Ann. Zool. Fennici 30:239–245
Helsinki 13 September 1993
ISSN 0003-455X

Factors affecting litter size in *Clethrionomys gapperi*

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Received 13 March 1993, accepted 19 May 1993

Litter size of 207 parous *Clethrionomys gapperi* in the front range of the Canadian Rocky Mountains, was examined by means of embryo counts, births in live-traps and births in the laboratory from wild inseminated females. The overall mean was 5.5, with a mode of 6 and a range of 1–10. Litter size and maternal weight were not correlated in either primi- or multiparous females. No differences were found in litter size among years, among the different collection methods, or between overwintered and young-of-the-year in months in which they co-occurred. However, litter size was significantly influenced by both month and parity. Litter size of multiparous females was relatively constant over the season, but it continuously increased from May to August in primiparous females. The seasonal change in litter size was atypical of other microtine populations, which usually show a decline late in the season. The determinants of litter size among *Clethrionomys* appear to be numerous, but are also inconsistant among species or populations.

1. Introduction

"Variation in litter size is one of the most striking features of eutherian life history diversity" (Read & Harvey 1989). Among rodents, females may produce only one young or more than 10 per litter. Within genera, mean litter size can vary considerably among species (e.g. Keller 1985, Millar 1989) and within species it may vary in relation to a variety of factors such as year, month, habitat, method of collection, age and/or size of the female and her parity. However, in many studies, sample sizes are inadequate to partition the variance among these factors. Pelikán (1979) suggested that a sample of 60–80 pregnant females in mid-breeding season would be needed to obtain a reliable estimate of the mean for a population, but clearly a larger sample is needed for in-depth analyses.

Here we report on the litter size from 207 parous *Clethrionomys gapperi* (red-backed vole) collected over a four year period in the Rocky Mountains, Canada. We examined the data in relation to year, month, method of collection, age, parity and maternal weight. Post-implant and post-natal mortality were also documented.

2. Methods

Animals were live- and snap-trapped at two elevations (approximately 790 m apart) in the Kananaskis Valley, Alberta, Canada (50°N, 115°W). Longworth live-traps and Museum Special snap-traps were set in lines of 20 to 125 traps to secure voles for laboratory studies or necropsy. Additional live-traps were used on grids for mark-recapture studies. Trapping was conducted from early May to late September or early October. More details on trapping techniques, laboratory procedures and habitat types can be found in Innes (1984) and, Innes & Millar (1990).

Estimates of litter size were derived from four sources. First, litter sizes of females which conceived in the wild, but gave birth in the laboratory were recorded within 24 h of parturition. At that time, maternal weight and the number of stillborns were also noted. Second, the number of viable and regressing embryos was determined from snap-trapped females. The body weights of these females were recorded minus the weight of the gravid uterus. Third, litter size as well as maternal weight were noted for those females that gave birth in traps on the mark-recapture grids. Fourth, estimates of litter size were taken from embryo counts from females that died in live-traps. In these cases, maternal weights were not used in any analyses.

Females were divided into two parity classes. Pregnant females that showed evidence of lactation (nipples prominent, nipples visible but flat, or with placental scars) were considered multiparous, while those pregnant females with no signs of a previous lactation were considered primiparous. Females were also classified as either overwintered or young-of-the-year based on weight, reproductive condition and time of the year they were caught. Animals that could not be assigned to an age class were excluded from all analyses involving age.

Although monthly changes in mean litter size are well documented, it is unclear on what basis a pregnant female should be assigned to a particular month. A female could be assigned to the month she was caught in, regardless of her stage of pregnancy. Alternatively, she could be assigned to the month she conceived in, or her month of parturition. In order to standardize our data, we assigned all females to their month of parturition. For kill-trapped females, we used the equation for mouse embryos relating foetal weight and age (Hugget & Widdas 1951) to determine the approximate age of the vole embryos. Both species have similar gestation lengths (19–20 days) (Hugget & Widdas 1951, Innes 1984).

Throughout, means are given ± 1 standard error (*SE*) and ANOVA represents analysis of variance.

3. Results

3.1. Pre- and postnatal mortality

Litter size may change as the result of intrauterine mortality or mortality at birth or shortly thereafter. However, prenatal mortality, based on the number of resorbing embryos of snap-trapped females was quite low. Only two of 283 embryos (0.71%) were found to be substantially smaller than other embryos within a litter. In the laboratory colony, postnatal mortality was also low. Five of 668 offspring (0.75%) were stillborn and 12 young (1.8%) died within one or two days postpartum. These data suggest that litter size at birth in this population is an adequate reflection of the possible reproductive potential of females throughout (visible) pregnancy and early lactation.

3.2. Influence of maternal weight

A oneway ANOVA showed no differences in maternal weight among years ($F = 0.70$, $P > 0.05$). Pooled data showed that litter size and maternal weight were correlated ($r = 0.17$, $P < 0.01$, one-tailed, $n = 189$), although the relationships were no longer significant within each parity group (multiparous: $r = 0.15$, $P > 0.05$, $n = 96$; primiparous: $r = 0.001$, $P > 0.05$, $n = 93$). Maternal weight increased from May to July, but decreased in August when the mean weight of young-of-the-year (23.6 ± 0.7 g, $n = 25$) was much lower than over-wintered females (29.2 ± 0.9 g, $n = 21$) ($t = 4.91$, $P < 0.001$, one-tailed) (Fig. 1). Also, multiparous females were usually heavier

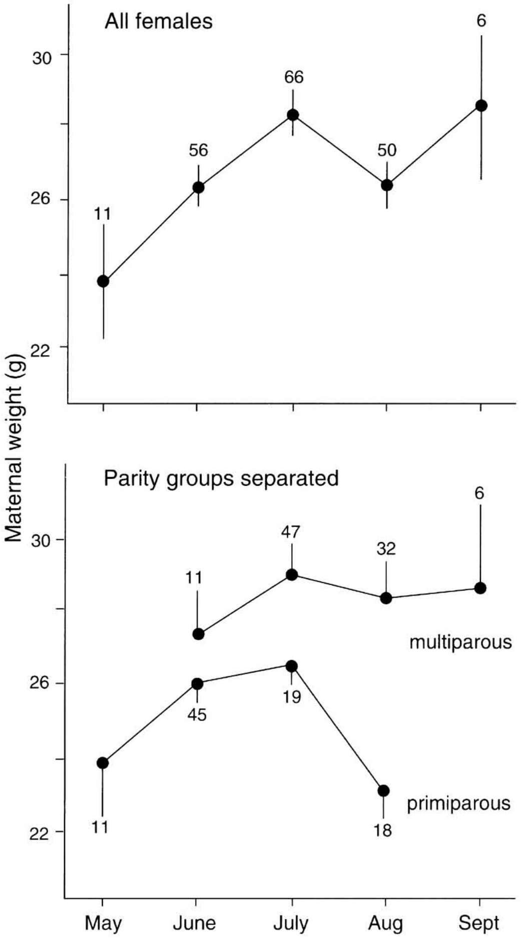

Fig. 1. Monthly variation in maternal weight (mean ± *SE*). Numbers represent sample sizes.

than primiparous females. A two-way ANOVA (excluding May and September) revealed a significant interaction term which indicated that maternal weight differed between parity groups depending on the month ($F = 3.11$, $P < 0.05$).

3.3. Litter size

In a previous analysis, Innes & Millar (1990) found no difference in litter size between elevations or among months, but a significant parity effect. Further analyses assumed no difference

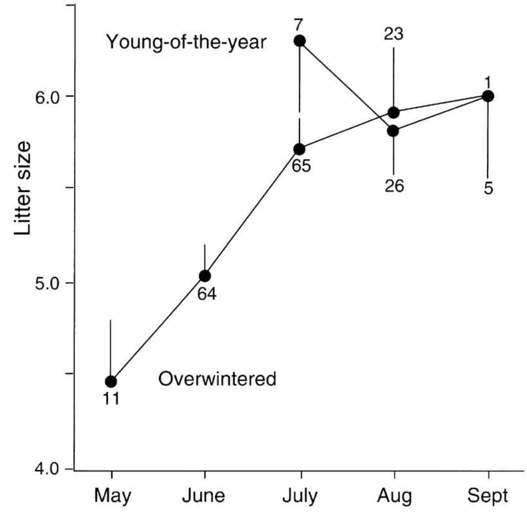

Fig. 2. Monthly variation in litter size with respect to age (mean ± *SE*). Numbers represent sample sizes.

between elevations and the estimates were pooled. The data approximated a normal distribution with a mean of 5.47 ± 0.10 ($n = 207$, mode = 6, range = 1–10). No differences were found in litter size among years ($F = 0.90$, $P > 0.05$) (Table 1). Nor were there any differences among the different methods of collection ($F = 1.49$, $P > 0.05$): Laboratory births: 5.31 ± 0.13, $n = 126$; snap-traps: 5.66 ± 0.19, $n = 50$; live-trap grids: 5.89 ± 0.26, $n = 15$; dead in live-traps: 5.75 ± 0.27, $n = 16$. Also age differences (overwintered versus young-of-the-year) did not appear to be important when data were compared from July to September ($t = 0.57$, $P > 0.05$) (Fig. 2).

Litter size for all females increased from May to July and then leveled off at about 5.8 young

Table 1. Yearly variation in litter size of *Clethrionomys gapperi*.

Year	Mean ± *SE*	Mode	Range	*n*
1978	5.69 ± 0.55	5	3–10	13
1979	5.23 ± 0.19	6	2–9	60
1980	5.51 ± 0.14	6	1–8	79
1981	5.62 ± 0.19	5	1–8	55

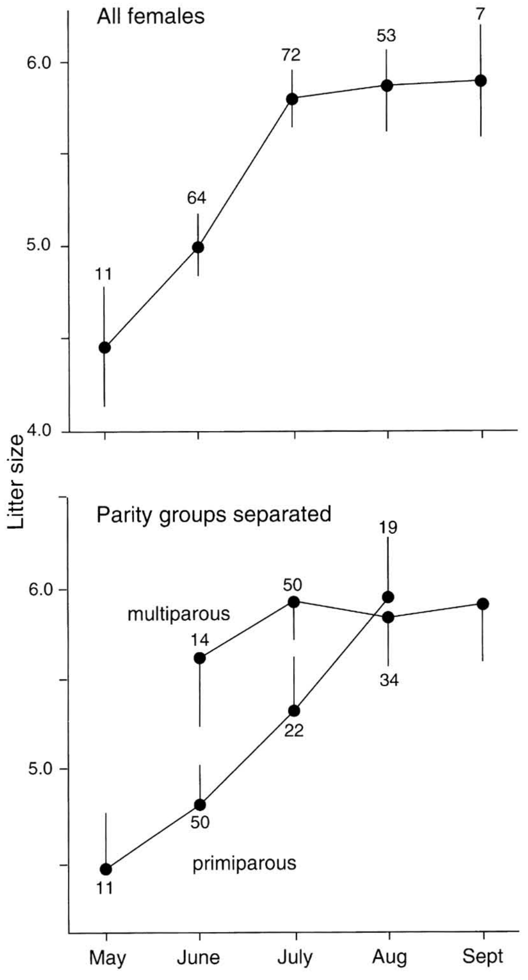

Fig. 3. Monthly variation in litter size (mean ± *SE*). Numbers represent sample sizes.

for August and September (Fig. 3). However, this approach concealed parity effects. The litter size of primiparous females increased throughout the trapping season. (No primiparous females were caught in September). The litter size of multiparous females remained relatively constant between 5.6 to 5.8 offspring during the season. A two-way ANOVA (excluding May and September showed a significant month ($F = 3.39$, $P < 0.05$) and parity effect ($F = 4.92$, $P < 0.05$). The interaction term was not significant ($F = 1.56$, $P > 0.05$).

4. Discussion

Fuller (1969), Mihok (1979), Martell (1983) and Bondrup-Nielsen (1987) as well as this study found no yearly variation in litter size in *C. gapperi*. However, Fuller (1985) reported a significant yearly difference in the same general area as his previous study. Patric (1962) found significant yearly differences in *C. gapperi* and suggested that litter size was inversely related to population density. Kalela (1957) concluded there was little yearly variation in *C. rufocanus*, and Krebs & Wingate (1985) presented data which suggested little yearly variation in litter size in *C. rutilus*. Nakata (1984) found no yearly differences in *C. rufocanus*, but when he grouped the data according to population phase, litter size was large during the increase phase and depressed during the decline phase. Also, he found that it was positively correlated with absolute population density among overwintered females, but not young-of-the-year. In Sweden, northern populations of *C. glareolus* appear to undergo population fluctuations, while southern populations do not. Conflicting evidence suggests that litter size may or may not be related to the degree of cyclicity in this species (Gustafsson & Batzli 1985, Hansson & Henttonen 1985). Martell & Fuller (1979) found that litter size was not related to density in *C. rutilus*.

In some species of *Microtus*, habitat (i.e. vegetation quality) can have a strong influence on litter size (e.g. Cole & Batzli 1979, Krohne 1980), but available data on *Clethrionomys* suggests habitat effects may be uncommon. Innes & Millar (1990) found no differences in litter size between two elevations which were represented by two different types of coniferous forests. Similarly, Bondrup-Nielsen (1987) found no difference in litter size when he sampled *C. gapperi* in deciduous and coniferous forests. Martell (1983) reported no differences in litter size between clear-cuts and control areas for the same species. However, Martell & Fuller (1979) found that the first litters of both overwintered and young-of-the year *C. rutilus* were greater on the tundra than in the taiga.

Few studies on *Clethrionomys* have examined whether litter size varies with the method of collection. Brambell & Rowlands (1936) (*C.*

glareolus), Iverson & Turner (1976) (*C. gapperi*) and Nakata (1984) (*C. rufocanus*) reported that placental scars gave higher means than embryo counts. Fuller (1985) found the opposite pattern in two of three years. Also, in *C. gapperi*, embryo counts from snap-trapping gave higher means than births in live-traps (Elliot 1969), although the comparison is confounded by differences among age groups. We found no differences in mean litter size with the method of collection. Most of our data were obtained from females that bred in the wild, but gave birth in the laboratory. Therefore, there were no biases resulting from laboratory matings.

We also concluded that age effects were not important in those months in which the two age groups co-occurred. However, if we had included all months, then overwintered females would have averaged smaller litters than young-of-the-year because of low means in May and June. Most other studies on *Clethrionomys* have concluded that overwintered females have larger litters than young-of-the-year (Kalela 1957, Zejda 1966, Iverson & Turner 1976, Mihok 1979, Stenseth et al. 1985, Tsvetkova 1990), although the mean difference between groups may be less than half an embryo. Elliot (1969) reported that overwintered females had slightly larger litters than young-of-the-year based on births in live-traps and near-term embryos. However, data from embryo counts that were not near-term suggest the opposite pattern. In general, assigning a female to an age group based on external appearance may result in considerable error variation, especially when multiparous females of both age groups co-occur in a population. A number of studies have used a more quantitative aging technique using changes in tooth morphology. Martell (1979) reported that young-of-the-year had larger litters than their overwintered counterparts, while Martell & Fuller (1979) found that overwintered females had larger litters than young-of-the-year in both taiga and tundra habitats. Nakata (1984) documented that litter size increased in females up to eight months after which there was a slight decline. Similar results were found by Fujimaki (1981) and Zejda (1966). However, when Fujimaki (1981) examined litter size concurrently by age and month, no clear pattern emerged.

Beer et al. (1957) showed that litter size generally increased with body length in *C. gapperi*. In other *Clethrionomys* species, litter size usually increased with body weight (Brambell & Rowlands 1936, Kalela 1957, Fujimaki 1981, Nakata 1984), but see Ims (1987). None of these studies examined this relationship within parity groups and we found no significant relationships between maternal weight and litter size within either primi- or multiparous females.

A number of other studies have also examined variation in litter size by month and/or parity group. Ten studies have examined monthly variation in either *C. gapperi*, *C. glareolus* or *C. rufocanus* and they can be categorized into two more or less distinguishable patterns. It has been found that litter size is usually greater in the spring (in May) than in any other month (Brambell & Rowlands 1936, Zejda 1966, Aulak 1973, Nakata 1984) or that it is greatest in the summer (usually June and/or July) than in any other month (Ryszkowski & Truszkowski 1970, Iverson & Turner 1976, Fujimaki 1981, Campbell & Clark 1980). Two other studies (Baker 1930, Fuller 1969) found that seasonal changes differed in different years. Of seven studies, three found that litter size was greater in multiparous females than primiparous females (Kalela 1957, Zejda 1966, Stenseth et al. 1985), while the others found no differences (Mihok 1979, Fujimaki 1981, Nakata 1984, Ims 1987).

Our mean litter size (5.5) appears similar to other northerly studies of *C. gapperi* (with large samples): 6.1 (n = 107) (Beer et al. 1957), 5.7 (n = 84) (Fuller 1969), 5.7 (n = 90) (Iverson & Turner 1976) and 5.5 (n = 100) (Mihok 1979). Unfortunately, a direct comparison with these studies is not possible because they did not examine both month and parity effects. However, the monthly pattern of litter size change is atypical of other *C. gapperi* populations as well as other microtines. It does not show the usual seasonal decline that is characteristic of almost all vole species (Dobson & Myers 1989, and references therein). Our data showed a sharp increase from May to July and then a more or less constant mean after that. This pattern resulted from a continuous increase in litter size among primiparous females from May to August, while it was relatively constant for multiparous females over the season. Presumably, multiparous females have larger litters than primiparous females because the reproductive tract becomes more efficient after the first litter (Reading 1966) and/or more ova are shed on subsequent pregnancies (Roberts 1961). However, as pointed out above, differences between parity groups is not universal among *Clethrionomys* species. Nutritional factors are often suggested for seasonal shifts in litter size among microtines (e.g. Batzli 1985), although strong evidence is restricted to a few *Microtus* species. *C. gapperi* appears more omnivorous than most *Microtus* species, eating primarily green vegetation early in the season and then changing to mushrooms and berries throughout the summer and autumn (Dyke 1971). The switch in food types and presumably an increase in food abundance over time seems correlated with the monthly increase of litter size in our primiparous females. Why the litter size of multiparous females did not show even a slight parallel pattern remains unknown.

Clearly, the determinents of litter size in *Clethrionomys* are numerous, but quite inconsistent. Some variables may be important for some species/populations, but not others. However, at another level, we need to know how successful a particular litter size is under natural conditions. Only a limited amount of effort has been made in this area (Sleeper 1980, Boutin et al. 1988, Morris 1992).

Acknowledgements. The technical assistance of K. Czaharynski, A. Holcroft and T. Lawton is greatly appreciated as well as the use of facilities at the Kananaskis Centre for Environmental Research (University of Calgary). This study was primarily funded by the Natural Sciences and Engineering Research Council, the Department of Indian and Northern Affairs and the Canadian National Sportsman's Fund. We thank H. Ylönen and one anonymous referee for their comments. The writing of this manuscript was, in part, supported by an NSERC grant to M. Kavaliers, Faculty of Dentistry, University of Western Ontario.

References

Aulak, W. 1973: Production and energy requirements in a population of the bank vole in deciduous forest of Circaeo-alnetum type. — Acta Theriol. 18:167–190.

Baker, J. R. 1930: The breeding-season in British wild mice. — Proc. Zool. Soc. (London) 1:113–126.

Batzli, G. O. 1985: Nutrition. — In: Tamarin, R. H. (ed.), Biology of New World Microtus. Spec. Publ. Amer. Soc. Mammal. 8:779–811.

Beer, J. R., MacLeod, C. F. & Frenzel, L. D. 1957: Prenatal survival and loss in some cricetid rodents. — J. Mammal. 38:392–401.

Bondrup-Nielsen, S. 1987: Demography of Clethrionomys gapperi in different habitats. — Can. J. Zool. 66:277–283.

Boutin, S., Moses, R. A. & Caley, M. J. 1988: The relationship between juvenile survival and litter size in wild muskrats (Ondatra zibethicus). — J. Anim. Ecol. 57:455–462.

Brambell, F. W. R. & Rowlands, I. W. 1936: Reproduction of the bank vole (Evotomys glareolus Schreber). I. The oestrous cycle of the female. — Phil. Trans. London Ser. B 226:71–79.

Campbell, T. M. III & Clark, T. W. 1980: Short-term effects of logging on red-backed voles and deer mice. — Great Basin Nat. 40:183–189.

Cole, F. R. & Batzli, G. O. 1979: Nutrition and population dynamics of the prairie vole, Microtus ochrogaster, in central Illinois. — J. Anim. Ecol. 48:455–470.

Dobson, F. S. & Myers, P. 1989: The seasonal decline in the litter size of meadow voles. — J. Mammal. 70:142–152.

Dyke, G. R. 1971: Food and cover of fluctuating populations of northern cricetids. — Ph.D. thesis, Univ. Alberta.

Elliot, P. W. 1969: Dynamics and regulation of a Clethrionomys population in central Alberta. — Ph.D. thesis, Univ. Alberta.

Fujimaki, Y. 1981: Reproductive activity in Clethrionomys rufocanus bedfordiae 4. Number of embryos and prenatal mortality. — Japanese J. Ecol. 31:247–256.

Fuller, W. A. 1969: Changes in numbers of three species of small rodent near Great Slave Lake, N.W.T. Canada, 1964–1967, and their significance for general population theory. — Ann. Zool. Fennici 6:113–144.

— 1985: Clethrionomys gapperi: Is there a peak syndrome? — Ann. Zool. Fennici 22:243–255.

Gustafsson, T. O. & Batzli, G. O. 1985: Effects of diet and origin of animals on growth and reproduction of Clethrionomys glareolus. — Ann. Zool. Fennici 22:273–276.

Hansson, L. & Henttonen, H. 1985: Regional differences in cyclicity and reproduction in Clethrionomys species: Are they related? — Ann. Zool. Fennici 22:277–288.

Huggett, A. S. G. & Widdas, W. F. 1951: The relationship between mammalian foetal weight and conception age. — J. Physiol. (London) 114:306–317.

Ims, R. A. 1987: Differential reproductive success in a peak population of the gray-sided vole, Clethrionomys rufocanus. — Oikos 50:103–113.

Innes, D. G. L. 1984: The life-history tactics of the voles, Clethrionomys gapperi and Microtus pennsylvanicus, at two elevations. — Ph.D. thesis, Univ. Western Ontario.

Innes, D. G. L. & Millar, J. S. 1990: Numbers of litters, litter size and survival in two species of microtines at two elevations. — Holarctic Ecol. 13:207–216.

Iverson, S. L. & Turner, B. N. 1976: Small mammal radioecology: natural reproductive patterns of seven species. — Atomic Energy of Canada, AECL-5393.

Kalela, O. 1957: Regulation of reproduction rate in subarctic populations of the vole Clethrionomys rufocanus (Sund.). — Ann. Acad. Sci. Fennicae (A IV) 34:1–60.

Keller, B. L. 1985: Reproductive patterns. — In: Tamarin, R. H. (ed.), Biology of New World Microtus. Spec. Publ. Amer. Soc. Mammal. 8:725–778.

Kreb, C. J. & Wingate, I. 1985: Population fluctuations in the small mammals of the Kluane Region, Yukon Territory. — Can. Field-Nat. 99:51–61.

Krohne, D. T. 1980: Intraspecific litter size variation in Microtus californicus II. — Variation between populations. — Evolution 34:1174–1182.

Martell, A. M. 1983: Demography of southern red-backed voles (Clethrionomys gapperi) and deer mice (Peromyscus maniculatus) after logging in north-central Ontario. — Can. J. Zool. 61:958–969.

Martell, A. M. & Fuller, W. A. 1979: Comparative demography of Clethrionomys rutilus in taiga and tundra in the low Arctic. — Can. J. Zool. 57:2106–2120.

Mihok, S. 1979: Demography, behavior and protein polymorphism in subarctic Clethrionomys gapperi. — Ph.D thesis, Univ. of Alberta.

Millar, J. S. 1989: Reproduction and development. — In: Kirkland, G. L. & Layne, J. N. (eds.), Advances in the study of Peromyscus (Rodentia): 169–232. Texas Tech. University Press, Lubbock.

Morris, D. W. 1992: Optimum brood size: tests of alternative hypotheses. — Evolution 46:1848–1861.

Nakata, K. 1984: Factors affecting litter size in the red-backed vole, Clethrionomys rufocanus bedfordiae, with special emphasis on population phase. — Res. Pop. Ecol. 26:221–234.

Patric, E. F. 1962: Reproductive characteristics of red-backed mouse during years of differing population densities. — J. Mammal. 43:200–205.

Pelikán, J. 1979: Sufficient sample size for evaluating the litter size in rodents. — Folia Zool. 28:289–297.

Read, A. F., & Harvey, P. H. 1989: Life history differences among the eutherian radiations. — J. Zool. (London) 219:329–353.

Reading, A. J. 1966: Effects of parity and litter size on the birth weight of inbred mice. — J. Mammal. 47:111–114.

Roberts, R. C. 1961: The lifetime growth and reproduction of selected strains of mice. — Heredity 16:369–381.

Ryszkowski, L. & Truszkowski, J. 1970: Survival of unweaned and juvenile bank voles under field conditions. — Acta Theriol. 15:223–232.

Sleeper, R. A. 1980: Litter survival of deer mice (Peromyscus maniculatus) in nest boxes. — Southwestern Nat. 25:259–260.

Stenseth, N. C., Gustafsson, T. O., Hansson, L. & Ugland, K. I. 1985: On the evolution of reproductive rates in microtine rodents. — Ecology 66:1795–1808.

Tsvetkova, A. A. 1900: Abundance dynamics and specifics of reproduction in two vole species with differing ecological specialization. — Soviet J. Ecol. 21:26–32.

Zejda, J. 1966: Litter size in Clethrionomys glareolus Schreber 1780. — Zool. Listy 15:193–206.