AGE-SPECIFIC EFFECT OF PARITY ON LITTER SIZE IN THE COMMON VOLE (*MICROTUS ARVALIS*)

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The ''triangular'' pattern of reproduction in arvicoline rodents predicts small fecundity early and late in life and high fecundity in the middle. In producing this pattern, the effects of maternal age and parity are typically highly confounded. We present results of a laboratory study designed to disentangle these effects in the common vole (*Microtus arvalis*) by analyzing variation in sizes of the first 2 litters born to 3 age classes of females subjected to photoperiods of 8 h and 16 h of light. Although the youngest females, paired at 2 weeks of age, decreased size of the 2nd litter in either light environment, the older 2 classes, paired at 3–4 months and 1 year of age, increased their 2nd litters, as predicted by the triangular pattern. This age-specific effect of parity could be explained by differences in the size of 1st litters.

Key words: age-specific fecundity, arvicolines, cost of reproduction, litter-size variation, photoperiod, reproduction

Variation in litter size in arvicoline rodents has long been a subject of extensive empirical and theoretical investigations (Leslie and Ranson 1940; Ranson 1934). The broad general pattern that has emerged from this long-term effort is that the size of the first 3 litters increases progressively, after which litter size reaches a plateaulike maximum, followed by a slow, highly variable decline (Frank 1956; Hasler 1975; Negus and Pinter 1965). Roff (1992:122) called such an age-specific pattern of reproduction ''triangular.'' However, in many laboratory and field studies, disentangling effects of age and parity has been difficult, because both are involved in shaping the pattern of successive litters (Hasler 1975; Stenseth and Framstad 1980). This is particularly important in such short-lived organisms as voles (*Microtus*), which are

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characterized by a limited breeding season because of seasonality of the environment. As a consequence, their age at 1st reproduction exhibits bimodal variation (Tkadlec and Zejda 1998b), shifting reproduction either very early or relatively late in life. Thus, we are uncertain of how consistently parity affects litter size over the life span of an individual and how flexible this pattern is under the influence of other changing environmental factors, such as photoperiod, temperature, food availability, or population density.

Recently, we found that the vagina of young, laboratory-bred, female common voles (*M. arvalis*) opened by 13 days of age (Tkadlec 1997), and 14-day-old females were already fully capable of fertile mating (Tkadlec and Zejda 1995). More surprisingly, these young mothers produced 1st litters larger than those produced by old mothers. This result challenges the generalization

TABLE 1.—Litter size in female common voles with respect to age class and photoperiod.

Photoperiod (h)	Age class	First litter			Second litter		
		n	$\bar{X}$	SE	n	$\bar{X}$	SE
8L:16D	I	16	5.12	0.36	13	3.85	0.36
	II	22	3.64	0.21	22	3.86	0.24
	III	16	3.44	0.32	15	4.53	0.38
16L:8D	I	19	6.05	0.28	16	5.25	0.45
	II	21	4.38	0.33	18	5.00	0.31
	III	17	4.06	0.37	15	5.27	0.38

that fecundity in small mammals increases with maternal age and size (Roff 1992). To test the hypothesis that parity affects litter size independently of maternal age, resulting always in a triangular pattern of reproduction, we designed a laboratory study involving 3 age classes of female common voles. We chose 2 light environments to check the effect of another potentially confounding variable, photoperiod. The triangular pattern of fecundity predicts that the 1st litter is smaller than the 2nd. Therefore, we focused on the variation in size of the first 2 litters and analyzed effect of parity with respect to its consistency over 3 age classes and 2 light regimes.

MATERIALS AND METHODS

We used laboratory-reared common voles derived from an outbred colony at Studenec, Czech Republic. The effect of parity was studied in 3 age classes, 2 of which were selected to mimic, at least partially, 2 distinct cohorts emerging in field populations; the 3rd was intermediate. Age class I involved very young female voles paired at 14–15 days of age (14.6 days ± 0.1 *SE*; range = 14–15 days), representing the spring-born cohort. Age class II was an intermediate category of females paired at 3–4 months of age (95.0 ± 1.0 days; range = 87–108 days). Age class III females were overwintered voles paired at about 1 year of age (333.0 ± 3.9 days; range = 309–385 days).

Breeding experiments were conducted in 2 constant light environments, 1 with 8L:16D and another with 16L:8D. Female voles were paired with proven adult male breeders and kept as monogamous pairs until they gave birth to the 2nd litter and young were weaned. We excluded females showing no signs of pregnancy within 60

days after pairing to ensure that no age overlap existed between age classes. We applied the same rule to 2nd litters by omitting those born >60 days after delivering the 1st litter.

Voles were housed in 15 by 30 by 45-cm metal cages with a nesting chamber. Hay was provided as nesting material and shavings were provided for bedding. Voles were offered pelletized vole diet (oats, wheat, dry alfalfa, dry milk, and mineral and vitamin supplement) and water ad libitum. The diet was supplemented regularly with apples and fresh grass. Animals were weighed daily and checked for presence of a litter, and young were weaned at 20 days of age. When newborns were discovered, the mother was weighed for her body mass at parturition.

General linear models were fitted to the data using procedure GLM in the SAS package (SAS Institute Inc. 1997) followed, if appropriate, by Scheffé tests (with 95% *CI*) for unplanned contrasts (Sokal and Rohlf 1995). We used either litter sizes at birth or change in size between 1st and 2nd litter (subtracting size of the 1st from the 2nd) as dependent variables. The criterion for statistical significance was $P < 0.05$.

RESULTS

We analyzed 111 first litters and 99 second litters with 4.44 ± 0.15 and 4.61 ± 0.15 (*SE*) offspring per litter, respectively; 12 females failed to produce the 2nd litter within 60 days of observation. In both light environments, the youngest female voles produced the largest 1st litters and the oldest females the smallest 1st litters (age, $F = 20.3$, *d.f.* = 2, 107, $P < 0.0001$; Table 1). Litter size at birth increased with length of photoperiod in all age classes ($F = 9.3$, *d.f.* = 1, 107, $P = 0.003$). The effect of both age and light were purely additive (age ×

TABLE 2.—Body mass (g) of female common voles at pairing and 1st parturition with respect to age class and photoperiod.

Photoperiod (h)	Age class	At pairing			At parturition		
		n	$\bar{X}$	SE	n	$\bar{X}$	SE
8L:16D	I	16	12.0	0.4	13	25.1	0.8
	II	22	22.8	1.3	22	26.2	0.6
	III	16	27.8	2.0	15	30.0	1.6
16L:8D	I	19	11.2	0.2	16	27.1	0.7
	II	21	23.1	1.4	18	26.5	0.9
	III	17	28.6	2.1	15	30.8	1.2

photoperiod, $F = 0.11$, $d.f. = 2, 105$, $P = 0.89$). However, variation in maternal body mass showed a different pattern (Table 2). The oldest females were heavier than those in the 2 younger age classes both at the time of pairing and at 1st parturition (at pairing, $F = 68.4$, $d.f. = 2, 108$, $P < 0.0001$; contrast III versus I + II, difference = 11.0, 95% $CI = 7.8–14.0$, $P < 0.05$; at parturition, $F = 12.0$, $d.f. = 2, 108$, $P < 0.0001$; contrast III versus I + II, difference = 4.2, 95% $CI = 1.9–6.4$, $P < 0.05$). Maternal mass at pairing ($F = 0.03$, $d.f. = 1, 109$, $P = 0.87$) and at parturition ($F = 1.30$, $d.f. = 1, 109$, $P = 0.26$) did not differ by photoperiod.
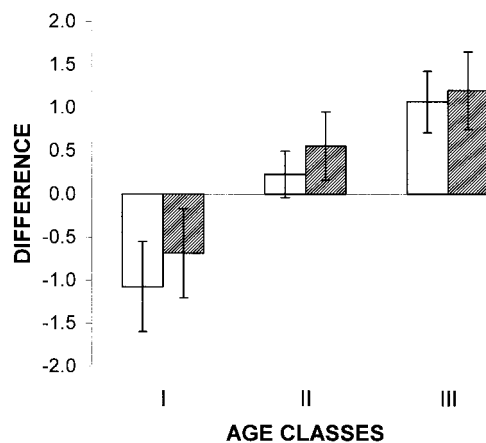
The oldest mothers increased the size of

FIG. 1.—Mean (± 1 SE) differences between size of 2nd and 1st litters in 3 age classes of female common voles for 2 photoperiods. Clear bars represent 8L:16D; shaded bars represent 16L:8D.

their 2nd litters, but 2nd litters of young mothers were smaller. The effect of maternal age on the change in size of successive litters was significant ($F = 11.0$, $d.f. = 2, 96$, $P < 0.0001$; Fig. 1), suggesting an important interaction between age and parity. We applied a model containing age class, photoperiod, parity, and interaction between age class and parity as predictor variables and litter size as a response variable to the entire data set involving 1st and 2nd litters. Sizes of litters differed by maternal age ($F = 8.1$, $d.f. = 2, 203$, $P = 0.0004$), photoperiod ($F = 23.9$, $d.f. = 1, 203$, $P < 0.0001$), and interaction between age and parity ($F = 10.5$, $d.f. = 2, 203$, $P < 0.0001$), indicating that the effect of parity depended on maternal age. When we modeled the change in litter size by adding sizes of 1st litters into the model as a covariate ($F = 35.5$, $d.f. = 1, 95$, $P < 0.0001$), the effect of age of the mother was marginally nonsignificant ($F = 2.91$, $d.f. = 2, 95$, $P = 0.06$). That suggests that most of the age effect can be accounted for by differences in 1st litters. Dependence of the change in litter size on size of the 1st litter (as measured by regression slopes of -0.71, -0.61, and -0.54 for age classes I, II, and III, respectively) did not differ among the age classes ($F = 0.22$, $d.f. = 2, 93$, $P = 0.80$).

Another confounding variable embedded in the effect of age might be the interval between the 2 successive litters. Within the limited 60-day period of observation, the youngest mothers had the greatest interlitter interval (29.0 days $\pm$ 1.5 SE), and the old-

est mothers had the shortest interval (21.0 $\pm$ 1.5 days; $F = 6.87$, $d.f. = 1$, 92, $P = 0.002$). Longer intervals were coupled with small 2nd litters, resulting in a negative difference between the 2nd and 1st litters ($F = 21.4$, $d.f. = 1$, 97, $P < 0.0001$). Accounting for variation in both interlitter interval and 1st litters, the effect of maternal age on difference in sizes of 1st and 2nd litters disappeared ($F = 0.88$, $d.f. = 2$, 94, $P = 0.42$).

The effect of photoperiod was significant ($F = 7.28$, $d.f. = 1$, 93, $P = 0.008$). No significant interaction existed between photoperiod and 1st litters ($F = 1.14$, $d.f. = 1$, 92, $P = 0.29$) or photoperiod and interlitter interval ($F = 0.34$, $d.f. = 1$, 92, $P = 0.56$). Sizes of the 2nd litter were greater at 16L: 8D for all age classes. Because young mothers reduced and old mothers increased the subsequent litter, we found no differences in sizes of 2nd litters among the age classes ($F = 1.05$, $d.f. = 2$, 96, $P = 0.35$; Table 1). However, differences between photoperiods persisted ($F = 15.3$, $d.f. = 1$, 97, $P = 0.0002$).

DISCUSSION

Under laboratory conditions, the effect of parity is age-specific, and the triangular shape of reproduction (Roff 1992) need not be a necessary outcome of sequences in litter size in voles. Unlike old mothers, which delivered small 1st litters and larger 2nd litters, the youngest female common voles gave birth to large 1st litters and smaller 2nd litters. These results differ from those of previous studies (Frank 1956; Reichstein 1964) and were obtained by lowering experimental age for the youngest category of breeding females to include those <20 days of age, as suggested by Tkadlec and Zejda (1995). Field observations indicate that early breeding in such female common voles is not confined to the laboratory (Boyce and Boyce 1988; Stein 1957). Experimental evidence for other arvicolines that young mothers are able to produce larger or same-size 1st litters as old mothers does exist

(Gustafsson et al. 1980; Hagen and Forslund 1979; Tkadlec and Zejda 1995).

Although evidence is substantial that the 1st litter in voles is significantly smaller than succeeding litters (see review in Hasler 1975), enough empirical data indicate an opposite pattern or at least no difference due to maternal age (Christian and Davis 1966; Hoffmann 1958; Keller and Krebs 1970; Mullen 1968:9; Stein 1957; Tupikova and Konovalova 1971; Zejda 1966) or parity (Dobson and Myers 1989). Even the decrease in size of the 2nd litter in young mothers can be reconciled with field data. Young female voles produce their 1st litters in the middle of breeding season when the yearly population maximum in litter size is usually observed. The subsequent decrease in litter size toward the end of breeding season is likely caused by young mothers, because the proportion of overwintered ones in the population is negligible at that time.

High fecundity of young and small mothers is contrary to the generalization that fecundity increases with maternal mass and age across a broad range of taxa (Roff 1992). In seasonal environments, high fecundity of young females may be adaptive in short-lived mammals whose probability of being alive and breeding in the next year is low (Tkadlec and Zejda 1998a). If so, the lower the life expectancy, the larger the 1st litter born to young mothers should be compared with old mothers. The common vole is a small arvicoline with high turnover rates in field populations (Frank 1957; Nabagło 1981). The disappearance rate of 6– 12%/week is indicative of intense mortality and emigration (Adamczewska-Andrzejewska and Nabagło 1977), although more detailed field data on survival rates of this species are needed. Thus, large 1st litters may be an adaptation for females unlikely to breed again. Unfortunately, we have no definite explanation of the pattern of small 1st litters born to old mothers. However, the common postweaning laboratory practice of keeping animals in small unisexual groups is likely to depress fecundity.

The age-specific effect of parity could be explained largely by differential fecundity in 1st litters. Life-history theory predicts that high investments in current reproduction may lower future reproduction or survival of parents and offspring (Williams 1966). Some empirical evidence from natural populations indicates that cost of reproduction may increase with decreasing age at 1st reproduction in female mammals (Harvey et al. 1989; Promislow and Harvey 1990). Our experimental data do not contradict this view but provide only limited support for higher reproductive costs (increased interlitter intervals and small 2nd litters) in young mothers. However, higher reproductive cost should be expected if young novice mothers, in addition to being energetically less efficient than multiparous mothers (Künkele and Kenagy 1997), must allocate additional resources to their own growth. Some cost of reproduction in field populations is implied by the observation that female voles entering reproduction the year they were born did not survive to the next (Tkadlec and Zejda 1998b). A manipulative approach controlling for litter size could further increase our understanding of arvicoline life histories and provide important data for investigating population dynamics of voles through mathematical modeling.

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