ARCTIC INSTITUTE OF NORTH AMERICA

TECHNICAL PAPER NO. 15

THE LEMMING CYCLE AT BAKER LAKE, NORTHWEST TERRITORIES, DURING 1959–62

By

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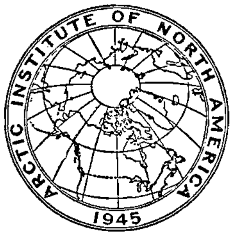

PUBLISHED SEPTEMBER 1964

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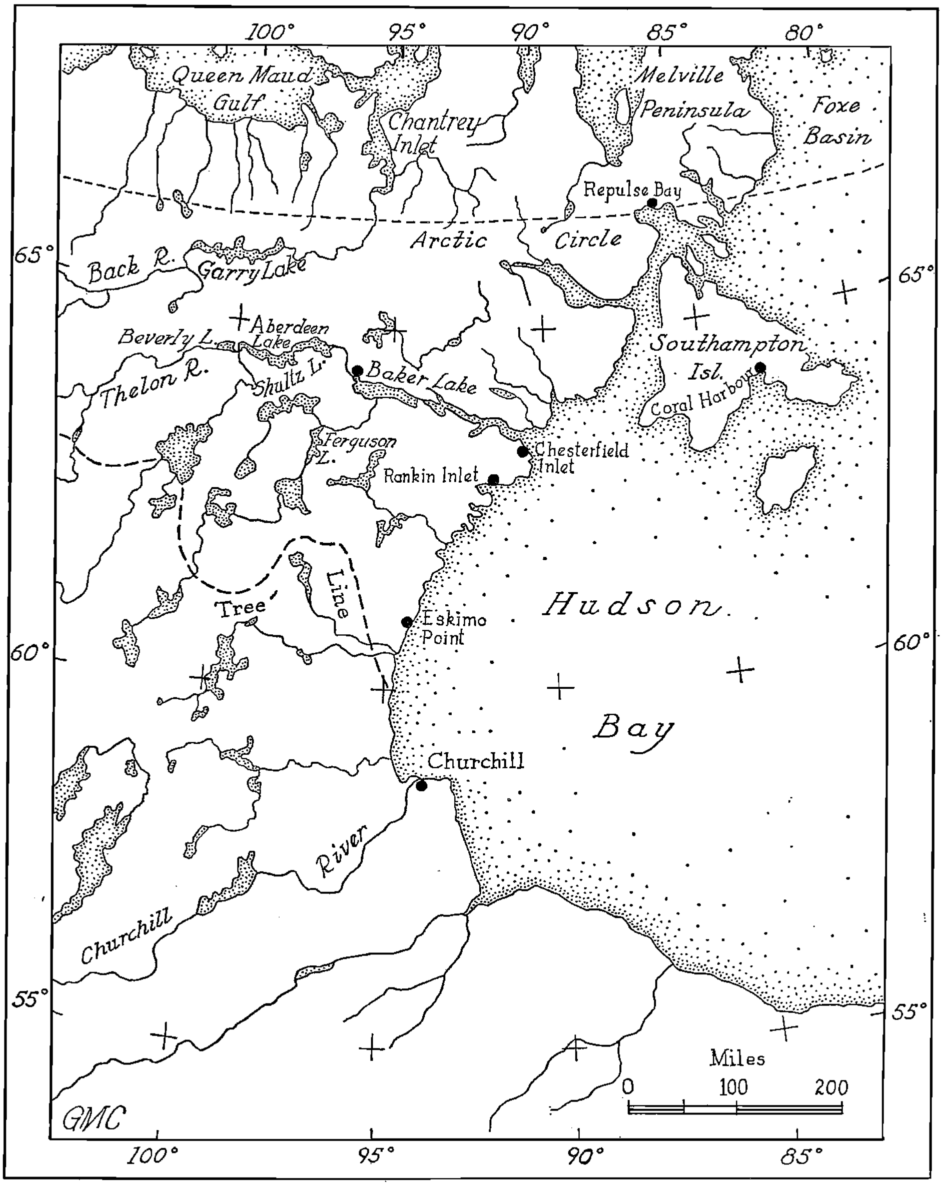

General sketch-map

THE LEMMING CYCLE AT BAKER LAKE, NORTHWEST TERRITORIES, DURING 1959–62

Charles J. Krebs[1]

Abstract

A four-year study covering one cycle in numbers of the brown and varying lemmings has been carried out at Baker Lake, Keewatin, N.W.T. An attempt was made to describe the events of the cycle in detail by snap-trapping and live-trapping techniques and by detailed autopsies on about 4,000 animals and from this to determine what explanations would fit the observations.

Increase began from very low numbers in the summer of 1959 with tremendous population growth occurring over the winter of 1959–60. Little further increase occurred in the peak summer of 1960. A great decline occurred over the winter of 1960–1, and this decline continued through the summer of 1961 on the Main Study Area. Little change occurred over the winter of 1961–2 and the phase of increase began again in the summer of 1962.

Two changes in reproduction were associated with this cycle—changes in the length of the breeding season and in the weight at sexual maturity. Winter breeding occurred in the period of increase but not in the decline, and a shortened summer breeding season occurred in the peak and to some degree in the decline. Young male *Lemmus* matured in the summers of increase but not in the peak or in the decline; young females matured in the increase and decline summers but not in the peak.

The major change in mortality was a very high juvenile mortality in the summer of the decline.

Changes in the quality of the animals were manifested not only by these reproductive and mortality changes but also by a 20–30 per cent increase in mean body weights of the adults in the peak summer compared with the increase or decline summers.

The role of the extrinsic factors is considered. There was no widespread destruction of the habitat, or any evidence of quantitative or qualitative food shortage in the animals of the decline. Neither predators, disease, nor parasites seemed to be the cause of the observed changes in mortality.

The role of the intrinsic factors is also considered. Summer adrenal and spleen weights showed no clear relationship to the cycle. The amount of wounding on skins showed strong seasonal changes and was not a simple function of density.

It was concluded from these observations that this lemming cycle could not be adequately explained by the conventional extrinsic factors such as food supply, but rather that it is essentially a self-regulatory phenomenon. The stress hypothesis proposed by Christian was also rejected as an adequate explanation of these events. The idea of Chitty that populations change in quality during changes in density was fully supported by these results. Behavioural changes in the population may constitute the crux of the lemming cycle, and Chitty's suggestion that these fluctuations may represent a genetic polymorphism involving aggressive behaviour is not refuted by these data.

Acknowledgments

I wish to express my gratitude to Dr. Dennis Chitty and Dr. Ian McT. Cowan for their stimulation and help throughout this study. I am also indebted to Mr. Andrew H. Macpherson of the Canadian Wildlife Service for information and assistance in the field work.

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Support for the field work was provided by the Arctic Institute of North America. I was supported during 1959–61 by the National Research Council of Canada, and during 1961–2 by the National Science Foundation of the United States. Many of the ideas were collected from discussions with friends and associates both at the Bureau of Animal Population, Oxford, and at the Department of Zoology, University of British Columbia. I am indebted to Dr. John McInerney and Dr. Douglas G. Chapman for careful reading and criticism of this manuscript. Thanks are also due to my wife who served as a field assistant for three summers. Finally, I want to thank the people of Baker Lake whose cooperation has made this study most pleasant.

Introduction

All animal populations fluctuate in numbers. These fluctuations may be small or large, regular or irregular. Some small mammals in particular show fluctuations which are large in magnitude and relatively regular in occurrence, and these fluctuations are referred to as "cycles". We are concerned here with a well-known example of these fluctuations–the lemming cycle of the tundra.

Two species of lemmings inhabit the Central Canadian Arctic, the brown lemming (*Lemmus trimucronatus*) and the varying lemming (*Dicrostonyx groenlandicus*). Both are small furry rodents with very short tails and ears, and usually weigh 60–100 grams when fully grown. The brown lemming remains brown all year round, but the varying lemming is white in winter and grey in summer. Both species are active throughout the year, burrowing under the snow in the winter and occupying burrows dug in the ground during the summer. Their food consists of green plants in summer and dormant buds and roots in winter. In summer the varying lemming tends to occupy the drier habitats and the brown lemming the wetter sites. There is an annual overturn of population; very few individuals live more than one year. Breeding may occur at any time of the year and young animals may mature at 3–4 weeks of age in both species. The gestation period is 19–21 days and the litter size varies seasonally between three and nine. Thus these species have a tremendous potential rate of increase.

This research program was planned to study the population dynamics of the brown lemming and the varying lemming over a full cycle in numbers at Baker Lake, Keewatin, N.W.T., in the Canadian Barren Grounds. The first purpose was to describe the events of the lemming cycle of the Barren Grounds, and this has been realized for one cycle. The second purpose was to explain these events in a comprehensive theory; while this is not yet realized, the results suggest which of the current explanations are inadequate. A hypothesis which is not inconsistent with the observed events is considered and the information still needed is noted.

Field work for this study was carried out from 25 May–10 September 1959, 10 May–8 September 1960, 16 May–12 September 1961, and 29 May–21 August 1962.

The plan of this paper is as follows. After a brief description of the study area, the habitats occupied by the two species of lemmings is described and population density changes are considered. Then reproduction, mortality, and movements are assessed in relation to the density changes. Changes in extrinsic and intrinsic factors which affect the population are next considered. Finally, a discussion of the entire work is given and an attempt made to integrate these results with contemporary ideas.

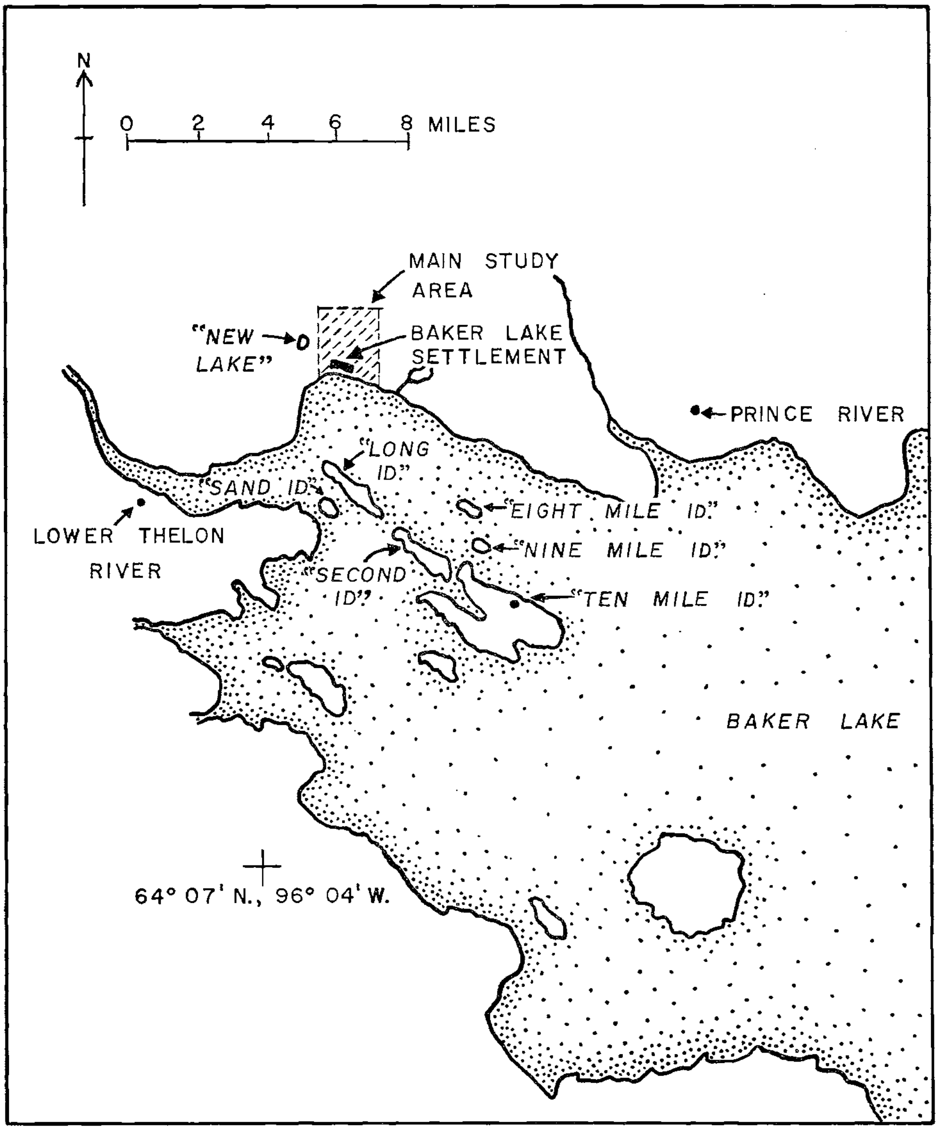

Fig. 1. Map showing the location of Baker Lake, the Main Study Area, and the peripheral sampling areas.

AREA AND CLIMATE

The Baker Lake settlement is on the northwest corner of Baker Lake near the mouth of the Thelon River in the east central Barren Grounds. The whole area lies in the Canadian Shield. The terrain in general is flat to gently rolling, mostly covered with glacial drift with few outcrops of bedrock. Lakes dot the landscape, occupying perhaps 30 per cent of the area. Drainage is poor and even light summer rains can cause considerable local flooding.

All intensive work was carried out in the Main Study Area (Fig. 1), occupying about 3 square miles just north of the Baker Lake settlement. Other outlying areas marked on Fig. 1 were sampled once or twice during each summer. In addition some sampling was carried out at the Canadian Wildlife Service camp on Aberdeen Lake (64° 37N., 99° 44W.), about 115 miles west of Baker Lake.

The weather for Baker Lake is summarized in Table 1 for 1959–62, and the mean values for ten years' records are given for comparison.

Summer weather varied considerably between the different years. The summer of 1959 was cold and very wet, while the summer of 1960 was warm and rather dry. The summer of 1961 was intermediate, cool and again dry, and the summer of 1962 was cool and wet.

The spring phenologies of the four years were quite different (Krebs, 1964). Spring 1960 was the earliest. In 1959 the spring events began about 10–20 days behind those of 1960; in 1961, 2–6 days behind; and in 1962, 10–20 days behind. This is reflected in the dates at which Baker Lake was free of ice: 31 July 1959, 12 July 1960, 17 July 1961, and 30 July 1962. There were corresponding differences in the time of onset of summer breeding in lemmings.

Events over the autumn freeze-up are also of considerable importance for lemmings. The 1959 freeze-up was characterized by a lack of freezing rain and a quick buildup of a protective snow cover, thus minimizing ground icing and burrow flooding. By contrast the 1960 freeze-up was accompanied by very wet conditions, oscillating freezing-thawing, and a lack of a good snow cover until mid-December. The 1961 freeze-up was similar to that of 1959, but somewhat wetter. The depth of snow on the ground (rough estimates by the Meteorological Station) was 9 inches on 1 November 1959, but only 2 inches on 1 November 1960. The depth of snow at the same date in 1961 was 11 inches, and for comparison the ten-year mean snow depth for this date at Baker Lake is about 3 inches.

VEGETATION AND HABITATS

One of the most striking characteristics of arctic vegetation is its extreme variability from one small area to the next. This produces a correspondingly great interspersion of habitats and gives the impression of one great continuum of vegetation rather than distinct habitats. Nevertheless, there are distinct habitats which can be recognized even though transitions are very common, and an attempt was made to divide the vegetation of the Baker Lake area into habitats which in principle might be applied to the entire Barren Grounds.

The dominating influence seems to be water, and thus we can recognize a vegetation continuum from dry to wet, the lichens occurring in dry areas, the heath (Ericaceae) plants in moderately dry areas, and the sedges and mosses in wet areas. I have introduced microtopographical relief into the habitat classification, as it is important for lemmings. This involves *hummocks* (low rounded mounds, 10–18 inches tall, 1–2 feet in diameter) and *tussocks* (thick clumps of *Eriophorum*, usually about 10 inches tall and less than one foot in diameter). Both these structures occur in wetter areas.

The type of habitat at each trapping station was recorded. This was done subjectively by looking at the vegetation, drainage, and microtopography, and included at most stations subjective appraisal of the two or three dominant species within a five-foot radius of the trapping station. There was not enough time to do anything more objective.

The principal eleven habitats are listed in Table 2, which also gives the area covered by each on the Main Study Area. These figures were obtained from interpretation of air photographs combined with a foot survey of the area.

The habitats found on the Main Study Area are similar to those at "New Lake",[1] Prince River, and Aberdeen Lake. The dominant plant species in these habitats are similar on the first three of these four areas, and Table 3 gives these data. In the Aberdeen Lake area somewhat different species dominate the same habitats; there is no *Cassiope tetragona* and extremely little *Dryas integrifolia*, but *Ledum groenlandicum* and *Eriophorum* are more abundant (Table 4).

Again, a slightly different series of habitats, characterized by a dominance of mosses, occurs on the islands at the west end of Baker Lake and on the sand-plain along the south bank of the Thelon River mouth (Table 5).

POPULATION DENSITY

The first requirement of all population work must be reasonably accurate information about changes in density. To determine trends in population density I have used five methods: live trapping, snap trapping, visual estimates, trace indices for faeces, and dropping boards. Of these only live trapping provides a direct census of numbers; the other four merely give an index more or less proportional to actual density.

Live trapping

A considerable effort was expended in a live-trapping program, but various difficulties plagued the results. The most serious problem was trap deaths; this was not solved until 1961 and even then not entirely. The basic technique was not fixed until 1961 and consequently the data for 1959 and 1960 are less complete.

Three quadrats for live trapping were established during the course of this study (Fig. 2). Their specifications are as follows:

	Area (acres)	*Length of one side* (feet)	*Trap spacing* (feet)	*No. of traps* (stakes)
Quadrat 1	1.9	288	18	289
Quadrat 2	11.3	700	50	225
Quadrat 3	3.5	350	50	64

Quadrat 1 was set up in 1959. Quadrat 2 was established in 1960 when it became apparent that movements and home ranges were far larger than could be measured by Quadrat 1. Quadrat 3 was also set up in 1960 primarily to sample *Dicrostonyx*, since the first two quadrats were mainly *Lemmus* habitat. Quadrat 1 was trapped in all four years, Quadrat 2 only in 1960, and Quadrat 3 in

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[1] Place names not officially adopted by the Permanent Board on Geographical Names are given in quotes.

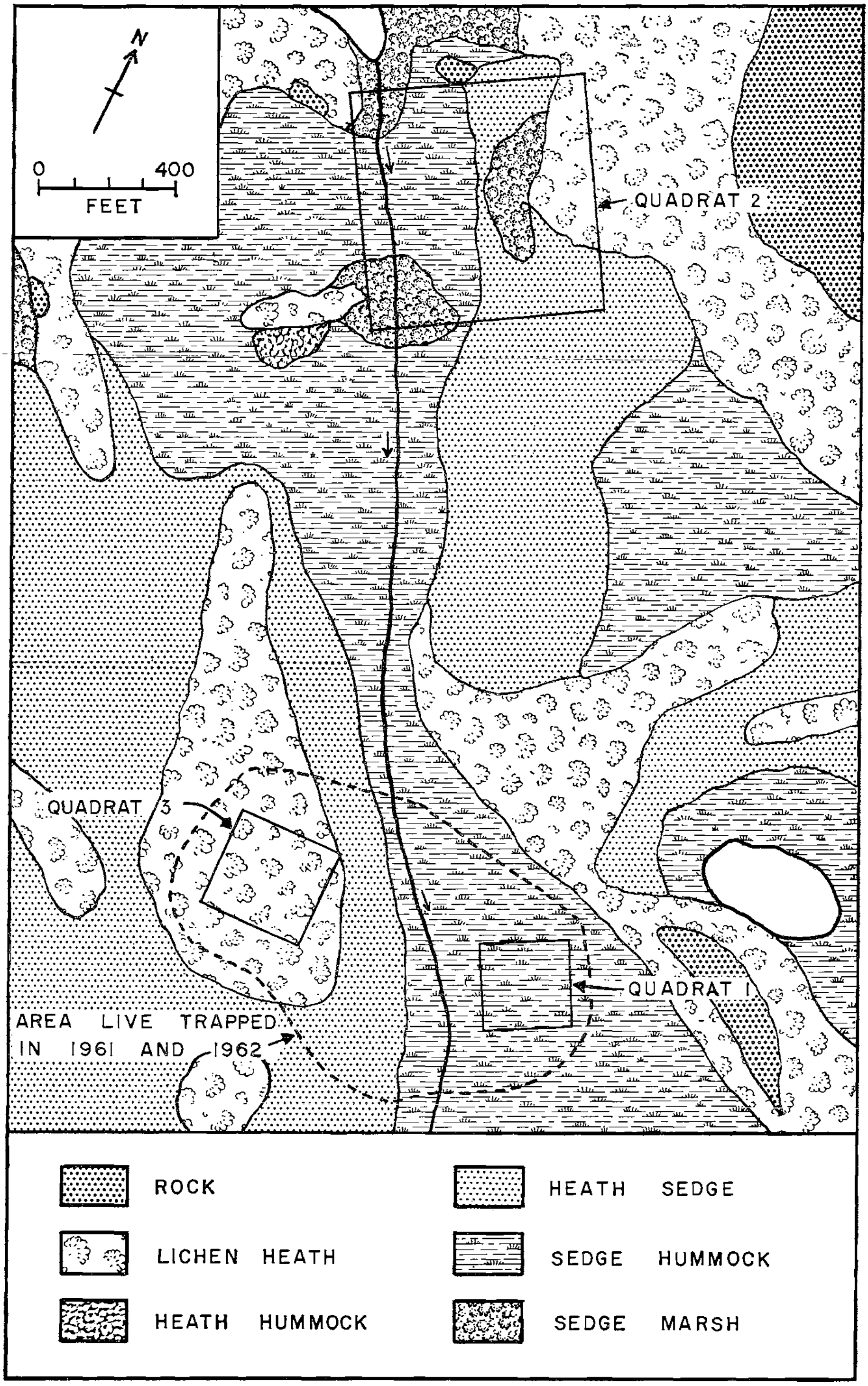

Fig. 2. Location of the live-trapping quadrats of the Main Study Area.

1960–2. In 1961 and 1962 additional traps were placed throughout the area enclosed by the dotted line in Fig. 2, so that this area of 18–19 acres was treated in effect as one quadrat.

The aim was to make a complete census of all the animals living in the quadrats; this approach avoids the difficulties inherent in Lincoln Index type of estimates. Since very few new animals were captured on the third day's trapping, almost the entire population was presumably marked each time. In most cases we have no independent evidence (e.g. snap trapping from the same area) to show that this is the case, and it can only be assumed that the figures given below represent the total trappable population on the given area at the given time. A small attempt to test this assumption was carried out in 1962 at the end of the program. Quadrat 3 was live-trapped on August 10–12 and then saturated with snap traps on August 15–17. The results were as follows:

	Number of *Dicrostonyx* trapped		
	Adults	*First summer litter* Y_1 *young*	*Second summer litter* Y_1' *young*
Live trapping Aug. 10–12	5	5	0
Snap trapping Aug. 15–17	4	4	3

The three Y_1' young (second summer litter) which were snap trapped were just out of the nest (10–12 grams) and thus could not have been live trapped the previous week. Two of the four Y_1 young (25–30 grams) (first summer litter) were unmarked; one of these was caught on the edge of the quadrat. All the adults were marked. The results are not conclusive but do suggest that the live trapping did census the majority of animals on the quadrat at the time.

Each trapping period lasted three days, one trap being used at each stake in the quadrats. All traps were placed in runways or at burrows if possible. They were frequently moved to cover all the area around the stakes. Traps were checked every 2–6 hours. Excess traps were always present, the maximum percentage of traps occupied at any one check being 35 per cent. No bait was used in any of the live traps. Night trapping was stopped in August 1960 because of high trap mortality and trapping thereafter was confined to the 9 a.m. to 11 p.m. period. In 1961 and 1962 trapping was carried out every week from June through August, but in earlier years only every 2–4 weeks. Both Longworth and Sherman traps were used and seemed to be equally effective. Extreme heat and cold had to be avoided with both traps to prevent mortality. *Lemmus* were marked with fingerling fish tags in the ear in 1959 and 1960. *Dicrostonyx* were marked with both ear tags and leg bands in 1959 and 1960. Both species were given toe clips as marks in 1961 and 1962 and this technique proved far superior to other tagging methods.

Animals caught in the live traps were aged according to their weight. The adult animals present at the beginning of the summer breeding are referred to as the *winter generation.* Since summer breeding tends to occur synchronously throughout the population, summer young appear in waves during the summer. These summer litters are referred to as follows: Y_1 summer young = first summer litter; Y_1' summer young = second summer litter; and Y_1'' summer young = third summer litter. These groups of young are readily separated by body weights until late summer, when growth rates decline. A full discussion of ageing problems is given in a later section (see Body weights).

Results

Table 6 gives the numbers of *Lemmus* on Quadrat 1 (1.9 acres) in 1959–62, and Table 7 gives the numbers of *Dicrostonyx* on Quadrat 3 (3.5 acres) in 1959–62.[1] While there were few or no *Dicrostonyx* on Quadrat 1 in any of the years, Quadrat 3 had a *Lemmus* population of about 20 animals in August 1960, but none in 1959, 1961, or 1962.

The first point that emerges from these tables is the great increase in numbers from 1959 to 1960 and subsequent decline in 1961. We can estimate these changes quantitatively. In *Lemmus* the increase from August 1959 to June 1960 is 28-fold, and if we accept the argument from snap trapping given below, that the population before the 1960 melt-off was approximately equal to the August 1960 population, we have an estimated 58-fold increase over the winter of 1959–60. This must be considered as a crude estimate only of the actual increase. There was probably a minimal 25-fold increase in *Lemmus* over the winter of 1959–60 and this increase may have been as much as 50-fold.

The 1959–60 winter increase of *Dicrostonyx* cannot be estimated in the same way, since Quadrat 3 was not set up until 1960. If we assume that the May 1960 population equalled that in August 1960, and that there were about 3–6 animals on the area in August 1959 (see Table 7), the estimated increase is 5- to 10-fold over the winter of 1959–60. These crude estimates suggest that *Dicrostonyx* probably did not increase as much as *Lemmus* over the winter of 1959–60 on the Main Study Area.

The *Lemmus* population at least doubled its numbers in the summer of 1960. From the amount of trap mortality involved in this estimate and additional data from Quadrat 2, a reasonable estimate of this summer increase is 2- to 3-fold between 15 June and 31 August 1960 in *Lemmus*. No estimate can be made for *Dicrostonyx* from live-trapping data.

Finally, we can estimate the decline over the winter of 1960–1. The *Lemmus* population on Quadrat 1 declined from 58 to 5 between August 1960 and June 1961, a 90–95 per cent decrease. The *Dicrostonyx* population on Quadrat 3 declined from 38 to 11 over the same period, a 70–80 per cent decrease. These crude figures allow us to conclude that *Dicrostonyx* probably did not decrease as much as *Lemmus* over the winter of 1960–1 on the Main Study Area.

The decline continued in both species through the summer of 1961 on the live-trapping area. There were very few summer young in the 1961 samples, an important point which I will discuss later, and there was no recovery of numbers.

There were no *Lemmus* on the live-trapping area in 1962. *Dicrostonyx* numbers on Quadrat 3 were about the same in the early summer of 1961 and 1962, the difference being that in 1961 they declined through August while in 1962 they maintained their numbers and began to increase by August.

Although it is possible to estimate the number of lemmings per acre, I have not done so. Actual densities are very much a local phenomenon and do not help us to understand the cycle. We are interested more in the relative changes than in the absolute levels of density.

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[1] The 1959 figures refer to live trapping along a line in the region where Quadrat 3 was set out in 1960.

Snap trapping

Snap trapping was done both systematically and non-systematically. The systematic lines were set up as Type B lines of the North American Census of Small Mammals (Calhoun, 1948), i.e. 20 stations spaced at 50 feet in a straight line with three traps per station within a five-foot radius of the stake. With a few exceptions these lines were set up in pairs spaced 100 feet apart (Calhoun, 1948, recommends 400 feet) and parallel. Eight pairs of lines were set out on the Main Study Area in 1959. No new lines were added there in 1960, but four additional pairs were set out in 1961. On the outlying areas two pairs of lines were set out in 1959, two additional pairs in 1960, five and one-half additional pairs in 1961, and one new pair in 1962. In general on the Main Study Area each line was trapped twice during the summer (June and August). These lines are referred to as *standard lines* because they are retrapped each year. Each single standard line run for one period (three days) represents 180 *standard trap nights* and all snap-trapping indices in this paper are expressed in numbers of lemmings per 100 standard trap nights.

Non-systematic snap trapping was done primarily to obtain specimens for autopsy. Stations with two traps were placed at irregular intervals wherever there seemed to be any chance of catching a lemming. The traps were removed after three days and the same place was never trapped twice. These lines caught two to three times as many lemmings per trap night as the standard lines.

Museum Special traps with raisins as bait were used throughout this study. Bait was probably unnecessary, but until the matter could be investigated it was thought best to continue the use.

Some differences between the two species for standard snap-trap sampling should be pointed out. *Lemmus* is found in the wet habitats and uses well-defined runways in moving about; its occupied holes are difficult to find because there are so many possible sites. *Dicrostonyx*, on the other hand, more often lives in the drier habitats and does not move along well-defined runways; its occupied holes are often easy to find and are marked by a mound of freshly dug sand or peat. Thus runway trapping is most effective for catching *Lemmus*, and burrow- or den-trapping is most effective for catching *Dicrostonyx*. The different habitats of the two species introduce a further complication. In the Baker Lake area the wet habitats are reasonably extensive and the distribution of *Lemmus* is fairly uniform over these. But, although the *Dicrostonyx* habitats are equally or even more extensive, areas suitable for digging burrows are restricted and this results in a contagious type of distribution for *Dicrostonyx*. This complicates sampling considerably, because standard trap-lines may completely miss these "colonies". The result is that *Lemmus* densities are estimated with more reliability by standard snap-trapping lines than are *Dicrostonyx* densities in the Baker Lake area.

Two questions about the snap-trapping technique should be considered at this point. First, does snap trapping provide a good index of population density? The number of animals caught in a trap-line depends not only on population density but also on the weather, habitat, amount of activity, home range size, and proportion of young animals. Trends in density are shown quite well, but the actual amount of the density change must remain vague. In particular, statistical confidence limits for these indices are meaningless unless the effects of all the secondary variables mentioned above can be neglected or assumed to cancel out over the census periods. In this study there are independent sources of density estimates, such as live trapping, and these can be used to check the snap-trapping indices.

The second question is whether repeated trapping of the same lines both within and between years has interfered with the cyclic changes we are attempting to observe. This question can be answered indirectly, since new standard lines were set out every year. We can enquire whether any catch differences occurred between new lines in year *x* and old lines in the same year, taking into account habitat differences between lines. Comparing the numbers caught in new and old lines, I found no differences in catch either in 1960 or in 1961, and so I conclude that snap trapping the same lines does not affect the cyclic changes we are attempting to observe. Other indirect evidence supports this. The number of traps set off without a catch is almost always equal to or greater than the number of lemmings caught, which suggests that a fair number of lemmings escape being trapped even in the immediate vicinity of the trap-line. In addition, if we consider the size of the area over which the trap-lines are spread and the mobility of the lemmings, it is clear that only a minute fraction of the population is being removed by trapping.

Results

Tables 8 and 9 give the snap-trapping indices for *Lemmus* and *Dicrostonyx* and show in a general way the great changes from scarcity in 1959 to abundance in 1960 and the subsequent decline in 1961. These changes in abundance occurred in both species and on all the areas trapped.

These data suggest that the *Lemmus* cycle was more pronounced than the *Dicrostonyx* cycle. The indices for the Main Study Area changed proportionally as follows:

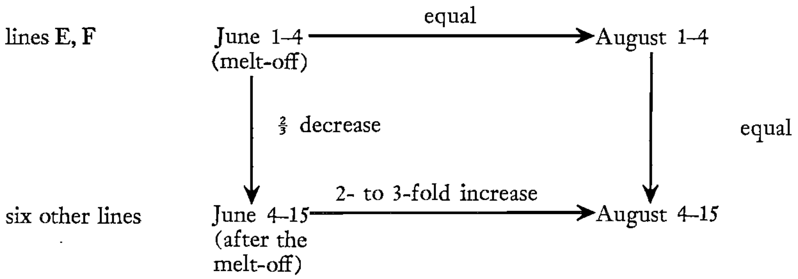
	1959	*1960*	*1961*	*1962*
Lemmus	1	125	7	8
Dicrostonyx	5	50	18	25

However, we must beware of comparing *Lemmus* indices with *Dicrostonyx* indices because the differences in biology between these species must affect the absolute value of these indices.

The snap-trapping indices in the summer of 1961 are particularly variable (e.g., compare *Lemmus* on "Nine Mile Island" at 12.22 with *Lemmus* on the Main Study Area in August at 0.62). This variability is due partly to the fact that two different types of declines occurred in 1961. On some areas there was moderate abundance in spring and a steady decrease through the summer with *no recovery* (Main Study Area, Prince River, Lower Thelon River). On other areas there was moderate abundance in spring with *some recovery* of numbers through the summer (Aberdeen Lake, "New Lake", "Ten Mile Island", "Nine Mile Island", "Long Island", "Second Island"). The significance of these different types of declines (respectively types G and H according to Chitty, 1955a, p. 59) and their associated characteristics will be discussed later.

One further detail of density changes during the cycle was shown by snap-trapping results. There was a sharp drop in density in the spring of 1960 in

Lemmus just as the snow was melting and summer breeding began. This drop was registered in the standard trap-line estimates as follows:



Given this set of relationships, we estimate a 67 per cent decline in density of *Lemmus* over the melt-off, but this is probably an overestimate because of increased movements of animals during the melt-off (thus increasing trap-line catches). Perhaps a 30 per cent mortality estimate is closer to the truth. This spring decline occurred in spite of the absence of bird predators and only sparse populations of mammalian predators. Whether this spring decline also occurred in *Dicrostonyx* could not be determined.

The summer trapping data reflect a change in habitat distribution between the two species over the cycle. If we divide the habitats into dry, medium, and wet (as in Tables 8 and 9) and plot the percentage of the total numbers caught in each type of habitat, we obtain the results shown in Fig. 3. There is an inverse relationship between *Dicrostonyx* and *Lemmus* such that the species which is most abundant occupies the greatest range of habitats. Thus *Lemmus* greatly expanded its habitat range in the peak summer of 1960, while *Dicrostonyx* contracted its habitat range although it also increased considerably in numbers. These changes complicate somewhat the interpretation of density

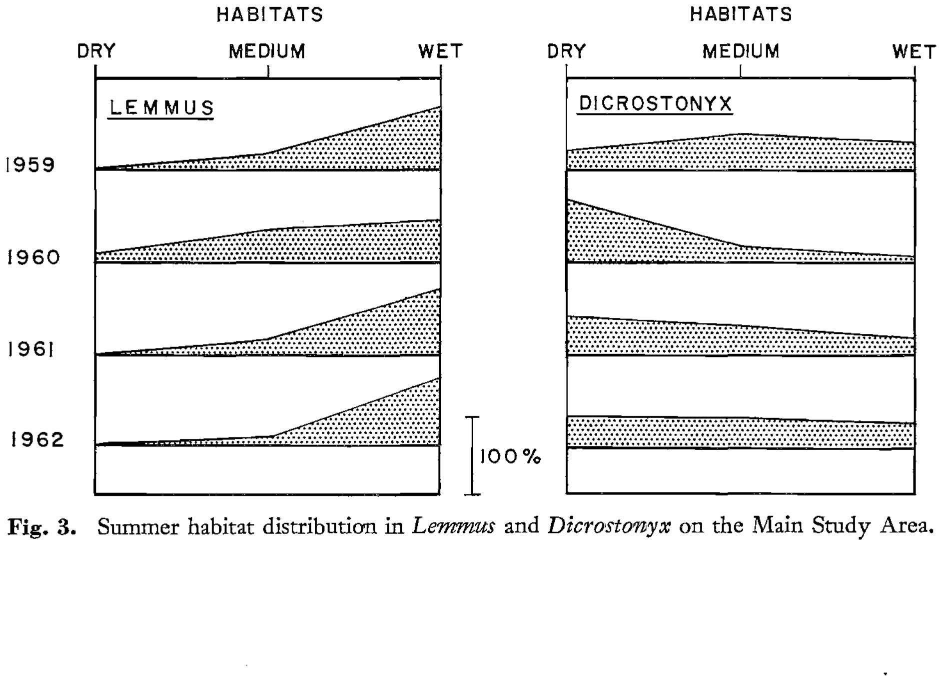


Fig. 3. Summer habitat distribution in *Lemmus* and *Dicrostonyx* on the Main Study Area.

changes observed in a single habitat, because a given number of animals spread over many habitats will obviously be less dense than the same number in one habitat only. The explanation of these changes in habitat segregation probably lies in some form of interspecific interference, but we have no direct evidence that this is the case.

Other census methods

Visual estimates of density changes were obtained by counting the number of lemmings seen per hour of walking on the tundra. This is obviously a crude index of density but it does provide valuable supplementary information for areas where no live trapping was done.

Trace indices of fresh faeces were made in 1959 and 1960 by doing line transects through habitat types, dropping a 3-foot by 1-foot rectangle every 10 feet, and recording presence or absence of fresh green droppings. Again this is a crude index but it has the advantage of being done very quickly.

Results

Visual estimates were obtained for *Lemmus* as follows:

1959	0.43	*Lemmus*	seen	per	100	hours	walking	(based	on	465	hours)
1960	85.00	”	”	”	”	”	”	”	”	316	”
1961	0.51	”	”	”	”	”	”	”	”	393	”
1962	0.81	”	”	”	”	”	”	”	”	247	”

These estimates apply only to the summer. During the spring melt-off and the fall freeze-up lemmings may become much more noticeable.

The extent of the 1960 cyclic high may be indicated from visual reports of lemming abundance as follows: May–Chesterfield Inlet, Rankin Inlet, Coral Harbour, Eskimo Point; July–Garry Lake, Beverly Lake; August–Chantrey Inlet; and September–Repulse Bay, Ferguson Lake. It is apparent from these reports that the 1960 high occurred over at least an area 500 miles by 400 miles of the Central Arctic, thus showing that the cycle at Baker Lake was not merely a local effect.

Data obtained from trace indices and dropping boards will not be given here because they add nothing new to the observations above.

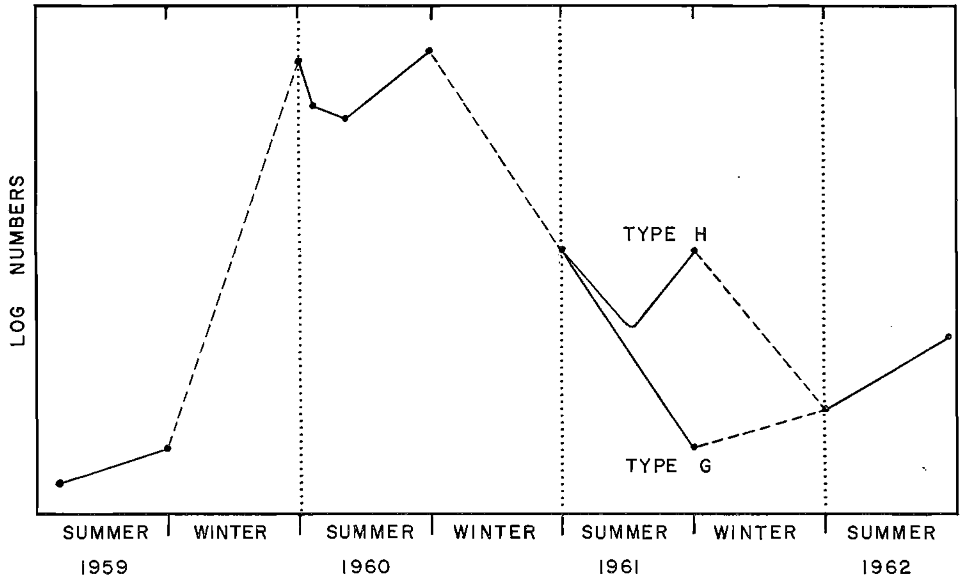
Finally, dropping boards were used as suggested by Emlen *et al.* (1957). This technique was tried in 1959 and 1960 but discontinued in 1961 because it involved a considerable amount of work and merely duplicated other census information.

Summary and conclusions

Figure 4 summarizes the density changes in *Lemmus* and *Dicrostonyx* over 1959–62.

1959 Summer: This was a summer of very low numbers of both species, with *Dicrostonyx* somewhat more abundant than *Lemmus*. It was evident by September that some increase had occurred but numbers were still very low.

1959–60 Winter: Tremendous population growth occurred over this winter in both species, the crude estimates of this increase being 25- to 50-fold in *Lemmus* and 5- to 10-fold in *Dicrostonyx* from September 1959 to May 1960.



LEMMUS								
	<1	1	28	58	5	1	<1	2?
DICROSTONYX								
	?	4?	20	38	11	2	6	11

Fig. 4. Generalized density changes, 1959–62.

1960 Summer: The spring population of *Lemmus* declined considerably when the snow melted and summer breeding began. This mortality was probably between 67 per cent and 30 per cent and was concentrated in a few days. By August the *Lemmus* population had risen 2- to 3-fold from its lowest point in June and was then slightly above the spring density. The *Dicrostonyx* population also increased during this summer, but it is not known whether it showed the same drop in numbers at the melt-off. Densities were highest in this cycle during August 1960.

1960–1 Winter: A severe decrease in population density occurred over this winter, estimated at 90–95 per cent in *Lemmus* and 70–80 per cent in *Dicrostonyx* from August 1960 to June 1961. This decrease had already occurred before the spring melt-off and there was no indication of a melt-off mortality such as occurred in 1960.

1961 Summer: There were two patterns found in this summer of decline. On the Main Study Area and two outlying areas the decline continued in both species through the summer with no recovery (Type G decline; Chitty, 1955a, p. 59). On five other outlying areas partial recovery occurred through the summer (Type H decline). By the end of this summer on the Main Study Area densities in both species were about equal to those at the start of the study.

1961–2 Winter: Numbers remained low over this winter with probably a slight increase in *Dicrostonyx* and perhaps also in *Lemmus*.

1962 Summer: This was a summer of low numbers in both species, comparable to 1959 although densities were somewhat higher than in 1959. By late summer numbers were building up again and it appeared that a phase of increase had begun.

Reports were received that lemming numbers were also high within a large area of the Central Arctic in 1960.

REPRODUCTION

Population density changes because of reproduction, mortality, or migration. In this section we shall deal with the first of these primary population factors.

Reproductive data can be obtained only from dead animals, and since most of these were obtained by snap trapping we must hope that snap trapping samples the population randomly. The difficulties of this assumption are partly avoided in the analysis which follows by treating separately each generation, the different summer litters, and the various time periods. For example, to lump old adult and summer young females together for an analysis would tax the assumption that this group is sampled randomly, whereas if we treat old and young females separately the assumption that sampling is random within each group is probably valid.

Complete autopsies were performed on almost all animals trapped; skins and skulls were saved and the following data were recorded:

All specimens: date, species, sex, weight, total length, hind foot length, fat index, adrenal weight, spleen weight, lens weight, stomach weight, location and habitat where caught.

Males only: testes position and weight, epididymis tubules visible or not, size of seminal vesicles.

Females only: whether lactating or not, vagina perforate or not, size of uterus, number of placental scars, number, size, and age of embryos, number of corpora lutea and corpora albicantia in each ovary, combined weight of uterus and embryos.

Males were judged as fecund or non-fecund by whether or not the epididymis tubules were visible to the naked eye (Jameson, 1950). There was almost no ambiguity in determining this, but in the few doubtful cases accessory data on the size of the seminal vesicles and the weight and position of the testes were used.

Females were classed as mature or immature by the presence or absence of corpora lutea in the ovaries. This criterion is more refined than the criterion of perforate or non-perforate vagina (Leslie, Venables, and Venables, 1952).

Females were classed as pregnant if the uterus showed macroscopically visible swellings. The gestation period of *Lemmus* has been measured in only a few cases. Thompson (1955 a) gives 20 and 20½ days for two individuals, and in the present study two pregnancies were timed at 21 and 21½ days. Thus an approximate gestation of 21 days is indicated for *Lemmus*. For *Dicrostonyx* Manning (1954) gives 19–21 days for two cases, and Quay and Quay (1956) give 21 days as a maximum for five observations. Thus an approximate gestation of 19–21 days is indicated for *Dicrostonyx*. Assuming that both species of lemmings follow, in general, the type of development shown by laboratory rats and mice, we may estimate that pregnancy becomes macroscopically visible on the sixth day after impregnation.

Embryos were aged in the following way in order to calculate back to the date of insemination. Birth weights were determined to average 3.3 grams in *Lemmus* (Thompson, 1955 a; this study) and about 3.0 grams in *Dicrostonyx* (Quay and Quay, 1956). Laboratory mouse embryo growth curves for weight and crown-rump length (Enzmann, 1935) were converted to the gestation period and birth weight of each species of lemming, and tables of expected weight and crown-rump length for each day of gestation were constructed. As a further check anatomical changes associated with development in the rat (Henneberg, 1937) were adapted in the same way to the lemmings. The use to which these ageing data are put is such that accuracy only within ± 2 days is necessary, and thus the assumptions made here are not really critical for the results which follow.

Placental scars are formed at the implantation sites of embryos and show up as areas of black pigmentation on the mesometrial side of the uterus (Conaway, 1955). Although these scars were counted, the only use made of these data was in the classification of females as *nulliparous* (no embryos or placental scars), *primiparous* (embryos or one set of placental scars present), or *multiparous* (embryos and placental scars present, or two or more sets of scars). These scars tend to fade with age, but this causes few problems in animals of short life-span like lemmings. Corpora albicantia (degenerate corpora lutea) were also counted; but, as with the placental scars, the only use made of these data was to classify females as nulliparous, primiparous, or multiparous.

Corpora lutea were counted in the ovaries of pregnant females with the aid of a binocular dissecting microscope. These structures show up very clearly in the small ovary of a lemming, particularly in animals freshly dead. In ovaries preserved in formalin they are much more difficult to count without detailed histological work. In order to assess ovulation rate we must assume that each corpus luteum represents one ovulated ovum and thus that there are no polyovular follicles or accessory corpora lutea formed. There is almost no experimental or histological evidence on lemmings for these points. Quay (1960) found very few (about 0.1 per cent) binuclear and trinuclear primordial follicles in *Dicrostonyx*, and this suggests that polyovular follicles are not important in this species. In general, corpora lutea counts agree with embryo counts for both species; only rarely are there fewer corpora lutea than embryos, and rarely more than one to three more corpora lutea than embryos. Until further studies are made, the analysis which follows must rest on the unproven assumption that corpora lutea counts accurately and consistently measure ovulation rate. There is no reason yet to doubt this assumption.

Resorbing embryos were recognized because they were smaller than normal embryos. Obviously these size differences are easier to detect in larger embryos late in pregnancy, and this introduces some uncertainty in assessing one aspect of prenatal mortality. In calculating litter size only live embryos were counted. Prenatal mortality is discussed in the section on mortality.

Reproduction is a complex variable which may be broken down into several components. Figure 5 gives a schematic analysis of these components for polyoestrous mammals, and an attempt will be made to assess some of these.

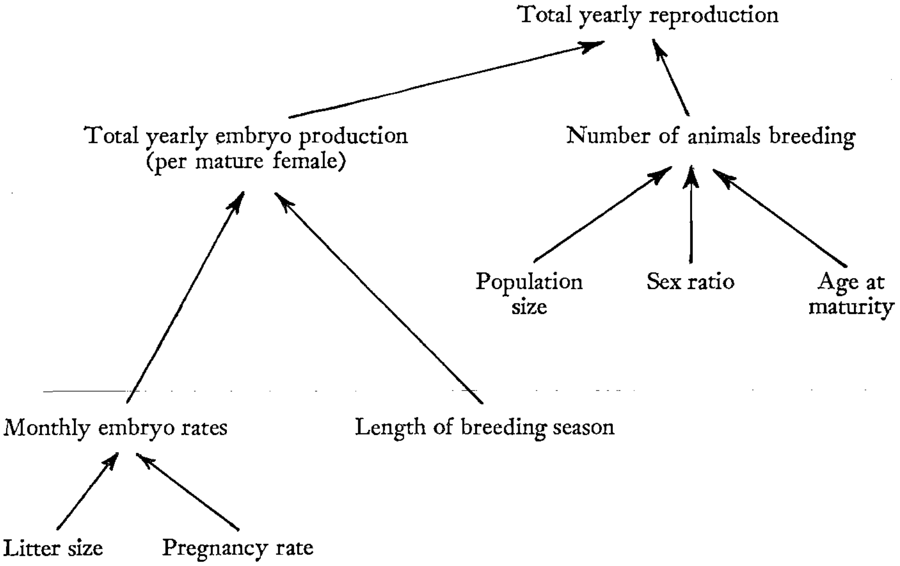


Fig. 5. Components of reproduction in polyoestrous mammals.

Length of breeding season

Summer breeding in lemmings begins when the snow melts in spring and this tends to synchronize breeding periods for the rest of the summer. Almost all mature females (the winter generation) are impregnated within a 5- to 10-day period at the melt-off; 20–21 days later this litter is dropped. Post-partum breeding is very common in both species, and thus three weeks later a second litter is dropped. A third litter and a fourth litter may be produced, but by late summer the original synchrony breaks down. This synchronous breeding tendency makes it possible to treat summer reproduction in terms of biological periods rather than chronological ones. Tables 10 and 11 give the timing of summer breeding periods in *Lemmus* and *Dicrostonyx.*

The length of the summer breeding seasons of 1959–62 in *Lemmus* and *Dicrostonyx* on the Main Study Area are given in Table 12. The beginning of breeding in every case coincides with the melting of the snow, and it is variations in the end of the summer breeding season that must be accounted for here. In 1959 there was no evidence that breeding ceased in the fall in *Lemmus,* as pregnant specimens were still being obtained in the first half of September when I left. Whether *Dicrostonyx* behaved in the same way or not is not known because only three small young and one lactating adult female were caught after the end of August. In 1960 summer breeding stopped at the end of July, no *Lemmus* being impregnated after July 20 or *Dicrostonyx* after July 25. In 1961 breeding seemed to have stopped by the end of July in *Dicrostonyx* and by the first week of August in *Lemmus.* There were very few mature females left in either species by August and no mature males were caught on the Main Study Area after August 1 in *Lemmus* or August 3 in *Dicrostonyx.* It is thus rather difficult to pinpoint the end of summer breeding in 1961. In 1962 pregnant *Lemmus* and *Dicrostonyx* were still being obtained in the last week of August and there was no indication that breeding was stopping. Thus 1962 resembled 1959.

At Aberdeen Lake changes in the length of the summer breeding season of *Dicrostonyx* seemed even more striking than the changes on the Main Study Area. In 1960 widespread evidence was obtained that breeding had stopped by July 15, and in 1961 by July 25. The precise end of the breeding season at Aberdeen Lake cannot be given for either year because of no August data. Thus breeding seemed to be curtailed in both summers but slightly earlier in 1960 than in 1961. *Lemmus* at Aberdeen Lake behaved like those on the Main Study Area.

The extent of winter and spring breeding (i.e. breeding under the snow) in both species is quite variable. Spring breeding (April, May) apparently occurred in 1959 at least in *Dicrostonyx*; a few young *Dicrostonyx* were found in June which must have been born during the spring, but no young *Lemmus*. Both species bred extensively in the winter and spring of 1959–60. Pregnant *Lemmus* were obtained in April and May, and breeding males in December, February, and April. Pregnant *Dicrostonyx* were obtained on November 18, January 17, and March 24, and breeding males in November, January, February, March, April, and May. Since only a few winter specimens were obtained (57 *Dicrostonyx* and 21 *Lemmus*), these data give only a qualitative idea of the 1959–60 winter breeding. In the winter of 1960–1, on the other hand, there was no breeding detected in either species (based on 65 *Dicrostonyx* and 245 *Lemmus* collected throughout the winter). Spring breeding did occur in 1961, and pregnant *Dicrostonyx* were obtained on April 16 and May 3. Although no pregnant *Lemmus* were obtained, females with fresh placental scars and young animals were caught in late May. In the winter and spring of 1961–2 breeding was detected in *Dicrostonyx*. Breeding males were obtained in December, January, March, April, and May, but no breeding females were obtained (based on 13 males and 4 females). No *Lemmus* were obtained over this winter. It was clear from the June weight distributions that a considerable amount of breeding had occurred under the snow during the spring in both *Lemmus* and *Dicrostonyx*. Thus spring breeding seems to occur every year irregardless of the cycle.

In summary, the major changes in the length of the breeding season over the lemming cycle were: (1) extensive winter breeding in the phase of increase (1959–60) but not in the decline (1960–1); and (2) shortening of the summer breeding season both of the peak year (1960) and of the decline (1961). These effects occurred in both species.

Litter size

Litter size at birth is a function of the ovulation rate and the prenatal mortality rates. An approximation to litter size is obtained by counting embryos in pregnant females. We need to find out whether there are any changes in number of corpora lutea or number of embryos per pregnant female over the lemming cycle.

There are at least eight interrelated variables that may affect litter size: season, food supply, body weight, age, parity, lactation, population density and social structure, and physiological and genetic changes in constitution. Thus to say that litter size differs between year *x* and year *y*, or group *a* and group *b*, is to say very little. It is necessary to correct for as many of these variables as possible in an assessment of litter size changes and to compare only groups of similar composition. These facts have not always been appreciated by workers assessing reproduction and much confusion has thus resulted.

A preliminary analysis of the data indicated that body weight *per se* (independent of parity and season) had no effect on corpora lutea or embryo counts, and this variable was deleted from the final analysis.

Tables 13 and 14 give the number of corpora lutea of pregnant *Lemmus* and *Dicrostonyx* from the Main Study Area, and from these data we are led to the following conclusions: (1) ovulation rate in both species changed seasonally, declining from higher values at the start of the summer to lower values in the late summer. (2) Primiparous females tended to have lower ovulation rates than multiparous females in both species but the differences are slight, as far as can be generalized from the few samples which contained both groups. (3) Primiparous summer young had significantly lower ovulation rates than multiparous winter generation adults breeding at the same time. (4) Finally, and most important for our purposes, there were no significant differences in ovulation rates of either species between the years, when we compare similar groups of animals.

Tables 15 and 16 give the number of embryos of pregnant *Lemmus* and *Dicrostonyx* from the Main Study Area. Precisely the same four conclusions drawn from the corpora lutea data can be applied to these embryo data.

Since all these data pertain only to the Main Study Area, it is reasonable to enquire whether these results are local or general. Fortunately data are available from Aberdeen Lake, 115 miles west of Baker Lake, for 1960–2. Table 17 gives the corpora lutea and embryo counts for *Lemmus* at Aberdeen Lake, and Table 18 the same data for *Dicrostonyx*. These data show the seasonal change observed above in ovulation rate and litter size. The *Lemmus* do not show any difference between ovulation rate or litter size in summer young and winter generation adults, contrary to what was observed above. Finally, there are no significant differences between the years in either variable for either species.

The seasonal trend in litter size carries through into the winter, as far as our meagre winter records indicate. Litter sizes of the pregnant females obtained in winter are listed below.

Date	*Number of embryos*	
	Lemmus	*Dicrostonyx*
18 November 1959		3
17 January 1960		3
24 March 1960		3
25 April 1960	4	
21 May 1960		5?
24 May 1960	3	
16 April 1961		3
3 May 1961		4

In conclusion, there seemed to be no significant change over the cycle in either ovulation rate or litter size in *Lemmus* or *Dicrostonyx*. There was a seasonal trend in these variables independent of the cycle in numbers.

Pregnancy rates

Given a summer breeding season of a certain length, we may enquire what proportion of mature females is pregnant at various times in this breeding season and whether or not there are differences between the years. The analysis of pregnancy rates used here follows that of Leslie *et al.* (1952).

Tables 19 and 20 give the crude (observed) pregnancy rates for *Lemmus* and *Dicrostonyx* respectively from the Main Study Area. Since animals in very early pregnancy will not be classified as pregnant macroscopically, these crude rates tend to underestimate the actual pregnancy rates such that a 0.750 crude rate (i.e. 15/20) for *Dicrostonyx* and a 0.762 crude rate (i.e. 16/21) for *Lemmus* will be equivalent to every female in the population being pregnant all the time. The rates are expressed per female of > 20.5 grams for *Lemmus* and of > 30.5 grams for *Dicrostonyx* because these are the weights above which a majority of females can be mature under good conditions. The data were not converted to standardized pregnancy rate (Leslie *et al.*, 1952) because after standardization of the data there was hardly any difference between the two rates.

If we examine these data (Tables 19, 20) we see that there is a general rise in the pregnancy rate from zero in May to high values by June 15 and a subsequent decline in August. We are not interested here in the timing of this rise and fall because this has been treated under the previous section on the length of the breeding season. What we are interested in is the period of midsummer when breeding is neither starting up nor beginning to stop, and we wish to enquire whether there are significant differences between the years in the rates during this period.

The tendency to synchrony in breeding may complicate comparisons of pregnancy rates between different years, particularly if spot samples only are taken. However in this study sampling was continuous through the summer on the Main Study Area, and this, coupled with the fact that the breeding synchrony is not absolute, permits us to compare the different years with statistical validity.

Pregnancy rates during midsummer (June 15–July 31) were compared for the Main Study Area in both *Lemmus* and *Dicrostonyx*. Chi-square tests (Snedecor, 1956, p. 228) showed no significant differences between years for winter generation animals of both species ($P > .10$).

Leaving the winter generation adults and looking at the pregnancy rates for the summer young, we find considerable variation between years. However, the pertinent factors involved here are changes in the length of the breeding season and related changes in the age at sexual maturity of these young; the former was treated above, the latter will be dealt with below. Consequently, a statistical analysis was not done on the data for these summer young.

One aspect of Tables 19 and 20 has not been discussed yet, the figures for total litter production. These are obtained in the manner described by Leslie *et al.* (1952) by applying the observed rates to the length of their particular time period and summing the results. Unfortunately it is not possible to attach statistical confidence limits to these numbers because they are sums of weighted averages. These figures are hypothetical in that they indicate the number of litters an average mature female would produce if she lived over the entire period between June 1 and August 31 for the winter generation, or in the case of the summer young over the period between reaching a mature weight and the end of August. Furthermore, these production figures are rather arbitrarily limited to June 1 to August 31 because most of the sampling was done at this time.

For *Lemmus* there is a slight depression of total litter production in the peak summer of 1960, but this is small in view of the fact that this summer had a shortened breeding season. For *Dicrostonyx,* on the other hand, there is an apparent increase in total litter production in the peak summer, a fact that seems to clash with the previous observation that this summer was characterized by a shortened breeding season. This anomaly is explained in part by the fact that in 1960 summer breeding began earlier than in the other years and in part by random sampling variations in the observed pregnancy rates.

In conclusion, on the Main Study Area the midsummer pregnancy rates did not change significantly from year to year in either species of lemming. All observed changes in pregnancy rates were reflections of changes in the length of the breeding season or the age at sexual maturity.

Age at reproductive maturity

The age at which reproduction begins is of the utmost importance in determining the intrinsic rate of increase of a population (Cole, 1954 a). Since we do not know the age of the specimens obtained in this study, it is necessary to use body weight as an index of age.

The method of Leslie, Perry, and Watson (1945) was used to determine the median body weight at maturity for the various groups. In brief this technique involves converting the weight data into logarithms and percent mature data into probits, fitting a straight line to this, and then calculating the 50 per cent point and its standard error. When the data were not sufficient to calculate the median body weight, the upper or lower limits possible for the median were indicated. Data from the Main Study Area for the whole summer were grouped in this analysis, but in the actual calculations the winter generation results are based mainly on the May and June samples and the summer generation results on July and August information. The results are summarized in Table 21.

These data show striking changes in the median body weight at maturity between the different years. In every case in the peak summer of 1960 there was an increase in the median body weight at maturity. In the 1961 summer of decline three patterns could be found: (1) in winter generation *Dicrostonyx* of both sexes and *Lemmus* males median weights remained the same as 1960; (2) in the winter generation *Lemmus* females median weights declined to a position intermediate between 1959 and 1960 levels; and (3) in the summer young *Lemmus* females median weights declined to the same levels as 1959. Missing from this classification are the summer young males of both species because none of these became sexually mature in either the summer of 1960 or the summer of 1961.

The summers of 1959 and 1962 closely resemble each other and seem to have had the most rapid rates of maturation found in both species, with the exception of the 1961 young females. Thus *Lemmus* females in 1959 and 1962 were mature at 20–25 grams, and males at 25–35 grams, roughly 3–4 weeks and

4–5 weeks of age respectively. *Dicrostonyx* males and females were mature at about 30–35 grams, roughly 4–5 weeks of age.

To sum up, there are striking changes in the median weight at sexual maturity over the cycle. In all groups the median weight was higher in the peak summer and remained high in most groups in the summer of the decline (except for young females). Young *Lemmus* males did not mature in either the peak summer or the summer of decline, whereas young females did mature in the decline but not in the peak summer.

MORTALITY

The second major factor which causes changes in population density is mortality. This factor begins its operation at ovulation and may be conveniently subdivided into pre-natal mortality and post-natal mortality.

Prenatal mortality is assessed by comparing counts made of corpora lutea, implantation sites, and living embryos. Data on post-natal mortality were obtained from live trapping.

Prenatal mortality

Prenatal mortality was assessed as far as possible by the methods of Brambell and Mills (1947, 1948). Prenatal mortality may be subdivided as follows:

1. Partial prenatal loss (at least one embryo survives until parturition)
    a. pre-implantation
    b. post-implantation
2. Total litter loss
    a. pre-implantation
    b. post-implantation

Partial pre-implantation mortality is estimated from discrepancies between corpora lutea counts and implantation site counts. From these data the loss of ova in litters that survive implantation can be estimated. Partial post-implantation mortality is estimated from discrepancies beween the number of implantation sites and the number of living embryos in the uterus. From these data we can estimate the number of implanted embryos which fail to survive, and this may include whole litters in the process of being lost. This estimate is always an underestimate because the females counted come from varying stages between implantation and birth. Ideally counts should be made on females in the very late stages of pregnancy only, but too few were obtained in this study.

Tables 22 and 23 summarize the data on partial prenatal mortality in *Lemmus* and *Dicrostonyx.* All data from each summer were grouped to obtain these estimates. Differences between the years were tested by chi-square (Snedecor, 1956, p. 228). In *Dicrostonyx* there was no significant difference in the partial prenatal mortality for 1959–62. In *Lemmus* there was a significant increase in both pre- and post-implantation loss in 1960 compared with the other three years ($.01 < P < .05$). However, variation between years was relatively small; in *Lemmus* the total loss of ova amounted to 4–9 per cent and in *Dicrostonyx* to 17–26 per cent. *Dicrostonyx* suffered considerably more partial prenatal loss than did *Lemmus.*

No information on the loss of whole litters before or during implantation is given by the above analysis. No litters were found undergoing complete resorption in middle or late pregnancy in this study. However, indirect evidence suggests that under some conditions in *Lemmus* complete resorption of litters just after implantation does occur especially in young animals. In late July 1960 young *Lemmus* 25–35 grams in weight with very faint placental scars, small corpora albicantia, and no active mammary tissue began to appear in the samples. Since it was quite impossible for these animals to have weaned a litter already (they were only 4–5 weeks old) and since the scars were so faint, a reasonable interpretation is that they lost their entire litters just after implantation. Although some of these animals were probably missed during autopsy because of the very small size of these scars and corpora, a minimal assessment of this total litter loss may be made from the snap-trapping samples. No *Dicrostonyx* has yet been seen with these characteristics, and it appears to be found only in *Lemmus* summer young. The following samples from the Main Study Area could have contained this type of young *Lemmus*:

	No. young females >20.5 grams	*No. mature (with corpora lutea)*	*No. showing evidence of total litter loss*
1959			
August 1–Sept. 10	16	16	0
1960			
July 16–August 15	93	31	12
1961			
July 16–August 31	15	7	4
1962			
August 1–31	22	20	0

If these data are approximately correct, we reach the conclusion that of all the summer *Lemmus* young which matured in 1960 and 1961 about 40–60 per cent lost their entire litters just after implantation. More information is needed to support this suggestion.

To sum up our assessment of prenatal mortality: partial prenatal mortality in *Dicrostonyx* showed no relationship to the cyclic density changes, but was significantly higher in the peak summer of 1960 for *Lemmus*. Total litter loss after implantation did not seem to occur in *Dicrostonyx* or in adult *Lemmus*, but in *Lemmus* summer young it seemed to be high in the peak summer and in the summer of the decline. Total litter loss before implantation could not be assessed in this study. These changes in prenatal mortality are not large enough to account for the changes in numbers described previously.

Post-natal mortality

(a) *Adults*

Adult mortality here includes all winter mortality as well as the summer mortality of winter generation animals. The specific conclusions made here apply to the live-trapping area in particular and probably sharp (Type G) declines in general.

Some observations on adult mortality may be made from snap-trapping records. There is an annual overturn in population. Adults of the winter generation, which comprise the entire population at the start of summer breeding, are gradually replaced through the summer by their own young, and by late August and September there are very few old adults left.

If we assume that snap-trapping mortality is negligible in comparison with natural mortality, we can estimate the summer mortality rate of adults by the decline in catch of adults from June to August on the standard trap-lines (Ricker, 1958). The results of this calculation are as follows:

	Estimated summer survival rate (per 28 days)	
	Lemmus	*Dicrostonyx*
1959	0.51 ?	0.42 ?
1960	0.58	0.67
1961	0.29	0.49
1962	0.53	0.71

The 1959 estimates are based on very few animals and must be considered unreliable. There are a great many assumptions involved in calculations of this type (Ricker, 1958, p. 45) and some caution must be used in their interpretation, but the data do suggest an increased summer mortality rate of adults in the decline.

Additional observations on adult mortality may be made from the live-trapping data. No mortality estimates were obtained in 1959. Tables 24 and 25 give the minimum survival factors for *Lemmus* in 1960 and 1961, and Tables 26–28 for *Dicrostonyx* in 1960–2. Minimum survival factors are obtained by marking a cohort of animals at time t and determining the number known to be alive at time $t + w$ (Chitty, 1952). These factors always underestimate the true survival factor and consequently care must be exercised in interpreting them. To facilitate direct comparisons the observed minimum survival factors were converted to a standard 28-day period, and these data are given in Tables 29 (*Lemmus*) and 30 (*Dicrostonyx*).

Considering only the winter generation, we see first that over-all summer survival appears to have been better in 1960 than in 1961 for both species. This supports the conclusion suggested previously from the snap-trapping records. In 1961 after mid-July survival seems to decrease moderately in *Dicrostonyx* and considerably in *Lemmus*, resulting in a complete absence of adults by early to mid-August. These differences between 1960 and 1961 seem to be real, although it is impossible to estimate their magnitude from these data.

Overwinter mortality cannot be estimated for 1959–60 or for 1961–2 because breeding was occurring, but we can obtain a block estimate for the 1960–1 winter because no breeding occurred. As was shown above in discussing density changes, only 5–10 per cent of the *Lemmus* and 20–30 per cent of the *Dicrostonyx* survived the interval from August 1960 to June 1961. There was no breeding over this period (the few animals born in May are excluded from these estimates) and no major movements occurred. As an approximation we may enquire what mean monthly mortality rate would produce the observed declines over this 10-month period with no recruitment or migration. For *Dicrostonyx* an 11–15 per cent monthly mortality would produce a 70–80 per cent decline over this period, and for *Lemmus* a 20–25 per cent monthly mortality would produce the observed 90–95 per cent reduction.

There is some indirect evidence that the winter mortality rate in 1960–1 was not constant in *Lemmus* but may have been so in *Dicrostonyx*. The local Eskimos brought in all lemmings they found during the winter, and these were recorded as "caught alive" or "found dead". There was a sharp drop in the number of live *Lemmus* found by the Eskimos about December 15–31 and thereafter almost all specimens were found dead. This same change did not seem to occur in *Dicrostonyx*. Figures obtained were as follows:

	Proportion of winter specimens caught alive	
	Before December 31	*After January 1*
Lemmus	30 of 98	3 of 99
Dicrostonyx	9 of 20	8 of 23

These data suggest a period of increased mortality for *Lemmus* sometime around December. We can introduce these data by adding one month with an increased mortality rate of 50 per cent, all other months having a constant rate. Then a 15–20 per cent monthly mortality with one month increased to 50 per cent predicts a decline in *Lemmus* similar to that observed. It is interesting that this increased mortality rate during one month has very little effect on the absolute value of the final predicted decline; for example,

20 per cent monthly mortality = 89 per cent decline
20 per cent monthly mortality plus one month at 33 per cent = 91 per cent decline
20 per cent monthly mortality plus one month at 50 per cent = 93 per cent decline

over 10 months. The reasons for this apparent mid-winter sharp decline in *Lemmus* are not known. The above hypothetical results suggest, however, that unless this increased mortality extended over a considerable length of time or was exceptionally severe it need have little absolute effect on spring densities in 1961.

Even though the winter decline in 1960–1 was very great in both species, the average monthly mortality rates which could produce the observed declines are reasonable for small mammals (Leslie, Chitty, and Chitty, 1953; Golley, 1961); indeed if anything they seem to be low rather than high.

In summary, mortality of the winter generation appeared somewhat higher in the summer of 1961 than in the summers of 1960 or 1962. Winter mortality rates during 1960–1 were moderate to low but produced a great numerical decline because of the lack of breeding over this 9- to 10-month period. Nothing is known of summer mortality in 1959 or winter mortality in 1959–60 or 1961–2. The data are not sufficient to assess possible differences in mortality between the sexes.

(b) *Juveniles*

Juvenile mortality refers to the mortality of summer young during the summer of birth, and thus includes birth to weaning mortality and early post-weaning mortality.

For a general idea of changes in juvenile mortality we may return to Tables 24–30 for the summer generation data. These tables show for *Lemmus* that apparently no young survived on the live-trapping area in 1961, while at least some survived in 1960 on the same area. For *Dicrostonyx* the 1960 data are not very extensive, but in 1961 there was apparently no survival of young until after August 1 and even then survival was not very good (first litter young should have been in the traps by 15 July 1961). These data suggest that juvenile survival was poor in both species during the summer of the decline.

A more refined estimate of this mortality may be made as follows. Since we know the mean timing of breeding periods and the mean litter size, as well as the number of adult females living on the quadrat at the various times, we may estimate the number of young born on the quadrat for each breeding period. At a subsequent trapping period (late enough after weaning to ensure that all the young are trappable) we get a tally of how many of these young are alive on the quadrat, and by comparing this with the calculated number born we can estimate the juvenile mortality rate directly. We assume in this analysis (1) that the females breed at the average rates determined previously, (2) that all females have their litters on or adjacent to the quadrat, (3) that all the young on the quadrat have been caught, as well as all the females, and (4) that there is no net immigration or emigration of young. Assumptions (1), (2), and (3) are probably valid, and assumption (4) could not be evaluated. These calculations were done for both species in 1960 and 1961 and for *Dicrostonyx* in 1962, and the results are presented in Tables 31–5.

These survival estimates are a composite of birth to weaning mortality and a variable length of early post-weaning mortality, and hence some caution must be exercised in comparing the survival rates converted to the standard 28-day base. These data show very low survival rates of summer young in the decline. There was some further suggestion that the second *Dicrostonyx* litter (Y_1') survived better than the first litter. This suggestion is confirmed in the snap-trapping data for 1961 in which the late August samples of both species are dominated by Y_1' young with almost no Y_1 young and only a few Y_1'' young (since the breeding adults are dying out through the summer, one would expect to get many Y_1 young, fewer Y_1' young, and very few Y_1'' young). There is no striking differential mortality between the sexes in these data. Extensive snap-trapping data support these results obtained from live trapping and render improbable any suggestion that these differences between years are due to emigration of young from the live-trapping area.

Birth to weaning mortality could not be separated from early post-weaning mortality in these estimates. If much loss occurred at birth or shortly thereafter, particularly losses of whole litters, this should show up in a regression of active mammary tissue in breeding females. However, there was no difference macroscopically between lactating females in 1960, 1961, and 1962. During the breeding seasons of these years virtually every female showed active mammary tissue, and there was no evidence that lactation had stopped in any of the females, such as occurs at the end of the breeding season. This indirect evidence suggests that the loss of whole litters at birth or in early suckling stages is not the cause of the observed poor survival of juveniles. More direct evidence on this point is needed.

In summary, juvenile mortality between birth and 1–4 weeks after weaning was very high in the summer of decline on the live-trapping area (Type G decline). Almost no young of the first litter seemed to survive and only moderate numbers of the second and third litters. This high mortality was probably not due to the loss of whole litters at birth or in the early suckling stages, but probably occurred just shortly before or shortly after weaning.

MOVEMENTS AND MIGRATIONS

The third factor which can cause changes in population density is dispersal. Dispersal may take the form of small local movements or mass movements ("migrations") of the whole population. On small areas dispersal can affect density through immigration or emigration. On large areas immigration usually balances emigration and consequently dispersal affects density only indirectly by causing changes in reproduction or mortality.

Almost all data on local movements were obtained by live trapping, and these methods have already been discussed. A few results were obtained by snap-trapping animals which had previously been live trapped.

Local movements

The live-trapping program used in this study was not designed primarily to study movements, and consequently the data leave much to be desired. The many problems of measuring home ranges and movements of small mammals have been discussed by Chitty (1937), Davis (1953), Godfrey (1954), Stickel (1954), and Brown (1956). No attempt to estimate actual home-range sizes will be made because very few animals were recaptured more than two or three times during any one trapping period of three days; at least 5–7 recaptures are necessary for home-range estimates. The appropriate method for the lemming data is to analyse distances between successive captures (Brown, 1956) because this allows animals captured only twice during a trapping period to be used. This type of analysis is confined to short-term movements within trapping periods.

Table 36 gives the length of every movement recorded within trapping periods for *Lemmus* in 1960 and 1961, and Table 37 gives the same information for *Dicrostonyx* for 1960–2. Differences between the years were tested by chi-square (Snedecor, 1956) and both species showed a significantly greater number of long movements of adults recorded in 1961 than in 1960 ($.01 < P < .05$). The suggestion is that the low density of 1961 was accompanied by a greater mobility of the adults at least, compared with 1960. No data on movements were obtained in 1959. The 1962 *Dicrostonyx* movements did not differ significantly from those of 1961.

Although these results are reasonable, there are several reservations which render their significance somewhat questionable. The primary difficulty is that the spacing of the traps was not identical in 1960 and 1961–2. In 1961 and 1962 live traps were scattered at irregular intervals outside the quadrat boundaries, and this increased the probability of detecting longer movements. Furthermore, many of the 1960 data come from Quadrat 2 and this area had so few lemmings in 1961 and 1962 that it was not trapped.

Observed range lengths (Stickel, 1954, p. 2) could be estimated for only a few *Lemmus* winter generation males with the following results:

1960 $N = 4$ $\bar{x} = 286$ feet 63 feet (1 SE)
1961 $N = 3$ $\bar{x} = 631$ feet 170 feet (1 SE)

These data conform to the suggestion of greater mobility in the summer of 1961 made above, but again reservations must be made about their significance. Observed range lengths could not be estimated for other groups because only animals having five or more recaptures within one trapping period can be used.

Whether lemmings occupy a definite territory or home range is not known. The general impression I have gathered from live trapping is that the males of both species are wide ranging and almost continually on the move. Untagged adult males continually appeared on the live-trapping areas through the summer. This effect was particularly striking in 1960 on the *Lemmus* quadrat (see Table 6) where ¼ to ⅓ of the adults were inadvertently killed each trapping period, and yet the adult population on the quadrat through the summer declined at a very low rate. Net immigration almost completely offset the artificial mortality. This same observation applies to a lesser degree to the summer young males and females. The adult females of both species seem to move around less than the males, but even so they range over rather large areas. Thus any complete study of movements under these conditions must involve very large live-trapping areas, possibly as big as 15–20 acres, in order to be certain of recording most of an individual's movements.

Movements of individuals from one week or month to the next during the summer will not be analysed in detail because the data are too fragmentary. A few examples will be given to indicate the sort of movements that can occur.

	Distance between capture points (feet)	*Dates of capture*
1960		
Lemmus adult male	3700	June 2–July 8
Lemmus Y_1 female	2600	July 7–28
Lemmus Y_1 male	525	July 23–August 4
1960–1 (the following are 1960 summer young recaptured alive as adults in June 1961)		
Lemmus female	2400	August 1960–June 1961
Lemmus female	365	” ”
Lemmus female	2500	” ”
Dicrostonyx female	165	” ”

The significance of these movements is simply not known. On the one hand, they may be extremely abnormal samples biased toward long movements; on the other hand, they may represent the normal sort of movements which go on in these populations. I am inclined to believe the latter alternative after having seen movements of 500–800 feet take place in less than 24 hours within a trapping period.

Migrations

Perhaps the one thing most people know about lemmings is that periodically they all march down to the sea and drown themselves. Obviously if this is true it must have a profound effect on the population dynamics of the animal.

Local movements of individual animals can be very pronounced at certain times of the year. At Baker Lake in the spring of 1960 lemmings began to appear in particular areas as the melt-off proceeded. Individuals and 'groups' of *Lemmus* were reported on the lake ice in front of the settlement on May 26, and the major activity occurred during the night hours (twilight all night at this time of year). From 2 a.m. to 4 a.m. on June 2 I observed 25 lemmings moving individually on the lake ice in front of the settlement. Fifteen of these were caught and tagged (1 *Dicrostonyx* male; 7 *Lemmus* males; 7 *Lemmus* females), and all were in breeding condition. None of these animals seemed to do anything on the ice except move in a straight line, usually toward the nearest land, running at top speed. All were very aggressive when caught. It was not possible to determine whether the lemmings on the ice came from the opposite side of the lake (3–5 miles) or whether they had moved out from the area of the settlement on to the ice and then later moved back again. One of the *Lemmus* males tagged was recovered five weeks later on the live-trapping area after having moved 3,700 feet (see above). Most of this movement on the ice was over by June 4, having lasted about 9 days. I never saw any evidence of group movements on the ice, and never saw even two lemmings moving together. An Eskimo brought in a bucketful of 70 *Lemmus* which he killed on the ice during the night of May 26, but whether these represented a real group or merely a lot of individuals could not be determined. Very few dead lemmings were found on the ice.

Apparently these spring movements are not common at Baker Lake. Mr. S. Lunan, who was manager of the Hudson Bay Company post at Baker Lake for about thirty years (until 1957), told me that only once had he seen lemmings so abundant that they were common on the ice in the spring.

Many other areas around Baker Lake reported movements of lemmings on the ice in the spring of 1960: Chesterfield Inlet, Rankin Inlet, Eskimo Point, Aberdeen Lake, and Schultz Lake. These spring movements are thus quite common in particular years of higher than average peak densities.

Many of the people living in the north, even the Eskimos, rarely see a live lemming. Thus when spring movements do occur, there is a tendency to exaggerate their size. A few tens of lemmings quickly become a few hundreds in the mind, and to the next person the number is in the thousands.

Another local movement of brown lemmings was reported in late August 1960 by an Eskimo at the east end of Baker Lake. The reliability of the observations could not be established. There are no other records of fall movements from the area.

No other "migrations" were observed during either 1959, 1961, or 1962 in the area.

The general conclusion is that no large-scale migration played any part in this lemming cycle. Local movements were pronounced in the spring of the peak year, but these were a relatively minor event in the cycle. The whole problem of lemming migrations will be treated in detail in the Discussion.

CHANGES IN EXTRINSIC FACTORS

Factors which affect reproduction and mortality may be broadly classified as intrinsic or extrinsic factors. Extrinsic factors include weather, predators, disease, parasites, and food. These factors are normally studied as distinct and independent variables which exert an effect on the population from the outside. They thus represent the first and simplest level of enquiry into the causes of population density changes.

Weather

The winter of 1959–60, when the lemmings increased, began with a dry freeze-up and a quick build-up of snow cover. The winter of 1960–1, when they declined, began with a wet freeze-up and a slow build-up of snow cover until December. However, because of the drifting of the snow and the tendency of lemmings to seek out the more deeply drifted areas, there probably were some locally favourable areas in 1960–1. Yet no winter breeding was found in 1960–1, which suggests that bad winter weather was not sufficient to cause the observed absence of breeding. The 1961–2 winter was apparently even more favourable for lemmings than that of 1959–60, and yet the population did not expand even though winter breeding was found. The suggestion from this is that whereas a favourable winter may be sufficient to allow winter breeding, it is clearly not sufficient to produce a population increase.

One of the most striking facts about this 1959–62 lemming cycle was its synchrony over a very large area of the Central Canadian Arctic. This does not appear to be a simple coincidence. It was impossible to find a population around Baker Lake which was not at a peak in 1960. If this synchrony is more than a mere coincidence, the agent acting over these large areas would most likely be weather.

Summer weather seemed to bear no relationship to the cycle. The summer of 1959 was very wet and cold and yet the population was beginning to increase locally. The summers of 1960 and 1961 were both warm and dry, and yet in 1960 the population remained at a peak whereas in 1961 it declined.

There are a sufficient number of climatic variables that if we investigate enough of them we shall surely find one or more close correlations with this lemming cycle. For this reason *post hoc* climatic correlations must always be suspect.

To sum up, favourable deviations from the average winter weather were associated with a large increase in density in 1959–60 and no change in density in 1961–2, and unfavourable deviations were associated with a decline in numbers in 1960–1. The significance of these associations is not known. Summer weather seemed of little importance.

Predators

Predatory birds were not very numerous near Baker Lake compared with the numbers reported for northern Alaska (Pitelka, Tomich, and Treichel, 1955). Only three long-tailed jaegers (*Stercorarius longicaudus*), three parasitic jaegers (*S. parasiticus*), one rough-legged hawk (*Buteo lagopus*), and one short-eared owl (*Asio flammeus*) were seen in 1959. In 1960 the first jaeger appeared on June 7, and birds of prey were still very scarce during this summer in spite of the dense lemming populations. No attempt was made to take a census of these birds in 1960. Three parasitic jaeger nests were found on the Main Study Area in 1960, and this seemed to represent most if not all of the jaegers nesting in this area. In 1961 predatory birds were again scarce. Only one snowy owl (*Nyctea scandiaca*), two long-tailed jaegers, and two parasitic jaegers were seen on the Main Study Area; no nests were found. Long-tailed jaegers were much more common during all four years on the islands in Baker Lake which support considerable numbers of nesting birds. In 1962 predatory birds were more common than in all the other years; at least four pairs of parasitic jaegers were nesting in the Main Study Area, and one nest which was followed hatched and the downy young was seen alive three weeks after hatching. Flocks of 15–25 long-tailed jaegers were seen over the Main Study Area on several occasions.

Only one mammalian predator was at all abundant on the Main Study Area —the weasel or ermine (*Mustela erminea*). Other larger predators, such as the arctic fox (*Alopex lagopus*), wolf (*Canis lupus*), and wolverine (*Gulo luscus*), were virtually absent. Weasels were very scarce in 1959 and none was seen; they were still uncommon in 1960 and only two were caught by the Eskimos. In 1961 weasels were very numerous. One was caught by an Eskimo on 1 February 1961, another on May 17, another on June 29, and from August 7 on weasels were seen everywhere. Over 70 specimens were caught by the Eskimos by the end of August and many more in early September. Complete autopsies were done on 26 of the August specimens. Of these 25 were males (286–341 mm. total length) and only one was a female (261 mm. total length). None was breeding, and almost all were moderately fat. Stomach contents were classed as follows: empty, 8; bird feathers and bones, 3; lemming fur and bones, 4; fish (?), 3; caribou meat (?), 4; berries and plant matter, 3; unidentifiable matter, 1. It is clear that not all these weasels could have lived on lemmings during the early summer because of the very sparse lemming population. The date at which weasels began to appear commonly (August 7) coincided with the time when all the young birds were finally able to fly, and this suggests that the weasels may have fed on birds during much of the summer. It seems probable that many weasels were drawn to the settlement in August and September to feed on refuse. Weasels were very scarce again in 1962.

It seems doubtful that the weasels were having an important effect on the lemming population of the live-trapping area for three reasons (1) no weasels were caught in the live traps until August 4 and six weasels were caught in these traps during the rest of August. If weasels were pursuing lemmings on this area during June and July it seems inconceivable that one or more of them would not have been caught, since the area was covered with live traps. (2) There is no evidence of high death rates in the adults during June and July such as would be expected if weasel predation was common. (3) The survival of the second litter of summer young (August) was relatively better than that of the first litter, even though the weasels should have exerted more predation pressure on this second litter. There is thus no evidence that weasel predation did account for the observed mortality changes during the decline.

Disease and parasites

No detailed studies on disease or parasites were made in this research program, but in the course of autopsying some 3,000–3,600 lemmings only 8 specimens were found with any gross abnormalities such as cysts in the liver and spleen. There was no macroscopic evidence that most of the animals were not healthy. Parasite loads were superficially quite low and there was no evidence of debilitation even in the few specimens with considerable numbers of stomach and intestinal parasites.

About 50 *Dicrostonyx* were shipped to Toronto and Ottawa in August 1960. Most of these specimens died either on route or just after arrival in spite of rapid transport and apparently adequate food and bedding (Fisher, pers. comm.; Manning and Macpherson, pers. comm.). The question arises whether these animals died because of a latent disease which could be responsible for the decline. There is no field evidence to support this view. Certainly there was no spectacular mortality in either *Dicrostonyx* or *Lemmus* during August, September, or October 1960. As we have seen previously, the winter mortality in *Dicrostonyx* over 1960–1 was not excessive for a population in which no recruitment was occurring. We seem to have the alternative of ascribing most of this winter decline to an epidemic and assuming all other mortality factors to be almost negligible, or of placing disease on a par with many other mortality factors which comprise the winter mortality. Furthermore, even if we could ascribe all this winter mortality to disease, we would be left without an explanation for most of the observed changes in reproduction or mortality described previously.

Food

Forage production was assessed by clipping the standing crop of green vegetation at the end of each summer (September 1–10) on 15 pairs of quadrats, one of which was open and the other enclosed. Each open quadrat was paired as closely as possible with an enclosed quadrat to reduce sampling variation. All clipped vegetation was dried in an oven at 225° F to constant weight and all weights given here are dry weights. The quadrats were 2 square metres in size and one-fourth of this total was clipped each year. Ten pairs of quadrats were set out in 1959 and the other five in 1960. Each enclosed quadrat was surrounded by ⅜ inch hardware cloth screening which was buried 8–12 inches in the ground and extended 24–28 inches above ground. There was no evidence that any lemmings got inside any of these enclosed quadrats during the period of study. All the quadrats could not be clipped in 1962. This general approach was the same as that of Thompson (1955 b).

Table 38 gives the standing crop measurement at the end of the 1959–62 growing seasons on the Main Study Area. These data may be considered in two parts. Quadrats 1–10 were present during all four years; quadrats 11–15 were installed in 1960 and serve as a further check on the 1960–2 changes. In the analysis of these data we are interested in the differences between the pairs of open and enclosed quadrats.

Because there were very few lemmings in 1959 we may adopt the 1959 data as our base and relate all changes to it. Two major effects cause deviations —weather effects and lemming effects—and the problem is to separate these (I shall use the term "weather effects" in a loose sense to include all non-lemming effects, weather being the major component of this category). This was done in the following way.[1] The difference between each 1960 enclosed quadrat and the same quadrat in 1959 must be caused very largely by weather differences. Similarly, the difference between each 1960 open quadrat and the same quadrat in 1959 must be caused by the interaction of lemming and weather effects. But since we know the weather effects alone from the enclosed quadrats, we may subtract this element to estimate the lemming effects (we assume these two effects to be independent and additive). We can apply the t-test to these

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[1] I am indebted to Dr. Monte Lloyd, Bureau of Animal Population, Oxford, for this statistical technique.

differences and thereby test the significance of these effects. The same procedure may be applied to the 1961 and 1962 data.

The weather effects are significant between all four years ($P < .01$), the progression in the size of the standing crop being 1959 < 1960 < 1961 < 1962. Thus in terms of the quantity of food, more was available at the end of the summer of decline than either the summer of increase or the peak summer. The relative changes in standing forage were: 1959—100; 1960—139; 1961—168; 1962—175. The significance of this steady increase in forage production from 1959 to 1962 is not known. Presumably it was not an enclosure effect because it occurred on both open and enclosed quadrats. It is improbable that my clipping technique could have changed so much, and these differences were not due to improperly dried samples, because I rechecked the 1959–61 samples in 1962.

Lemmings significantly depressed the standing crop in both 1960 and 1961 ($.01 < P < .05$). There was no difference in the lemming effect on quadrats 1–10 between 1960 and 1961, and it showed up in 1961 on the new quadrats 11–15 as would be expected ($P < .01$). Since quadrats 11–15 were not installed until July 1960, one would not expect any lemming effect to show up in the 1960 data for these. The depressing effect of the lemmings on the forage is very nearly the same in 1960 and 1961. If we take the theoretical standing crop to be what would occur in the absence of lemmings, the lemmings are found to depress standing crop by 14.5 per cent in 1960 and 16.4 per cent in 1961 on quadrats 1–10, and by 14.1 per cent in 1961 on quadrats 11–15. There is no significant lemming effect in the 1962 data, which thus resembles 1959.

The limitations of these quadrat data must be stressed. These quadrats are not a random sample of the whole area. They are put almost invariably in sedge marsh type, in the greenest, densest vegetation where high utilization might be expected. As such they are not even a random sample of sedge marsh, and thus the conclusions from such data can strictly be applied only to the area on which the actual quadrats occur. A further difficulty arises from the effect of the enclosures on the microclimate of the quadrat. We must assume that these microclimatic changes are negligible, but this may not be true. All these difficulties in interpreting quadrat data do not appear to have been appreciated by Thompson (1955 b). If we locate quadrats in the best habitats, where maximum utilization is expected, we should not be surprised to find high utilization and depressed forage production. However, while this does give us an estimate of maximal effects, it tells us very little about the relationship of lemmings to their food supply in general.

Forage utilization was estimated in the spring of 1961 by systematic sampling along line transects. A three-by one-foot rectangle was dropped every ten feet along these transects until the lines ran out of the wetter habitats. The habitat was classified at each station. All the cut grass and moss was removed from the three square feet and a visual estimate was made of the proportion and type of the forage that had been clipped. No transects were done in the dry habitats because utilization was so low as to be unmeasurable with this technique. All these estimates were made before the new season's growth of plants had begun, i.e. when the quantity of green food was at its lowest point for the year.

Table 39 gives these forage utilization estimates made in the spring of the decline. No transects were made in 1959, 1960, or 1962 because utilization was too small to be conveniently measured. These data for 1961 show an average utilization of 30 per cent at the most for the wetter habitats. It was rather difficult to estimate the moss removed but this was attempted because moss is a very important food item during the winter. The pattern of forage use appeared very spotty in the spring of 1961. Small areas two to six feet in diameter would be completely devastated of all live plants down to the roots, and these areas were surrounded by untouched vegetation. There was no evidence that the boundaries of these small feeding places coincided with packed snow, ice, or any vegetation or topographical changes. In no case did these devastated areas coalesce over large areas; no place was more than four to five feet from relatively untouched vegetation. It is difficult to see how food supply could be short under these conditions.

The dry tundra areas were hardly touched during the winter of 1960–1. Small local areas were devastated but on the whole less than 5 per cent had been consumed. Since the plants of the dry tundra areas grow very slowly (heath recolonization may take fifty years or more), any widespread destruction of this vegetation would be evident for decades afterward. The same point may be made about dwarf birch and willows. There was very little girdling of these shrubs during 1960–1 either on the Main Study Area or on the outlying areas where they are more common.

All the previous points have been concerned with food quantity. Food quality may also be important. No attempt was made to analyse the quality of the food in this study. There was no evidence of any obvious deficiency diseases such as occur in domestic animals having vitamin or mineral shortages (Maynard and Loosli, 1956).

With all the difficulties involved in measuring forage changes directly, it seems easier to turn the problem upside down and to look at the animal as a measure of the adequacy of the food supply (Bandy *et al.*, 1956). I have used a fat index to measure this, and these data will be presented in the next section.

Thus there was no evidence of a quantitative shortage of food over this lemming cycle. Nor was there any obvious evidence of a deficiency disease associated with changes in the quality of the food.

CHANGES IN INTRINSIC FACTORS

Changes in reproduction and mortality may also result from changes in factors intrinsic to the population, as well as in the extrinsic factors just discussed. Other animals of the same kind may produce behavioural and physiological changes in the individual organism. The intrinsic factors are behaviour and physiology; these may be studied directly in themselves or indirectly by their effects. In this section I will analyse some changes which occur over the cycle in the following properties of individuals: weight distributions and mean body weights; organ weights; fat index; and social relationships.

Age determination

Many different techniques for measuring chronological age have been proposed, but the majority of small mammal workers still use body weight as a criterion of age (e.g. Chitty, 1952; Hoffmann, 1958). Frank and Zimmermann (1957) found that the body weight to age relationship in the vole *Microtus arvalis* was greatly affected by both inherent variability and seasonal changes in growth. Body weight is more a criterion of physiological age than chronological age, and as such it is more useful for our purposes than chronological age would be. An attempt was made to use the lens of the eye as an age indicator (Lord, 1959) in this study and this information will be treated in a later publication. Body weights were used rather than total lengths because it is easier to compare data on weights with those of other workers.

Body weight distributions

Much information can be learned from age or weight distributions (Bodenheimer, 1938; Leslie and Ranson, 1940). Tables 40 and 41 give the weight distributions for *Lemmus* and *Dicrostonyx* males during 1959–62 on the Main Study Area; the data for the females are very similar. All the weight data discussed here were obtained from the snap-trapping samples; weight data from live trapping are not given but they showed similar changes. Some care must be taken in comparing weight distributions between the years because 1959 and 1962 were biologically 2–3 weeks behind 1960, and 1961 was about one week behind 1960.

Several points are shown by these data. First, the peak summer of 1960 was characterized by higher adult body weights than either 1959, 1961, or 1962. There were very few *Lemmus* above 76 grams in either of these three years, but in 1960 a majority of the adults were above this weight. In *Dicrostonyx* the difference between 1960 and 1961 was evident but not so marked. Second, there is a gap in the 1961 summer weight distributions where the early young should be. Again this was shown more clearly by *Lemmus* than by *Dicrostonyx*. Figure 6 shows graphically the late July *Lemmus* male weight distributions for 1960 and 1961 on the Main Study Area and illustrates these points, i.e., the higher body weights of 1960 and the shortage of summer young in 1961 for the Main Study Area.

The body weight distributions for Aberdeen Lake (Tables 42, 43) show interesting differences in 1961 data from those of the Main Study Area. There is very little difference between the 1960 and 1961 distributions in either species; high body weights were found in both years, and there does not seem to be a missing group of summer young in 1961. The 1960 and 1962 distributions on the two areas are very similar.

With these two differing patterns in mind let us look at the weight distributions found on the other outlying areas in 1961 (Table 44). Only data for *Lemmus* males are given; *Dicrostonyx* is sparse on all these trapping areas. "New Lake", Lower Thelon River, "Ten Mile Island", and the Prince River were sampled in 1959 and 1960 also, but the data are virtually identical with those for the Main Study Area. The 1961 data are based on small numbers of animals, but if we compare these samples with the corresponding ones from the Main Study Area we find some differences. "New Lake", "Long Island", "Second Island", "Ten Mile Island", and "Nine Mile Island" show the weight distribution pattern found at Aberdeen Lake in 1961. The Prince River and Lower Thelon River show the Main Study Area pattern (see Fig. 6).

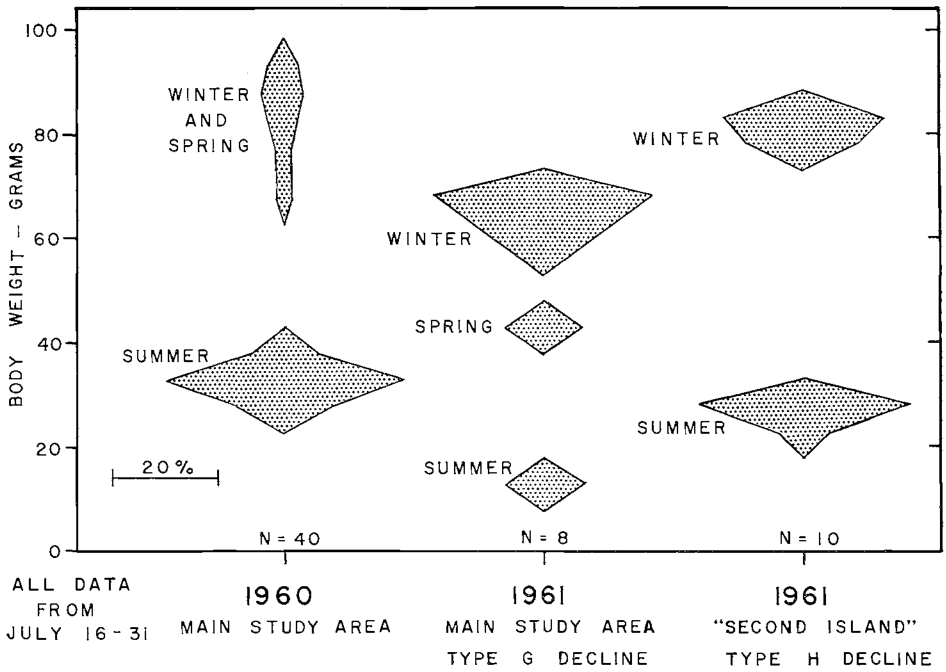

Fig. 6. Body weight distributions for *Lemmus* males, July 16–31, 1960 and 1961.

We can summarize these relationships in the following way:

	1960		*1961*	
	Weights ad. males	*Recruitment Y_1 young*	*Weights ad. males*	*Recruitment Y_1 young*
Main Study Area[1]	high	+	low	—
Aberdeen Lake[1]	high	+	high	+
"New Lake"	high	+	high	+ ?
Lower Thelon River	high	+	?	—
"Ten Mile Island"	high	+	high	+
Prince River	high	+	low	—
"Nine Mile Island"			high	+
"Long Island"			high	+
"Second Island"			high	+

([1]*Dicrostonyx* and *Lemmus*. Others refer to *Lemmus* only.)

In the summer of decline those areas which show recruitment are undergoing a Type H decline (slight recovery) by definition, and those areas showing no recruitment of these early young are undergoing a Type G decline (no recovery). Thus we reach two conclusions which apply to both species: (1) that Type H declines were associated with high body weights and Type G declines with low body weights; and (2) that the adult body weight change was associated with population phenomena and was not simply a side effect irrelevant to the cycle. It is clear from the 1959 and 1962 data that low body weights *per se* are not sufficient to cause a lack of recruitment of young but that something else must also be necessary.

Unfortunately there is no evidence to show what did cause this lack of recruitment. It was not apparently due to either the quality of the habitat or the population density of the area in 1960:

	Type of vegetation	*Density in 1960*	*Type of decline*
Lower Thelon River	thick	very high	no recovery
"New Lake"	thick	very high	some recovery
Main Study Area	sparse	mod. high	no recovery
"Ten Mile Island"	sparse	mod. high	some recovery

It is also clear that the weather cannot be the only cause because opposite effects were found within 1–2 miles of each other. While we cannot rule out other extrinsic effects such as disease, this difference in the quality of the individuals as measured by body weight may be caused by differences in the intrinsic factors of the various populations independent of the absolute density. There is no information from this study to test this suggestion. Finally, all the four island populations sampled in 1961 were undergoing Type H declines; the significance of this is not understood.

To sum up the results of analysing body weight distributions, we have seen that the peak summer was characterized by adults of high body weight, and that two patterns appeared in the decline: (1) low body weights and no recruitment of Y_1 young, in Type G declines; and (2) high body weights and recruitment of Y_1 young, in Type H declines.

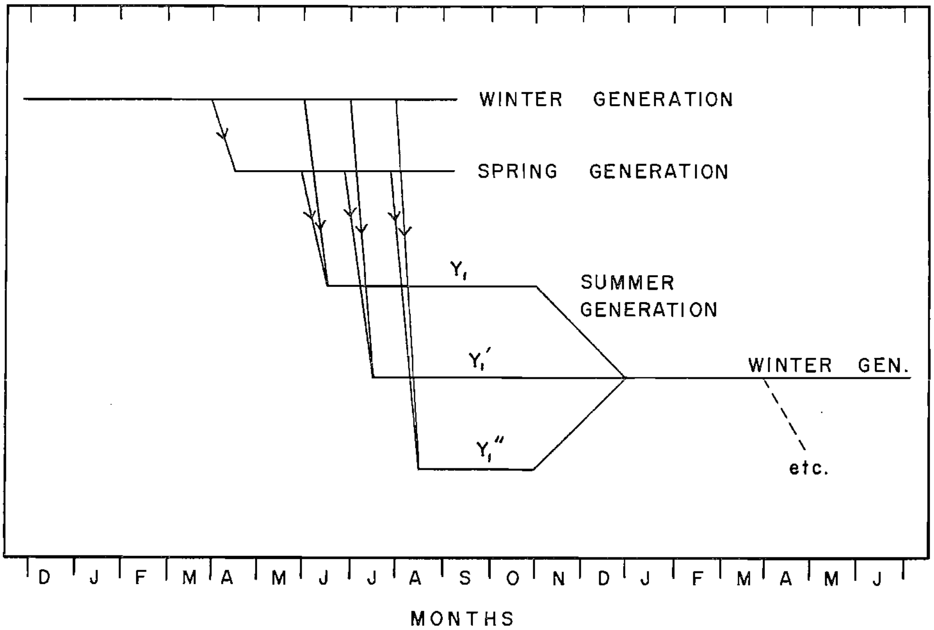

Fig. 7. Generalized annual chronology of generations and litters for *Lemmus* and *Dicrostonyx.*

Mean body weights

In computing mean body weights it is desirable to follow discrete generations so that the resulting means have a clear biological significance, rather than being a mere statistical collection of data from diverse groups of animals. Figure 7 gives a generalized chronology and classification of the litters and generations of both species of lemmings. There is no problem in separating summer-born animals from winter or spring animals, but the difficulty arises in trying to keep the spring generation (born April–May) separate from the winter generation. In *Lemmus* this difficulty arose only for the May 16–31 and June 1–15 samples for 1960; these were separated on the basis of breeding or non-breeding, the breeding animals being referred to as the winter generation. These spring animals in *Lemmus* are absorbed into the rest of the winter generation adults by the end of June and cannot be recognized as a distinct element of the samples after then.

In *Dicrostonyx* the problem is much more difficult. The spring generation appears in all four years and persists as a distinct entity even into August. Data on body weight, total length, lens weight, and reproductive condition were used in trying to separate the winter from the spring-born animals. In 1961 the two groups were easiest to distinguish because although the body weights overlapped there was a gap in the lens weights between the winter generation (born in the summer of 1960) and the spring generation (born April–May 1961). For example, in the June 1–15 sample winter animals had lens weights over 6.0 mg. while spring animals had lens weights of less than 4.0 mg. In 1960 gaps in the body weight distributions were taken as break points. In 1959 and 1962 gaps in body weight and total length distributions were mainly used for separating these groups. While there is a considerable subjective element involved in these separations (particularly for 1959), I believe the results are biologically more helpful than they would be if these two groups were mixed.

The mean body weights for adults clearly illustrate the observation that high body weights were associated with the peak summer and Type H declines. Tables 45 and 46 give the mean body weights for the winter and spring generations of *Lemmus* and *Dicrostonyx* males for 1959–62. We are mainly concerned here with the winter generation.

The *Lemmus* data (Table 45) are very clear. On the Main Study Area the peak summer of 1960 showed mean body weights about 28 per cent greater than 1959 and 20 per cent greater than 1961 or 1962. These differences are highly significant as tested by analysis of variance ($P < .01$). For Aberdeen Lake the 1960 and 1961 data are not significantly different, high body weights occurring in both years, and the 1962 weights are significantly below the 1960–1 weights ($.01 < P < .05$). The other areas sampled in 1961 all have high mean body weights except for the Prince River; in 1962 all these areas had low body weights.

The *Dicrostonyx* data (Table 46) are not so clear. On the Main Study Area the peak summer of 1960 showed mean body weights about 40 per cent greater than 1959 and 11 per cent greater than 1961 or 1962. The difference between 1960 and 1961–2 is highly significant as tested by analysis of variance ($P < .01$). For Aberdeen Lake the 1960 and 1961 data are not significantly different, as in *Lemmus*, and the 1962 weights are significantly lower than the 1960–1 weights ($.01 < P < .05$).

Growth of adult animals is mostly complete by early June in both species. Individual adults captured in the live-trapping program from June to August showed growth rates averaging about 0.2 per cent per day in both 1960 and 1961 for both species. It thus appears that the critical growth period for the adults is April and May, before the snow melts or the new season's plant growth begins.

In summary, an analysis of mean body weights for the winter generation confirms quantitatively the observation that high body weights ($\bar{x} = 70$–85 grams) were found in the peak summer on all areas and in Type H declines in 1961. Lower mean body weights ($\bar{x} = 50$–65 grams) prevail at the other times for both species.[1] Most of the growth which produces these differences occurs in April and May before the snow melts, and adult growth rates during the summer are low.

Organ weights

All organs were preserved in 10 per cent neutral formalin and weighed either on an electric balance or on a torsion balance during the winter after collection. Organs weighing more than 200 mg. were weighed to the nearest 5 mg.; organs weighing less than 200 mg. were usually weighed to the nearest 0.1 mg. All organs were cleaned of surface fat under a binocular microscope and rolled dry on filter paper before weighing. Repeated weighings indicated an accuracy of ± 3 per cent in normal weighings. Some of the larger organs were weighed fresh in the field during 1961 and 1962.

The expression of organ weights normally used by physiologists as well as most ecologists is that of milligrams of organ weight per gram of body weight. However, few workers have heeded the advice of Chester Jones (1957, pp. 6–7) that such figures may be misleading when different body-weight groups are compared. There are only two circumstances under which the above expression may be used validly: (1) if all the animals compared are of very similar body weights; or (2) if the arithmetic regression of organ weight on body weight is linear and passes through the origin. I know of no instance in which the latter is true, and the former is not true in this study.

The problem, however, still remains of correcting for differences in body weight and obtaining a measurement of organ weight which is independent of the particular body weights in the sample. This difficulty was overcome by Chitty (1961) by using standardized means (Hill, 1959). These means are calculated as follows (see Hill, 1959, Chap. 18 for details). All the data are grouped and mean organ weights for each 10-gram weight class were determined, as well as a grand mean for the whole data. The standardized mean is then obtained by the formula:

$$S = O/E \times G$$

where G = grand mean of the whole data
O = observed sample mean
E = expected sample mean
S = standardized mean for the sample

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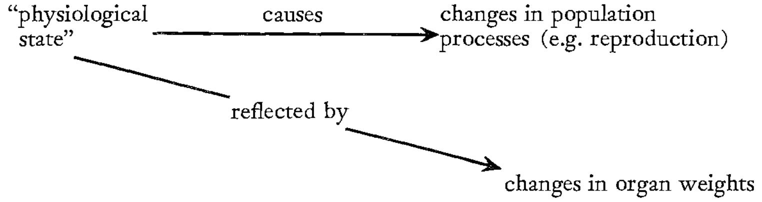
[1] Mr. S. D. MacDonald of the National Museum of Canada has kindly given me his weight records for *Dicrostonyx* from the Queen Elizabeth Islands; a peak population at Mould Bay in 1949 had high body weights (maximum, 100 grams), and a low population at Alert in 1951 had low body weights (maximum, 67 grams). He also collected *Lemmus* and *Dicrostonyx* at Eskimo Point, Keewatin, in the peak summer of 1960 and found both species with high body weights.

The observed and expected sample means are calculated in the same way as in chi-square problems. One difficulty of using standardized means is that confidence limits cannot be placed on them and no significance tests may be applied. This difficulty, as will be seen, will not affect the analysis which follows, and the conclusions reached could not be any different if we were able to apply the standard tests of significance.

The technique used by Christian and Davis (1956) and apparently in all of Christian's work is somewhat similar to the standardized mean method but the final results are expressed in percentages (i.e. by substituting X 100 for X G in the above equation). The difference is that he does not weight the means of the component body-weight groups in relation to their sample size, i.e. a weight group with only one animal in it contributes as much to the mean as a weight group with 25 animals in it. These means are thus less reliable than true standardized means which are used in this study.

Over 7,500 organs from about 3,000 lemmings were weighed in the course of this study in an attempt to find a physiological index which is correlated with the previously described population processes. The idea that certain physiological changes in individuals cause profound changes in population processes is very widely held, particularly because of the work of Christian (1950, 1957, 1961). The assumption is that each individual has a certain internal physiological state which can be conveniently measured by weighing one or more of several internal organs such as the adrenals, testes, and spleen. The further assumption is made that this physiological state causes changes in population processes. Thus we have diagrammatically:



Now it is of course possible that the real "physiological state" is not measured by these organ weights. But the point here is that many workers do rely on organ weights for evidence (e.g. Christian, 1961, pp. 439–40), and hence we may begin by using this assumption.

Table 47 gives the mean standardized organ weights for *Lemmus* males, and Table 48 gives the same data for *Dicrostonyx* males. Data for females are not given, even though they have been analysed in detail, because the conclusions merely duplicate those from the male data. The organs included in these tables are adrenals, testes, and spleen. All adrenal and testes weights given are paired weights. Fat indices are also given and will be discussed later. Two separate standardizations were performed for each organ (winter and summer generations) because the organ weights in each of these groups tend to be very different. For this reason comparisons should be made down the columns only and not across the rows of these tables. To correct to some extent for variation due to reproductive status, I have included only fecund males for the winter generation figures, and only non-fecund males for the summer generation figures. The groups omitted by these restrictions are small and discontinuous in time.

Adrenal gland

It is difficult to see any consistent relationship between the adrenal data and the population changes. There is a seasonal change in adrenal weights, rising to a peak in June or July, similar to that described by Chitty (1961) for *Microtus agrestis* and Christian (1962) for *Marmota monax*. At one point or another almost all the means overlap and thus it is not possible to say categorically that any one summer showed higher or lower adrenal weights than another summer. However, some years tend to be higher or lower than others, and we may broadly classify the years as follows:

	Summer				*Winter*
	1959	*1960*	*1961*	*1962*	*1960–1*
Lemmus					
Adult males	low	medium	low	high	—
Young males	high	low	high	high	high
Dicrostonyx					
Adult males	low	low	high	low	—
Young males	low	low	low	low	high

The mean difference between "high" and "low" adrenal weights was 5–14 per cent for the summer adults, and 23–33 per cent for the *Lemmus* summer young. High adrenal weights were found in all groups in the winter of 1960–1, but unfortunately comparative data from other winters are not available. There is a clear relationship of summer adrenal weights to the cycle if we look at single groups such as the *Dicrostonyx* adult males. These relationships, however, are not consistent between groups, as can be seen, for example, by comparing adults and young. Two conclusions follow from these data: (1) summer adrenal weights do not show a consistent relationship to the phase of the cycle; and (2) winter adrenal weights seemed high in 1960–1 relative to the summer weights.

This analysis of adrenal weight changes may be criticized because it involves no statistical tests, since a basic deficiency of the standardized mean technique is that standard errors cannot be estimated. It is difficult to see what additional light would be thrown on the relationship between adrenal weight changes and the cycle by any statistical tests of significance. The fact is that changes in population size of 10- to 50-fold are not reflected in consistent adrenal weight changes either within sex and age groups or between these groups, and thus significance tests are superfluous.

Testis

There is some correlation between testes weights and population density changes, which shows up as follows:

	Summer			
	1959	*1960*	*1961*	*1962*
Lemmus				
Adult males	high	low	high	low
Young males	high	low	low	high
Dicrostonyx				
Adult males	high	low	low	high
Young males	high	low	low	low

The mean differences between "high" and "low" testes weights was 14–21 per cent for the summer adults and 49–78 per cent for the summer young. Testes weights were highest in both species during 1959. The peak summer was characterized by low testes weights in all groups, but in the decline *Lemmus* adults showed a different trend from the others. The results for the young agree with those discussed previously regarding reproduction. Young male *Lemmus* did not mature either in 1960 or 1961. Young male *Dicrostonyx* did not ever seem to mature in their first summer; nonetheless they seem to show the same type of changes in testes weights (cf. August weights) as do the *Lemmus* young. Because this inhibition of gonadal development in young male lemmings occurred in the summer of decline as well as in the peak summer, density *per se* cannot be the factor directly involved here, but rather the important variable must be capable of acting at very low densities in the decline.

Spleen

The spleen in lemmings varies considerably in size, weighing from 5–600 mg. in *Dicrostonyx* and 5–1,200 mg. in *Lemmus*. The very heaviest spleens are found only in midsummer animals (late July–August) and there is thus a very strong seasonal variation in average weights. There was little difference in *Lemmus* from 1959–61; the 1962 spleen weights were the highest. In *Dicrostonyx* spleen weights were low in 1959 but high in all the other years. Thus spleen weights showed no clear relationship to the cycle in numbers. The striking seasonal change in spleen size is not understood but may be associated with blood parasites transmitted by mosquitoes during the midsummer insect season (Baker, Chitty, and Phipps, 1963) or by mosquito or other ectoparasite bites directly (Chitty and Phipps, 1960). This hypothesis is consistent with the observation that *Lemmus* has a greater spleen enlargement than *Dicrostonyx*, because *Lemmus* lives in the wetter places where mosquitoes are more abundant.

To sum up, summer adrenal and spleen weights showed no clear relation to the cycle in numbers. Winter adrenal weights were high in 1960–1 but comparative data from other winters are lacking. Testes weights tended to change systematically over the cycle, being high in 1959, low in 1960, and somewhat variable in 1961 and 1962. All these organs showed a seasonal cycle of weight changes independent of the population cycle.

Fat changes

The amount of fat stored by lemmings may be used as another index of general physiological condition. This was assessed by an arbitrary fat index scale of 1–5, 1 being the value for an animal with no fat and 5 for a very fat animal. This index was estimated purely subjectively by observing the amount of fat on the skin, between the shoulders, around the hind legs, and around the viscera and gonads. Animals with no fat to be seen (except around the gonads where it is almost always present) were classified as fat index 1. The skins of animals of fat 3 or more were always greasy and had to be wiped or scraped after drying. These data on fat changes were analysed in the same way as the organ weight data.

Fat index data for *Lemmus* and *Dicrostonyx* males are given in Tables 47 and 48 along with the organ weight data. The fat index shows a seasonal variation, being at its lowest in midsummer when breeding is intense and highest in the winter (particularly fall and spring). If we compare the spring and summer data of the different years, there does not seem to be any difference between the years 1960–2 in this index. In particular, the spring and summer of 1961 have fat indices equal to or greater than either 1960 or 1959. There is thus no indication of undernourished animals in the spring of the decline. Low fat indices may have prevailed in the mid-winter of 1960–1, but data from the previous winter are not sufficient for a good comparison. The July and August 1959 indices were higher than any other year for the winter generation animals.

Social relationships

Very little is known about social relationships in natural populations of cyclic rodents. Some indirect evidence and a few observations of social relationships will be noted here with the clear understanding that they are very inadequate.

In early June 1960 both species of lemmings were extremely hostile in behaviour, at least towards humans. On several occasions while walking across the tundra, I encountered loud squeaking lemmings (both species). Often they were heard squeaking long before I could actually see them (in one particular instance squeaking began when I was 20 feet away). As mentioned previously, lemmings caught on the ice in this spring of 1960 were also very aggressive. This type of behaviour contrasted sharply with their behaviour later in the summer when they tried to hide as soon as I approached. Collett (1895) and Curry-Lindahl (1961) also report this curious behaviour for the Norwegian lemming. The significance of these observations is not known.

Some crude measure of aggressive behaviour may be obtained by the incidence of wounding in a population (Southwick, 1958). All lemming skins collected in this study were examined and classified on an arbitrary scale as follows: no recent wounds or obvious scars showing on inside of skin; light wounds; moderate wounds; or severe wounds. Skins were selected and set out as standards for each of these four categories, and these were constantly used for comparisons. All the classification for 1959–61 was done in a two-week period to minimize the subjective element.

Tables 49 and 50 give the incidence of wounding shown on skins for *Lemmus* and *Dicrostonyx* males over the cycle. Differences in the amount of wounding between years were tested by chi-square for June, July, and August separately.

In both species the peak summer of 1960 had a significantly higher amount ($P < .01$) of wounding in June, the time before the summer young have appeared. In spite of very large differences in density between years, the amount of wounding found in July and August was not markedly different. This implies that fighting may occur even at very low densities. Both *Lemmus* and *Dicrostonyx* showed the same general patterns, although there was less wounding shown on *Dicrostonyx* skins than on *Lemmus* skins.

Only one sample of *Lemmus* summer young contained both mature and immature animals, and the data on these are as follows:

	Sample size	*Per cent showing wounds*	*Mean body weight*	*Range of body weights*
August 1959				
Immature males	11	9.1	21.7 gm.	13.5–30.8
Mature males	8	75.0	33.5 gm.	27.8–38.5

These differences in wounding are significant (chi-square for independence = 6.04, d.f. = 1, .01 < P < .05). Since the mean body weights of these samples differ considerably, some of this difference in wounding may be explained on this basis. However, this is probably not the entire explanation because in 1960 and 1961 none of the samples of immature animals with as high or higher body weights showed as much wounding as this mature sample from 1959. This suggests that it was the maturation of summer young males during their first summer which led to the great increase in the amount of fighting in the August 1959 *Lemmus*. It also suggests that a function of the observed inhibition of maturation of males in the peak and decline summers is to prevent a considerable amount of fighting in these populations. Summer young *Lemmus* females did not seem to show this difference, for a July 1960 sample of 18 immature and 14 mature females had no wounds. However more positive evidence is needed on this point.

Indirect evidence from snap trapping suggests some sort of antagonism between old and young *Lemmus* during the summer of 1960. Given the August 1960 snap-trapping data, we may make the null hypothesis that the proportion of adult and young *Lemmus* in the habitat types is the same. The relevant data are as follows:

	Lichen-heath	*Heath-sedge and h-s hummock*	*Sedge hummock*	*Sedge marsh*	*Totals*
August adults	0	21	20	9	50
August young	23	188	102	53	366

If young animals tend to disperse from the densely occupied habitats to the less densely occupied ones, the proportion of young in the poorer habitats (i.e. dry for *Lemmus*) should be greater than that of adults, and conversely for the better habitats. These data were tested by chi-square and the null hypothesis was not rejected, although the result is close (chi-square = 6.49, d.f. = 3, .05 < P < .10). Thus although the data suggest fewer young in the sedge hummock and more young in the lichen-heath habitats, compared with the adults, the differences are not statistically significant.

It is clear that the data available on social relationships is very meagre and almost all indirect. We know that at times lemmings were very aggressive, that there were large changes in the amount of wounding shown on skins, and that there may have been some antagonism between old and young *Lemmus*. Taken together this is enough to point out that behavioural changes represent the largest gap in our knowledge of the intrinsic factors operating in the cycle.

DISCUSSION

The amount of literature published about "cycles" is truly voluminous, but the proportion which presents original thought or solid evidence is very low indeed. In this discussion I will first give a brief historical review and will then attempt to integrate the main changes discussed in the previous sections with the results of other workers. Finally, I will consider the current theories about microtine cycles and their status in the light of these data from lemmings.

Historical approaches and background

The history of cycles is not very long in terms of years, but two general approaches to the problem can be recognized. The original observation (Elton, 1924) was that animal populations fluctuated in size and in some species there appeared to be some regularity to this change. Given these initial data, some workers emphasized the regularity of the cycles and concentrated much effort on an attempt to determine the precise period of these cycles for each species. An example from this group is Siivonen (1948). Another approach emphasized "cycles" as a particular problem of population regulation and concentrated study on the factors operating on the population to cause these increases and declines. A blending of both these approaches is illustrated by the work of Elton (1924, 1931, 1942).

The first approach was challenged by Palmgren (1949) and Cole (1951, 1954 b, 1958) who demonstrated that "cycles" similar in length to those found in nature could be interpreted as essentially random fluctuations with some serial correlation between successive years. It is essential to understand Cole's argument or we risk a complete misunderstanding of what he has shown. Given a set of "cyclic" data on population size for any animal, Cole has shown that you can produce a similar "cycle" in random numbers by introducing some serial correlation. Now this suggests that, given only these data, we could interpret the "cycle" as a random fluctuation, and this would be the simplest interpretation if no other data were available. In other words, if we wish to understand "cycles" we must study something more than changes in numbers. Cole (1958, p. 646) states: "We should seek to understand the causes of each case of population growth and decline instead of looking for some hypothetical and cryptic phenomenon capable of generating cycles".

The second approach is the one now emphasized by a majority of workers on cycles. Attention has turned away from the periodicity and toward the population aspects of cycles. A supposition of this approach is that the problem of cyclic length will be solved once the mechanism of these cycles is understood. In this study I have followed the second approach.

Much of the difficulty of talking about "cycles" arises because several meanings are given to the term (e.g. Slobodkin, 1961), giving rise to much confusion. We must therefore attempt to delimit the particular phenomenon to be discussed here from all other "cycles". Chitty (1952, 1960) has discussed this problem and claims that a specific type of cycle may be recognized in microtine rodents. Using this approach, we may adopt the following definition for the particular type of cycle studied here: *a cycle is a typically 3- to 4-year fluctuation in numbers in microtine rodents characterized by high body weights of adults in the peak summer.* I do not propose this as a definition everyone is supposed to accept, but I am merely stating the way I shall use the word *cycle* in this paper. Chitty (1960) defined the problem somewhat more widely and includes this definition as only a particular instance of the more general problem of why populations fail to maintain a high rate of increase.

I shall assume, until there is evidence to the contrary, that these cycles (as defined above) are a single class of events and have a common explanation. The two facts (1) that they are usually 3- to 4-year cycles and (2) that high body weights seem always to be associated with peak populations present a strong argument for this working hypothesis. Furthermore, this is a sound approach to the problem in the present state of knowledge. Another approach is to begin with the assumption that all these rodent cycles have a different explanation. This implies that each cycle is a unique, local event and that successive cycles in the same locality or different localities cannot be compared, and consequently this makes it impossible to test hypotheses or to predict future phenomena. Again, a limited number of different types of cycles based on, for example, groups of species or climatic zones could be distinguished. I have not used this approach because I do not feel that it is the most fruitful one at present. I am thus interested primarily in the things common to all cycles and only secondarily in those things restricted to a given area or circumstance.

However, I do recognize that there is no guarantee that these cycles are a single class of events. It is possible that the class is larger than I have indicated, perhaps including the gallinaceous birds and the snowshoe hare. But it does not seem to me to be prudent to extend it beyond the limits set by the body-weight characteristic until more evidence becomes available. It cannot, I feel, be restricted to include less than that mentioned above.

I suggest therefore that these cycles as defined above seem to represent a single class of events and have a common explanation. Thus a single explanation may be sought for lemming cycles at Baker Lake, in Alaska, Scandinavia, and Russia, and vole cycles in England and elsewhere. This is essentially the same belief expressed by Chitty (1952).

Reproduction

Several authors have described winter breeding in lemmings. Thompson (1955 a) working in northern Alaska on *Lemmus trimucronatus* found that winter breeding occurred only during the period of increase which he claimed occupied two winters, although evidence for breeding during the second winter is not very conclusive (as we have seen, lemmings may breed under the snow every spring). Dunaeva and Kucheruk (1941) found winter breeding in both *Dicrostonyx torquatus* and *L. sibiricus* in Russia during the period of increase. Sutton (Sutton and Hamilton, 1932) found winter breeding in both *D. groenlandicus* and *L. trimucronatus* on Southampton Island during the period of increase. Nasimovich, Novikov, and Semenov-Tyan-Shanskii (1948) believed that winter breeding of the Norwegian lemming was limited to the phase of increase. Recently, Koshkina and Khalansky (1962), Curry-Lindahl (1961), and Koponen, Kokkonen, and Kalela (1961) have reported winter breeding in the Norwegian lemming during the period of increase, and Koshkina and Khalansky (1962) found no winter breeding in the winter following the peak. Thus it is clear that the only reports of winter breeding in lemmings are from the period of increase. However, during the period of low numbers it would be very difficult to detect winter breeding. In this study breeding was detected in *Dicrostonyx* in the low winter of 1961–2. The suggestion is that winter breeding is very pronounced in the phase of increase and absent in the decline, but may also occur in the period of low numbers in some circumstances.

There is good evidence that the summer breeding season in the peak year is shortened in lemmings, compared with the increase or decline summers. Thompson (1955 a) reported this for *Lemmus trimucronatus* in Alaska. Dunaeva and Kucheruk (1941) reported that breeding had ceased by August in the peak summer for *D. torquatus.* Nasimovich *et al.* (1948) and Kalela (1961) both found this shortened summer breeding season in peak populations of *L. lemmus.* Wildhagen (1953) did not report either winter breeding or a shortened summer breeding season in the peak year for *L. lemmus* in Norway; his samples however are very scattered and discontinuous.

The available data on litter-size changes and pregnancy-rate changes over the lemming cycle are very scarce. Thompson (1955 a) reported no change in litter size, and his data seem to agree with what was found in this study, and do not appear to bear out his conclusions that reproduction proceeded at a reduced level in summers of low population density and reached great peaks of intensity in the summers of high densities. Unfortunately his data are presented in such a way that no statistical assessment or detailed comparisons can be made. Koshkina and Khalansky (1962) reported that reproduction was most intense during the increase and was reduced in peak and declining populations, but their data on litter size do not support this conclusion.

There is also little information from these other lemming studies on the question of changes in the age or weight at sexual maturity over the cycle. Nasimovich *et al.* (1948) state that most of the summer young females do not mature in the peak year; nothing comparable is said about young males. Wildhagen (1953) states that both male and female *L. lemmus* become fecund during their first summer in the peak year, but his criterion of maturity for the male has been questioned by Newson (pers. comm.), and furthermore his samples are very discontinuous.

Considering other cyclic mocrotines besides lemmings, we find a close parallel in Kalela's (1957) study of *Clethrionomys rufocanus* in Finnish Lapland. From his data on the reproduction of this cyclic vole he concluded: (1) in peak populations nearly all the summer young males and some of the summer young females failed to mature; (2) a shortened summer breeding season occurred in the peak and decline years; and (3) there was no change in litter size over the cycle. The similarity of these results to those given previously for this study is quite impressive.

Chitty (1952) reported a shortened summer breeding season in the peak year for *Microtus agrestis* in Wales. Godfrey (1953) suggested that a delay in reaching maturity for *M. agrestis* young may occur only in years of peak population. Stein (1957) found no change in litter size over the cycle for *M. arvalis* and a decrease in the percentage of young females maturing during the peak summers. Adams, Bell, and Moore (quoted by Christian, 1961) found in *Microtus montanus* that breeding ceased early in the peak summer and apparently most of the summer young males did not mature either in the peak or in the decline. Zejda (1961) reported a shortened peak breeding season and a failure of summer young to mature in the peak summer for *Clethrionomys glareolus* in Czechoslovakia.

These observations suggest that cycles of the type defined previously are associated with a fairly specific set of reproductive changes. It is important to look for contrary instances to see how far this generalization holds. Hamilton (1937 a, 1941) reported an accelerated breeding rate, increased litter size, and longer reproductive season in increasing and peak populations of *M. pennsylvanicus.* No statistical data were given for the litter size changes so it is not possible to tell if they are significant. Also, Hamilton does not discount possible body weight or parity effects and his increased litter sizes might be explained by the heavier animals in his high populations (1937 b). He found winter breeding only in the peak year and no curtailment of the peak summer breeding season. His data also show an increase in the amount of post-partum breeding in the peak year. Hamilton's observations are at complete variance with those described above for lemmings, and they have never been repeated.

Hoffmann (1958) studied reproduction and mortality in *M. montanus* and *M. californicus.* He defined the phases of the cycle in terms of changes in fall population densities, and a completely different pattern is seen if we consider changes in his spring densities, which Chitty and Chitty (1962 a) considered to be the indicator of cyclic phase. From this point of view Hoffmann has no data for the period of increase in spring densities for either species or for the period of decline for *M. californicus,* and his data essentially refer to populations at peak phase only. He found no change in age at maturity or incidence of post-partum breeding over the period studied and only minor changes in litter size and ovulation rate. He concluded that reproductive changes were a relatively minor part of the cycle and that the important changes must have been in mortality. This is the exact antithesis of Hamilton's conclusions, but part of this apparent conflict of views may arise because Hamilton's data cover the period of increase and Hoffmann's do not.

Much more critical data on reproduction in relation to cyclic events is needed. There is clear evidence from the more northerly lemmings and voles that at least some cycles are accompanied by striking changes in the length of the breeding season and age at maturity. We must now ask if this is a universal characteristic of these cycles. Hamilton's (1937 a) and Hoffmann's (1958) data suggest that it is not and that other patterns are possible. If this is true, how and why do these patterns differ from one another?

What could have been the cause of the reproductive changes observed in this study? Let us first consider extrinsic factors. It seems unlikely that changes in the food supply were the direct cause of these reproductive changes. Maynard and Loosli (1956, p. 387) point out that the nutritive requirements of breeding females are greater than those for males, and yet in this study males were affected much more than females (cf. Table 21), which suggests that the factors involved are not nutritional. Mild winter weather in 1959–60 may have been necessary for the extensive winter breeding to occur but there was no evidence that it was sufficient (cf. 1961–2 winter) to cause the increase. There was no evidence that any climatic factor could have caused the midsummer breeding changes found in the peak summer or the summer of decline. If we turn to the intrinsic factors, there is no evidence that these reproductive changes were a function of density *per se* because they persisted into the decline in some cases and affected the sexes differentially. There is also no evidence that these reproductive changes were caused by stress as defined by Christian (1959); and, although one can obtain reproductive changes by stressing animals, there are other ways to do this as well (e.g. Parkes and Bruce, 1961), and we are thereby no closer to knowing what happens in the field. Nevertheless, this is not to say that the reproductive changes observed in this study do not have a physiological explanation. I conclude that these reproductive changes were not caused primarily by extrinsic factors or by stress or density *per se*, but rather were caused by some intrinsic change in the population, probably associated with intraspecific strife.

To sum up, at least some cycles are accompanied by a set of specific reproductive changes involving winter breeding during the increase, a shortened summer breeding season at the peak, and a lack of maturation in young males and to some extent in young females during the peak summer. The available evidence suggests that while this is a common pattern it may not be found in all cases, and it is important to seek information on contrary instances such as described by Hamilton (1937 a). The reproductive changes described here cannot be explained by extrinsic factors but seem to be caused by intrinsic changes in the population.

Mortality

Very little work has been done on quantitative mortality measurements for cyclic microtines. This is important because there is a tendency to disregard variables which have not been studied intensively, or else to put forward reasonable but quite unverified explanations for the cyclic mortality which would not be tenable if quantitative data were available.

Partial prenatal mortality does not seem to play a necessary part in the cycle. Kalela (1957) reported no obvious change in prenatal mortality for *Clethrionomys rufocanus*, and Hoffmann (1958) found only a slight change in partial prenatal mortality between peak and declining populations of *Microtus montanus*. This agrees with the results of this study. Information on total litter loss is almost completely lacking for cyclic microtines because this type of loss is difficult to measure. We may conclude that partial prenatal mortality may show small changes over the cycle; whether there is some change in total litter losses, particularly among young animals (as shown in this study), is not yet known. Total litter losses among adults are probably not significant (Hoffmann, 1958; this study).

Hoffmann (1958) found that weanling and juvenile mortality increased considerably in *M. montanus* during a decline, and he suggested that this change was the key to the decline. Godfrey (1955) found that high mortality of juveniles was associated with the decline of two *M. agrestis* populations, and juvenile male mortality was also high in the peak summer. Elton, Davis, and Findlay (1935) have recorded another instance of high juvenile mortality in a decline of *M. agrestis*. Chitty (1952) found that high juvenile mortality was associated with peak and declining populations of the same species.

The results of this study agree with those on *Microtus* and indicate that a high juvenile mortality rate occurred at least in all the declining populations which showed no recovery (G). Juvenile mortality in those declines which showed some recovery (H) must be less than in Type G declines, but no quantitative data are available. Some workers have found high juvenile mortality also in the peak summer, but there was no clear suggestion of this in the present study, and this may not be a constant feature of the cycle.

Chitty (1952) reported increased adult mortality in the spring of the decline, and the data of Godfrey (1955) suggest the same thing. This increased mortality however may be confined to a short period in the spring when breeding begins (Chitty and Chitty, 1962 a). Very few extensive measurements of adult mortality rates during the cycle have been made (Leslie *et al.*, 1953; Chitty and Chitty, 1962 a).

We may conclude from the above data that juvenile mortality changes are important and exceed any changes in adult mortality which may occur over the cycle. Studies on non-cyclic mice by Bendell (1959) and Martin (1956) also pointed to the importance of juvenile mortality in determining density changes, and Lack (1954) concluded that in all animals the death rate is higher in the juveniles than in the adults. We do not yet know the reason for this high juvenile mortality in the decline.

Migrations

Migrations of lemmings have been reported from Scandinavia in particular but also from various parts of North America. In view of the preoccupation of many people with these migrations it may be profitable to enquire how these migrations differ from the spring unrest and wandering found at Baker Lake in 1960.

Thompson (1955 c) has described a brown lemming emigration at Point Barrow, Alaska that seems to resemble closely my observations. For about six days at the beginning of June of the peak summer, when the snow was melting and summer breeding had just begun, individual lemmings moved haphazardly through the camp and out on to the sea ice. Only a small percentage of the total population took part in this emigration. Thompson noted that this emigration was very different from the mass migrations of Scandinavian lemmings.

The only report of a mass migration of lemmings in the North American Arctic is that of Gavin (1945); perhaps local conditions exaggerated the kind of movement described by Thompson. There is no question that lemmings do move individually on sea ice, lakes and the land during the spring melt-off in peak years and that they may move quite long distances on ice. There is no question that one may see ten or fifteen lemmings at a time on the bare patches of ground during the melt-off and that sled dogs may gorge themselves on lemmings while travelling across country. But these are not solid masses of lemmings marching in a particular direction. I have been told by people at Baker Lake that during the 1960 spring there were "millions" of lemmings marching across the tundra toward Hudson Bay, and that there were "thousands" of lemmings all over the lake ice when in fact fewer than 50 lemmings were actually seen by the persons involved. The Eskimos of the Barren Grounds have no legends of mass lemming migrations and it is difficult to believe that they would overlook such an event if it ever occurred. I therefore do not believe that mass migrations of lemmings occur in North America.

Let us now look at the Scandinavian lemming migrations. Collett (1895, 1911; summarized by Elton, 1942) has given one of the most extensive descriptions of these movements. The evidence for migrations which he gives seems to be as follows: (1) lemmings are found in the lowlands in great numbers during some years; (2) individual lemmings may appear on city streets, swimming in the ocean, or other abnormal places during the peak years; and (3) various observers report "migrating swarms". But it has never been shown that lemmings are absent from the woodland and lowland zones as a normal habitat even in low years, and yet the whole argument that a migration has occurred rests on the truth of this assumption. Collett (1895, p. 17) states that one rarely sees lemmings even in the best habitats during normal years, and yet the bulk of the evidence that lemmings do not inhabit the woodland and lowland zones is that they are never seen there. Again there is no doubt that individual lemmings do move into abnormal places during a peak year such as Collett describes. Collett (1895), portraying the type of movement, states:

> "They are not sociable in the sense of several individuals deliberately joining company for long distances. . . . Therefore they seldom, if ever, advance in close ranks as generally depicted in drawings. . . ." (p. 43)

and again (1911):

> "They migrate chiefly by night, but also partly by daylight, always singly or some few near together, never in close formation. . . ." (trans.)

If this is true, then how do we decide when a "migration" is occurring? There is not a single quantitative observation on the extent of these movements. Kalela (1949) states that the Norwegian lemming extended its range by more than 100 kilometres over three subsequent cycles, but there is no evidence why the simpler explanation of permanent low density populations in the "invaded" areas is not acceptable. Nasimovich *et al.* (1948) recorded the following observations on Norwegian lemmings:

> "[In spring the] lemmings ran singly on the ice, never forming groups, and only in a few cases were more than three animals seen simultaneously. . . . On an excursion on the ice of [a lake] from end to end (about 18 km.) 20–32 running lemmings were counted. Thus the spring migrations observed by us are far different from the picture of mass 'flows' described by other writers. . . ." (trans. p. 27)

Recently Kalela (1961) and Koponen *et al.* (1961) have discussed lemming migrations in northern Lapland. They distinguish (1) spring migrations which go on for about one week, and (2) fall migrations which may go on for two or three months. Koponen *et al.* (1961) have described a spring migration on lake ice which was extremely similar to the movements described by me and by Thompson (1955 c). Each lemming on the ice moved independently, and only very small numbers of lemmings were involved. The beginning of these movements coincided with the start of the spring breeding season and seemed to be associated with a seasonal change of habitat. Kalela (1961) and Myllymaki *et al.* (1962) have described fall migrations associated with a seasonal change of habitat. Not a single animal was marked and recaptured in this work, and all the evidence for migratory movements consists of the facts that (1) lemmings were found in farmyards, swimming in lakes, and other unusual places at the peak, (2) no lemmings were *seen* in an area at one time and at a later date some lemmings were *trapped* there, and (3) observations on a path and a waterway over short intervals have shown a predominance of movements in one direction compared with the other (Myllymaki *et al.*, 1962). No one doubts that individual lemmings do wander into strange places at times of peak densities, and no evidence is presented why local reproduction along with movements of several hundred metres at the most between seasonal habitats could not account for most of the changes observed. The apparently directional movements reported by Myllymaki *et al.* (1962) are based on so few observations that they cannot be considered as indicating that a directional migration was in fact occurring (cf. for example, Pearson, 1960, Fig. 19, for runway use in a "non-migratory" situation), and are viewed simply as a sample of the local movements which occur at high densities. It is indeed surprising to find that there is no objective evidence for mass migrations of the Norwegian lemming. Until evidence to the contrary becomes available, it seems best to regard mass lemming migrations as a fiction and to confine our attention to the individual movements found sometimes at peak densities.

Thompson (1955 c) states that the mass unrest in the spring of the peak year at Point Barrow was probably caused by changes in available food and cover and seemed to have a very minor effect on local population densities. He does not consider the fact that this unrest marks the onset of summer breeding. The sudden environmental changes associated with the melt-off may not even be a necessary cause of this unrest, because the same type of shuffle is also found in voles at the start of summer breeding (Chitty and Phipps, 1961). It would be difficult of course to find a natural situation in the lemmings to test this hypothesis that the onset of summer breeding is a sufficient cause of the mass unrest observed, and so we must let the matter stand for the moment.

Weather and synchrony

The problem of synchrony of cycles over large areas of country has long intrigued workers. I do not propose to discuss any of the cosmic theories that have at one time or another been put forward to explain synchrony. Weather seems to be the only reasonable variable which could account for this synchrony. Thus an attempt must be made to discover what effect ordinary weather phenomena, such as deep snow covers, warm springs, and wet summers, have on reproduction and mortality of cyclic animals.

As Chitty (1952, p. 540) has pointed out, if everything about a cycle in numbers was explained by an intraspecific process (or, for that matter, by the food supply hypothesis), we would expect non-synchronous fluctuations, which is not what we observe at all. Thus weather must play a necessary part in these cycles. It seems clear at the other extreme that weather changes cannot be a sufficient cause of the cyclic increase or decline because we would not normally get 3- to 4-year cycles if this were true (assuming there are no weather cycles of this periodicity). We conclude that weather changes must be a necessary cause of synchronous increase or decline or both in these cyclic species but cannot be the entire cause.

Shelford (1943) concluded that *Dicrostonyx* populations at Churchill tended to increase with average or above average snowfall which gave protection over the entire winter and with warm temperatures in July and August, and tended to decline over cold winters with little snow. It is clear from his data, however, that weather changes alone were probably not responsible for the increases or declines observed because some favourable winters were not accompanied by increases and at least one favourable winter was followed by a decline. Collett (1895) pointed out that spring and summer weather need have little effect on *Lemmus lemmus* populations. The suggestion, therefore, for lemmings is that summer weather normally has little or no effect on the cycle, but that winter weather may be a partial cause of the increases and declines.

Chitty (1952, 1960) and Chitty and Chitty (1962 a) have reported instances of asynchrony in populations very close to each other and concluded from this that bad weather alone was not sufficient to cause a decline in *Microtus agrestis* populations. There are few other reports of populations in the same locality fluctuating out of phase such as Chitty found. Pitelka (1961) reports some instances from northern Alaska of asynchrony, but it seems clear that it is not easy to find these, and the areas involved seem to come back into phase rather quickly.

Pitelka (1957) has discussed some aspects of regional synchrony in northern Alaska. He has concluded (p. 85) from the available data that the short-term cycle is not a normal characteristic of tundra microtines everywhere, and that cyclic fluctuations among several microtines in the same area are not typically in phase. Now it is probably true that very strong cycles such as occur at Point Barrow do not occur in the areas more toward the interior of Alaska, but this does not mean that the same phenomenon may not be occurring there to a lesser extent. In other words, the absolute densities at the "peak" and the "low" may be very different from area to area (this is one problem to be explained) while the same cyclic process may occur in all these areas (and this is another problem). To map the extent of cyclic "highs" by means of aircraft observations on the abundance of predators and drifted winter-cut vegetation, such as was done for northern Alaska, seems to me to miss the whole point at issue. If we applied this same technique to the Canadian Barren Grounds we would conclude some very misleading things about cyclic "highs" (i.e. that the lemming cycle was confined to a very small part of the total area, in habitats of very thick marshy vegetation), and yet the vegetation of the Foothills sector of northern Alaska (Britton, 1957) is rather similar to that of the Barren Grounds. Even casual observations on the ground can be very misleading in these respects. It seems premature to decide whether cycles are or are not characteristic of tundra microtines everywhere. However, we must look for instances of non-cyclic populations as it would be most interesting to compare this type of population with a normal cyclic population.

A second problem regarding synchrony treated by Pitelka (1957) is whether sympatric microtines cycle in phase. Elton (1942, p. 439) stated that both species of lemmings probably fluctuated in phase. Watson (1956, p. 295) believed that when *Lemmus* and *Dicrostonyx* were sympatric they tended to fluctuate in phase, although this synchrony was never exact. The data given in this paper support this belief. No intensive work has yet been done on areas where three or more cyclic microtines commonly occur.

The role of weather in cyclic fluctuations remains very poorly understood, and this generalization probably applies to almost all animal populations

(Andrewartha and Birch, 1954). We cannot study a natural population in the absence of weather and we have not yet learned to set up laboratory populations which are comparable to field populations. It is certainly possible to ascribe almost all population changes to weather changes by *ad hoc* hypotheses (e.g. Schindler, 1960), but this hardly furthers our understanding of the changes. To date the only plausible explanation of the role of weather in promoting synchrony is that of Chitty (1952, 1955 b, 1960) which is illustrated in a model by Leslie (1959). Chitty postulates that the effect of weather on a population will be determined in part by the past history of the population. In this way, for example, a mild winter would accelerate the increase of a population which was low, and retard the decline of a population already at a peak, thus tending to bring the populations into phase.

Predators

Very few workers today support the idea that the cycle is caused by predators (Lack, 1954, p. 213; Pitelka *et al.*, 1955). There is no doubt that under certain conditions predators do kill many lemmings, and Pitelka (1959) believes that they may dampen the fluctuations of the lemmings at least in northern Alaska. While it is reasonable to suppose that predation might alter the length and pattern of the cycle, a sharp spring decline in *Lemmus* occurred in 1960 in this study in the virtual absence of predators; similar spring declines were described by Thompson (1955 a) and Pitelka (1958) and attributed to predators.

Disease and parasites

Elton (1942, p. 201) and Chitty (1954) have shown that disease cannot be regarded as a sufficient cause for a decline in numbers. Disease is believed to be a local factor of variable intensity and occurrence and not an essential part of the cyclic process. Nothing from this study opposes these ideas.

Body weight changes

High body weights in the peak year have been described by Chitty (1952) for *Microtus agrestis*, Zimmermann (1955) and Stein (1957) for *M. arvalis*, Thompson (1955 a) for *Lemmus trimucronatus*, Kalela (1957) for *Clethrionomys rufocanus*, Stein (1956) and Zejda (1961) for *C. glareolus*, and by this study for *L. trimucronatus* and *Dicrostonyx groenlandicus*. It is important to enquire why this weight change occurs.

A change in mean body weight of adults may be produced in two general ways: (1) by a change in the growth rate of individuals; or (2) by a change in the normal age class structure of the population. The first would be a real effect, the second a statistical effect. Zimmermann (1955) believed that these weight changes did not represent mere changes in the proportions of the age classes but were partly caused by changes in the growth rate of individuals. He states that probably the same extrinsic factors cause the density changes and the growth changes (e.g. favourable weather). Stein (1956) found that the lower age groups were missing from peak and declining populations of *C. glareolus* in Germany and this caused the mean body weight in the spring to be greater in peak populations. He believed that these changes were not produced by extrinsic variables which caused a change in growth rate, but rather that they were due to a selective elimination of the younger animals by some form of intraspecific strife (i.e. that the effect was statistical). Zejda (1961) offered a different interpretation of Stein's results based on his own work on *C. glareolus* —that these lower age groups were missing because of the shortened reproductive season in the peak year. Thus populations descended from normal spring to fall breeding seasons would have on the average normal body weights, but those descended from curtailed summer breeding seasons would include only the larger spring animals and not the smaller fall animals, and those from which the spring litters are eliminated would produce on the average below-normal size animals.

It is difficult to reconcile any of these hypotheses with the results found in this study. Presumably lemmings born during the winter should have the lowest growth rates, and yet it was these animals that formed the bulk of the high weight adults of summer 1960. As we have seen, adult lemmings do not grow much after the first week of June. Thus we have the anomalous situation in which the 1960 adult animals were produced at a time of the year when there is no vegetative growth and had reached their high weights before any summer plant growth began. Furthermore, a 3- to 4-year cyclical change of extrinsic factors would be needed to verify Zimmermann's hypothesis for cyclical species. These considerations seem to rule out Zimmermann's explanation as sufficient. Also, the curtailed summer breeding season of 1960 produced small adults the following year on some areas (Type G decline) and large adults on other areas (Type H declines). This seems to rule out the interesting hypothesis of Zejda. Finally, the hypothesis of Stein is excluded because the youngest adults were also the largest (winter generation 1960), and the greatest amount of strife seemed to produce smaller animals (winter generation 1961) not larger ones. Furthermore, the large animals of the peak lemming populations are bigger animals in every way than those from declining or low populations. These large animals occupy weight classes which are not even approached in the low years, and thus this change represents more than a statistical change of proportions within certain size groups.

Chitty and Chitty (1962 b) found that weather differences could not account for the differences in growth since opposite effects were observed on two areas subject to the same weather within one season. They also found that high population density at the time of poor growth was not an adequate explanation. There is no indication that age differences are responsible for the observed differences; indeed in the present study the low weight animals of the Type G declines were at least 3–4 months older on the average than the high weight animals of the peak.

Stein (1956) seems to have been the first to postulate that this size change associated with density changes might involve genetic changes in the population. Newson and Chitty (1962) found that some voles from declining populations would grow if brought into the laboratory but none grew in the field. This demonstrated that the intrinsic condition of the animals was not a sufficient explanation of low body weights during the decline, and hence that some environmental variable must be involved, probably some aspect of behaviour.

The conclusion which emerges from this discussion is that the weight changes associated with cyclic fluctuations represent a change in the growth rates of individuals and thus a change in population quality. We do not know why growth rates should change over the cycle. One way to change the growth rate of laboratory animals is to modify the diet (e.g. Osborne and Mendel, 1926), but it is possible to change growth rates in other ways as well (e.g. MacArthur, 1949; Crowcroft and Rowe, 1961), and so we cannot conclude what factors are necessarily involved in these weight changes until further study is made. It is possible that these body weight changes discussed here are not a single class of events but are produced by several different factors. But, until we have evidence to the contrary, I believe that we should look for a common explanation.

In summary, we know that high body weights are associated with peak populations of several different types of microtines. We do not understand why animals do not grow during certain phases of the cycle, except that these differences seem to be a result of intraspecific interactions. The relevant change is in the growth rates of individual animals, and genetic changes may be involved.

Three current hypotheses

I would now like to consider three current hypotheses which attempt to explain these cyclical fluctuations.

(1) *Food supply hypothesis*

This hypothesis, first suggested by Lack (1954, p. 215) and supported by Pitelka from his work and that of Thompson at Point Barrow, Alaska on the brown lemming, is shown in Fig. 8. The essence of the change involved in the decline is a qualitative and quantitative change in the forage; predation does not seem to be an essential part of the decline (Pitelka *et al.*, 1955). We may enquire whether this hypothesis fits the observations of this study.

First, there was no extensive forage utilization at Baker Lake and this would seem to cripple this hypothesis at the start (Table 39). Second, there was no evidence of starvation in animals alive in the spring of the decline (Tables 47, 48). However, this is apparently not an objection to the hypothesis because Thompson (1955 a) reported no evidence of malnutrition in Point Barrow lemmings in the spring of the decline either. We are left with the qualitative forage change as the supposed cause of the decline. Yet there was no evidence of deficiency diseases in the young of the decline; indeed, the whole difficulty is to account for the loss of very normal-looking young. Thus the deficiencies must be such that they are not noticeable macroscopically. They must prevent the young males from maturing in the decline but allow the young females to mature. They must account for the cessation of breeding in mid-summer of the peak year and yet allow the summer young to grow well through the entire peak summer. Furthermore, they must account for an increasing survival rate in the later summer litters of the decline compared with the first litter. Such effects seem highly unlikely to be the result of qualitative forage changes. For these reasons I reject the food supply hypothesis as an adequate explanation of the Baker Lake lemming cycle.

Yet the same effects of the lemmings on the standing crop of forage as were reported by Thompson (1955 b) at Point Barrow were also found in this

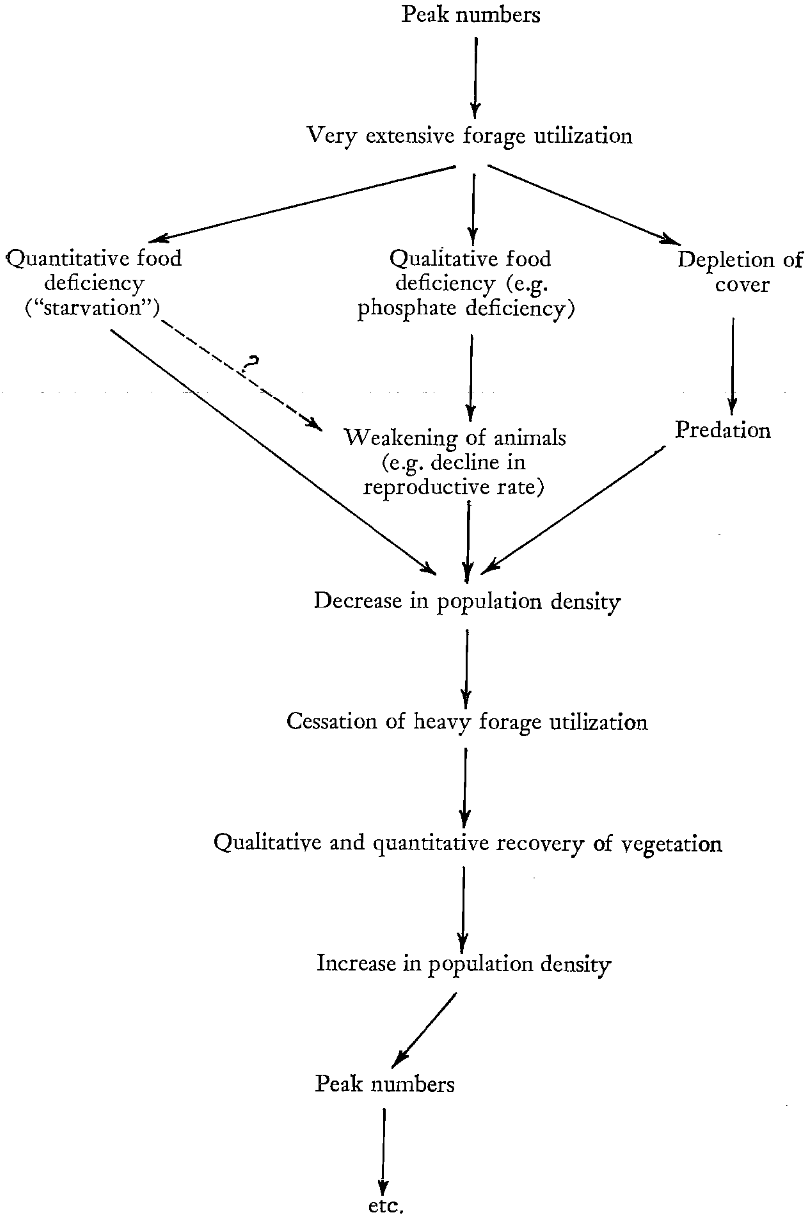


Fig. 8. Pitelka's food supply hypothesis.

study. There is no doubt that lemmings exert a strong influence on vegetation but this is hardly evidence for the above hypothesis. All the evidence for this hypothesis consists of an observed association between lemming declines and extensive forage utilization (Thompson, 1955 b; Pitelka, 1958), and until more conclusive evidence is available it is necessary to remain sceptical of this interpretation.

Rausch (1950, p. 176) states that there was nothing to indicate that the decline in numbers in 1949 at Point Barrow resulted from starvation. Elton (1942, 1955) and Chitty (1952, 1960) have presented reasons for rejecting the food supply hypothesis as an explanation of *Microtus agrestis* cycles. Kalela (1957) came to the same conclusion for *Clethrionomys rufocanus*. Nasimovich *et al.* (1948) state that the food supply was not responsible for *Lemmus lemmus* fluctuations.

Kalela (1962) has suggested that fluctuations in arctic small rodents are most easily explained by variations in plant production caused by weather, coupled with some biological rhythms inherent in the rodent populations. The question is whether any of the biological changes which accompany these cycles can be attributed to variations in plant production; Kalela has presented no evidence on this, and his own data (1957) serve as a rebuttal to this suggestion.

(2) *Christian's stress hypothesis*

The idea that cycles were caused by stress and that declines could be associated with changes in adrenal-pituitary functions and shock disease was proposed by Christian (1950) from the basic work of Selye (1946). The basic hypothesis has not changed much since then, with the exception of the added effects of stress on later generations (Christian and Lemunyan, 1957), and Fig. 9 outlines the stress hypothesis summarized in Christian (1961). A long series of papers presents the evidence for this idea (Christian, 1955 a, 1955 b, 1956, 1957, 1959, 1961, and others).

We must distinguish a general and a specific aspect of Christian's ideas. His general thesis is that all mammals limit their own densities by a combination of behavioural and physiological changes. His specific thesis is that the mechanism of this limitation involves the General Adaptation Syndrome and is purely phenotypic. I will limit my discussion to the cyclic rodents.

There are two conditions which must be fulfilled to verify this specific hypothesis:

(1) there must be increased adrenal activity and decreased reproductive activity at high densities;
(2) this increased adrenal activity must cause an increased death rate.

It is not sufficient merely to find increased adrenal activity at high densities and to claim that the hypothesis has been confirmed.

Christian has amassed a large amount of data to support his hypothesis. The sheer bulk of data from at least partly controlled laboratory studies is considered by some to be the strongest point of this hypothesis, but Chitty (1960, p. 104) considers this the weakest point. There is no evidence that these laboratory situations correspond to anything that goes on in nature.

No consistent relationship between summer adrenal weights and the phases of the cycle was found in this study (Tables 47, 48), and Chitty (1961) reported the same result from *Microtus agrestis*. Data from *M. montanus* given by Christian (1961) shows no relationship between adrenal weights and population size, contrary to what Christian says. Given these data, we seem to have two choices. We can reject Christian's hypothesis, or we can save the hypothesis by saying that adrenal weights are not always a valid index of the General Adaptation Syndrome. If we accept the second alternative we must also question the majority of the evidence in favour of the hypothesis, since it is

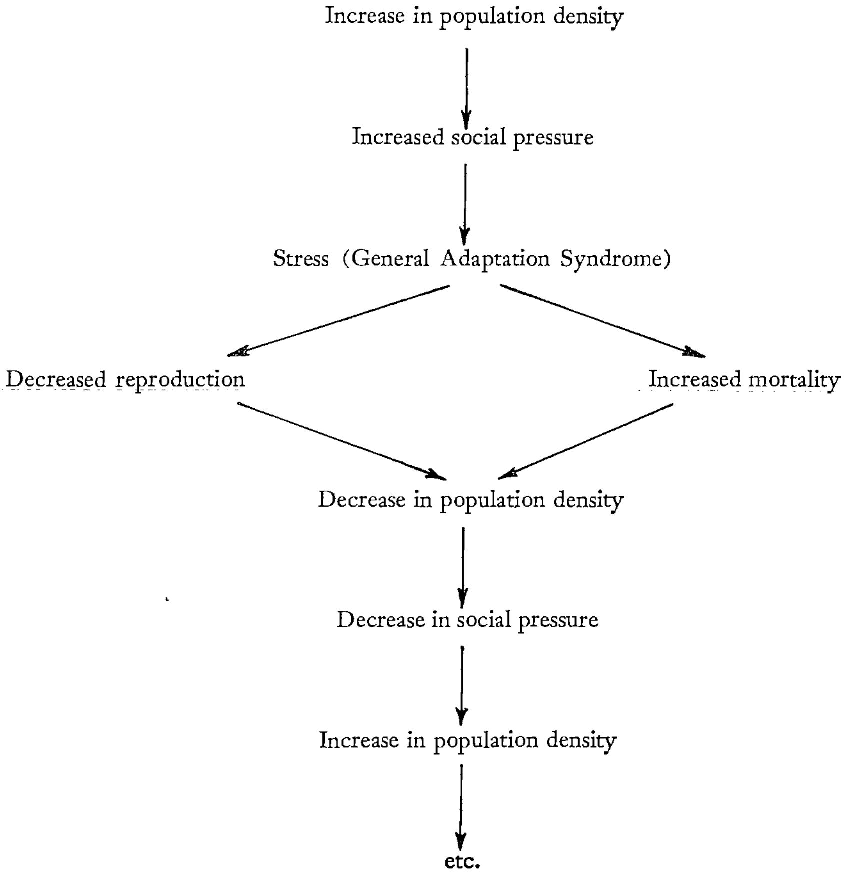


Fig. 9. Christian's stress hypothesis. The system is purely phenotypic and operates through the General Adaptation Syndrome.

mostly based on adrenal weights. Neither horn of the dilemma is very favourable to the current hypothesis.

One reason adrenal weights may give a poor index of adrenal function is that cortical zonation may differ greatly between the sexes and between mature and immature animals (Chester Jones, 1957, pp. 109–12). An attempt was made to avoid this pitfall by separating sexes, winter and summer generations, and breeding and non-breeding animals in this study. The validity of my conclusions must rest on the assumption that, given this separation of groups, the size of the adrenals in lemmings bears a close statistical relationship to their functional endocrine output under field conditions.

Munday (1961) has critically reviewed the evidence that stress may explain cyclic declines and has concluded that there is as yet no evidence that normal stressors can induce disease in either normal individuals or succeeding generations. Turner (1960, p. 265) has concluded much the same thing. Chitty (1959) has shed considerable doubt on the existence of shock disease in nature. There is little conclusive evidence of any correlation in natural populations between adrenal hypertrophy and a regression of reproductive function, and finally the idea that stress has an effect on subsequent generations has received little support (Munday, 1961).

(3) *Chitty's polymorphic behaviour hypothesis*

Chitty (1952) found that intraspecific strife during the peak summer produced little effect on the adults but rather the progeny of these animals appeared to be less viable. He emphasized the indirect effect on the progeny rather than the direct effects on the adults, and pointed out that Christian's views (1950) could not explain the long continued declines which may occur (Chitty, 1955 a, p. 60). Chitty (1952, 1958, 1960) proposed the following concept: that mutual antagonism associated with high breeding densities brings about a change in the properties of the contemporary population, and of the subsequent generations, which become less resistant to the normal sources of mortality. It is important to distinguish this concept of a change in quality of the population from the explanation (mechanism) of this concept (Conant, 1951, p. 106). Chitty (1960) reviewed the evidence for this concept and concluded that there was no evidence against it, although a mechanism had not yet been demonstrated. Christian's (1961) general ideas have much in common with this concept.

The relevant changes produced by mutual antagonism might involve two mechanisms: (1) changes in maternal physiology which are transmitted to the offspring (i.e. similar to the stress hypothesis of Christian); or (2) changes in the genetic composition of the population by selection. The first explanation was tested extensively in the laboratory by Chitty and rejected as an adequate explanation because, although striking effects could be produced in the adults by mutual antagonism, their offspring did not show the changes in quality found in natural populations (Chitty, 1958, 1960). Attention was thus turned to the second possibility, genetic changes. The first possibility investigated was hereditary haemolytic anaemia (Dawson, 1956; Chitty, 1958). This has been rejected as an explanation of the recurring declines by Newson and Chitty (1962).

Chitty has thus modified his views regarding the mechanism involved, while retaining the primacy of mutual interference as a necessary agent in these declines. His current view on the mechanism of the cycle is shown in Fig. 10 (Chitty, pers. comm.). This polymorphic behaviour mechanism proposed by Chitty does not act independently of the external environment. This is extremely important because we must explain not only the cyclic fluctuations but also the synchrony. This is introduced in Fig. 10 by the effects of contingencies (e.g. weather) on reduced viability or fertility.

Evidence from this study fully supports the general concept that populations change in quality during changes in abundance. Peak populations showed these qualitative differences by (1) high body weights and (2) reproductive changes which carried over into the decline. The high juvenile mortality during the decline could not be predicted from the population density at the time. Finally, the different types of declines could not be explained by differences in extrinsic factors.

There is no direct evidence from this study to test the mechanism proposed by Chitty (Fig. 10). We have seen that a considerable amount of wounding

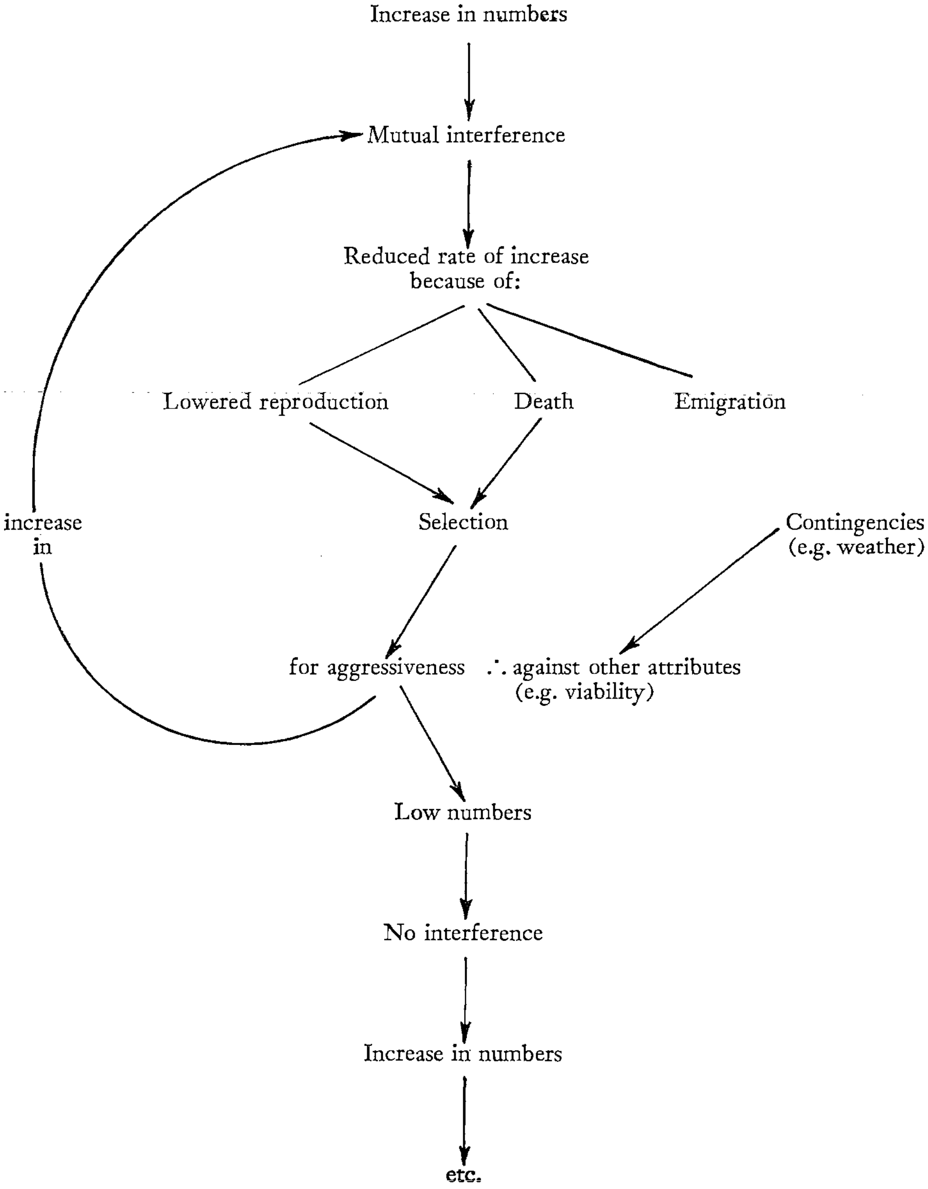


Fig. 10. Chitty's hypothesis. The system is partly genetic and primarily behavioural.

occurs in these lemming populations (Tables 49, 50). Adult males may range over very large areas (Tables 36, 37) and the most probable hypothesis about the disappearing young of the decline is that these adult males kill them. None of these points are good evidence for this mechanism, and neither are they good evidence against this mechanism.

Birch (1960) has discussed the fact that natural selection acts to bring the actual rate of increase *r* to a maximum. If this is the case, we may assume that in peak and declining lemming populations there is some survival value in a failure to mature (for males at least). It is very important to determine whether this change in maturation is genotypic or phenotypic; as yet we do not know. In either case, it would seem possible that a very high rate of selection against the early maturing young could occur because of increased fighting associated with sexual maturation, and we could thereby get a complete change in quality of the population over a very short period of time at high densities. If the maturation change were phenotypic, it would be secondary in importance to aggressive behaviour. On the other hand, if this change were genotypic, it could be of primary importance in the cycle.

One of the interesting points that has come from this lemming work is the similarity between this lemming cycle and the cycles in *Microtus agrestis* described in detail by Chitty. That similar types of events should occur in two such different ecological situations argues quite strongly for a unified view of cyclic processes.

Conclusions

I have attempted to give a semi-complete description of a single lemming cycle, and with this single observation on a very complex natural event have attempted to examine the current ideas on population cycles. The wider our horizon of facts has become, the less and less adequate seem the conventional ideas. As long as we stick to small parts of local problems and seek only confirmatory evidence we shall have to be content with *ad hoc* explanations and conventional ideas.

I have tried to penetrate to the core of the phenomenon studied, and have seen that extrinsic factors could not explain the cycle. Of the intrinsic factors I discarded the purely physiological ideas because the interactions of individuals which could produce physiological changes were severe enough that attention was turned directly to the underlying behaviour and possible selective forces that might result.

Future work on the mechanism of cyclical fluctuations should consider the role of behaviour in far more detail than has been done in the past. The suggestion of Chitty that these fluctuations may represent a genetic polymorphism deserves considerable attention. The problem remains far from being solved.

SUMMARY

1. A four-year study covering one cycle in numbers of the brown lemming (*Lemmus trimucronatus*) and the varying lemming (*Dicrostonyx groenlandicus*) has been carried out at Baker Lake, N.W.T. in an attempt to describe a lemming cycle from the Canadian Barren Grounds and to see what explanations would fit the observed events.
2. Increase began from very low numbers in 1959 and tremendous population growth occurred over the winter of 1959–60. Little further increase occurred in the peak summer of 1960. A great decline occurred over the winter of 1960–1, and this decline continued through the summer of 1961 on the Main Study Area. Numbers changed little over the winter of 1961–2 and increase was beginning again in the summer of 1962.

3. Two major changes in reproduction occurred over the cycle. A lengthened summer breeding season and winter breeding occurred during the increase in 1959–60, but no winter breeding and a shortened summer breeding season characterized the peak and decline. Young male *Lemmus* did not mature in either the peak or decline summers, nor did young females in the peak. No changes in midsummer pregnancy rates or litter size occurred over the cycle.
4. Partial prenatal mortality changed only slightly over the cycle. Adult mortality may have been slightly higher in the summer of decline than in the peak summer. Juvenile mortality was very high in the summer of decline, particularly for the first summer litter.
5. Spring movements of individual lemmings on the ice were found in the peak year. The existence of mass lemming migrations is questioned both for North America and Scandinavia. There is no good evidence of any oriented long-distance group movements of lemmings.
6. Favourable fall and winter weather was associated with the increase in numbers during 1959–60 and no change in numbers during 1961–2; unfavourable fall and early winter weather was associated with the decline.
7. Predatory birds were uncommon throughout the cycle. The weasel was the only common mammalian predator but could not have accounted for the observed mortality changes. Diseases and parasites did not seem to play any significant role in the cycle.
8. Lemmings reduced the forage crop by about 15 per cent in the peak and decline. Forage utilization averaged 30 per cent or less in the wet habitats and was negligible in the dry habitats after the critical winter of 1960–1. There was no evidence of quantitative food shortage nor any suggestion of deficiencies in food quality over the cycle. Lemmings in the spring of the decline were as fat as usual.
9. High body weights (20–30 per cent above 'normal') were associated with all peak populations.
10. Organ weights (adrenals, spleen) did not give any clue to what was causing the cycle. Summer adrenal weights showed no consistent relationship to the density changes.
11. Intraspecific strife, as measured by wounds on skins, showed strong seasonal changes which were not a simple function of density.
12. Three current hypotheses were considered in the light of these data. The food supply hypothesis of Pitelka was rejected as an adequate explanation. The stress hypothesis of Christian was also rejected. Chitty's general concept that populations change in quality during changes in density is supported by this study. Chitty's specific explanation that these cycles represent a genetic polymorphism involving aggressive behaviour was not refuted by these data, which suggest that behavioural changes may constitute the crux of the cycle.

Table 1. Temperature and precipitation data during 1959–62 and the mean values for 1950–60 as recorded by the Baker Lake meteorological station.

	Jan.	*Feb.*	*Mar.*	*Apr.*	*May*	*June*	*July*	*Aug.*	*Sept.*	*Oct.*	*Nov.*	*Dec.*	*Whole year*
Mean monthly temperature (°F)													
1959	−22	−28	−18	−2	15	35	50	46	38	14	−4	−6	9.8
1960	−26	−25	−22	1	28	46	54	52	38	19	−7	−14	12.0
1961	−31	−21	−25	2	16	41	53	46	30	10	−4	−14	8.6
1962	−35	−32	−12	−4	12	36	52	50					
Mean 1950–60	−28	−27	−15	2	22	39	52	50	38	18	−4	−19	10.7
Total rainfall (in.)													
1959	—	—	—	—	Tr[1]	0.89	1.78	2.71	1.07	Tr	Tr	—	6.45
1960	—	—	—	—	Tr	0.14	1.28	1.11	1.76	1.60	Tr	—	5.89
1961	—	—	—	—	Tr	0.37	0.24	1.98	2.05	Tr	Tr	—	4.64
1962	—	—	—	Tr	Tr	1.24	1.49	1.73					
Mean 1950–60	—	—	—	Tr	0.22	0.73	1.55	1.72	1.16	0.20	Tr		5.58
Total snowfall (in.)													
1959	3.2	0.8	1.4	1.5	6.1	Tr	—	—	1.0	8.7	2.1	7.6	30.0 (1959–60)
1960	1.6	1.0	2.3	4.9	0.8	—	—	—	0.8	7.3	1.5	1.7	25.6 (1960–61)
1961	0.6	4.4	3.1	4.2	1.0	1.0	—	Tr	8.4	6.9	8.7	6.0	43.9 (1961–62)
1962	0.2	0.5	7.6	3.4	2.2	Tr	—	Tr					
Mean 1950–60	1.8	1.8	2.3	3.6	1.8	0.6	—	Tr	0.9	3.8	3.6	2.9	23.1

[1] Tr = trace.

Table 2. Area covered by the principal habitat types on the Main Study Area.

Habitat type	*Number of acres*	*% of total land surface*
Rock and rock-lichen	294	15.0
Lichen	53	2.7
Lichen-heath	742	38.0
Heath and heath hummock	5	0.2
Heath-sedge and heath-sedge hummock[1]	506	25.9
Sedge tussock	3	0.1
Sedge hummock	290	14.9
Sedge marsh	67	3.3
Total area cover typed (exclusive of lakes)	1960 (3.05 square miles)	100.1

[1] Heath-sedge hummock contributes about 30 per cent of these figures, heath-sedge the remaining 70 per cent.

Table 3. Dominant plant species in the habitats of the Main Study Area, "New Lake", and Prince River, given a. a percentage of the frequency with which they were recorded as dominant at trapping stations in the given habitats

Species	*Lichen heath*	*Heath*	*Heath hummock*	*Heath sedge*	*Heath sedge hummock*	*Sedge tussock*	*Sedge hummock*	*Sedge marsh*
Lichens	*97.5*[1]	—	18.2	31.5	24.4	7.9	7.0	—
Dryas integrifolia	*28.8*	—	9.1	43.1	32.5	2.6	20.4	—
Betula glandulosa	*28.8*	*66.7*	*81.8*	26.2	48.0	47.4	24.6	1.0
Vaccinium uliginosum	26.3	*72.2*	*100.0*	8.5	26.8	7.9	6.3	—
Cassiope tetragona	23.8	27.8	45.5	3.8	—	—	0.7	—
Ledum groenlandicum	21.3	5.6	9.1	0.8	1.6	2.6	2.1	—
Empetrum nigrum	25.0	38.9	27.3	2.3	1.6	—	1.4	—
Arctostaphylos rubra	18.8	5.6	—	—	—	2.6	—	—
Rhododendron lapponicum	2.5	—	—	0.8	—	2.6	—	—
Rubus chamaemorus	—	—	—	—	—	2.6	—	—
Salix spp.	2.5	5.6	—	8.5	4.9	5.3	4.2	1.9
Eriophorum spp.	—	—	—	4.6	18.7	*100.0*	*43.0*	*61.0*
Carex spp.	—	—	—	*86.9*	*77.2*	26.3	*94.4*	*94.3*
Juncus spp.	—	—	—	34.6	15.4	—	28.2	50.5
Mosses	23.8	61.1	9.1	*47.7*	*48.8*	*47.4*	38.7	30.5
Total number of stations	80	18	11	130	123	38	142	105

[1] The two most common dominants for each habitat are given in italics.

Table 4. Dominant plant species in the habitats of the Aberdeen Lake area, given as a percentage of the frequency with which they were recorded as dominant at trapping stations in the given habitat.

Species	*Lichen heath*	*Heath-sedge and H-S hummock*	*Sedge tussock*	*Sedge hummock*	*Sedge marsh*
Lichens	*96.9*[1]	25.7	11.8	9.1	—
Ledum groenlandicum	*100.0*	*91.4*	*58.8*	*72.7*	—
Betula glandulosa	—	5.7	—	4.6	—
Vaccinium vitis-idaea	43.8	28.6	—	—	—
Empetrum nigrum	3.1	—	—	—	—
Rubus chamaemorus	6.3	14.3	17.6	9.1	—
Eriophorum spp.	3.1	*45.7*	*94.1*	*68.2*	*75.0*
Carex spp.	—	31.4	41.2	59.1	*95.8*
Mosses	6.3	40.0	47.1	63.6	70.8
Grasses	12.5	11.4	—	9.1	12.5
Total number of stations	32	35	17	22	24

[1] The two most common dominants for each habitat type are given in italics.

Table 5. Dominant plant species in the moss habitats on the islands of Baker Lake and the south bank of the Thelon mouth, given as a percentage of the frequency with which they were recorded as dominant at trapping stations in the given habitat.

Species	*Lichen heath*	*Moss heath*	*Moss*	*Moss sedge*
Lichens	*100.0*[1]	44.1	—	—
Dryas integrifolia	9.5	*58.8*	27.3	—
Vaccinium uliginosum	9.5	5.9	4.5	2.0
Vaccinium vitis-idaea	*52.4*	—	4.5	—
Betula glandulosa	23.8	11.8	27.3	11.8
Empetrum nigrum	19.0	26.5	4.5	—
Ledum groenlandicum	42.9	5.9	—	2.0
Salix spp.	—	14.7	*59.1*	64.7
Carex spp.	—	2.9	31.8	*82.4*
Mosses	14.3	*97.0*	*100.0*	*96.1*
Grasses	9.5	8.8	13.6	29.4
Other species	—	2.9	4.5	2.0
Total number of stations	21	34	22	51

[1] The two most common dominants for each habitat type are given in italics.

Table 6. Numbers of *Lemmus* on Quadrat 1 during 1959–62.*

Date of sampling	*Winter generation*		*Summer generation*†		*Total animals*
		Y_1	Y_1'	Y_1''	
1959					
August 5–10	—	—	—	—	0
August 11–23	—	—	1^{1}	—	1
1960					
June 18–20	28^{7}	—	—	—	28
July 6–8	22^{7}	8	—	—	30
July 28–30	12^{6}	25^{4}	4^{2}	—	41
August 25–7	8^{2}	16	20^{1}	14^{1}	58
1961					
June 12–18	2^{2}	—	—	—	2
June 19–25	3	—	—	—	3
June 26–July 2	5^{1}	—	—	—	5
July 3–9	3^{1}	—	—	—	3
July 10–16	2	2^{1}	—	—	4
July 17–23	2	—	—	—	2
July 24–30	2	—	—	—	2
July 31–August 6	—	—	—	—	0
August 7–13	—	—	1	—	1
August 14–20	—	—	—	—	0
August 21–7	—	—	—	—	0
August 28–September 1	—	—	—	1	1
1962					
July 16–August 11	—	—	—	—	0

*Superscripts in the table give trap mortalities.
†Y_1 = first summer litter, Y_1' = second summer litter, Y_1'' = third summer litter.

Table 7. Numbers of *Dicrostonyx* on Quadrat 3 in 1960–2.*

Date of sampling	*Winter generation*		*Summer generation*†		*Total animals*
		Y_1	Y_1'	Y_1''	
1959‡					
July 24–August 1	(3)	(3)	—	—	(6)
August 6–10	(1)	(2)	—	—	(3)
1960					
August 25–7	10^{1}	13	11	4	38
1961					
June 5–11	1	—	—	—	1
June 12–18	9	—	—	—	9
June 19–25	11^{3}	—	—	—	11
June 26–July 2	5	—	—	—	5
July 3–9	1	—	—	—	1
July 10–16	8	—	—	—	8
July 17–23	5	—	—	—	5
July 24–30	4	1	—	—	5
July 31–August 6	1	—	4	—	5
August 7–13	2	—	1	—	3
August 14–20	—	—	1	—	1
August 21–7	—	—	2	—	2
August 28–September 1	—	—	—	—	0
1962					
June 18–24	6	—	—	—	6
June 25–July 1	5	—	—	—	5
July 2–8	10	—	—	—	10
July 16–22	5	—	—	—	5
July 23–9	7	1	—	—	8
July 30–August 5	2	—	—	—	2
August 6–12	5	5	—	—	10
August 13–19	4	4	3	—	11

*Superscripts in the table give trap mortalities.
†Y_1 = first summer litter, Y_1' = second summer litter, Y_1'' = third summer litter.
‡The 1959 figures refer to live trapping along a line in the region where Quadrat 3 was set out in 1960. They are thus not strictly comparable with the 1960–2 figures.

Table 8. *Lemmus* snap-trapping indices, 1959–62.

Location and time period	*Dry habitats*[1]		*Medium habitats*		*Wet habitats*	
	N[2]	*Lemmus*[3]	*N*	*Lemmus*	*N*	*Lemmus*
Main Study Area						
1959						
June	711	0.0	1332	0.15	2268	0.09
July	504	0.0	1377	0.0	990	0.10
August	504	0.0	1377	0.0	990	0.20
September 1–10	153	0.0	810	0.0	477	0.21
1960						
June	504	0.79	1377	4.87	999	6.91
July	378	0.0	180	6.11	198	6.57
August	684	5.56	1377	15.54	999	21.42
1961						
June	576	0.0	1647	0.24	1449	1.10
July	1017	0.0	1017	0.30	1764	1.42
August	1260	0.0	1773	0.11	1935	0.62
1962						
June	684	0.0	2061	0.05	1971	0.61
July	378	0.0	1737	0.35	3645	1.56
August	522	0.0	1449	0.07	1629	1.90
Other areas						
1959						
August 12–17						
Prince River	18	0.0	126	0.79	576	2.43
"Ten Mile Island"	—	—	24	0.0	216	1.85
Lower Thelon River	213	0.0	—	—	387	0.78
August 26–September 5						
"New Lake"	—	—	—	—	1620	1.11
1960						
July 13–18						
Aberdeen Lake	201	0.0	226	3.54	218	18.35
July 20–3						
"New Lake"	—	—	54	33.30	306	27.12
August 15–18						
Prince River	15	6.67	96	23.95	391	17.65
"Ten Mile Island"	—	—	24	12.50	216	18.06
Lower Thelon River	213	17.37	—	—	387	27.13
1961						
July 1–13						
"New Lake"	—	—	171	0.0	540	1.48
July 26–9						
Aberdeen Lake	306	0.0	279	2.15	486	8.44
July 17–20						
"Long Island"	126	0.0	207	2.90	207	7.73
July 24–7						
"Second Island"	369	2.98	27	0.0	144	6.25
August 14–19						
Prince River	18	0.0	90	0.0	432	3.01
"Ten Mile Island"	126	2.38	54	3.70	180	7.78
"Nine Mile Island"	81	12.34	—	—	90	12.22
Lower Thelon River	153	0.0	27	3.70	360	3.33
September 1–10						
"New Lake"	—	—	297	0.67	696	3.02
1962						
July 2–8						
"New Lake"	—	—	567	0.71	954	1.15
July 11–16						
Aberdeen Lake	1086	0.18	393	2.54	747	5.35
July 17–21						
"Long Island"	108	0.0	—	—	450	0.67
"Second Island"	387	0.78	—	—	171	2.92
"Sand Island"	54	0.0	—	—	306	0.98
August 5–9						
Prince River	18	0.0	108	0.0	594	2.19
"Ten Mile Island"	198	0.0	—	—	342	0.88
"Nine Mile Island"	189	0.53	—	—	171	2.92
"Eight Mile Island"	225	4.89	—	—	135	5.93
Lower Thelon River	153	0.0	—	—	567	1.06

[1] Dry habitats = lichen heath, heath, heath hummock, and moss heath.
Medium habitats = heath sedge and heath sedge hummock.
Wet habitats = sedge hummock, sedge tussock, sedge marsh, moss, and moss sedge.

[2] Number of standard trap nights.

[3] Number of *Lemmus* caught per 100 standard trap nights.

Table 9. *Dicrostonyx* snap-trapping indices, 1959–62.

Location and time period	*Dry habitats*[1]		*Medium habitats*		*Wet habitats*	
	N[2]	*Dicro.*[3]	*N*	*Dicro.*	*N*	*Dicro.*
Main Study Area						
1959						
June	711	0.42	1332	0.68	2268	0.26
July	504	0.20	1377	0.51	990	0.20
August	504	0.20	1377	0.29	990	0.0
September 1–10	153	0.0	810	0.12	477	0.63
1960						
June	504	2.98	1377	1.31	999	0.30
July	378	10.05	180	2.22	198	0.51
August	684	7.31	1377	1.09	999	0.40
1961						
June	576	1.04	1647	1.40	1449	0.48
July	1017	2.56	1017	0.88	1764	0.62
August	1260	0.79	1773	0.85	1935	0.56
1962						
June	684	1.02	2061	1.16	1971	1.27
July	378	2.65	1737	1.96	3645	1.18
August	522	0.77	1449	1.38	1629	1.10
Other areas						
1959						
August 12–17 Lower Thelon River	213	0.0	—	—	387	0.52
1960						
July 13–18 Aberdeen Lake	201	14.43	226	6.64	218	2.29
August 15–18 Lower Thelon River	213	4.69	—	—	387	0.26
1961						
July 26–9 Aberdeen Lake	306	5.56	279	6.45	486	2.06
August 14–19 Lower Thelon River	153	0.0	27	0.0	360	0.0
1962						
July 11–16 Aberdeen Lake	1086	1.66	393	0.25	747	0.54
August 5–9 Lower Thelon River	153	0.65	—	—	567	0.18

[1] Dry habitats = lichen heath, heath, heath hummock, and moss heath.
Medium habitats = heath sedge and heath sedge hummock.
Wet habitats = sedge hummock, sedge tussock, sedge marsh, moss, and moss sedge.

[2] Number of standard trap nights.

[3] Number of *Dicrostonyx* caught per 100 standard trap nights.

Table 10. Timing of summer breeding periods in *Lemmus* females, 1959–62. Dates given are insemination dates; to obtain periods of birth add 21 days.

Year	*Period*			
	I	*II*	*III*	*IV*
Winter generation				
1959	June 12–20	July 3–11	July 24–August 6	?
1960	May 29–June 10	June 16–30	July 8–19	No breeding
1961	June 5–14	June 26–July 6	July 18–28	August 6–?
1962	June 15–22	July 7–15	July 29–August 3	?
Y_1 Summer young				
1959	—	—	July 24–August 6	?
1960	—	—	July 8–19	No breeding
1961	—	—	July 18–28	August 7–?
1962	—	—	July 22–31	August 15–?
Y_1' Summer young				
1959	—	—	—	August 19–31
1960	—	—	—	No breeding
1961	—	—	—	August 8–?
1962	—	—	—	?

Table 11. Timing of summer breeding periods in *Dicrostonyx* females, 1959–62. Dates given are insemination dates; to obtain periods of birth add 20 days.

Year	*Period*			
	I	*II*	*III*	*IV*
Winter generation				
1959	June 18–28	July 10–18	August 1–10?	?
1960	May 31–June 8	June 22–8	July 16–24	No breeding
1961	June 2–14	June 28–July 10	July 21–?	No breeding
1962	June 17–27	July 9–18	July 31–August 6	August 20–?
Y_1 Summer young				
1959	—	—	?	No breeding ?
1960	—	—	No breeding	No breeding
1961	—	—	July 17–21	No breeding
1962	—	—	August 3–?	?
Y_1' Summer young				
1959	—	—	—	No breeding ?
1960	—	—	—	No breeding
1961	—	—	—	No breeding
1962	—	—	—	?

Table 12. Length of the summer breeding seasons of *Lemmus* and *Dicrostonyx*, Main Study Area, 1959–62.

Year	*Length in days*[1]	*Time period*[2]
Lemmus		
1959	81	June 12 – September 15+
1960	70	May 29 – August 9
1961	85	June 5 – August 28
1962	78	June 15 – September 5+?
Dicrostonyx		
1959	74	June 18 – August 30+ ?
1960	74	May 31 – August 13
1961	70	June 2 – August 10
1962	76	June 17 – September 10 ?

[1] Only June, July, and August counted in this figure.
[2] First insemination date to last birth date.

Table 13. Number of corpora lutea in *Lemmus* females, Main Study Area, summers 1959–62.

Group	*I Period*			*II Period*			*III Period*			*IV Period*		
	N	*Mean*	*SE*	*N*	*Mean*	*SE*	*N*	*Mean*	*SE*	*N*	*Mean*	*SE*
Winter generation												
1959												
Primiparous	12	6.92	±.36		—			—			—	
Multiparous		—			—		3	7.33	±.67		—	
1960												
Primiparous	15	7.80	±.39		—			—			Not breeding	
Multiparous	10	8.10	±.28	18	7.72	±.24	13	6.62	±.33			
1961												
Primiparous	8	7.25	±.31		—			—			—	
Multiparous		—		5	8.20	±.37	8	6.75	±.31	1	7.00	
1962												
Primiparous	10	6.50	±.48		—			—			—	
Multiparous	1	7.00		11	7.73	±.19	5	7.00	±.84		—	
Y_1 Summer young												
1959												
Primiparous		—			—		7	5.57	±.37		—	
1960												
Primiparous		—			—		10	5.20	±.36		Not breeding	
1961												
Primiparous		—			—		13	5.31	±.29		—	
1962												
Primiparous		—			—		13	4.54	±.18	1	4.00	
Y_1' Summer young												
1959												
Primiparous		—			—			—		5	3.80	±.37
1960												
Primiparous		—			—			—			Not breeding	
1961												
Primiparous		—			—			—		1	4.00	
1962												
Primiparous		—			—			—			—	

Table 14. Number of corpora lutea in *Dicrostonyx* females, Main Study Area, summers 1959–62.

Group	*I Period*			*II Period*			*III Period*		
	N	*Mean*	*SE*	*N*	*Mean*	*SE*	*N*	*Mean*	*SE*
Winter generation									
1959									
Primiparous	9	7.00	±0.50		—			—	
Multiparous		—		2	6.50	±0.50	1	5.00	
1960									
Primiparous	9	7.00	±0.47	1	6.00			—	
Multiparous	2	9.50	±1.50	9	7.33	±0.80	6	5.67	±0.84
1961									
Primiparous	23	6.96	±0.35		—			—	
Multiparous	1	7.00		7	8.43	±0.72	1	9.00	
1962									
Primiparous	17	6.12	±0.26	1	4.00			—	
Multiparous	6	8.50	±1.06	14	6.86	±0.54	3	5.00	±0.58
Y_1 Summer young									
1959									
Primiparous		—			—			—	
1960									
Primiparous		—			—			—	
1961									
Primiparous		—			—		2	4.50	±0.50
1962									
Primiparous		—			—		1	5.00	

Table 15. Number of embryos in *Lemmus* females, Main Study Area, 1959–62.

Group		*I Period*			*II Period*			*III Period*			*IV Period*	
	N	*Mean*	*SE*	*N*	*Mean*	*SE*	*N*	*Mean*	*SE*	*N*	*Mean*	*SE*
Winter generation												
1959												
Primiparous	12	6.33	±.36		—			—			—	
Multiparous		—			—		3	6.67	±.67		—	
1960												
Primiparous	15	7.27	±.37		—			—			Not breeding	
Multiparous	10	7.50	±.34	18	7.11	±.28	13	6.23	±.28			
1961												
Primiparous	8	7.00	±.38		—			—			—	
Multiparous		—		5	7.80	±.49	8	6.75	±.31	1	6.00	
1962												
Primiparous	10	6.30	±.52		—							
Multiparous	1	7.00		11	7.36	±.28	5	7.00	±.84		—	
Y_1 Summer young												
1959												
Primiparous		—			—		7	5.43	±.48		—	
1960												
Primiparous		—			—		10	5.00	±.30		Not breeding	
1961												
Primiparous		—			—		13	4.92	±.33		—	
1962												
Primiparous		—			—		13	4.23	±.26	1	4.00	
Y_1' Summer young												
1959												
Primiparous		—			—			—		5	3.80	±.37
1960												
Primiparous		—			—			—			Not breeding	
1961												
Primparous		—			—			—		1	4.00	
1962												
Primiparous		—			—			—			—	

Table 16. Number of embryos in *Dicrostonyx* females, Main Study Area, summers 1959–62.

Group		*I Period*			*II Period*			*III Period*	
	N	*Mean*	*SE*	*N*	*Mean*	*SE*	*N*	*Mean*	*SE*
Winter generation									
1959									
Primiparous	9	6.11	±0.46		—			—	
Multiparous		—		2	6.00	±1.00	1	1.00	
1960									
Primiparous	9	6.11	±0.51	1	6.00			—	
Multiparous	2	6.00	±2.00	9	5.00	±0.58	6	4.67	±0.49
1961									
Primiparous	23	5.61	±0.41		—			—	
Multiparous	1	4.00		7	5.29	±0.64	1	8.00	
1962									
Primiparous	17	5.35	±0.32	1	3.00			—	
Multiparous	6	7.17	±0.54	14	5.50	±0.42	3	4.67	±0.88
Y_1 Summer young									
1959									
Primiparous		—			—			—	
1960									
Primiparous		—			—			—	
1961									
Primiparous		—			—		2	2.50	±1.50
1962									
Primiparous		—			—		1	4.00	

Table 17. Number of corpora lutea and embryos in *Lemmus* females at Aberdeen Lake, summers 1960–2.

Group		*I Period*[1]			*II Period*			*III Period*	
	N	*Mean*	*SE*	*N*	*Mean*	*SE*	*N*	*Mean*	*SE*
NUMBER OF CORPORA LUTEA									
Winter generation									
1960									
Primiparous	4	9.00	±0.41		—			—	
Multiparous		—		5	7.20	±1.07	4	5.50	±0.91
1961									
Primiparous	1	9.00			—			—	
Multiparous		—			—		3	6.00	±0.00
1962									
Primiparous	7	6.57	±0.20		—			—	
Multiparous		—		4	7.25	±0.48		—	
Y_1 Summer young									
1960									
Primiparous		—			—		3	6.00	±0.47
1961									
Primiparous		—			—		1	6.00	
1962									
Primiparous		—			—			—	
NUMBER OF EMBRYOS									
Winter generation									
1960									
Primiparous	4	8.75	±0.63		—			—	
Multiparous		—		5	7.00	±1.00	4	5.50	±0.91
1961									
Primiparous	1	9.00			—			—	
Multiparous		—			—		3	6.00	±0.00
1962									
Primiparous	7	6.29	±0.29		—			—	
Multiparous		—		4	7.25	±0.48		—	
Y_1 Summer young									
1960									
Primiparous		—			—		3	6.00	±0.47
1961									
Primiparous		—			—		1	6.00	
1962									
Primiparous		—			—			—	

[1] Insemination dates. I Period: 4–9 June 1960; 10–12 June 1961; 12–20 June 1962; II Period: 24–7 June 1960; 2–8 July 1962; III Period: 6–10 July 1960; 10–20 July 1961.

Table 18. Number of corpora lutea and embryos in *Dicrostonyx* females at Aberdeen Lake, summers 1960–2.

Group		*I Period*[1]			*II Period*			*III Period*	
	N	*Mean*	*SE*	*N*	*Mean*	*SE*	*N*	*Mean*	*SE*
NUMBER OF CORPORA LUTEA									
Winter generation									
1960									
Primiparous	7	7.00	±0.72		—			—	
Multiparous		—		9	5.67	±0.64		—	
1961									
Primiparous		—			—			—	
Multiparous		—		2	4.00	±1.00	1	5.00	
1962									
Primiparous	3	5.33	±0.88	1	6.00			—	
Multiparous	1	11.00		1	7.00			—	
NUMBER OF EMBRYOS									
Winter generation									
1960									
Primiparous	7	5.57	±0.57		—			—	
Multiparous		—		9	4.00	±0.65		—	
1961									
Primiparous	4	5.50	±0.64		—			—	
Multiparous		—		8	4.00	±0.38	2	2.50	±1.50
1962									
Primiparous	3	4.67	±1.45	1	6.00			—	
Multiparous	1	9.00		1	5.00			—	

[1] Insemination dates. I Period: 3–9 June 1960; 5–14 June 1961; 15–24 June 1962; II Period: 21 June–9 July 1960; 26 June–7 July 1961; 4–10 July 1962; III Period. 16–20 July 1961.

Table 19. Crude pregnancy rates per 16[1] days per female >20.5 grams, *Lemmus*, summers 1959–62.

Location and time period	*Winter generation*		*Summer young*			
			Y1 litter		*Y1′ litter*	
	N	*Preg. rate*	*N*	*Preg. rate*	*N*	*Preg. rate*
Main Study Area						
1959						
June 15–30	14	0.714	—	—	—	—
July	3	0.667	1	1.000	—	—
August	4	0.500	12	0.583	5	1.000
1960						
May 16–31	140	0.007	—	—	—	—
June 1–15	31	0.516	—	—	—	—
June 16–30	21	0.667	—	—	—	—
July 1–15	16	0.812	1	0.000	—	—
July 16–31	26	0.538	47	0.234	—	—
August 1–15	20	0.050	49	0.020	11	0.000
August 16–31	4	0.000	13	0.000	20	0.000
1961						
May 16–31	6	0.000	—	—	—	—
June 1–15	20	0.150	—	—	—	—
June 16–30	5	0.800	—	—	—	—
July 1–15	2	1.000	—	—	—	—
July 16–31	6	0.333	3	1.000	—	—
August 1–15	3	0.333	—	—	3	0.000
August 16–31	—	—	1	0.000	6	0.000
1962						
June 1–15	10	0.000	—	—	—	—
June 16–30	8	0.750	—	—	—	—
July 1–15	15	0.400	—	—	—	—
July 16–31	15	0.733	1	1.000	—	—
August 1–15	11	0.636	19	0.632	—	—
August 16–31	—	—	4	0.250	—	—
Total litter production for June, July, and August						
1959		2.841		1.568		0.813
1960		2.613		0.253		0.000
1961		2.996		1.469		0.000
1962		3.043		1.155		?

[1]Estimated portion of the 21-day gestation period for which pregnancy can be recognized macroscopically.

Table 20. Crude pregnancy rates per 15[1] days per female >30.5 grams, *Dicrostonyx*, summers 1959–62.

Location and time period	*Winter generation*		*Y_1 summer young*	
	N	*Preg. rate*	*N*	*Preg. rate*
Main Study Area				
1959				
June 15–30	3	0.667	—	—
July	9	0.889	—	—
August	3	0.333	—	—
1960				
May 16–31	6	0.000	—	—
June 1–15	22	0.364	—	—
June 16–30	5	1.000	—	—
July 1–15	10	1.000	—	—
July 16–31	6	0.833	2	0.000
August 1–15	7	0.143	5	0.000
August 16–31	10	0.000	13	0.000
1961				
May 16–31	3	0.000	—	—
June 1–15	50	0.060	—	—
June 16–30	25	0.760	—	—
July 1–15	10	0.600	—	—
July 16–31	5	0.800	14	0.214
August 1–15	4	0.250	—	—
August 16–31	4	0.000	1	0.000
1962				
June 1–15	12	0.083	—	—
June 16–30	23	0.348	—	—
July 1–15	21	0.810	—	—
July 16–31	17	0.765	—	—
August 1–15	10	0.500	—	—
August 16–31	8	0.250	3	0.000
Total litter production for June, July, and August				
1959		3.190		?
1960		3.394		0.000
1961		2.524		0.228
1962		2.823		0.000

[1] Estimated portion of the 20-day gestation period for which pregnancy can be recognized macroscopically.

Table 21. Median body weights at maturity for *Lemmus* and *Dicrostonyx* males and females, 1959–62.

Group and year	*Males*		*Females*	
	Median weight[1]	*95% conf. limits*	*Median weight*	*95% conf. limits*
Lemmus				
Winter generation				
1959	<30.5	—	<26	—
1960	36.7	34.2–39.4	51.6	49.8–53.6
1961	31–41	—	41.2	37.4–45.4
1962	29.3	27.5–31.2	32.4	27.9–37.6
Y_1 Summer young				
1959	33.8	24.6–46.6	<26	—
1960	>61	—	29.1	26.6–31.8
1961	>41	—	21.3	20.1–22.6
1962	36–40 ?	—	20.3	18.5–22.3
Y_1' Summer young				
1959	26.5	—	20–25	—
1960	>51	—	>41	—
1961	>41	—	24.4	22.6–26.4
1962	?	—	?	—
Dicrostonyx				
Winter generation				
1959	28.3	23.2–34.5	30.5	23.2–40.3
1960	43.3	38.5–48.8	49.9	43.5–57.3
1961	38.8	36.7–41.0	49.3	46.9–51.7
1962	34.1	32.6–35.7	40.7	37.9–43.7
Y_1 Summer young				
1959	?	—	?	—
1960	>51	—	>41	—
1961	>31	—	24.0	22.3–27.1
1962	>36	—	>31 ?	—

[1] Weights in grams.

Table 22. Partial prenatal mortality data for *Lemmus* females, summers 1959–62, Main Study Area.

Type of loss	*1959*	*1960*	*1961*	*1962*
Pre-implantation loss				
% litters showing loss	16.7 N = 18	31.3 N = 67	14.7 N = 34	14.6 N = 41
% ova lost	3.9 N = 102	5.3 N = 476	2.3 N = 216	2.3 N = 257
Post-implantation loss				
% litters showing loss	5.6 N = 18	17.9 N = 67	8.8 N = 34	9.8 N = 41
% embryos resorbing	2.0 N = 98	4.2 N = 451	1.9 N = 211	1.6 N = 251

Table 23. Partial prenatal mortality data for *Dicrostonyx* females, summers 1959–62, Main Study Area.

Type of loss	*1959*	*1960*	*1961*	*1962*
Pre-implantation loss				
% litters showing loss	63.6 N = 11	44.0 N = 25	55.9 N = 34	45.5 N = 44
% ova lost	16.9 N = 77	19.7 N = 178	18.2 N = 242	11.1 N = 287
Post-implantation loss				
% litters showing loss	18.2 N = 11	20.0 N = 25	32.3 N = 34	18.2 N = 44
% embryos resorbing	7.8 N = 64	6.3 N = 143	9.1 N = 198	7.1 N = 255

Table 24. Minimum survival factor estimates for *Lemmus*, summer 1960.

Time period	*Winter generation*			*Summer generation*		
	N[1]	*Nt*	*M.S.F.*	*N*	*Nt*	*M.S.F.*
Quadrat 1						
June 18–20	19	12	0.63	—	—	—
July 6–8	16	8	0.50	8	2	0.25
July 28–30	9	6	0.67	20	5	0.25
August 25–7	8	—		50	—	
Quadrat 2						
June 29–July 2	15	8	0.53	1	1	1.00
July 20–3	14	5	0.36	45	17	0.38
August 4–6	6	—		69	—	

[1] N = number released, Nt = number known to be alive next time, M.S.F. = minimum survival factor over the time period shown.

Table 25. Minimum survival factor estimates for *Lemmus*, summer 1961, Quadrat 1.

Time period	*Winter generation*			*Summer generation*		
	N[1]	*Nt*	*M.S.F.*	*N*	*Nt*	*M.S.F.*
June 5–11	2	2	1.00	—	—	
June 12–18	4	3	0.75	—	—	
June 19–25	5	5	1.00	—	—	
June 26–July 2	4	4	1.00	—	—	
July 3–9	3	3	1.00	—	—	
July 10–16	3	1	0.33	1	0	0.00
July 17–23	3	1	0.33	—	—	
July 24–30	2	0	0.00	—	—	
July 31–August 6	—	—		—	—	
August 7–13	—	—		1	0	0.00
August 14–20	—	—		—	—	

[1] N = number released, Nt = number known to be alive next time, M.S.F. = minimum survival factor over the time period shown.

Table 26. Minimum survival factor estimates for *Dicrostonyx*, summer 1960, Quadrat 2.

Time period	*Winter generation*			*Summer generation*		
	N[1]	*Nt*	*M.S.F.*	*N*	*Nt*	*M.S.F.*
June 29–July 2	6	5	0.83	—	—	
July 20–3	8	4	0.50	5	2	0.40
August 4–6	8	—		7	—	

[1] N = number released, Nt = number known to be alive next time, M.S.F. = minimum survival factor over the time period shown.

Table 27. Minimum survival factor estimates for *Dicrostonyx*, summer 1961, Quadrat 3.

Time period	*Winter generation*			*Summer generation*		
	N^1	N_t	*M.S.F.*	N	N_t	*M.S.F.*
June 5–11	2	1	0.50	—	—	
June 12–18	16	11	0.69	—	—	
June 19–25	14	11	0.79	—	—	
June 26–July 2	12	11	0.92	—	—	
July 3–9	11	11	1.00	—	—	
July 10–16	11	8	0.73	—	—	
July 17–23	8	6	0.75	—	—	
July 24–30	6	3	0.50	2	0	0.00
July 31–August 6	3	2	0.67	5	3	0.60
August 7–13	2	0	0.00	4	4	1.00
August 14–20	—	—		6	3	0.50
August 21–7	—	—		6	2	0.33
August 28–September 1	—	—		2	—	

[1] N = number released, N_t = number known to be alive next time, M.S.F. = minimum survival factor over the time period shown.

Table 28. Minimum survival factor estimates for *Dicrostonyx*, summer 1962, Quadrat 3.

Time period	*Winter generation*			*Summer generation*		
	N^1	N_t	*M.S.F.*	N	N_t	*M.S.F*
June 18–24	10	7	0.70	—	—	
June 25–July 1	13	11	0.85	—	—	
July 2–8	17	12	0.71	—	—	
July 16–22	15	14	0.93	—	—	
July 23–9	17	10	0.59	5	4	0.80
July 30–August 5	11	7	0.64	5	3	0.60
August 6–12	7	4	0.57	5	2	0.40
August 13–19	4	—		8	—	

[1] N = number released, N_t = number known to be alive next time, M.S.F. = minimum survival factor over the time period shown.

Table 29. Minimum survival rates for *Lemmus* converted to a 28-day period. Original data in Tables 24 and 25.

	Minimum survival rate per 28 days	
	Winter generation	*Summer generation*
1960		
Quadrat 1		
June 18–July 6	0.49	—
July 6–July 28	0.41	0.17
July 28–August 25	0.68	0.26
Quadrat 2		
June 29–July 20	0.43	1.00
July 20–August 4	0.15	0.17
1961		
Quadrat 1		
June 5–20	0.56	—
June 21–July 4	1.00	—
July 5–18	0.11	0.00
July 19–31	0.00	—
August 1–31	0.00	0.00

Table 30. Minimum survival rates for *Dicrostonyx* converted to a 28-day period. Original data in Tables 26, 27, and 28.

	Minimum survival rate per 28 days	
	Winter generation	*Summer generation*
1960		
Quadrat 2		
June 29–July 20	0.78	—
July 20–August 4	0.27	0.18
1961		
Quadrat 3		
June 5–20	0.13	—
June 21–July 4	0.53	—
July 5–18	0.53	—
July 19–31	0.14	0.00
August 1–15	0.00	0.36
August 16–31	—	0.03
1962		
Quadrat 3		
June 18–30	0.35	—
July 1–15	0.50	—
July 16–29	0.30	0.41
July 30–August 17	0.13	0.06

Table 31. Survival estimates for juvenile *Lemmus* on Quadrat 1, summer 1960.

		Period of breeding	
	I	*II*	*III*
Mean date at which weaning is complete	July 9	July 28	August 18
No. adult females alive then	7	8	4 ad., 6 yg.[1]
Mean litter size	7.37	7.11	6.23 ad., 5.00 yg.
Calculated no. of young born	51.5	56.9	39.9
Date of subsequent trapping	July 28–30	August 25–7	August 25–7
No. of these juveniles in traps	25	20	14
Estimated survival rate from birth to trapping	0.49 (per 34 days)	0.35 (per 43 days)	0.35 (per 22 days)
Estimated survival rate converted to 28-day period	0.56	0.50	0.25

[1]Pregnancy rate of young = 0.50: continuous breeding assumed for adults.

Table 32. Survival estimates for juvenile *Lemmus* on Quadrat 1, summer 1961.

		Period of breeding	
	I	*II*	*III*
Mean date at which weaning is complete	July 14	August 4	August 27
No. adult females alive then	1	1	0
Mean litter size	7.00	7.80	6.75
Calculated no. of young born	7.0	7.8	0
Date of subsequent trapping	July 13–15	August 10–12	August 29–31
No. of these juveniles in traps then	2	1	1
Estimated survival rate from birth to trapping time	0.29 (per 14 days)	0.13 (per 21 days)	—
Estimated survival rate converted to 28-day period	0.09	0.07	—

Table 33. Survival estimates for juvenile *Dicrostonyx* on Quadrat 2, summer 1960.

	Period of breeding	
	I	*II*
Mean date at which weaning is complete	July 7	July 29
No. adult females alive then	3	3
Mean litter size	6.11	5.00
Calculated no. of young born	18.3	15.0
Date of subsequent trapping	July 20–3	—
No. of these juveniles in traps then	7	—
Estimated survival rate from birth to trapping time	0.38 (per 28 days)	—
Estimated survival rate converted to 28-day period	0.38	?

Table 34. Survival estimates for juvenile *Dicrostonyx* on Quadrat 3, summer 1961.

		Period of breeding	
	I	*II*	*III*
Mean date at which weaning is complete	July 12	August 7	August 27
No. adult females alive then	7	2	0
Mean litter size	5.61	5.29	8.00
Calculated no. of young born	39.3	10.6	0
Date of subsequent trapping	July 27–9	August 3–5	August 24–6
No. of these juveniles in traps then	2	4	2
Estimated survival rate from birth to trapping time	0.05 (per 29 days)	0.38 (per 14 days)	?
Estimated survival rate converted to 28-day period.	0.05	0.14	?

Table 35. Survival estimates for juvenile *Dicrostonyx* on Quadrat 3, summer 1962.

	Period of breeding	
	I	*II*
Mean date at which weaning is complete	July 25	August 15
No. adult females alive then	5	3
Mean litter size	5.35	5.50
Calculated no. of young born	26.7	16.5
Date of subsequent trapping	August 8–10	August 16–18
No. of these juveniles in traps then	7	5
Estimated survival rate from birth to trapping time	0.26 (per 29 days)	0.30 (per 17 days)
Estimated survival rate converted to 28-day period	0.28	0.14[1]

[1] This estimate is probably low because these young were just coming out of the nest when the last trapping was performed.

Table 36. Length of every movement recorded within periods of live trapping for *Lemmus*, summers 1960–1[1].

Group and time period	*Length of movement (feet)*									
	< 50	*51–100*	*101–150*	*151–200*	*201–300*	*301–400*	*401–500*	*501–700*	*701–900*	*Mean*
1960										
Winter generation										
Males	8	6	5	3	3	5	–	–	–	143
Females	17	13	10	9	1	2	1	–	–	105
Y$_1$ Summer young										
Males	15	7	4	3	3	–	1	–	–	95
Females	12	10	7	6	3	2	–	–	–	111
1961										
Winter generation										
Males	1	2	6	2	3	–	1	1	1	229
Females	–	–	–	–	–	–	–	–	–	–
Y$_1$ Summer young										
Males	–	–	–	–	–	–	–	–	–	–
Females	–	–	–	–	–	–	–	–	–	–

[1] 1960 data from Quadrat 2; 1961 data from Quadrat 1 and vicinity.

Table 37. Length of every movement recorded within periods of live trapping for *Dicrostonyx*, summers 1960–2.[1]

Group and time period	*Length of movement (feet)*								
	< 50	*51–100*	*101–150*	*151–200*	*201–300*	*301–400*	*401–500*	*501–600*	*Mean*
1960									
Winter generation									
Males	15	6	1	1	2	2	–	–	86
Females	8	3	1	2	2	–	–	–	84
Y$_1$ Summer young									
Males	2	1	1	–	–	–	–	–	62
Females	–	1	–	–	–	–	–	–	71
1961									
Winter generation									
Males	1	1	5	0	1	–	1	1	201
Females	1	6	2	3	1	–	–	–	112
Y$_1$ Summer young									
Males	–	1	–	–	–	–	–	–	71
Females	–	–	–	–	–	–	–	–	–
1962									
Winter generation									
Males	10	7	6	7	6	5	3	–	167
Females	6	6	4	2	1	–	1	–	108
Y$_1$ Summer young									
Males	3	1	1	–	–	–	–	–	55
Females	–	2	–	–	–	–	–	1	–

[1] 1960 data from Quadrats 2 and 3; 1961–2 data from Quadrat 3 and vicinity.

Table 38. Standing forage in grams per 0.5 sq. metre dry weight at the end of summer.

Quadrat	*1959*		*1960*		*1961*		*1962*	
	Enclosed	*Open*	*Enclosed*	*Open*	*Enclosed*	*Open*	*Enclosed*	*Open*
1	14.6	20.0	19.5	27.9	44.7	57.8	—	—
2	118.3	70.0	149.8	90.5	157.2	105.6	—	—
3	36.7	29.9	51.2	37.1	72.8	49.1	82.3	56.3
4	48.9	31.9	58.8	36.5	100.8	68.3	97.8	77.1
5	28.7	26.0	50.9	31.1	72.3	42.3	—	—
6	28.1	27.0	31.5	43.8	36.2	35.1	49.4	45.3
7	24.7	25.4	43.0	35.1	42.0	32.8	44.2	50.6
8	37.1	47.6	57.0	53.7	79.4	49.5	95.9	79.7
9	74.5	73.2	115.8	86.2	109.3	90.9	124.2	131.8
10	46.5	37.3	57.1	40.9	54.9	53.5	68.1	80.0
11	—	—	62.2	55.6	75.1	67.4	—	—
12	—	—	47.1	53.2	97.6	83.1	—	—
13	—	—	91.2	101.9	104.3	95.5	—	—
14	—	—	57.1	63.7	86.4	79.9	—	—
15	—	—	75.3	89.5	93.6	93.2	91.0	93.2
Mean 1–10	45.8	38.8	63.5	48.3	77.0	58.5	80.3	74.4
Mean 11–15			66.6	72.8	91.4	83.8	91.0	93.2

Table 39. Estimate of percentage forage utilization in the spring of the decline, June 1961. Figures represent a total of seven different line transects.

Habitat type	*No. quadrats*	*% With runways*	*% With winter cuttings*	*% Estimated utilization*		
				Sedge	*Moss*	*Heath*
Heath-sedge hummock	52	65.3	55.8	15.2	7.2	4.1
Sedge hummock	171	86.5	67.8	25.3	29.3	2.1
Sedge marsh	53	39.6	26.4	6.0	5.0	—

Table 40. Body weight distributions for *Lemmus* males on the Main Study Area, 1959–62. Dotted lines separate summer generation from winter and spring generations.

Weight class (gm.)	*Jan.*	*Feb.*	*Mar.*	*Apr.*	*May 1–15*	*May 16–31*	*June 1–15*	*June 16–30*	*July 1–15*	*July 16–31*	*Aug. 1–15*	*Aug. 16–31*	*Sept.*	*Oct.*	*Nov.*	*Dec.*
	1959															
11–											3					
16–											1					
21–											3		1		2	
26–											3		2		1	
31–								3			2		1		1	
36–								2			2		1		–	
41–								1			–				1	
46–								3	1		–				–	
51–								2	1		–				1	
56–								3	1		2					
61–									1		–					
66–											1					
71–											3					
76–											–					
81–											1					
								14	4		21		5		6	
	1960															
11–						7′			4		7					
16–						21	1		5		2	5				
21–						11	–		–		3	3				
26–		1				7	2		–	7	11	6				
31–		1				10	–		–	18	35	14	1	2		3
36–		1				12	2		1	5	18	10	9	7		13
41–		–				11	3		–	–	9	9	8	6		11
46–		1				11	6	1	–	–	1	2	7	1		5
51–		–				22	5	1	–	–	2	3	1	1		–
56–		1				20	10	1	–	–	–	–	–			–
61–						29	10	3	1	–	–	–	1			–
66–						42	5	5	2	1	–	–	–			–
71–						25	7	4	1	1	–	3	1			2
76–						21	2	3	1	1	–	–	–			
81–						25	5	3	1	2	5	–	–			
86–						9	3	6	3	3	4	3	–			
91–						9	2	4	3	2	–	1	–			
96–						4	1	1	–		2		1			
101–						1	1	1	1		3					
106–								2	1							
		5				297	65	35	24	40	102	59	29	17		34

Table 40—*Continued*

Weight class (gm.)	*Jan.*	*Feb.*	*Mar.*	*Apr.*	*May 1–15*	*May 16–31*	*June 1–15*	*June 16–30*	*July 1–15*	*July 16–31*	*Aug. 1–15*	*Aug. 16–31*	*Sept.*	*Oct.*	*Nov.*	*Dec.*
	1961															
11–						1				1	1					
16–						–	1		1	–	1	2				
21–						1	–		–	–	2	6	4			
26–						–	–		–	–	3	6	1			
31–	3	1		1		–	–		–	–		3	2			
36–	6	5	2	1		–	–		–	–						
41–	6	6	1	1	1	–	3		–	1						
46–	2		1			–	2	1	–	–						
51–	1					–	4	1	–	–						
56–	1					–	2	4	–	1						
61–						–	2	2	–	2						
66–						–	2	1	2	3						
71–						1	2	2								
76–						1	3									
81–							1									
	19	12	4	3	1	4	22	11	3	8	7	17	7			
	1962															
11–							1				1					
16–							1			2	6					
21–							1			1	1					
26–							3	1		1	1	4				
31–							4	–	1	–	–	6				
36–							2	–	–	–	–	1				
41–							3	3	–	2	–					
46–							–	5	1	–	–					
51–							1	–	2	4	–					
56–							3	1	7	3	1					
61–							2	1	2	1	1					
66–							1	–	4	5	1					
71–								1	–	2	3					
76–								–	1	1						
81–								–								
86–								–								
91–								1								
							22	13	18	22	15	11				

Table 41. Body weight distributions for *Dicrostonyx* males on the Main Study Area, 1959–62. Dotted lines separate summer generation from winter and spring generations.

Weight class (gm.)	*Jan.*	*Feb.*	*Mar.*	*Apr.*	*May 1–15*	*May 16–31*	*June 1–15*	*June 16–30*	*July 1–15*	*July 16–31*	*Aug. 1–15*	*Aug. 16–31*	*Sept.*	*Oct.*	*Nov.*	*Dec.*
1959																
11–									3		2					
16–									–		–					
21–									1		1					
26–								1	–		2					
31–								1	2		1			1		
36–								3	3		–			–		
41–								1	2		1			2		
46–								1	2		–					
51–								3	2		1					
56–									1							
61–																
66–																
								10	16		8			3		
1960																
11–						1						1				
16–						5	1		1	3	1	2				
21–						2	1		–	1	1	–				
26–						–	2		–	2	1	2				
31–						–	2		–	–	–	2				
36–				1		–	2	1	–	1	–	6	2			
41–	1			1		–	–	–	2	4	1	5	4			
46–	–			4		–	–	–	2	–	2	3	1	1		2
51–	–			3		1	3	1	2	–	–	2	2	1		2
56–	–			4		–	3	1	2	–	–	1				3
61–	1			2		–	1	2	1	–	–	–				–
66–	1			3		3	1	–	2	–	2	–				1
71–	–			1		–	3	3	3	1	–	–				
76–	1			–		1	2	–	–	1	1	–				
81–	1			–		2	2	–	–			–				
86–				–		1	–	1	1			–				
91–				–		2	–		1			–				
96–				–			–					–				
101–				1			2					–				
106–												1				
	5			20		18	25	9	17	13	9	25	9	2		8

Table 41—*Continued*

Weight class (gm.)	*Jan.*	*Feb.*	*Mar.*	*Apr.*	*May 1–15*	*May 16–31*	*June 1–15*	*June 16–30*	*July 1–15*	*July 16–31*	*Aug. 1–15*	*Aug. 16–31*	*Sept.*	*Oct.*	*Nov.*	*Dec.*
	1961															
11–						1	1			1						
16–						–	2			1	5	2				
21–						–	4			1	–	7	1			
26–						–	6	1	1	–	6	2	–			
31–						1	2	3	2	–	1	2	1			
36–			1			1	3	–	4	–	–	1				
41–		1	1			1	7	–	–	1	1					1
46–	1		1			1	2	1	1	1	–					–
51–	1					1	6	2	3	–	–					–
56–	2				2	–	10	4	2	1	3					2
61–	–				–	–	7	2	2	2	3					–
66–	–				1	–	8	1	1	1	–					1
71–	1					2	2	2	–		1					
76–						–	4	–	1							
81–						1	2	–								
86–							1	2								
91–							1	1								
	5	1	3		3	9	68	19	17	9	20	14	2			4
	1962															
11–							1			4	3	1				
16–							2	1		–	4	–				
21–							1	5	1	–	3	1				
26–							1	2	3	–	2	2				
31–							8	3	8	–	–	3				
36–							–	8	5	3	1	2				
41–							1	5	4	3	2	1				
46–							–	4	4	6	4	–				
51–		2					–	5	1	7	1	1				
56–		–					1	7	1	4	3	1				
61–		–					1	2	3	3	4	1				
66–		2					2	7	3	3	1	–				
71–		1					2	2	1	1	2	–				
76–		2					2		1		–	–				
81–							2				–	1				
86–							1	1			1					
91–								1								
		7					25	53	35	34	31	14				

Table 42. Body weight distributions for *Lemmus* males at Aberdeen Lake, 1960–2. Dotted lines separate summer generation from winter and spring generations.

Weight class (gm.)	*1960* *May 27– June 2*	*June 15–16*	*July 10–18*	*1961* *June 1–5*	*June 22– July 10*	*July 26–9*	*1962* *June 23*	*July 12–16*
11–						2		
16–			1			7		
21–			6			2		
26–			1			3		1
31–			–			–		1
36–			–			–		1
41–	2		–			–	1	4
46–	–		1			–	–	1
51–	–		2			–	–	4
56–	1	1	3			–	1	1
61–	–	–	–			–		8
66–	1	1	2	1		1		6
71–	–	1	2	1	1	1		4
76–	–		2		–	2		1
81–	2		3		1	3		1
86–	1		–		–	–		
91–			2		2	–		
96–			1			1		
101–			–					
106–			2					
	7	3	28	2	4	22	2	33

Table 43. Body weight distributions for *Dicrostonyx* males at Aberdeen Lake, 1960–2. Dotted lines separate summer generation from winter and spring generations.

Weight class (gm.)	*1960* *May 27– June 2*	*June 15–16*	*July 10–18*	*1961* *May 28– June 7*	*June 13–22*	*July 10–19*	*July 26–9*	*1962* *June 25–7*	*July 12–16*
11–						1			
16–			3			–	1		
21–	1		2	1		–	1		
26–	–		–	–	1	–	2		1
31–	–		–	–	–	–	2		1
36–	–		2	–	–	–	1		2
41–	1		5	1	–	–	3	1	5
46–	–	1	3	–	1	2	2	–	–
51–	–	2	2	–	–	–	1	1	1
56–	–	–	2	–	2	–	2		2
61–	–	–	–	1	1	2	2		1
66–	–	–	2	–	2	–	1		1
71–	1	–	1	3	–	1	1		
76–	2	1	2	–	1	2	2		
81–	–	–	3	–	1		1		
86–	1	1	–	–	–		2		
91–	1		2	–	1		2		
96–	–			1	–				
101–	–				1				
106–	1								
111–	1								
	9	5	29	7	11	8	26	2	14

Table 44. Body weight distributions for *Lemmus* males on the outlying areas, summer 1961. Dotted lines separate summer generation from winter and spring generations.

Weight class (gm.)	*"New Lake" July 4–12*	*"Long Island" July 17–20*	*"Second Island" July 24–7*
11–			
16–			
21–		3	1
26–		—	4
31–		—	—
36–		—	—
41–		—	—
46–		—	—
51–		—	—
56–		—	—
61–	2	—	—
66–	—	—	—
71–	1	3	—
76–	1	—	2
81–	4	1	3
86–		2	
	8	9	10

Weight class (gm.)	*Lower Thelon R. August 14–19*	*"Ten Mile Id." August 14–19*	*"Nine Mile Id." August 14–19*	*Prince River August 14–17*
11–				1
16–	1			—
21–	3			1
26–	4	4		1
31–		4	2	—
36–		1	2	—
41–		—	—	—
46–		—	—	—
51–		—	—	—
56–		—	—	—
61–		—	—	3
66–		1	—	1
71–		—	—	
76–		—	—	
81–		1	1	
86–				
91–				
	8	11	5	7

Table 45. Mean body weights for *Lemmus* males of the winter and spring generations, summers 1959–62.

Location and time period		*Winter generation*			*Spring generation*	
	N	*Weight*	*SE*	*N*	*Weight*	*SE*
Main Study Area						
1959						
June 16–30	10	50.21	±1.83	4	34.38	±1.00
July 1–15	3	56.60	±3.07	—	—	—
July 16–31	—	—	—	1	49.40	—
August 1–15	4	69.10	±4.40	—	—	—
August 16–31	3	71.30	±7.74	—	—	—
1960						
May 16–31	241	66.92	±0.95	56	22.23	±0.88
June 1–15	57	67.20	±1.83	8	36.00	±3.51
June 16–30	35	79.33	±2.52	—	—	—
July 1–15	15	81.77	±4.53	—	—	—
July 16–31	10	83.79	±2.50	—	—	—
August 1–15	14	91.06	±2.20	—	—	—
August 16–31	7	82.61	±3.30	—	—	—
1961						
May 16–31	2	76.60	±1.80	2	19.40	±4.80
June 1–15	21	62.58	±3.28	1	19.00	—
June 16–30	11	61.56	±2.10	—	—	—
July 1–15	2	67.80	±1.30	—	—	—
July 16–31	7	62.84	±3.50	—	—	—
August 1–15	—	—	—	—	—	—
August 16–31	—	—	—	—	—	—
1962						
June 1–15	7	60.17	±2.25	15	31.56	±2.29
June 16–30	4	72.30	±7.64	9	44.57	±2.08
July 1–15	14	63.36	±1.50	4	46.70	±4.79
July 16–31	12	66.55	±1.89	6	50.17	±2.14
August 1–15	6	67.83	±2.63	—	—	—
August 16–31	—	—	—	—	—	—
Aberdeen Lake						
1960						
May 27–June 2	5	77.08	±5.46	2	41.60	±0.60
June 15–16	3	66.40	±4.57	—	—	—
July 10–18	14	84.69	±3.57	6	55.15	±1.67
1961						
June 1–5	2	70.45	±1.35	—	—	—
June 22–July 10	4	85.17	±4.78	—	—	—
July 26–9	8	79.80	±2.96	—	—	—
1962						
June 23	1	60.00	—	1	41.60	—
July 12–16	21	67.34	±1.41	12	45.17	±2.30
Other areas						
1961						
"New Lake" July 4–12	8	75.99	±3.14	—	—	—
"Long Island" July 17–20	6	79.97	±3.14	—	—	—
"Second Island" July 24–7	5	81.04	±1.52	—	—	—
Lower Thelon R. August 14–19	—	—	—	—	—	—
"Ten Mile Island" August 14–19	2	75.75	±5.74	—	—	—
"Nine Mile Island" August 14–19	1	84.40	—	—	—	—
Prince River August 14–17	4	65.03	±1.45	—	—	—

Table 46. Mean body weights for *Dicrostonyx* males of the winter and spring generations, summers 1959–62.

Location and		*Winter generation*			*Spring generation*	
time period	*N*	*Weight*	*SE*	*N*	*Weight*	*SE*
Main Study Area						
1959						
June 15–30	5	50.00	±2.22	5	33.60	±1.98
July 1–15	2	51.70	±2.60	4	37.10	±1.68
July 16–31	2	52.95	±0.45	4	41.80	±3.00
August 1–15	1	51.40	—	1	42.00	—
August 16–31	—	—	—	—	—	—
1960						
May 16–31	10	77.50	±4.11	8	18.63	±1.13
June 1–15	17	71.02	±3.79	8	29.72	±2.56
June 16–30	8	67.68	±3.72	1	39.20	—
July 1–15	12	67.58	±3.49	4	45.20	±2.08
July 16–31	2	74.95	±0.75	—	—	—
August 1–15	3	70.73	±4.16	—	—	—
August 16–31	1	106.00	—	—	—	—
1961						
May 1–15	3	59.77	±3.57	—	—	—
May 16–31	5	66.40	±6.78	4	33.22	±6.95
June 1–15	36	67.33	±1.58	32	35.94	±2.16
June 16–30	12	70.32	±3.60	7	40.34	±3.90
July 1–15	8	61.71	±2.95	9	39.28	±2.62
July 16–31	4	62.95	±2.70	2	45.95	±0.45
August 1–15	7	62.26	±1.97	1	40.60	—
August 16–31	—	—	—	—	—	—
1962						
June 1–15	11	73.88	±3.07	14	29.72	±2.18
June 16–30	25	64.16	±1.98	28	35.81	±1.64
July 1–15	10	65.02	±2.21	25	37.18	±1.31
July 16–31	13	62.35	±1.65	17	47.19	±1.30
August 1–15	11	66.70	±2.84	8	45.84	±1.59
August 16–31	4	65.05	±6.50	—	—	—
Aberdeen Lake						
1960						
May 27–June 2	8	84.70	±7.71	1	23.10	—
June 15–16	2	81.75	±4.85	3	50.77	±1.49
July 10–18	12	76.90	±2.94	12	44.47	±1.55
1961						
May 28–June 2	5	75.54	±6.14	2	32.00	±9.60
June 13–22	9	75.58	±5.53	2	38.85	±8.35
July 10–19	5	70.76	±3.60	2	48.55	±1.05
July 26–9	10	80.90	±3.28	10	49.53	±2.46
1962						
June 25–7	1	51.00	—	1	40.70	—
July 12–16	5	60.00	±1.84	9	39.54	±1.49

Table 47. Standardized mean organ weights (milligrams) and fat index for *Lemmus* males, 1959–62.

Location and time period	*Adrenals*				*Testes*				*Spleen*				*Fat index*			
	Winter[1]		*Summer*[2]		*Winter*		*Summer*		*Winter*		*Summer*		*Winter*		*Summer*	
	N	*Wt.*	*N*	*Wt.*	*N*	*Wt.*	*N*	*Wt.*	*N*	*Wt.*	*N*	*Wt.*	*N*	*Ind.*	*N*	*Ind.*
Baker Lake																
1959																
June 16–30	12	25.2	–	–	14	646	–	–	14	231	–	–	14	1.7	–	–
July	4	26.0	–	–	4	521	–	–	4	243	–	–	4	1.8	–	–
August	7	24.8	11	12.0	7	361	11	86	7	353	11	63	7	2.0	11	1.7
Sept.–Oct.	–	–	2	10.2	–	–	–	–	–	–	1	58	–	–	3	1.9
December	2	16.9	–	–	2	186	–	–	2	83	–	–	3	2.4	3	2.4
1960																
Feb.–April	–	–	3	11.0	2	154	–	–	–	–	1	18	–	–	3	1.0
May 16–31	88	23.2	–	–	89	545	–	–	88	66	–	–	207	2.1	–	–
June 1–15	56	26.2	–	–	58	512	–	–	57	109	–	–	57	1.4	–	–
June 16–30	35	27.5	–	–	31	510	–	–	35	199	–	–	35	1.2	–	–
July 1–15	23	28.8	8	11.9	23	490	7	30	23	249	6	33	22	1.2	9	1.5
July 16–31	14	24.8	38	7.3	14	380	31	15	14	401	33	77	14	1.1	33	1.3
August 1–15	14	25.0	86	7.8	14	305	87	16	14	284	85	72	13	1.5	94	1.8
August 16–31	–	–	50	9.7	–	–	50	15	–	–	49	56	–	–	52	2.0
Sept. 15–30	–	–	27	7.6	–	–	27	13	–	–	27	69	–	–	27	2.7
Oct. 27–Nov.	–	–	17	16.1	–	–	17	15	–	–	17	38	–	–	17	1.4
December	–	–	32	16.3	–	–	32	20	–	–	31	35	–	–	31	1.5
1961																
January	–	–	19	13.7	–	–	19	17	–	–	19	30	–	–	19	1.5
February	–	–	12	11.5	–	–	12	15	–	–	12	31	–	–	12	1.2
March	–	–	4	13.8	–	–	4	14	–	–	4	44	–	–	4	1.8
April	–	–	3	14.1	–	–	3	31	–	–	3	44	–	–	3	2.0
May 1–15	–	–	–	–	–	–	–	–	–	–	1	43	–	–	1	1.9
May 16–31	2	25.3	–	–	2	635	–	–	2	140	–	–	2	4.2	–	–
June 1–15	22	24.4	–	–	22	634	–	–	22	96	–	–	22	2.5	–	–
June 16–30	8	21.8	–	–	11	576	–	–	11	156	–	–	11	1.1	–	–
July 1–15	10	26.7	–	–	10	556	1	43	10	267	1	45	10	1.3	1	1.5
July 16–31	7	25.7	1	11.8	7	437	1	35	6	516	1	59	7	1.0	1	1.2
August 1–15	–	–	7	11.4	–	–	7	14	–	–	7	90	–	–	7	1.4
August 16–31	–	–	17	12.5	–	–	17	10	–	–	16	74	–	–	17	2.1
September	–	–	7	7.5	–	–	7	24	–	–	7	51	–	–	7	2.2
1962																
June 1–15	16	22.4	–	–	16	542	–	–	16	92	–	–	16	2.9	–	–
June 16–30	12	30.6	–	–	12	523	–	–	12	264	–	–	12	1.3	–	–
July 1–15	18	31.9	–	–	18	503	–	–	18	289	–	–	18	1.1	–	–
July 16–31	18	23.4	4	11.6	20	465	4	52	18	647	4	76	18	1.2	4	1.4
August 1–15	6	25.2	9	13.2	6	474	9	66	6	695	9	88	6	1.6	9	1.6
August 16–31	–	–	3	12.4	–	–	3	198	–	–	3	115	–	–	3	1.1
Aberdeen Lake																
1960																
May 27–June 2	7	22.5	–	–	7	666	–	–	7	86	–	–	7	2.3	–	–
July 10–18	20	24.7	8	8.2	20	512	8	17	20	265	7	48	20	1.3	8	1.6
1961																
July 26–9	8	23.6	14	9.7	8	535	14	21	8	403	14	60	8	1.2	14	1.7
1962																
July 12–16	33	24.5	–	–	33	510	–	–	33	383	–	–	33	1.2	–	–

[1] Winter generation — fecund animals only.
[2] Summer generation — non-fecund animals only.

Table 48. Standardized mean organ weights (milligrams) and fat index for *Dicrostonyx* males, 1959–62.

Location and time period	*Adrenals*				*Testes*				*Spleen*				*Fat index*			
	Winter[1]		*Summer*[2]		*Winter*		*Summer*		*Winter*		*Summer*		*Winter*		*Summer*	
	N	*Wt.*	*N*	*Wt.*	*N*	*Wt.*	*N*	*Wt.*	*N*	*Wt.*	*N*	*Wt.*	*N*	*Ind.*	*N*	*Ind.*
Baker Lake																
1959																
June 16–30	6	14.8	–	–	6	261	–	–	6	31.5	–	–	7	1.5	–	–
July	12	12.4	–	–	12	273	–	–	12	55.3	–	–	12	2.0	–	–
August	2	13.8	6	9.1	2	202	6	51	2	37.6	6	25.3	2	1.9	6	1.6
November	1	11.1	2	6.2	1	89	2	45	1	18.8	2	23.7	1	1.2	2	2.4
1960																
Jan.–Mar.	–	–	–	–	3	69	2	17	–	–	–	–	3	2.6	2	2.7
April	8	14.7	5	8.3	11	115	9	38	4	61.3	–	–	11	1.9	9	2.6
May 16–31	2	12.1	–	–	2	241	–	–	2	31.3	–	–	2	2.3	–	–
June 1–15	14	13.7	–	–	14	224	–	–	14	49.2	–	–	14	1.1	–	–
June 16–30	9	15.5	–	–	9	196	–	–	9	60.8	–	–	9	1.0	–	–
July 1–15	13	14.9	1	7.1	13	230	1	41	13	77.4	1	40.8	12	1.2	1	1.6
July 16–31	2	12.7	10	8.1	2	139	11	20	2	73.1	9	39.4	2	1.2	11	1.2
August 1–15	3	13.6	7	8.8	1	132	7	23	3	132.3	7	48.8	3	1.7	7	1.7
August 16–31	–	–	24	9.4	1	100	24	22	1	124.0	24	59.9	1	1.8	24	2.2
Sept. 15–30	–	–	9	7.3	–	–	9	25	–	–	9	41.7	–	–	9	2.5
November	–	–	2	10.8	–	–	2	19	–	–	2	37.0	–	–	2	2.4
December	–	–	8	11.2	–	–	8	37	–	–	8	42.3	–	–	8	1.6
1961																
January	–	–	5	9.3	–	–	5	34	–	–	5	33.1	–	–	5	1.7
February	–	–	1	7.6	–	–	1	36	–	–	1	24.9	–	–	1	0.9
March	–	–	3	13.6	–	–	3	56	–	–	3	28.2	–	–	3	1.0
May 1–15	1	13.4	–	–	1	124	–	–	1	22.6	–	–	1	2.6	–	–
May 16–31	7	15.3	–	–	7	169	–	–	7	35.6	–	–	7	3.0	–	–
June 1–15	47	16.0	–	–	47	217	–	–	46	49.0	–	–	47	2.4	–	–
June 16–30	16	16.6	–	–	16	186	–	–	16	69.8	–	–	18	1.4	–	–
July 1–15	16	14.6	–	–	16	235	–	–	16	98.4	–	–	16	1.3	–	–
July 16–31	6	12.3	2	7.6	6	253	3	46	6	65.4	3	37.5	6	1.4	3	2.0
August 1–15	7	11.8	12	9.3	7	241	12	27	6	112.0	12	38.6	7	1.2	11	1.6
August 16–31	–	–	14	9.4	–	–	14	25	–	–	14	34.9	–	–	14	1.7
December	3	11.7	–	–	3	143	–	–	3	98.4	–	–	3	1.3	–	–
1962																
Jan.–April	5	15.4	–	–	5	134	–	–	5	56.9	–	–	5	2.2	–	–
June 1–15	13	12.4	–	–	12	244	–	–	12	58.5	–	–	12	2.6	–	–
June 16–30	36	15.4	–	–	35	263	–	–	36	53.5	–	–	36	1.4	–	–
July 1–15	27	15.1	–	–	27	247	–	–	27	81.9	–	–	27	1.1	–	–
July 16–31	30	13.0	3	4.4	29	258	4	17	29	118.9	3	45.7	29	1.6	4	2.0
August 1–15	16	13.0	12	7.5	14	244	11	31	15	110.1	12	40.4	16	1.1	12	1.6
August 16–31	3	9.3	5	8.2	–	–	5	22	3	80.0	5	84.3	3	1.3	5	2.1
Aberdeen Lake																
1960																
May 27–June 2	7	15.2	–	–	8	250	–	–	8	34.2	–	–	8	2.3	–	–
June 15–16	5	12.3	–	–	5	224	–	–	5	47.3	–	–	5	1.7	–	–
July 10–18	11	12.7	5	7.3	9	178	5	32	9	109.1	4	87.3	9	1.2	5	1.7
1961																
July 26–9	5	15.6	5	7.3	5	160	5	16	5	91.2	5	43.8	5	1.4	5	1.8
1962																
July 12–16	11	12.5	–	–	9	240	–	–	11	67.8	–	–	11	1.0	–	–

[1] Winter generation — fecund animals only.
[2] Summer generation — non-fecund animals only.

Table 49. Amount of wounding shown on skins of *Lemmus* males from the Baker Lake area, 1959–62.

Time period	Winter generation[1]				Summer generation[2]			
	N	% *Light*	% *Mod.*	% *Heavy*	*N*	% *Light*	% *Mod.*	% *Heavy*
1959								
June 16–30	7	28.6	—	—	—	—	—	—
July	5	20.0	—	—	—	—	—	—
August	7	28.6	42.9	—	11	9.1	—	—
1960								
May 16–31	138	21.7	0.7	—	—	—	—	—
June 1–15	65	40.0	—	1.5	—	—	—	—
June 16–30	34	58.8	5.9	5.9	—	—	—	—
July 1–15	25	48.0	8.0	12.0	8	—	—	—
July 16–31	14	50.0	21.4	—	36	2.8	—	—
August 1–15	14	28.6	7.1	—	85	25.9	1.2	1.2
August 16–31	—	—	—	—	55	36.4	1.8	—
Sept. 15–30	—	—	—	—	25	28.0	8.0	—
Oct.–Dec.	—	—	—	—	46	52.2	6.5	2.2
1961								
Jan.–Apr.	—	—	—	—	36	19.4	8.3	2.8
May 16–31	4	25.0	—	—	—	—	—	—
June 1–15	21	19.1	—	—	—	—	—	—
June 16–30	12	16.7	—	—	—	—	—	—
July 1–15	8	25.0	12.5	12.5	—	—	—	—
July 16–31	18	66.7	5.6	—	10	—	—	—
August 1–15	—	—	—	—	7	28.6	—	—
August 16–31	—	—	—	—	18	38.9	—	—
Sept.–Dec.	—	—	—	—	10	20.0	—	—
1962								
Jan.–May	—	—	—	—	—	—	—	—
June 1–15	20	15.0	—	—	—	—	—	—
June 16–30	12	25.0	—	—	—	—	—	—
July 1–15	18	22.2	5.6	5.6	—	—	—	—
July 16–31	18	55.6	38.9	—	4	50.0	25.0	—
August 1–15	6	50.0	33.3	—	9	22.2	11.1	—
August 16–31	—	—	—	—	3	100.0	—	—

[1] Winter generation — mature animals only.
[2] Summer generation — immature animals only.

Table 50. Amount of wounding shown on skins of *Dicrostonyx* males from the Baker Lake area, 1959–62.

Time period	*Winter generation*[1]				*Summer generation*[2]			
	N	*% Light*	*% Mod.*	*% Heavy*	*N*	*% Light*	*% Mod.*	*% Heavy*
1959								
June 16–30	11	9.1	9.1	—	—	—	—	—
July	13	15.4	—	—	3	—	—	—
August	2	50.0	—	—	6	—	—	—
1960								
May	6	—	—	—	—	—	—	—
June 1–15	28	28.6	10.7	—	—	—	—	—
June 16–30	9	44.4	11.2	—	—	—	—	—
July 1–15	16	37.5	—	—	1	—	—	—
July 16–31	4	25.0	—	—	11	9.1	—	—
August 1–15	4	—	—	—	8	25.0	—	—
August 16–31	—	—	—	—	22	18.2	—	—
Sept. 15–30	—	—	—	—	9	44.4	—	—
Oct.–Dec.	—	—	—	—	11	27.3	9.1	—
1961								
Jan.–March	—	—	—	—	8	37.5	—	—
May	9	—	11.1	—	—	—	—	—
June 1–15	65	20.0	—	—	—	—	—	—
June 16–30	17	23.5	—	—	—	—	—	—
July 1–15	17	47.1	—	—	—	—	—	—
July 16–31	6	66.7	16.7	—	2	—	—	—
August 1–15	8	50.0	—	—	12	8.4	—	—
August 16–31	—	—	—	—	13	7.7	—	—
Sept.–Dec.	4	25.0	—	—	2	—	—	—
1962								
Jan.–May	8	12.5	—	—	—	—	—	—
June 1–15	12	—	—	—	—	—	—	—
June 16–30	13	—	—	—	—	—	—	—
July 1–15	28	14.3	3.6	—	—	—	—	—
July 16–31	27	40.8	—	—	4	—	—	—
August 1–15	8	75.0	—	—	12	16.7	—	—
August 16–31	3	—	—	—	4	25.0	—	—

[1] Winter generation — mature animals only.
[2] Summer generation — immature animals only.

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