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Litter Size Variation in Captive Wood Lemmings (*Myopus schisticolor*)

M. I. Cheprakov

Institute of Plant and Animal Ecology, Ural Division, Russian Academy of Sciences, ul. Vos'mogo Marta 202, Yekaterinburg, 620144 Russia

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Material for this study was collected between 1988 to 1992 in the vivarium of the Institute of Plant and Animal Ecology (Ural Division, Russian Academy of Sciences). The founders of the captive wood lemming colony (five females and three males) were captured in the Malaya Sos'va Nature Reserve located in the northern part of Western Siberia. A total of 102 females participated in mating and produced 202 litters. The animals were kept under standard conditions (Pokrovskii and Bol'shakov, 1979).

The photoperiod, ambient temperature, and diet changed during the experiment. The monthly average air temperature ranged from 12.1–12.4°C (January–March) to 16.8–19.5°C (June–August); the daylight period, from 9.0 (November–January) to 16.2–17.5 h (May–July). In September through May, the animal diet consisted of fresh carrot, green moss, and oats. In June through August, carrots were replaced by freshly cut mixed herbage (mainly sedges). The cages were equipped with drinking bowls and treadmills.

The data were processed using three-way ANOVA with constant effects and the methods of multiple comparisons. Calendar season and female body weight at the moment of probable conception (30 days before delivery) and age at the moment of delivery were taken into account.

Several types of females differing in the pattern of reproduction were distinguished. Type 1 comprised females occurring only in summer and participating in reproduction early; the first litter appeared in females no more than two months old and included 3.92 ± 0.26 young (n = 12). Seasonal differences in the size of the second and subsequent litters were nonsignificant (p > 0.10). The average litter size during all the seasons was 3.04 ± 0.26 (n = 24), this was significantly lower than the average size of the first litter (p < 0.05). Multiparous females of type 1 were older than primiparous females; their weight was 26.4 ± 0.6 g, greater than the average weight of primiparous females (18.8 ± 0.8 g, p < 0.05). At the moment of the first conception, these females weighed no more than 23.1 g. This value was taken as the weight boundary between females of types 2 and 3. The age boundary for females of the latter two types was considered to be 2.4 months, as the minimal age of females having the first litter at the age of at least 2.0 months was 2.5 months.

In females of types 2 and 3, the variation of litter size depending on the serial number of litters and seasons was examined by two-way ANOVA. In females of type 2, the effect of the number of litter is significant (p < 0.05), whereas the effects of seasons and interaction between the factors are nonsignificant (p = 0.10 and p = 0.14, respectively). The seasonal variation in the first litters is nonsignificant (p > 0.05); in subsequent litters, the litter size in the summer season is greater than in the other seasons (2.52, p < 0.05). An increase in the size of summer litters is responsible for a larger average annual litter size in multiparous females (3.10) than in primiparous females (2.37, the difference for p = 0.05 is 0.72, Tables 1 and 2). In females of type 3, the effect of seasons (three gradation: summer, autumn, and others) is significant (p < 0.05), whereas the effects of the serial number of litter and interaction between the factors are nonsignificant (p > 0.20). Seasonal differences are significant only in the case of the first litters; the mean for the winter and spring seasons is 2.50, and this is lower than the mean for the autumn season (the difference for p = 0.05 is 1.12).

Multiparous females of all types are of a greater weight than primiparous females (p < 0.01). Each

Table 1. Seasonal changes in the size of the first litter in female wood lemmings older than 2.4 months depending on female body weight at the moment of conception (mean / sample size)

Weight at the moment of conception, g	Winter	Spring	Summer	Autumn
<23.2	2.56/9	2.26/23	2.40/5	2.33/6
>23.1	2.33/3	2.54/13	3.27/22	3.78/9

female type is characterized by a special dependence of litter size on the age and weight parameters. In some females, repeated litters are more numerous; in others, they are smaller in size; and in some cases, litter size did not change significantly.

A correlation between body weight and litter size in the females of types 2 and 3 can be considered in terms of the critical point concept. In primiparous females, the critical weight point is 23.1 g. I proposed the existence of such a point at the moment of conception in repeatedly mating females. Empirically, it was determined at 25.4 g. A criterion for determining the critical point is based on the principle of maximal differences in seasonal dynamics between the animals characterized by body weights above and below this point. Three-way ANOVA of data on all females with retarded maturation with respect to season, serial number of litter, and body weight shows that the effects of season and weight and the interaction of the three factors are significant ($p < 0.05$). The other effects and interactions between the factors are nonsignificant ($p > 0.22$). In multiparous females with smaller body weight, in contrast to primiparous females, the seasonal dynamics of litter size is well-pronounced. This occurs because of an increase in the size of summer litters, as the data on the winter and spring season (2.00) significantly differ from the data on the summer season (Tables 1 and 3, $p < 0.05$). Among females of greater weight, the seasonal dynamics of litter size is distinct in primiparous females ($p < 0.06$), whereas litter size in multiparous females varies nonsignificantly from season to season (Tables 1 and 3, $p > 0.20$). In other words, primiparous females show an increase in the sizes of summer and autumn litters when their weight is above the critical point; among multiparous females, a peak in the summer season is observed in the animals with a body weight below the critical point.

In primiparous females, litter size depends on body weight; in lightweight animals, the mean litter size is smaller (2.26) than in heavier animals (3.18, $p < 0.05$). In multiparous females, the difference is nonsignificant ($p > 0.10$).

Thus, rodents bred under conditions of almost natural photoperiod and smoothed seasonal fluctuations of ambient temperature usually demonstrate more or less distinct seasonal changes in litter size (Pokrovskii and Bol'shakov, 1979).

At constant photoperiod and ambient temperature, the seasonal variation of litter size is weak or absent (Gustavson *et al.*, 1980; Rychnovsky, 1985). Under conditions of constant illumination and ambient temperature, litter size in wood lemmings is 3.8–3.9, and seasonal variation is nonsignificant (Kalela and Oskala, 1966). I recorded similar litter sizes in some female groups in summer, under conditions of the longest daylight period. This agrees with previous studies showing that litter size in rodents increases when the daylight period becomes longer (Baker and Ranson, 1932; Pinter and Negus, 1965).

Table 2. Seasonal changes in the size of the second and subsequent litters in females weighing no more than 23.2 g (type 2) and at least 23.1 g (type 3) at the moment of the first conception (mean / sample size)

Female	Winter	Spring	Summer	Autumn
Type 2	2.66/3	2.53/15	3.67/12	2.00/1
Type 3	2.54/11	2.91/11	3.29/7	2.94/16

Table 3. Seasonal changes in the size of the second and subsequent litters in female wood lemmings older than 2.4 months depending on female body weight (mean / sample size)

Weight at the moment of conception, g	Winter	Spring	Summer	Autumn
<25.5	2.25/4	1.90/10	3.71/7	2.75/4
>25.4	2.70/10	3.19/16	3.42/12	2.92/13

The absence of response to the seasonal factor in female wood lemmings appears to be based on the phenomenon of insensitivity to a short daylight period revealed in some other rodents (Blank *et al.*, 1992).

The results described above suggest that the absence or presence of a response to the seasonal factor in female wood lemmings is not an individual property that manifests itself throughout ontogeny; more likely, it is the state of organism depending on parameters such as the age of the first birth, weight at the moment of conception, and the presence or absence of preceding pregnancies. Only one study showed that in primiparous voles, in contrast to multiparous ones, the mean litter size was independent of body weight but depended on the season (Innes and Miller, 1993). I believe that the female types distinguished in wood lemmings will occur in some other rodent species as well. Thus, in Mongolian gerbils (*Meriones unguiculatus*), litter size was greater in early-maturing than in late-maturing females (Clark and Galef, 1986).

Thus, it appears that, at least in the wood lemming, the combination of such factors as female age, body weight, and the presence or absence of preceding births exerts direct influence on the seasonal dynamics and intensity of summer reproduction, the presence or absence of reproduction under snow, and, consequently, on the dynamics of rodent population size.

CONCLUSIONS

(1) It is shown that litter size depends on female body weight, serial number of litter, individual age, and the season of reproduction. In some cases, the interaction of these factors is observed; i.e., they modify each other's effects.

(2) Based on age and weight parameters and taking into account preceding births, females can be divided into several types differing in the pattern of seasonal changes in litter size. The response to the seasonal factor in females of a certain type can change in the course of individual development, which is observed in multiparous females.

(3) In female wood lemmings, which reach sexual maturity after day 40 of life, a critical point of body weight at the moment of conception was revealed. This point can be used as a criterion for dividing females into two groups characterized by the presence and absence of a well-pronounced response to the seasonal factor.

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