Growth, reproduction and resource allocation in the Norwegian lemming *Lemmus lemmus* (L.) under controlled conditions

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Lemmings from a laboratory colony did not show statistically significant differences in growth between the sexes up to an age of 50 days. After this, growth slowed down, but adult individuals continued to gain weight, some reaching more than 100 g. Reproductive females gained more weight than non-reproductive. Maximal longevity was between 2 and 3 years. The Norwegian lemming has high reproductive potentials. Females became sexually mature at about 3 weeks of age, even down to two weeks, and remained sexually active until the last periods of life. With 8 mammae and an average litter size of 4, our material confirmed the one-half rule. Litter size up to 16 was recorded. With post-partum oestrus, litters were born at 21 day intervals. Pregnancy and lactation therefore overlapped. Resource allocation between the mother's demands and those of the two sets of progeny, is achieved partly because the lactation period is so much shorter than the gestation period. Thus competition for energy is reduced. We did not observe any negative effects of the presence of sucklings on the ensuing litter. Even with concurrency in pregnancy and lactation the female herself gained some weight. The Norwegian lemming is thus capable of rapid population growth.

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INTRODUCTION

Small mammals in northern and arctic areas undergo spectacular 3-5 year cycles in population abundance (review in Stenseth & Ims 1993). The causes of these cycles are still extensively debated. A better understanding of demographic processes is considered vital to understanding population dynamics in general (Tuljarpurkar & Caswell 1997). Information regarding demography of lemmings under controlled conditions is scarce, despite the fact that such information may be valuable to better understand trade-offs between for example growth and reproduction (e.g. Stearns 1992). This was why we started to maintain a colony of the Norwegian lemming *Lemmus lemmus* (L.) in the laboratory in order to accumulate data on growth and reproduction of this species. Some of the findings regarding reproduction are published elsewhere (Semb-Johansson et al. 1993). Additional data, concerning growth and reproduction, presented in this paper, are supplementary to information already given by Finnish (Kalela et al. 1961), Swedish (Marcström 1966), German (Frank 1962) and American scientists (Morrison et al. 1976, 1977a,b) on this species. We address questions of resource allocation concerning progeny demands and the trade-off between mother and offspring. Our findings contribute to the general problem of resource allocation in mammalian growth and reproduction as part of life history theory in general (Stearns 1992), and in small mammals in particular (Stenseth & Ims 1993).

MATERIAL AND METHODS

The laboratory colony originated from wild animals collected in Southern Norway in 1963-64 and 1967-68 (Semb-Johansson et al. 1979, 1993). The animals were kept under controlled conditions in wooden cages with metal screened top, front and bottom. They were fed rolled oats, bread and apples (fresh daily) *ad lib.* and once a week with moss, mostly *Pleurozium schreberi*. Further details are given in Semb-Johansson et al. (1993). During the first three weeks the animals were, when possible, weighed each day.

RESULTS AND DISCUSSION

Growth

The body growth of the captive animals was at first linear, followed by a short period (around day 10-14) of slightly reduced growth (Figure 1). The reduced rate of growth corresponds to the period of weaning: the eyes open, locomotory activity increases, thermoregulation is attained, and there is a gradual shift from milk to solid food (Østbye 1965). There was no difference between male and female body mass before 52 days of age (Figure 1, ANCOVA, r^2=0.699, n=70, F=0.005, p=0.942) when simultaneously correcting for age (F=526.465, p=0.000). This agrees with the observations of Frank (1962), with regard to both the lack of early sexual differences, and the various phases of growth. At about age 50 days, growth slowed down. After 52 days of age, males were significantly heavier than females (Figure 1, ANCOVA, r^2=0.858, n=74, F=181,229, p=0.000) when simultanously correcting for age (F = 239.759, p = 0.000).

Morrison et al. (1977a) describes the growth curves of rodents, including lemmings, as comprising sets of linear segments which reach a stable phase at adult weight. The data from our animals compare fairly well with those of Morrison et al. (1977a). However, Morrison et al. (1977a) calculated the stable adult weight (one year old) as 60 g in males and 52 g in females, while our animals continued to gain weight even in the adult phase, although at a slower rate than in the early phase of life. Several old males reached weights of more than 100 g. The maximal weight was 135 g for a male (670 d. old) and 111 g for a non-pregnant female (620 d. old). These data are slightly higher than those reported by others (e.g. Kalela et al. 1961: male 110 g, non-pregnant female 104 g) and may partly be the result of inactivity and surplus of food. Autopsies sometimes documented an excess of fat deposits.

The growth curve for females shown in Figure 1 is based on non-reproductive females only. If females became sexually active and reproduced, they grew much faster. Five examples are shown in Figure 1, based on the pregestation and postparturition weights of caged, reproducing females. This difference in growth rates may explain why we found a higher growth rate for females in freely growing populations as compared with isolated non-reproducing individuals (Semb-Johansson et al. 1979).

Sexual maturation, length of reproductive life and longevity

In our colony, perforation of the vagina normally took place when the female was around 3 weeks old. The earliest pregnancy was observed in a female only 2 weeks old. This is remarkable because this is about the time when weaning takes place, but sexual maturation as early as 15 days was also reported by others (Kalela et al. 1961, Frank 1962). In contrast to this, one female was 413 days old when she delivered her first litter, and she ended up with a total of 8 litters before she died. Females may remain sexually active up to the last part of their lives. Thus one female delivered her last (8th) litter when she was 691 days old. This agrees with Marcström (1966) who also reported fertile females more than 600 days old.

The oldest female became 784 days old (i.e. 2.1 years) and the oldest male 1037 days (2.8 years). Several individuals reached an age of more than two years, but none became three years old. The Norwegian lemming can become older than that, as Marcström (1966) reported males being at least 3 years and 9 months old.

Interbirth intervals

In the Norwegian lemming 74% *post partum* oestrus was prevalent (Morrison et al. 1976). In our colony, when a male and a female were caged together, mating was normally observed 2-4 hours after the delivery of a litter. The delivery could last for more than 4 hours, and in one case where a female gave birth to a litter of 16 young ones, mating took place several times before the last young one was born. Marcström (1966) reports that in

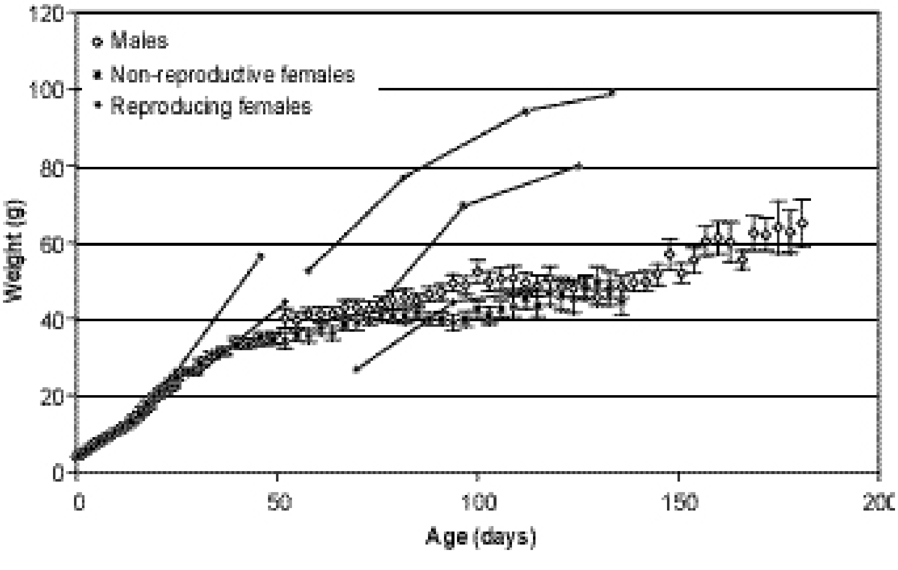

Figure 1
Growth of lemmings in the laboratory. Males and non-reproducing females have equal growth rates up to about 52 days of age, after which males grew faster. Females that started reproducing gained weight much faster than non-reproducing females.

one case mating took place only hours after parturition, but that the majority of the females did not come into heat until several hours after parturition. If *post partum* oestrus did not take place in his captive animals, the females entered a period of lactation anoestrus of 4-18 days.

Several females showed a remarkable regularity in deliveries when they were caged together with the same male for a substantial period of time, a situation we refer to as ”permanent pairs”. This was the case both for field-caught females (Figure 2a) and for females born in captivity (Figure 2b). Litters may be overlooked if the offspring is totally lost because of cannibalism by the female immediately after parturition, or abortions or resorbtions may affect interbirth intervals. Thus we are inclined to assume that one litter was missed, resulting in the interval of 43 days in Figure 2b. The inter-birth intervals showed a mode of 21 days (31%) with no significant differences between small and large litter sizes (Semb-Johansson et al. 1993). Litters were born all year around, as already reported by Kalela et al. (1961).

Litter size

The average litter size for our total material was 4, and numbers of 3-5 made up for 61% of the variation (Semb-Johansson et al. 1993). The range was from 1 to 16 young ones, but only 7 of the 630 litters were above 8 young. The Norwegian lemming has only 8 mammae, but 12 of the 16-litter survived to weaning. In the field a female with 14 young ones has been reported from Finse, Norway (E. Leslie, pers. comm.), and Collett (1911-12) reported up to 11 embryos, and Wildhagen (1953) up to 13. Among mammals, and particularly rodents, the mean litter size is about half the number of mammae, and maximum litter size approximates mammary numbers (Sherman et al. 1999). Our material confirms these rules. Litter size in small rodents may vary with litter sequence (parity) and age (weight) of the mother (e.g. Semb-Johansson et al. 1993, Sikes & Ylönen 1998). This will be taken into consideration in our analysis of resource allocations.

Female output

The total reproductive output for our laboratory females was very variable. Based on females (n=12) with 10 or more litters during their lifetime, the average number of litters and young per female per year was 13 litters (range 7-17) and 51 young (range 23-76). Laboratory observations are usually not representative for field conditions (cfr. Millar & Threadgill 1987). Thus the average litter size in small rodents has a tendency to be lower in laboratory animals than what is observed in the field. This goes also for the Norwegian lemming (Stenseth & Ims 1993: p. 272). On the other hand, age at maturation is reported to be higher in the field (Koponen 1970). Realisation of the reproductive potential in the field also varies with seasons and from one year to another. The breeding season is shorter, with winter breeding as an interesting adjustment primarily found in years prior to peak years (Stenseth & Ims 1993, Krebs 1993), but even in peak years immediately before the population crash (Østbye et al. 1993).

It has earlier been concluded that under natural conditions lemmings do not seem to have exceptionally high reproductive rates compared with other microtines (Stenseth & Ims 1993: p 271). What is evident from our laboratory studies is that the reproductive potentials of the Norwegian lemming are extremely high, thus making possible the remarkable population growth which takes place before and during peak years.

Female investments

Realisation of the reproductive potential requires an efficient use of the resources, of both time and energy. Investments of a female lemming may follow three main channels, often concurrent: (1) Maintenance of her own life, including growth, (2) prenatal growth and development of the progeny, and (3) postnatal growth and development of the sucklings, often from the preceeding litter. The analysis of energy partitioning, which we present here, is based on observations of weight, not on measurements in energy equivalents. With these restrictions and despite large individual differences, some general patterns are evident.

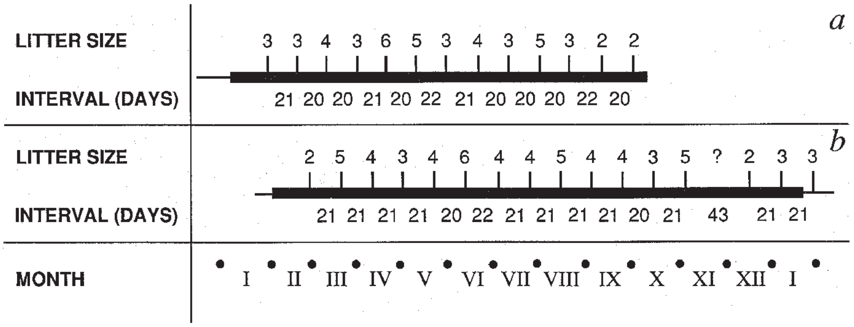

Figure 2
Litter sizes and birth intervals between births in (A) a field-caught and (B) a laboratory bred female.

Female growth

In Figure 1 we have shown the growth of non-reproductive females. For females in an active period of reproduction growth was quite different. During the period of pregnancy, female weight increased up to the time of delivery (Figure 3a). Most of this increase was due to the growth of the embryos and their supporting apparatus, and was therefore influenced by the number of embryos. Thus the female giving birth to 16 young ones, increased more than 58 g in the last seven days of pregnancy, i.e. more than 8 g per day. Therefore, Figure 3 is restricted to females with litter size 3-5 and pregestation weight 30-70 g. If we compare the pregestation and postparturition weights (i.e. the "basal weights") of females without sucklings (Figure 3a), this weight increased during pregnancy, with an average of about 15.7 ± 4.4 g. (n=17), i.e. 33% of the pregestation weight. This increase in basal weight is also evident for the 5 reproducing females in Figure 1.

The increase in female basal weight was quite different if she had concurrent sucklings (Figure 3b). The weight usually dropped during the 1st to 2nd week of pregnancy, but increased during the last part, the final result being an average increase in basal weight of only 5.5 ± 3.8 g (n=8), i.e. 10% of the pregestation weight. This difference was also evident from Figure 5.

The increase in basal weight was also evident if we look at the changes in weight of individual females. As shown in Figure 4a, the female basal weight increased steadily during the period of (6) pregnancies. Periods of increasing and decreasing female basal weights were correlated with periods of pregnancies and non-pregnancies (Figure 4b). Basal weight was not influenced by the female becoming sexually mature (opening of the vagina) or by the presence of a male in the cage.

The rate of increase in female basal weight depended not only upon the breeding situation, but also upon the female pregestation weight (or age) (Figure 5, litter size 3-5). For small females the relative gain in basal weight was about 50-60%, but declined to less than 20% for the heaviest females. For females with concurrent lactation the relative increase was less.

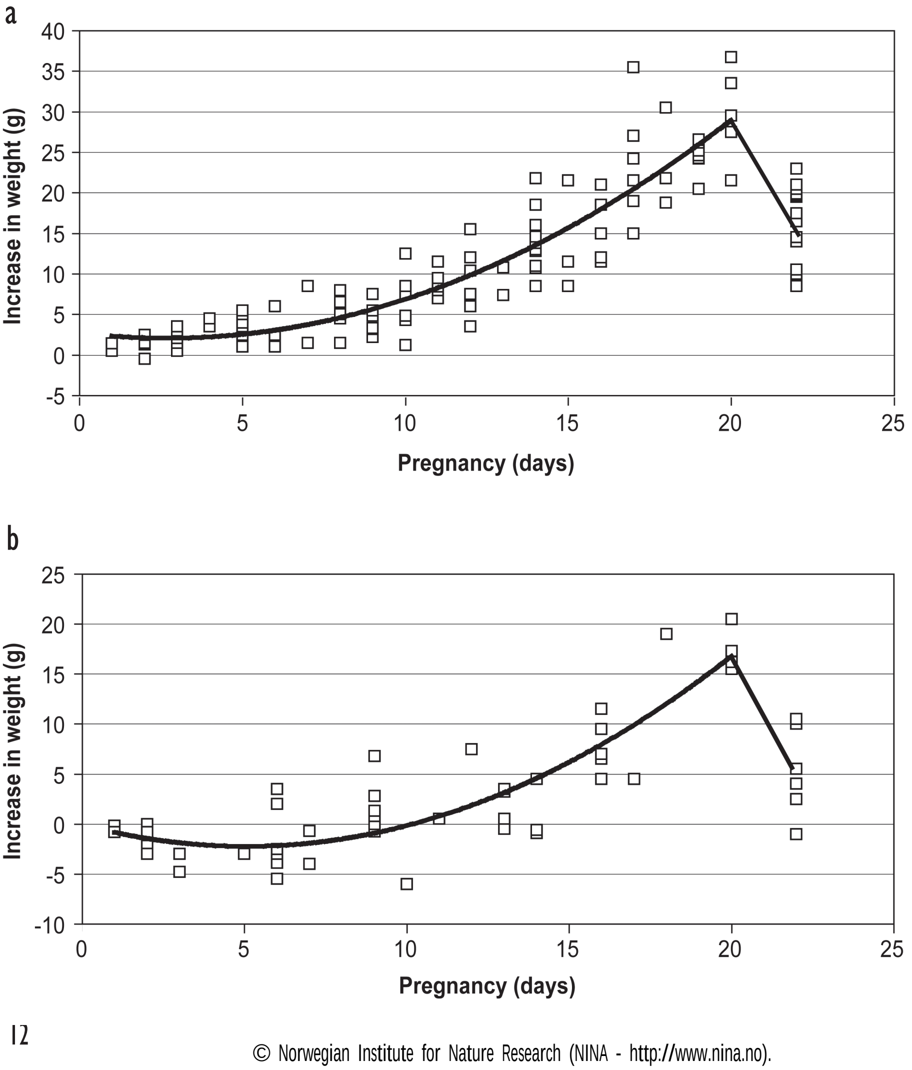

Figure 3
Changes in weight during the period of pregnancy for (A) females without sucklings and (B) females with concurrent sucklings. The trendline up to 20 days is a second-order polynomial line, whereas a straight line was drawn from there to the mean at 22 days.

Increased female body-weight after parturition was also observed in other rodents (Weiner 1987) and may last for a period of several months after the end of reproductive activity (Dewsbury 1992). Also in sciurids *post-partum* females are significantly heavier than non-reproductive females (Humphries & Boutin 1999). On the other hand, in the shrew *Crocidura russula monacha* the female returned to her pre-pregnant body-mass immediately after delivery (Mover et al. 1988).

Lactation is a strong energetic burden on the mother, and it is remarkable that the female Norwegian lemming will increase in weight even after lactation in addition to pregnancy. This is not so in all mammals, and in some species the body mass of lactating females immediately after weaning may be 10-15% less than before conception (Thompson 1992).

Investment in fetuses

The growth of fetuses of the Norwegian lemming has been described by Østbye & Gult (1980). Weight of the new-borns is an indication of the gestation effort of the mother. The average weight of a new-born was for our total material 3.92 g (n=2541) (Semb-Johansson et al. 1993). The weight of the new-born depends on several conditions. With increasing litter size it decreases, but there is of course a lower limit for the weight of the new-born. Thus for the 16-litter, the four smallest youngones with weights from 2.6-3.1 g died within the first week, whereas the others (weights 3.2-3.9) survived beyond weaning. For the present analysis, we therefore selected females with litters of 3-5, and a pre-gestation body weight of 30-70 g. The females were divided in two groups with no significant differen-

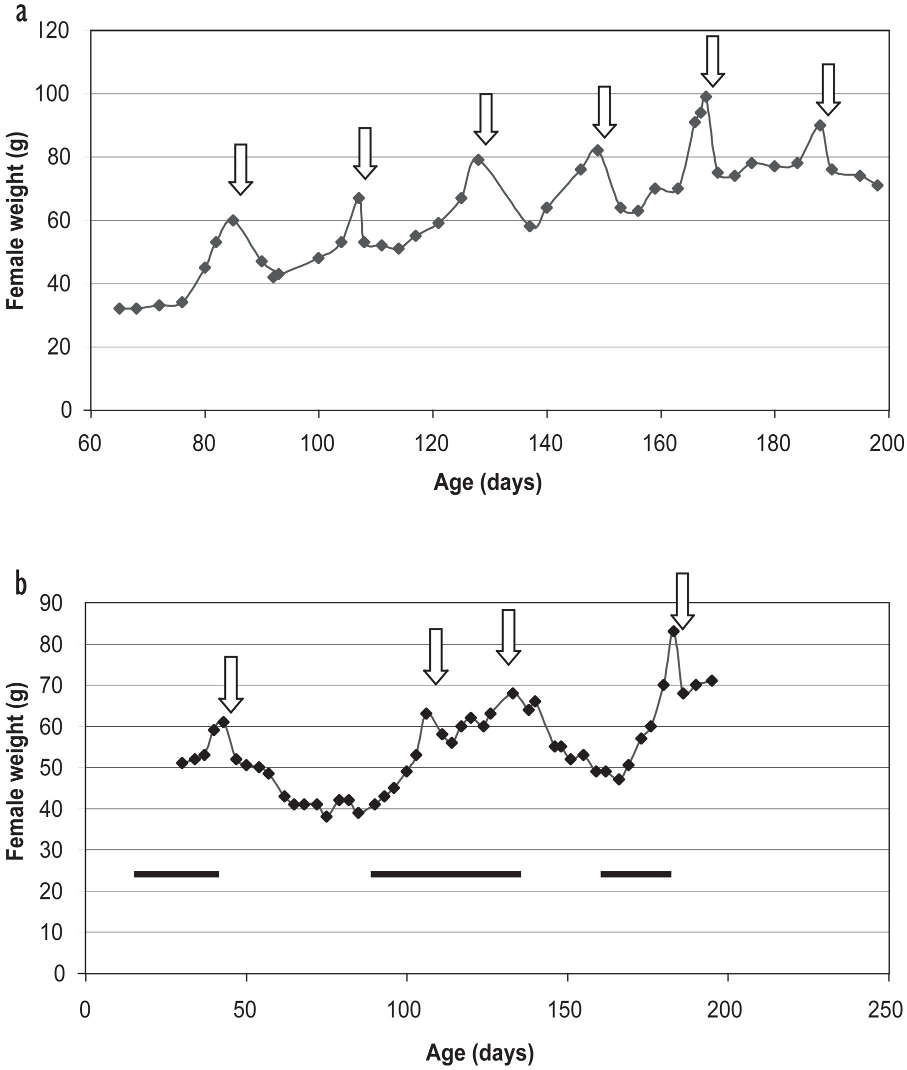

Figure 4
Changes in weight during periods of pregnancies and non-pregnancies in two field-caught female lemmings. Arrows indicate births. (A) Permanent pairs (continuous reproduction). (B) Discontinuous reproduction. Solid horizontal bars mark periods when a male was present.

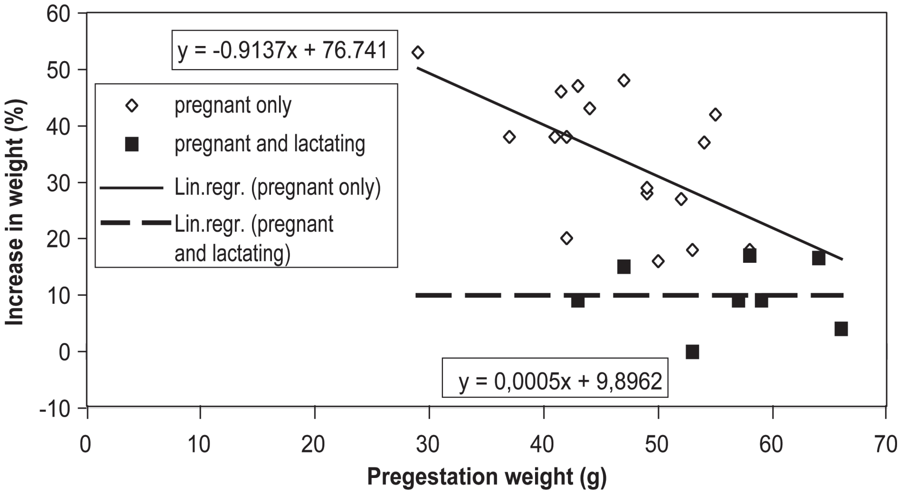

Figure 5
Increase in female weight in relation to her pregestation weight for females that are pregnant only or pregnant and lactating.

ces in body weights between the groups. Females which did not have any sucklings to take care of during the present pregnancy, delivered young ones with an average body weight of 4.0±0.66 g (n=55). When the mother had sucklings at the same time, the weight of the new-borns was, to our surprise, 4.70±0.68 g (n=29). This difference was highly significant (t=4.59, df=56, $p<0.005$). At the time of weaning there was no significant difference in weight between the two groups, nor was there any difference in the rate of survival between the two groups up to this age.

The investment in fetuses may be expressed as a percentage of the pre-gestation weight of the mother. In our study (litter size 3-5, female weight 45-65 g) the total litter mass at birth was on the average 33% of the pre-gestation weight of the female (range 17-45; n=24). In extreme cases it was much higher. Thus for one 27 g female which gave birth to 4 young, it was 67%, and in the female with a litter of 16, the total litter mass was 58% of the pre-gestation weight.

Leitch et al. (1959) lists the relationship between maternal weight and litter mass in 114 mammalian species. The Norwegian lemming is close to the upper range for small rodents (35-50%), but our extreme observations (above 60%) are only matched by laboratory strains of the guinea-pig.

Postnatal investments

An expression for the lactation effort is the gain in weight of the sucklings up to the time of weaning. The gain in weight may be expressed as a percentage of the post-parturition weight of the female. This percentage is influenced by litter size and female weight, but also by concurrency in reproduction. Thus it is seen from Figure 3a and b that the increase in post-parturition weight was lower in females with concurrent sucklings. If we use our average data, the investment in a litter of 4 sucklings will therefore be about 53% of the post-parturition weight if the mother did not have another litter to take care of at the same time, and 63% with concurrency in reproduction. Our data agree well with what is found in other mammalian species. Thus relative size at weaning averages 37% in mammals, but in some rodents it exceeds 65% of adult size (Millar 1977).

Resource allocations: progeny demands

Simultaneous energetic investment in both embryonic and neonatal development is a hard job for small mammals. A female with concurrent fetuses and sucklings therefore has to make priorities in resource investments. In the Norwegian lemming, this is achieved by differences in timing between different demands. During the first 10-12 days of pregnancy the lemming mother will give priority to mammary nourishment of the neonates, whereas later she will switch to transplacental nourishment of the next litter. Lactation is energetically demanding, and the bottleneck is the late lactation period (e.g. König & Markl 1987). In the Norwegian lemming, embryonic development is very slow during the first week. By the time the sucklings of the preceding litter are about to be weaned, the embryos of the new litter have reached less than 10% of their weight at birth (Østbye & Gult 1980). In this way the maximal energy requirements during the last part of the lactation period do not interfere with the development of the embryos.

Another question is whether the female lemming in this way is able to reduce energy-competition so much that the effect is negligible. In other words, does the presence of sucklings during pregnancy have any negative effects on the ensuing litter? With regard to the weight of the new-born, we have already pointed out that the neonates weighed more when the mother in addition had sucklings to take care of. The presence of sucklings had no observable effect on the duration of a concurrent pregnancy (cfr. Figure 2), nor on the survival of the young of the litter (Semb-Johansson et al. 1993). What about litter size? In order to observe the effect of having sucklings on the size of the ensuing litter, we compared the effect of small and of large litters. To our surprise we found that a large litter (of 7 or more sucklings) was generally followed by a litter larger ($\bar{X}$ = 4.9; n= 26) than the average of 4, whereas a small litter of sucklings (3 or less) was generally followed by a litter smaller ($\bar{X}$ = 3.7; n= 156) than the average. This was not due to the fact that our material consisted of some females having generally large litters and others having generally small litters. Thus we did not observe any negative effect on litter size.

As a conclusion we may therefore state that we did not observe any negative effects (i.e. trade-offs) from the presence of sucklings during pregnancy on the ensuing litter. This is in agreement with observations made on other small rodents, such as *Neotoma floridana* and *Sigmodon hispidus,* with regard to growth and survival when food was available *ad lib*. (McClure 1987, Oswald & McClure 1990). Nor did lactation affect gestation time in *Zygodontomys microtinus* (Aguillera 1985). On the other hand, nursing of a litter during pregnancy affected the number of young in the subsequent litter in *Peromyscus maniculatus* (Myers & Master 1983), and in the house mouse the offspring were smaller at weaning (König & Markl 1987).

Resource allocations: The mother

In life-history studies much emphasis has been put on the utilisation of energy and the trade-off between traits of mother and offspring (e.g. Stearns 1992, Thompson 1992). In the Norwegian lemming, the presence of sucklings in addition to fetuses did reduce the increase in weight of the mother (Figure 3). But even with concurrent lactation and pregnancy she was able to gain some weight. In cases with conflicts over patterns of resource allocation between mother and offspring these conflicts are settled in a manner consistent with the mother's rather than the offsprings' best interest (Millar 1975, Rogowiz 1996, Sikes & Ylönen 1998). It is generally assumed that breeding is proportionately more costly for small females. As expected, the strategies of resource allocation in the Norwegian lemming differed with female size (Figure 3). A light (young) female would invest relatively more in her own growth, as compared to a larger female (cfr. Figure 5), who will invest relatively more in her offspring. Such differences in reproductive tactics between small and large females have been demonstrated in several species of rodents (e.g. Derrickson 1988). From the point of view of evolution it is understandable that a young mother make priority to her own demands, whereas an older female would favour the offspring.

Concluding remarks

Lemmings have high rates of metabolism, a small body mass, and are well known for their population fluctuations (McNab 1980). The Norwegian lemming is such an r-selected species, well adapted to rapid population growth. First of all, it has high reproductive capacity. As emphasized in this paper, it may become sexually mature at an early age (down to 2 weeks), it has the capacity of raising large litters (at least up to 12), and with short intervals (normally 21 days) between litters. Thus it may achieve a high reproductive rate during the short periods of favourable conditions and compares well with other opportunistic small rodents (e.g. Delany 1986).

A premise for efficient use of the reproductive capacity is an optimal combination of food consumption and utilisation. When the female Norwegian lemming enters an active reproductive period, she also prepares for the increased energy demands. This is shown by the fact that a reproductive female will increase more in basal weight than a non-reproductive female (Figure 1). A probable explanation is that pregnancy stimulates food intake. Thus in the bank vole, *Clethrionomys glareolus,* food consumption and assimilation both increase during pregnancy and lactation (Kaczmarski 1966), as was the case in most female mammals (Thompson 1992).

The problem of investment priorities is solved in different ways in small rodents. It is first of all important to avoid concurrency of the peaks of energy demands in late pregnancy and late lactation, as simultaneous energetic investment in these two processes is beyond the physiological capacity of many small mammals (Mover et al. 1988). In the Norwegian lemming, early embryonic development coincides with late lactation and thus energetic competition is avoided. The hispid rat *Sigmodon hispidus* seems to represent a case similar to the Norwegian lemming. In this species the lactation period is so short that there is minimal energetic overlap with concurrent pregnancy and lactation (McClure 1987). Another way of avoiding accumulated energy demands when pregnancy is concurrent with lactation, is by delayed implantation and/or repressed post-implantation development. This was the case in the bank vole *Clethrionomys glareolus* where the lactating period and the pregnancy period were of similar length (Andersson & Gustafsson 1979, Gustafsson et al. 1980) and in the house mouse (McLaren & Michie 1963). In the collared lemming *Dicrostonyx groenlandicus,* the interval between births is extended in lactating females, probably as a result of delayed implantation (Manning 1954). In the shrew *Crocidura russula monacha* the gestation period is prolonged and thus energy competition is reduced (Mover et al. 1988). In the Norwegian lemming (Koponen 1970), as well as in *Lemmus trimucronatus* (Mullen 1968), no such effect was found. Here, the amount of energy available for the offspring is so large and the timing so perfect, that no negative effects from lactation on the development of the next litter could be observed.

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SAMMENDRAG

Vekst, reproduksjon og ressursfordeling hos lemmen, *Lemmus lemmus* (L.) under kontrollerte betingelser

De dramatiske og spektakulære svingningene i lemenbestander i høyfjellet har fascinert forskere i lang tid. Bedre kunnskaper om demografien til lemen er grunnleggende for en bedre forståelse av svingningsmønsteret. I denne artikkelen presenteres data på reproduktive rater og på avveininger mellom vekst og reproduksjon i livshistorien til lemen som ble holdt under kontrollerte forhold. Det var ingen kjønnsforskjeller i vekstrate hos lemen fra laboratorie-kolonien de første 50 levedagene. Etter denne fasen ble veksten seinere, men også voksne individer økte i vekt, enkelte ble over 100 g. Reproduserende hunner vokste lenger enn ikke-reproduserende. Maksimal levealder var mellom 2 og 3 år. Lemen hadde tydelig et høyt reproduksjons-potensiale. Hunner ble seksuelt modne ved omtrent 3 ukers alder, noen allerede etter 2 uker, og de forble seksuelt aktive inntil den siste perioden av livet. Materialet støttet den såkalte "halveringsregelen", idet det var 8 patter, mens gjennomsnittlig kullstørrelse var 4. Maksimal kullstørrelse var 16. Kullene ble født med 21 dagers mellomrom. Graviditet og laktasjon overlappet derfor i tid. Ressurs-deling mellom morens behov og de to sett med avkom oppnås delvis siden laktasjonsperioden er så mye kortere enn graviditetsperioden. På det vis fordeles energikravet for et gitt tidspunkt. Det var ingen negativ effekt av tilstedeværelsen av tidligere kull på neste kull. Selv hunner som både var gravide og i laktasjon vokste også i kroppsstørrelse. Lemen har altså forutsetninger for rask bestandsvekst. Betydningen av resultatene i forhold til studier av andre smågnagerarter diskuteres.

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