

# REMARKS ON THE REPRODUCTION, SEX RATIO, AND LIFE EXPECTANCY OF THE VARYING LEMMING, *DICROSTONYX GROENLANDICUS*, IN NATURE AND CAPTIVITY

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**I**N 1949 a colony was started in Ottawa from 16 Greenland Varying Lemming, *Dicrostonyx groenlandicus groenlandicus*, which had been captured at Igloolik on 14 September 1949 (see Manning, 1950). Three females and 3 males bred, and the colony reached a peak of 76 in April 1951, but declined during the following summer. A single female Mackenzie Varying Lemming, *D. g. kilangmiutak*, from Tuktoyaktuk, was added to the colony that fall, and mated with one of the *D. g. groenlandicus* males to produce six litters, after which most of the colony consisted of intergrades. There was a considerable decline in numbers during the summer of 1952, and no attempt was made to rebuild the colony the next winter. By September 1953 only one lemming was left.

The captive colony was established primarily to obtain growth data for the more accurate aging of specimens collected in the field, and no deliberate experiments were made to determine reproduction rates under specific conditions. However, owing to scarcity of published information on this aspect of the biology of the Varying Lemming, it appeared worth analysing the records of the colony and comparing them with field observations as well as with some of the more detailed work which has been done on related genera. In view of the small numbers involved and the lack of adequately controlled conditions, the results should be treated with caution, particularly as the continuity of the records was broken each summer when I was absent in the Arctic<sup>1</sup>. The need for further experiments and field observations may also be stressed.

## Age of sexual maturity

Throughout the life of the colony there was a shortage of males, and it was felt, possibly erroneously, that the best way to build up the population was to mate the available males with females of mature age, particularly those

<sup>1</sup>I am indebted to my wife for looking after some of the lemmings through two summers, and for checking the calculations. Dr. J. S. Hart very kindly made arrangements to house some of the lemmings for two summers at the National Research Council. Mr. Andrew Macpherson helped take care of the original 16 captives during their month-long journey by boat, aircraft, and train from Igloolik to Ottawa as well as the single *D.g. kilangmiutak* which had almost as long a journey from Tuktoyaktuk. Dr. E. O. Höhn, Mr. Charles Handley, and Mr. S. D. MacDonald generously supplied me with information from their field notes.

**Table 1.** Distribution of young in litters

Litter size or embryo count											Total no. of litters or pregnant ♀♀	Mean no. per litter or pregnant ♀ ± S.E.	Standard deviation $\sqrt{\frac{\sum(f d^2)}{N}}$
	1	2	3	4	5	6	7	8	11				
1. Frequency in each group of litters counted within 24 hours of birth. Live and dead young included	7	12	11	8	14	3	1				56	3.41 ± .21	1.57
2. Frequency in each group of litters first counted at an average of 4 days after birth	8	7	5	5	2						27	2.48 ± .25	1.29
3. Frequency in each group of litters from 4 feral-born ♀♀		3(5)	5(5)	4(4)	7(5)	2(2)					21	3.98 ± .27	1.23
4. Frequency in each group of litters born to 9 ♀♀ when known to be under 250 days old	3(4)	2(1)	3(6)	7(6)	5(5)	2	1(1)				23	3.80 ± .34	1.61
5. Frequency in each group of litters born to 7 ♀♀ when known to be over 250 days old	4(10)	14(13)	8(4)	2(2)	6(5)	1(1)					35	2.83 ± .23	1.36
6. Frequency in each group of litters (counted within 24 hours of birth) in which all deaths were recorded until after weaning	5	11	9	7	11	3	1				47	3.45 ± .23	1.57
7. Frequency in each group of litters recorded in line 6 when recounted on 4th day	6	12	7	5	12	2					44	3.25 ± .23	1.54
8. Frequency of embryo and placental scar counts in feral ♀♀		1	2	5	11	3	4	3	1		30	5.47 ± .33	1.80
9. Frequency in each group of feral litters	2	1	6	6	1	2	1				19	3.68 ± .35	1.52

In lines 3, 4, and 5 the actual counts made are given in brackets; the other figures show the size and frequency after one lemming has been added to adjust for deaths prior to counting in those litters not counted until 24 hours or more after birth (see line 2). In calculating the means for these three lines the more accurate figure of .93 (the difference between the means of lines 1 and 2) has been used.

There do not appear to be many records of embryo or nestling counts of Varying Lemming in the literature. The figures in lines 8 and 9 are derived as follows: Ross (1835, p. xiv), March, 4 embryos, July, 6 nestlings; Preble (1902) [August, 3, 3 nestlings, 3, 3 embryos]. Actually Preble says, "Three young at a birth seems to be the usual number. Every litter we found consisted of three, and in each pregnant female we secured were three embryos". MacFarlane (1908), June, 5, 5 embryos; Allen (1919, pp. 533, 523, 537), June, 4, 5, 8, 7, 11 embryos, July, 5 embryos, August, 4 nestlings; Sutton and Hamilton (1932), January-April, 3 nestlings, 2, 5, 5, 7 embryos; Shelford (1943), July, 6 nestlings; Strecker and Morrison (1952), August, 4 nestlings; Hanson *et al.*, (unpubl.), July, 6, 8, 5 embryos, 5, 4 placental scars; Manning and Macpherson (1949, Field Notes), August, 3, 5 nestlings, Manning (1953, Field Notes), June, 7, 7, 8, 6, 5 embryos, July, 5 embryos, August, 4, 4 nestlings. MacDonald (1949, Field Notes), April, 4 embryos, July, 2, 3, 1 nestlings, August, 4 nestlings, September, 1 nestling; MacDonald (1951, Field Notes), July, 4 nestlings; Handley (1949, Field Notes), June, 6 embryos, August, 5 embryos, 3, 7 nestlings. Additional more generalized information is also sometimes given. Thus Shelford (1943) says that 5 to 8 young were reported by Twomey in 1933, and 4 to 6 in 1936, both years of abundance. Ross (1835) gives the number of young as 4 to 8. Freuchen (Degerböl and Freuchen, 1935) found 7 foetuses in a female in July 1922, but remarks that other females had not nearly so many. Armstrong (1857, p. 558) says, "They generally bring forth from two to six at a birth; in a few instances as many as eight or nine", and Feiden (1877) that the young number 3 to 5. See also Degerböl and Möhl-Hansen (1943).

which had already bred but had lost their first mate.<sup>1</sup> However, since full-grown females had a tendency to kill younger lemmings, the males were seldom mated until 80 to 100 days old. There were therefore few opportunities for early breeding, but in spite of this one female produced a litter at 84 days of age, one male sired a litter at 46 days, and another at 61 days (allowing 20 days as the gestation period).

**Litter size**

*Comparison of counts at birth and later.* The distribution of young in 83 litters counted between February 1950 and April 1952 is given in Table 1.

<sup>1</sup>One reason for this belief was that the three pairs of original captives, which were probably a month to 6 weeks old when caught, did not produce young for the first 5, 6, and 7 months respectively. It is now of interest to speculate if there is a connection between this delay and the period (near the peak or possibly the start of decline of the population cycle) at which they were captured. The single female, taken at Tuktoyaktuk in 1951 when the cycle was near a low point, had its first litter within 5 weeks of being mated, but there was little sign of an increase in the Tuktoyaktuk area the following year.

Fifty-six of these counts were made within 24 hours (usually within 12 hours) of birth, and have been assumed to represent the actual number born alive or dead. Records of deaths in 47 of these litters, selected at random, were kept until after weaning. Their mean size at the first count was 3.45. All the 4 young of one litter were dead when first found, and all in two of the remaining litters were dead by the second day. By the fourth day after birth, the mean size of the surviving 44 litters had been reduced by natural deaths to 3.25, and by the eighth day to 3.20 young.

Ranson (1941, p. 55) reported a reduction of .52 young per litter in 411 litters of captive Field Voles, *Microtus agrestis*, kept under optimum conditions, between birth and weaning at 14 days. He excluded from his first calculations young found dead at the first count, but included litters completely exterminated later. A comparable figure for the 46 lemming litters which had live young on the first day is .41 young per litter, a difference of only .11 from Ranson's figure. The mean number of young in the 44 lemming litters surviving on the fourteenth day was  $3.07 \pm .24$ .

Twenty-seven litters not found within the first 24 hours after birth were counted at varying intervals thereafter, an average being at about 4 days. The mean size of these litters was then 2.48, which is  $.77 \pm .34$  less than the mean size on the fourth day of the 47 litters for which detailed records were kept from birth. Since most of the 27 late counts were made during the summer when I was away, it is possible that either some of the young were missed in the counts or the litter size was affected by the higher temperature or other changed conditions.

Table 2. Number of young per litter according to litter sequence in 69 litters

Litter sequence	1	2	3	4	5	6	7	8	9
No. of litters recorded within 24 hours of birth + no. recorded later	12+6	10+5	7+4	3+3	5+0	5+0	1+2	1+2	1+2
Mean no. of young in litters	3.42	3.50	3.50	3.30	3.75	5.40	3.28	3.94	4.61

In calculating the mean number of young in the litters, .93 has been added to those litters which were not recorded within 24 hours of birth. This figure is the difference between the mean of those counted within 24 hours of birth and the mean of those not counted until later (see Table 1, lines 1 and 2), and here assumed to be due to death before counting or to the different conditions under which the lemmings were living when most of the late counts were made.

*Effect of age of mother on litter size.* Table 2 shows that there was no obvious correlation between litter size and litter sequence in the captive lemming for the first 9 litters.<sup>1</sup> However, the material is obviously heterogeneous since some of the mothers were feral-born and some captive-born. Also, there was a great disparity in age of the mothers, and, perhaps more important, the earlier litters were heavily weighted by mothers which died young and may therefore have been constitutionally unsound. The large mean size of the sixth litters is noteworthy, but since only 5 litters are involved, it is probably due to chance.

Table 4, which groups the litters according to the age of the mother, indicates that there was a gradual decline in the average size of litters born to mothers after the 101-150 age group, using a 25-day grouping for the

<sup>1</sup>Only 2 females had more than 9 litters. The details of these are shown in Table 3.

**Table 3.** Number of young and interval in days between litters for the two pairs producing the largest number of litters

Pair A		Pair B	
No. young in litters	Interval in days from birth of preceding litter	No. young in litters	Interval in days from birth of preceding litter
2*		5*	
4	21½-24½	4*	39 approx.
4	23¼-24½	3*	27 "
5	21¼-22¼	3	19 "
6	26 -27	2	21 "
6	21¼-22¼	5	21 "
4*	22 approx.	2	23 -24
3*	23 "	3	20½-21½
2*	20 "	5	20 -21
4*	22 "	3	25 approx.
2	58 "	1	22 "
2	22 -22½	1	20 -22
5	17½-18½	2	35 -37
		1*	24 approx.
		1*	18 "
		1*	24 "

Both sets of parents were kept paired. Pair A were at least half-grown when captured at Igloodik on 14 September 1949. The first litter was born 158 days later when the estimated age of the parents was 190 days. Four hundred and fifty-nine days after capture, the female was found dead after having given birth, probably prematurely, to one of its 5 embryos. She had produced 13 litters in 302 days at an average interval of 25.2 days between litters. The mean litter size was 3.77, or 4.12 if corrected for the 5 (starred) litters which were not found within 24 hours of birth. The male died soon after siring its last litter, about 456 days after capture.

Pair B were unrelated first generation captives. The female was 158 days old when the first litter was born, and 520 days old at the birth of her last litter. She died on the 667th day after producing 16 litters in 362 days with an average interval of 24.2 days between litters. The male was about 110 days old at the birth of the first litter, sired its last litter with another female at about 661 days, and died at 748 days. The mean litter size was 2.63, or 2.97 if corrected for the 6 (starred) litters not found within 24 hours of birth.

**Table 4.** Mean size of 58 litters born to mothers in different age groups

Age in days	51-100	101-150	151-200	201-250	251-300	301-350	351-400	401-450	451-500	501-555
No. of litters in each age group	1+0	8+3	4+3	2+2	6+1	7+3	5+3	3+0	1+4	0+2
Mean size of litters from 13 ♀♀ of known age	4.0	4.53	3.11	2.96	2.99	2.98	2.85	2.33	2.74	2.43

The first figure in each age group shows the number of litters which were found within 24 hours of birth; the second figure, those which were not counted until later. To obtain the mean litter size, .93 young was added to the size of each of the latter. This figure is the difference between the mean of those counted within 24 hours of birth and the mean of those not counted until later (see Table 1, lines 1 and 2).

mother's age, it was found that there was a statistically significant negative correlation ( $r = -.33, P < .02$ ) between the mother's age from 100 days onward and litter size. The coefficient of regression was  $.10 \pm .04$ . Leslie and Ranson (1940, p. 50), grouping their data in 8-week periods, found the litter size of captive Field Voles, *M. agrestis*, increased with the advancing age of the mother to a maximum in the 20 (16-24)-week period before it gradually declined. Since the mid-point of the group with the greatest litter size in the lemmings is only 14 days short of the mid-point of the group with the greatest litter size in the voles, and since the two species appear to reach sexual maturity at about the same age (see Leslie and Ranson, 1940, p. 34 for data on sexual maturity in *M. agrestis*) it is probable that the absence of small early litters in the lemmings is caused by the artificially late date at which they were mated.<sup>1</sup> The age of the mothers at the birth of the first litter, shown

<sup>1</sup>However, in the rat, *Rattus rattus*, first litters average smaller than second even when the female is mated late (Asdell *et al.*, 1941).

by Asdell *et al.* (1941) to affect the mean size of litters produced by rats, did not produce a demonstrable effect in the lemmings. The small negative, non-significant correlation ( $r = -.16$ ,  $P > .1$ ) between the age of the mothers at birth of their first litters and the average size of their subsequent litters, was due to the average age of the mothers at birth of all litters.

Since there appears to be a difference in the size of litters produced by the younger and older mothers, it is possible that litters born after a cyclic decline in lemming numbers, during which it seems probable that few if any young are born,<sup>1</sup> would be smaller than at other periods because of the comparatively old age of the breeding population. Thus recovery would be delayed for a generation.

*Comparison of embryos and nestling numbers from field counts.* Turning to the figures in Table 1 (lines 8 and 9) for the embryo and litter counts made in the field, it will be seen that the mean number of young per litter has dropped from 5.47 in the embryo counts, which, being mostly casual observations, probably included few records for the earlier stages of development, to 3.68 in the litter counts, which may be assumed to have been made about a mean of 8 days after birth. Ranson (1941) palpated 382 pregnant captive Field Voles, *M. agrestis*, about the fourteenth day of pregnancy to obtain an estimated mean of 3.91 embryos per female. These females produced 340 litters<sup>2</sup> with a mean number of 3.64 young, found alive or dead, showing a wastage of .27 per litter during the latter part of pregnancy. If a similar wastage is assumed in the lemming during the prenatal period and added to the figure, .25, obtained for wastage in 44 litters of lemming between birth and the eighth day, the total expected wastage between the average period of the feral lemming count and the average period of the litter counts would be .52. But since there are more young in the larger litters of the feral lemming, more deaths per litter are to be expected, and the figure for the mean size of the litters must be adjusted accordingly. The adjusted figure will be

$$\frac{5.47}{3.91} \times .27 + \frac{3.68}{3.20} \times .25 = .38 + .29 = .67.$$

This expected wastage is distinctly smaller than that obtained from the records of feral embryo and nestling counts, namely, 1.79 young per litter.

<sup>1</sup>There is as yet no good evidence for this in the Varying Lemming. However, it is my impression that no embryos were found in 23 females, over 125 mm. in total length, collected in northern Foxe Basin in late August and early September 1939, when the cycle was thought to have passed the peak, but the negative evidence was not recorded, and it is probable that all the females were not examined internally. Mammary tissue was present in one female, and a number of young in the 3- to 6-week class were obtained. In June 1952, on southern Banks Island when lemming were increasing, 5 of the 13 females over 125 mm. in total length were pregnant. The smallest female measured 128 mm. and contained 6 embryos. One only, taken July 30, of the 12 females over 125 mm. collected on northern Banks Island in late July and August was pregnant, but recently weaned young were common in the latter month. None of the 59 Brown Lemmings, *Lemmus trimucronatus*, examined by Rausch (1950, p. 176) in the Point Barrow region prior to and during the cyclic decline in 1949 was pregnant or had placental scars, although a few showed perforate vaginae.

<sup>2</sup>We are not here concerned with the 42 palpated pregnancies which resulted in no young found alive or dead.

The difference may or may not be significant. The standard errors have not been calculated since the data for expected wastage are heterogeneous, and seasonal or more probably cyclic variations in litter size may have biased the feral counts, as the number of litter and embryo counts of individual observers in single seasons are not always well balanced. It is clearly desirable to obtain additional data and look more closely for possible causes of wastage in feral litters. Under field conditions there is of course a considerable wastage of whole litters caused directly by predation on the litters or indirectly by predation on the mother, but there is no apparent reason for a greater wastage within feral than within captive litters.

*Comparison of litter size in feral and captive lemmings.* If the best available corrections, .38 and .29, are respectively subtracted from and added to the field counts of lemming embryos and litters and an unweighted mean of the result taken, a figure of  $4.53 \pm .28$  is obtained as an estimate of the litter size at birth under natural conditions. The difference between this and the mean for the 56 captive litters counted at birth (Table 1) is  $1.12 \pm .35$ , which is probably significant even though the corrections used are also subject to error.

A number of causes may have contributed to a reduced litter size in the captives, although no single one appears sufficient to account for the whole difference. As shown above, some reduction may have been due to the advanced age of the mothers when most of the litters were born, but on the other hand, the small litters expected from females under 100 days are likely to have reduced the mean litter size of the feral animals.

The inbreeding inevitable in a colony which was derived from 4 feral females and 3 males only may have tended to reduce litter size, and Table 1 shows that the mean size of litters born to the 4 feral females was slightly larger than those of the second and subsequent generations, in spite of the average age of the former at the birth of their litters being 290 days when based on a conservative estimate of their age when captured. Of the 8 Varying Lemming litters recorded by Degerbøl and Møhl-Hansen (1943, p. 10), the 5 born in captivity of feral parents had a mean size of 4.40, while the 3 born to their offspring had a smaller mean, 3.67. In both instances the litters may originally have been larger, as they were not counted until some days after birth.

The experiments of Baker and Ranson (1932, and 1933) with the Field Vole, *M. agrestis*, suggest that lowering the temperature or decreasing the period of light does not reduce litter size, although it does reduce fertility of the female. It would be surprising if a comparable reduction in daily exposure to light would cause a similar loss of fertility in the Varying Lemming (cf. Hamilton, 1941, p. 21) which are known to breed during the arctic winter (Ross, 1835; Sutton and Hamilton, 1932), while Field Voles apparently do not breed in the winter even in Britain (Asdell, 1946; Chitty, 1952).

Most of the paired captive lemmings were kept at about 60°F during the winter, and light was supplied for an average of 14 hours a day by a 60-watt bulb. One pair was exposed to full room daylight, including some sun, plus

electric light until 11 p.m. A few during one winter were given no light except a little diffuse daylight and occasional distant electric light for not more than 3 hours a day. A few pairs were kept outside in cages with a minimum of nest material throughout the winter, and were therefore perhaps subjected to more severe conditions than they would encounter under the snow in the Arctic. Only one of the pairs kept outside produced young: a litter of 4 on February 28, and one of 5 on April 5. The number of pairs under the varied conditions was not sufficient to draw any definite conclusions, but none of the conditions had any obvious effect on litter size. It is still possible that 24 hours of light, which is normal for lemmings under natural spring and summer conditions, would increase either fertility or litter size, although it must be remembered that feral lemmings spend a considerable period below ground, and there was some indication that the captive lemmings exposed to the most light were the most aggressive and irritable. It is also possible that 60°F is above the optimum temperature for lemmings, and that a temperature nearer that of summer arctic conditions would increase litter size and/or fertility. The apparent failure of the captive lemmings to produce as large litters in the summer as in the winter may have been an effect of temperature.

The staple winter food of the captive lemmings consisted of rolled oats to which had been added wheat-germ oil (vitamin E), orange and grapefruit peel, some green vegetable material, occasional carrots, and usually some green bark. In summer the green food and carrots were increased, and the wheat-germ oil was often omitted, but fresh grass was added in most cases. There was almost always an excess of food in the runs. Water was also supplied, and contrary to the reports of Degerbøl and Møhl-Hansen (1943, p. 37) and Strecker and Morrison (1952, p. 182), it was frequently drunk. Naturally the food differed greatly from that eaten by lemmings in their natural habitat, but there does not appear to be any obvious deficiency.<sup>1</sup> Also, Bodenheimer (1949, p. 45) gives evidence of special foods which influence fertility, at least in species with the rabbit-ferret type of oestrus cycle, while the experiment of Baker and Ranson (1933) on the effect of winter and summer foods in *M. agrestis* gave the unexpected result of a considerable excess in the total number of young born to the mice supplied with winter food over those supplied with summer food. The increase amounted to .83 young per litter when pregnancies resulting in the absorption of all young are included, but a reduction of .18 when such pregnancies are excluded.

It is not known if there is any variation in the average size of summer and winter litters of feral lemmings, or even if they breed every winter. A suggestion of the possible behaviour may be obtained from Hamilton (1937), who found that the Meadow Vole, *Microtus pennsylvanicus*, in central New

<sup>1</sup>It was noted that the second and third generation of captives were in general less friendly than the feral-born individuals, and much more inclined to fight with each other. Two strange adults of the same sex could seldom be put together without one being killed, but the original group was brought to Ottawa in one box and lived together for over 6 weeks with no serious fighting. It is very tentatively suggested that the cause of this apparent difference may have been a dietary deficiency.

York state bred in winter only when the population was near peak numbers. Even then, the number of embryos per pregnant female was considerably fewer than in summer. There was also a reduction in embryo numbers following and preceding the winter non-breeding period of other years. Hamilton also shows that the mean number of embryos per pregnancy during the summer preceding the cyclic maximum was distinctly higher than in other years. Confirmation of this for another species is given by Bodenheimer and Sulman (1946), who state that the litter size of *Microtus guentheri* increases from the normal 3-8 to 6-12 in the initial phase of vole outbreaks in Palestine, possibly because of seasonal and cyclic fluctuation in a plant gonadotropin. Shelford (1943) suggested an increase in litter size during the up-swing of the lemming cycle, but as yet there is little direct evidence for or against this, although it may be noted that my Banks Island embryo counts in the spring of 1953, when the lemming were first recovering from a crash two years earlier, are higher than those of Handley and MacDonald for the summer of 1949 (Table 1), when the latter believed lemming to be at a peak in Prince Patrick Island. Any factor causing larger litters at certain periods of the cycle might account in part for the apparent difference between the mean size of the feral and captive litters.

#### Gestation period and litter frequency

The females of two pairs which had been breeding regularly were isolated and their respective mates later introduced into their runs for 24 hours: in the first pair, 14 days after the birth of the preceding litter of one young which was weaned on that day, and in the second, two days after the birth of one young which was also weaned about the fourteenth day. The minimum possible gestation period in both tests was 19 days, and the maximum, 20 days 10 hours in the first (when one young was born) and 21 days in the second (when 6 young were born). When, as in most cases, the pairs were left unbroken, re-fertilization was normally effected at post-partum oestrus (see Table 5). Since there is a significant correlation ( $r = .52$ ,  $P$  about  $.02$ )<sup>1</sup> between litter size and interval to birth of next litter for the 20 litters of Table 5 with intervals between 20 and 26½ days, the intervals of 22 to 26½ days are probably occasioned by delayed implantation caused by lactation, as has been observed in the related genus *Clethrionomys* (Brambell and Rowlands, 1936), though not in *M. pennsylvanicus* (Hamilton, 1941). The 36½-day interval could be due to the same cause, as the preceding litter of 5 young was not removed from the parents until they were 20 days old. The remaining three long intervals were probably due to fertilization at a post-lactation oestrus after failure at post-partum oestrus, since there were only 1, 1, 2 young respectively in the preceding litters, and the single young born prior to the 35-day interval died when it was 12 days old. In five instances involving 8 litters with mean size of 4.12 young per litter, Degerbøl and Møhl-Hansen (1943, p. 10) reported the interval between litters to be about a month, but the young were not always found until some days after birth.

<sup>1</sup>The regression of interval on litter size is  $2.2 \pm 0.8$  days.

**Table 5.** Intervals between litters for pairs kept mated

Interval (max. error 1 day) between litters in days	20	20½	21	21½	22	22½	23	23½	24	24½	26½	35	36	36½	42	
No. litters	2	2	5	1	6	-	-	2	-	1	1	1	1	1	1	
Mean no. young at birth in litter preceding interval	2.5		2.2		4.3		4.5		3		5		1	1	5	2
Mean no. young in litter following interval	4.0		2.8		3.8		3.0		1		6		1	2	5	2

The young were usually weaned between the 14th and 18th day. Two died in one litter of 4 young about the third day. The interval between it and the following litter was 21½ days. None of the other litters lost more than one young before the 14th day.

Hamilton (1949) points out that copulation immediately after parturition is not merely a response to captivity, but occurs naturally in several mammals, including the Red-backed Vole, *Clethrionomys gapperi*, and the Muskrat, *Ondatra zibethica*. He (1937) also found up to 83.3 per cent of nursing *M. pennsylvanicus* pregnant at a period of maximum production, while Brambell and Rowlands (1936) concluded that most female Bank Voles, *Clethrionomys glareolus*, must become pregnant again at post-partum oestrus. In the Varying Lemming I know of only two records of pregnant nursing females. Preble (1902) reports a female near Churchill which was suckling 3 young and contained 3 embryos, and I recorded one on Banks Island with degenerating mammary tissue and 7 small embryos. Handley (Field Notes) found a nest at Mould Bay which contained young from two litters of different ages. Further careful observations are desirable, and will probably show that at certain stages in the population cycle pregnant nursing females are not uncommon.

### Sex ratios

The pooled specimens of the five collectors shown in Table 6 were obtained in northern Canada without selection for sex. In a total of 410 *D. groenlandicus* and 26 *D. hudsonius*,  $50 \pm 2.4$  per cent, were male. Of course all that is here proved is that half the sum of the number caught by trap (about two-thirds) and by hand (about one-third) were male. The actual proportion of males in the population can only be assumed, as one of the sexes may be more susceptible to being trapped or dug out from burrows. When the major collections are considered separately, it is seen that the one from Piling has a chi-square value which is surely too high to be consistent with the hypothesis of a 50 per cent male population, while there are two others, from southern Banks Island and from Mould Bay, which have probably inconsistent values. The Piling collection differs from the others, except perhaps the Igloolik, in that it was obtained from a restricted area probably under a quarter of a mile square. It would appear that either there was a local concentration of females, or the females, which were apparently not at that time breeding, were more susceptible to traps. The other two collections from Baffin Island or the nearby islands of Foxe Basin including Igloolik, which were taken about the same period and, it is thought, at about the same stage of the cycle, do not show the same discrepancy, and are, in fact, the most consistent with the hypothesis of a 50 per cent male population. It is true that these two

**Table 6.** Sex ratios from random counts of 436 feral and 119 captive Varying Lemming

	Collector	No. specimens	Per cent ♂ ± σ	Adjusted chi-sq.
Piling, Baffin Id., 31 Aug.-4 Sept. 1949	A. H. Macpherson T. H. Manning	30	23.3 ± 7.7	7.5
Igloolik Id., Foxe Basin, 14 Sept. 1949	T. H. Manning	31	45.2 ± 8.9	0.1
Other Baffin Id. and Foxe Basin areas, chiefly C. Dorset, 12 Aug.-11 Sept. 1949	T. H. Manning	38	55.3 ± 8.1	0.1
S. Banks Id., 6 June 1953	E. O. Höhn T. H. Manning	54	63.0 ± 6.6	3.1
N. Banks Id., 5 July-28 Aug. 1953	T. H. Manning	43	39.6 ± 7.5	1.5
Mould Bay, Prince Patrick Id., 26 Apr.-5 Aug. 1949	C. O. Handley S. D. MacDonald	166	57.8 ± 3.8	3.8
All above collections and some smaller collections <sup>1</sup>		436	50.0 ± 2.4	-
Captive lemmings, Feb. 1950-Apr. 1952		119	31.0 ± 4.2	16.3

The standard deviations of the percentages are based on the relative proportions of the sexes in the respective samples. The chi-square values are based on the hypothesis of a population equally divided between the sexes.

Specimens from Igloolik and Cape Dorset were all hand-caught by digging burrows or searching under stones. Nearly all those from Piling and Banks Island were caught in baited traps, usually placed in runways. The Prince Patrick Island specimens were partly trapped and partly dug out.

<sup>1</sup> These latter were taken between 1944 and 1953 by S. D. MacDonald, A. H. Macpherson, and T. H. Manning and include 26 *D. hudsonius* from the east side of Hudson Bay.

collections were taken principally by hand, but the southern Banks Island collection, which was nearly all trapped, was 63 per cent male, so that it cannot be said that the females are necessarily more susceptible to traps. Hantzsch (1913, p. 150) records an even greater disproportion in favour of the males at Blacklead Island in the spring of 1909 when only one out of 30 specimens was female. It appears, therefore, that whereas the total lemming population is approximately equally divided between males and females, local concentrations of either sex may occur at certain places and seasons, or alternatively, one or other sex may at times be more easily taken, especially by trapping.

The captive lemmings were usually sexed between the ages of 25 and 60 days. In their case the proportion of males is presumably representative of the population of the colony, although it is thought that males had a shorter life expectancy, so that the proportion born may have been distinctly higher than the 31 per cent of Table 6, but probably significantly less than 50 per cent. It is tentatively suggested that one or more of the small number of feral lemming contributing to the colony may have had an inheritable tendency to produce more than the normal proportion of females. Although less pronounced, this might be comparable to the genetic condition known as "sex-ratio" in the fruit fly, *Drosophila* (Wallace, 1948).

### Care of young

Both sexes of the segregated captive pairs tended the young. The male was often almost as assiduous as the female in carrying the young back to the nest when they were old enough to crawl out. Both sexes would remove the young from a disturbed nest. MacDonald found two nests at Mould Bay containing a pair of adults and half-grown young, which suggests that even under natural conditions lemmings remain paired after the birth of the young.

### Life expectancy and disease

There is no direct evidence of the normal age limit of the Varying Lemming in their natural habitat, but in some other small microtine rodents (e.g., *M. agrestis* (Chitty, 1952), *C. glareolus* (Brambell and Rowlands, 1930)) survival through a second winter is exceptional, if indeed it occurs at all.

In captivity, the mean life span of 87 live-born Varying Lemming calculated from the grouped data of Table 7 was 105 days, or 143 days if calculated from the number surviving on the twentieth day. The latter figure may be compared with 34.57 weeks (242 days) given by Leslie and Ranson (1940, p. 50) for 144 Field Voles observed from the age of 3 weeks.

**Table 7.** Deaths of 87 captive lemmings recorded by age groups

Age in days, mid periods	20-day periods					50-day periods							
	10	30	50	70	90	125	175	225	275	325	375	425	450 upward
No. of deaths	25	11	10	7	6	10	5	1	4	3	2	1	2

The two lemmings living beyond 450 days died respectively on their 667th (♀) and 748th (♂) day.

Table 7 was included with some misgivings. It is inevitably biased because the greatest number of births occurred in the late winter and early spring, whereas the greatest number of deaths occurred during the summer when records were not kept. Furthermore, the number of natural deaths, the only ones included in the table, in middle and old age were disproportionately reduced by accidental deaths, by escapes (about half the lemmings were kept in boxes or open runs), and by gifts of animals for experimental or other purposes, so that the 87 deaths recorded are in effect selected individuals from the 255 births which were noted. The maximum life span of the lemmings recorded in Table 7, 748 and 667 days for a male and female respectively, is very similar to that for Leslie and Ranson's voles (1940), but in addition, two females, which had never bred and were kept as pets for the latter part of their lives by Mr. and Mrs. G. W. Rowley, reached the age of about 2½ years and 3 years and 2 months respectively.

The oldest female to bear young was aged 555 days at the time of its last litter, and the oldest male was 661 days old when it sired its last litter.

The cause of death of most of the younger captive lemmings is unknown, but it was noted that several might die within a period of a few days, and there then might be two weeks or more with no deaths. Sometimes the lemmings became thin before dying; at other times they were fat and apparently healthy until about 24 hours before death. About 8 lemmings which died from unknown causes were sent to the Animal Diseases Research Institute, Hull, P.Q., for autopsy, but the cause of death could not be determined. One lemming died from cancer (Rowley, 1953).

The original captives were brought to Ottawa with 7 Brown Lemming, *Lemmus trimucronatus*, with which they occasionally had direct contact. Six of the Brown Lemming died shortly after arrival, and *Listeria monocytogenes* was isolated from the 4 sent to the Animal Diseases Research Institute (Plummer and Byrne, 1950), but the Varying Lemming were apparently not affected.

### Summary

The mean number of young born, alive or dead, in 56 captive litters counted within 24 hours of birth was  $3.41 \pm .21$ . Records for 47 litters were kept until after weaning. On the fourteenth day, 44 of these had some surviving young, and their mean litter size was then  $3.07 \pm .24$ .

There was a significant correlation between the age of the mother when over 100 days and litter size:  $r = -.33$ ,  $P < .02$ .

The mean of 30 feral embryo and placental scar counts was  $5.47 \pm .33$ , the mean of 19 feral litter counts,  $3.68 \pm .35$ . The apparent wastage, therefore, was 1.79 young per litter against an estimated wastage in captive litters of .67.

The mean size at birth of 49 feral litters was estimated at  $4.53 \pm .28$ ; the difference between this and the mean size of 56 captive litters was  $1.12 \pm .35$  young. Possible causes are discussed.

The normal gestation period is believed to be between 19 and 21 days. When pairs were left mated, conception apparently occurred usually at post-partum oestrus, but the interval between litters was sometimes increased to  $26\frac{1}{2}$ , and perhaps in one case to  $36\frac{1}{2}$  days. There was a significant positive correlation ( $r = .52$ ,  $P$  about .02) between this interval and the size of the preceding litter, presumably owing to delayed implantation caused by lactation.

Fifty  $\pm 2.4$  per cent of 410 *Dicrostonyx groenlandicus* plus 26 *D. hudsonius* taken in northern Canada were males, but some collections from localized areas showed a significant variation. Only  $31 \pm 4.2$  per cent of the captive lemmings, usually sexed between the ages of 25 and 60 days, were males.

The mean life span of 87 live-born captive lemmings dying from natural or unknown causes was 105 days, but this figure is probably biased by interruptions in the records and therefore too low. The oldest male died on its 748th day, and the oldest female at about 3 years 2 months. The oldest male sired its last litter about the 661st day, and the oldest female to bear young was aged 555 days. One lemming died of cancer; the cause of death in other cases was not determined.

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