

THE LEMMING CYCLE AT BAKER LAKE, N.W.T., DURING 1959-61

by

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B.S., University of Minnesota, 1957

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A Thesis Submitted in Partial Fulfilment of  
The Requirements for the Degree of  
Doctor of Philosophy  
In the Department  
of  
Zoology

We accept this thesis as conforming to the  
required standard

THE UNIVERSITY OF BRITISH COLUMBIA

April, 1962

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Date April 1, 1962

# The University of British Columbia

FACULTY OF GRADUATE STUDIES



PROGRAMME OF THE  
FINAL ORAL EXAMINATION  
FOR THE DEGREE OF  
DOCTOR OF PHILOSOPHY

*of*

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B.S., University of Minnesota, 1957

M.A., University of British Columbia, 1959

IN ROOM 3332, BIOLOGICAL SCIENCES BUILDING

THURSDAY, APRIL 19th, 1962 AT 3:00 P.M.

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## THE LEMMING CYCLE AT BAKER LAKE, N.W.T., DURING 1959-61

A three 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, 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 3000 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 1960-61, and this decline continued through the summer of 1961 in the Main Study Area.

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 only in the period of increase, and a shortened summer breeding season occurred in the peak and to some degree in the decline. Young male *Lemmus* matured in the summer 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% increase in mean body weights of the adults in the peak summer compared to 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 qualitative or quantitative 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 and yearly changes and was not a simple function of density.

It was concluded from these observations that the 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. Behavioral 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 behavior is not refuted by these data.

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Dynamic Oceanography .....	G. L. Pickard
Biogeography .....	R. W. Pillsbury



## ABSTRACT

A three 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 3400 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 1960-61, and this decline continued through the summer of 1961 on the Main Study Area.

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 only in the period of increase, and a shortened summer breeding season occurred in the peak and to some degree in the decline. Young male Lemmus matured in the summer 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% increase in mean body weights of the adults in the peak summer compared to 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 and yearly changes and was not a simple function of density.

It was concluded from these observations that the 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. Behavioral 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 behavior is not refuted by these data.

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## 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 and the Canadian Wildlife Service for information and assistance in the field work. 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 1961-62 by the National Science Foundation of the U.S. It is a great presumption to put my name to this manuscript because 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, U.B.C. Thanks are also due to my wife who served as a field assistant for two summers. Finally, I want to express my thanks to the people of Baker Lake whose cooperation has made this study most pleasant.

## INTRODUCTION

All animal populations fluctuate in numbers. In some these fluctuations are small, in others large. In some again these fluctuations are irregular, in others they tend to be regular. 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 weight 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, no individuals living 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.

The objective of this research program was 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 of this study was to describe the events of the lemming cycle of the Barren Grounds. The second purpose was to explain these events in a comprehensive theory. The basic question directing my approach is this: what are the necessary and sufficient conditions for the occurrence of a lemming cycle. The first purpose (description) has now been realized for one cycle. The second purpose (explanation) is not yet realized, but the results suggest which of the current explanations are inadequate. A hypothesis is considered which is not inconsistent with the observed events and the information needed from future work is noted.

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 will be described and then population density changes will be considered. Then reproduction, mortality, and movements will be assessed in relation to the density changes. Changes in extrinsic and intrinsic factors which affect the population will then be considered. Finally, a discussion of the entire work will be given with an attempt to integrate these results with contemporary ideas.

## DESCRIPTION OF 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 showing. Lakes dot the landscape, occupying perhaps 30% of the total area. Drainage is poor and even light summer rains can cause considerable local flooding.

This study was carried out in the area shown in Figure 1. The Main Study Area occupies about 3 sq. miles just north of the Baker Lake settlement. All intensive work was carried out on this area. Other areas marked on the map are outlying areas sampled once or twice during each summer. In addition some sampling was carried out at the Canadian Wildlife Service camp on Aberdeen Lake ( $64^{\circ} 37' N$ ,  $99^{\circ} 44' W$ ), about 115 miles west of Baker Lake.

The weather for Baker Lake is summarized in Table 1 for 1959-61, 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 wet, while the summer of 1960 was warm and rather dry. The summer of 1961 was intermediate, cool to warm and again dry.

The spring phenologies of the three years were quite different. Spring 1960 was the earliest. The spring events of 1959 began about 8-20 days behind those of spring 1960, and the spring events of 1961 were 2-6 days behind those of 1960. This is reflected in the dates at which Baker Lake was entirely free of ice: 31 July 1959, 12 July 1960, and 17 July 1961. There were corresponding differences in the time of onset of summer breeding in lemmings.

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

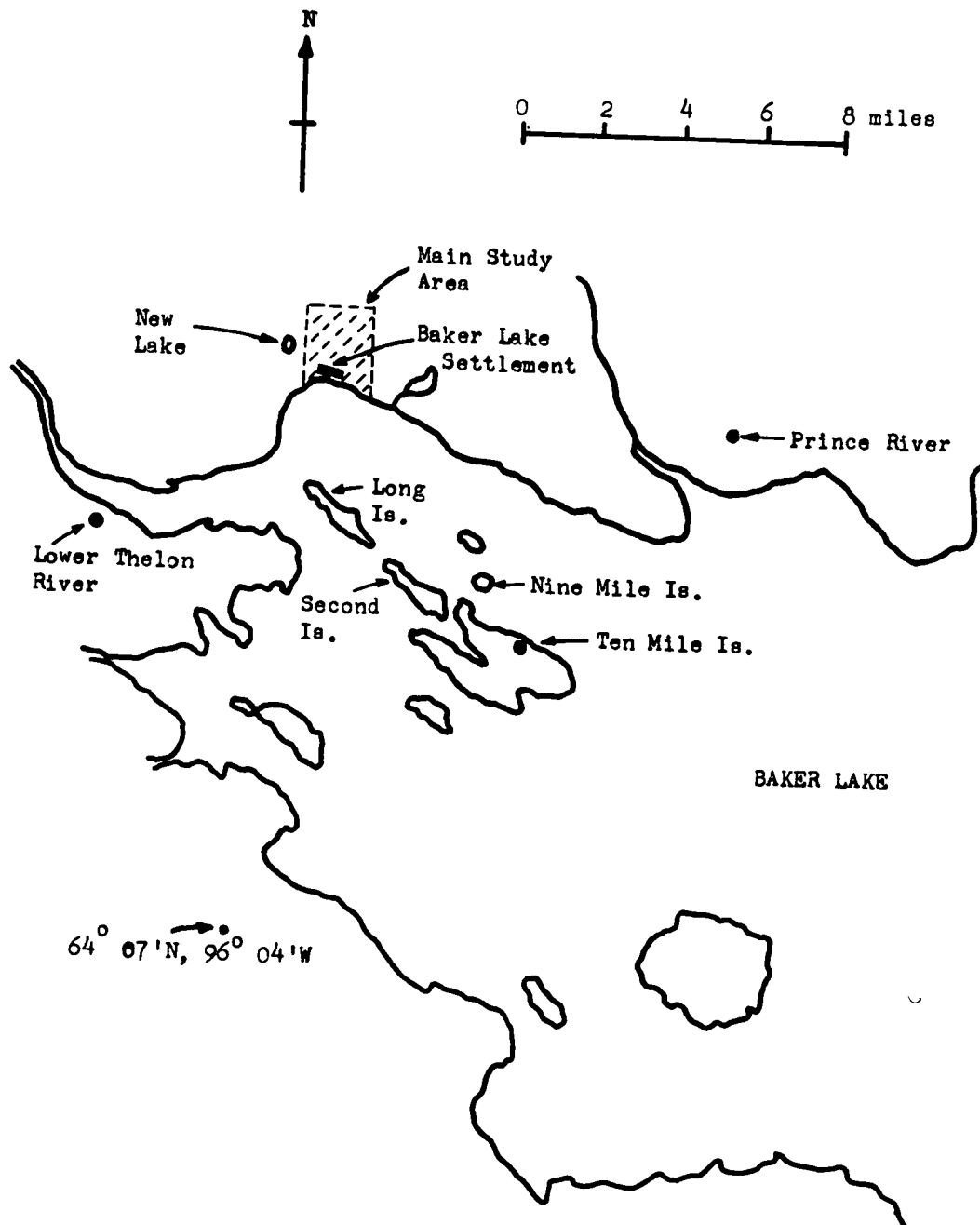




TABLE 1. Temperature and precipitation data during 1959-61 and the mean values for 1950-60 as recorded by the Baker Lake Meteorological Station.

	JAN.	FEB.	MAR.	APR.	MAY	JUNE	JULY	AUG.	SEPT.	OCT.	NOV.	DEC.	WHOLE YR.
<u>Mean Monthly Temperature</u> (°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					
Mean 1950-60	-28	-27	-15	+2	22	39	52	50	38	18	-4	-19	+10.7
<u>Total Rainfall</u> (in.)													
1959	-	-	-	-	Tr*	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					
Mean 1950-60	-	-	-	Tr	0.22	0.73	1.55	1.72	1.16	0.20	Tr	-	5.58
<u>Total Snowfall</u> (in.)													
1959	3.2	0.8	1.4	1.5	6.1	Tr	-	-	1.0	8.7	2.1	7.6	30.0
1960	1.6	1.0	2.3	4.9	0.8	-	-	-	0.8	7.3	1.5	1.7	30.0
1961	0.6	4.4	3.1	4.2	1.0	1.0	-	Tr					25.6
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

\* Tr = trace

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. This contrast between 1959 and 1960 is brought out in Table 2.

To sum up, the summer of 1959 was cold and wet but was followed by a quick, dry freeze-up and an ideal winter. The summer of 1960 was warm and dry but was followed by a slow, wet freeze-up and a bad early winter. The summer of 1961 was warm and dry also.

TABLE 2. Depth of snow on ground during early winter.

	Depth of Snow (inches)				
	Oct. 1	Oct. 15	Nov. 1	Nov. 15	Dec. 1
1959-60	0	2	9	9	11
1960-61	Tr*	2	2	2	3
Mean 1950-60	0	1	3	5	7

\* Trace.

## VEGETATION AND HABITATS

Not much is known about plant associations in the Canadian Arctic. Nevertheless, some scheme of habitat classification was needed in this study. What follows is an attempt to divide the vegetation of the Baker Lake area into habitats which in principle might be applied to the entire Barren Grounds.

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.

Three criteria were used to distinguish habitats. As a first approximation, the dominating influence seems to be water, and thus we can recognize a vegetation continuum from dry to wet. From this perspective the lichens occur in dry areas, the heath (*Ericaceae*) plants in moderately dry areas, and the sedges and mosses in wet areas. I have introduced a further factor into the habitat classification, that of microtopographical relief. This involves hummocks (low rounded mounds, 10-18" tall, 1-2' in diameter) and tussocks (thick clumps of *Eriophorum*, usually about 10" tall and less than one foot in diameter). Both these structures occur in wetter areas. This microtopographical relief is important for lemmings.

The type of habitat at each trapping station was recorded. All habitat classification in this study was done subjectively by looking at the vegetation, drainage, and microtopography. A subjective appraisal of the two or three dominant species within a five foot radius of the trapping station was also made for most stations. There was not enough time to do

anything more objective.

The principal habitats are listed in Table 3 which also gives the area covered by each on the Main Study Area. These figures were obtained from a combination aerial photo and foot survey of the area.

The habitats found on the Main Study Area are similar to those at New Lake, Prince River, and Aberdeen Lake. The dominant plant species found in these habitats are similar on the first three of these four areas, and Table 4 gives these data. The Aberdeen Lake area shows somewhat different species dominating the same habitats, and these data are given in Table 5. The chief difference is that there are no Dryas integrifolia and Cassiope tetragona at Aberdeen Lake, but Ledum groenlandicum and Eriophorum are more abundant there.

A slightly different series of habitats occurs on the islands at the west end of Baker Lake and on the sandplain along the south bank of the Thelon River mouth. These habitats are characterized by a dominance of mosses, as shown in Table 6.

In summary, because there is no satisfactory botanical classification of tundra plant associations 11 habitat types have been established to describe the vegetation of the Baker Lake area. The criteria used to distinguish habitats were drainage, plants and microtopographical relief. The plant species found in these habitats vary slightly from area to area.

TABLE 3. 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 *	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)	1958	100.1
(3.05 sq. miles)		

\* Heath-sedge hummock contributes about 30% of these figures, heath sedge the remaining %70.

TABIE 4. Dominant plant species in the habitats of the Main Study Area, New Lake, and Prince River. Figures in the table refer to the frequency with which the plant species was recorded as dominant at trapping stations in the given habitat.

SPECIES	LICHEN HEATH	HEATH	HEATH HUMM.	HEATH SEDGE	HEATH SEDGE HUMM.	SEDGE TUSSOCK	SEDGE HUMM.	SEDGE MARSH
Lichens	<u>97.5%</u> *	-	18.2%	31.5%	24.4%	7.9%	7.0%	-
<i>Dryas integrifolia</i>	<u>28.8</u>	-	9.1	43.1	32.5	2.6	20.4	-
<i>Betula glandulosa</i>	<u>28.8</u>	<u>66.7</u>	<u>81.8</u>	26.2	48.0	47.4	24.6	1.0
<i>Vaccinium uliginosum</i>	26.3	<u>72.2</u>	<u>100.0</u>	8.5	26.8	7.9	6.3	-
<i>Cassiope tetragone</i>	23.8	27.8	45.5	3.8	-	-	0.7	-
<i>Ledum groenlandicum</i>	21.3	5.6	9.1	0.8	1.6	2.6	2.1	-
<i>Empetrum nigrum</i>	25.0	38.9	27.3	2.3	1.6	-	1.4	-
<i>Arctostaphylos rubra</i>	18.8	5.6	-	-	-	2.6	-	-
<i>Rhododendron lapponicum</i>	2.5	-	-	0.8	-	2.6	-	-
<i>Rubus chamaemorus</i>	-	-	-	-	-	2.6	-	-
<i>Salix</i> spp.	2.5	5.6	-	8.5	4.9	5.3	4.2	1.9
<i>Eriophorum</i> spp.	-	-	-	4.6	18.7	<u>100.0</u>	<u>43.0</u>	<u>61.0</u>
<i>Carex</i> spp.	-	-	-	<u>86.9</u>	<u>77.2</u>	26.3	<u>94.4</u>	<u>94.3</u>
<i>Juncus</i> spp.	-	-	-	34.6	15.4	-	28.2	50.5
Mosses	23.8	61.1	9.1	<u>47.7</u>	<u>48.8</u>	<u>47.4</u>	38.7	30.5
Total Number of Stations	80	18	11	130	123	38	142	105

\* The two most common dominants for each habitat are underlined.

TABIE 5. Dominant plant species in the habitats of the Aberdeen Lake area. Figures in the table refer to the frequency with which the plant species was 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	<u>96.9%</u> *	25.7%	11.8%	9.1%	-
Ledum groenlandicum	<u>100.0</u>	<u>91.4</u>	<u>58.8</u>	<u>72.7</u>	-
Betula glandolusa	-	5.7	-	4.6	-
Vaccinium vitis-idea	43.8	28.6	-	-	-
Empetrum nigrum	3.1	-	-	-	-
Rubus chamaemorus	6.3	14.3	17.6	9.1	-
Eriophorum spp.	3.1	<u>45.7</u>	<u>94.1</u>	<u>68.2</u>	<u>75.0</u>
Carex spp.	-	31.4	41.2	59.1	<u>95.8</u>
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

\* The two most common dominants for each habitat type are underlined.



TABLE 6. Dominant plant species in the moss habitats on the islands of Baker Lake and the south bank of the Thelon mouth. Figures in the table refer to the frequency with which the plant species was recorded as dominant at trapping stations in the given habitat.

SPECIES	LICHEN HEATH	MOSS HEATH	MOSS	MOSS SEDGE
Lichens	<u>100.0%</u> *	<u>44.1%</u>	-	-
<i>Dryas integrifolia</i>	9.5	<u>58.8</u>	27.3	-
<i>Vaccinium uliginosum</i>	9.5	5.9	4.5	2.0
<i>Vaccinium vitis-idea</i>	<u>52.4</u>	-	4.5	-
<i>Betula glandulosa</i>	23.8	11.8	27.3	11.8
<i>Empetrum nigrum</i>	19.0	26.5	4.5	-
<i>Ledum groenlandicum</i>	42.9	5.9	-	2.0
<i>Salix</i> spp.	-	14.7	<u>59.1</u>	64.7
<i>Carex</i> spp.	-	2.9	31.8	<u>82.4</u>
Mosses	14.3	<u>97.0</u>	<u>100.0</u>	<u>96.1</u>
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

\* The two most common dominants for each habitat type are underlined.

## POPULATION DENSITY

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

### METHODS

#### Live Trapping

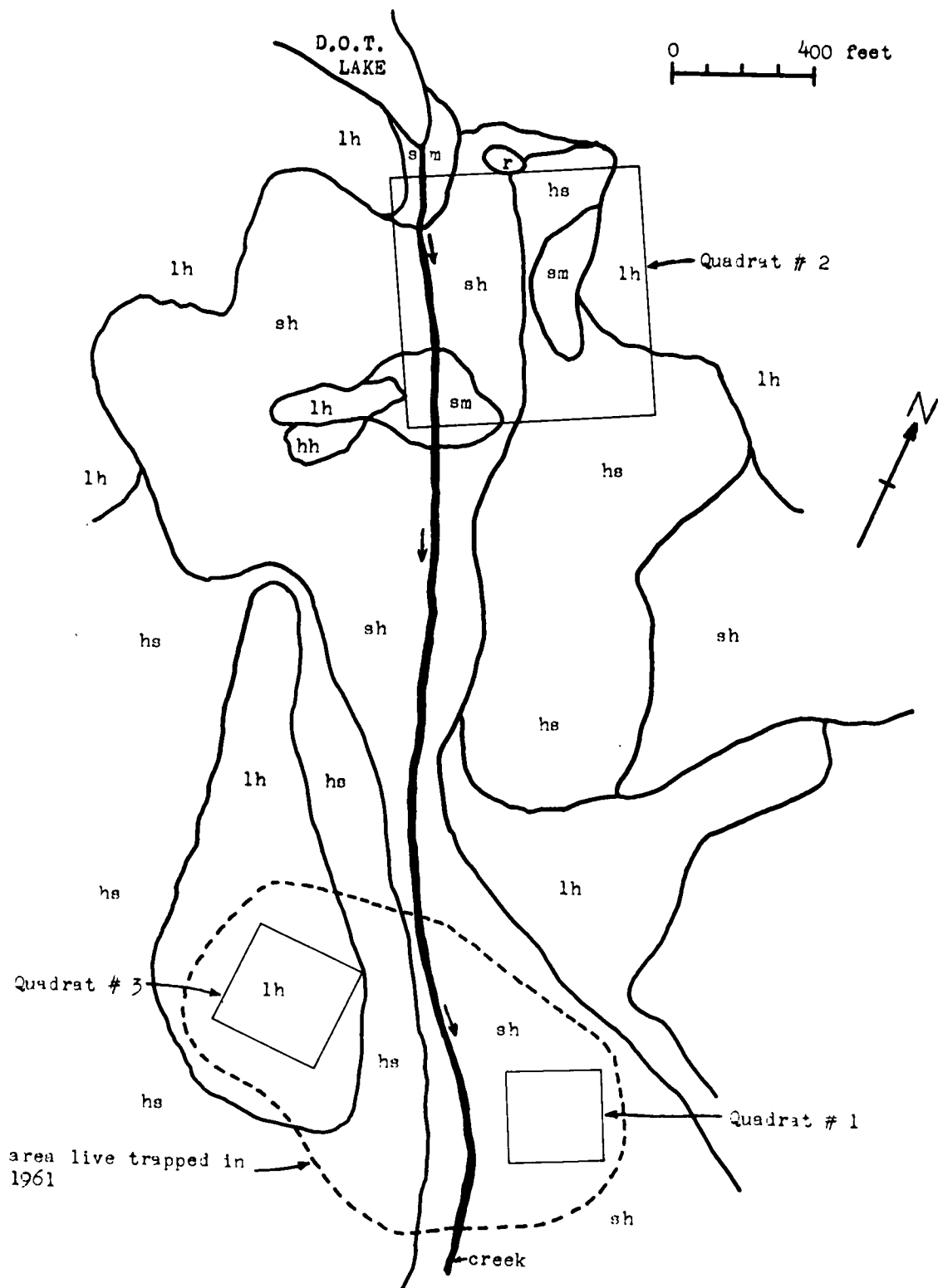
Live trapping is the best technique for estimating density because it gives a direct count. A considerable amount of effort was expended in a live trapping program in this study, but various difficulties plagued the results. The most serious problem was trap-deaths; this was not solved until 1961 and 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 (Figure 2). Their specifications are as follows:

	Area (acres)	Length of one side (feet)	Trap spacing (feet)	No. of traps
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

FIGURE 2. Location of the live trapping quadrats of the Main Study Area. Abbreviations refer to habitat types (r = rock, lh = lichen heath, hh = heath hummock, hs = heath sedge and heath sedge hummock, sh = sedge hummock, and sm = sedge marsh).



weight. The cohort of 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 aging problems is given in a later section (see Body Weights).

### 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' 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' apart (Calhoun, 1948, recommends 400') 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, and five and one-half additional pairs in 1961. 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 were placed at irregular intervals wherever

there seemed to be any chance of catching a lemming. Two traps were placed around each station. 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 were used throughout this study and raisins were used as bait. Although it was probably unnecessary, bait was used on all snap traps throughout this study until the matter could be investigated.

Some difference between the two species for standard snap trap sampling should be pointed out. Lemmus is a creature of 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, is more often a creature of 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 (Lemmus) 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" and thus give a biased idea of the actual density. The result is that Lemmus densities are estimated better 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. For this reason numerical indices from snap trapping must be treated with caution. Trends in density are shown quite well, but the actual numerical value of these trends 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. In this study there are independent sources of density estimates, such as live trapping, and these can be compared to the snap trapping indices to see how well these different estimates agree.

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, we 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.

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

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

## RESULTS

### Live Trapping

Table 7 gives the numbers of Lemmus on Quadrat # 1 (1.9 acres) in 1959-61, and Table 8 gives the numbers of Dicrostonyx on Quadrat # 3 (3.5 acres) in 1959-61. While there were few or no Dicrostonyx on Quadrat # 1 in any of the years, Quadrat # 3 had a Lemmus population of 20 animals in August 1960, but none in either 1959 or 1961.

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 only a crude estimate of the actual increase. There was probably a minimal



TABLE 7. Numbers of Lemmus on Quadrat # 1 during 1959-61.<sup>1</sup>

DATE OF SAMPLING	WINTER GENERATION	SUMMER GENERATION <sup>2</sup>			TOTAL ANIMALS
		$Y_1$	$Y_1'$	$Y_1''$	
1959					
August 5-10	-	-	-	-	0
August 11-23	-	-	1 <sup>1</sup>	-	1
1960					
June 18-20	28 <sup>7</sup>	-	-	-	28
July 6-8	22 <sup>7</sup>	8	-	-	30
July 28-30	12 <sup>6</sup>	25 <sup>4</sup>	4 <sup>2</sup>	-	41
August 25-27	8 <sup>2</sup>	16	20 <sup>1</sup>	14 <sup>1</sup>	58
1961					
June 12-18	2 <sup>2</sup>	-	-	-	2
June 19-25	3	-	-	-	3
June 26-July 2	5 <sup>1</sup>	-	-	-	5
July 3-9	3 <sup>1</sup>	-	-	-	3
July 10-16	2	2 <sup>1</sup>	-	-	4
July 17-23	2	-	-	-	2
July 24-30	2	-	-	-	2
July 31-Aug. 6	-	-	-	-	0
August 7-13	-	-	1	-	1
August 14-20	-	-	-	-	0
August 21-27	-	-	-	-	0
August 28-Sept. 1	-	-	-	1	1

<sup>1</sup> Superscripts in the table give trap mortalities.

<sup>2</sup>  $Y_1$  = first summer litter,  $Y_1'$  = second summer litter,

$Y_1''$  = third summer litter.

TABLE 8. Numbers of Dicrostonyx on Quadrat # 3 in 1960-61. <sup>1</sup>

DATE OF SAMPLING	WINTER GENERATION	SUMMER GENERATION <sup>2</sup>			TOTAL ANIMALS
		$Y_1$	$Y_1'$	$Y_1''$	
1959 <sup>3</sup>					
July 24-Aug. 1	(3)	(3)	-	-	(6)
August 6-10	(1)	(2)	-	-	(3)
1960					
August 25-27	10 <sup>1</sup>	13	11	4	38
1961					
June 5-11	1	-	-	-	1
June 12-18	9	-	-	-	9
June 19-25	11 <sup>3</sup>	-	-	-	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-Aug. 6	1	-	4	-	5
August 7-13	2	-	1	-	3
August 14-20	-	-	1	-	1
August 21-27	-	-	2	-	2
August 28-Sept. 1	-	-	-	-	0

<sup>1</sup> Superscripts in the table give trap mortalities.

<sup>2</sup>  $Y_1$  = first summer litter,  $Y_1'$  = second summer litter,  
 $Y_1''$  = third summer litter.

<sup>3</sup> The 1959 figures refer to live trapping done along a line in the vicinity of where Quadrat # 3 was set out in 1960. They are thus not strictly comparably to the 1960-61 figures.

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 8), the estimated increase is 5-10 fold over the winter 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 2-3 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 1960-61. The Lemmus population on Quadrat # 1 declined from 58 to 5 between August 1960 to June 1961, a 90-95% decrease. The Dicrostonyx population on Quadrat # 3 declined from 38 to 11 over the same period, a 70-80% decrease. These crude figures allow us to conclude that Dicrostonyx probably did not decrease as much as Lemmus over the winter of 1960-61 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 to which we shall return later, and there was no recovery of numbers.

Although it is possible to estimate the number of lemmings per acre, I have not done so because the data are too imprecise. Actual densities are very much a local phenomenon and do not help us to understand the cycle.

### Snap Trapping

Tables 9 and 10 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 change proportionally as follows:

	1959	1960	1961
<u>Lemmus</u>	1	50	10
<u>Dicrostonyx</u>	5	40	15

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. So all that we can say is that the data suggest that Lemmus fluctuated more strongly than Dicrostonyx.

The snap trapping indices in the summer of 1961 are particularly variable (compare, for example, 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, 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, 1955) 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

TABLE 9. Lemmus snap trapping indices, 1959-61.

LOCATION AND TIME PERIOD	DRY HABITATS <sup>1</sup>		MEDIUM HABITATS		WET HABITATS	
	N <sup>2</sup>	LEMMUS <sup>3</sup>	N	LEMMUS	N	LEMMUS
<u>Main Study Area</u>						
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	0.00	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
<u>Other Areas</u>						
1959						
August 12-17						
Prince River	18	0.0	126	0.79	576	2.43
Ten Mile Is.	-	-	24	0.0	216	1.85
Thelon River	213	0.0	-	-	387	0.78
August 26-Sept. 5						
New Lake	-	-	-	-	1620	1.11
1960						
July 13-18						
Aberdeen Lake	201	0.0	226	3.54	218	18.35
July 20-23						
New Lake	-	-	54	33.30	306	27.12
August 15-18						
Prince River	15	6.67	96	23.95	391	17.65
Ten Mile Is.	-	-	24	12.50	216	18.06
Thelon River	213	17.37	-	-	387	27.13
1961						
July 1-13						
New Lake	-	-	171	0.0	540	1.48
July 26-29						
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

(continued)

TABLE 9 (continued).

LOCATION AND TIME PERIOD	DRY HABITATS <sup>1</sup>		MEDIUM HABITATS		WET HABITATS	
	N <sup>2</sup>	LEMMUS <sup>3</sup>	N	LEMMUS	N	LEMMUS
1961 (Cont'd)						
July 24-27						
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 Is.	126	2.38	54	3.70	180	7.78
Nine Mile Is.	81	12.34	-	-	90	12.22
Thelon River	153	0.0	27	3.70	360	3.33
September 1-10						
New Lake	-	-	297	0.67	696	3.02

<sup>1</sup> Dry Habitats = lichen heath, heath, heath hummock and moss heath.

Medium Habitats = heath sedge and heath sedge hummocked.

Wet Habitats = sedge hummock, sedge tussock, sedge marsh, moss, and  
moss sedge.

<sup>2</sup>N = number of standard trap nights.

<sup>3</sup>LEMMUS = number of Lemmus caught per 100 standard trap nights.

TABLE 10. Dicrostonyx snap trapping indices, 1959-61.

LOCATION AND TIME PERIOD	DRY HABITATS <sup>1</sup>		MEDIUM HABITATS		WET HABITATS	
	N <sup>2</sup>	DICRO. <sup>3</sup>	N	DICRO.	N	DICRO.
<u>Main Study Area</u>						
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
<u>Other Areas</u>						
1959						
August 12-17						
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						
Thelon River	213	4.69	-	-	387	0.26
1961						
July 26-29						
Aberdeen Lake	306	5.56	279	6.45	486	2.06
August 14-19						
Thelon River	153	0.0	27	0.0	360	0.0

<sup>1</sup> Dry Habitats = lichen heath, heath, heath hummock, and moss heath.

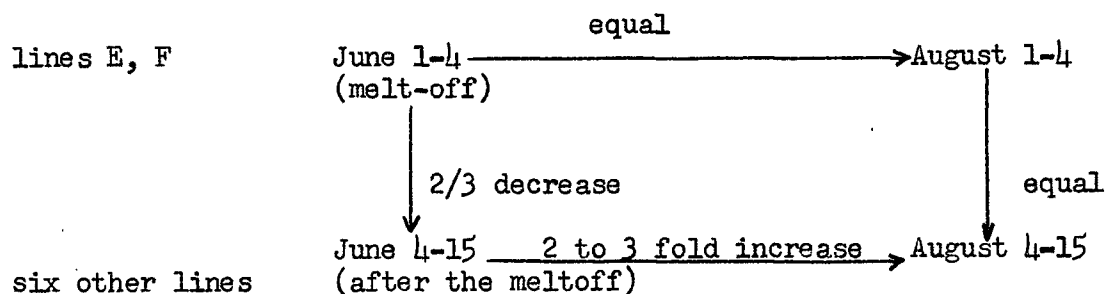
Medium Habitats = heath sedge and heath sedge hummock.

Wet Habitats = sedge hummock, sedge tussock, sedge marsh, moss and moss sedge.

<sup>2</sup>N = number of standard trap nights.

<sup>3</sup>DICRO. = number of Dicrostonyx caught per 100 standard trap nights.

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% decline in density of Lemmus over the melt-off, but this is probably an overestimate because of increased movements of animals during this period (thus increasing trap line catches). Perhaps a 30% 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 spring 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 9 and 10) and plot the percentage of the total numbers caught in each type of habitat, we obtain the results shown in Figure 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 spectrum in the peak summer of 1960, while Dicrostonyx contracted its habitat spectrum although it also increased considerably in numbers. These changes complicate somewhat the interpretation of density 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



FIGURE 3. Summer habitat distribution in Dicrostonyx and Lemmus on the Main Study Area. Ordinate is the percentage of total numbers caught in each type of habitat.

DRY



MEDIUM



WET



HABITATS

DICROSTONYX

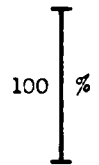
1959



1960



1961



LEMMUS

1959



1960



1961



interference, but we have no direct evidence that this is the case.

#### Other Census Methods

Visual estimates were obtained for Lemmus as follows:

1959 -	0.43	<u>Lemmus</u>	seen	per	100	hours	walking	(based on 465 hours)
1960 -	85.0	"	"	"	"	"	"	( " " 316 " )
1961 -	0.51	"	"	"	"	"	"	( " " 393 " )

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 Harbor, Eskimo Point; July -- Garry Lake, Beverly Lake; August -- Chantry 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 presented here because they add nothing new to the observations above.

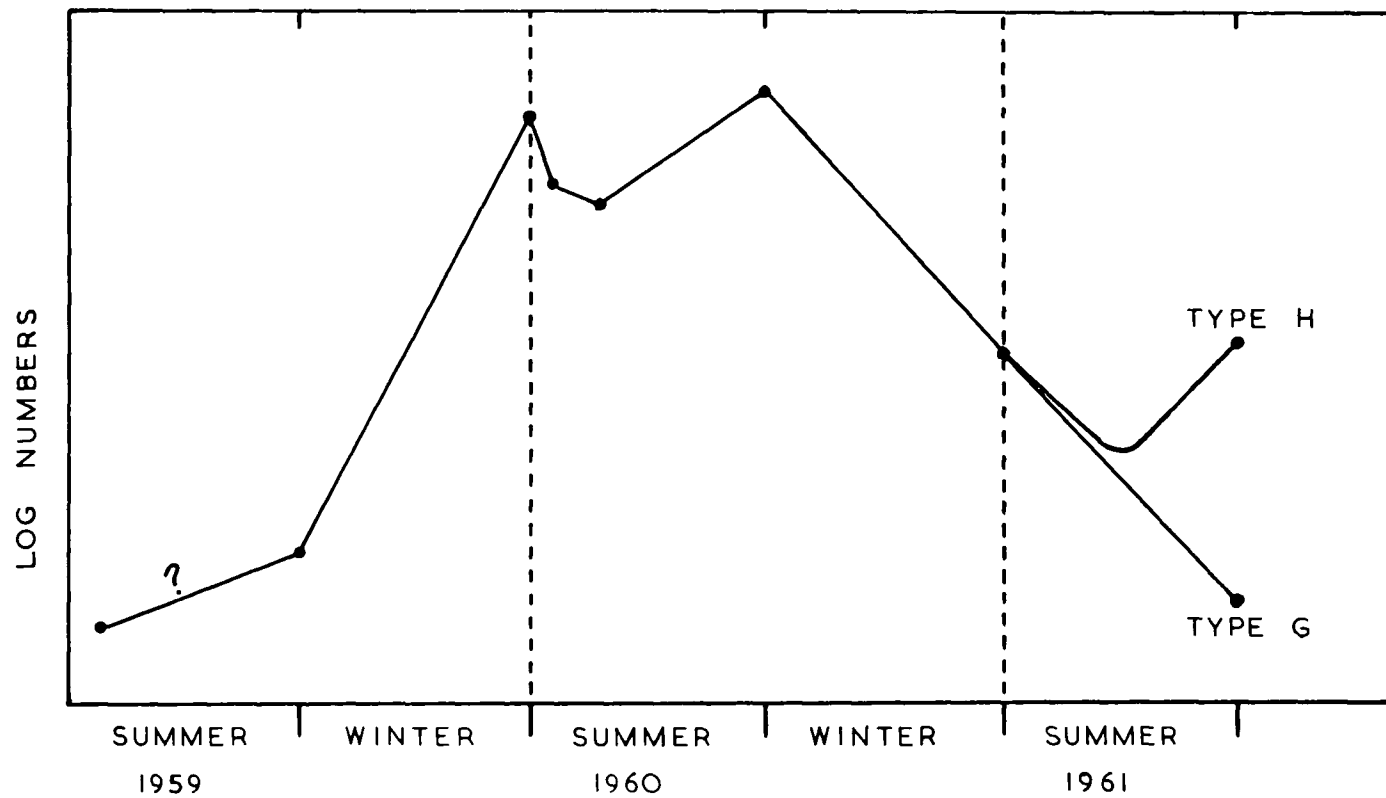
#### SUMMARY AND CONCLUSIONS

Figure 4 summarizes the density changes in Lemmus and Dicrostonyx over 1959-61.

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 25-50 fold in Lemmus and 5-10 fold in Dicrostonyx from September 1959 to May 1960.

FIGURE 4. Generalized density changes, 1959-61. Numbers indicate relative changes in numbers for each species based on live trapping. See text for details.



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

1960 Summer: The spring population of Lemmus declined considerably when the snow melted and summer breeding began. This mortality was probably between 67% and 30%. By August the Lemmus population had risen 2-3 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 they showed the same drop in numbers at the melt-off. Densities were highest in this cycle during August 1960.

1960-61 Winter: A severe decrease in population density occurred over this winter, estimated at 90-95% in Lemmus and 70-80% in Dicrostonyx from August 1960 to June 1961.

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, 1955). 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.

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.

## METHODS

Reproductive data can only be obtained 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 albicans 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 utilized.

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  $20\frac{1}{2}$  days for two individuals, and in the present study two pregnancies were timed at 21 and  $21\frac{1}{2}$  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 aging data are put is such that accuracy only within  $\pm 2$  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. Ovaries preserved in formalin 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 egg 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%) 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 very 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 and embryo rates only live embryos were counted. Prenatal mortality is discussed in the section on mortality.

## RESULTS

Reproduction is a complex variable which may be broken down into several components. Figure 5 gives a schematic analysis of the components of reproduction in polyestrous mammals, and in the remainder of this section we will attempt to assess some of these particular components.

### 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 5-10 day period at the melt-off; 20-21 days later this litter is dropped (the  $Y_1$  summer young). Post-partum breeding is very common in both species, and thus 3 weeks later a second litter is dropped (the  $Y_1'$  summer young). A third litter ( $Y_1''$  young) 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 11 and 12 give the timing of summer breeding periods in Lemmus and Dicrostonyx.

The length of the summer breeding seasons of 1959-61 in Lemmus and Dicrostonyx on the Main Study Area are given in Table 13. 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

FIGURE 5. Components of reproduction in polyestrous mammals.

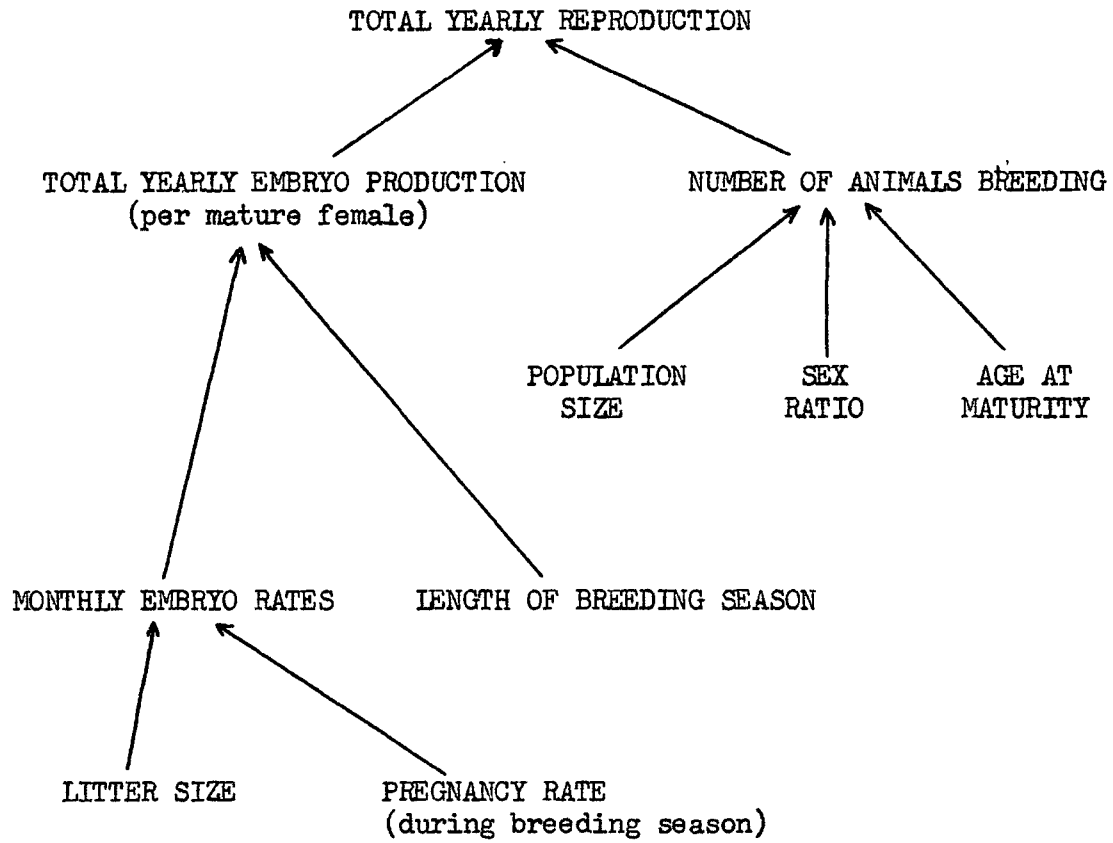


TABLE 11. Timing of summer breeding periods in Lemmus females, 1959-61.

Dates given are insemination dates; to obtain periods of birth add 21 days.

YEAR	PERIOD			
	I	II	III	IV
<u>Winter Generation</u>				
1959	June 12-20	July 3-11	July 24-Aug. 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-?
<u>Y<sub>1</sub> Summer Young</u>				
1959	-	-	July 24-Aug. 6	?
1960	-	-	July 8-19	NO BREEDING
1961	-	-	July 18-28	August 7-?
<u>Y<sub>1</sub> ' Summer Young</u>				
1959	-	-	-	August 19-31
1960	-	-	-	NO BREEDING
1961	-	-	-	August 8-?

TABLE 12. Timing of summer breeding periods in Dicrostonyx females, 1959-61. 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 22-28	July 16-24	NO BREEDING
1961	June 2-14	June 28-July 10	July 21- ?	NO BREEDING
Y <sub>1</sub> SUMMER YOUNG				
1959	-	-	?	NO BREEDING ?
1960	-	-	NO BREEDING	NO BREEDING
1961	-	-	July 17-21	NO BREEDING
Y <sub>1</sub> ' SUMMER YOUNG				
1959	-	-	-	NO BREEDING ?
1960	-	-	-	NO BREEDING
1961	-	-	-	NO BREEDING

TABIE 13. Length of the summer breeding seasons of Lemmus and Dicrostonyx, Main Study Area, 1959-61.

YEAR	LENGTH IN DAYS <sup>1</sup>	TIME PERIOD <sup>2</sup>
<u>LEMMUS</u>		
1959	80	June 12 - September 15 +
1960	70	May 29 - August 9
1961	84	June 5 - August 28
<u>DICROSTONYX</u>		
1959	73	June 18 - August 30 + ?
1960	74	May 31 - August 13
1961	69	June 2 - August 10

<sup>1</sup> Only June - August counted in this figure.

<sup>2</sup> First insemination date to last birth date.

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 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 mid-August in Dicrostonyx and by the end 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. Under such circumstances it is rather difficult to pinpoint the end of summer breeding in 1961, and some care must be exercised in interpreting these figures.

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 was stopping 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 given in Table 14. The data for 1958-59 are based on body weight distributions of June 1959. A few young Dicrostonyx were found which must have been born during the spring, but no young Lemmus. Both species bred extensively in the winter of 1959-60. Pregnant female Lemmus were obtained in April and May, and breeding males in December, February, and April. Pregnant female Dicrostonyx were obtained on November 18, January 17, and March 24, and breeding males in November, January,

TABLE 14. Winter and spring breeding of Lemmus and Dicrostonyx, 1958-61.

YEAR	WINTER BREEDING <sup>1</sup>	SPRING BREEDING <sup>2</sup>
<u>LEMNUS:</u>		
1958-59	none ?	none ?
1959-60	extensive	extensive
1960-61	none	some
<u>DICROSTONYX</u>		
1958-59	none ?	some
1959-60	extensive	some
1960-61	none	some

<sup>1</sup> Winter - September to April 15

<sup>2</sup> Spring - April 16 to May 31



February, March, April, and May. Since only a few winter specimens were obtained from this winter (57 Dicrostonyx and 21 Lemmus), these data give only a qualitative idea of winter breeding. In the winter of 1960-61, 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 female Dicrostonyx were obtained on April 16 and May 3. Although no pregnant female Lemmus were obtained, females with fresh placental scars and young animals were caught in late May.

In summary, the major changes in the length of the breeding season over the lemming cycle were: (1) extensive winter breeding only in the phase of increase (1959-60); 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 15 and 16 give the number of corpora lutea of pregnant Lemmus and Dicrostonyx females from the Main Study Area, and from these data we are led to the following conclusions: (1) Ovulation rate in both species changes seasonally, declining from higher values at the start of the summer to lower values in the late summer. (2) Primiparous females tend to have lower ovulation rates than multiparous females in both species but the differences are slight, in so far as can be generalized from the few samples which contain both groups. (3) Primiparous summer young have significantly lower ovulation rates than multiparous winter generation adults breeding at the same time. (4) Finally, and most important for our purposes, there are no significant differences in ovulation rates of either species between the years, when we compare similar groups of animals.

Tables 17 and 18 give the number of embryos of pregnant Lemmus and Dicrostonyx females 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 and 1961. Table 19 gives the corpora lutea and embryo counts for Lemmus at Aberdeen Lake in 1960 and 1961, and Table 20 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

TABIE 15. Number of Corpora Lutea in Lemmus females, Main Study Area, Summers 1969-61.

[illegible]

TABLE 16. Number of corpora lutea in Dicrostonyx females, Main Study Area, summers 1959-1961.

GROUP	I PERIOD			II PERIOD			III PERIOD		
	N	MEAN	SE	N	MEAN	SE	N	MEAN	SE
WINTER GENERATION									
1959									
Primiparous	9	7.00	$\pm 0.50$		-			-	
Multiparous		-		2	6.50	$\pm 0.50$	1	5.00	
1960									
Primiparous	9	7.00	$\pm 0.47$	1	6.00			-	
Multiparous	2	9.50	$\pm 1.50$	9	7.33	$\pm 0.80$	6	5.67	$\pm 0.84$
1961									
Primiparous	23	6.96	$\pm 0.35$		-			-	
Multiparous	1	7.00		7	8.43	$\pm 0.72$	1	9.00	
Y <sub>1</sub> SUMMER YOUNG									
1959									
Primiparous		-			-			-	
1960									
Primiparous		-			-			-	
1961									
Primiparous		-			-		2	4.50	$\pm 0.50$

TABLE 17. Number of embryos in Lemmus females, Main Study Area, summers 1959-61.

GROUP	I PERIOD			II PERIOD			III PERIOD			IV PERIOD		
	N	MEAN	SE	N	MEAN	SE	N	MEAN	SE	N	MEAN	SE
<u>WINTER GENERATION</u>												
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	
<u>Y<sub>1</sub> SUMMER YOUNG</u>												
1959												
Primiparous	-			-			7	5.43	±.48	-		
Multiparous	-			-			-			-		
1960												
Primiparous	-			-			10	5.00	±.30	NOT BREEDING		
Multiparous	-			-			-					
1961												
Primiparous	-			-			13	4.92	±.33	-		
Multiparous	-			-			-			-		
<u>Y<sub>1</sub> : SUMMER YOUNG</u>												
1959												
Primiparous	-			-			-			5	3.80	±.37
Multiparous	-			-			-			-		
1960												
Primiparous	-			-			-			NOT BREEDING		
Multiparous	-			-			-					
1961												
Primiparous	-			-			-			1	4.00	
Multiparous	-			-			-			-		

TABLE 18. Number of embryos in Dicrostonyx females, Main Study Area, summers 1959-61.

GROUP	I PERIOD			II PERIOD			III PERIOD		
	N	MEAN	SE	N	MEAN	SE	N	MEAN	SE
WINTER GENERATION									
1959									
Primiparous	9	6.11	$\pm 0.46$	-	-	-	-	-	-
Multiparous		-		2	6.00	$\pm 1.00$	1	1.00	
1960									
Primiparous	9	6.11	$\pm 0.51$	1	6.00		-	-	
Multiparous	2	6.00	$\pm 2.00$	9	5.00	$\pm 0.58$	6	4.67	$\pm 0.49$
1961									
Primiparous	23	5.61	$\pm 0.41$	-	-	-	-	-	-
Multiparous	1	4.00		7	5.29	$\pm 0.64$	1	8.00	
Y <sub>1</sub> SUMMER YOUNG									
1959									
Primiparous		-		-	-	-	-	-	
1960									
Primiparous		-		-	-	-	-	-	
1961									
Primiparous		-		-	-	-	2	2.50	$\pm 1.50$

TABLE 19. Number of corpora lutea and embryos in Lemmus females at Aberdeen Lake, summers 1960-61.

GROUP	I PERIOD <sup>1</sup>			II PERIOD			III PERIOD		
	N	MEAN	SE	N	MEAN	SE	N	MEAN	SE
<u>NUMBER OF CORPORA LUTEA</u>									
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
Y <sub>1</sub> Summer Young									
1960									
Primiparous		-			-		3	6.00	±0.47
1961									
Primiparous		-			-		1	6.00	
<u>NUMBER OF EMBRYOS</u>									
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
Y <sub>1</sub> Summer Young									
1960									
Primiparous		-			-		3	6.00	±0.47
1961									
Primiparous		-			-		1	6.00	

<sup>1</sup> Insemination dates: I Period - June 4-9, 1960; June 10-12, 1961;  
II Period June 24-27, 1960; III Period - July 6-10, 1960; July 10-20, 1961.

TABLE 20. Number of corpora lutea and embryos in Dicrostonyx females at Aberdeen Lake, summers 1960-61.

GROUP	I PERIOD <sup>1</sup>			II PERIOD			III PERIOD		
	N	MEAN	SE	N	MEAN	SE	N	MEAN	SE
<u>NUMBER OF CORPORA LUTEA</u>									
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	
<u>NUMBER OF EMBRYOS</u>									
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

<sup>1</sup> Insemination dates: I Period -- June 3-9, 1960; June 5-14, 1961; II Period -- June 21-July 9, 1960; June 26-July 7, 1961; III Period July 16-20, 1961.



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 meager winter records indicate. Litter sizes of the pregnant females obtained in winter are listed below.

Date	Number of Embryos	
	<u>Lemmus</u>	<u>Dicrostonyx</u>
November 18, 1959		3
January 17, 1960		3
March 24, 1960		3
April 25, 1960	4	
May 21, 1960		5?
May 24, 1960	3	
April 16, 1961		3
May 3, 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 subsequently whether there are differences between years in this variable. The analysis of pregnancy rates used here follows that of Leslie et al. (1952).

Table 21 gives the crude (observed) pregnancy rates for Lemmus and Table 22 the rates for Dicrostonyx from all areas during this study. Since animals in very early pregnancy will not be classified as pregnant macroscopically, these crude pregnancy rates tend to underestimate the actual pregnancy rates such that a 0.750 crude pregnancy rate (i.e. 15/20) for Dicrostonyx and a 0.762 pregnancy rate (i.e. 16/21) for Lemmus will be equivalent to every female in the population being pregnant all the time. These rates are expressed per female >20.5 grams for Lemmus and >30.5 grams

TABLE 21. Crude pregnancy rates per 16<sup>1</sup> days per female >20.5 grams,  
Lemmus, summers 1959-61.

LOCATION AND TIME PERIOD	WINTER GENERATION		SUMMER YOUNG			
	N	PREG. RATE	Y <sub>1</sub> LITTER		Y <sub>1</sub> ' LITTER	
			N	PREG. RATE	N	PREG. RATE
MAIN STUDY AREA						
1959						
June 18-30	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
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
ABERDEEN LAKE AREA						
1960						
May 27-June 2	9	0.000	-	-	-	-
June 15-16	4	1.000	-	-	-	-
July 10-18	12	0.750	8	0.375	-	-
1961						
June 2-5	3	0.000	-	-	-	-
June 22	1	1.000	-	-	-	-
July 26-29	7	0.429	5	0.200	-	-

<sup>1</sup> Estimated portion of the 21 day gestation period for which pregnancy can be recognized macroscopically.

TABLE 21 (continued). Lemmus crude pregnancy rates.

LOCATION AND TIME PERIOD	WINTER GENERATION		SUMMER YOUNG			
			Y <sub>1</sub> LITTER		Y <sub>1</sub> ' LITTER	
	N	PREG. RATE	N	PREG. RATE	N	PREG. RATE
OTHER AREAS						
1961						
Long Island						
July 17-20	4	0.250	6	0.667	-	-
Second Island						
July 24-27	3	0.667	6	0.833	-	-
Prince River						
August 14-17	-	-	1	0.000	4	0.000
Nine Mile Is.						
August 14-19	1	1.000	2	0.000	1	0.000
Ten Mile Is.						
August 14-19	1	1.000	3	0.333	2	0.000
Thelon River						
August 14-19	-	-	-	-	4	0.000

TABLE 22. Crude pregnancy rates per 15<sup>1</sup> days per female >30.5 grams,  
Dicrostonyx, summers 1959-61.

LOCATION AND TIME PERIOD	WINTER GENERATION		Y <sub>1</sub> 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
TOTAL LITTER PRODUCTION FOR JUNE, JULY AND AUGUST				
1959		3.190		?
1960		3.394		0.000
1961		2.524		0.228
ABERDEEN LAKE AREA				
1960				
May 27-June 2	4	0.000	-	-
June 15-16	7	1.000	-	-
July 10-18	26	0.347	-	-
1961				
May 28-June 7	5	0.200	-	-
June 15-22	11	0.364	-	-
July 10-19	17	0.412	-	-
July 26-29	17	0.176	3	0.000

<sup>1</sup> Estimated portion of the 20 day gestation period for which pregnancy can be recognized macroscopically.

for Dicrostonyx because these are the weights above which a majority of females can be mature under good conditions. Finally, these data are given in terms of crude pregnancy rates instead of standardized pregnancy rates (Leslie et al. 1952) because after a complete standardization of the data there was hardly any change in the rates and consequently there was no need to include the standardized rates.

If we examine these data (Tables 21, 22) 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.

Pregnancy rates during midsummer (June 15-July 31) were compared for the Main Study Area and for Aberdeen Lake in <sup>6</sup>both Lemmus and Dicrostonyx. Chi-square tests (Snedecor, 1956, p 228) were made with the following results for the winter generation animals:

#### Significant Differences

	<u>Lemmus</u>	<u>Dicrostonyx</u>
(1) Between years:		
Main Study Area, 1959-61	-	-
Aberdeen Lake, 1960-61	-	*
(2) Between areas:		
Main Study Area vs. Aberdeen Lake		
1960	-	**
1961	-	**

( - =  $P > .10$ ; \* =  $P < .025$ ,  $> .01$ ; \*\* =  $P < .005$ )

While Lemmus showed no differences in pregnancy rates whatever either over

the cycle or between different areas, Dicrostonyx showed a significant lowering of the midsummer pregnancy rate in the decline (1961) at Aberdeen Lake but no differences on the Main Study Area. Furthermore, in each year 1960 and 1961 the pregnancy rates were significantly lower at Aberdeen Lake compared with Baker Lake.

Looking more closely at the Aberdeen Lake Dicrostonyx data, we see that these differences can be explained by a curtailment of breeding in early July, i.e. that the summer breeding season was shortened drastically in 1960 and 1961. The one point that is then left to be explained is the mid-June 1961 rate of 0.364, but this may be due to the late spring phenology of 1961 such that these animals were just beginning to breed.

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 21 and 22 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 either 1959 or 1961 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. The same was true at Aberdeen Lake for Lemmus but not for Dicrostonyx which seemed to show depressed pregnancy rates in the summer of the decline. All other observed changes in pregnancy rates were reflections on 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. As mentioned above, the criteria of maturity were the presence of corpora lutea in females and of visible epididymal tubules in males.

Tables 23-26 give the percentage of mature animals in the various weight classes for Lemmus and Dicrostonyx males and females. 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

TABLE 23. Weight at reproductive maturity in Lemmus males, summers 1959-61.

WEIGHT CLASS (g)	WINTER GENERATION			SUMMER GENERATION					
				Y <sub>1</sub> YOUNG			Y <sub>1</sub> ' YOUNG		
	1959	1960	1961	1959	1960	1961	1959	1960	1961
11-20.5 g.	-	0* (28)	0 (2)	-	0 (9)	0 (11)	0 (2)	0 (12)	0 (5)
21-30.5	-	10 (20)	0 (1)	0 (2)	0 (10)	0 (12)	50 (6)	0 (16)	0 (27)
31-40.5	100 (5)	58 (24)	-	80 (5)	0 (65)	0 (9)	100 (1)	0 (28)	0 (3)
41-50.5	100 (5)	81 (31)	100 (6)	-	0 (19)	-	-	0 (2)	-
51-60.5	100 (9)	98 (59)	100 (12)	-	0 (5)	-	-	-	-
61-70.5	100 (2)	99 (98)	100 (14)	-	-	-	-	-	-
71-80.5	100 (3)	96 (65)	100 (9)	-	-	-	-	-	-
81-90.5	100 (1)	96 (72)	100 (1)	-	-	-	-	-	-
91-100.5	-	97 (29)	-	-	-	-	-	-	-
101-110.5	-	100 (10)	100 (1)	-	-	-	-	-	-

\* Percentage mature; sample size in parentheses.



TABLE 24. Weight at reproductive maturity in Lemmus females, summers 1959-61.

WEIGHT CLASS (g)	WINTER GENERATION			SUMMER GENERATION					
				Y <sub>1</sub> YOUNG			Y <sub>1</sub> ' YOUNG		
	1959	1960	1961	1959	1960	1961	1959	1960	1961
11-20.5	-	0 * (19)	0 (1)	-	13 (8)	0 (18)	0 (2)	0 (7)	0 (3)
21-30.5	100 (1)	0 (12)	0 (2)	100 (1)	40 (10)	75 (16)	100 (3)	0 (4)	32 (19)
31-40.5	50 (6)	5 (21)	50 (6)	100 (8)	39 (61)	100 (7)	100 (2)	0 (25)	100 (1)
41-50.5	100 (6)	21 (48)	64 (11)	100 (2)	80 (15)	100 (2)	-	0 (1)	-
51-60.5	100 (4)	52 (52)	100 (16)	-	100 (7)	100 (1)	-	-	-
61-70.5	100 (4)	92 (48)	100 (14)	-	100 (2)	-	-	-	-
71-80.5	100 (1)	100 (25)	88 (8)	-	-	-	-	-	-
81-90.5	-	100 (26)	100 (1)	-	-	-	-	-	-
91-100.5	-	100 (16)	-	-	-	-	-	-	-
101-110.5	-	100 (3)	-	-	-	-	-	-	-

\* Percentage mature; sample size in parentheses.

TABLE 25. Weight at reproductive maturity in Dicrostonyx males, summers 1959-61.

WEIGHT CLASS (g)	WINTER GENERATION			SUMMER GENERATION					
				Y <sub>1</sub> YOUNG			Y <sub>1</sub> ' YOUNG		
	1959	1960	1961	1959	1960	1961	1959	1960	1961
11-20.5	-	0 * (7)	0 (3)	-	0 (4)	0 (2)	0 (2)	0 (1)	0 (5)
21-30.5	50 (2)	0 (4)	0 (12)	-	0 (3)	0 (7)	0 (3)	0 (4)	0 (3)
31-40.5	78 (9)	40 (5)	71 (14)	0 (1)	0 (3)	0 (1)	-	0 (6)	0 (1)
41-50.5	100 (7)	75 (4)	69 (13)	-	0 (12)	-	-	0 (2)	-
51-60.5	86 (7)	77 (13)	97 (31)	-	0 (3)	-	-	-	-
61-70.5	-	83 (12)	96 (27)	-	-	-	-	-	-
71-80.5	-	80 (15)	100 (10)	-	-	-	-	-	-
81-90.5	-	100 (7)	100 (5)	-	-	-	-	-	-
91-100.5	-	100 (3)	100 (2)	-	-	-	-	-	-
101-110.5	-	67 (3)	-	-	-	-	-	-	-

\* Percentage mature; sample size in parentheses.

TABLE 26. Weight at reproductive maturity in Dicrostonyx females, summers 1959-61.

WEIGHT CLASS (g)	WINTER GENERATION			SUMMER GENERATION					
				Y <sub>1</sub> YOUNG			Y <sub>1</sub> ' YOUNG		
	1959	1960	1961	1959	1960	1961	1959	1960	1961
11-20.5	0 * (1)	0 (6)	0 (11)	0 (2)	0 (1)	7 (15)	0 (1)	0 (10)	0 (3)
21-30.5	25 (4)	0 (3)	9 (11)	0 (1)	0 (2)	33 (3)	0 (7)	0 (6)	0 (2)
31-40.5	100 (3)	0 (4)	10 (10)	-	0 (9)	100 (1)	-	0 (7)	0 (1)
41-50.5	100 (5)	60 (5)	64 (25)	-	12 (17)	-	-	-	-
51-60.5	100 (5)	89 (9)	80 (25)	-	0 (2)	-	-	-	-
61-70.5	100 (3)	100 (19)	93 (28)	-	-	-	-	-	-
71-80.5	-	100 (11)	78 (7)	-	-	-	-	-	-
81-90.5	-	100 (9)	100 (2)	-	-	-	-	-	-
91-100.5	-	100 (4)	100 (1)	-	-	-	-	-	-
101-110.5	-	100 (1)	100 (1)	-	-	-	-	-	-

\* Percentage mature; sample size in parentheses.

converting the weight data into logarithms and percent mature data into probits, fitting a straight line to this, and then calculating the 50% point and its standard error. The results are summarized in Table 27. Some of the data were not sufficient to calculate the median body weight at maturity and in these classes 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.

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) median weights remained the same as 1960, as in winter generation Dicrostonyx of both sexes and Lemmus males; (2) median weights declined to a position intermediate between 1959 and 1960 levels, as in the winter generation Lemmus females; and (3) median weights declined to the same levels as 1959, as in the summer young Lemmus and Dicrostonyx females. 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 summer of 1959 seems to represent the most rapid rates of maturation found in both species. Thus Lemmus females were mature at 20-25 grams and males at 25-35 grams, representing roughly 3-4 weeks and 4-5 weeks of age respectively. Dicrostonyx males and females were mature at about 30 grams, representing roughly 4-5 weeks of age. In neither of the other years were these rapid rates of maturation found, with the exception of the 1961 young females, and it is these deviations from the possible rates of maturation that must be explained.

TABLE 27. Median body weights at maturity for Lemmus and Dicrostonyx males and females, 1959-61.

GROUP AND YEAR	MALES		FEMALES	
	MEDIAN WEIGHT *	95% CONF. LIMITS	MEDIAN WEIGHT	95% CONF. LIMITS
<u>LEMMUS</u>				
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
Y <sub>1</sub> 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
Y <sub>1</sub> ' SUMMER YOUNG				
1959	26.5	-	20-25	-
1960	> 51	-	> 41	-
1961	> 41	-	24.4	22.6 - 26.4
<u>DICROSTONYX</u>				
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
Y <sub>1</sub> SUMMER GENERATION				
1959	?	-	?	-
1960	> 51	-	> 41	-
1961	> 31	-	24.0	22.3 - 27.1

\* Weights in grams.

To sum up, there are striking changes in the median weight at sexual maturity over the cycle. These changes consist in a general increase in the median weight at maturity in the peak summer in all sexes and generations, and a complete lack of maturation of all summer young males in both the peak summer and the summer of decline. In only one summer out of three did either species show maximal rates of maturation.

### Embryo Rates

It is convenient to have one figure which sums up most of the components of reproduction to give some assessment of total productivity. This can be done by the use of embryo rates, following the method of Leslie et al. (1952). If we observe a sample of N mature females, P of which are pregnant and which contain a total of E live embryos, we have for the embryo rate

$$E/N = P/N \times E/P$$

that is, the embryo rate is the proportion of mature females pregnant multiplied by the mean litter size. Since the pregnancy rate reflects changes in the length of the breeding season, changes in the weight at maturity, and changes in the proportion pregnant during the breeding season, this equation effectively sums up most of the components of reproduction (c.f. Figure 5).

Tables 28 and 29 give the crude embryo rates for Lemmus and Dicrostonyx. Crude rates are given here instead of standardized rates because there is very little difference between the two. Total embryo production was obtained in the same way as total litter production above, by applying the observed rates to the length of their particular time period and summing the results. These production figures are hypothetical; for the winter generation they give the number of embryos a mature female would produce if she lived throughout the whole summer and bred at the

TABLE 28. Crude embryo rates per 16<sup>1</sup> days per female >20.5 grams,  
Lemmus, 1959-61.

LOCATION AND TIME PERIOD	WINTER GENERATION				SUMMER GENERATION			
			Y <sub>1</sub> YOUNG				Y <sub>1</sub> <sup>1</sup> YOUNG	
	N	EMBRYO RATE	N	EMBRYO RATE	N	EMBRYO RATE	N	EMBRYO RATE
MAIN STUDY AREA								
1959								
June 15-30	14	4.57	-	-	-	-	-	-
July	3	4.67	1	6.00	-	-	-	-
August	4	3.50	12	3.17	5	3.80	-	-
1960								
May 16-31	140	0.02	-	-	-	-	-	-
June 1-15	31	3.94	-	-	-	-	-	-
June 16-30	21	4.86	-	-	-	-	-	-
July 1-15	16	5.69	1	0.00	-	-	-	-
July 16-31	26	3.46	47	1.17	-	-	-	-
August 1-15	20	0.25	49	0.10	11	0.00	-	-
August 16-31	4	0.00	13	0.00	20	0.00	-	-
1961								
May 16-31	6	0.00	-	-	-	-	-	-
June 1-15	20	0.90	-	-	-	-	-	-
June 16-30	5	6.00	-	-	-	-	-	-
July 1-15	2	8.50	-	-	-	-	-	-
July 16-31	6	2.16	3	4.00	-	-	-	-
August 1-15	3	2.00	-	-	3	0.00	-	-
August 16-31	-	-	1	0.00	6	0.00	-	-
Total Embryo Production for June, July and August								
1959		19.54		8.76		3.09		
1960		17.27		1.27		0.00		
1961		22.39		5.88		0.00		
ABERDEEN LAKE								
1960								
May 27-June 2	9	0.00	-	-	-	-	-	-
June 15-16	4	8.75	-	-	-	-	-	-
July 10-18	12	4.75	8	2.25	-	-	-	-
1961								
June 2-5	3	0.00	-	-	-	-	-	-
June 22	1	9.00	-	-	-	-	-	-
July 26-29	7	2.57	5	1.20	-	-	-	-

<sup>1</sup> Estimated portion of the 21 day gestation period for which pregnancy can be recognized macroscopically.

TABLE 29. Crude embryo rates per 15<sup>1</sup> days per female >30.5 gramsDicrostonyx, 1959-61.

LOCATION AND TIME PERIOD	WINTER GENERATION		SUMMER GENERATION	
	N	EMBRYO RATE	N	EMBRYO RATE
MAIN STUDY AREA				
1959				
June 15-30	3	4.00	-	-
July	9	5.22	-	-
August	3	0.33	-	-
1960				
May 16-31	6	0.00	-	-
June 1-15	22	2.23	-	-
June 16-30	5	6.40	-	-
July 1-15	10	5.10	-	-
July 16-31	6	4.00	2	0.00
August 1-15	7	0.57	5	0.00
August 16-31	10	0.00	13	0.00
1961				
May 16-31	3	0.00	-	-
June 1-15	50	0.48	-	-
June 16-30	25	3.96	-	-
July 1-15	10	2.70	-	-
July 16-31	5	4.00	14	0.71
August 1-15	4	2.00	-	-
August 16-31	4	0.00	1	0.00
TOTAL EMBRYO PROD.				
June - August				
1959		15.48		?
1960		18.56		0.00
1961		13.41		0.76
ABERDEEN LAKE AREA				
1960				
May 27-June 2	4	0.00	-	-
June 15-16	7	5.57	-	-
July 10-18	26	1.28	-	-
1961				
May 28-June 7	5	0.60	-	-
June 15-22	11	2.00	-	-
July 10-19	17	1.59	-	-
July 26-29	17	0.59	3	0.00

<sup>1</sup> Estimated portion of the 20 day gestation period for which pregnancy can be recognized macroscopically.



observed rates, and for the summer generation the number of embryos a female would produce from the time of reaching minimum mature weight to the end of August.

The most striking changes in total reproductive effort occur in Lemmus. If we assume for the moment that female mortality rates were the same in all years, the ratio of total reproductive output for the summers of 1959-61 is 31.4 - 18.5 - 28.3 embryos, or approximately 1.70 - 1.00 - 1.53. As we have seen, these differences arise principally because of changes in the length of the breeding season and in the age at maturity in the young.

In Dicrostonyx, on the other hand, total embryo production was apparently highest in the peak summer of 1960. This contrast with Lemmus is brought about in part by biological differences (i.e. young Dicrostonyx mature at an older age than Lemmus and  $Y_1$  young Dicrostonyx never seem to mature in their first summer; the breeding season of 1961 in Dicrostonyx was apparently shorter than that of 1960) and in part by statistical difficulties (i.e. 1959 and 1961 Dicrostonyx sampling in August and September was insufficient to determine accurately if and when breeding stopped or young matured). For these reasons I do not place too much confidence in the total embryo production figures of 1959 and 1961 for Dicrostonyx. There is a suggestion of decreased productivity during the decline on the Main Study Area; the data from Aberdeen Lake also suggest this.

Total embryo production for the entire year cannot be determined because there are insufficient winter and spring data, and it is necessary to bear in mind that the above figures are only summer production.

Comparison of total summer production of Lemmus with that of Dicrostonyx shows that the potential rate of increase of Lemmus is about

twice as great as that of Dicrostonyx under good conditions.

To sum up, total embryo production during the summer in Lemmus was high in 1959 and 1961 and low in 1960, but in Dicrostonyx seemed to be lower in 1961 than in 1960.

#### SUMMARY AND CONCLUSIONS

(1) There was no significant change in litter size or midsummer pregnancy rates over the cycle.

(2) There were two changes in the length of the breeding season: first, extensive winter breeding occurred only in the winter of increase; and second, there was a shortened summer breeding season in the peak summer and also to some degree in the decline.

(3) The median weight at sexual maturity was higher in the peak summer in all groups 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 or the 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. The purpose of this section is to assess the importance of these components.

## METHODS

Prenatal mortality is assessed by comparing counts made of corpora lutea, implantation sites, and living embryos. The methods of collecting these data were discussed in the section on reproduction.

Data on post-natal mortality were obtained from live trapping. The methods used in live trapping were discussed in the section on population density.

## RESULTS

### 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 we estimate the amount of loss of ova in litters that survive implantation. Partial

post-implantation mortality is estimated from discrepancies between the number of implantation sites and the number of living embryos in the uterus. From these data we 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 only on females in the very late stages of pregnancy, but too few were obtained in this study.

Tables 30 and 31 summarize these 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) and all found to be non-significant. Variation between years was slight; in Lemmus the total loss of ova amounted to 4-9% and in Dicrostonyx to 23-26%. Dicrostonyx suffers considerably more partial prenatal loss than does 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 these animals 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 the frequency of

TABLE 30. Partial prenatal mortality data for Lemmus females, summers 1959-61, Main Study Area.

TYPE OF LOSS	1959	1960	1961
<u>Pre-implantation loss</u>			
% litters showing loss	16.7 N=18	31.3 N = 67	14.7 N = 34
% ova lost	3.9 N = 102	5.3 N = 476	2.3 N = 216
<u>Post-implantation loss</u>			
% litters showing loss	5.6 N = 18	17.9 N = 67	8.8 N = 34
% embryos resorbing	2.0 N = 98	4.2 N = 451	1.9 N = 211

TABIE 31. Partial prenatal mortality data for Dicrostonyx females, summers 1959-61, Main Study Area.

TYPE OF LOSS	1959	1960	1961
<u>Pre-implantation loss</u>			
% litters showing loss	63.6 N = 11	44.0 N = 25	55.9 N = 34
% ova lost	16.9 N = 77	19.7 N = 178	18.2 N = 242
<u>Post-implantation loss</u>			
% litters showing loss	18.2 N = 11	20.0 N = 25	32.3 N = 34
% embryos resorbing	7.8 N = 64	6.3 N = 143	9.1 N = 198

this total litter loss may be made from the snap trapping samples.

No Dicrostonyx have yet been seen with these characteristics. No winter generation Lemmus showing these peculiarities have been found, and thus the condition appears to be found only in Lemmus summer young. The following samples 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
<u>Main Study Area</u>			
1959			
August-Sept. 10	16	16	0
1960			
July 16-31	41	15	6
August 1-15	52	16	6
1961			
July 16-31	2	2	0
August 1-15	3	1	1
August 16-31	10	4	3

If these data are approximately correct, we reach the conclusion that of all the summer young which matured in 1960 about 35-40% lost their entire litters just after implantation, and in 1961 about 50-75% suffered total loss of their litters. Thus these data show a sharp contrast to the partial prenatal loss data given above by suggesting a considerable increase in total litter loss in Lemmus summer young over the cycle.

To sum up our assessment of prenatal mortality: partial prenatal mortality in Lemmus and Dicrostonyx showed no relationship to the cyclic density changes. 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.

#### 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 Type G declines in general.

Some general observations on adult mortality may be made from snap trapping records. Unfortunately snap trapping data cannot give valid quantitative estimates of mortality rates but qualitative observations may be made. There is an annual overturn in population. Adults of the winter generation, which comprise the entire population at the start of the 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. This is reflected in the snap trapping samples as follows:

	% of winter generation adults in snap trap samples	
	<u>Lemmus</u>	<u>Dicrostonyx</u>
1959-61 combined		
June 1-15	100	100
June 16-30	100	100
July 1-15	79	93
July 16-31	60	42
August 1-15	23	35
August 16-31	11	17
September 1-15	2	8

Quantitative observations on adult mortality may be made from the live trapping data. No mortality estimates were obtained in 1959. Tables 32 and 33 give the minimum survival rates for Lemmus in 1960 and 1961, and Tables 34 and 35 for Dicrostonyx in 1960 and 1961. Minimum survival rates 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 rates always underestimate the true survival rate and consequently care must be exercised in interpreting them. To facilitate direct comparisons the observed minimum survival rates were converted logarithmically to a standard 28 day period, and these data are given in Table 36 (Lemmus) and 37 (Dicrostonyx).



TABLE 32. Minimum survival rate estimates for Lemmus, summer 1960.

TIME PERIOD	WINTER GENERATION				SUMMER GENERATION			
	N *	N <sub>t</sub>	N <sub>t+1-∞</sub>	M.S.R.	N	N <sub>t</sub>	N <sub>t+1-∞</sub>	M.S.R.
<u>Quadrat # 1</u>								
June 18 - 20	19	10	2		-			
				0.63				
July 6 - 8	16	5	3		8	2	0	
				0.50				0.25
July 28-30	9	6	0		20	5	0	
				0.67				0.25
August 25-27	8	-	-		50	-	-	
<u>Quadrat # 2</u>								
June 29 -	15	8	0		1	0	1	
July 2				0.53				1.00
July 20 - 23	14	5	0		45	17	0	
				0.36				0.38
August 4 - 6	6	-	-		69	-	-	

\* N = number released, N<sub>t</sub> = number known to be alive next time,

N<sub>t+1-∞</sub> = number included from later sampling, M.S.R. = minimum survival rate over the time period shown.

TABLE 33. Minimum survival rate estimates for Lemmus, summer 1961,  
 Quadrat # 1.

TIME PERIOD	WINTER GENERATION				SUMMER GENERATION			
	N *	$N_t$	$N_{t+1-\infty}$	M.S.R.	N	$N_t$	$N_{t+1-\infty}$	M.S.R.
June 5 -	2	2	0		-			
				1.00				
June 12 -	4	1	2		-			
				0.75				
June 19 -	5	5	0		-			
				1.00				
June 26 -	4	3	1		-			
				1.00				
July 3 -	3	2	1		-			
				1.00				
July 10 -	3	0	1		1	0	0	
				0.33				0.00
July 17 -	3	1	0		-			
				0.33				
July 24 -	2	0	0		-			
				0.00				
July 31 -	-				-			
August 7 -	-				1	0	0	
								0.00
August 14 -	-				-			
August 21 -	-				-			
August 28 -	-				-			
Sept. 1								

\* N = number released,  $N_t$  = number known to be alive next time,  
 $N_{t+1-\infty}$  = number included from later sampling, M.S.R. = minimum  
 survival rate over the time period shown.

TABLE 34. Minimum survival rate estimates for Dicrostonyx, summer 1960, Quadrat # 2.

TIME PERIOD	WINTER GENERATION				SUMMER GENERATION			
	N *	$N_t$	$N_{t+1-\infty}$	M.S.R.	N	$N_t$	$N_{t+1-\infty}$	M.S.R.
June 29 -	6	4	1		-			
July 2				0.83				
July 20 - 23	8	4	0		5	2	0	
				0.50				0.40
August 4 - 6	8	-	-		7	-	-	

\* See Table 33 for explanation of symbols.

TABLE 35. Minimum survival rate estimates for Dicrostonyx, summer 1961, Quadrat # 3.

TIME PERIOD	WINTER GENERATION				SUMMER GENERATION			
	N *	$N_t$	$N_{t+1-\infty}$	M.S.R.	N	$N_t$	$N_{t+1-\infty}$	M.S.R.
June 5 -	2	0	1	0.50	-			
June 12 -	16	7	4	0.69	-			
June 19 -	14	6	5	0.79	-			
June 26 -	12	2	9	0.92	-			
July 3 -	11	9	2	1.00	-			
July 10 -	11	5	3	0.73	-			
July 17 -	8	4	2	0.75	-			
July 24 -	6	2	1	0.50	2	0	0	0.00
July 31 -	3	2	0	0.67	5	1	2	0.60
August 7 -	2	0	0	0.00	4	2	2	1.00
August 14 -	-				6	2	1	0.50
August 21 -	-				6	2	0	0.33
August 28 - Sept. 1	-				2	-	-	

\* See Table 33 for explanation of symbols.

TABLE 36. Minimum survival rates for Lemmus converted to a 28 day base.  
Original data in tables 32 and 33.

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-Aug. 25	0.68	0.26
Quadrat # 2		
June 29-July 20	0.43	1.00
July 20-Aug. 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	-
Aug. 1-31	0.00	0.00

TABIE 37. Minimum survival rates for Dicrostonyx converted to a 28 day base. Original data in tables 34 and 35.

MINIMUM SURVIVAL RATE PER 28 DAYS		
	WINTER GENERATION	SUMMER GENERATION
1960		
Quadrat # 2		
June 29-July 20	0.78	-
July 20-Aug. 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
Aug. 1-15	0.00	0.36
Aug. 16-31	-	0.03

Considering only the winter generation, we see first that overall summer survival appears to have been better in 1960 than in 1961 for both species. 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 because breeding was occurring, but we can obtain a block estimate for the 1960-61 winter because no breeding occurred. As was shown above in discussing density changes, there was a 90-95% decrease in Lemmus and a 70-80% decrease in Dicrostonyx over the period 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% monthly mortality would produce a 70-80% decline over this period, and for Lemmus a 20-25% monthly mortality would produce the observed 90-95% reduction.

There is some indirect evidence that the winter mortality rate in 1960-61 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
<u>Lemmus</u>	30 of 98	3 of 99

## Proportion of winter specimens caught alive

before December 31

after January 1

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 into our model by adding one month with an increased mortality rate of 50%, all other months having a constant rate. Then a 15-20% monthly mortality with one month increased to 50% predicts a decline in Lemmus similar to that observed. The interesting thing to note is that the magnitude of this increased mortality rate during one month has very little effect on the final predicted decline; for example,

20% monthly mortality	= 89% decline over 10 mo.
20%    "        "        plus one month at 33%	= 91%    "        "        "
20%    "        "        "        "        "        "        50%	= 93%    "        "        "

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

The conclusion to this discussion on winter mortality in 1960-61 is that although the decline in both species over this time is very great numerically, the average monthly mortality rates which could produce the observed declines are reasonable for small mammals (Leslie, Chitty, and Chitty,<sup>1953;</sup> Golley, 1961); indeed if anything they seem to be low rather than high.

In summary, mortality of the winter generation appeared slightly higher in the summer of 1961 than in the summer of 1960. Winter mortality rates during 1960-61 were moderate to low but produced a great numerical



decline because of the lack of breeding over this 9-10 month period. Nothing is known of summer mortality in 1959 or winter mortality in 1959-60. The data are not sufficient to investigate 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-weaning mortality and early post-weaning mortality.

For a general idea of changes in juvenile mortality we may return to Tables 32-37 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. Knowing from the reproductive data given previously the mean timing of breeding periods and the mean litter size, and knowing from live trapping 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 all the young being 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 the results are presented in Tables 38-41.

These survival estimates are a composite of birth-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 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  $Y_1'$  and very few  $Y_1''$ ). 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-weaning mortality could not be separated from early post-weaning mortality in these estimates. If much loss occurred at birth or shortly after, 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 and 1961. During the breeding season of both 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.

TABLE 38. 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. <sup>1</sup>
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	Aug. 25-27	August 25-27
No. of these juveniles in traps then	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 base	0.56	0.50	0.25

<sup>1</sup> Pregnancy rate of young = 0.50; continuous breeding assumed for adults.

TABIE 39. 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	7.00	7.80	0
Date of subsequent trapping	July 13-15	Aug. 10-12	Aug. 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 a 28 day base	0.09	0.07	-

TABLE 40. 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 20-23	-
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 a 28 day base	0.38	?

TABLE 41. 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. of 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 27-29	Aug. 3 - 5	Aug. 24-26
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 base	0.05	0.14	?

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.

#### SUMMARY AND CONCLUSIONS

(1) Partial prenatal mortality showed no change in either species over the cycle, but the complete loss of litters just after implantation for summer young Lemmus seemed to be high in the peak summer and in the summer of decline.

(2) Adult mortality seemed to increase slightly in the summer of the decline in both species, and winter mortality rates in 1960-61 were low to moderate in both species. Nothing is known about mortality during 1959 or the 1959-60 winter.

(3) Juvenile mortality between birth and shortly after weaning was very high in the summer of the decline particularly for the first summer litter. This conclusion probably applies only to Type G declines as will be shown in a later section.

## 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 through reproduction or mortality changes.

### METHODS

Almost all data on local movements were obtained by live trapping, and these methods have been discussed in a previous section. A few movements were obtained by snap trapping animals which had previously been live trapped.

### RESULTS

#### 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 Davis (1953), 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 analyze distances between successive captures (Brown, 1956) because this allows us to use animals captured only twice during a trapping period. This type of analysis is confined to short term movements within trapping periods.

Tables 42 and 43 give the length of every movement recorded within trapping periods for Lemmus in 1960 and 1961, and Tables 44 and 45 give the same information for Dicrostonyx. Differences between the years were tested by chi-square (Snedecor, 1956) and both species showed a



TABLE 42. Length of every movement recorded within periods of live trapping for Lemmus, summer 1960, Quadrat # 2.

LENGTH OF MOVEMENT	WINTER GENERATION		Y <sub>1</sub> SUMMER YOUNG	
	MALES	FEMALES	MALES	FEMALES
≤ 50'	8	17	15	12
51-100'	6	13	7	10
101-150'	5	10	4	7
151-200'	3	9	3	6
201-300'	3	1	3	3
301-400'	5	2	0	2
401-500'	0	1	1	0
501-700'	-	-	-	-
701-900'	-	-	-	-
	N = 30 $\bar{x}$ = 143.3'	N = 53 $\bar{x}$ = 105.1'	N = 33 $\bar{x}$ = 94.6'	N = 40 $\bar{x}$ = 111.2'

TABLE 43. Length of every movement recorded within periods of live trapping for Lemmus, summer 1961, Quadrat # 1, and vicinity.

LENGTH OF MOVEMENT	WINTER GENERATION		Y <sub>1</sub> SUMMER GENERATION	
	MALES	FEMALES	MALES	FEMALES
≤ 50'	1			
51-100'	2			
101-150'	6			
151-200'	2			
201-300'	3	?	?	?
301-400'	0			
401-500'	1			
501-700'	1			
700-900'	1			

N = 17

$\bar{x}$  = 229.3'

TABLE 44. Length of every movement recorded within periods of live trapping for Dicrostonyx, summer 1960, Quadrats # 2 and # 3.

LENGTH OF MOVEMENT	WINTER GENERATION		Y <sub>1</sub> SUMMER YOUNG	
	MALES	FEMALES	MALES	FEMALES
≤ 50'	15	8	2	0
51-100'	6	3	1	1
101-150'	1	1	1	-
151-200'	1	2	-	-
201-300'	2	2	-	-
301-400'	2	0	-	-
401-500'	-	-	-	-
501-600'	-	-	-	-
	N = 27	N = 16	N = 4	N = 1
	$\bar{x}$ = 86'	$\bar{x}$ = 84'	$\bar{x}$ = 62'	$\bar{x}$ = 71'

TABLE 45. Length of every movement recorded within periods of live trapping for Dicrostonyx, summer 1961, Quadrat # 3 and vicinity.

LENGTH OF MOVEMENT	WINTER GENERATION		Y <sub>1</sub> SUMMER YOUNG	
	MALES	FEMALES	MALES	FEMALES
≤ 50'	1	1	0	-
51-100'	1	6	1	-
101-150'	5	2	-	-
151-200'	0	3	-	-
201-300'	1	1	-	-
301-400'	0	-	-	-
401-500'	1	-	-	-
501-600'	1	-	-	-
	N = 10	N = 13	N = 1	N = 0
	$\bar{x} = 201'$	$\bar{x} = 112'$	$\bar{x} = 71'$	

significantly greater number of long movements recorded in 1961 than in 1960 (Lemmus winter generation males,  $P < .05, > .025$ ; Dicrostonyx winter males,  $P < .005$ ; and Dicrostonyx winter females,  $P < .05, > .025$ ). The suggestion is that the low density of 1961 was accompanied by a greater mobility of the adults at least, compared to 1960. No data on movements were obtained in 1959.

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 the two years. In 1961, in particular, 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 that it was not trapped.

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

1960     $N = 4$      $\bar{x} = 286$  feet     $\pm 63$  feet (1 SE)

1961     $N = 3$      $\bar{x} = 631$  feet     $\pm 170$  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 any other group except this 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 7) where  $1/4$  to  $1/3$  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 analyzed 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		
<u>Lemmus</u> adult male	3700	June 2-July 8
<u>Lemmus</u> Y <sub>1</sub> female	2600	July 7-28
<u>Lemmus</u> Y <sub>1</sub> male	525	July 23-August 4
1960-61 (the following are 1960 summer young recaptured alive as adults in June 1961)		
<u>Lemmus</u> female	2400	Aug. 1960 - June 1961
<u>Lemmus</u> female	365	" "
<u>Lemmus</u> female	2500	" "
<u>Dicrostonyx</u> 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 more in the latter alternative after having seen movements of 500-800 feet take place in less than 24 hours within a trapping period (see Tables 43 and 45).

## 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 lemmings.

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, as each local center of density began to be affected by the snow melting. 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 AM to 4 AM 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 onto the ice and then later moved back again. One of the Lemmus males tagged was later recovered on the live trapping area five weeks later after having moved 3700 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 30 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 or 1961 in the area.

The general conclusion regarding these "migrations" of lemmings is that they assume a mental status disproportionate to their biological significance for the lemmings. The actual events are far less striking than the legend, and not all peak populations even show these events.

#### SUMMARY AND CONCLUSIONS

(1) Whether lemmings occupy a definite territory or home range is not known.

(2) There is a suggestion that the average distance moved between traps was greater during the decline of 1961 compared to the peak summer of 1960 in adults of both species.



(3) Individual animals can move over large distances; instances of animals having moved 800 feet in less than one day have been recorded.

(4) True group movements ("migrations") are very rarely if ever recorded, but the spring melt-off during the peak year may be accompanied by considerable local movement of individuals.

(5) There is no evidence that "migrations" or even these spring movements are a necessary part of the cycle in numbers.

## 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, and we must enquire whether extrinsic factors can adequately explain the observed density changes of lemmings.

### Weather

The winter of 1959-60, when the lemmings increased, began with a dry freeze-up and a quick buildup of snow cover. The winter of 1960-61, when they declined, began with a wet freeze-up and a slow buildup 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, probably there were some areas in 1960-61 that were as favorable weather-wise as areas in 1959-60. Yet no winter breeding was found in 1960-61, which suggests that bad winter weather was not sufficient to cause the observed absence of breeding.

One of the most striking facts about this 1959-61 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. We do not know if good winter weather is the only thing needed for an increase in numbers, or whether some other factor must also be present.

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. Because of this post hoc climatic correlations must always be suspect. Only by replicating and diversifying our observations on the association between types of weather and cyclic changes can we hope to obtain a better idea of its role until experimental work can be done.

To sum up, favorable deviations from the average winter weather were associated with a large increase in density, and unfavorable deviations were associated with a decline in numbers. Summer weather seemed of little importance.

### Predators

Avian predators 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 census 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 on this area. In 1961 avian predators were again scarce. Only one snowy owl, 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 three years on the islands in Baker Lake which support

considerable numbers of nesting birds.

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), wolves (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 end of August and many more in early September. Complete autopsies were done on 22 of the August specimens. Of these 21 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, 7; bird feathers and bones, 3; lemming fur and bones, 2; fish (?), 3; caribou meat (?), 4; berries and plant matter, 2; 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.

We must now see whether these weasels could have been responsible for the mortality changes of the lemming population. It seems doubtful whether 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.

#### Disease and Parasites

No detailed studies on disease or parasites were made in this research program, but in the course of autopsying some 2500-3000 lemmings only eight specimens have been 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 1960-61 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.

There is thus little evidence that disease or parasites can adequately explain the cyclic events.

### 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 sq. meters 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 3/8" hardware cloth screening which was buried 8-12" in the ground and extended 24-28" above ground. There was no evidence that any lemmings got inside any of these enclosed quadrats during the period of study. This general approach was the same as that of Thompson (1955 b).

Table 46 gives the standing crop measurements at the end of the 1959, 1960, and 1961 growing seasons on the Main Study Area. These data may be considered in two parts. Quadrats # 1-10 were present during all three years; quadrats # 11-15 were installed in 1960 and serve as a further check on the 1960-61 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 from this base -- weather effects and lemming effects --, and the problem is to separate these. This was done in the following way. \*

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\* I am indebted to Dr. Monte Lloyd, Bureau of Animal Population, for this statistical technique.

TABLE 46. Standing forage in grams per 0.5 sq. meter dry weight at the end of summer.

QUADRAT #	1959		1960		1961	
	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
4	48.9	31.9	58.8	36.5	100.8	68.3
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
7	24.7	25.4	43.0	35.1	42.0	32.8
8	37.1	47.6	57.0	53.7	79.4	49.5
9	74.5	73.2	115.8	86.2	109.3	90.89
10	46.5	37.3	57.1	40.9	54.9	53.5
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
$\bar{x}_{1-10}$	45.8	38.8	63.5	48.3	77.0	58.5
$\bar{x}_{11-15}$			66.6	72.8	91.4	83.8

The difference between each 1960 enclosed quadrat and the same quadrat in 1959 must be caused only 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 differences and thereby test the significance of these effects. The same procedure may be applied to the 1961 data.

The weather effects are significant between all three years ( $P < .01$ ), the progression in the size of the standing crop being  $1959 < 1960 < 1961$ . 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.

Lemmings significantly depressed the standing crop in both 1960 and 1961 ( $P < .05$ ,  $> .01$ ). There is no difference in the lemming effect on quadrats # 1-10 between 1960 and 1961, and the lemming effect shows up in 1961 on the new quadrats # 11-15 as would be expected ( $P < .01$ ). The depressing effect of the lemmings on the forage is very nearly the same in 1960 and 1961 on both sets of quadrats. If we set theoretical standing crop at what would occur in the absence of lemmings, the lemmings are found to depress standing crop by 14.5% in 1960 and 16.4% in 1961 on quadrats # 1-10, and by 14.1% in 1961 on Quadrats # 11-15.

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 one might expect high utilization from prior knowledge. 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 enclosures' subsequent altering of the microclimate of the quadrat. We must assume that these microclimatic changes are negligible, but this may not be true. 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 3' by 1' 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 3 sq. feet and a visual estimate was made of the proportion of the forage that had been eaten. Transects were done only in the wetter habitats and utilization was estimated separately for sedges, mosses, and heaths on each plot. 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 and quality of the food supply was at its lowest point for the year.

Table 47 gives these forage utilization estimates made in the spring of the decline. No transects were made in either 1959 or 1960 because total utilization was too small to be conveniently measured. These data for 1961 show average utilization of 30% at the most for the wetter habitats. It was rather difficult to estimate the moss utilization but this

TABLE 47. 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		
				SEDGES	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	-

was attempted because moss is a very important food item during the winter. The pattern of forage utilization was very spotty in 1961. Small areas 2-6 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 4-5 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 utilized at all during the winter of 1960-61. Small local areas were devastated but on the whole utilization must have been less than 5%. Since the plants of the dry tundras grow very slowly (heath recolonization may take 50 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 1960-61 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 analyze 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.

#### SUMMARY AND CONCLUSIONS

(1) Favorable winter weather was associated with the increase in numbers, and unfavorable winter weather was associated with the decline. Summer weather showed no correlation with density changes.

(2) Avian predators were uncommon throughout the cycle and did not appear to play a necessary role in it. The weasel or ermine was the only important mammalian predator and these were not common until 1961, especially during August and September. However, there was no evidence that weasel predation accounted for the mortality changes observed in the lemmings.

(3) There was no evidence that disease or parasites played any necessary role in this cycle.

(4) Lemmings significantly reduced the standing crop of forage in both 1960 and 1961 by about 15%. Forage utilization averaged 30% or less in the wetter habitats just after the winter of 1960-61, and the dry habitats were scarcely touched. There was no evidence of quantitative food shortage, nor any clear suggestion of a deficiency in food quality over the cycle.

## 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 behavioral and physiological changes in the individual organism. The intrinsic factors are behavior and physiology; these may be studied directly in themselves or indirectly by their effects. In this section we shall analyze 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.

### METHODS

#### Age Determination

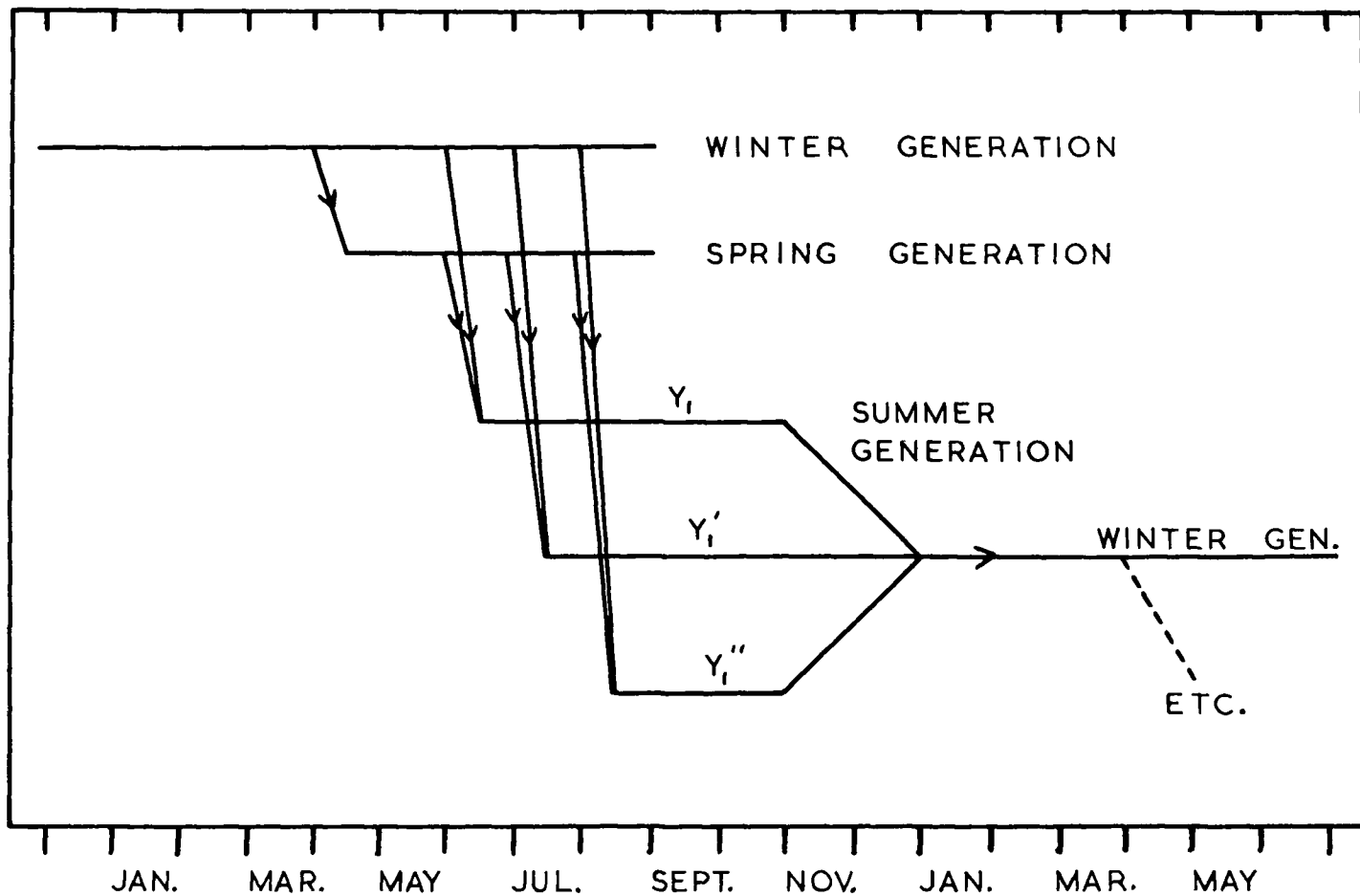
Many different techniques for measuring chronological age have been proposed, but the majority of small mammal workers still use body weight as a criterion of age (e.g. Chitty, 1952; Hoffmann, 1958). Frank and Zimmermann (1957) found that the body weight - age relationship in Microtus arvalis was greatly 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 but analysis showed that lens weight was normally proportional to body weight. Whatever caused the body weight to change also caused the lens weight to change, and so no additional information accrued from weighing lenses (one exception to this is discussed below). Body weights were used rather than total lengths because there is much less variability both within and between workers when using measurements than when using total length measurements.

Mean Body Weights

Figure 6 gives a generalized chronology and classification of the litters and generations of both species of lemmings and is necessary for the discussion that follows. This basic pattern varies slightly in the different phases of the cycle. The winter generation consists either of overwintered animals (1959 ? and 1961) or of animals born during the fall and winter (1960). The spring generation appears each year before the snow melts but is not very large numerically; it essentially behaves like the winter generation during the summer. The summer litters follow in rapid sequence; it is probable that some adult females produce only two litters and others four litters, and this may vary with the cyclic phase, but the general pattern is about three summer litters per adult female. By fall only summer born young are left and these form next year's winter generation. Summer young females may breed in their first summer and add a further generation to the fall population, but this complication has been left out of this diagram.

In computing mean body weights we would like 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. 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, 1960 samples. Since breeding occurred throughout this winter it was somewhat arbitrary to distinguish a winter generation and a spring generation, but this was done for the above two samples on the basis of breeding vs. non-breeding animals, 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.

FIGURE 6. Generalized annual chronology of generations and litters for Lemmus and Dicrostonyx.





In Dicrostonyx the problem is much more difficult. The spring generation appears in all three years and persists as a distinct entity even into August. Data on body weight, total length, lens weight, and reproductive condition were utilized 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 utilized as break points. In 1959 gaps in body weight and total length distributions were mainly utilized 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 meaningful than they would be if these two groups were mixed.

#### Organ Weights

All organs were preserved in 10% neutral formalin and weighed in the winter after collection either on an electric balance or on a torsion balance. 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  $\pm 3\%$  in normal weighings. Some of the larger organs were weighed fresh in the field during 1961.

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, p 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. All the data are grouped and mean organ weights for each 10 g 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

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.

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 results would be expressed in percentages). 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.

## RESULTS

### Body Weight Distributions

Much information can be learned from age or weight distributions (Bodenheimer, 1938; Leslie and Ranson, 1940). Tables 48 and 49 give the weight distributions for Lemmus and Dicrostonyx males during 1959-61 on the Main Study Area. The data for the females are not given here because they are very similar to that for the males. All the weight data discussed here were obtained from the snap trapping samples; weight data from live trapping are not presented but they show the same changes described here. Some care must be taken in comparing weight distributions between the years because 1959 was biologically 2-3 weeks behind 1960, and 1961 was about 1 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 or 1961. There were very few Lemmus above 76 g in either 1959 or 1961, but in 1960 a majority of the adults were above this weight. In Dicrostonyx the difference between 1960 and 1961 was not so well marked but the same tendency was shown. Second, if we consider the winter data, Lemmus did not appear to increase in weight through the winter whereas the Dicrostonyx weight distributions suggest that they did increase in weight at least slowly during the winter. A sudden spurt of growth seems to occur in May for each species. Third, there was a gap in the 1961 summer weight distributions where the early summer young should be. Again this was shown more clearly by Lemmus than by Dicrostonyx. The left part of Figure 7 shows graphically the late July Lemmus male weight distributions for 1960 and 1961 on the Main Study Area and illustrates two of these points, i.e. the higher body weights of 1960

TABLE 48. Body weight distributions for Lemmus males on the Main Study Area, 1959-61. Dotted lines separate summer generation from winter and spring generations.

WEIGHT CLASS (grams)	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.
<u>1959</u>																
11-												3				
16-												1				
21-												3			2	
26-												3			1	
31-								3				2			1	
36-								2				2			-	
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
<u>1960</u>																
11-						7				4		7				
16-						21		1		5		2				
21-						11		-		-		3				
26-		1				7		2		-		5				
31-		1				10		-		7		11				
36-		1				12		2		18		35		1	2	3
41-		-				11		3		5		18		9	7	13
46-		1				11		6	1	-		9		8	6	11
51-		-				22		5	1	-		1		7	1	5
56-		1				20		10	1	-		3		1	1	-
61-						29		10	3	-		-		1	-	-
66-						42		5	5	2		1		-	-	-
71-						25		7	4	1		3		1	-	2
76-						21		2	3	1		-		-	-	-
81-						25		5	3	1		5		-	-	-
86-						9		3	6	3		4		3	-	-
91-						9		2	4	3		2		1	-	-
96-						4		1	1	-		2		1	-	-
101-						1		1	1			3			-	-
106-								2	1						-	-
						297		65	35	24		40		102	59	29
															17	34
<u>1961</u>																
11-						1				1		1				
16-						-		1		-		1		2		
21-						1		-		-		2		6		
26-						-		-		-		3		6		
31-	3	1				-		-		-				6		
36-	6	5				-		-		-				3		
41-	6	6				-		3		-		1		-		
46-	2					-		2		-		-		-		
51-	1					-		4		-		-		-		
56-	1					-		2		-		1		-		
61-						-		2		-		2		-		
66-						-		2		2		3		-		
71-						1		2		2				-		
76-						1		3						-		
81-								1						-		
86-														-		
91-														-		
96-														-		
101-														-		
	19	12				4		3	1	4		23		11		3
												8		7		17

TABLE 49. Body weight distributions for Dicrostonyx males on the Main Study Area, 1959-61. Dotted lines separate summer generation from winter and spring generations.

WEIGHT JAN. FEB. MAR. APR. MAY MAY JUNE JUNE JULY JULY AUG. AUG. SEPT. OCT. NOV. DEC.  
CLASS 1-15 16-31 1-15 16-30 1-15 16-31 1-15 16-31  
(grams)

1959

11-									3		2				
16-									1		1				
21-									1		2				
26-							1		1		1				
31-							1		2		1			1	
36-							3		3		1			1	
41-							1		2		1			2	
46-							1		2		1				
51-							3		2		1				
56-									1						
61-															
66-															
71-															

10 16 8 3

1960

11-					1										
16-					5		1		1	3	1	2			
21-					2		1		1	1	1	1			
26-					1		2		1	2	1	2			
31-					1		2		1	1	1	2			
36-				1	1		2	1	1	1	6	2			
41-	1			1	1		1		2	4	1	5	4		
46-	1			4	1		1		2	1	2	3	1	1	2
51-	1			3	1		3	1	2	1	1	2	2	1	2
56-	1			4	1		3	1	2	1	1	1	1		3
61-	1			2	1		1	2	1	1	1	1	1		1
66-	1			3	3		1	1	2	1	2	1	1		1
71-	1			1	3		3	3	3	1	1	1	1		
76-	1			1	2		2	1	1	1	1	1	1		
81-	1			1	2		2	1	1	1	1	1	1		
86-				1	1		1	1	1	1	1	1	1		
91-				2	1		1	1	1	1	1	1	1		
96-				1	1		1	1	1	1	1	1	1		
101-				1	2		2	1	1	1	1	1	1		
106-															

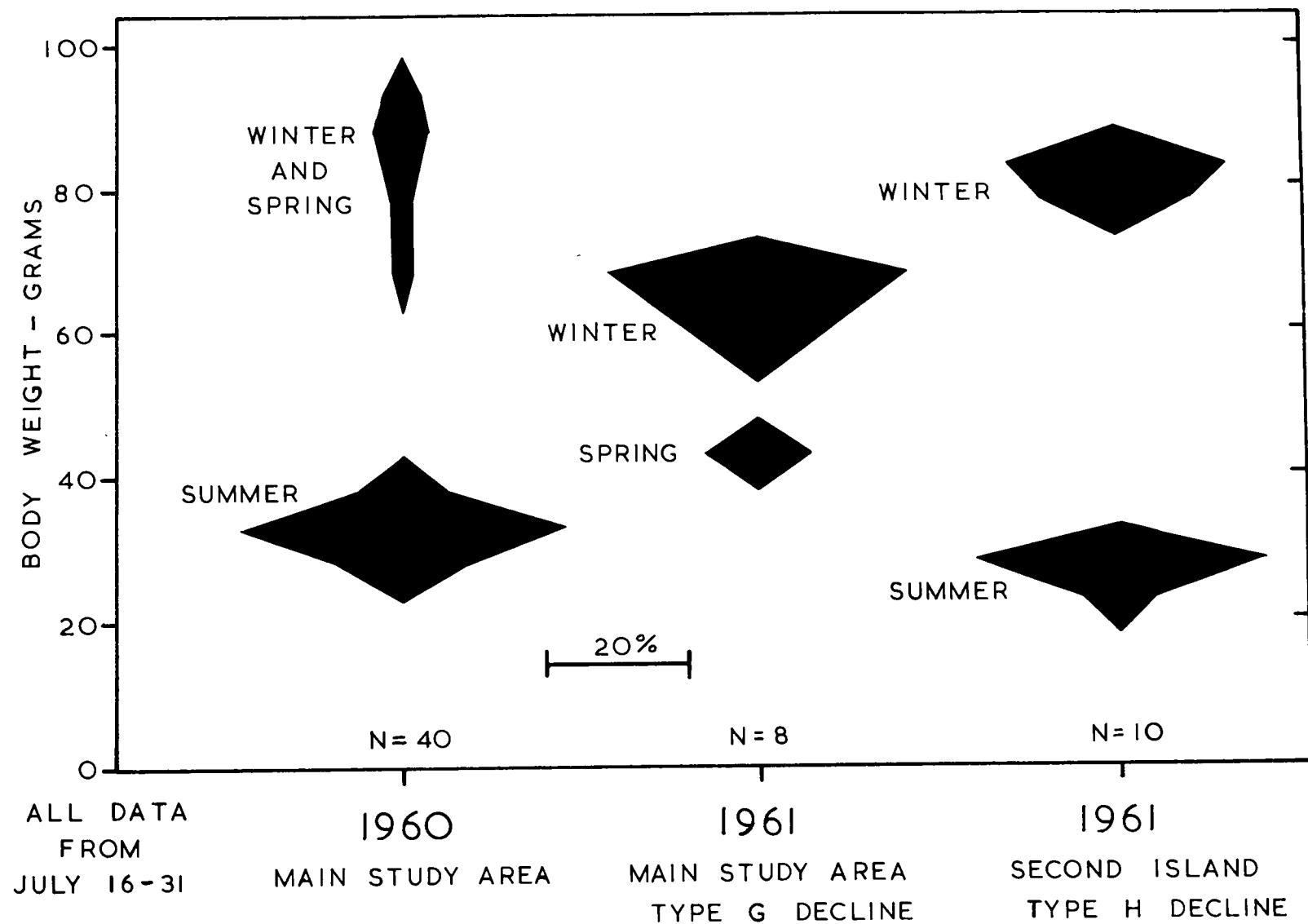
5 20 18 25 9 17 13 9 25 9 2 8

1961

11-					1	1				1					
16-					1	2				1	5	2			
21-					1	4				1	1	7			
26-					1	6	1		1	1	6	2			
31-					1	2	1		2	1	1	2			
36-				1	1	3	1		4	1	1	1			
41-		1	1	1	1	7	1		1	1	1	1			
46-	1		1	1	1	2	1		1	1	1	1			
51-	1				1	6	2		3	1	1	1			
56-	2				2	10	4		2	1	3	3			
61-	1				1	7	2		2	2	3	3			
66-	1				1	8	1		1	1	1	1			
71-	1				2	2	2		1	1	1	1			
76-					1	4	1		1	1	1	1			
81-					1	2	1		1	1	1	1			
86-					1	1	2		1	1	1	1			
91-					1	1	1		1	1	1	1			
96-															

5 1 3 3 9 68 19 17 9 20 14

FIGURE 7. Body weight distributions for Lemmus males, July 16-31, 1960 and 1961. Winter, spring, and summer indicate generations.



and the missing summer young of 1961 for the Main Study Area.

It is instructive to compare the body weight distributions for Aberdeen Lake during 1960 and 1961 with those of the Main Study Area. Tables 50 and 51 give the data for Lemmus and Dicrostonyx males at Aberdeen Lake. The first point to notice about these data is that there is very little difference between the 1960 and 1961 distributions in either species, contrary to the result found on the Main Study Area. High body weights are found in both years and there does not seem to be a missing group of summer young in 1961. This difference between Aberdeen Lake and the Main Study Area does not appear until 1961, as the 1960 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. These data are given in Table 52. Only data for Lemmus males are given; Dicrostonyx is very sparse on all these trapping areas. New Lake, Lower Thelon River, Ten Mile Island, and the Prince River were sampled in 1960 also, but these data are not given here because they are virtually identical with that previously given for the Main Study Area in 1960. These 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 striking differences. New Lake, Long Island, Second Island, Ten Mile Island, and Nine Mile Island show the weight distribution pattern found at Aberdeen Lake and not that found on the Main Study Area. The Prince River shows the Main Study Area pattern. These two different patterns are shown graphically in the right part of Figure 7.

We can summarize these relationships in the following way:



TABLE 50. Body weight distributions for Lemmus males at Aberdeen Lake, 1960-61.

WEIGHT, CLASS	1960			1961		
	MAY 27- JUNE 2	JUNE 15-16	JULY 10-18	JUNE 1-5	JUNE 22- July 10	JULY 26-29
11-						2
16-			1			7
21-			6			2
26-			1			3
31-			-			-
36-			2			-
41-	2		-			-
46-	-		1			-
51-	-		2			-
56-	1	1	3			-
61-	-	-	-			-
66-	1	1	2	1		1
71-	-	1	2	1	1	1
76-	-		2		-	2
81-	2		3		1	3
86-	1		-		-	-
91-			2		2	-
96-			1			1
101-			-			-
106-			2			-
	<u>7</u>	<u>3</u>	<u>28</u>	<u>2</u>	<u>4</u>	<u>22</u>

TABLE 51. Body weight distributions for Dicrostonyx males at Aberdeen Lake, 1960-61. Dotted lines separate summer generation from winter and spring generations.

WEIGHT CLASS	1960			1961			
	MAY 27- JUNE 2	JUNE 15-16	JULY 10-18	MAY 28- JUNE 7	JUNE 13-22	JULY 10-19	JULY 26-29
11-			3			1	
16-			2			-	1
21-	1		2	1		-	1
26-	-		-	-	1	-	2
31-	-		-	-	-	-	2
36-	-		2	-	-	-	1
41-	1		5	1	-	-	3
46-	-	1	3	-	1	2	2
51-	-	2	2	-	-	-	1
56-	-	-	2	-	2	-	2
61-	-	-	-	1	1	2	2
66-	-	-	2	-	2	-	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						
	<hr/>	<hr/>	<hr/>	<hr/>	<hr/>	<hr/>	<hr/>
	9	5	29	7	11	8	26

TABLE 52. Body weight distributions for Lemmus males on the outlying areas, summer 1961. Dotted lines separate summer generation from winter and spring generations.

WEIGHT CLASS	NEW LAKE July 4-12	LONG ISLAND July 17-20	SECOND ISLAND July 24-27
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	
	<u>8</u>	<u>9</u>	<u>10</u>

WEIGHT CLASS	LOWER THELON R. August 14-19	TEN MILE IS. Aug. 14-19	NINE MILE IS. Aug. 14-19	PRINCE R. Aug. 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-				
	<u>8</u>	<u>11</u>	<u>5</u>	<u>7</u>

	1959		1960		1961	
	Weights Ad. ♂	Recruit. Y <sub>1</sub> young	Weights Ad. ♂	Recruit Y <sub>1</sub> young	Weights Ad. ♂	Recruit. Y <sub>1</sub> young
1. Main Study Area *	Low	+	High	+	Low	-
2. Aberdeen Lake *			High	+	High	+
3. New Lake			High	+	High	+ ?
4. Thelon River			High	+	?	-
5. Ten Mile Is.			High	+	High	+
6. Prince River			High	+	Low	-
7. Nine Mile Is.					High	+
8. Long Island					High	+
9. Second Island					High	+

( \* 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 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.

It is pertinent to enquire what differences there are between the areas showing no recovery of numbers in 1961 and the areas showing some recovery. There is no apparent relationship with either the quality of the habitat or the population density of the area in 1960. This is illustrated in the following table:

	Type of Vegetation	Density in 1960	Type of Decline
Thelon River	thick	very high	no recovery
New Lake	thick	very high	some recovery
Main Study Area	sparse	mod. high	no recovery
Ten Mile Is.	sparse	mod. high	some recovery

It is also clear that 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 were undergoing Type H declines. The significance of this is not understood.

To sum up the results of analyzing 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.

#### Mean Body Weights

We may quantify the observation that high body weights were associated with the peak summer and Type H declines by computing mean body weights for the adults. Tables 53 and 54 give the mean body weights for the winter and spring generations of Lemmus and Dicrostonyx males for 1959-61. We are mainly concerned here with the winter generation.

The Lemmus data (Table 53) are very clear. On the Main Study Area the peak summer of 1960 showed mean body weights about 28% greater than 1959 and 20% greater than 1961. In both cases the differences are clearly significant. For Aberdeen Lake the 1960 and 1961 data are not significantly different, high body weights occurring in both years. The other areas sampled in 1961 all have high mean body weights except for the Prince River.

The Dicrostonyx data (Table 54) are not so clear. On the Main Study Area the peak summer of 1960 showed mean body weights about 40% greater than 1959 and 11% greater than 1961. The question arises whether the latter figure is statistically significant. A non-parametric ranking test

TABLE 53. Mean body weights for Lemmus males of the winter and spring generations, summers 1959-61.

LOCATION AND TIME PERIOD	WINTER GENERATION			SPRING GENERATION		
	N	WEIGHT	S.E.	N	WEIGHT	S.E.
<u>Main Study Area</u>						
1959						
June 16-30	10	50.21	$\pm 1.83$	5	34.38	$\pm 1.00$
July 1-15	4	56.60	$\pm 3.07$	-	-	-
July 16-31	-	-	-	1	49.40	-
August 1-15	4	69.10	$\pm 4.40$	-	-	-
August 16-31	3	71.30	$\pm 7.74$	-	-	-
1960						
May 16-31	241	66.92	$\pm 0.95$	56	22.23	$\pm 0.88$
June 1-15	57	67.20	$\pm 1.83$	8	36.00	$\pm 3.51$
June 16-30	35	79.33	$\pm 2.52$	-	-	-
July 1-15	15	81.77	$\pm 4.53$	-	-	-
July 16-31	10	83.79	$\pm 2.50$	-	-	-
August 1-15	14	91.06	$\pm 2.20$	-	-	-
August 16-31	7	82.61	$\pm 3.30$	-	-	-
1961						
May 16-31	2	76.60	$\pm 1.80$	2	19.40	$\pm 4.80$
June 1-15	22	62.58	$\pm 3.28$	1	19.00	-
June 16-30	11	61.56	$\pm 2.10$	-	-	-
July 1-15	2	67.80	$\pm 1.30$	-	-	-
July 16-31	7	62.84	$\pm 3.50$	-	-	-
August 1-15	-	-	-	-	-	-
August 16-31	-	-	-	-	-	-
<u>Other Areas</u>						
1960						
Aberdeen Lake						
May 29-June 2	7	66.94	$\pm 7.56$	-	-	-
June 15-16	3	66.40	$\pm 4.57$	-	-	-
July 10-18	20	75.83	$\pm 4.00$	-	-	-
1961						
Aberdeen Lake						
June 1-5	2	70.45	$\pm 1.35$	-	-	-
June 22-July 10	4	85.17	$\pm 4.78$	-	-	-
July 26-29	8	79.80	$\pm 2.96$	-	-	-
New Lake						
July 4-12	8	75.99	$\pm 3.14$	-	-	-

TABLE 53. (continued) Lemmus male mean body weights.

LOCATION AND TIME PERIOD	WINTER GENERATION			SPRING GENERATION		
	N	WEIGHT	S.E.	N	WEIGHT	S.E.
Other Areas (cont'd)						
1961						
Long Island						
July 17-20	6	79.97	$\pm 3.14$	-	-	-
Second Island						
July 24-27	5	81.04	$\pm 1.52$	-	-	-
Lower Thelon R.						
Aug. 14-19	-	-	-	-	-	-
Ten Mile Is.						
Aug. 14-19	2	75.75	$\pm 5.74$	-	-	-
Nine Mile Is.						
Aug. 14-19	1	84.40	-	-	-	-
Prince River						
Aug. 14-17	4	65.03	$\pm 1.45$	-	-	-

TABLE 54. Mean body weights for Dicrostonyx males of the winter and spring generations, summers 1959-61.

LOCATION AND TIME PERIOD	WINTER GENERATION			SPRING GENERATION		
	N	WEIGHT	S.E.	N	WEIGHT	S.E.
<u>Main Study Area</u>						
1959						
June 15-30	5	50.00	$\pm 2.22$	7	33.60	$\pm 1.98$
July 1-15	2	51.70	$\pm 2.60$	4	37.10	$\pm 1.68$
July 16-31	2	52.95	$\pm 0.45$	4	41.80	$\pm 3.00$
August 1-15	1	51.40	-	1	42.00	-
August 16-31	-	-	-	-	-	-
1960						
May 16-31	10	77.50	$\pm 4.11$	8	18.63	$\pm 1.13$
June 1-15	17	71.02	$\pm 3.79$	8	29.72	$\pm 2.56$
June 16-30	8	67.68	$\pm 3.72$	1	39.20	-
July 1-15	12	67.58	$\pm 3.49$	4	45.20	$\pm 2.08$
July 16-31	2	74.95	$\pm 0.75$	-	-	-
August 1-15	3	70.73	$\pm 4.16$	-	-	-
August 16-31	1	106.00	-	-	-	-
1961						
May 1-15	3	59.77	$\pm 3.57$	-	-	-
May 16-31	5	66.40	$\pm 6.78$	4	33.22	$\pm 6.95$
June 1-15	36	67.33	$\pm 1.58$	32	35.94	$\pm 2.16$
June 16-30	12	70.32	$\pm 3.60$	7	40.34	$\pm 3.90$
July 1-15	8	61.71	$\pm 2.95$	9	39.28	$\pm 2.62$
July 16-31	4	62.95	$\pm 2.70$	2	45.95	$\pm 0.45$
August 1-15	5	63.46	$\pm 2.59$	3	53.03	$\pm 6.25$
August 16-31	-	-	-	-	-	-
<u>Aberdeen Lake</u>						
1960						
May 27-June 2	8	84.70	$\pm 7.71$	1	23.10	-
June 15-16	2	81.75	$\pm 4.85$	3	50.77	$\pm 1.49$
July 10-18	12	76.90	$\pm 2.94$	12	44.47	$\pm 1.55$
1961						
May 28-June 2	5	75.54	$\pm 6.14$	2	32.00	$\pm 9.60$
June 13-22	9	75.58	$\pm 5.53$	2	38.85	$\pm 8.35$
July 10-19	5	70.76	$\pm 3.60$	2	48.55	$\pm 1.05$
July 26-29	10	80.90	$\pm 3.28$	10	49.53	$\pm 2.46$



(Snedecor, 1956, p 115) was applied to the 1960 vs. 1961 data for the winter generation and gave a significant difference ( $P < .05, > .01$ ).

For Aberdeen Lake the 1960 and 1961 data are not significantly different, as in Lemmus.

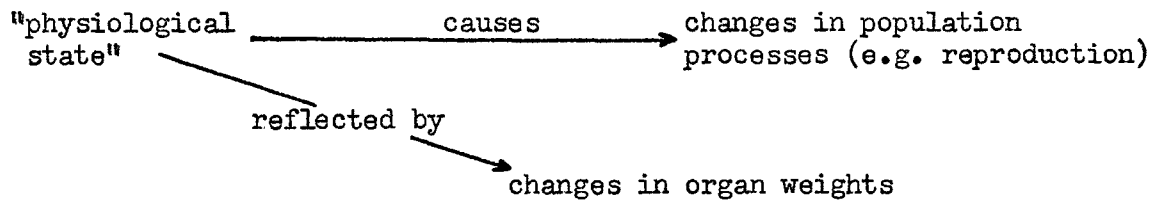
Growth of adult animals is mostly complete by early June in both species. Individual adults captured in the live trapping program from June to August show growth rates averaging about 0.2% per day in both 1960 and 1961 for both species. It thus appears that the critical growth period for the adults is 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 prior observation that high body weights ( $\bar{x} = 70-85$  g) were found in the peak summer on all areas and in Type H declines in 1961. Lower mean body weights ( $\bar{x} = 50-65$ g) prevail at the other times for both species. 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

Over 6000 organs from about 2400 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 testes, adrenals, 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 all the upholders of these "physiological" theories do rely on organ weights and have based their supposed confirmations on organ weights. Hence we may begin by using their assumption.

Tables 55 and 56 give the mean standardized organ weights for Lemmus males and females, and Tables 57 and 58 give the same data for Dicrostonyx males and females. The organs included are: for the males -- testes, adrenals, and spleen; and for the females -- adrenals and spleen. All testes and adrenal weights given are paired weights. Fat indices are also given and will be discussed later. Four separate standardizations were performed for each organ: males and females, and winter and summer generations. 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 and pregnant or lactating females for the winter generation figures, and only non-fecund males and nulliparous females for the summer generation figures. The groups omitted by these restrictions are small and discontinuous in time.

The first organ we may consider is the adrenal gland, and we may enquire whether population density changes were associated with adrenal weight changes. It is difficult to see any consistent relationship between these adrenal data and the population changes. There is a seasonal change

TABLE 55. Standardized mean organ weights (milligrams) and fat index for Lemmus males, 1959-61.

LOCATION AND TIME PERIOD	ADRENALS				TESTES				SPLEEN				FAT INDEX			
	W*		S*		W		S		W		S		W		S	
	N	WT.	N	WT.	N	WT.	N	WT.	N	WT.	N	WT.	N	IND.	N	IND.
<u>Main Study Area</u>																
1959																
June 16-30	12	25.2	-	-	14	646	-	-	14	231	-	-	15	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	-	-	-	-	-	-	-	-	-	-	12	43	-	-	13	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	9	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
<u>Other Areas</u>																
1960																
Aberdeen Lake																
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																
Aberdeen Lake																
July 27-29	8	23.6	14	9.7	8	535	14	21	8	403	14	60	8	1.2	14	1.7
Long Island																
July 17-20	6	24.8	3	7.2	6	486	3	25	6	375	2	52	6	0.9	3	1.4
Second Island																
July 24-27	5	25.7	5	8.4	5	576	5	43	5	464	5	55	5	0.9	5	1.4
Prince River																
August 14-17	4	24.3	3	12.8	4	399	3	9	4	674	3	64	4	1.3	3	1.9
Nine Mile Island																
August 14-19	1	22.1	4	7.9	1	422	4	35	1	231	4	79	1	1.7	3	1.9
Ten Mile Island																
August 14-19	2	22.7	9	13.4	2	538	9	32	2	213	9	62	2	0.9	8	1.5
Thelon River																
August 14-19	-	-	8	11.2	-	-	8	12	-	-	8	73	-	-	8	1.8

\* W = winter generation (fecund animals only).

\* S = summer generation (non-fecund animals only).

TABLE 56. Standardized mean organ weights (milligrams) and fat index for Lemmus females, 1959-61.

LOCATION AND TIME PERIOD	ADRENALS				SPLEEN				FAT INDEX			
	WINTER * N	WT.	SUMMER * N	WT.	WINTER N	WT.	SUMMER N	WT.	WINTER N	IND.	SUMMER N	IND.
<u>Main Study Area</u>												
1959												
June 16-30	4	38.0	-	-	6	243	-	-	9	1.8	-	-
July	2	32.3	-	-	2	259	-	-	2	2.4	-	-
August	4	29.0	3	10.7	5	267	3	47.6	-	-	4	1.7
Oct.-Dec.	-	-	3	14.0	-	-	1	21.9	-	-	4	4.0
1960												
April	2	30.0	-	-	2	119	-	-	-	-	1	2.3
May 16-31	3	25.3	-	-	3	81	-	-	45	1.7	-	-
June 1-15	18	32.7	-	-	18	166	-	-	21	1.1	-	-
June 16-30	21	38.1	-	-	21	130	-	-	11	1.4	-	-
July 1-15	16	36.5	8	12.3	16	198	8	53.9	-	-	9	1.7
July 16-31	21	32.7	26	7.1	24	285	25	108.0	2	1.3	26	1.8
August 1-15	14	32.2	41	7.2	14	211	40	59.6	6	1.3	40	1.9
August 16-31	-	-	37	10.2	-	-	37	69.4	2	1.3	37	2.2
Sept. 15-30	-	-	15	6.8	-	-	15	50.1	-	-	15	2.5
Oct.-Nov.	-	-	18	13.1	-	-	18	14.3	-	-	18	1.7
December	-	-	26	15.4	-	-	26	27.7	-	-	26	1.7
1961												
January	-	-	32	13.3	-	-	32	22.7	-	-	32	1.5
February	-	-	8	15.4	-	-	8	34.8	-	-	8	1.1
March	-	-	6	10.9	-	-	6	20.3	-	-	6	2.0
April	-	-	3	15.3	-	-	4	26.0	-	-	4	1.4
May 1-15	-	-	11	20.4	-	-	11	44.2	-	-	13	1.3
May 16-31	-	-	-	-	-	-	-	-	4	2.5	-	-
June 1-15	4	27.3	-	-	4	149	-	-	8	1.8	-	-
June 16-30	5	37.3	-	-	5	188	-	-	4	1.8	-	-
July 1-15	2	29.7	-	-	2	215	-	-	-	-	-	-
July 16-31	6	33.2	-	-	6	466	-	-	-	-	-	-
August 1-15	3	26.5	4	11.8	3	174	4	62.1	-	-	4	1.7
August 16-31	-	-	8	15.6	-	-	8	70.1	-	-	8	2.0
<u>Other Areas</u>												
1960												
Aberdeen Lake												
May 27-June 2	-	-	-	-	-	-	-	-	5	1.5	-	-
June 15-16	4	35.1	-	-	4	157	-	-	4	1.0	-	-
July 10-18	12	28.6	7	8.9	12	179	5	32.8	1	1.5	8	1.6
1961												
Aberdeen Lake												
July 26-29	7	30.3	16	10.7	7	374	14	77.7	-	-	16	1.8
Long Island												
July 17-20	4	28.0	5	9.5	4	201	5	49.9	-	-	5	1.7
Second Island												
July 24-27	3	30.9	2	10.5	3	189	2	156.1	-	-	2	1.6
Prince River												
August 14-17	-	-	2	14.7	-	-	2	51.0	-	-	2	2.4
Nine Mile Is.												
August 14-19	1	22.3	1	8.1	-	-	1	85.8	-	-	1	1.6
Ten Mile Is.												
August 14-19	1	27.6	3	13.3	-	-	3	34.9	-	-	3	1.9
Thelon River												
August 14-19	-	-	4	10.8	-	-	4	73.6	-	-	4	2.0

\* Winter Generation : adrenals and spleen - pregnant or lactating only  
fat index - pregnant or parous only (not lactating).  
Summer Generation : nulliparous animals only.

TABLE 57. Standardized mean organ weights (milligrams) and fat index for Dicrostonyx males, 1959-61.

LOCATION AND TIME PERIOD	ADRENALS				TESTES				SPLEEN				FAT INDEX			
	W *		S *		W		S		W		S		W		S	
	N	WT.	N	WT.	N	WT.	N	WT.	N	WT.	N	WT.	N	IND.	N	IND.
<u>Main Study Area</u>																
1959																
June 15-30	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	2	11.1	3	6.2	1	89	2	45	2	18.8	3	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
<u>Other Areas</u>																
1960																
Aberdeen Lake																
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																
Aberdeen Lake																
July 26-29	5	15.6	5	7.3	5	160	5	16	5	91.2	5	43.8	5	1.4	5	1.8

\* W = winter generation (fecund animals only).

S = summer generation (non-fecund animals only).

TABLE 58. Standardized mean organ weights (milligrams) and fat index for Dicrostonyx females, 1959-61.

LOCATION AND TIME PERIOD	ADRENALS				SPLEEN				FAT INDEX			
	WINTER *		SUMMER *		WINTER		SUMMER		WINTER		SUMMER	
	N	WT.	N	WT.	N	WT.	N	WT.	N	IND.	N	IND.
<u>Main Study Area</u>												
1959												
June 15-30	3	27.3	-	-	3	108	-	-	4	1.1	-	-
July	9	22.5	2	8.3	9	102	2	41	6	2.2	2	2.5
August	4	17.7	8	9.0	4	71	8	24	-	-	8	2.0
Oct. - Nov.	1	12.8	-	-	1	65	-	-	3	2.9	2	1.8
1960												
Jan.-March	2	17.0	-	-	2	20	-	-	3	2.1	6	3.1
Apr.-May 15	-	-	-	-	-	-	-	-	2	0.9	11	1.8
May 16-31	1	11.9	-	-	1	25	-	-	-	-	7	1.7
June 1-15	9	29.4	-	-	10	73	-	-	17	1.3	-	-
June 16-30	5	25.6	-	-	5	165	-	-	5	1.6	-	-
July 1-15	10	23.6	-	-	10	79	-	-	1	1.8	-	-
July 16-31	6	25.3	15	7.3	6	71	15	58	2	1.3	15	1.4
August 1-15	5	24.0	14	8.8	4	73	14	41	2	1.2	13	1.7
August 16-31	1	16.0	25	8.7	1	22	26	48	9	1.6	27	2.3
Sept. 15-30	-	-	6	6.1	-	-	6	29	4	1.7	6	2.5
Oct. - Nov.	-	-	5	9.2	-	-	5	33	-	-	5	1.3
December	-	-	5	7.6	-	-	5	33	-	-	5	1.6
1961												
January	-	-	2	7.1	-	-	2	34	-	-	3	1.5
February	-	-	3	10.4	-	-	3	28	-	-	2	0.9
March	-	-	-	-	-	-	-	-	-	-	1	3.7
April	-	-	2	10.1	-	-	2	52	-	-	4	2.1
May 1-15	1	11.2	-	-	1	16	-	-	1	1.7	2	1.6
May 16-31	-	-	-	-	-	-	-	-	1	1.6	-	-
June 1-15	7	25.9	-	-	5	69	-	-	22	1.6	-	-
June 16-30	19	23.5	-	-	20	82	-	-	22	1.7	-	-
July 1-15	9	22.2	4	7.3	8	106	4	56	5	1.4	4	2.0
July 16-31	5	16.9	11	7.0	5	56	10	41	2	1.2	11	1.6
August 1-15	3	20.2	5	8.0	3	68	5	44	2	0.8	5	1.6
August 16-31	3	15.7	10	9.0	3	85	10	35	1	1.8	9	1.5
<u>Other Areas</u>												
1960												
Aberdeen Lake												
May 27-June 2	-	-	-	-	-	-	-	-	4	1.9	-	-
June 15-16	7	25.0	-	-	7	97	-	-	7	1.1	-	-
July 10-18	21	21.2	9	6.6	21	93	8	64	11	1.1	9	1.6
1961												
Aberdeen Lake												
July 26-29	9	21.3	10	7.3	9	95	11	49	9	1.5	13	1.8

\* Winter Generation (incl. Spring Gen.) : adrenals and spleen - pregnant or lactating only.  
: fat index - pregnant or parous only (not lactating).  
Summer Generation: nulliparous animals only.

in adrenal weights, rising to a peak in June or July, similar to that described by Chitty (1961) for Microtus agrestis. 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	1960-61
<u>Lemmus</u>					
Adult males	Low	High	Low	-	
Adult females	Low ?	High	Low	-	
Young males	High	Low	High	High	
Young females	Low ?	Low	High	High	
<u>Dicrostonyx</u>					
Adult males	Low	Low	High	-	
Adult females	High	High	Low	-	
Young males	Low	Low	Low	High	
Young females	Low	Low	Low	High	

The mean difference between "high" and "low" adrenal weights was 5-14% for the summer adults, and 23-33% for the Lemmus summer young. High adrenal weights were found in all groups in the winter of 1960-61, but unfortunately comparative data from the previous winter are not available. There is a clear relationship of summer adrenal weights to the cycle if we look at single groups such as the Lemmus 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 1960-61 relative to the summer weights.

The second organ to be considered is the testis. There is some correlation between testes weights and density changes, which shows up as

follows:

		Summer		
		1959	1960	1961
<u>Lemmus</u>				
	Adult males	High	Low	High
	Young males	High	Low	Low
<u>Dicrostonyx</u>				
	Adult males	High	Low	Low
	Young males	High	Low	Low

The mean differences between "high" and "low" testes weights was 14-21% for the summer adults and 49-78% 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. These 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 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.

The final organ to be considered is the spleen. The spleen in lemmings varies considerably in size, weighing from 5-600 mg in Dicrostonyx and 5-1200 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 between the different years, and the 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 and Chitty, ms.) 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 1960-61 but comparative data from 1959-60 are lacking. Testes weights tended to change systematically over the cycle, being high in 1959, low in 1960, and somewhat variable in 1961. 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 always classed 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 analyzed in the same way as the organ weight data.

Fat index data for Lemmus and Dicrostonyx males and females are given in Tables 55-58 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 in fall and spring). If we compare the spring and summer data of the different years, there does not

seem to be any difference between years 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 winter of 1960-61, but data from the previous winter are not sufficient for a good comparison.

### Social Relationships

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

In early June 1960 both species of lemmings were extremely hostile in behavior, 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 one 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 behavior contrasts sharply with their behavior later in the summer when they try to hide as soon as one approaches. Collett (1895) and Curry-Lindahl (1961) also report this curious behavior for the Norwegian lemming. The significance of these observations is not known.

Some crude measure of aggressive behavior 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 this classification was done in a two week period at the end of the study so as to minimize the subjective element.

Tables 59 and 60 give the incidence of wounding shown on skins for Lemmus and Dicrostonyx males over the cycle. For both species 1959 showed the lowest over-all amount of wounding both for old and young animals. The 1960 adults of both species showed a high incidence of wounding in late June and July, and this declined by August when breeding had ceased. The 1960 young showed a considerable amount of wounding as they moved under the snow in the fall of 1960. The 1961 adults showed the highest wounding percentages for all years in late July and early August. Unlike 1960 however, there appeared to be very little wounding until early July in 1961, a time just after the first summer young had been born and the females were breeding again. The significance of these year to year and seasonal differences are not understood, and much more detailed work must be done on these points. However, these crude data do illustrate three general points: (1) there is a considerable seasonal variation in the amount of fighting which causes skin wounds; (2) this fighting was not a simple function of density because at certain times in the summer of the decline wounding was more extensive than in the peak summer; (3) both Lemmus and Dicrostonyx showed the same general pattern, although there was less wounding shown on Dicrostonyx skins than on Lemmus skins.

Maturation of summer young males during their first summer was associated with a considerable amount of wounding. Only one sample of Lemmus summer young contained both mature and immature animals, and the data on these are as follows:

TABLE 59. Amount of wounding shown on skins of Lemmus males from the Main Study Area, 1959-61.

TIME PERIOD	WINTER GENERATION <sup>1</sup>				SUMMER GENERATION <sup>1</sup>			
	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	2.0	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.-Nov.	-	-	-	-	16	62.5	-	-
December	-	-	-	-	30	46.7	10.0	3.3
1961								
January	-	-	-	-	18	27.8	-	5.5
February	-	-	-	-	12	8.3	25.0	-
March	-	-	-	-	4	25.0	-	-
April	-	-	-	-	2	-	-	-
May 1-15	-	-	-	-	1	-	-	-
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	-	-

<sup>1</sup> Winter Generation - mature animals only.  
 Summer Generation - immature animals only.

TABLE 60. Amount of wounding shown on skins of Dicrostonyx males from the Main Study Area, 1959-61.

TIME PERIOD	WINTER GENERATION <sup>1</sup>			SUMMER GENERATION <sup>1</sup>				
	N	% LIGHT	% MOD.	% HEAVY	N	% LIGHT	% MOD.	% HEAVY
1959								
June 15-30	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.-Nov.	-	-	-	-	2	50.0	-	-
December	-	-	-	-	9	22.2	11.1	-
1961								
January	-	-	-	-	5	60.0	-	-
Feb.-March	-	-	-	-	3	-	-	-
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	-	-

<sup>1</sup> Winter Generation - all mature.  
Summer Generation - all immature.

	Sample Size	% showing wounds	Mean body weight	Range of body weights
August 1959				
Immature males	11	9.1	21.7 g	13.5 - 30.8
Mature males	8	75.0	33.5 g	27.8 - 38.5

These differences in wounding are significant (chi-square for independence = 6.04, df 1,  $P < .05, > .01$ ). Since the mean body weights of these samples differ considerably, some of the 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 a reason why there seems to be a great increase in the amount of fighting in the August 1959 Lemmus. It also suggests a function for the observed inhibition of maturation of males in the peak and decline summers, i.e. it prevents a considerable amount of fighting in these populations. Summer young Lemmus females did not seem to show this difference:

July 1960	Immature females	N = 18	% showing wounds = 0.0
	Mature females	N = 14	% showing wounds = 0.0

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
" 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, df 3,  $P < .10, > .05$ ). Thus although the data suggest fewer young in the sedge hummock and more young in the lichen-heath habitats, compared to 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 behavioral changes represent the largest gap in our knowledge of the intrinsic factors operating in the cycle.

#### SUMMARY AND CONCLUSIONS

(1) High body weights were associated with all peak populations and Type H declines. These high weights were about 20-30% greater on the average than the normal low body weights found during the period of low numbers and Type G declines.

(2) Midsummer weight distributions for Type G declines showed a conspicuous gap where the first summer young should have been.

(3) Organ weights did not appear to give us any insight into the causes of the cycle. Summer adrenal weights and spleen weights did not show any consistent relationship to the density changes. Winter adrenal weights during 1960-61 seemed to be high in both species. Testes weights showed a fairly consistent relation to the cycle similar to the changes described under reproduction.

(4) Spring and summer fat indices showed no relation to the cycle, and lemmings in the spring of the decline were as fat as or fatter than animals from the other years, thus eliminating any doubt about the quantity of food available during the decline. Winter fat indices for 1960-61 may have been lower than those for the previous winter but not enough data are available for an adequate comparison.

(5) Intraspecific strife, as measured by the wounds on the skin, showed strong seasonal and year to year changes. This strife was not a simple function of density because the highest amount of wounding was recorded in the summer of the decline. The changes in the amount of strife shown by the skins are not understood.

(6) Sexually mature young Lemmus males suffered more wounding than immature young males in the August 1959 sample.



## DISCUSSION

We have now presented the results of this study on lemming cycles and must integrate these results with contemporary ideas and studies by other workers. The amount of literature published about "cycles" is truly voluminous, but the proportion of this which presents original thought or solid evidence is very low indeed. The pattern followed in this discussion will be as follows. After a brief historical review and some methodological discussion we shall consider the main changes discussed in the previous sections and integrate these with the results of other workers. Finally, we shall 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 we can recognize two general approaches to the problem. 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 does not prove anything. It 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) 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, and failure to distinguish between them (e.g. Slobodkin, 1961) gives 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: in this paper a cycle is defined as a typically 3-4 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 3-4 year cycles and (2) that high body weights seem to be always associated with peak populations present a strong argument for this working hypothesis. Furthermore, this is a sound methodological approach to the problem in the present state of knowledge. One alternative is to begin with the assumption that all these rodent cycles have a different explanation. This implies that each cycle is 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. Another alternative is to distinguish a limited number of different types of cycles based on, for example, groups of species or climatic zones. I have not used this approach because I do not feel it is the most fruitful one in the present state of knowledge. 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, we must recognize that there is no guarantee that this is a single class of events. It is possible that the class is larger than we have indicated, perhaps including the gallinaceous birds and the snowshoe hare. I do not wish to argue with those who wish to make the class larger, but it does not seem to me to be prudent to extend the class beyond the limits set by the body weight characteristic until more evidence becomes available. But I do object to a restriction of the class to include less than that given above. However, if one believes the body weight characteristic to be unimportant, one can define the problem differently.

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 Lemmus sibiricus in Russia during the period of increase. Sutton and Hamilton (1932) found winter breeding in both Dicrostonyx groenlandicus and Lemmus 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, Curry-Lindahl (1961) and Koponen, Kokkonen, and Kalela (1961) reported probable winter breeding in the Norwegian lemming during the period of increase. 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.

There is equally 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 L. 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 indicate no difference in midsummer pregnancy rates over the cycle. Unfortunately the data are presented in such a way that no statistical assessment or detailed comparisons may be made. His data seem to agree with what was found in this study, and even his own data fail to bear out his conclusion that reproduction proceeded at a reduced level in summers of low population density but reached great peaks of intensity in the summers of high densities.

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 Lemmus lemmus become fecund during their first summer in the peak year, but his criterion of maturity for the males has been questioned by Newson (pers. comm.), and furthermore his samples are very discontinuous.

Considering other cyclic microtines 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 England. Godfrey (1953) suggested that a delay in reaching maturity for M. agrestis young may only occur 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 M. 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 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.

This series of positive instances suggests that cycles of the type defined previously are associated with a fairly specific set of reproductive changes. It is important to look for negative 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 (Hamilton, 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 (1960 a) considered to be the indicator of cyclic phase. From this point of view he 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 whether 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?

It is pertinent to enquire 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, p387) 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 27), which suggests that the factors involved are not nutritional. Mild winter weather may have been necessary for the extensive winter breeding

to occur, but 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 assessments for cyclic microtines. This is an important point because there is a tendency to disregard variables which have not been studied intensively, or else to posit reasonable but 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 M. 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 probably partial prenatal mortality does not change over the cycle, but 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 found high juvenile mortality also in the peak summer, but there was no suggestion of

this in the present study, and this characteristic 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, 1960 a). Very few extensive measurements of adult mortality rates have been made (Leslie et al., 1953; Chitty and Chitty, 1960 a), and we must be careful not to extrapolate too much from observations on midsummer adult mortality such as were made in this study.

We may conclude from the above data that juvenile mortality changes are most important over the cycle and exceed any changes in adult mortality which may occur. This is not an unusual situation, for 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.

### 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 given previously. 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 onto the sea ice. Only

a small percentage of the total population took part in this emigration. Thompson remarked that this emigration was very different from the mass migrations of Scandinavian lemmings.

There is no good evidence for the North American arctic that any other type of lemming movements occurs besides that described by Thompson. The report of Gavin (1945) of a ten day mass migration of brown lemmings at a density of one per sq. yard is hardly credible. 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 engorge themselves on lemmings while travelling across country. But it is a complete myth to extrapolate such events, as Gavin (1945) did, into a solid mass of lemmings marching in a particular direction for days on end. I have been seriously 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. I therefore reject the suggestion 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 do not inhabit the woodland and lowland zones as a normal habitat even in low years, and yet this is a critical point regarding whether

or not a migration is necessary to account for the presence of these animals. 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 kilometers 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..." (translation page 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 1 week, and (2) fall migrations which may go on for 2-3 months. Koponen et al. (1961) have described a spring migration on lake ice which was extremely similar to that described above for this study and that described 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) has 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 and other unusual places at the peak, and (2) no lemmings were seen in an area at one time and at a later date some lemmings were trapped there. 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 meters at the most between seasonal habitats would not be enough to account for all the changes observed by Kalela (1961). I reject his claim that fall migrations occur in the Norwegian lemming because the data presented have a much simpler explanation.

It is indeed surprising to find that there is no objective evidence for mass migrations of the Norwegian lemming. The spring "migrations" described seem to be no different from the local movements found by Thompson (1955 c) and by this study. There is no good evidence that the fall "migrations" are anything but local movements of individuals at high densities. No oriented long distance movements of groups have ever been demonstrated. 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 rest for the moment.

To sum up, there is no convincing evidence that mass migrations of lemmings occur either in North America or in Scandinavia. The descriptions published for spring "migrations" can be explained as small local emigrations of individuals such as described by Thompson (1955 c). These local emigrations may be caused by the onset of summer breeding activity in dense populations perhaps coupled with the strong environmental changes during the melt-off. The fall "migrations" seem to be nothing but local movements of individuals caused in part by high densities.

#### 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 we must attempt to discover what effect ordinary weather phenomena -- deep snow covers, warm springs, wet summers, etc. -- have on reproduction and mortality of cyclic animals.

As Chitty (1952) 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 the cycle. 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 3-4 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 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 favorable winters were not accompanied by increases and at least one favorable winter was followed by a decline. Collett (1895) pointed out that spring and summer weather had little effect on L. 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) has 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 b) has discussed some aspects of regional synchrony in northern Alaska. He has concluded 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 airplane 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 b) is whether sympatric microtines cycle in phase. Elton (1942, p 439) stated that both species of lemmings probably fluctuated in phase. Watson (1957) 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 sum up, weather must be regarded as a necessary cause of the cyclic increase or decline because (1) if weather was not necessary, cycles would not tend to be synchronous, and (2) if weather was sufficient to cause the increase or decline, cycles would not tend to be 3-4 years in length. To date the only plausible explanation of this role of weather is that of Chitty (1952, 1955 b, 1960) which is illustrated in a model by Leslie (1959).

#### 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. 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 (1957 a) and attributed to predators. While it is reasonable to suppose that predation might alter the length and pattern of the cycle, mere association of events must be viewed critically.

#### Disease and Parasites

Elton (1942, p 201) and Chitty (1954, 1960) have shown that disease cannot be regarded as a sufficient condition 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 summer 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 Lemmus 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. favorable weather). Stein (1956) found that the lower age groups were missing from peak and declining populations of Clethrionomys 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, i.e. 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 3-4 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 (1960 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 lab 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 behavior.

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

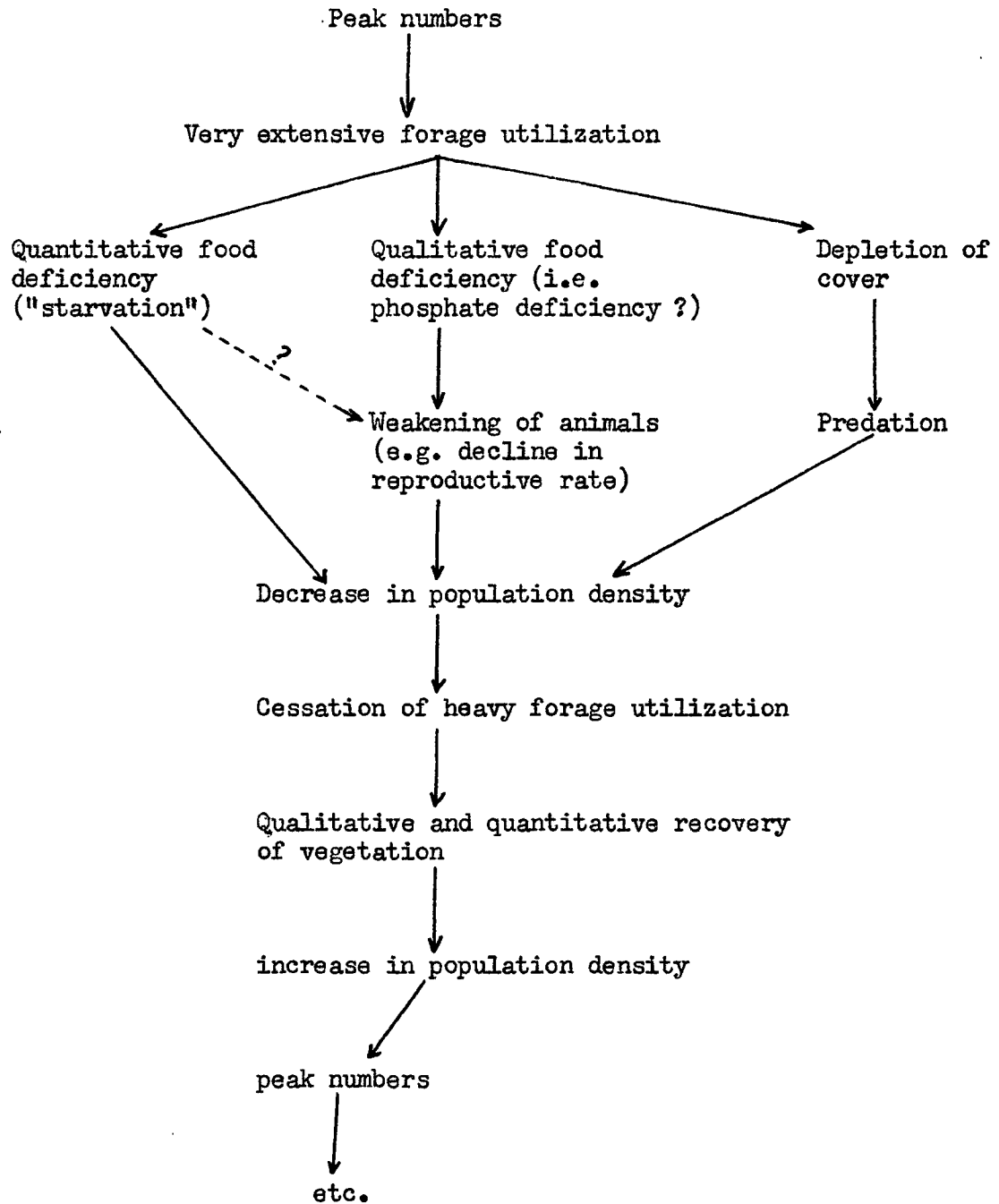
I would now like to consider three current hypotheses which attempt to explain these cyclical fluctuations.

#### (1) Food Supply Hypothesis:

The hypothesis supported by Pitelka from his work and that of Thompson at Point Barrow, Alaska on the brown lemming is shown in Figure 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 47). Second, there was no evidence of starvation in animals alive in the spring of the decline (Tables 55-58). 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. Furthermore, they must

FIGURE 8. Pitelka's food supply hypothesis.



account for an increasing survival rate in the later summer litters of the decline compared to 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. The events to be explained are mainly intrinsic changes involving both reproduction and mortality and are of such a general nature that ad hoc hypotheses regarding extrinsic factors in local situations are entirely insufficient.

Yet the same effect of the lemmings on the standing crop of forage as were reported by Thompson (1955 b) at Point Barrow were also found in this study. There is no doubt that lemmings exert a strong effect on the 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, 1957 a), and until more conclusive evidence is available it is necessary to remain skeptical of this interpretation.

Rausch (1950) states that there was nothing to indicate that the decline in numbers in 1949 at Point Barrow resulted from starvation. Chitty (1952, 1960) has presented his 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.

## (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 Figure 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 behavioral and physiological changes. His specific thesis is that the mechanism of this limitation involves the General Adaptation Syndrome and is purely phenotypic. I shall not discuss the applicability of this scheme to all mammals, but 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.

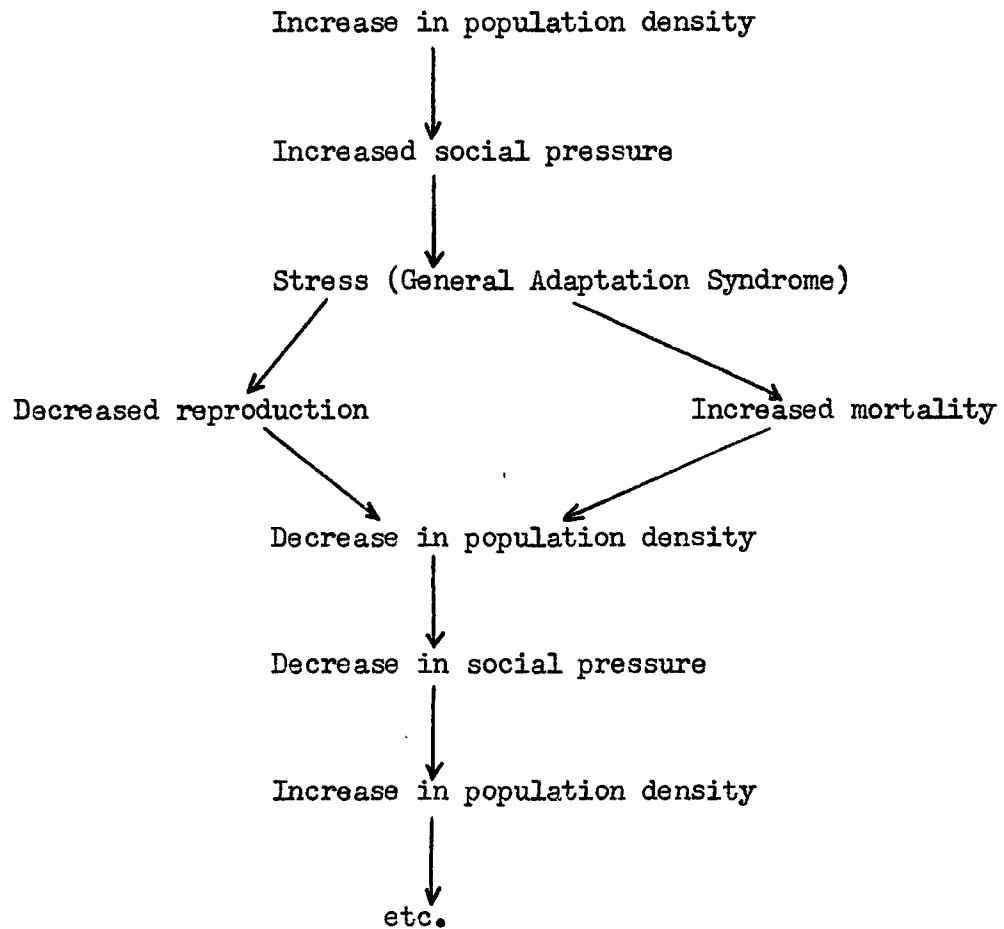
It is not sufficient merely to find increased adrenal activity at high densities and to claim that the hypothesis has been confirmed.

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) considers this the weakest point. There is no evidence that these laboratory situations correspond to anything that goes on in nature, and thus the extrapolation from the lab to the field is not justified.

No consistent relationship between summer adrenal weights and the phases of the cycle was found in this study (Tables 55-58), 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



FIGURE 9. Christian's stress hypothesis. The system is purely phenotypic and operates through the general adaptation syndrome.



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 favor of the hypothesis, since it is mostly based on adrenal weights. Neither horn of the dilemma is very favorable to the current hypothesis.

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).

To sum up, there is no evidence from adrenal weights that stress (sensu Selye) played any major role in this lemming cycle and thus Christian's specific hypothesis was rejected as an explanation.

### (3) Chitty's 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). Chitty (1952, 1957, 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

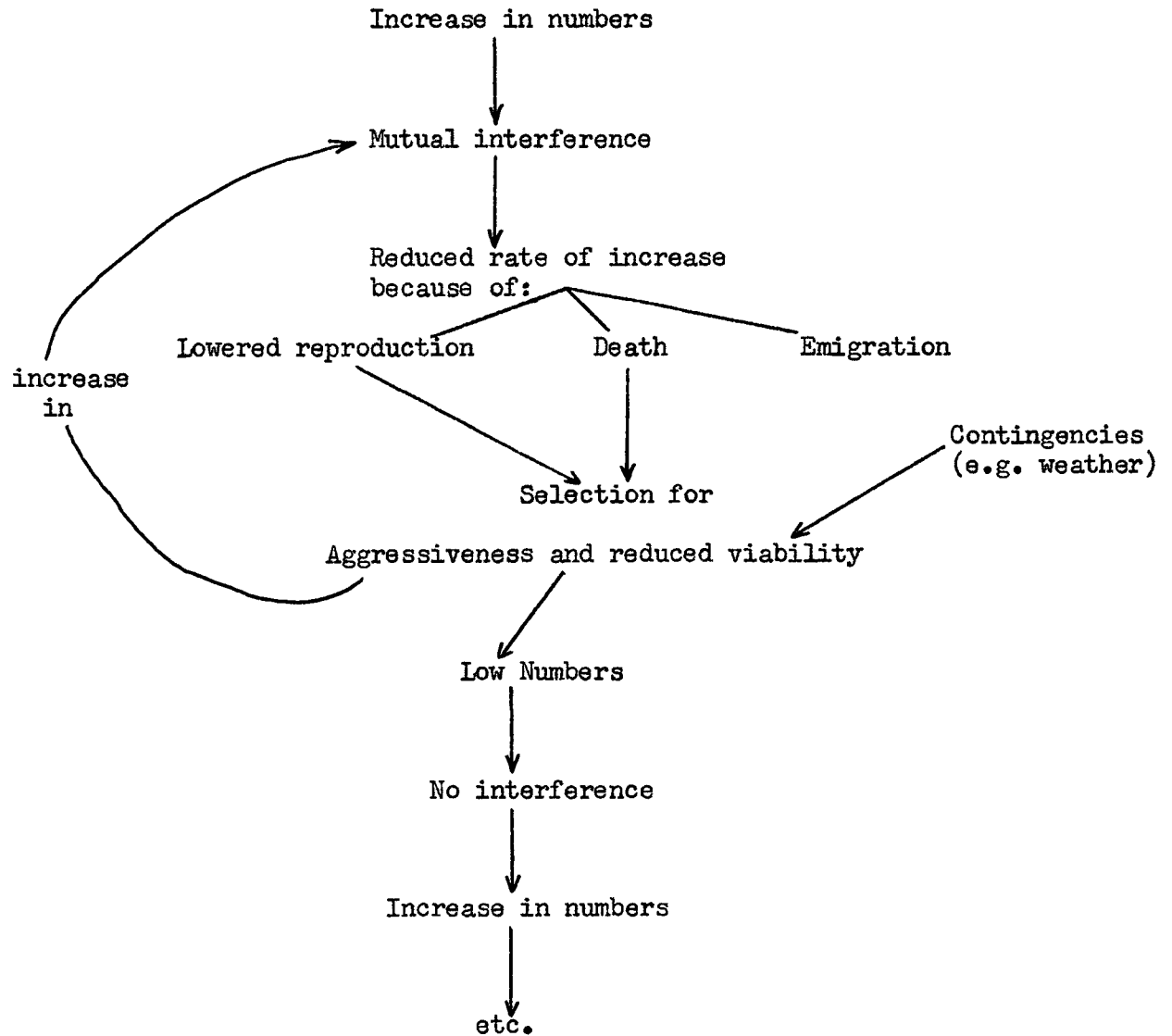
generations, which become less resistant to the normal sources of mortality. It is important to distinguish this concept of a change in quality of the population from the explanation (mechanism) of this concept (Conant, 1951, p 106). Chitty (1960) reviewed the evidence for this concept and concluded 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, 1957, 1960). Attention was thus turned to the second possibility, genetic changes. The first possibility investigated was hereditary splenic anemia (Dawson, 1956; Chitty, 1957). 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 Figure 10 (Chitty, pers. comm.).

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

FIGURE 10. Chitty's hypothesis. The system is partly genetic and primarily behavioral.



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 (Figure 10). We have seen that a considerable amount of wounding occurs in these lemming populations (Tables 59-60). Adult males may range over very large areas (Tables 42-45) and the most probably hypothesis about the disappearing young of the decline is that these adult males kill them. None of these points is 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 behavior. 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.

To sum up, Chitty's concept of a change in quality of the population during changes in density is fully supported by this study. His view that the mechanism involved is behavioral and genetic is not refuted by my data which suggest that behavioral changes may constitute the crux of the lemming cycle.

### 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 be content with ad hoc explanations and conventional ideas.

We have tried to penetrate to the core of the phenomenon studied. We have seen that extrinsic factors could not explain the cycle. Of the intrinsic factors we 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 behavior and possible selective forces that might result.

Future work on the mechanism of cyclical fluctuations should consider the role of behavior 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 three 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 1960-61, and this decline continued through the summer of 1961 on the Main Study Area. This cycle was synchronous in both species over a wide zone of the central arctic.
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.
4. Partial prenatal mortality did not change 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. Favorable fall and winter weather was associated with the increase, and

unfavorable fall and early winter weather was associated with the decline.

7. Avian predators 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% in the peak and decline. Forage utilization averaged 30% or less in the wet habitats and was negligible in the dry habitats after the critical winter of 1960-61. 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% 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 and yearly 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 behavior was not refuted by these data, which suggest that behavioral changes may constitute the crux of the cycle.



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