

Population cycles of lemmings near Barrow, Alaska: a historical review

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Current hypotheses regarding the causes of population cycling of brown lemmings *Lemmus trimucronatus* (Richardson, 1828), developed during long-term studies from 1950–1974. We maintain that three factors largely determine the timing and amplitude of population cycles in brown lemmings. First, a basic interaction between lemmings and vegetation sets the stage because dense populations of lemmings severely damage the vegetation, at which point lemming populations decline and remain low until the vegetation recovers. Second, opportunistic predators, mainly jaegers and owls, assemble as the snow melts during peak years and drive already declining populations to extremely low densities. Weasels are effective predators under the snow, but they appear irregularly. If weasel populations increase early in the cycle, lemming populations that normally increase dramatically during the winter in a peak year can be decimated before the snow melts. Finally, both wet summers that result in extensive flooding of the preferred habits of lemmings and freezing rains or winter thaws that cause ice formation reduce food availability, disrupt the cycle and extend the period between peak densities. Numerous observations, experimental results and simulation models support these views. Similar results regarding the importance of the available food supply, particularly in winter, and of the predation regime also have been reported for arvicoline populations at lower latitudes.

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Introduction

Brown lemmings *Lemmus trimucronatus* (Richardson, 1828), in northern Alaska hold a special place in mammalian population ecology. Long-term data for their population dynamics

present the most convincing demonstration of high-amplitude population cycles (alternating peaks and valleys in density over a period of 3–5 years) for arvicoline rodents in North America (Turchin 2003). Although intensive studies of arvicoline rodents continued in northern Alaska from the early 1950's to the late-1980's, regret-

tably few investigations have occurred since then. Our objectives in this review are: 1) to provide a historical account of progress in understanding the fascinating population cycles of brown lemmings on the North Slope of Alaska and 2) to stimulate further research on this problem.

Because we were involved in much of the research, this review reflects our personal experience, and we report not only the results of published studies but also background information to indicate how others influenced our views. We do not review information on population cycles in general, as our main concern is with the historical development of understanding the cycles near Barrow, Alaska. We include a section reviewing other studies that emphasize the factors we use to explain events at Barrow, even though done on different species and at different latitudes, to suggest the possibility of more general application of our results. We do not attempt to review the many studies that have suggested alternative explanations for population cycles, however, and make no pretense that this is a complete review. To do so would require a monograph because of the many hypotheses proposed to explain cycles (Batzli 1992 presented a list of 22 hypotheses and several more have been proposed since).

Early observations

Shortly after they first arrived in Northern Alaska, the Iñupiaq people probably became aware of periodic outbreaks of lemmings, but the scientific study of brown lemmings in tundra near Barrow, Alaska did not begin until the first biological surveys of the area in the late 1800's. By the early 1900's Charles Brower, a local merchant and self-styled "King of the Arctic", had begun to sell lemming skins to natural history museums (Brower 1942). The timing of peak densities of lemmings near Barrow based upon the scientific literature can only be traced back to the end of World War II. Earlier records probably could be reconstructed from the number of specimens that museums across North America received each year from Brower. Serious study

of the population ecology of lemmings, however, did not begin until the early 1950's after establishment of the Naval Arctic Research Laboratory (NARL) just southwest of Point Barrow, the northernmost point of Alaska (71°20'N, 156°40'W). A brief history of the first 25 years of NARL can be found in Britton (1973). A more expansive work provides additional details and reminiscences for the first 50 years (Norton 2001).

Robert Rausch was the first mammalogist to visit NARL regularly. Although his main interests were parasitology and systematics, he reported that a lemming peak had occurred in 1946, and he published observations on the collapse of a peak population during late winter and spring of 1949 (Rausch 1950). He observed lemmings scurrying everywhere and found dead and dying lemmings on the snow, but they showed no obvious lesions or signs of disease. Unfortunately, no reliable estimates of population densities were made for these cycles.

Neal Weber, an entomologist on the scene in 1948 and 1949, observed the destruction that the lemmings had wrought on the vegetation, which included clipping of nearly all the monocot stems and extensive digging for rhizomes. He suggested that the deaths before snow melt occurred because of starvation (Weber 1950), an interpretation supported by a later finding that lemming carcasses found frozen in the snow had extraordinarily low fat content (1.1% for frozen carcasses versus 2.0% for animals that starved in the laboratory, Batzli and Esseks 1992).

Spurred on by these early reports, Daniel Thompson began a four-year study of lemmings (1950–1954) that culminated in his Ph. D. thesis (Thompson 1955a). This was the first of several theses on the ecology of lemmings, their forage and their predators during the next two decades (Maher 1961, Pieper 1964, Mullen 1965, Gesamen 1968, Underwood 1971, Bunnell 1973, Coady 1975, Osborn 1975, Barkley 1976). Thompson (1955a) monitored lemming populations (indices of density in three habitat types), their food supply (primarily monocots), and their predators (primarily weasels, foxes, owls, and jaegers) from 1950–54. He also constructed exclosures to assess the effects of lemming activity on the subsequent production of vegetation.

Although surprisingly comprehensive, this study only provided reliable data on relative, not absolute, densities of lemmings.

Thompson found that intensive grazing (nearly 100% of the stem bases of monocots clipped by lemmings during winter) and digging for rhizomes dramatically reduced the standing crop of new forage by about 50% during summer following the peak density of lemmings in 1953. Because lemmings depend on the green bases of monocot shoots for energy during the winter (mosses provide a nutrient supplement but far less digestible energy – see Batzli 1993), and because reproduction of lemmings declined after peak densities (less reproduction in late summer and no winter reproduction), Thompson concluded that lemming cycles resulted from a dominant herbivore interacting with its forage. Although the major cause of population decline immediately after peak densities in 1953 appeared to be predation, he did not think that predation was a necessary feature of the cycle because other factors would have led to a decline in the absence of predation (Thompson 1955b). Finally, Thompson observed a “lemming emigration” before snow melt in 1953, but he found fewer dead lemmings than Rausch reported for 1949, and regarded losses from these apparently random, pre-melt movements as relatively unimportant for the lemming decline in 1953 (Thompson 1955c).

In 1951 James Bee began his survey of the mammals of the North Slope of Alaska and added valuable information on the distribution and natural history of lemmings (Bee and Hall 1956), but the geographic extent of his work precluded detailed treatment of local population dynamics. In that same year the senior author (FAP) arrived to study bird populations. He soon realized that the lemming cycle was a major ecological event in the tundra ecosystem near Barrow, one that had implications for many other aspects of ecosystem dynamics, and he decided to start a long-term study of lemmings and their predators. The work began modestly in 1952 by asking local villagers (mostly children) to capture lemmings by hand so that changes in their population structure and reproductive activity could be documented for different phases of the

cycle. It slowly burgeoned into regular trapping on permanent trap lines at Barrow and across the North Slope of Alaska, and the study continued in various forms for over two decades.

The development of long-term studies of lemmings at Barrow can be traced back to the formal training in ecology of FAP at the University of Illinois at Urbana-Champaign where he arrived in 1937 to complete his last two years of college. Victor E. Shelford, founding president of the Ecological Society of America, and his student S. Charles Kendeigh, a later president of ESA, were the leading ecologists at Illinois. At this time Shelford still went to Churchill, Manitoba every summer, where, among other things, he observed population cycles in collared lemmings *Dicrostonyx richardsoni* (Shelford 1943). Courses taken with Shelford and Kendeigh introduced FAP to an expanded view of ecology, including topics such as, the impact of physical and biotic factors on patterns of distribution and abundance of populations, the patterns and processes of succession, and the patterns of community structure and organization.

Because of his enthusiasm for birds, FAP soon came under the wing of Kendeigh, served as his research assistant, and had access to his private library of ecology. One of the first books that he borrowed was Charles Elton's small, but influential, volume on animal ecology (Elton 1927), which opened his mind to the world of trophic interactions and their role in population dynamics and community organization. Later, in 1952–1953, when FAP observed the striking damage to vegetation and the impressive gathering of predators associated with peak lemming populations at Barrow, these early lessons became an important backdrop for the explanation of lemming cycles in terms of trophic interactions.

Of course, FAP was not alone in this approach to lemming populations. David Lack's important book on the regulation of animal numbers appeared in 1954 (Lack 1954). It emphasized the role of food in population fluctuations and included a chapter on population cycles. Impressed with a variety of lines of evidence that pointed to food shortage for voles, lemmings, and hares at high densities, Lack pro-

posed that population cycling in herbivorous small mammals occurred because of a strong interaction with the vegetation, a classical predator-prey cycle but at a lower trophic level. Furthermore, FAP was a contemporary of and interacted with Thompson, whose work we have already discussed, and the arguments in Lack's book influenced both of their views regarding the lemming cycle at Barrow.

The nutrient-recovery hypothesis

By 1956 ecological research at NARL was thriving. Max Britton, a plant ecologist (Britton 1957), became director of the Arctic Section of the Office of Naval Research in 1954, and Max Brewer, a permafrost geologist, became Director of NARL in 1956 (permafrost refers to the perennially frozen ground that underlies the shallow active layer of tundra soil that thaws each summer – see Brown and Sellman 1973). Britton and Brewer proved to be extraordinarily supportive of ecological research at tundra sites. One result was the development of a team to investigate interactions of soils, vegetation, lemmings, and predators. John Tedrow had responsibility for soil (Tedrow 1973), Arnold Schultz for vegetation-lemming interactions (Schultz 1964, 1969), and FAP for lemming-predator interactions (Pitelka *et al.* 1955a, 1955b, Pitelka 1957a, 1957b, 1964, 1973).

In 1958 Schultz began intensive study of changes in vegetation and soils associated with lemming activity (Schultz 1964). New exclosures confirmed Thompson's results that clipping of plants and digging of rhizomes by lemmings reduced the standing crop of vegetation during the summer following a lemming peak (1960), by about 20% for just clipping and about 90% for digging rhizomes. Furthermore, concentration of phosphorus, calcium, and nitrogen in the forage plants outside of exclosures cycled in concert with lemming populations, increasing as lemming density increased and declining dramatically after peak densities. Within the exclosures nutrient concentrations changed relatively little from year to year. The depth of thaw of soil dur-

ing summer also cycled outside the exclosures, increasing after a peak population removed most of the insulating vegetation and declining as the vegetation recovered in subsequent years. Again, much less annual variation in depth of thaw occurred within exclosures. Finally, measurement of nutrients in soil cores indicated that concentrations of phosphorus and calcium dropped off sharply with depth.

In addition to increased mortality during the population crash, reproduction by lemmings was curtailed, particularly during winter following peak densities, as had been reported by Thompson (1955b). Christian (1950) had proposed that physiological effects of stress associated with crowding at high densities could account for a subsequent decline in reproduction, but a physiological study of brown lemmings in the field by Mullen (1968) found no evidence of such stress. To account for all these results, Pitelka (1964) and Schultz (1964) developed the nutrient-recovery hypothesis, which extended Lack's simple view of lemming-plant interactions to encompass additional aspects of the ecosystem, particularly the processes of decomposition and nutrient cycling (Fig. 1).

In outline, the nutrient-recovery hypothesis stated that peak lemming populations decimate the vegetation to such an extent that the populations begin to starve and a population crash ensues. Devastation of the vegetation substantially lowers plant productivity and accumulation of litter during the growing season. With substantial reduction of standing vegetation and litter, more solar radiation reaches the soil surface, which warms the soil so that depth of thaw increases. Because decomposition and, therefore, soil nutrients are concentrated at upper levels of soil, lower concentrations of nutrients become available to plants as their roots penetrate lower levels of soil, and total uptake of nutrients decreases. As a result, new growth of forage contains low levels of nutrients, which curtails reproductive success of lemmings. Lemming populations only recover their high reproductive output and associated population growth when plant production and accumulation of litter have increased, normal depth of thaw has returned, and nutrient levels in forage plants have recovered.

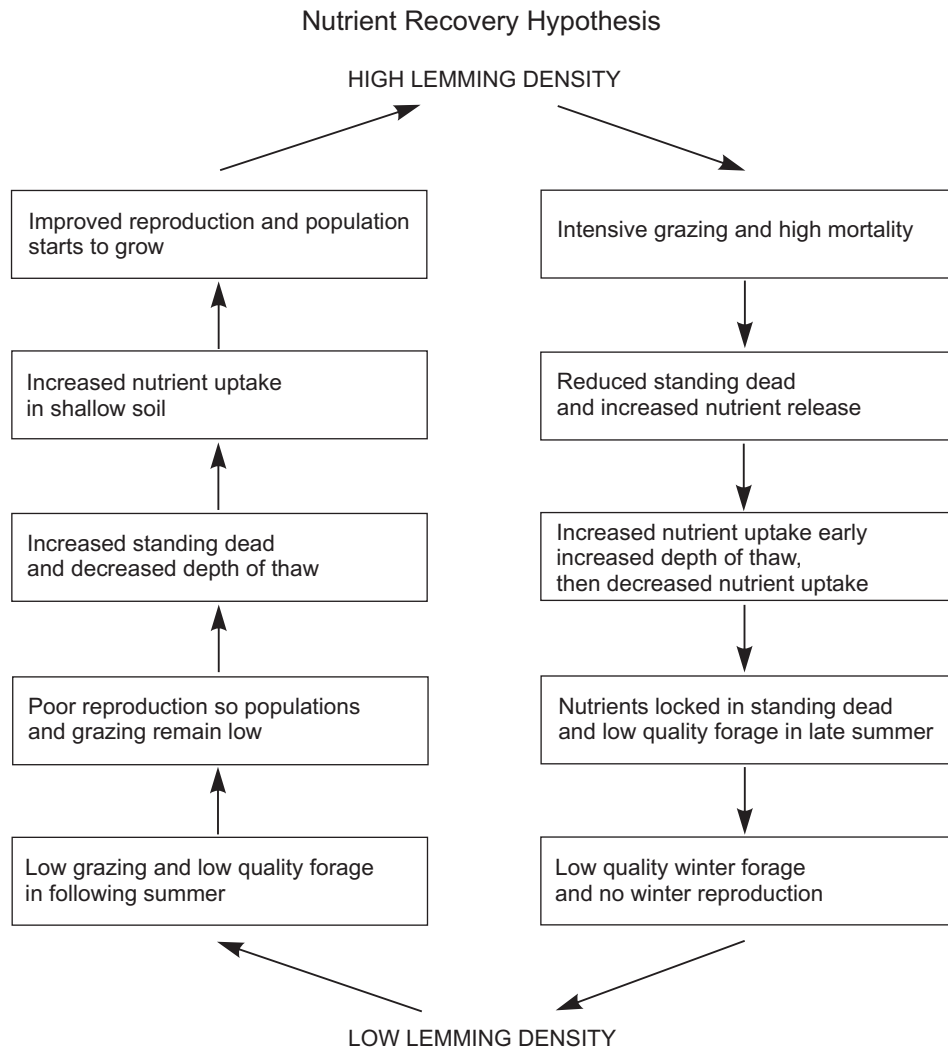


Fig. 1. Summary of major steps in the nutrient-recovery hypothesis as proposed by Pitelka (1964) and Schultz (1964, 1969).

A fertilization experiment that Schultz (1969) conducted to test the nutrient-recovery hypothesis produced disappointing results. If interactions of soil nutrients, plant quality, and lemming activity drove the lemming cycle, fertilization should have broken the cycle by maintaining high levels of nutrients in the soil and in the vegetation. This in turn should have maintained high densities of lemmings or at least caused an earlier recovery of populations following peak densities. The work began at low population densities in 1961 (peak densities occurred in 1960) and continued through 1964, during which time a general population increase

and decline occurred under the snow in the winter of 1962–1963. Addition of nitrogen, phosphorus, potassium, and calcium to a 2.4 ha plot in wet meadow (a favored lemming habitat) quickly increased net production and nutrient concentrations in plants (3 to 4 times compared to the control plot) and stopped cyclic fluctuations in nutrients. No response of the lemming population was seen until the winter of 1963–1964, however. A survey of winter nests of lemmings in early summer of 1964 found densities 300 times greater on the fertilized plot than on a nearby control plot, which indicated a huge local increase of lemming densities during the pre-

vious winter. After snowmelt, however, lemming populations were relatively low on both the fertilized plot and on surrounding tundra. Schultz (1969) explained that "jaegers had found this 6-acre pantry and picked it clean." This "pantry effect" illustrated the difficulty of interpreting results of field experiments when predators can concentrate on experimental plots.

Subsequent research supported some, but not all, of the tenets of the nutrient-recovery hypothesis. Because of high energetic requirements and low digestibility of forage, high lemming populations must eat virtually all the available stem bases of monocots during winter (Batzli 1975a). The activities of lemmings do impact rates of nutrient cycling and monocot growth, slowing both over the short term of 1 to 2 years but increasing both over the long term of 10 to 20 years (Batzli 1975b, 1978). Grazing by lemmings does reduce vegetative cover, which does increase the depth of thaw, and nutrient concentrations in forage do change dramatically from year to year, though not simply because of changes in depth of thaw (Batzli *et al.* 1980, Chapin *et al.* 1980). Low nutrients in food can reduce reproductive success of arvicoline rodents (Batzli 1986), and reproducing female lemmings do face nutrient depletion (Barkley *et al.* 1980). Nevertheless, the growth of brown lemming populations does not simply track the concentration of nutrients in their forage. In some years lemming populations did not increase even though nutrient concentration in their forage was relatively high (Batzli *et al.* 1980). Thus, the nutrient recovery hypothesis did not provide the sole explanation for population fluctuations of lemmings at Barrow, but it did faithfully describe several aspects of a remarkable series of events in the nutrient dynamics of the tundra ecosystem.

Long-term studies and multiple factors

Starting with Thompson's work, lemming populations near Barrow were the subjects of investigation every summer from 1950 through 1974, sometimes by more than one laboratory.

By 1955, after Thompson had completed his field work, FAP decided to quantify changes in density of lemming populations by intensive snap-trapping along eight pairs of 300-m trap lines in a variety of habitats within 6-km of NARL. The data from these trap lines provided a consistent index of density two or three times each summer for 19 years (1955–1973) and became the basis for long-term estimates of fluctuations in density, reproduction, and population structure that were used to synthesize the dynamics of the herbivore food chain by the U. S. IBP Tundra Biome (Batzli *et al.* 1980). By using mark and recapture procedures before snap trapping, the trap indices of FAP were transformed to estimates of absolute density (Fig. 2, Batzli 1981). Note that collared lemmings *D. groenlandicus*, only occurred at very low numbers near Barrow, except for 1971. Although qualitative information exists for peak densities of brown lemmings in 1946 and 1949, and indices of density exist for 1953, estimates of absolute densities for these early peaks, as reported in Schultz (1969), remain little more than educated guesses.

After 22 years of studying brown lemming populations at Barrow, Pitelka (1973) concluded that multiple environmental factors affect their pattern of population dynamics. In the early years of study at Barrow populations rose and fell in a repeated pattern with population peaks occurring every 3–4 years (1946, 1949, 1953, 1956, 1960). The build-up to population peaks generally occurred in winter under the snow, but was heralded by a population increase the prior summer. The population crash started in late winter or in spring before snow melt, at which time emaciated, dead or dying lemmings were often found in the snow. Apparently driven by the great influx of predators at snow melt, the decline continued to low population levels by the end of summer in spite of substantial reproduction (Pitelka *et al.* 1955a). In 1956, however, the population crash appeared to come early; population densities were only moderate when the snow melted, although abundant winter nests and signs of winter grazing indicated that densities had been much higher (Fig. 2).

In 1960 the population did not decline during summer, even though the predator influx oc-

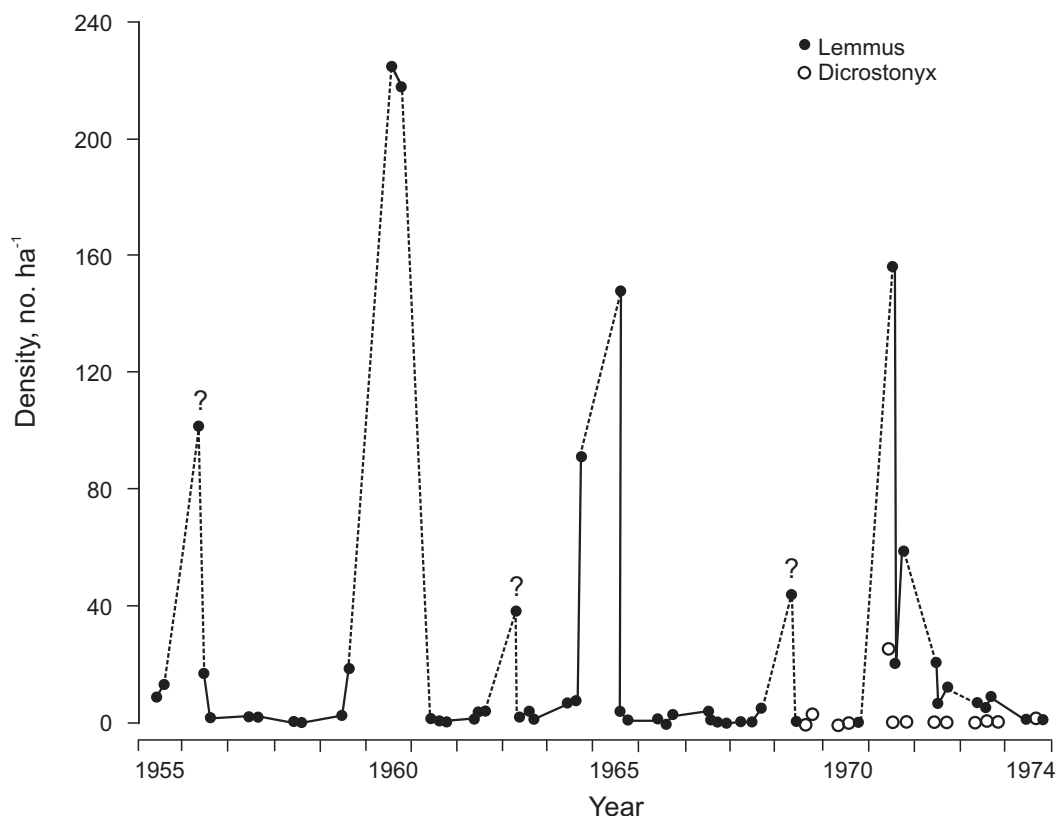


Fig. 2. Overall estimates of densities of lemmings in a variety of habitats based upon catches from trap lines. Mark and recapture estimates from live trapping were used to transform snap-trap indices to densities (Batzli 1981). Dashed lines represent changes in density during winter, and question marks indicate estimates of likely densities reached sometime before snowmelt based upon signs of winter nests and grazing. From Batzli *et al.* (1980).

curred, perhaps because much of the population increase occurred later in the winter so that some food remained when the snow melted. After that, rapid growth of the vegetation could sustain the population until late summer. Very low densities occurred during the next three summers, rather than just the usual one or two summers. During the winter of 1962–1963 lemming populations increased, as indicated by the extent of clippings and winter nests, but weasels appeared earlier in the cycle than usual, and lemming populations were again low by snowmelt. The summer of 1963 was unusually wet and cold, which likely had two effects: (1) reduced production of monocots, the major food supply for lemmings (Batzli and Pitelka 1983), and (2) continued flooding of low-lying habitats, where the greatest concentration of high quality

food occurred (Batzli *et al.* 1983). As a result, populations did not increase during the winter of 1963–1964, and lemming populations did not reach their next peak until 1965. Populations crashed during the summer of 1965 as they had in the early years, but again the peak was followed by a series of summers with low population densities (this time from 1966–1970). In the winter of 1968–1969 a population that increased under the snow was again invaded by weasels and returned to low densities by snowmelt (MacLean *et al.* 1974), a pattern similar to the winter of 1962–1963. The following winter (1969–1970) was severe and started with freezing rain that coated the tundra surface with ice, thereby locking up much of the food supply for lemmings. Finally, in 1971 a strong peak occurred and crashed but with a relatively slow de-

cline (Fig. 2). This peak occurred with the usual influx of avian predators, but without the usual warning of increasing lemming densities the preceding summer and without a marked increase in weasel populations (MacLean *et al.* 1974). These events (Pitelka 1973 provides more details) convinced us that weather, predators, and food supply all have a role to play in the timing and magnitude of density fluctuations of brown lemmings.

In addition to the studies at Barrow, FAP embarked on a geographical survey to determine the spatial extent of small mammal cycles on the North Slope of Alaska, the degree of synchrony of population fluctuations of lemmings at different sites and among different species at the same site (four species of arvicoline rodents in addition to the brown lemming occur on the North Slope), and the patterns of distribution of predators. The methods used in these studies and the distribution and fluctuations in density of arvicoline rodents across the North Slope are summarized in Pitelka and Batzli (1993).

Results from these extensive studies confirmed that the population peaks of brown lemmings and the associated increase of predator populations only occur synchronously within a 50-km radius of Barrow. Population cycles occur over a more extensive portion of the coastal plain to the east and west of Barrow, but not in synchrony with those near Barrow.

Moving inland, as greater topographic relief creates a mosaic of drier habitats, other species of arvicoline rodents become important and population cycles disappear (Batzli and Jung 1980, Batzli and Henttonen 1990, Pitelka and Batzli 1993, Batzli and Lesieutre 1995). Substitutions for some of the dominant predators also occur along this gradient (rough-legged hawks *Buteo lagopus*, instead of snowy owls *Nyctea scandiaca*, long-tailed jaegers *Stercorarius longicaudus*, instead of pomarine jaegers *S. pomarinus*, and red foxes *Vulpes vulpes*, instead of arctic foxes *Alopex lagopus*). The mustelid predators remain the same, however, (least weasels *Mustela nivalis* and ermine *M. erminea*). Pomarine jaegers and snowy owls probably drop out because they depend on high densities of lemmings for successful reproduction (Pitelka *et al.* 1955b). This

pattern suggests that only the unique landscape and vegetation of northern coastal tundra, where large expanses of wet sedge meadow and low polygon troughs contain concentrations of preferred food for brown lemmings (several species of sedges *Eriophorum* spp., and the grass *Dupontia fisheri*) provide the necessary conditions for spectacular, cyclic interaction of lemmings, vegetation and predators.

Modeling efforts

Modeling efforts, while not providing definitive results, can support or contradict hypotheses that are based on empirical observations. Five models have provided additional insight into the factors influencing lemming populations near Barrow. Collier *et al.* (1975) modeled the acquisition and use of energy and supported the notion that insufficient quantity of food (energy) can account for lack of reproduction during winter, particularly by small females. Using the energetic model to drive forage intake, Barkley *et al.* (1980) found that in years with low nutrient concentration adult female lemmings face severe nutrient depletion when reproducing in late summer or winter, which supported an important tenet of the nutrient-recovery hypothesis. Osborn (1975) used the data of Pitelka and his students to model lemming demography and consumption by avian predators, thereby simulating the impact of these predators on lemming populations. He concluded that the percentage of mortality accounted for by owls and jaegers peaked in June at snowmelt with moderate densities of lemmings (~ 25 per ha) and dropped off rapidly at lower and higher densities. Apparently, the reduction in per capita predation on higher densities of lemmings occurred because territorial defense by breeding predators prevented a concentration of nomadic predators from developing. From this, Batzli *et al.* (1980) concluded that predation alone could not account for the rapid declines in lemming populations that occurred during summer in most peak years.

Two models addressed the overall dynamics of lemming populations at Barrow. Bunnell (1973) included information on nutrient cycling,

plant production, lemming foraging, lemming demography, and predation based largely on the results of Pitelka, Schultz, and their students. He concluded that "predation, forage quantity and quality, density dependent and dispersal phenomena are all active in generating lemming cycles." However, although studies of lemming activity and home range exist for the Barrow region (Banks *et al.* 1975, Peterson and Batzli 1975), there are no data, only anecdotes, regarding lemming dispersal.

Using more analytical models and additional data generated by the IBP Tundra Biome (Brown *et al.* 1980), Turchin and Batzli (2001) concluded that interactions between lemmings and forage quantity could explain the basic population cycle. The authors noted, however, that interactions with mosses, an important food in winter, needed to be included because their slow regrowth provided the most likely source of delayed density dependence in vegetation. This conclusion depended upon an assumption of nearly linear regrowth of graminoids, which reflected the large underground nutrient reserves in their rhizomes. That assumption would not be correct if extensive damage to rhizomes occurred at high lemming densities and caused a delay in the recovery of vascular plants, a phenomenon often reported but not adequately quantified.

The results of modeling reinforced our conclusions from empirical studies that food and predation are central elements in the cyclic dynamics of brown lemming populations near Barrow. Food plays a critical role because its decimation during winter acts to slow population growth before snow melt of most peak years, and because changes in its availability or quality prevent successful reproduction during the winter following a peak population. Avian predators play an important role in the rapid decline of populations during a peak year, and they help drive lemming populations to extremely low levels, but they appear insufficient to initiate the decline. Mammalian predators, particularly weasels, show a less reliable pattern, sometimes appearing relatively early in the cycle and sometimes not appearing at all. Finally, the timing of events during the course of a cycle can be altered by unusually severe weather that

affects availability of food or by the early appearance of weasels before a population increase has gained momentum.

Other arvicoline cycles

A rich literature exists on the problem of population cycles in arvicoline rodents in general, far too extensive to be adequately covered by this review. Nevertheless, we would be remiss if we did not point out that some of these studies, particularly those in Fennoscandia, have entertained themes similar to ours for brown lemmings at Barrow. As pointed out by Stenseth (1999), although population cycling per se only requires the operation of a delayed density-dependent factor, mathematical analyses of cycles of arvicoline rodents (lemmings and voles) generally indicate that both a direct density-dependent factor and a delayed density-dependent factor must be involved.

Models developed for population cycles of voles at lower latitude have emphasized the importance of specialized predators, such as weasels, in the generation of population cycles (Hanski *et al.* 2001). Specialist predators have been singled out because, by definition, their populations can only increase when the prey population is sufficiently abundant, but their response will be delayed owing to a lag in reproduction as the prey population increases and a lag in mortality due to starvation as the prey population declines. More elaborate demographic models for both lemmings and voles included their interactions with both predators and vegetation and also suggested that interactions with specialist predators strongly influence arvicoline population dynamics (Klemola *et al.* 2003). These latter models never succeeded in producing very realistic population cycles, however.

More recent work on low amplitude cycles of collared lemmings also implicated predation as a strong influence of population dynamics. Over a period of 15 years workers in Greenland were able to estimate the functional and numerical responses of the four predator species (arctic fox, ermine, long-tailed jaeger and snowy owl) that take the only rodent present, the collared lem-

ming (Gilg *et al.* 2006). These data indicated that only predation by ermine showed the delayed density dependence required for cycling. A simulation model based on these data produced population cycles of the appropriate length and amplitude, but the empirical data had two years of increase and two years of decline for each lemming cycle, whereas the model produced three years of increase and one year of decline (Gilg *et al.* 2003). Experimental studies on collared lemmings in northern Canada confirmed predation as an important factor, although not necessarily the only factor, limiting population densities of lemmings (Reid *et al.* 1995, Wilson *et al.* 1999).

Other theoretical analyses indicated that generalist predators acting alone could also drive arvicoline cycles, but such cycles have higher minimum densities and lower amplitude than do lemmings and voles at northern latitudes (Oksanen *et al.* 2001, Korpimäki *et al.* 2005). In addition, an empirical analysis suggested that delayed density dependence by both specialist and generalist predators accounts for arvicoline cycles in western Finland (Norrdahl and Korpimäki 2002).

To mimic actual arvicoline population cycles most models include a self-limiting (direct density-dependent) term for the prey as well as delayed density dependence by the predator. Otherwise, the population growth of predators, which have lower reproductive potential, is insufficient to catch the booming vole populations. This density-dependent effect often has been interpreted as a result of social interaction, but Turchin and Batzli (2001) showed that available food supply provides a viable alternative direct density-dependent factor for these models. In recent years empiricists, largely based upon field experiments, also seem to be converging on food supply during winter, as the best candidate for a direct density-dependent factor (Batzli 1996, Klemola *et al.* 2000, Huitu *et al.* 2003, Korpimäki *et al.* 2005, Huitu *et al.* 2007).

Given that many arvicoline populations do not cycle, comparative information on allopatric populations of the same species with and without cycling can also help to assign causes of cycling. Much comparative work and modeling for populations in Fennoscandia, reviewed in Han-

ski *et al.* (2001), indicated that noncycling populations at more southerly latitudes likely reflect the increased importance of generalist and nomadic predators and the shorter period of snow cover (the specialist weasels hunt under the snow with protection from avian predators). Analysis of another geographic gradient in cycling, based on an extensive data set for the grey-sided vole *Myodes rufocanus*, on Hokkaido Island, Japan, indicated that the increasing frequency of population cycling along a geographic gradient reflected the shortening of summer breeding season (Stenseth and Saitoh 1998). Although the direct cause of the shift in pattern of cycling could not be discerned, subsequent modeling by Klemola *et al.* (2003) suggested that longer winters favor the effectiveness of specialist predators in driving population cycles.

These studies provide a promising beginning, but predation regime alone seems unlikely to explain patterns of population cycling in North America. There population cycles appear at lower latitudes (mid-western and western USA) even in the presence of abundant generalist predators (Pearson 1966, 1971, Batzli and Pitelka 1971, Getz and Hoffman 1999). Furthermore, in mid-western USA cycling and non-cycling populations of the prairie vole, *Microtus ochrogaster*, can exist in neighboring fields (Cole and Batzli 1979, Getz and Hoffman 1999). Much higher population densities are reached in old fields with higher quality food, even though they have less cover, and only then do populations reach sufficient densities to detect population cycles. Thus, higher quality food and increased predation may act in concert, but generalists dominate the suite of predators (Lin and Batzli 1995).

Future work

Clearly, more research needs to be done at Barrow and elsewhere to test our hypotheses, but what should have priority? A common problem for both empirical and theoretical analyses of lemming dynamics is the paucity of data for winter (Batzli *et al.* 1980, Turchin and Batzli 2001, Klemola *et al.* 2003). Neither the mortality of lemmings due to predators (primarily foxes

and weasels), nor the variability in lemming reproduction and densities, nor the availability and quality of forage have been well documented during winter. All represent critical areas for completion of quantitative analyses of lemming cycles. Modeling efforts have also revealed the need to quantify the amount of destruction of rhizomes, the rate of regrowth of monocots after winter grazing and after digging for rhizomes at snowmelt and the rate of recovery of mosses after heavy use during winter. Of course winter data are much more difficult to obtain, which explains their paucity, but further progress depends upon someone making the effort.

The need for additional field experiments to test the food and predation hypotheses is just as important as the need for more quantitative information on trophic relationships among lemmings, predators and forage. Such experiments have been attempted, with varying success, on a variety of arvicoline rodents (Schultz 1969, Lindroth and Batzli 1986, Korpimäki and Norrdahl 1998, Wilson *et al.* 1999, Klemola *et al.* 2000, Graham and Lambin 2002, Sundell 2003, Ekerholm *et al.* 2004), but, while informative, they rarely provide definitive results. Difficulties include the scale of manipulations, replication of treatments and movements of animals.

Often the space required for adequate manipulation of populations, largely owing to the low densities reached by arvicoline and the large areas used by predators, make adequate replication difficult. It may be, as some have argued (Oksanen 2001), that we can only expect to detect large effects with field experiments, in which case lack of replication can be tolerated. Unfortunately, however, the high mobility of the animals makes some treatments, such as reducing predator densities or increasing lemming densities, difficult to maintain even without replication. One possibility is the use of large pens in natural habitat so that movements of lemmings and predators in and out of the pens can be controlled. Because cycling lemming populations apparently reach very low densities (< 1/ha) and because of the possibility of a fence effect caused by disrupting emigration/immigration (Krebs 1996, but see Ostfeld 1994), however, the pen size would need to be very large (> 10 ha).

The pen also should maintain its integrity, which can be difficult during winter when drifting snow can cover the fencing (Ekerholm *et al.* 2004). Taken together these requirements may not be logistically feasible. In the long run perhaps only repetition of experiments in a variety of contexts, even though each has little replication, will sort out the competing hypotheses.

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