every three to six years and may drop to less than 1 in the years between.

A simulation model shows that a dramatic increase in the population can be produced by a slight improvement in the survival rate of adult females and their young. The population increases occur during those winters when the structure of the snowpack allows access to food, when forage quality is high, and when predatory mammals are scarce. The high reproductive potential of lemmings then allows the population to increase greatly before the snow melts.

Only catastrophic mortality can explain the radical declines. Current evidence suggests that the mortality, at least early in the summer, is caused by overgrazing accompanied by a rise in the number of predatory birds. However, the effects of increased social interactions on the dispersal and genetics of high populations have not been studied sufficiently.

Examination of the nutrient-recovery hypothesis as an explanation for cyclic fluctuations in lemming density leads to the conclusion that it requires modification. Although changes in the nutritional quality of the vegetation may affect lemming populations, lemming activity does not appear to produce the short-term effects required to alter nutrient concentrations in soil and plants as proposed.

The herbivore community in the Prudhoe Bay region is more diverse and more stable than that at Barrow. Caribou (*Rangifer tarandus*) provide the greatest herbivore biomass. The brown lemming and the collared lemming (*Dicrostonyx torquatus*) exist in about equal numbers, but their density is an order of magnitude less than at Barrow. Even so, lemmings may consume three to six times as much vegetation as caribou because their metabolic rates are higher and their forage is less digestible. Ground squirrels (*Spermophilus parryii*) are also important herbivores in more restricted habitats.

Comparison of ungulate and microtine grazers reveals two very different, but equally successful, suites of adaptation to herbivory on tundra. The short development times and large litters of the microtines give them a high population growth rate. In order to fuel its high metabolic rate a microtine must fill its gut often. But because it eats faster and has a

faster turnover rate of gut contents than an ungulate, it requires less time for foraging. Caribou, on the other hand, being large and mobile, are less vulnerable to predators and can therefore spend more time foraging. During the summer they must make up for the undernutrition they suffer during winter. Their grazing patterns can be interpreted as an attempt to maximize their intake of high quality forage. But on some days harassment by mosquitoes and warble flies prevents them from obtaining adequate nutrients.

Owing to their periodic abundance lemmings can strongly affect vegetational composition and production on the coastal tundra at Barrow. There is little evidence of this in the Prudhoe Bay region, however, and the effects of grazing are not conspicuous there. Both lemmings and caribou influence soil characteristics by burrowing, trampling and manuring.

A proposed nutrient-transport hypothesis ascribes the uneven distribution of soil nutrients and biological activity in polygonized terrain to the redistribution of nutrients by animals.